THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1934

VOL. LIX

WITH NINETEEN PLATES
and 351 Text-figures.

SYDNEY:

PRINTED AND PUBLISHED FOR THE SOCIETY BY

AUSTRALASIAN MEDICAL PUBLISHING CO., LTD.,
Seamer Street, Glebe, Sydney,

and

SOLD BY THE SOCIETY.

1934.

CONTENTS OF PROCEEDINGS, 1934.

PARTS I–II (Nos. 251–252).

(*Issued 15th May, 1934.*)

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(*Issued 15th September, 1934.*)

PARTS V–VI (Nos. 255–256).

(*Issued 15th December, 1934.*)

CORRIGENDA.

Page 68, line 2 from bottom of page, for *Chimaera nova-zelandiae* read *Chimaera novae-zelandiae.*

Page 102, line 1, *for* 2S (χ^2)–2S (n)–1, *read* $\sqrt{2S\ (\chi^2)} - \sqrt{2S\ (n-1)}$

Page 145, line 43, *for* climbing fern, *read* epiphyte

Page 149, line 5, *for* in the leaf axils, *read* at the bases of the leaf stalks

Page 149, line 6, *for* in this situation, *read* in the leaf axils

(Issued 15th May, 1934.)

Vol. LIX. **Nos. 251-252.**
Parts 1-2.

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Parts I–II (Pages i–xxviii; 1–100).

CONTAINING THE PROCEEDINGS OF THE ANNUAL MEETING AND PAPERS READ IN MARCH-APRIL.

With three plates.

[Plates i-iii.]

SYDNEY:
PRINTED AND PUBLISHED FOR THE SOCIETY BY
AUSTRALASIAN MEDICAL PUBLISHING CO., LTD.,
Seamer Street, Glebe, Sydney,
and
SOLD BY THE SOCIETY,
Science House, Gloucester and Essex Streets, Sydney.

1934.

PRICE 6/6.

Registered at the General Post Office, Sydney, for transmission by post as a periodical.

Agent in Europe:
Messrs. DULAU & Co., 32 Old Bond Street, London, W.1.

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ANNUAL GENERAL MEETING.

WEDNESDAY, 28th MARCH, 1934.

The Fifty-ninth Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 28th March, 1934.

Professor A. N. Burkitt, M.B., B.Sc., President, in the Chair.

The minutes of the preceding Annual General Meeting (29th March, 1933) were read and confirmed.

PRESIDENTIAL ADDRESS.

I feel deeply the honour which the position of President carries with it, and have endeavoured in my Address to summarize work which has occupied my attention for some time.

My own contributions to the field are as yet negligible, but I believe I have brought together observations and data which few have either the time or the training to co-ordinate. Any shortcomings, and I am only too well aware of some, are due to the width of the field which I have attempted to portray in bird's-eye view.

The concluding part of Volume lviii of the Society's Proceedings was issued in December. The complete volume (469 plus lxiv pages, twenty-nine plates and 319 text-figures) contains thirty papers from twenty-eight authors, five papers being by Linnean Macleay Fellows and one by the Macleay Bacteriologist. The papers covered a wide range of Natural History subjects. Although the general trend of conditions during 1933 has been one of improvement, it is still very necessary to exercise strict economy with regard to publication, and authors are again requested to assist the Council by keeping their papers within the smallest possible limit, whilst preserving effective presentation of their results.

The Honorary Treasurer's report and financial statement will show that we have emerged from another year of financial stress, having spent just a little less than we received. This is satisfactory in view of the fact that some of our mortgagors are in arrears and the amount of interest outstanding at 1st March, 1934, was £725 15s. 1d. Some of this may never be recovered, but it is hoped that in due course the bulk of it will be received.

Exchanges from scientific societies and institutions perhaps show some effects of the difficult times inasmuch as receipts totalled only 1,703, as compared with 2,236, 2,084 and 1,866 for the three preceding years. Several applications for exchanges of publications were received and the following were added to our exchange list: Sociedad Entomologica Argentina, Index Horti botanici Universitatis Budapestinensis, University of California at Los Angeles, Waite Agricultural Research Institute, Adelaide, and the Botanical Institute of the Faculty of Sciences, Lisbon.

Since the last Annual Meeting seven Ordinary Members have been added to the roll, four have resigned and the names of four have been removed on account of arrears of subscription.

The first application for Associate Membership was received by the Council in February, and there are now three Associate Members.

Harold Wynne Hamilton, who died suddenly on 27th March, 1933, at the age of fifty-six, had been a member of the Society since 1931. He was born at Guntawang, near Mudgee, and after leaving school entered the Education Department; at the time of his death he held the post of lecturer in Geography at the Teachers' Training College. His great interest was the Gould League of Bird Lovers, of which he had been Honorary Secretary for seventeen years.

On 29th October, 1933, the Society lost an old and faithful servant by the death of William Stapleton, who had been in the Society's employment since the end of 1907, having been appointed as caretaker soon after his father's death in October, 1907. His father had been associated with the Macleay family and the Society for about fifty years, so that Stapleton's death breaks up a family association with the Macleays and the Linnean Society of about seventy-five years—an association which must have begun just about the time of William Stapleton's birth. He had continued in active work until about a year before his death when he had a heart attack and was unable to resume duty. The Council thereupon granted him a pension in view of his long and satisfactory service, but unfortunately he did not for long enjoy the leisure he had so well earned.

The Fifth Pacific Science Congress was held in Canada at Vancouver and Victoria in June, 1933, and was attended by an Australian delegation which included Mr. E. C. Andrews (leader), Dr. R. J. Tillyard, Mr. E. Cheel and Dr. Ida A. Brown.

The Sixteenth International Geological Congress, held at Washington, D.C., in July, 1933, was attended by Dr. A. B. Walkom, on the invitation of the Geological Society of America.

The Society was represented at the Centenary of the Entomological Society of London by Commander J. J. Walker.

We offer our hearty congratulations to the following: Miss Sarah Hynes, on her inclusion in the list of recipients of New Year Honours as a Member of the Order of the British Empire; Sir T. W. Edgeworth David and Dr. Patrick Brough on being admitted to the degree of Doctor of Science in the University of Sydney; Mr. N. A. Burges and Misses Joyce Vickery and Enid Edmonds, on attaining the degree of Master of Science in the University of Sydney; and Miss Germaine Joplin on being awarded a Junior Fellowship by the International Federation of University Women.

The year's work of the Society's research staff may be summarized thus:

Mr. H. L. Jensen, Macleay Bacteriologist to the Society, completed his periodical counts of the numbers of soil microorganisms (bacteria, actinomycetes and fungi) and carried out calculations of the correlations between these numbers and external factors. The results show that in a given soil the bacterial numbers depend, under the conditions with which he dealt, chiefly upon moisture content; the numbers of actinomycetes showed a very definite correlation with the numbers of bacteria; and the number of fungi exhibited a definitely positive correlation with the moisture. A paper on this subject

has been completed and will be presented before the Society during 1934. The systematic work which Mr. Jensen has been carrying out on the Actinomycetes and Corynebacteria is now mainly finished. This systematic work has been necessitated by our imperfect knowledge of these groups and the paper to appear shortly in the Proceedings—"Studies on Saprophytic Mycobacteria and Corynebacteria"—may be regarded as an introduction to problems of decomposition of lignin and similar mother substances of soil humus, and the absence of humus accumulation in soils under arid conditions. Before these and the related problems of the production of plant food from organic matter can be solved, however, more experimental work on the activity of various groups of microorganisms in the processes of decomposition of organic matter under different conditions of moisture and temperature and in soils of different types is required.

Mr. F. A. Craft, Linnean Macleay Fellow of the Society in Geography, completed a paper on "The Coastal Tablelands and Streams of New South Wales", which appeared in the Proceedings for 1933. He spent the greater part of the year working on erosional problems in the Murray Valley above the Hume Weir. This work consisted of a reconnaissance survey of the Hume Catchment and an analysis of various river flow and rainfall statistics for the area. He is now preparing two papers, one dealing with the regime and secular changes of the Upper Murray and Snowy Rivers, and the other with problems of erosion in the Hume Catchment in New South Wales. On completion of these he proposes to extend certain aspects of these studies to cover the whole State, his work for the coming year including (1) determination of the regimes of the principal rivers in the State with special reference to low and high water in comparison with rainfall data, (2) location and distribution of the principal catchments of the State, and (3) correlation of land forms with stream volumes and behaviour.

Dr. H. Claire Weekes, Linnean Macleay Fellow of the Society in Zoology, obtained further material for her studies of the structure and function of the corpus luteum in lizards which may be regarded as the forerunner of an investigation into the part played by the pituitary in the reptilian reproductive cycle and into the nature of the mechanisms controlling the retention of the eggs within the uterus and the mechanisms concerned with the birth of the young. She is now preparing her final paper on the results obtained during her tenure of the Fellowship and expects to submit this to the Council before her departure in June for London. This paper will deal with the structure and functions of the corpus luteum in oviparous and viviparous reptiles and will contain a comparative account of this gland in a wide series of lizards, both European and Australian. We may take this opportunity of expressing our appreciation of the high standard of work carried out by Dr. Weekes and of wishing her every success for the future.

Miss Lilian Fraser, Linnean Macleay Fellow of the Society in Botany, continued her work on sooty moulds. Two papers were published in the Proceedings during the year, viz., (1) An Investigation of the Sooty Moulds of New South Wales. i. Historical and Introductory Account, and (2) The Mycetozoa of New South Wales. Another paper was completed and will appear during the coming year. In order to deal with the physiology of the sooty moulds it has been found necessary first to classify and review the species of fungi occurring in the sooty moulds in New South Wales. While this work is

in progress an investigation of the Capnodiaceae is also being carried on, the life history of *Capnodium salicinum* being studied in order to find a basis for the classification of the Capnodiaceae. In regard to the distribution of sooty moulds it has been found that in open country they consist chiefly of *Capnodium salicinum*, *Hendersoniella* sp., and members of the *Fungi imperfecti*; in rain forest areas these are absent and such fungi as *Chaetothyrium*, *Aithaloderma*, *Capnodium* spp., are present. The Trichopeltaceae are restricted to rain forests. Preliminary experiments in the work on the physiology of the sooty moulds indicate that the fungi in culture have not the same powers of resistance to heat and desiccation as under natural conditions, and reasons for this are being sought. The work of identification of *Meliola*, *Asterina* and related fungi begun last year has been continued. During the coming year Miss Fraser aims to complete the study of the life history of *Capnodium salicinum* and *Aithaloderma* sp., and make a thorough examination of the affinities of the family to which they belong; also to complete the study of the sooty mould fungi with regard to resistance to light, heat and desiccation; to complete the classification of the Capnodiaceae which occur in New South Wales; to investigate the biology of *Asterella Hakeae* and to continue the work of classification of *Meliola*, *Asterina* and related fungi.

Dr. I. V. Newman, Linnean Macleay Fellow of the Society in Botany, completed the investigation of the life-history of *Acacia Baileyana* and is now preparing the results for publication. This paper will describe the germination of the microspore and megaspore with details of the gametic chromosome number and some indications of chromosome morphology, and contain an account of germination tests in culture to find the viability of the pollen, and a suitable medium for its germination. The changes in the male nuclei during fertilization, and the fact that they show the gametic number of chromosomes, namely thirteen, on entry into the embryo-sac are recorded. The development of the embryo and endosperm is followed out in detail, together with some developments in the ovule that are unusual after fertilization. Evidence of polyspermy in connection with the endosperm is educed. There is also a discussion of the results of experiments on the germination of green seeds, carried out before the Fellowship was taken up. Work on the genetics of *A. Baileyana* was continued in a small way. An apparatus was designed for bagging the parts of the tree used, to allow of them being enclosed for a long period. Several cross pollinations were attempted without success; but normal seedlings were raised from seeds resulting from selfing. During the coming year Dr. Newman hopes to complete his investigation of the cytology of *Acacia Baileyana*, to begin a comparative study of the morphology of diverse species of *Acacia*, and to do some further genetical work in selfing and crossing *A. Baileyana*.

Six applications for Linnean Macleay Fellowships were received in response to the Council's invitation of 27th September, 1933. I have pleasure in reminding you that the Council reappointed Mr. F. A. Craft to a Fellowship in Geography and Miss Lilian Fraser and Dr. I. V. Newman to Fellowships in Botany, and also appointed Mr. Norman Alan Burges, M.Sc., to a Fellowship in Botany for one year from 1st March. We may all wish them a successful year's research.

Mr. Norman Alan Burges graduated as Bachelor of Science in 1931 with First Class Honours and University Medal in Botany. In 1932 he was awarded the John Coutts Scholarship and a Science Research Scholarship in Botany. In

1933 he obtained the degree of Master of Science for a thesis embodying the results of his research while holding the above Scholarships. For two periods, December, 1930, to February, 1931, and December, 1931, to March, 1932, he acted as temporary assistant in the Plant Pathology Laboratory of the Division of Plant Industry at Canberra. During 1933 he was Acting Lecturer and Demonstrator in Botany in the University of Sydney. His published research includes a study of the mycorrhiza of *Eriostemon Crowei* (with Asst. Professor J. McLuckie) and of the Mosses of New South Wales. For his work as a Fellow he proposes during the coming year (1) a study of the morbid anatomy of the galls produced by *Uromycladium* and *Uromyces*, (2) cytological study of *Uromycladium Tepperianum*, (3) an attempt to determine the function of the pycnium of *Uromycladium*, and (4) an examination of the physiologic specialization occurring in *U. Tepperianum*.

This review of the activities of the Society and its Research Fellows leads fittingly to the subject of my Address tonight, for they are striking evidence of progress toward that aim which, as Sherrington has stated, seems the universal goal of animal behaviour, namely, to dominate more completely the environment, and the instrument which has above all rendered this possible in man is his brain.

What more striking examples over a wide range could we have than the researches of Mr. Jensen on agricultural bacteriology, Mr. Craft on the permanence of the Hume Reservoir, Dr. Claire Weekes on the evolution of the mechanisms for development of the young, and so on.

Some Aspects of the Vertebrate Nervous System.

My subject is the vertebrate nervous system, and more especially that part of it upon whose activity consciousness depends. Hence it is necessarily concerned with the human nervous system in particular.

My endeavour will be to outline some aspects of the progress which has been made, in recent years, in gaining a more rational understanding of the nervous system, either from anatomical, physiological, pathological or psychological studies. These studies have been greatly aided by researches upon the nervous system of lower vertebrates.

The importance of the subject cannot be over-estimated. I need merely quote Sir Gowland Hopkins, in the last Presidential Address to the British Association for the Advancement of Science, wherein he says, "A few years ago the Cambridge philosopher, Dr. C. D. Broad, who is much better acquainted with scientific data than are many philosophers, remarked upon the misfortune involved in the unequal development of science; the high degree of our control over inorganic nature combined with relative ignorance of biology and psychology. At the close of a discussion as to the possibility of continued mental progress in the world, he summed up by saying that the possibility depends on our getting an adequate knowledge and control of life and mind before the combination of ignorance on these subjects with knowledge of physics and chemistry wrecks the whole of the social system. He closed with the somewhat startling words: 'Which of the runners in this very interesting race will win it is impossible to foretell. But physics and death have a long start over psychology and life!' . . . But, to repeat, the need for recognising biological truth as a necessary guide to individual conduct and no less to statecraft and social policy needs emphasis today. With frank acceptance of the truth that his own nature is congruent with all those aspects of nature at

large which biology studies, combined with intelligent understanding of its teaching, man would escape from innumerable inhibitions due to past history and present ignorance, and equip himself for higher levels of endeavour and success."

Need I remind you that this is the instrument that has made man what he is, that its history is the history of human thought, and, as Pavlov long ago expressed it, science is now faced with the problem of attempting to understand its own creator, the human brain.

The more or less logical order in which I shall approach the subject is:

(1) The constituent elements of the nervous system, the nerve cells or neurones.

(2) The external world and the sense organs and their connection with the central nervous system. Here we must not forget also the internal world, from which, as it has been said, the central nervous system receives a running proprioceptive commentary and from which arise the "drives" which influence us, such as hunger, thirst, sex and subtler influences.

(3) The influence of the special senses, more especially vision, upon the evolution of the nervous system.

(4) The lower reflex mechanisms.

(5) The thalamus, especially concerned with the affective side of sensations, and already so well developed in birds.

(6) The cerebral cortex. These last two, the thalamus and cortex, seem to be chiefly linked with subjective consciousness.

(7) Finally, the expressor mechanisms, muscles and their control.

(1) *The constituent elements of the nervous system, the nerve cells or neurones.*

Let us briefly examine some aspects of the progress in our knowledge of the conducting units, or neurones, which compose the nervous system. Here, undoubtedly one of the most important advances is given in the summary of Sherrington's Ferrier Lecture, and I make no apology for quoting it to you in full:

"Though trains of impulses are the sole reactions which enter and leave the central nervous system, nervous impulses are not the sole reactions functioning within that system. States of excitement which can sum together, and states of inhibition which can sum together, and states which represent the algebraical summation of these two, are among the central reactions. The motor neurone lies at a focus of interplay of these reactions, and its motor unit gives their net upshot, always expressed in terms of motor impulses and contractions. The central reactions can be much longer lasting than the nerve impulse of nerve trunks. Further, these central states and reactions are, as compared with the processes of nerve-trunk conductions, relatively very sensitive to physiological conditions, and are delicately responsive to fatigue, blood supply, drugs, etc. *The specific cell units, the neurones, far from behaving merely as passive recipients and transmitters of impulses, modify as well as transmit what they receive. They can develop rhythm of their own and their rate of discharge can rise and fall with intensity of central excitation and inhibition respectively.*"

The fundamental importance of this last statement is obvious.

As regards the structure of the various component units or neurones, it is impossible to mention the immense number of morphological and physiological observations upon nerve cells and fibres, upon the synapse, etc. The meaning of much of our knowledge is as yet unknown.

Long ago Cajal and, more recently, Kappers and others have pointed out how the varying anatomical structure of nerve cells can result in varying functions, e.g., the avalanche conduction phenomena in the neurones of the cerebellar cortex. Kappers has further elaborated a theory of neurobiotaxis, an attempt to explain the phenomena of growth and development of the units of the nervous system and the marvellous process by which they link up into that complex network of the human nervous system.

I think it is undoubted that with further progress we shall find some correlation between varying anatomical structural types and arrangements of the neurones and their physiological and psychological functioning. The summation of sensory processes which is necessary to give us our perception of space, must surely find some correlation with the pouring in of nerve impulses from sense organs of all kinds, into nerve cells of the thalamus, and probably into a fairly localized cortical area linking up sensorimotor (both proprioceptive and exteroceptive), visual, auditory and vestibular impulses, and possibly lying between them. As Kappers has expressed it: "The ability of the neurone to receive at the same time more than one stimulus by different dendrites and to lead their compound along one axis cylinder, may be considered as the material expression of the formation of a compound impression from different perceptions, and this compound again acts as a factor in the formation of the higher, more complicated compounds, if the axis-cylinder runs in the cerebral direction. If it runs in the aboral direction, the axis cylinder is the final common path leading to a somatic effector centre."

Actual attempts to correlate morphological differences in the neurones with physiological and psychological differences are as yet only in their infancy, but we may mention the work of Hoff who has, by degeneration methods and careful histological examination, examined the terminal "boutons" of the pyramidal tracts, where these synapse with the dendrites and cell bodies of the anterior horn motor neurones. Again, the peculiar form of the various cells and their synapses in the cerebellar cortex would seem undoubtedly to be correlated with motor co-ordination which this cortex is believed to exercise. Jelgersma has elaborated a complex theory based upon the histology of the cerebellar cortex. In the cerebral cortex Economo and others have pointed out that the granular cells are probably characteristic of sensory receptive areas and the Betz cells have long been known in the motor area.

Finally, I would like to mention one of Kappers' recent speculations. He points out (1919, 1926) that the neurones which build up our nervous system are, after all, cells similar fundamentally to those that build up the rest of the body, and that, therefore, we must concede to all cells the germ of powers which find their highest expression in the nerve cells. Kappers himself supports the Aristotelian conception of a "psyche" in all cells, and attempts to find a parallelism between certain mental phenomena, characteristic of the activity of the highest neurones, and certain general phenomena characteristic of cells in general, e.g., growth and development. Logical correlation, for instance, he compares with the power of adaptive growth, with the natural correlation of organs among

themselves, and with the surrounding world, and so on. He even goes so far as to suggest that the centrosome of the cell may be the actual site of this function.

Whatever be one's philosophical outlook upon the problem of life and mind, these speculations of Kappers are interesting and probably, from any point of view, represent, in part, truths which will persist.

(2) *The external world and the sense organs and their connection with the central nervous system.*

When we examine recent advances in our knowledge of the sense organs and the relation between the stimuli received from the external world and the subjective phenomena which occur as a result, the researches of Adrian and others are of outstanding importance. They have been rendered possible by the wireless valve, with its powers of amplification of minute electrical currents.

Briefly these astonishing results may be summarized as follows:

"Our mind receives all the information which can be got out of the messages from those receptors which are in touch with it, but it means also that the *mental correlate is a very close copy of the physical events in the sensory nerves.*—The only kind of distortion which takes place in the transference from body to mind (or in the parallelism of bodily and mental events) is that the sensations rise and fall smoothly, whereas the nervous message consists of a series of discrete impulses with pauses in between. Somewhere on the way between the two there must be a smoothing process which converts the disconnected impulses into a change of much slower period. If the succession of action currents were recorded by a galvanometer of long period, instead of a capillary electrometer, the mirror would move slowly and its deflection at any moment would be roughly proportional to the frequency of the impulses at that moment. In the same way we can imagine that the impulses are conducted to some part of the nervous apparatus of the brain where the excitatory process rises and declines much more slowly than in the nerve fibre.

"The existence of such regions has been demonstrated by Liddell and Sherrington in some of the reflex arcs of the spinal cord, where a brief influx of sensory impulses provokes a motor discharge of much more gradual onset and decline. There is, therefore, no need to look outside the central nervous system for the smoothing process which integrates the series of impulses into a quasi-steady effect. The sequence of events between the stimulus and the mind can be seen most clearly in a diagram. The stimulus is represented as appearing suddenly and remaining at a constant value. The excitatory process in the receptor declines gradually, and as it declines the intervals between the impulses in the sensory fibre become longer and longer. The impulses are integrated by some central process, and the rise and decline of the sensation is a fairly close copy of the rise and decline of the excitatory process in the receptor. The *quality* of the sensation seems to depend on the path which the impulses must travel, for apart from this there is little to distinguish the message from different receptors."

Adrian has studied not only sense organs and sensory nerves, but also motor nerves, and concludes that their normal activity in the body consists in the transmitting of impulses of the same type as those which are set up in isolated nerves by electrical stimulation.

How powerful a weapon this new implement of wireless valve amplification is proving is indicated by the recent work of Saul and Davis (1933) upon action currents in the central nervous system. By linking a loud speaker to their amplifying apparatus and connecting it by electrodes to the auditory nerve, they were able to reproduce musical tones applied to the cat's ear up to 1,000 double vibrations per second. Words came back blurred and so on. Similar experiments were made with vision and smell.

Our knowledge of the sense organs is steadily increasing whether we consider the eye and vision (Parsons, 1926; Lythgoe, 1933), hearing (Wever, 1933), or the work of Adrian which has shown that the sensory receptors in the skin and muscles, etc., may be classified into "postural" and "phasic", corresponding closely to the types of reflexes which they elicit, as was clearly pointed out long ago by Sherrington.

These two groups of end organs are characterized by their rate of discharge of impulses when stimulated. The postural receptors or end organs give a prolonged discharge, and exhibit a very slow adaptation to a constant stimulus, whereas the phasic receptors have a rapid adaptation rate, and respond especially to sudden changes in the environment. The further analysis of what happens to these sensory impulses, of whatever kind, has been rendered possible partly by the work of Pavlov on conditioned reflexes or responses.

Steady progress is being made in our knowledge of the analysing activity of the various sense organs and their receptive centres in the central nervous system. Sherrington long ago showed that in binocular vision the fusion of the images takes place at what may be called the "psychical" level (Creed, 1931).

To quote Head (1920, p. 741): "The forms assumed by sensation are ordered and predestined on the physiological level, as a result of innumerable integrations, which take place outside consciousness. These processes are not open to conscious analysis; it is only the interplay of sensations that can be discovered by introspection. The psychologist, who attempts to discover a strict psychophysical parallelism, ignores the central link of the problem. He assumes that the nature and conditions of the physical stimulus can be brought into direct relation with the psychical act of sensation. . . . This fundamental error vitiates much of the work on the psychology of the senses. It is only under artificial conditions that the physiologist can foretell exactly what reaction will follow a given physical stimulus; previous occurrences in the tissue may entirely change the nature of the response. Adaptation, biphasic activity, and facilitation form a normal part of the vital activity of the nervous system; they may intervene between a measured physical stimulus and the physiological effect, and make it impossible to establish a direct and immediate correlation. Therefore, between the impact of some physical force on the tissues of the body and the psychical act of sensation, are interposed reactions which, in many cases, cannot be predicted."

Nevertheless, as Adrian has shown, there is a very close correspondence between the physical stimulus and the psychical sensation, and our outlook on the matter may well be coloured by our philosophical outlook. The view taken as to the relation between the physical impulse and the sensation in consciousness may vary from that expressed by J. S. Haldane (1933), who states: "Ultimately, therefore, sense-experiences are manifestations of personality", a thorough-going Berkeleyan concept, to the opposite monistic and materialistic view expressed by his son

J. B. S. Haldane (1932), who quotes Lenin's words, "For every materialist the laws of thought that reflect the forms of the real existence of things are totally like and in no way different from, those forms."

Whatever view one may privately hold, it seems to me unquestioned that a monistic materialism which does not assume any distinction between mind and matter is the outlook which is leading to progress in our knowledge.

(3) *The influence of the special senses, more especially vision, upon the evolution of the nervous system.*

As regards the eye, let us examine what is known of its architecture and functions.

The exact structure and function of the rods and cones is as yet imperfectly understood, but it would seem that the basis for colour discrimination may lie in three different chemical substances somewhere in the light reception apparatus (Roaf, 1933). Just what happens in the nerve cell linkages immediately related to the rods and cones is as yet imperfectly understood, but apparently large numbers of rods and cones only link up with one nerve fibre of the optic nerve in the periphery of the retina, while in the macular region there is a point for point representation and each cone links up with only one nerve fibre, and there is practically no interaction.

The passage of the nerve impulse along the optic nerve is being studied by Adrian and Matthews, in relation to intensity and size of the image. They also found evidence of interaction between retinal neurones peripherally. When we come to the first relay station for the reception of visual images, e.g., the external geniculate body, it is not yet known to what extent there is a point to point representation of each macular fibre, but the broad details have recently been elucidated and summarized by Brouwer and his fellow workers.

Turning to the area striata of the cortex, we now come to the important problem, for it is the activity of the nerve cells in and around the area striata, or visual cortex, which is probably more important for thinking processes than any other part of the cortex, with the possible exception of the auditory cortex. The actual area is about one-fortieth to one-fiftieth (2–2½%) of the total cortical area, and there seems to have been a progressive increase in the cortex other than projection cortex, when we examine the visual cortex in apes (10%, Brodmann) and lemurs (15%). At the moment I can find no exact figures as to the area parastriata, and peristriata, which are generally believed to be associated with vision also, or at least visual memories. Economo's estimate of the number of cells in the visual cortex is $1{,}400 \times 10^6$.

If now we assume that the number of cells in the lateral geniculate body is such that each optic nerve fibre synapses with one cell in the geniculate body, and that each geniculate body cell sends a fibre to the visual cortex, then we have a framework of nerve cells in the visual cortex in which, for every entering optic radiation fibre, there are 2,800 neurones. When we multiply this and find that there are 500,000 entering fibres, and $1{,}400 \times 10^6$ neurones, then it becomes apparent that however we conceive visual memory processes, the number of possible linkages is quite adequate to the prodigious capabilities of human visual memories.

It is probable, of course, that we must conceive of mental processes, including memory, not as any crude series of nerve impulses passing through particular pathways, but rather as a time pattern of nerve impulses in an immense net-

work. To quote Professor Adrian in his recent address to the British Association for the Advancement of Science (*Nature*, 9th Sept., 1933, p. 401): "The electric changes taking place in such groups [e.g., small groups of nerve cells such as ganglia] and in the cerebral cortex show that the different neurones often pulsate synchronously, as though they formed a mass through which waves of activity are freely conducted. In such a mass the waves due to incoming signals and to the spontaneous activity of nerve cells may produce nodes of vibration and interference figures, patterns in time as well as in space. Such patterns might be independent of precise neurone connexions. It is possible that they may supply the basis for an appropriate motor response, though how they can do so is a problem to which no answer can be given in the present state of our knowledge."

We thus see that the physical correlates of vision are only very partially known, but the importance of stereoscopic vision (with a macula in each eye) in the evolution of the brain has been ably summarized by G. Elliot Smith (1930), and we may quote verbatim his remarks:

"Binocular vision enriched by macular efficiency provided the conditions which made possible the attainment of stereoscopic powers, the conscious appreciation of a third dimension of space, the recognition of solidity and perspective. A vision of the world was thus revealed to man, with an appreciation of form, colour, size, and space, and a fuller understanding of distance and movement. The most significant enrichment of the sensory basis of the mind is conferred by the macula. To paraphrase the account given by the late Dr. Henry Watt, it 'refines and distinguishes positions and forms, and, aided by the more precise accommodation which becomes evolved in association with it, it sharpens the objects of attention and dissipates the rest. Stereoscopy adds a new character to a group of forms that may persist for indefinite periods of observation; delicate skin gives greater sensitivity to variations of pressure, and the prehensile hand implies a very great refinement in the positions and forms of the derived articular sense. In the hand this becomes a fine mobile tridimensional sense which, like the stereoscopic eye, can go round and through things, so almost isolating them from their surroundings.'

"When in response to the visual curiosity excited by the new vision of the forms, textures, and colours of objects, the hand, under the guidance of the eyes, examines these objects, and explores their positions in space, not only is tactile information added to visual knowledge and integrated with it, but also the impulses from the joints, muscles, tendons, and in fact from the whole body, recording the effects upon the organism of the accomplishment of the action, are added to the visual, tactile and motor sources of knowledge. Hence, as Dr. Watt expresses it, 'the articular sense is the conscious correlate of action and of the individual's share in his experiences'. Thus 'action enters into the data of sense to integrate with it and so build up psychical mind-stuff'.

"The consciousness of action makes possible 'the integrations of percept and probably of concept that are the beginnings of intellect'. It adds the essential personal element in the process of interaction of mind and mechanism, and the interpretation of the means whereby motor skill creates mind. For 'the first purpose of the mind is to serve the ends of action. It is not merely a speculative instrument given to man that he may form for himself a disinterested knowledge of the world, create and enjoy works of art, and plan an elysium

of happiness and love.' It is primarily a means for seeking actively, under the guidance of attention and interest, the objects of its own desire, and for expressing in movement and other forms of behaviour the satisfaction of the impelling appetites. Vision and touch are closely integrated with movements and feelings and the affective results of such expressions of the mind's searchings for satisfaction."

(4) *The lower reflex mechanisms.*

The story of the lower reflex mechanisms in the spinal cord has been elucidated specially by Sherrington (1932) and his fellow workers; this work must form the basis for further work upon the function of the neurones in the higher parts of the brain for, as Sherrington has said, "The motoneurone, specialized nerve cell though it be, may yet typify for us the reactions of nerve cells in general." For whether we examine the lower reflex regions of the nervous system, or those regions where mental processes take place, we find the same essential features, neurones set end-to-end in neurone chains, and evidently, just as before, serving as lines for travel of nerve impulses, and nodal points for their convergence and irradiation, their further launching by excitation, and their restriction by inhibition.

Our aim must surely be to interpret the subjective functions of the higher nerve centres as correlates of physiological functions similar to those so ably elucidated by Sherrington in the spinal cord and brain stem especially.

(5) *The thalamus, especially concerned with the affective side of sensations, and already so well developed in birds.*

Let us now examine the activity of the thalamus, a mass of nerve cells in the base of the forebrain, which has become increasingly complex in structure as we ascend the vertebrate scale. Its anatomical structure and connections have only been partly elucidated within the last few years, though in 1910-11 Elliot Smith emphasized its importance, when he stated that the key to the interpretation of the structure of the cerebral cortex or neopallium in mammals lies in an intensive study of the thalamus.

In the words of Le Gros Clark (1932): "Into the thalamus there come fibres conveying sensory impulses of every possible kind, somatic and visceral, impulses which convey intimation of changes within the organism itself, and of changes in the external environment. Here, long before the neopallium has appeared in evolutionary history, a mechanism is provided for the interaction and blending of these diverse afferent impulses, and in relation to this plain anatomical fact, there is accumulating evidence based on clinical and psychopathological observations that the thalamus is the anatomical equivalent of the very threshold of consciousness."

Further, the work of the clinicians, and more recently of the experimental physiologist, has within recent years shown that there is a differentiation of function within consciousness itself and that, as Head (1920) has expressed it so clearly, ". . . the essential organ of the thalamus is the centre of consciousness for certain elements of sensation. It responds to all stimuli capable of evoking either pleasure and discomfort, or consciousness of a change in state. The feeling tone of somatic or visceral sensation is the product of thalamic activity and the fact that a sensation is devoid of feeling tone shows that the impulses which underlie its production make no thalamic appeal."

More recently still, the detailed structure of the thalamus and its connections have been further elucidated, especially by Le Gros Clark, and we know that it probably consists of direct reception groups of neurones or nuclei of a lower level, and upper level nuclei which in some way elaborate the impulses received in the lower levels. These upper level nuclei appear to be a distinctive feature (both topographically and functionally speaking) of the mammalian thalamus.

"These upper levels receive no significant afferent connections from lower sensory centres except by relays through the lower level of the thalamus. They are related rather to the 'association' areas of the cortex, whereas the nuclei of lower thalamic levels are connected with the sensory projection areas, and they exhibit a progressive increase in relative size and elaboration in higher mammalian types culminating in the primates where the association areas of the cortex attain to their fullest development" (Le Gros Clark, 1932).

Of these upper level nuclei, the lateral nucleus seems to represent a higher intra-thalamic functional level related principally to the sensory impulses which reach the ventral nucleus by the fillet (which conveys tactile impulses, deep sensibility, and proprioceptive impulses). These impulses, having reached the ventral nucleus where they are represented in a relatively elementary form, may be there brought into relation with, and modified by, afferent impulses which come in from other thalamic nuclei of an equivalent functional level (e.g., the geniculate bodies concerned with vision and hearing and the anterior nucleus, originally olfactory) and passed on to the main part of the lateral nucleus by short internuclear connections where they acquire a re-representation. Further, the thalamus lies next to another structure, the hypothalamus, which is a visceral correlation centre, and in close relation to the pituitary gland, both by vascular channels and nerve fibre connections.

Again quoting Le Gros Clark (1932): "In view of the part which the pituitary gland is known to play in controlling growth in fœtal and post-natal life, its dominating influence over the endocrine system generally, its power of regulating fundamental rhythms of sexual life and development, etc., it is not unreasonable to suppose that through its connections with the gland, the hypothalamus provides a region of the brain in which the basic vital activities of the organism may be echoed in terms of neurogenic processes. These considerations lead to the suggestion that the hypothalamus is the recipient of those vague indefinable impressions which arise in association with all sorts of visceral activities and metabolic processes and which, in their totality, represent sensory material by which the organism is enabled to appreciate itself as a unified being, an individual existing as an organised entity without special reference to the external environment (and with definite needs, such as hunger, thirst, sex, etc.). In general, then, the hypothalamus may be regarded as part of the diencephalon which, by its nervous connections and through the direct liaison which it establishes with the hormonic regulatory system via the pituitary, mediates the integration of visceral impulses, and plays an essential part in the control of the internal milieu of the organism. Thus it stands in direct contrast to the functional implications of the dorsal part of the diencephalon. While the latter is the recipient of impulses on the basis of which the organism may develop an awareness of its external milieu and adapt its overt behaviour accordingly, the former is the recipient of impulses on the basis of which the organism may develop an awareness of its internal organic activities and through which sensory experiences are endowed with an affective tone."

The story of the gradual evolution of this marvellous mechanism in the vertebrates has been ably told by Elliot Smith, Kappers, Le Gros Clark, and others. We see the gradual increase of somatic or bodily impulses received into this basal forebrain, with all its possibilities of sensory fusion and correlation, and release from or at least dominance over the relatively inaccurate olfactory mechanisms which originally prevailed in the forebrain. Further, the increasing number and perfection of the various bodily sensory impulses, whether tactile, visual, auditory, vestibular, or proprioceptive, leads to an ever improving accuracy in our perception of the outside world. Nevertheless, this dorsal part of the thalamus always remains linked by specialized or unspecialized nerve fibre bundles with the hypothalamus, thus providing "a basic mechanism whereby the organism is enabled to equate consistently the impressions which it derives from the outside world with the organic functions of its own being" (Le Gros Clark, 1932).

Examining this relationship of the thalamus with the hypothalamus in detail, one of the most important contributions recently made by Le Gros Clark and others is to show that what is known as the *dorso-medial nucleus* of the thalamus links up with the hypothalamus on the one hand, and with the frontal cortex of the brain on the other hand. Thus the dorso-medial nucleus occupies "a significant position, forming as it does an intermediate station through which the whole periventricular system (which includes hypothalamus) can be brought under the dominating influence of the frontal cortex of the cerebral hemisphere. In other words, the dorso-medial nucleus provides a mechanism whereby the highest functional levels of the brain are enabled to control the more primitive elements of mental activity, such as are represented in emotional reactions, instinctive impulses, etc." (Le Gros Clark, 1932).

In support of this hypothesis we have not only the experimental work of J. F. Fulton and F. D. Ingraham (1929), quoted by Le Gros Clark, but also the work of Bard and others. Fulton and Ingraham found that by inflicting certain lesions which had probably involved the nerve fibres connecting the frontal cortex with the dorso-medial nucleus of the thalamus, they were able to alter profoundly the emotional behaviour of animals.

Bard's work (1928) showed that following removal of the cerebral cortex "sham rage", as he calls it, could be elicited. This sham rage failed to appear after removal of the thalamus and hypothalamus, and hence he concluded that the expression of anger in the cat is dependent upon central mechanisms which are located in this part of the brain stem. The close relation of these mechanisms to the sympathetic system is also discussed by Bard. "The prefrontal areas may thus be regarded as a final product of the cerebral development where the activities of the purely cortical mechanisms underlying the intellectual components of personality are equated with the activities of the hypothalamic region which are associated with the more fundamental and primitive components. In this way a mean is provided for harnessing the impulses which are indissolubly linked up with elementary forms of emotional experience to the intentions and resolves which have their origin in ideational processes taking place at the highest intellectual levels" (Le Gros Clark, 1932).

The psychological importance of the activity of the thalamus has as yet been scarcely realized, but we may cite some instances derived from actual clinical experience and consider the light which modern concepts of thalamic activity possibly throw upon many phenomena, whether human, or otherwise.

Head and Holmes have analysed the response to all forms of stimuli, whether painful or pleasureable, in a number of patients who had lesions which destroyed either a part of the thalamus or its connections with the cerebral cortex. In one case, though the patient could not recognize any thermal stimulus as such, yet over the affected half of the chest large tubes containing water at from 38°C. to 48°C. evoked intense pleasure. "Oh, that's lovely, it's soothing, so very pleasant" (Head, 1920).

Again, in states of emotion, we see some remarkable phenomena in these cases. "One patient was unable to go to his place of worship because he could not stand the hymns on his affected side." "A highly educated patient confessed that he had become more amorous since the attack, which had rendered the right half of his body more responsive to pleasant and unpleasant stimuli. 'I crave to place my right hand on the soft skin of a woman. It's my right hand that wants consolation. I seem to crave for sympathy on my right side.' Finally, he added, 'My right hand seems to be more artistic'." "Thus, not only does the abnormal half of the body respond more vigorously to the affective element of a stimulus, but on over re-action can also be evoked by purely mental states. The manifestations of this increased susceptibility to states of pleasure and pain are strictly unilateral, and may lead to many curious complications" (Head, 1920).

Full consideration of the evidence led Head to conclude that in these cases we had a lesion which interrupted controlling pathways from the cortex to the thalamus (cortico-thalamic) and more especially to the lateral nucleus of the thalamus, one of the upper level nuclei, thus leaving the remaining nuclei fairly intact. Pure cortical lesions cause no change in the threshold to pain.

Turning now to lower vertebrates, it is of interest to find that reptiles and lower forms have a relatively poorly developed and simple thalamus, and it is probable that the subjective "pain" which we feel is differentiated from a generalized sense of discomfort reaction to a harmful stimulus. That is, parallel with increasing anatomical complexity and differentiation, to be found as we ascend the vertebrate scale, we get an actual psychological differentiation and localization of various aspects of sensation, this differentiation being revealed by pathological conditions.

Obviously the above is pure speculation, but consideration of the behaviour of the lower vertebrates, so far as I am aware, does not contradict such an hypothesis. This differentiation and localization is to be seen not only in the thalamus, but also in the gradual evolution and differentiation out of the pain pathways in the spinal cord, as we ascend the vertebrate scale.

The difficult question as to whether there are sensory receptor organs which transmit painful impulses only to the central nervous system is not yet settled.

It is of interest to note that the only sensory impulses that we receive from the cornea, the drum of the ear and the pulps of the teeth, are pure pain impulses, with little, if any, degree of localization within these regions. The question of visceral sensation is very complex, while the sensations received from the male or female external sex organs, and also from the nipples, are almost purely thalamic and have very little direct cortical representation.

If, further, we examine the behaviour of birds, though any hypothesis as to the subjective character of the functioning of their brain must be very speculative, nevertheless the richness and varied quality of behaviour which in ourselves is strongly endowed with affective tone, would make it probable that they also are

endowed with some degree of emotional or affective consciousness analogous to our own. Their song and powers of vocal mimicry, their elaborate courtship and mating, the making of nests, brooding and care of the young when hatched, and finally flight and migration itself, all give some indication of these elaborate forms of behaviour; as Arthur Thomson says, "Song is a natural expression of emotional intensity".

Now, if we examine the forebrain of the bird, we find a fairly well developed thalamus, with considerable differentiation; the cortex, however, is almost absent, and seems to be replaced in part by another basal forebrain structure, the *corpus striatum*, which in birds develops a most elaborate structure with a special nucleus peculiar to birds, the hyperstriatum, which is possibly analogous in part to the mammalian cortex. However, the midbrain in birds has possibly greater functional value than in the mammalia, and the researches of Popa (1933) would suggest that the motor cortex of mammals is replaced by the superior colliculus of the midbrain, which is also tremendously enlarged in birds on account of their extraordinary powers of vision, which almost certainly exceed our own in certain respects, at least. Stimulation experiments of the superior colliculi, according to Popa, show that there is a definite localization of various movements in the colliculus.

(6) *The cerebral cortex.*

(*These last two, the thalamus and cortex, seem to be chiefly linked with subjective consciousness.*)

Turning now to the cerebral cortex, which contains the nerve cells upon whose activities the highest functions of the brain depend, the rough structure has been subjected to minute analysis by many observers, Campbell, Elliot Smith, Brodmann, Economo, Vogt and Cajal.

The results have been summarized by Elliot Smith, Vogt and others, but, as yet, attempts to interpret subjective function in terms of objective structure and function are in their infancy. The above observers, and earlier ones still, such as Ferrier, have shown that the cortex may be divided into various areas, up to 200 (Vogt), with definite differences of neuronal pattern, and with different intra-, inter-, or subcortical connections. These areas have been roughly grouped into *projection* areas which are definitely linked with lower centres, and are either sensory afferent areas, or motor efferent areas, and intermediate areas between these projection areas, which are only indirectly linked with subcortical centres; these latter are the so-called *association* areas, and reach their highest development and differentiation in the human brain. The tendency nowadays is rather to discount the idea of sharply defined and localized areas, each with a separate functional significance, and experimental evidence (Lashley, 1929) suggests that localization is only partial, and mass or quantity of cortical substance seems to determine the degree of general efficiency.

Though the work of Lashley on the objective level, and the work of the "Gestalt" psychologists on the subjective level has emphasized the importance of the functioning of the cortex as a whole, nevertheless both the morphological and clinical evidence indicates some degree of functional independence and differentiation. Otherwise, why the differences in pattern of the cells in the different areas? Further, we have a definite linkage, not only of the sensory projection areas with definite nuclear groups of neurones in the thalamus, but also some part of the prefrontal cortex links with the dorsomedial nucleus and

the hypothalamus, and seems to be closely associated with emotional activities. We may mention here the unsolved problem as to the interrelationships between the cerebral cortex of the right and left hemispheres of the brain. Dandy (1933) removed the greater part of the right cerebral hemisphere in several patients for tumour, and the only observable interference with their functions in several cases was the resulting hemiplegia. As regards their mental functions he states: "I am still not willing to say that the mentality of the patients was normal; but rather that abnormalities have not been disclosed." The exact relationship between the hemispheres, and the predominance of one hemisphere, the left hemisphere in right-handed people, is probably intimately linked up with the phenomenon of mirror-writing (Macdonald Critchley, 1928), with some strange pathological conditions such as certain kinds of apraxia (von Monakow, 1914), and with the possible predominance of one eye in vision, as has been suggested by Parson (1924) in his discussion of left-handedness.

The evidence of comparative anatomy would seem to show that man owes his peculiar mental powers to the development of the so-called "silent" association areas between the projection areas (G. Elliot Smith). We are, as yet, however, almost completely ignorant of the correlates between physiological functioning in these areas and subjective mental processes. Nevertheless, the work of Head (1926) upon aphasia and the processes concerned in speech, helps to give us a glimpse of the future, and it may not be without significance that among the areas which he has shown to be associated with different aspects of speech, that one which is concerned with semantic aphasia lies close to the ventral or head end of the sensorimotor cortex. In semantic aphasia, the patient can speak perfectly well, but has difficulty in giving general direction to his thought or in *formulating a general line of action.* "He has lost the power to co-ordinate details into a general formula for internal or external statement." The phenomena seen in abstruse mathematical calculation may also prove of value in interpreting the functions of different cortical areas. Some mathematicians think in terms of auditory symbols, and others in terms of visual symbols. We are all familiar with the early work of Galton in this field, linking up in part with Jung's psychological types.

It will thus be seen that conscious thinking is correlated with the activity of nerve cells in the cortex and thalamus. The stream of consciousness may be considered as a peak of activity in a more or less dormant field. In other words, as Denny Brown (1932) expresses it, this peak of activity corresponds to the phenomenon of attention, and the relatively dormant field corresponds to the "subconscious" of the psychologist.

A valuable concept has been formulated by Kubie (1930). In attempting to explain certain spontaneous involuntary movements which have long been known to the clinician, he has postulated as a theoretical possibility the occurrence in the central nervous system of closed circuits, with excitation waves running through them in circles. "Such a circular wave constitutes a delicately balanced system whose course can be changed, and indeed whose very existence can be terminated by slight changes in the inter-relations of four sensitive factors: (1) The initial intensity of the wave (which for any single pathway in which the All-or-None principle rules will depend upon the state of conductivity of the tissue); (2) the velocity of the wave; (3) the length of the circuit; (4) the duration of the relative or absolute refractory phase which follows the passage

of the wave." Kubie then suggests that within the association areas, more especially of the cerebral cortex, there is an activity, even when the body is otherwise at rest. Further, this activity can be plausibly pictured as consisting of innumerable excitation waves circling continually in *closed and silent pathways.* He contrasts these "silent" regions of the central nervous system with what he calls "active" regions in which there can be no play of impulses without either visible movement or sensible feeling, or some alteration of internal economy. He argues in favour of this concept as follows:

"At every moment the central nervous system is receiving proprioceptive and exteroceptive stimuli in great numbers. To these impulses one of three things may happen; they may pursue an unchecked course from afferent to efferent pathways (i.e., the horse-shoe circuits of the active areas of the brain); or they may enter refractory areas in which they are destroyed; or encountering refractory pathways in the active area, they may switch off into pathways that are open into the silent areas. Once within the silent areas they must either circle until they are destroyed, or ultimately come out again into active efferent expression."

On some such basis one may picture the circuits of the silent areas arising. (They could equally well arise in centres where they are spontaneously generated in the neurone bodies). The important thing is that in either case the impulses playing about within the nervous system face one of three possible fates; they must either go in open circuits which must ultimately lead to efferent expression, or they must become annihilated in refractory tissue, or they must wheel in regular or irregular circuits which ultimately bring them back on themselves. The subjective phenomena of the stream of consciousness and of thought would certainly lend colour to these relatively closed circuits. "If they exist at all, there must be countless such circuits; and at any one moment some will be stopping because they are encountering refractory tissue, others starting, still others travelling at diminished intensity through tissue of partial refractivity, etc. And of all this activity there may be outwardly no normal sign. It is, however, equally possible that the algebraic sum or the distribution of all of this activity may bear some relationship to many states of psychomotor activity—such as sleeping, waking, confusion, alertness, etc." (Kubie, 1930).

Incidentally, it is easy to understand how such silent circus rhythms could act as a source of spontaneous involuntary movements. "Again it is conceivable that such active circus rhythms may occur occasionally within an active receptive area of the cortex. If this occurs in the occipital cortex, is it hard to imagine that the result would be the scintillating phenomena of migraine, whose wheeling lights may be taken as giving support to some of these speculations? Or if certain cell layers of the motor system were involved, might not epilepsy be the expression of the process? The stability of such circus rhythms would depend upon wave velocity, circuit length, and the refractory phase" (Kubie, 1930). The recent work of Adrian would possibly lend support to these hypothetical closed circuits in the "silent" areas. The passage of an excitation wave in closed circuits from one neurone to another can be visualized in two ways; either along one of the divisions of a branching axone, or (unlikely) along what would ordinarily be called their dendrites. It is the *Golgi Type II cell* which would seem to lend itself most readily to this type of organization of closed circuits as a normal function (Sherrington).

"Such circus movements may occur abnormally in other parts of the brain and spinal cord and even in ganglia, and would explain many phenomena, such as the production of spontaneous sensations, spontaneous pain, etc. They may also explain many normal phenomena such as the relatively autonomous rhythm of discharge along post-ganglionic fibres of the sympathetic system. These circuits within 'silent' areas may possibly receive their 'cues' from the diversion of proprioceptive impulses from the active afferent system. Further these circling excitation waves may be closely related to the excitatory agent which Sherrington has found it necessary to postulate, and inhibition may find its mechanism, as Keith Lucas suggested, in some expression of the refractory phase" (Kubie, 1930). More recently, Lorente de Nó (1933) has independently elaborated this concept.

There would seem to be little doubt that many of the normal processes of thought (e.g., comparison, etc.) involve the activity of neuronal circuits whose further activity does not lead to immediate motor action. Further, it would seem probable that when we feel emotion in conjunction with any thought process, we are dealing with the activity of a neuronal circuit which includes either some of the thalamic nuclei, and probably hypothalamic centres, or the prefrontal cortex which is intimately linked with the dorso-medial thalamic nucleus. Hence the associated phenomena of pain or pleasure, e.g., pallor or blushing, quickened pulse and respiration, visceral activities, etc. Let us attempt to apply such a concept to certain abnormal psychological phenomena, to explain which a whole structure of purely subjective hypotheses has been built up. I refer especially to the Freudian hypotheses. Some of the mechanisms suggested by Freud as working hypotheses to explain many pathological and also more or less normal phenomena, are those of conflict, repression, and the effects upon consciousness and behaviour which a repressed complex is capable of producing.

I would here suggest that the clinico-anatomical findings, which have shown that thalamic activity is closely linked with the emotional or affective aspect of sensations and thoughts, would also make it a feasible possibility that the activity of thalamic centres once started into action, is of so "powerful" a nature (e.g., either because of the intensity of the nerve impulses initiated in the thalamic cells or because of some property of their synapses) that, if these impulses are unable to give rise to a normal activity via the cortex, they link up abnormally with other circuits in the cortex, and hence we could explain the abnormal behaviour following upon repression (i.e., inhibition). Conflict itself would be similar to that seen in the ordinary phenomena of reflex activity, but naturally on a more complex scale, and intimately associated with that dual activity of cortex and thalamus.

My own conviction is that with the knowledge now available to us from the researches of Pavlov, Sherrington, Denny Brown, Le Gros Clark, Head, etc., we are in a position to attempt to formulate more accurate hypotheses as to the physiological correlates of the Freudian concepts. If these concepts are valid, then it is obvious that any such hypotheses must prove to be valid also, and will further our understanding of mental processes. The importance of the linkage of some part of the prefrontal cortex to thalamus and hypothalamus is further emphasized by an actual observation of Penfield and Gage (1933). In a patient in whom the frontal lobe was exposed at operation, galvanic stimulation of certain sites in the mid frontal gyrus led the patient to weep and grind his

teeth, and sometimes to struggle wildly. It seems possible, in some conditions, that the height of the wave which, possibly, flickers during attention from place to place in the cortex, may sometimes occur in the thalamus, while the whole of the cortex is in a relatively quiescent state. Examples of such a condition are seen in cases of extreme emotion, such as in hysterical laughter (which leads to complete helplessness), at the height of the sex act, blind rage, etc.

It is perhaps pertinent here to refer to a very fundamental criticism of Pavlov's work by Denny Brown (1932). In order that a conditioned reflex (or response, as Brown prefers to call it) may be established, an essential feature is the *satisfaction* of the nervous state. As he remarks, it is this satisfaction, whether it be of hunger, of thirst, etc., that is a characteristic of cortical processes and is largely ignored by Pavlov. "The last step in the train of events must be the final proprioceptive sensory information reaching the cortex, implying repletion of the hunger need" (Denny Brown, 1932). It seems to me that until we have a clearer idea of what these various bodily satisfactions are, and how they supply their proprioceptive answer, many of the Freudian phenomena will remain without an objective restatement.

Denny Brown remarks that Troland (1928) has called this satisfaction "retroflex action". Much of this activity must take place at the thalamic level, being intimately associated with pleasure. Troland's work on Human Motivation is one of the few psychological works which attempt to correlate our modern knowledge of thalamic functions with normal psychological phenomena. Many other speculations of Denny Brown seem most attractive and in line with Sherrington's work on the lower reflex mechanisms to the elucidation of which Brown has himself made many contributions. Among these hypotheses, a very suggestive one is that which he puts forward to explain the process of attention in the alert state. It is, briefly, that there is "a subcortical primitive sensory mechanism (possibly thalamic) concerned in the appreciation of newness or vividness (primitive contrast) of stimulus, and having the power to facilitate the appropriate field of the cortical discriminating mechanism". Further, "the fatigue, or exhaustion, or simple lack of stimulation of such a mechanism accounts for the phenomenon of sleep without the postulation of any active negative process. The transitional states of hypnosis remain as transitional states both on the above hypothesis or on the hypothesis of irradiation of inhibition". In conclusion he states, referring to Pavlov's work, "Between the knowledge of sensory processes in the cerebral cortex thus gained, and the little definite knowledge that has been gained of the outgoing cortical motor pathway, there remains a complicated nervous mechanism still unexplored."

The most important development here undoubtedly is the development of auditory and visual symbols, these giving a sort of shorthand whereby the mind can handle more and more complex ideas. Some speculations have been made as to what is possibly happening in the cortical network during this process of handling symbols, in other words, in speech and writing, etc., but as yet they are too speculative to be of much value. Bolton's observations on the different layers of cells in different areas of the cortex, and the coarse disturbances in various diseases are well known. They have been ably summarized recently by Hines (1929) and Kappers (1929). When we examine subjective psychology we find an immense collection of observations, great differences of opinion and a multitude of theories, though probably the application of statistical methods by Spearman

(1923, 1927, 1930) and others is slowly sifting out the truth. Whether the qualitative and quantitative principles which Spearman educes will hold, will, I imagine, ultimately depend on the extent to which we can describe them in objective physiological terms. Proceeding still further, we have the doctrine of mental energy, so ably discussed by Spearman (1927), with the law of fatigue and the law of constant output.

It is interesting to note that two concepts which Kant considered as a priori, namely space and time, seem in part to be resolving themselves into concepts which, in the case of space at least, are built up by an integrative process in a localized nucleus of the thalamus and a localized area of the parietal cortex, and to a lesser degree also our cortex seems in some way to be able to estimate time, possibly by some measurement (largely unconscious) of, or concentration upon bodily rhythms, such as respiration, the heart beat, etc. The whole question of the relation between the Kantian ideas and our modern physiological ideas of space perception is discussed by Camis (1930).

Before passing on to the consideration of the efferent mechanisms, it is of interest to mention here the light which certain clinical cases throw upon the James-Lange hypothesis of the origin of the emotions. Although this theory had been shown not to be in accord with experimental evidence (Sherrington, 1906), further evidence on clinical grounds also tends to discount the hypothesis. Kinnier Wilson (1928) has collected some of the clinical evidence in cases of pathological laughing and crying. The bodily reverberation, as James calls it, is not the emotion. In cases of pseudo-bulbar palsy, which are characterized by attacks of laughing and crying, the patient may be extremely angry at the constant caricaturing of his real feelings. "A patient of my own (case 5) told me how one day his daughter had hinted plainly enough that she thought 'Dad was putting it on a bit'; incensed at her unbelief, he rose from his chair to give her a box on the ears, but his legs giving way, he had to throw his arms round her neck to keep himself from a fall, and in this (for his angry state of mind) ignominious position he burst into explosive laughter."

(7) *The expression mechanisms, muscles and their control.*

Let us turn now to another aspect of the cerebral cortex and the nervous system, namely the apparatus concerned in giving final expression to the thoughts and impulses which have been elaborated in the brain. This motor mechanism naturally, of course, has its final effect upon the muscles, glands, etc. Our knowledge of the mechanisms concerned, whether cortical or at lower levels, down to the "final common pathway", has been largely due to Sherrington and his fellow workers. These mechanisms for motor control have had profound repercussions upon the sensory processes. Their evolution is of extraordinary interest and has been ably summarized by Wood-Jones (1918) and Huber (1930), etc., and also by the clinicians (Hughlings Jackson, Kinnier Wilson, 1928, etc.). As Wood-Jones (1918) expresses it, the motor area is one in which an animal can, as it were, see and feel itself performing movements. This motor area becomes more defined and extended in its control as we ascend the scale to man. It is interesting to see that it commenced with facial and grasping or biting movements, next the forelimb and especially the hand movements developed their re-representation in this area and finally the major part of the body. To quote Wood-Jones, "The animal without a neopallial kinaesthetic area performs all its actions in the absence of any pictured consciousness of the action. An animal

with a kinaesthetic area performs actions of which it has a definite mental pictured conception. *It knows what it is doing.* An animal with a developing prefrontal association area has, in addition, memories of its past actions. *It knows what it is doing, and it remembers what it has done.* An animal with an elaborated prefrontal area has, in addition, the faculty for building up pictures of possible future actions. *It knows what it is doing, and it remembers what it has done, and it can estimate what it might do.*" Although this word picture given by Wood-Jones may not prove to be quite accurate, nevertheless it gives us some idea of the probable evolution of the "action" side of the brain.

Recent work, clinical and experimental, upon the premotor cortex in man and apes indicates that, especially as regards movements of the hand, certain inhibitory and grasping movements, etc., may be associated with this area immediately in front of the so-called "motor" area proper (Bucy, 1933; Walshe and Graeme Robertson, 1933; Fulton, 1933; etc.). One thing at least emerges from our clinical and experimental knowledge of the control of movements, and that is the extreme complexity of mechanisms concerned, whether in the spinal cord, the cerebellum and vestibular apparatus, the red nucleus and *substantia nigra*, the *corpus striatum*, and finally the motor cortex. This steadily increasing complexity has been associated with a "transference of function", as Hughlings Jackson called it, to higher and higher centres. As Sherrington pointed out long ago, this transference of function is associated with the increasing dominance of the distance receptors, the eye and the ear, and their organ, *par excellence*, the cerebral cortex, "a relatively enormous neural super-structure possessing million-sided connections with multitudinous other nervous arcs and representing untold potentialities for redistribution of so-to-say stored stimuli by 'associative recall'" (Sherrington, 1906).

Closely associated with these complex mechanisms for the control of movements is the increasing complexity of the sensory pathways for informing these motor mechanisms as to how the muscles are acting; "the running proprioceptive commentary" becomes of profound importance. The full significance of these is not understood as yet, particularly the cortical connections with the cerebellum, the red nucleus and the *corpus striatum*, but already many curious anomalies of movement, narcolepsy, catatonia, etc., are being explained in terms of disturbance of one or other of these aspects of the controlling mechanism (Kinnier Wilson, 1928; Worrall, 1931).

In this connection it is interesting to note that there is much clinical evidence to suggest that there are distinct and separate nerve pathways and mechanisms concerned in discriminatory cortical motor control on the one hand and in the expression of the emotions on the other hand. The large mass of nerve cells in the base of the forebrain which is intimately linked with the thalamus, namely the *corpus striatum*, is probably closely associated with this emotional motor control mechanism. It remains, however, as one of the "mysteries" of the brain. This structure, the *corpus striatum*, also shows marked evolutionary changes, and reaches its highest development in birds, but is also very large and well developed in man.

In concluding my remarks upon this aspect of the nervous system I shall again quote Sherrington (1931), "It may be that to decipher how nerve manages muscle is to decipher how nerve manages itself. If so, not without significance should be what we have just glimpsed, that there are in the nervous system

heights of excitation and depths of inhibition higher and deeper and with grades of adjustment ampler than muscle with all its subtleties can commensurately express."

Finally, we can but briefly refer to muscle itself. Coincident with the evolution of the brain has been an all-round refinement, and differentiation, not only of the sensory receptive mechanisms, as is, for example, so ably expressed by Elliot Smith's description of the evolution of binocular stereoscopic vision, but also of the muscular mechanisms, whether they be in the hand or the facial musculature concerned with facial expression, or in the apparatus for that most profound development of action, speech.

Our knowledge of the mimetic apparatus, especially, has been greatly advanced by Huber in America and Lightoller in Australia, while the details of muscle action have been in part elucidated here in Sydney by Hunter, Royle, Wilkinson and Phillips. In conclusion, may I remind you that it is these final aspects of my subject that matter so profoundly, it is this necessity for the control of nervous reactions which has possibly led to the evolution of consciousness, as Lloyd Morgan has suggested? The closing words of Sherrington's classic work, "The Integrative Action of the Nervous System" (1906), hold today and are the most profound and philosophical to be found in modern science: "We thus, from the biological standpoint, see the cerebrum, and especially the cerebral cortex, as the latest and highest expression of a nervous mechanism which may be described as the *organ of, and for, the adaptation of nervous reactions.* The cerebrum, built upon the distance-receptors and entrusted with reactions which fall in an anticipatory interval so as to be *precurrent* (Lecture IX), comes, with its projicience of sensation and the psychical powers unfolded from that germ of advantage, to be the organ *par excellence* for the readjustment and the perfecting of the nervous reactions of the animal as a whole, so as to improve and extend their suitability to, and advantage over, the environment.

"These adjustments, though not transmitted to the offspring, yet in higher animals form the most potent internal condition for enabling the species to maintain and increase in sum its dominance over the environment in which it is immersed. A certain measure of such dominance is its ancestral heritage; on this is based its innate right to success in the competition for existence. But the factors and elements of that competition change in detail as the history of the earth proceeds. The creature has to be partially readjusted if it is to hold its own in the struggle. Only by continual modification of its ancestral powers to suit the present can it fulfil that which its destiny, if it is to succeed, requires from it as its life's purpose, namely, the extension of its dominance over its environment. For this conquest its cerebrum is its best weapon. It is, then, round the cerebrum, its physiological and psychological attributes, that the main interest of biology must ultimately turn."

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The Secretary (for Dr. G. A. Waterhouse, Honorary Treasurer, who was absent through illness) presented the balance sheets for the year ended 28th February, 1934, duly signed by the Auditor, Mr. F. H. Rayment, F.C.A. (Aust.); and he moved that they be received and adopted, which was carried unanimously.

No nominations of other candidates having been received, the Chairman declared the following elections for the ensuing session to be duly made:

President: Professor W. J. Dakin, D.Sc.

Members of Council: Sir T. W. E. David, K.B.E., C.M.G., M.A., D.Sc., F.R.S., W. W. Froggatt, F.L.S., A. H. S. Lucas, M.A., B.Sc., H. S. H. Wardlaw, D.Sc., G. A. Waterhouse, D.Sc., B.E., F.E.S., W. L. Waterhouse, D.Sc.Agr.

Auditor: F. H. Rayment, F.C.A. (Aust.).

A cordial vote of thanks to the retiring President was carried by acclamation.

Linnean Society of New South Wales

GENERAL ACCOUNT. Balance Sheet at 28th February, 1934.

LIABILITIES.	£ s. d.	£ s. d.
Capital: Amount received from Sir William Macleay during his lifetime	14,000 0 0	
Further sum bequeathed by his Will	6,000 0 0	
		20,000 0 0
Contingencies Reserve		9,704 9 11
Fletcher Memorial Fund at 28th February, 1934		23 17 0
Commercial Banking Co. of Sydney, Ltd.		106 13 1
Income Account at 28th February, 1934		308 18 4
		£30,143 18 4

ASSETS.	£ s. d.
Society's Freehold	11,000 0 0
Consols	1,000 0 0
Loans on Mortgage	3,600 0 0
Science House (one-third share)	14,533 18 4
Cash in hand	10 0 0
	£30,143 18 4

INCOME ACCOUNT. Year Ended 28th February, 1934.

	£ s. d.	£ s. d.
To Salaries and Wages		1,079 6 8
„ Printing Publications	489 10 0	
„ Illustrations	72 9 6	
		561 19 6
„ Rates and Insurance		201 10 6
„ Library		14 0 10
„ Postage	41 3 5	
„ Petty Cash	15 9 2	
		56 12 7
„ Audit	8 11 6	
„ Printing	19 16 6	
„ Attendance and Cleaning	26 3 6	
„ Supplement, Catalogue Scientific Periodicals	10 0 0	
„ Expenses	24 4 6	
		88 16 0
„ Interest on Overdraft, etc.		21 8 0
„ Bank Expenses		2 6 2
„ Rent—Science House		169 19 11
„ Appropriation: Contingencies Reserve		7 7 0
„ Balance to 1934-35		308 18 4
		£2,512 5 6

	£ s. d.	£ s. d.
By Balance from 1933-34		259 5 0
„ Subscriptions: 1933-34	133 7 0	
Arrears	22 1 0	
In Advance	10 10 0	
		165 18 0
„ Entrance Fees		7 7 0
„ Interest		136 19 1
„ Rents		318 10 0
„ Sales (including 60 copies of Proceedings purchased by Government of New South Wales)		113 19 1
„ Bank Exchange		2 7 7
„ Fellowships Account (surplus income at 28th February, 1934, transferred)		777 19 9
„ Science House Returns		730 0 0
		£2,512 5 6

Examined and found correct. Securities produced.
F. H. Rayment, F.C.A. (Aust.),
Auditor.
13th March, 1934.

G. A. Waterhouse,
Hon. Treasurer.
5th March, 1934.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

BALANCE SHEET at 28th February, 1934.

LIABILITIES.	£	s.	d.	ASSETS.	£	s.	d.
Amount bequeathed by Sir William Macleay	35,000	0	0	Consols	10,900	0	0
Surplus Income Capitalized	14,216	1	4	Loans on Mortgage	37,700	0	0
				Homes Loan	477	10	0
				Commercial Banking Coy. of Sydney, Ltd.	138	11	4
	£49,216	1	4		£49,216	1	4

INCOME ACCOUNT. Year Ended 28th February, 1934.

	£	s.	d.		£	s.	d.
To Balance	232	8	0	By Interest	2,610	7	9
„ Salaries of Linnean Macleay Fellows	1,600	0	0				
„ General Account	777	19	9				
	£2,610	7	9		£2,610	7	9

Examined and found correct. Securities produced.
F. H. RAYMENT, F.C.A. (Aust.),
Auditor.
13th March, 1934.

G. A. WATERHOUSE,
Hon. Treasurer.
5th March, 1934.

BACTERIOLOGY ACCOUNT.

BALANCE SHEET at 28th February, 1934.

LIABILITIES.	£	s.	d.	ASSETS.	£	s.	d.	£	s.	d.
Amount bequeathed by Sir William Macleay	12,000	0	0	Consols				15,820	0	0
Accumulated Income Capitalized	3,820	0	0	Cash: Commercial Banking Company of Sydney, Ltd.	496	19	0			
Income Account at 28th February, 1934	518	7	9	Savings Bank	15	8	9			
				In hand	6	0	0			
								518	7	9
	£16,338	7	9					£16,338	7	9

INCOME ACCOUNT. Year Ended 28th February, 1934.

	£	s.	d.		£	s.	d.
To Salary	600	0	0	By Balance from 1933-34	507	1	3
„ Expenses (Storage and Cartage)	12	10	1	„ Interest	625	8	10
„ Petty Cash	1	12	3				
„ Balance to 1934-35	518	7	9				
	£1,132	10	1		£1,132	10	1

Examined and found correct. Securities produced.
F. H. RAYMENT, F.C.A. (Aust.),
Auditor.
13th March, 1934.

G. A. WATERHOUSE,
Hon. Treasurer.
5th March, 1934.

NOTES ON AUSTRALIAN DIPTERA. XXXIV.

By J. R. Malloch.
(*Communicated by F. H. Taylor.*)

(Two Text-figures.)

[Read 28th March, 1934.]

The data presented below are required in connection with some rearings of species by Australian workers and are presented to permit of certain specific names being available for publication of the records.

Family Agromyzidae.

Haplomyza imitans, n. sp.

♂, ♀. Very similar to *Agromyza pusilla* Meigen in size, colour markings and wing venation, the most striking distinction between them consisting of the lack of the outer cross-vein of the wing, which incidentally constitutes the principal generic character. The less evident forward inflection of the third vein, and the continuance of the costal vein to the apex of the fourth vein, distinguish the genus from *Phytomyza*.

Head yellow, ocellar triangle and occiput black, aristae, the bristles and hairs black. Thorax yellow, distinctly shining but not highly glossy; mesonotum with the lateral margins in front of wings yellow, the disc rather dull black owing to the presence of faint dusting; scutellum yellow, with the lateral margins narrowly black; mesopleura with a black mark on lower anterior angle, sternopleura black except on the upper margin, hypopleura with a black central mark; postnotum black. Abdomen shining black, with narrow yellow apices to the tergites; hypopygium of male, and the sheath of ovipositor and the ovipositor of female shining black. Legs yellow, tibiae and tarsi black, the fore tibiae paler, especially in male. Wings hyaline, veins black. Squamae dirty yellow, fringes fuscous.

Frons almost half the head-width, all the frontal bristles well developed, the orbitals three in number, the upper two pairs reclinate, the anterior pair incurved, and a few very fine short hairs laterad of the bristles; third antennal segment short, rounded at apex, about as wide as height of cheek below middle of eye; arista pubescent. Mesonotum with two strong pairs of postsutural dorsocentrals and a much weaker pair usually visible in front of these close to the suture, the intradorsocentral hairs in four irregular series anteriorly, and some rather well developed hairs in front in line with the dorsocentrals; scutellum with four equally long bristles; mesopleura and sternopleura each with one bristle, propleural distinct. Abdomen as in *Agromyza pusilla*. Legs normal. Fourth vein ending almost exactly in the wing tip, penultimate section of costa a little shorter than ultimate, the latter slightly shorter than section basad of the apex of first vein, inner cross-vein below apex of first, fifth vein complete. Length, 1–1·5 mm.

Type, female, allotype, and three paratypes, mining spinach, Sydney, N.S.W., 20.10.1931; paratypes, four, mining wall-flower, same locality, 26.10.1931, and two mining *Stellaria media*, same locality, 11.10.1931 (K. E. W. Salter). Type and allotype in the Macleay Museum; paratypes in the School of Public Health and Tropical Medicine collection.

Family Tachinidae.

Genus Froggattimyia Townsend.

This genus I have included in my key to the genera of Australian Tachinidae in a previous paper in this series, and I have also given a few notes on the type specimen of the genotype, *hirta* Townsend, in the same paper. I have had several specimens of the genus before me for two or three years, but did not care to deal with them until more material was available. Now I have received specimens from Mr. A. L. Tonnoir that call for an identification, and present below some data dealing with the species involved.

The genus is distinguished from its allies by the presence of propleural and prosternal hairs, the slightly carinate face, and the presence of fine hairs on the entire length of the parafacials.

Key to the Species.

1. Males 2
   Females 6
2. Mesopleura with bright fulvous yellow hairs on entire lower half, a patch of black hairs on central portion of the upper half 3
   Mesopleura entirely black-haired 5
3. Abdomen yellow-dusted on dorsum; parafacial at base of antenna not much more than half as wide as length of eye; genae with numerous black hairs on upper third of the raised part; the dark central part of the dorsum of abdomen not one-third of the width of disc ..... *wentworthi*, n. sp.
   Abdomen grey-dusted on dorsum, the black central part about half as wide as the disc and bluish in tone 4
4. Hairs on parafacials not extending much below level of middle of third antennal segment and quite long, the width of the parafacial not more than two-thirds as great as length of eye; genae black-haired on upper half or more of the raised part ..... *nicholsoni*, n. sp.
   Hairs on parafacials extending to or almost to level of apex of third antennal segment and quite short, the width of the parafacial about four-fifths the length of eye; genae entirely fulvous-yellow haired, or with but one or two darker hairs on upper margin of the raised part ..... *fergusoni*, n. sp.
5. Distance between the vibrissae greater than that from either to eye-margin; third antennal segment and aristae black, the former with a very narrow reddish mark at base on inner side; legs black, tarsi yellowish, fore pair more conspicuously so than the other pairs ..... *tillyardi*, n. sp.
   Distance between the vibrissae not as great as that from either to eye-margin; third antennal segment fulvous-yellow, the outer or upper surface more or less infuscated or browned; legs dark brown, apices of femora, the tibiae, and tarsi paler ..... *hirta* Townsend.
6. Mesopleura with all the hairs black 7
   Mesopleura with fulvous-yellow hairs on lower half 8
7. Distance between the vibrissae distinctly greater than that from either to eye-margin; legs tawny-yellow, apices of tarsi slightly darker; third antennal segment and aristae black, the former almost as wide as parafacial .... *lasiophthalma*, n. sp.
   Distance between the vibrissae not as great as that of either from eye-margin; legs fuscous or dark brown; third antennal segment brownish-yellow, the outer, or upper, half or more dark brown or fuscous ..... *hirta* Townsend.
8. Ventral surface of hind coxae with numerous fulvous-yellow bristles and hairs, no black bristles present; hind trochanter with one long black bristle; humeral angles not yellow, the lateral margins including the humeri with grey dust

which is not noticeably different in colour from that of the disc of mesonotum ..... *nicholsoni*, n. sp.

Ventral surface of hind coxae with a number of strong black bristles and a few fulvous-yellow hairs; hind trochanter with one black bristle; humeral angles yellowish, the lateral margins of the mesonotum with the dust ochreous-yellow and distinct in tone from the grey dust of the disc 9

9. Fourth visible abdominal tergite with the disc covered with quite fine hair-like bristles which become stronger and longer on sides; third antennal segment orange or fulvous-yellow, with a very narrow brown upper margin ..... sp.

Fourth visible abdominal tergite with numerous quite well developed bristles on disc; third antennal segment with the apical third brown, which colour extends along the upper edge almost to base ..... sp.

I describe the first species very fully, and it is to be taken that the others differ from it in the particulars listed in the above key and in the notes or abbreviated descriptions given below.

FROGGATTIMYIA WENTWORTHI, n. sp. Text-fig. 1.

♂. Head testaceous-yellow, with yellow dust, interfrontalia reddish-brown, becoming darker above, orbits blackened except in front and with grey dust on the blackened part, not distinctly shining, ocellar triangle coloured as upper orbits, occiput blackened except on the lower third, the dark part yellowish-grey dusted; antennae orange-yellow, dark brown or fuscous on apical third of third segment and with the dark colour extending to base on upper edge; aristae fuscous at apices, fulvous at bases; palpi orange-yellow, with short black hairs at apices and longer pale hairs basad of these; hairs of frons, parafacials, the upper third of raised part of genae, and immediately behind the postocular ciliae black, the others yellow. Thorax black, more yellowish on lower half of humeral angles, postalar region, and the sutures of pleura; scutellum testaceous-yellow; mesonotum with whitish-grey dust, when seen from behind with four linear dark vittae, the submedian pair not continued much behind suture, the sublateral pair continued to about midway between suture and posterior margin; lateral margins behind bases of wings yellowish-dusted; mesonotal hairs, all bristles and some hairs on central upper part of the mesopleura black, the others fulvous; scutellum black-haired except for some yellowish hairs on sides anteriorly. Abdomen testaceous, more red on sides above, and with a central blackish stripe of dorsum which tapers posteriorly and is not more than one-third of the dorsal width at any part, seen from behind with a narrow dark dorsocentral vitta and dark changeable lateral marks on second to fourth tergites, the entire surface very densely coated with yellow or ochreous dust; dorsal hairs and bristles black, those of venter, except on fourth tergite apically, fulvous-yellow. Legs orange to fulvous-yellow; fore coxae with numerous black bristles in front, hind pair with fulvous-yellow bristles and hairs on ventral surface, hind trochanter with one black bristle. Wings greyish hyaline, yellowish at bases, veins brown. Squamae brownish-yellow. Halteres fulvous-yellow.

Frons at vertex a little less than one-fourth of the head-width, widened to anterior margin, the orbits at anterior ocellus about half as wide as interfrontalia, widened anteriorly; inner vertical bristles moderately long, outer pair very fine and short; ocellar bristles proclinate and divergent, very short; each orbit with a series of about 18 incurved inner marginal bristles, the lower one close to level of apex of second antennal segment and diverging outward from the inner margin, the entire surface laterad of the bristles and the parafacials with fine black hairs which extend downward to lower level of eye; parafacial

at level of antennal base about half as wide as length of eye and about equal to 2·5 times the width of third antennal segment; face slightly receding below, vibrissae about the length of second antennal segment below apices of antennae and slightly more than that distance above mouth margin; cheek nearly half as high as eye and about 1·5 times as high as greatest width of parafacial; second segment of arista about as thick as long; palpi slightly thickened at apices. Thorax with the usual 3 + 4 dorsocentrals and 3 + 3 acrostichals, 2 + 1 sternopleurals, and the apical pair of scutellar bristles short and fine. First and second visible tergites of the abdomen each with a pair of apical central bristles, third with a complete series, fourth with surface quite regularly covered with long bristly hairs, none of which is nearly as strong as the apical series on third tergite. Hypopygium small (Text-fig. 1), base shining brown, with numerous fine hairs. Fore tibia with two posterior bristles, the anterodorsal series hardly developed, consisting of very short setulae; mid femur with about four long bristles on basal half of ventral surface; mid tibia with three bristles near middle, one, the longest, on anterodorsal, one on ventral, and one on posterior surface; hind femur with four or five bristles on basal third and one or two near apex of anteroventral surface, and only the basal series on posteroventral; hind

Text-fig. 1.—Hypopygium of *Froggattimyia wentworthi* male: *a*, forceps from the side; *b*, penis from the side; *c*, forceps from behind, denuded.
Text-fig. 2.—*Paropsivora grisea*, head in profile.

tibia with two posteroventral and one or two anteroventral bristles, the anterodorsal surface with a regular series of closely placed short bristles, one near middle longer than the others. Second costal section but little shorter than third, the latter about 1·33 times as long as fourth; bend of fourth vein angular, without an appendage; base of third vein with three or four bristles above and two below. Squamae large, the lower one not bulged up on inner margin, subtransverse on outer and hind margins. Length 12 mm., width at base of abdomen 5·5 mm.

Type, Wentworth Falls, N.S.W., 21 Dec., 1923 (Harrison).

FROGGATTIMYIA FERGUSONI, n. sp.

♂. Very similar in general appearance and coloration to the preceding species, differing essentially as noted in the foregoing key to species.

The upper portion of the parafacials and the entire frontal orbits in the type are rather distinctly shining, the parafacials are much wider than in *wentworthi*, the hairs on the latter are also much shorter, and the ocellars are stronger. It may be noted also that in the colour of the hairs on the palpi and

the bristles of the hypopleura there is a distinction, these being all fulvous in *fergusoni*, but this may not be a constant character in either species. Also the mid tibia in *fergusoni* has two posterior bristles and the outstanding bristle near the middle of the anterodorsal series of the hind tibia is much longer than in *wentworthi*, but here again there may be variation which can only be checked up with a series of specimens. The very wide central blue-black dorsal stripe on the abdomen appears to be a good character and undoubtedly one that will be less subject to variation than the others. In the other characters there is very little that can be utilized for specific distinction, although there are about twice the number of short bristles on the base of the third vein both above and below that there are in *wentworthi*, and the third section of the costa is fully 1·5 times as long as the second. Length 13 mm., width at base of abdomen 6 mm.

Type, Wyalkatchem, W.A., 1 Sept., 1926 (E. W. Ferguson).

Named in memory of the gentleman who induced me to take up the study of Australian Diptera.

FROGGATTIMYIA NICHOLSONI, n. sp.

♂. This species is also very similar to the first one, which obviates the necessity for a full description here.

The colour of the abdomen is similar to that of *fergusoni*, but the dark central stripe is narrower, occupying about one-third of the dorsal width, the dust on the dorsum of abdomen is more checkered or uneven, the parafacials are longer haired, as are also the genae, and the latter are more preponderantly black-haired. The mid tibia of the only leg of that pair intact has three posterior bristles, the hind tibia has three posterodorsal bristles as in *fergusoni*, the hypopleural bristles are mixed black and fulvous, and the bristle on the hind trochanter is yellow, differing thus from the two preceding species. Base of third wing-vein with four or five short bristles above and only one below; costal divisions as in *fergusoni*. Length 13 mm., width at base of abdomen 6 mm.

Type, Sydney, 25 Aug., 1923 (Nicholson).

Named in honour of the collector through whose efforts I have been able to see many interesting species from Australia.

The female described here, I believe, belongs to this species, though the conclusion requires confirmation in the field. My decision is based upon the fact that the base of the third wing-vein has but one bristle on the underside, and there is a second outstanding bristle in the anterodorsal series on the hind tibia, near the base, which is weakly but quite evidently represented in the male also, and not at all visible in the other two species of the group known to me in the male sex.

♀. Differs from the male in having the entire dorsum of the abdomen blue-black, rather densely and slightly changeably whitish-grey dusted, and the scutellum entirely or almost entirely dark. Frons almost one-third of the head width at vertex, outer verticals about half as long as inner pair, ocellars of moderate length, each orbit with the upper inner bristle reclinate, and one or two outer proclinate bristles. Abdomen more tapered than in male, fourth visible tergite with long hair-like bristles on entire dorsum, none of which are nearly as strong as the apical series on third tergite. Length 8–10 mm.

Allotype, and one paratype, Blue Mts., 25 Mar. and 15 Jan., 1922 (Health Dept.).

FROGGATTIMYIA HIRTA Townsend.

Canad. Ent., 48, 1916, 155; Malloch, PROC. LINN. SOC. N.S.W., 54, pt. 4, 1929, 323.

♂, ♀. A much darker species than any of the three just dealt with, the pleural hairs, except some on the extreme lower part of the humeral callus and those on the centre of the propleura, black. The legs are darker also, though in the material before me the colours are very obscure because the specimens have been killed before attaining absolute maturity. The type male in the collection of the United States National Museum unfortunately has lost all the legs except the hind femur on one side, and this is dark brown to beyond the middle and fulvous at apex. Because of immaturity and the presence of dirt the specimens of both sexes before me have the legs apparently dark brown, though held against the light the tibiae are evidently much paler. The dark-haired parafacials and genae, with the shorter hairs on the former and the greater width of the parafacials in profile, extensively reddish third antennal segment, and less extensive red marks on the sides of the abdomen in the male, distinguish the species from the next one. Length 8–9 mm.

Townsend in his original record stated that he had a male and a female from Mittagong, N.S.W., reared from Sawfly larvae. The male I accept as the type, the female I believe is not conspecific and is dealt with below. I place here two males and one female from Roma, Qld. (Department of Agriculture, Brisbane, Q.), reared from larvae of *Pterygophorus analis* Costa, 12.2.1915 (H. Tryon). This species is also a Sawfly, but there is no means of determining whether the host was the same in both cases.

FROGGATTIMYIA TILLYARDI, n. sp.

♂. Differs from *hirta*, as indicated in the foregoing key to species. It may be noted also that the abdomen is more tapered posteriorly in the male and is more extensively red on the sides, the second and third segments being broadly so. The black legs with their pale tarsi, especially the fore tarsi, are very distinctive. The widely spaced vibrissae are quite characteristic, and in profile these are almost in line with the lower level of the eye, which is not the case in any other male before me. The abdomen in the male has a more marked black dorsocentral vitta than in *hirta*, but none of the tergites has a dark hind margin. Eyes with a few very short sparse hairs. Length 8 mm., width at base of abdomen 3 mm.

Type, Blundell's, F.C.T., December, 1931, parasite of *Paropsis reticulata* Marsh. (W. K. Hughes).

FROGGATTIMYIA LASIOPHTHALMA, n. sp.

♀. This species rather closely resembles the preceding one and may possibly be but the female of it, though there are several striking distinctions in both structure and coloration that would appear to justify me in my present course of considering them distinct.

The general coloration is very similar, but the abdomen is nowhere red and has the dusting quite dense and somewhat checkered, the legs are tawny yellow with the coxae black and the apices of tarsi infuscated, the head is brownish-yellow, with only the occiput except the lower third blackened, and the third antennal segment is entirely black.

The eyes have more evident, longer, and denser hairs than in the above male, the third antennal segment is comparatively longer and wider, and the

parafacials are a little wider. None of these characters is more pronounced in females than in males as a general rule in this group as far as my experience goes. In both, the vibrissae are about equally widely placed, and the gena is about one-third as high as the eye. Length 7–8 mm.

Type and one paratype, Black Mt., F.C.T., December, 1931, parasite of larvae of *Gonipterus scutellaris* Gyll. (W. K. Hughes).

A peculiarity of the female consists of the heavily chitinized pointed subtriangular piercer which is curved forward below the venter.

FROGGATTIMYIA SP.

♀. This is the specimen which Townsend included as the female of *hirta* in his original description of that species, but I cannot agree with that decision because of the colour of the hairs of the mesopleura, which are fulvous except on the upper central portion. The legs are entirely fulvous-yellow, including the coxae and tarsi, and the third antennal segment has a very fine border of brown on its upper or outer side. The abdomen has a red mark on each side which covers the apex of first, all of second, and the base of third tergite, but does not extend far inward. The hairs on lower part of the parafacials and all of those on the genae are yellow. The abdominal bristles are much weaker than usual, even those in centre of the apex of third tergite being short and hair-like. Length 8·5 mm.

Locality, Sydney, N.S.W., labelled parasitic larva (W. W. Froggatt).

I prefer to allow this specimen to stand without a name pending the discovery of the male.

FROGGATTIMYIA SP.

♀. Similar to the preceding species but with a greater proportion of the abdomen red on sides, and the third antennal segment more largely dark brown. The abdomen has much stronger bristles, the series on the apex of third tergite and several of those on the disc of fourth being quite strong. Length 7–8 mm.

Locality, Narromine, Maroondah, N.S.W., no collector's name or date.

PAROPSIVORA, n. gen.

Generic characters.—Belongs to the group in which the centre of the propleura is haired. In addition to this character the prosternum has setulae on the sides, the parafacials are bare, the frontal bristles do not descend below the level of the apex of second antennal segment, the third antennal segment is about twice as long as the second and has the upper apex distinctly though not conspicuously pointed, the arista is bare, with the second segment not elongated, the palpi are normal, and the abdomen has no discal bristles. For other characters see description of genotype below.

PAROPSIVORA GRISEA, n. sp.

♀. Black, densely grey-dusted. Frontal stripe fuscous, darker than the orbits; antennae and aristae black; palpi testaceous-yellow; inner occipital hairs and the beard yellow. Mesonotum with four dark grey vittae which do not extend more than midway from the suture to hind margin. Abdomen with the dust checkered much as in typical species of the genus *Sarcophaga*, changeable according to the angle from which it is viewed. Legs black. Wings hyaline, veins brown. Calyptrae white. Halteres yellow.

Eyes with some very short sparse pale hairs; frons at vertex nearly one-fourth of the head-width, interfrontalia in front of anterior ocellus not as wide

as either orbit at that point, almost uniformly wide to anterior extremity, the orbits widened and quite strongly bristled, the inner margin with the upper two bristles recurved, the anterior four or five incurved, the anterior two divergent, proclinate outer bristles strong, two pairs; ocellars of moderate length, proclinate and divergent; outer verticals shorter than the inner pair; face shallowly and evenly concave; profile as in Text-figure 2. Dorsocentral bristles 3 + 4, acrostichals 3 + 3, the posterior presutural pair close to suture; presutural sublateral area with five bristles; sternopleurals three, two strong above and one very fine short one below midway between the others. Abdomen ovate, first two visible tergites each with a pair of central apical bristles, third with an apical transverse series, fourth with a number of strong bristles, forming two rather irregular transverse series, one median and the other apical. Fore tarsus with the apical four segments slightly widened; fore tibia with a posterior bristle, and the anterodorsal bristles short and present on more than the basal half; mid tibia with a strong ventral bristle, the anterodorsal surface with one long and one short bristle; hind tibia with a series of irregular bristles on anterodorsal and posterodorsal surfaces, the one near middle longest, beyond which the series stops. Venation as in *Phorocera*, first posterior cell open, ending before wing tip, outer cross-vein much closer to bend of fourth than to inner cross-vein, ultimate section of fifth vein subequal to outer cross-vein; third vein with two or three bristles at base above and below. Lower calypter as in preceding genus. Length 5·5 mm.

Type, Blundell's, F.C.T., December, 1931, parasite of larvae of *Paropsis reticulata* Marsh. (W. K. Hughes).

Type specimen slightly crushed, but the postscutellum apparently quite large.

THE EARLY STAGES OF *SCIADOCERA RUFOMACULATA* WHITE (DIPT. PHORIDAE).

By Mary E. Fuller, B.Sc.

(With a foreword by A. L. Tonnoir.)

(Eight Text-figures.)

[Read 28th March, 1934.]

Foreword (by A. L. Tonnoir).

In a previous paper (Tonnoir, 1926) I called attention to and discussed a fly, *Sciadocera rufomaculata* White,* which had been considered till then as belonging to the Empidae. I concluded that its affinities were with the Phoridae and that a new subfamily should be erected to receive it.

Father Schmitz, writing an account (1929) of a similar fly from Southern Chile, did not agree with my views and erected a new family to receive this genus; further, he concluded that the strongest affinities of *Sciadocera* were with the Platypezidae and not with the Phoridae.

Schmitz remarked that I had disregarded any possible connection between *Sciadocera* and the Platypezidae. This is not quite correct, because three years before (Tonnoir, 1923) I had placed *Sciadocera* in the Platypezidae; but later, after a closer study of the fly, I decided that its affinities were with the Phoridae and discussed them in detail. I did not give the reasons why this insect should not be placed with the Platypezidae, as I considered that the arguments in favour of its being placed with the Phoridae were quite sufficient.

As to the third view, to erect a new family, adopted by Schmitz and also suggested to me by Bezzi, I did not consider this possibility very long, because the Aschiza, being a transition group, is bound to contain a number of aberrant forms, for which it is more useful from the general taxonomic point of view to stress the affinities than to emphasize the differences. *Ironomyia* White would also be given family rank if one were to follow Father Schmitz' principle, instead of being placed with the Platypezidae, as I have done. There are probably a number of other unknown or still insufficiently known forms of the Aschiza for which new families could be erected. The final result would be that there would be a number of monogeneric families which would certainly not have the same status as the other families of the Diptera.

Schmitz concludes: "If we should nevertheless place this genus in this family (Phoridae), then we must have sounder reasons than those which Tonnoir indicates." These sounder reasons (or rather a few more of them) I find now in the recently gained knowledge of the early stages of *Sciadocera*, which it has been the good fortune of Miss Fuller to secure. These indubitably point to the conclusion that *Sciadocera* is a Phorid and that in these stages it is rather far removed from the Platypezidae.

I have previously mentioned having observed the female flies on the carcass of a Wombat, on which they were apparently trying to oviposit. I was therefore

* Through some unfortunate *lapsus calami* the species was mentioned throughout that paper as *S. maculata.*

not very surprised to find some specimens of *Sciadocera* among some insects captured by Miss Fuller in a trap baited with decaying liver. I pointed out to her then what a good opportunity this would be to secure the early stages of this much discussed fly, and she lost no time in obtaining them and describing them very adequately in the following paper.

In his classification of the larvae of the Diptera, Brauer (1883) placed both Phoridae and Platypezidae in the tribe Hypocera of the Aschiza, although he pointed out that there was not a single character in common between the larvae and pupae of the two families. Now that our knowledge of these stages is decidedly more extensive, there is yet no common character of importance to be found, as will be seen from the table I give here.

Platypezidae.	*Phoridae.*
LARVA.	
General shape oval, usually strongly flattened dorso-ventrally.	General shape similar to that of the Cyclorrhapha dipteron and usually elongate and subcylindrical.
Segmentation: Only ten or nine segments visible from above, the cephalic and the first thoracic segments being bent under the body (Text-fig. 2).	Twelve segments visible from above.
Cephalic segment not conspicuously bilobed. Metathoracic and first abdominal tergites sometimes fused together.	Cephalic segment projecting forward and strongly bilobed (Text-fig. 1).
Breathing system: Posterior spiracles placed on the anterior margin of the eighth abdominal segment and scarcely projecting above the dorsum.	Posterior spiracles placed right at caudal extremity of the body and usually borne by a more or less elongated process.
Mouth parts: of a very specialized type.* Oral hooks considerably modified in shape of large rasps and having lost all connection with the rest of the buccopharyngeal armature; they are embedded in the integument of the cephalic segment and move as a whole with that segment. Hypopharyngeal armature with single branches which are fused distally and project a long way out of the mouth but are bent backwards and provided with teeth. Floor of pharynx smooth. A small third median cornu present.	Generalized mouth parts. Two oral hooks articulated on the upper branch of the hypopharyngeal sclerite, whose lower branches are there fused together. The upper branches of this sclerite sometimes disconnected from the lower ones. Floor of the pharynx striated or corrugated. Only two cornua present.
PUPARIUM.	
The shape remains the same as in the larva.	The shape is different from that of the larva; flattened, often tortoise-shaped, the distal end conspicuously curved upwards.

* There is some disagreement about the structure of the mouth parts of the Platypezidae. Bergenstamm (1870) and later Brauer and Bergenstamm (1883) say that there are two well developed oral hooks, whereas de Meijere (1911) and Lundbeck (1927) are of the contrary opinion. From my own observations on a larva of *Platypeza* and judging from the position of the mouth opening, I cannot but conclude that the oral hooks are present in a very modified form as the lateral organs which Bergenstamm calls "radula" but do not homologize. I cannot believe that these organs are entirely new structures. The projecting median-toothed organ which de Meijere and Lundbeck seem to have identified as oral hooks cannot be anything else but a part of the hypopharyngeal armature since it is situated below the oral opening.

Platypezidae.	*Phoridae.*
Spiracles: Anterior spiracles placed on the first thoracic segment and but slightly protruding on the anterior margin of the body.	Anterior spiracles of the transpercing type and placed on the second abdominal segment, usually very elongated.
Dehiscence taking place along a semicircular line around the margin of the anterior part of the body and also sometimes between the first and second abdominal tergites, so that a piece composed of the meso- and metanotum plus the first abdominal tergite becomes detached.	Dehiscence taking place along a longitudinal median line on tergites of body segments 4 to 6 (abdominal 1 to 3), with further splits between segments 3 and 4 as well as 6 and 7, no piece getting detached.

A study of this table, after reading Miss Fuller's description of the early stages of *Sciadocera rufomaculata*, will convince anyone that this insect does belong to the Phoridae, as not a single one of its larval* or pupal characters can be considered as intermediate between those of the two families here analysed, but they all fall entirely on the side of the Phoridae.

Introduction.

During the winter of 1932 some curious flies were captured in a glass blowfly trap baited with liver. These were determined as *Sciadocera rufomaculata* White by Mr. Tonnoir, who pointed out the desirability of obtaining a knowledge of the early stages. The captured flies were all females, and several were placed in jars with fresh meat, wool or fungus. They did not oviposit on any of these materials. On the 18th July a female was put into a jar with a piece of old decayed liver in which *Calliphora stygia* larvae had been feeding. This was moist and putrid and was placed on soil. On 1st August small maggots, which on examination were found to be in their second instar, were present on the liver. They grew slowly and eventually pupated. In October a number of *Sciadocera* of both sexes emerged. Previously only females had been taken in this district. The flies which emerged were put into a cage provided with food, water and oviposition media. After a week, a small cluster of eggs, numbering about ten, was deposited on the soil near a piece of liver. These eggs did not hatch and eventually collapsed.

For comparison with *S. rufomaculata* a figure is given of the larval head of *Platypeza griseola* Tonn. which was bred from rotting mushrooms collected in April, 1932.

Length of Stages.

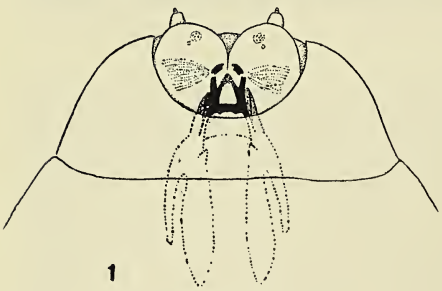
At the temperature in the laboratory (mean temperature for the period approximately 10°C.) the stages were as follows: The feeding period occupied 18 days, the prepupal stage 45 days and the pupal stage 14 days. Half-way through the prepupal period some of the prepupae were transferred to the hot room, which is kept at a temperature of approximately 23°C. The prepupal stage was then shortened to 25 days, but the pupal period was lengthened to 20 days. The longest that any of the flies lived in captivity was three weeks.

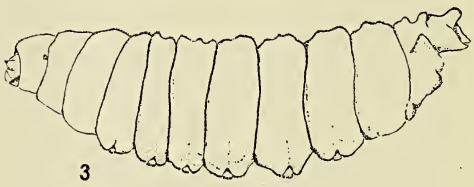
Description of Early Stages.

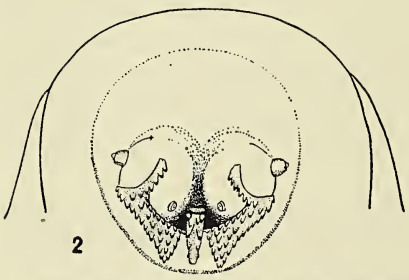
(*a*) *The Egg.*—The egg is creamy-white in colour. It is 0·64 mm. in length, of an elongate-oval shape, slightly more curved on one side than the other and rounded at both ends. The chorion is heavily sculptured with a pattern of raised, branched, irregularly broken lines.

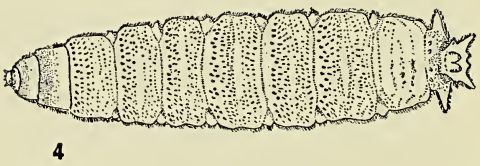
* With exception of the projecting hypopharyngeal armature.

(*b*) *Second Stage Larva* (Text-fig. 3).—No first instar maggots are available for description, as the larvae were not discovered until they were in the second instar. The maggots were then 2 mm. long and of a deep cream colour. The second stage larva is short and thick-set, narrowing at either end. Tiny colourless spines are present on the dorsal and ventral surfaces of each segment, particularly near the anterior border. These surfaces are undulating and folded, there being a spiny swelling in the centre of each segment ventrally. There are a pair of spiracles on the first thoracic segment, and a pair on the eighth abdominal segment situated at the ends of a pair of protuberances on the dorsal surface. The eighth segment has a number of other papillae which are described, along with the details of the mouth parts and spiracles, in the full grown maggot. The most noticeable differences in the two stages are the lack of close covering of scales and hairs in the second instar, and the thick cylindrical body, the full-grown maggot being flat and elongated and clothed with hairs.









Text-fig. 1.—Head of third stage larva of *S. rufomaculata,* ventral view. × 77.
Text-fig. 2.—Head of full-grown larva of *P. griseola,* ventral view. × 77.
Text-fig. 3.—Second stage larva of *S. rufomaculata,* lateral view. × 30.
Text-fig. 4.—Third stage larva of *S. rufomaculata,* dorsal view. × 8 approx.

(*c*) *Third Stage Larva* (Text-fig. 4).—The length of the full-grown maggot is from 7 to 8 mm. The skin is creamy coloured, thickly covered with brown hairs and spines, making the maggot a dirty, light brown colour. The form is typical of Cycloraphous Diptera, the body being formed of a small head, three thoracic, eight normal and two reduced abdominal segments. The larva is pointed at the head end and truncated posteriorly. It is comparatively broad and rather flattened dorso-ventrally, although the dorsal and ventral surfaces are actually slightly convex. The small pointed head is bilobed, with the oral hooks projecting ventrally between the lobes. Each lobe bears a pair of papillae representing maxillary palp and antenna. The antenna is anterior and is comparatively large, with a long narrow apical segment.

The first thoracic segment overarches the head dorsally. Its anterior third consists of a band of many rows of small spines directed backwards, which give place to long hairs in the last few rows. The hairs are more numerous on the sides. The rest of the segment is smooth. The anterior spiracles emerge about the middle of the segment laterally. Each anterior spiracle bears at the end a small plate which is surrounded by a thickened margin, and which has two slits close together. These slits are almost round in outline and resemble those in the posterior spiracles in structure. The second and third thoracic segments have bands of spines anteriorly, but the whole segment is haired, the hairs being most dense on the sides and fading away posteriorly. On the under surface the hairs diverge at the centre and sweep outwards to both sides, the third segment being more hairy underneath than the second.

The first to seventh abdominal segments are similar. Laterally the intersegmental membrane forms a small fleshy protuberance between each segment. Dorsally, on each side of the intersegmental line, the surface is smooth and slightly depressed. There is also on the dorsal surface a narrow shallow depression in the centre of each segment running parallel to the segmentation. The ornamentation on the dorsal surface of each segment is as follows: Near the anterior edge are a number of scattered scale-like spines, which are most numerous on the first abdominal segment. These give place to fine chitinous hairs which project backwards and become more sparse in the centre at the depression. Near the posterior border these hairs are smaller, more numerous and project forwards. They are most dense and conspicuous on the sides, giving the maggot a fringed appearance. The lateral protuberances are also each clothed with a tuft of hairs. All the hairs and spines are brown. The seventh segment is smoother than the others dorsally. It has no scales and the hairs are smaller and fewer.

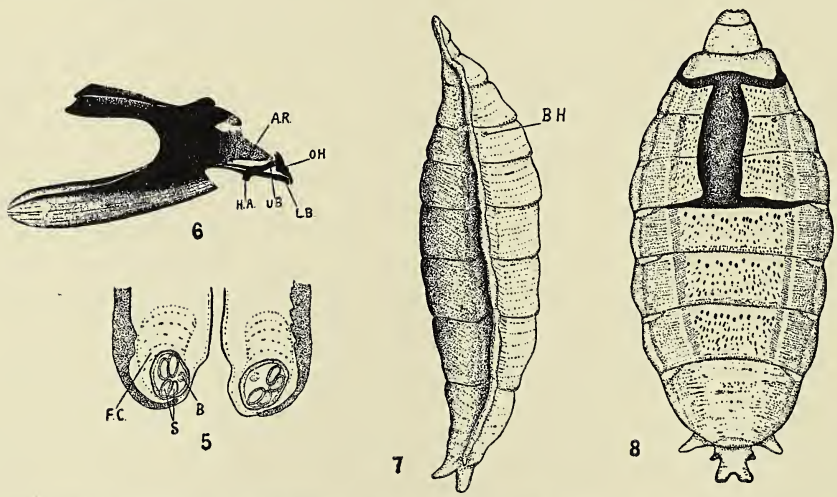
The ventral surfaces of the first seven abdominal segments are similar. They are undulating and covered with an arrangement of scales and hairs. The anterior border is marked in the centre by a number of flat pointed scales directed backwards. The posterior border has similar scales pointing forwards, these being larger and most noticeable on the last few segments. In the centre is a pair of bullae, one each side of the middle, corresponding to the depression on the dorsal surface. These swellings are clothed with very minute spinules and seem smooth by comparison with the rest of the surface. Surrounding them are two or three rows of scales pointed outwards. They become smaller passing outwards, and give place to hairs which cover the rest of the segment. In the centre between the bullae are several larger scales projecting backwards. Each abdominal segment has a lateral fold or ridge which is thickly haired.

The eighth abdominal segment is entirely different from the others. On the dorsal surface near the junction with the seventh are four papillae, two each side of the centre. These end in circlets of small dark spines. Near the anterior end, projecting laterally and slightly upwards and forwards are two large papillae covered with hairs. The dorsal surface of the segment between them is swollen into a ridge covered densely with small spines directed forwards. The segment narrows considerably about the centre and the posterior half of the dorsal surface is bare except along the edge. The segment ends in a pair of large papillae pointing backwards and outwards and covered with hairs. Between them is a pair of smaller papillae, and there is a similar lateral pair anterior to them. From the centre of the dorsal surface of the posterior half of the segment a pair of tubes arise (Text-fig. 5). They project upwards and backwards, and bear the

spiracular plates at their ends. The tubes are highly chitinized on the sides, especially on the outer edge. The plates are small, each with four slits arranged in two pairs.

The anterior half of the under surface of the eighth segment is swollen and densely covered with hairs projecting backwards. There is a depression in the centre, in which are a pair of smooth flaps surrounding the anus and representing the tenth segment. Anterior to this is a larger fold covered with hairs and ornamented on the edge with thick short spines. This probably represents the ninth segment.

Buccopharyngeal Armature (Text-fig. 6).—The mouth parts of *Sciadocera* show many of the general features described by Keilen (1911) for the genus *Phora*. The basal or pharyngeal sclerites are of similar form to those of Muscids and Calliphorids, each consisting of a broad vertical plate deeply incised at the posterior margin to form dorsal and ventral cornua. The incision or gap is very wide and the cornua narrow in *Sciadocera*. The dorsal cornu is narrower and shorter than the ventral which is pointed posteriorly. The floor of the pharynx, which is visible towards the ventral edge of the sclerite, is strongly ribbed or corrugated. The plate joining the dorsal edges of the pharyngeal sclerite anteriorly is prolonged upwards and forwards into a blunt projection. The anterior margin of each pharyngeal sclerite is also produced forwards above the hypopharyngeal sclerite, almost reaching the base of the oral hooks, a feature characteristic of *Phora*. The pair of narrow projections called by Miller (1933) the atrial rods, and by Keilen the *batonnets de la pièce basilaire*, occur along the lower edge of the forward projection of the pharyngeal sclerite, resembling the condition in *Phora*.



Text-fig. 5.—Posterior spiracles of the third stage larva of *S. rufomaculata*. × 48. *s*, slits; *b*, button; *f.c.*, felt chamber.

Text-fig. 6.—Mouth parts of third stage larva of *S. rufomaculata*. × 44. *a.r.*, atrial rod; *h.a.*, hypostomal arch; *l.b.*, lower fused branches of hypopharyngeal sclerite; *o.h.*, oral hooks; *u.b.*, upper branches of hypopharyngeal sclerite.

Text-fig. 7.—Puparium of *S. rufomaculata*. × 11. Lateral view. *b.h.*, breathing horns.

Text-fig. 8.—Pupal shell of *S. rufomaculata*. × 11. Dorsal view showing method of dehiscence.

The hypopharyngeal sclerite is of the usual H-shape, but the arms are very narrow and elongated and fused posteriorly with the pharyngeal sclerite. The bar of the H is Miller's hypostomal arch and shows in profile as a ventral projection in *Sciadocera*. The arms of the hypopharyngeal sclerite fork just anterior to the hypostomal arch. The lower branches are produced anteriorly as far as the end of the oral hooks, where they unite to form a short point, which is directed downwards and is less strongly chitinized than the rest. The oral hooks are very small and are situated above the anterior end of the hypopharyngeal sclerite. The basal portion of each is roughly triangular in shape, with a notch in the posterior margin and a small aperture near the centre. The hook part is narrow and curved with the point close to the end of the hypopharyngeal sclerite. The hooks articulate with the upper branches of the hypopharyngeal sclerite, which corresponds in position to the auxiliary piece described by Keilen in *Phora*.

(*d*) *Puparium* (Text-fig. 7).—The average length of the puparium is 6 mm. It is light brown in colour and is sufficiently thin to show the developing fly a few days before emergence, when it appears black. The puparium is shaped like a tortoise, but rather more elongated, being thin at the edges and convex in the middle. It is attached by the ventral surface, which is also convex, to some object such as a leaf or fragment of wood.

There are eleven segments. The first represents the prothoracic segment of the larva and shows two little projections which were the anterior spiracles. The last segment bears the papillae which characterized the eighth larval segment, the spiracular tubes being at the posterior extremity of the puparium. The small spines and hairs which clothed the skin of the maggot persist, but are darkened and hardened. The puparium is scalloped along the thin flattened edges and is narrowed and flattened on the anterior three segments. The fifth segment bears on the dorsal surface a pair of very minute breathing horns. Each is like a small black spine arising from a darkened spot. When emergence takes place the puparium splits in a line down the centre of the fourth, fifth and sixth segments and also opens between the third and fourth and sixth and seventh segments (Text-fig. 8). A few days before emergence of the fly dark lines appear where the dehiscence takes place.

This method of emergence is similar to that described for other Phorids.

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AUSTRALIAN RUST STUDIES. IV.

Natural Infection of Barberries by Black Stem Rust in Australia.

By W. L. Waterhouse, The University of Sydney.

(Plate iii.)

[Read 28th March, 1934.]

Introduction.

For long it was believed that black stem rust in Australia was unable to attack the barberry. McAlpine (1906) in his experiments failed to obtain any infection. In 1921 (Waterhouse, 1921) it was shown that rust on wheat from Glen Innes produced normal infections of the barberry under experimental conditions at the University of Sydney. Similar results (Waterhouse, 1929) have been repeatedly obtained in subsequent years. But, although search has been made, no natural infection of the barberry has yet been recorded. It is perhaps on this account that barberry eradication has so far not received attention in Australia.

Field Occurrence.

In early December, 1933, Messrs. S. L. Allman and R. E. Dwyer, officers of the New South Wales Department of Agriculture stationed at the Bathurst Experiment Farm, noticed a leaf infection of barberry and forwarded three young shoots for examination. These were found to be carrying a number of spermogonia and a few aecidia. Messrs. Allman and Dwyer had collected the material from plants growing in the shrubbery of Mr. C. Bland at Yetholme, N.S.W.

Examination of the few aecidiospores present showed that they conformed to the *Puccinia graminis* type. They were used to inoculate seedlings of wheat, oats, barley and rye in the plant house. The result, to be discussed later, was the production of a single uredo pustule on the wheat seedlings.

Upon receipt of the material, a brief visit was at once paid to the locality in company with Mr. Allman. Mr. and Mrs. Bland showed the utmost hospitality and gave every assistance in the examination. Growing in the shrubbery near the homestead were three well-established barberry bushes producing fruit which at that time was about half-grown (Plate iii, C). On the leaves of all the bushes many infections were found. Spermogonia and aecidia were clearly discernible on some leaves, but in most cases the infected areas had completely blackened owing to age, indicating that the visit was made about a month later than it should have been. On many twigs each successive shoot was infected. One of these is illustrated in Plate iii, C.

A number of grasses were found growing under and around the barberry bushes. They comprised *Agropyron scabrum*, *Bromus maximus*, *B. racemosus*, *Festuca Myuros*, *Lolium perenne*, and *Danthonia* sp., together with others not in head. Inflorescences of the first four listed were growing right up into the

barberries, some heads of the first-named being almost as tall as the barberries themselves. One of these emerging from the barberry is shown in Plate iii, B.

Rust in the uredospore stage was present on the grasses above named. The bromes and rye grasses showed leaf rust attack only, but *Agropyron scabrum* was attacked on both leaves and stems by stem rust. This proved to be a typical *P. graminis.*

In addition to the uredosori, abundant teleutosori were present. These occurred on old grass stems, definitely traced back in every case to the growing plants of *Agropyron scabrum.* Germination tests with the spores made upon return to the laboratory gave negative results. This was quite in accord with the expectancy (Waterhouse, 1929).

Thus, apart from the sporidia, there were associated in the closest proximity to each other, all the spore forms of stem rust.

At the time of the visit, a crop of oats was growing in a paddock distant about 200 yards from the infected barberries in the shrubbery. Enquiry elicited the information from Mr. Bland that attempts to grow wheat had resulted in failure owing to rust attack.

It was pointed out by Mr. Bland that other barberry bushes were growing in the neighbourhood. Owing to limited time, however, only one of these areas, skirting the "Old Sydney Road" in Yetholme, was visited. Here eight barberry bushes were found. The largest of them measured 8 ft. in height and 12 ft. across its largest diameter (Plate iii, A). Every one of these bushes showed rust-infected shoots. Nearly all the pustules had blackened with age. The grasses in this area were similar to those noted in Mr. Bland's property. It was stated that yet other patches of barberries occurred in the vicinity, and that some of them had been there for 60 years.

Plant House Determinations.

Upon return from the field, inoculations of cereal seedlings (wheat, oats, barley and rye) were made in the plant house. These dealt with three collections of rust, viz., aecidiospores from the barberries, uredospores from *Agropyron scabrum* growing intermixed with the barberries, and, thirdly, the same material collected in the open at a distance of about 200 yards from the barberries.

From the scanty aecidial material, only one pustule appeared on wheat. This inoculum was multiplied and then used to inoculate the standard set of differential hosts (Stakman and Levine, 1922). The rust proved to be *Puccinia graminis tritici,* form 34. This is not at variance with a considerable amount of work, yet unpublished, which proves clearly that form 34 is heterozygous. Had an extensive collection of aecidia been possible, others of the forms which have recently been separated out from barberry inoculations with form 34 would probably have been found.

Tests with the rust on *Agropyron scabrum* growing intermixed with the barberry proved this rust to be the same as the preceding, viz., *P. graminis tritici* 34. The same result was obtained with the rust on *A. scabrum* growing at a distance in the open paddock. This again was necessarily a scanty collection owing to time limitations.

It has previously been shown (Waterhouse, 1929) that stem rust occurs on *A. scabrum* growing in different localities. With one exception, when *P. graminis avenae* was present, the rust has proved to be the one or other of known forms of *P. graminis tritici.* In recent years it has always been form 34.

Conclusion.

The occurrence of natural infection of the barberry is vitally important in view of the proof that new physiologic forms of stem rust originate on the barberry (Waterhouse, 1929, et al.). Change in the rust flora may thus take place readily where infected barberries are present. The singularly fortunate circumstance, from a wheat breeder's point of view, that only the one form of wheat stem rust is now present in wheat, may be completely altered in this manner and the problem of breeding for rust-resistance made much more difficult. Especially does this danger exist with a heterozygous rust like form 34.

The climatic conditions at Yetholme, situated at an altitude of 4,000 ft., approximate to English conditions, and are not extensively replicated in New South Wales. Nevertheless, wheat-growing is carried on less than five miles in a direct line from the infected barberries. These wheat areas in turn link up with others and by means of these crops—not taking grasses into consideration—spread of uredospores throughout the wheat belt can readily take place under favourable conditions for rust development.

In view of the fact that under some conditions barberries may become naturally infected by stem rust, steps should be taken to eradicate the susceptible sorts and to prevent their dissemination. If it is desired to grow barberries, only immune sorts should be tolerated.

Acknowledgements.

Grateful acknowledgement is made of generous financial assistance given by the Trustees of the Science and Industry Endowment Fund, and of valuable help in the cultural work by Mr. J. G. Churchward.

Summary.

In December, 1933, Messrs. Allman and Dwyer found infected barberries growing under natural conditions at Yetholme, N.S.W. The rust proved to be *P. graminis tritici* 34. The same form was present on *Agropyron scabrum* growing intermixed with the barberries. Old stems of this grass were heavily infected with the teleutosori which were doubtless the source of the barberry infection. The same grass growing a considerable distance away from the barberries was attacked by the same rust. Rust-susceptible barberries should be eradicated.

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EXPLANATION OF PLATE III.

A. One of the old barberry bushes growing at the roadside in Yetholme. The fence post is 4 feet 6 inches high.

B. A barberry bush in Mr. Bland's shrubbery. At a spot 1 inch from the left of the photograph, and 1¼ inches above the bottom—i.e., almost above the "two-foot" rule—an inflorescence of *Agropyron scabrum* may be seen protruding from the barberry.

C. A twig of barberry showing infected leaves of successive shoots. × ¾.

STUDIES ON SAPROPHYTIC MYCOBACTERIA AND CORYNEBACTERIA.

By H. L. Jensen,
Macleay Bacteriologist to the Society.

(Plates i–ii; seven Text-figures.)

[Read 28th March, 1934.]

Introduction.

The genera *Mycobacterium* and *Corynebacterium* were introduced by Lehmann and Neumann in 1896 and had as type species, respectively, the tubercle bacillus, *Myc. tuberculosis*, and the diphtheria bacillus, *Cor. diphtheriae*, two important pathogens which, together with a few related forms, distinguished themselves from all other bacteria known at that period by their characteristic morphology. Since then, numerous saprophytic and parasitic species have been added to the two genera.

In Lehmann and Neumann's classical definition, *Mycobacterium* was distinguished by its formation of slender, frequently branched rods of irregular length, after staining with hot carbol-fuchsin not easily decolorized by treatment with mineral acids ("acid-fast"), and *Corynebacterium* by its tendency to form cells of irregular thickness, club- or wedge-shaped, sometimes branched, not acid-fast, but often showing an irregular bar- or belt-staining.

Because of the branching, Lehmann and Neumann regarded the two genera as closely related to the actinomycetes, from which they are distinguished by the lack of a typical mycelium (cf. Miehe, 1909; Haag, 1927).

Lehmann and Neumann's definitions have in all essential points been adopted in subsequent treatises upon these organisms, for instance, Andrews, Bullock *et al.* (1923), Bergey (1923–30), Haag (1927), but the distinction between the two genera is by no means simple, as the following survey of their general morphology and biology will show.

1. *Cell Morphology.*—The names *Corynebacterium* and *Mycobacterium* were designed to indicate a prevalence of club-shaped cells in the former genus, and a tendency to branching in the latter. It is generally conceded that the typical clubs are as a rule, but not constantly, present in *Cor. diphtheriae*, but mostly absent in the non-virulent "diphtheroids" (Andrews, Bullock *et al.*, 1923; Gins and Fortner, 1926; Kliewe, 1927). In older cultures of corynebacteria there is often an abundance of very big, spherical to lemon-shaped cells almost as big as yeast cells (Dale, 1910; de Negri, 1916; Bergstrand, 1918–23; Mellon, 1920–26; Brown and Orcutt, 1920; Grasset and Grasset, 1930), or smaller round cells appearing like true cocci (Madsen, 1896; Mellon, 1917–26; de Negri, 1916; Walker and Adkinson, 1917; Andrews, Bullock *et al.*, 1923); these coccoid forms can be made entirely predominant by special methods of cultivation (Smirnow, 1908; Malchereck, 1932; Pope and Pinfield, 1932). Mycobacteria do not produce clubs in young, but sometimes in old cultures (Metschnikoff, 1888; Rabinowitsch, 1897;

Korn, 1899; Tobler, 1901; Büttner, 1926; Haag, 1927); really big "cystites", as in the corynebacteria, seem only to have been observed in media containing KJ (Péju and Rajat, 1907). Coccoid cells may be formed in truly acid-fast saprophytic mycobacteria (Moeller, 1898; Korn, 1899; Söhngen, 1913; Ørskov, 1923) as well as in less acid-fast forms approaching the genus *Proactinomyces* (Gray and Thornton, 1928; Jensen, 1931–32). Branching is mostly an occasional phenomenon in corynebacteria (Bernheim and Folger, 1896; Hill, 1902; Abbott and Gildersleeve, 1904), although it may be very prevalent in certain strains of *Cor. diphtheriae* under special conditions of growth, such as media containing lithium chloride (Maassen, 1904), or reduced oxygen pressure (Martin *et al.*, 1924). Some authors (Enderlein, 1925; Kuhn and Sternberg, 1931) even deny the existence of branching in the said species. Also in the mycobacteria branching may be infrequent (Seiffert, 1932) or quite absent (Kuhn and Sternberg, 1931).

2. *Staining Properties.*—As Lehmann and Neumann (1920–27) point out, the mycobacteria are not always strongly acid-fast. Forms only weakly or inconstantly acid-fast were described by Olschanetzsky (1902), Bertani (1913), Ørskov and Jensen (1926), Büttner (1926), Haag (1927) and Eichbaum (1932); see also Gray and Thornton (1928) and Jensen (1931). The very type species, *Myc. tuberculosis*, is not acid-fast in quite young cultures (Krylow, 1912; Wherry, 1913). The same is true to a still higher degree of *Myc. phlei* (Cantacuzène, 1905). The acid-fastness may be lost, temporarily or even permanently, by special methods of cultivation, such as acid media, growth in mixture with other microorganisms, etc. (Frei and Pockschischewsky, 1910; Wherry, 1913; Thompson and O'Brien, 1920; Vaudremer, 1921; Machado, 1927; Schachschuwarly and Woldrich, 1929; Eberson and Sweeney, 1931; Kirchner *et al.*, 1930). Some corynebacteria, on the other hand, show some acid-fastness (Wolbach and Honeij, 1915; Bergstrand, 1918; Haag, 1927; Daines and Austin, 1932; Martinaglia, 1932; Knorr, 1932). Haag even found certain strains of *Cor. diphtheriae* as acid-fast as the weakly acid-fast *Myc. eos.* The mycobacteria have always been reported as grampositive, although they may be gramnegative while quite young (Krylow, 1912). The same applies to the corynebacteria, although some of them are but weakly grampositive. The so-called metachromatic granules, which are characteristic of the diphtheria bacillus, occur very inconstantly among other corynebacteria (Kliewe, 1927; Schroeder, 1931) and therefore afford no differentiation between the two genera.

3. *Motility* has sometimes been alleged in mycobacteria (Ferran, 1897; Schumowski, 1898; Moeller, 1899; Tobler, 1901; Courmont and Descos, 1902; Hawthorn, 1903), but as flagella have never been demonstrated, these statements might seem due to observational errors. Ferran, indeed, claims to have stained flagella, but his alleged transformation of *Myc. tuberculosis* is of such a character that one cannot but suspect a contamination. No doubtless corynebacteria have been found motile.

4. *Mode of Cell Division.*—Kurth (1898) first described the characteristic process of cell division in *Cor. diphtheriae*: a cell grows to a certain length, a line of division is formed at the middle, and the daughter cells bend suddenly into an angle, thereby producing the V- or L-shaped figures so eminently characteristic of microscopical preparations of these organisms. This phenomenon was later termed "snapping" growth by Hill (1902), and shown by Graham-Smith (1910) to be characteristic of all diphtheroids. Bergey (1923–30) has included it in the diagnosis of *Corynebacterium.* On this basis, too, did Kisskalt and Berend (1918) transfer several organisms, previously known as *Bacterium*, to *Coryne-*

bacterium. Ørskov found this mode of division, which he termed "angular growth", perfectly constant in mycobacteria, corynebacteria and certain actinomycetes. A different type of division was observed in *Myc. tuberculosis* by Miehe (1909): after division, the ends of the daughter cells bend, slip past each other, and grow into parallel bundles (the "slipping growth" of Graham-Smith, 1910). Similar observations were made by von Faber (1912) on quite different mycobacteria. Miehe's observations were confirmed and extended by Ørskov (1923–32), Haag (1927), and Gardner (1929), who showed that the growth starts with the "snapping" type, which is later superseded by the "slipping". Georgevitch (1916) has, independently of these authors, beautifully demonstrated both slipping and angular growth in an organism from the leaf nodules of *Pavetta* (cf. von Faber, 1912). A certain unequal division, resembling the budding of yeasts, has been observed in diphtheroids by Bergstrand (1918–19) and Mellon (1920); the latter author gave this phenomenon the somewhat bizarre name of "lapolar gemmation". It represents probably a breaking-off of side-branches (cf. Hill, 1902).

5. *Fermentative Reactions.*—The mycobacteria seem as a whole incapable of decomposing carbon-compounds with the formation of organic acids, according to Haag (1927), and particularly to the very careful studies of Merrill (1930–31). A slight formation of acetic acid was reported by Söhngen (1913); also Birch-Hirschfeld (1932) and Eichbaum (1932) mention a slight acid-formation (see also Thomson, 1932). There is a single instance recorded (Kersten, 1909) of an acid-fast bacterium forming gas in sugar-media; since no details were given, this isolated case may be regarded with scepticism. Most corynebacteria ferment sugars and related compounds with the formation of acids, but not of gas, and an enormous amount of work has been devoted to the classification of corynebacteria on the basis of these reactions (for references, see Andrews, Bullock *et al.*, 1923; Kliewe, 1927; Schroeder, 1931). These studies have shown that all corynebacteria with the exception of one group, known as "Hofmann's bacillus" or *Cor. pseudodiphtheriticum*, are able to produce acid from some carbohydrate or other.

6. *Nitrogen Requirements.*—Most mycobacteria are not fastidious in their requirements for nitrogenous food. Proskauer and Beck (1894) showed that simple amino-acids and ammonium-salts, but not nitrate, would serve as nitrogenous food for *Myc. tuberculosis*; this was confirmed by Kondo (1925) and Merrill (1931). Saprophytic mycobacteria grow well with nitrate (Haag, 1927). The diphtheria bacillus and the diphtheroids will, as a rule, demand a rather rich medium containing protein. Haag (1927) considered this a feature of distinction between mycobacteria and corynebacteria, but the difference is not absolute, since *Cor. diphtheriae* will grow in protein-free media under certain conditions (Braun and Mündel, 1929).

7. *Proteolysis.*—No mycobacteria are capable of liquefying gelatin or digesting milk. Dernby and Näslund (1922) found *Myc. tuberculosis* devoid of proteolytic ectoenzyme, but possibly containing small amounts of proteolytic endoenzyme (cf. Corper and Sweany, 1918); it is also capable of forming ammonia from peptone, probably through the action of endoenzymes (Merrill, 1930). *Cor. diphtheriae* does not liquefy gelatin or digest milk (Eijkmann, 1901), but possesses proteolytic endoenzymes (Dernby and Siewe, 1923). Those few authors who have studied the growth of diphtheroids in milk (v. Przewoski, 1912; Belenky and Popowa, 1930; Steck, 1932) do not report any proteolysis in this medium, but a few gelatin- or serum-liquefying diphtheroids have been described by Müller (1908), Mellon

(1917), Eberson (1918), Barratt (1924) and Süssmann (1928). Also *Cor. pyogenes* (Brown and Orcutt, 1920) is proteolytic, as well as some of the saprophytic corynebacteria of Kisskalt and Berend (1918) and some alleged variants of *Cor. diphtheriae* (Maver, 1931).

8. *Utilization of Paraffine.*—Söhngen (1913), Büttner (1926), Haag (1927) and Jensen (1932) have shown the ability of saprophytic mycobacteria and several actinomycetes to use paraffines as source of energy. Haag considered this a decisive point in the differentiation between mycobacteria and corynebacteria, which latter do not grow on paraffine.

9. *Oxygen Requirements.*—The tubercle bacillus is strictly aerobic, as well as most saprophytic mycobacteria. Acid-fast bacteria claimed to be facultative anaerobes were mentioned by Korn (1899), Karlinski (1901), and Olschanetzsky (1902), but since no technical details were given, this cannot be regarded as proved. Among the corynebacteria we find strictly aerobic, facultative anaerobic, and microaerophilic forms. *Cor. diphtheriae* will grow under more or less anaerobic conditions, although, according to Pesch and Gottschalck (1924), not in entirely oxygen-free atmosphere, whereas most diphtheroids are decidedly aerobic (Pesch and Gottschalck, 1924; Kliewe, 1927). Microaerophilic diphtheroids were described by Eberson (1918) and Thomson and Thomson (1926).

10. *Relation to Hydrogen Ion Concentration.*—According to Dernby and Näslund (1922), Ishimori (1924), Kondo (1925) and Kondo and Nodaki (1925), various strains of *Myc. tuberculosis* and *leprae* (?) as well as saprophytic mycobacteria are very inconsistent in their reaction requirements, the limit of acidity even varying from pH 4·5 to pH 6·6; the limits of optimal reaction vary almost equally as much. *Cor. diphtheriae* will under otherwise optimal conditions tolerate an acidity of pH 5·2–5·3, with optimum at approximately neutral reaction (Dernby and Siewe, 1922; Walbum, 1922). Other corynebacteria do not seem to have been studied in this respect.

11. *Alleged Complex Life Cycles and Stabilized Variants.*—Metschnikoff (1888) first suggested that the tubercle bacillus might really be a developmental form of a higher organized fungus. Several authors of recent time (Vaudremer, 1921; Arloing and Dufourt, 1925; Kedrowsky, 1928; Karwacki, 1930) claim to have stabilized actinomyces-like variants of it. The same has often been alleged in *Myc. leprae*, but there seems to be no uniformity among the many organisms isolated from leprous lesions, which probably comprise corynebacteria, real mycobacteria, and species of *Proactinomyces*. Non-acid-fast variants, besides those mentioned in section 2 above (p. 20), have been described by Sweany (1926). Thompson and O'Brien (1920) claimed to have transformed *Myc. tuberculosis* and other acid-fast bacteria into microaerophilic diphtheroids by cultivation in mixture with *Bact. proteus*. Kuhn and Sternberg (1931) mention the stabilization of a coccoid, non-acid-fast "C-form" of the tubercle bacillus, said to have its counterpart among all other bacteria.* Kahn (1928) described a complex life cycle in *Myc. tuberculosis*, but this may, according to Ørskov (1932), largely depend on observational errors. The whole question seems intimately bound up with the problem of the existence of an ultra-microscopic, filtrable form of *Myc. tuberculosis*—a question where no decision has been arrived at in spite of the existence of an already enormous literature. *Actinomyces*-like variants of *Cor. diphtheriae* have been described by Cache (1901), Spirig (1904), and Concetti

* Recent critical studies by W. Kruse and co-workers have shown that the existence of Kuhn's "C-forms" must in general be regarded with much scepticism.

(cit. after Lehmann and Neumann, 1920). Variants of other character were described by Maver (1931). de Negri (1916) and Bergstrand (1918–19) described the wide range of pleomorphism in corynebacteria, without drawing any definite conclusions as to any cyclical development. Complex life-cycles, including the phenomena described by Löhnis (1922) as reproductive bodies, gonidia, and symplasm, were alleged to occur in corynebacteria by Almquist and Koraen (1918), Mellon (1920–26), and Grasset and Grasset (1930); the last-named authors, like Mellon (1926), describe also certain mycelial forms.

The Distribution of Mycobacteria and Corynebacteria in Nature.

Severin (1895) first observed acid-fast bacteria as saprophytes in manure. Soon afterwards, saprophytic mycobacteria were isolated from butter by Rabinowitsch (1897), Korn (1899), and Tobler (1901), and from dung and plant materials by Moeller (1898–99). More recently they have been shown to be common in milk (Albiston, 1930) and tap-water (Eichbaum, 1932). Their frequent occurrence in soil was first discovered by Herr (1901), later confirmed by Kersten (1909), Büttner (1926), Haag (1927), who also found them very common in other habitats, and Frey and Hagan (1932). The soil "mycobacteria" of several other authors were probably largely actinomycetes of the *Proactinomyces*-type (Haag, 1927; Jensen, 1932).

While the common occurrence of mycobacteria as saprophytes has been known for a long time, a quite different view has prevailed in regard to the corynebacteria, which have generally been considered more or less strict parasites and, perhaps for that very reason, hardly studied at all from other than medical points of view. McClure (1898) isolated a diphtheroid from milk, but this may have been one of the udder-corynebacteria of Steck (1932). The first isolation of a corynebacterium from other than animal habitats was reported by Honing (1912), but this organism was probably not a real corynebacterium (motile!). Harris and Wade (1915) found numerous corynebacteria in the air, and were the first to call attention to their probable frequent occurrence as saprophytes, a view which Eberson (1918) shared. Kisskalt (1917) isolated a corynebacterium from water, but did not later (Kisskalt and Berend, 1918) find such organisms as common saprophytes. Several of those organisms which Kisskalt and Berend recognized as corynebacteria are found in air, water, dung, milk, etc. (Lehmann and Neumann, 1927). Barratt (1924) isolated a serum-liquefying diphtheroid from an oyster. Klieneberger (1932) found corynebacterium-like organisms occurring as contaminants on agar plates. The present writer found corynebacteria occurring in quite surprising numbers in soil (Jensen, 1933). During the attempts to identify these and a number of mycobacteria isolated at the same time, I became aware that a large number of previously recorded bacteria, many of them not adequately described, probably belonged to the same group, which therefore seems to need a thorough revision from a general microbiological point of view. The present paper represents an attempt thereat.

Methods.

The soils from which isolations were made, as well as the medium for isolation, were described previously (Jensen, 1933). Some organisms, especially mycobacteria, were isolated by accumulation in a mineral nutrient solution with paraffin wax, and plating on some suitable agar medium. The following media were used for the morphological and cultural studies:

1. *Asparagine-agar*: dextrose 10·0 gm.; asparagine 1·0 gm.; K_2HPO_4 1·0 gm.; $MgSO_4$ 0·5 gm.; NaCl 0·5 gm.; agar 20·0 gm.; H_2O 1,000 c.c.; pH 7·0–7·2.—2.

Glycerine-agar: like (1), dextrose and asparagine replaced by glycerine, 40·0 gm., and ammonium lactate 5·0 gm.—3. *Nutrient agar*: meat-extract 5·0 gm.; peptone-Witte 10·0 gm.; NaCl 5·0 gm.; agar 20·0 gm.; H_2O 1,000 c.c.; pH 7·0–7·2.—4. *Dextrose-agar*: like (3), plus 1% dextrose.—5. *Nutrient gelatine*: like (3), agar replaced by 16% gelatine.—6. Broth: like (3), without agar.—7. *Sabouraud's agar* (de Negri, 1916): milk is boiled for 5 minutes with 0·2% HCl; to the neutralized filtrate are added 1% dextrose, 1% peptone, and 2% agar; pH 7·0–7·2; the addition of urea was found unnecessary, and was omitted.—8. *Milk-agar*: 4–5 c.c. of sterile milk and 8–10 c.c. of sterile melted 2·5% tap-water agar were mixed in a sterile Petri dish.—9. *Milk*.—10. *Potato*.—*Utilization of various nitrogen compounds* was tested in a solution containing 1% dextrose, the same mineral nutrients as media 1–2, and 0·2% of the following compounds: sodium nitrate, ammonium phosphate, asparagine, and peptone. It may here be mentioned that none of the organisms studied gave any positive evidence of fixation of free nitrogen; several strains grew feebly in the N-free solution, such as many bacteria may do at the expense of small impurities in the medium or volatile N-compounds of the atmosphere (Kondo, 1925; Braun and Goldschmidt, 1927). *Reduction of nitrate to nitrite* was tested in the above solution with nitrate at the end of the experiment, and in broth with 0·2% sodium nitrate, with Gries's reagent. *Inversion of saccharose* was tested in a similar solution with 2% saccharose and 0·2% sodium nitrate (or peptone for organisms not utilizing nitrate), by means of Fehling's reagent. *Diastatic action* was tested, by means of iodine solution, in plate culture on agar containing 1% soluble starch, 0·2% peptone, and the mineral nutrients of media 1–2. *Proteolytic action* was tested by formaldehyde titration of 4-weeks-old milk cultures. *Indol formation* was tested by the Ehrlich-Böhme method in a 2% peptone solution. *Haemolysis* was tested on blood-agar plates. *Relation to hydrogen-ion concentration* was tested in a solution containing: dextrose 10·0 gm.; peptone 2·0 gm.; KH_2PO_4 and K_2HPO_4 in varying proportions, 5·0 gm.; $MgSO_4$ 0·5 gm.; NaCl 0·5 gm.; H_2O 1,000 c.c.; pH adjusted, by means of HCl, to pH-values from 3·8 to 7·2. *Fermentative properties* were tested in the following medium, which is composed on the basis of the studies of Schroeder (1931), and which was found to give a much clearer picture of the acid- or alkali-formation than broth media: carbon compound 10·0 gm.; casein dissolved in 1n NaOH, 1 gm.; K_2HPO_4 0·2 gm.; $MgSO_4$ 0·5 gm.; NaCl 0·5 gm.; agar 20·0 gm.; H_2O 1,000 c.c. Bromo-thymol-blue in alkaline aqueous solution was added to a concentration of 0·005%, and the reaction was adjusted to pH 6·6–6·8. Slope-cultures were incubated for 20 days. The following compounds were tested: arabinose, dextrose, levulose, galactose, maltose, saccharose, lactose, glycerine, mannite, and dulcite. *Dissociation*: Two special media were used in attempts to enforce dissociation of the organisms: (*a*) ("lithium-solution") containing dextrose 1%, peptone, 0·5%, LiCl 1%, mineral nutrients as in media 1–2; and (*b*) ("uranium solution") containing dextrose 1%, asparagine 0·1%, uranyl nitrate 0·2%, same mineral nutrients. All media were sterilized at 110°C.; a period of 10 minutes was sufficient to ensure sterility, and caused no change in the reaction of the sugar media. Neither did the gelatine fail to solidify after this treatment. Gelatine cultures were incubated at 18–22°C., all others at 28–30°C., unless otherwise stated.

The familiar method of plate-streaking was used regularly for the isolation of variants. This technique has recently been very severely criticized by Klieneberger (1932), whose paper was not seen by me until most of the experimental

work had been finished. In order to get an idea of the dangers to be expected, 50 control plates (dextrose agar, Sabouraud's agar, milk-agar) were poured and streaked with sterile needle. Result after incubation at 28–30°C. for 4–5 days:

Plates remaining sterile	33	(66%)
Plates infected by mould	4	(8%)
„ „ „ yeast	2	(4%)
„ „ „ actinomyces	1	(2%)
„ „ „ bacteria	10	(20%)

Mostly only one bacterial colony appeared, rarely two, but one plate showed that type of contamination which Klieneberger mentions as particularly dangerous: multiple colonies—11 in this case—probably due to the rubbing out of infecting bacterial clumps. Although thus Klieneberger's warning is undoubtedly very timely, I am convinced that the variants dealt with here are not contaminants, since each of them was recognizable as a modification of the strain from which it had been derived, and was obtained from this particular strain only. Variants which one would be inclined to regard as alien to the nature of mycobacteria and corynebacteria, such as spore-formers, motile forms or true cocci, were never found.

Authentic cultures of the following organisms were used for comparison: *Myc. tuberculosis*, avian type, from the Department of Medical Bacteriology, Sydney University; *Myc. phlei*, from the culture collection of the McMaster Laboratory of Animal Health, Sydney University; *Myc. coeliacum*, from the Rothamsted Experimental Station, Harpenden, England; *Cor. pseudodiphtheriticum*, one strain from the McMaster Laboratory, another from the Department of Medical Bacteriology; *Cor. equi*, two strains from the McMaster Laboratory, one isolated by Dr. Bull, Adelaide, another isolated at the Glenfield Veterinary Research Station, N.S.W.; *Mierobacterium flavum*, *lacticum* and *liquefaciens*, from the Biotechnical-Chemical Laboratory, Polytechnical College, Copenhagen, Denmark; *Aplanobacter michiganense*, from the Faculty of Agriculture, Dept. of Plant Pathology, Sydney University; *Cellulomonas fimi*, from the New Jersey Agricultural Experiment Station, U.S.A.; *Bact. fulvum*, from the National Collection of Type Cultures, Lister Institute of Preventive Medicine, London. I wish to express my sincere thanks to the scientists at the various institutions who have placed these cultures at my disposal.

The Genus Mycobacterium.

The strains of *Mycobacterium* formed two morphologically and biologically fairly distinct subgenera.

Subgenus *A*.—This group, comparatively rare in soil, resembles *Myc. tuberculosis* morphologically and conforms with the saprophytic mycobacteria of Haag (1927). These organisms are morphologically characterized by a typical combination of "snapping" and "slipping" cell division, the latter type superseding the former. During the first stages of growth after transfer to fresh medium the young cells occupy angular positions, but soon the ends of the cells separate at the place of division, the cells bend and continue to grow past each other, thereby, especially in *Myc. tuberculosis*, producing characteristic wisp-like colonies composed of bundles of parallel, uneven-sided rods. Text-figures 1–3 show good examples of this mode of growth. True branching occurs sometimes in the early stages, but never frequently. The acid-fastness against 20% sulphuric acid is well developed in the saprophytic species, although not so strongly as in *Myc. tuberculosis*. The cells are generally longer in young than in older cultures,

but this is not always equally pronounced. I have never observed any filaments or branching forms in old cultures. There is also little tendency to formation of swollen, club-like cells, although an irregular thickness is common. Acid-fast organisms with a marked club-formation have been described by Korn (1899) and Tiedemann (1930), but particularly the latter organism seems to be a *Proactinomyces*, in which such cell types are common (Ørskov, 1923; Jensen, 1932); indeed, the organism which Tiedemann considers identical with *Myc. luteum* Söhngen is very suggestive of the yellow variant of *Proact. polychromogenes*. In physiological respect these bacteria are, like *Myc. tuberculosis*, able to grow well on simple N-compounds, but they show no preference for glycerine as a source of energy. They utilize paraffine readily, but do not invert saccharose, hydrolyze starch or decompose cellulose. They are strictly aerobic, and show no or only a very faint acid-formation in sugar-media. They are immotile and gram-positive, and they show no haemolytic or, as discussed in detail below, proteolytic effect.

MYCOBACTERIUM LACTICOLA Lehmann and Neumann.

Synonyms: *Myc. berolinensis, friburgensis,* and *graminis* Bergey (1923–30).*— Other synonyms, see Haag (1927).

One strain, isolated from heavily manured garden soil.

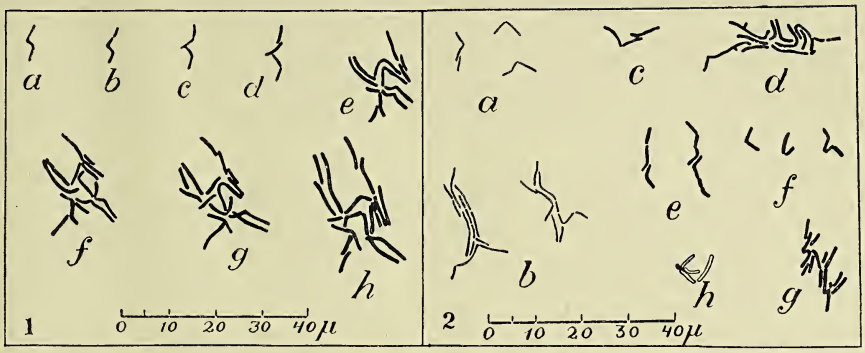
Morphology.—This organism shows by direct agar-microscopy, according to Ørskov (1923), a beautiful combination of snapping and slipping growth on asparagine-agar as well as in protein-media (Text-fig. 1). 2–3-day-old colonies show short projections of parallel cells, and on nutrient agar one sees at this time a number of small refractive external granules on the cells, visible by high focussing and doubtless identical with the rudimentary aerial mycelium in certain species of *Proactinomyces* (Jensen, 1932). 18–24-hours-old cells are long and slender, 0·5–0·7μ × 2–8μ, not staining well with ordinary dyes, after 2–3 days shorter, 1·2–3·0μ, and after 6–7 days almost coccoid. The organism is strongly acid-fast in synthetic as well as protein media, but only faintly so in dextrose-asparagine-solution of pH 5·0. The morphology does not vary much according to medium or temperature. Branching, if present at all, is quite infrequent.

Cultural characters.—Asparagine-agar: good growth, edges entire, surface convex, glistening, at first smooth, after 10–14 days somewhat folded; growth opaque, at first white with creamy tinge, later becoming ochre-yellow; consistence at first sticky, gum-like, becoming soft and mealy. *Dextrose-agar*: very much like previous, more rapid growth, consistence pasty, colour less intense. *Potato*: fair growth, restricted, convex, smooth, becoming slightly folded, glistening, light ochre-yellow. *Gelatine*: thin filiform growth in stab; small, round, convex, smooth, glistening, greyish-yellow surface colony; no liquefaction. *Broth*: faint uniform turbidity, small soft white sediment which gradually becomes yellow; thin, dry, silky surface pellicle after 3–4 weeks. *Milk*: small white granules on the surface and along the tube, later a dry, pale yellow surface pellicle; the milk is not coagulated, but after 3 weeks slightly cleared, after 10 weeks almost transparent, viscid, alkaline; at 37°C. the clearing is very strong after 3–4 weeks.

Physiological characters.—Nitrate, ammonia, asparagine and peptone are utilized almost equally well. Reduction of nitrate, doubtful. Slight production of acid from levulose. Optimal reaction, pH 6·8–7·2. Dextrose-NH_4Cl-solution is

* It is not obvious why Bergey has disregarded the priority of the unquestionably valid species-name *lacticola*.

acidified to pH 3·7–3·8 in 3 weeks. Excellent growth at 37°C. Growth stops at pH 4·3–4·6.



Text-figure 1.—*Myc. lacticola.* Successive stages in development on asparagine-agar, room temp. Direct agar-microscopy. *a-d* 20-24 hours, 2-hour intervals; *e-g* 44-48 hours, 2-hour intervals.

Text-figure 2.—*a. Myc. tuberculosis* (avian), Sabouraud's agar, 2 days, 37°C.; *b.* Same, 4 days, 37°C.; *c. Myc. phlei,* authentic, asparagine-agar, 1 day, 28°C.; *d.* Same, 3 days, 28°C.; *e. Myc. phlei* 282, plane type, glycerine-agar, 2 days, 20°C.; *f.* Same, perrugose type, asparagine-agar, 1 day, 20°C.; *g.* Same, 2 days, 20°C.; *h.* Same, with aerial "mycelium" (heavily shaded).—All by direct agar-microscopy.

Dissociation.—The above description agrees with the "plane" type of *Myc. lacticola* (Lehmann and Neumann, 1911–27; Haag, 1927). A variant of a somewhat "perrugose" character was obtained by plating from an 80-days-old culture in dextrose-peptone-solution of pH 4·6; its young agar cultures differed from the original by showing a more flat and spreading growth with lobate edges and a dull, finely rugose surface. A definitely "perrugose" variant was obtained by plating from 7-months-old culture in lithium-solution and from 2-months-old culture in uranium-solution. This variant produces in agar-media a spreading, flat, strongly wrinkled, dry and dull growth of a tough consistence; broth and other liquid media remain clear with a dry, thick pellicle and flaky sediment. Morphologically these variants are like the original type.

Mycobacterium phlei Lehmann and Neumann.

Synonym: *Myc. stercusis* Bergey (1930). Other synonyms, see Haag (1927).

One authentic strain; one (282) isolated from soil from Griffith, N.S.W.

Morphology.—Both strains appear as small, fairly straight rods, 0·5–0·7μ × 1·5–4·0μ, not varying much in different media or at different ages. The authentic strain shows distinct snapping and slipping growth, whereas 282 has a tendency to produce chain-like figures, somewhat like the "Harnbacillus" of Miehe (1909). Branching, although present, is rare (Text-fig. 2). The authentic strain is more acid-fast than 282, which after 1 day on asparagine- or dextrose-agar has only a minority of acid-fast cells; after 2–3 days the acid-fastness is good, but markedly granular and belt-like, in milk after 7 days complete, but in broth only partial.

Cultural characters.—The authentic strain, which is markedly perrugose, bears little resemblance to the plane soil strain. *Asparagine-agar*: good growth, becoming abundant; authentic strain spreading, edges lobate, surface flat, dull, dry, rugose, 282 restricted, convex, smooth, moist, glistening; both white, becoming ochre-yellow. *Dextrose-agar*: like previous, still better growth, authentic strain

more strongly wrinkled. *Potato*: good growth, becoming abundant, greyish-yellow; authentic granular, 282 smooth and glistening. *Gelatine*: granular yellowish growth in stab; wrinkled yellow surface colony; no liquefaction. *Broth*: authentic strain leaves the broth clear with dry white, later yellow pellicle; 282: uniform turbidity, later slimy cream-coloured pellicle and sediment. *Milk*: fragile yellowish pellicle on surface and along the tube; milk slowly cleared, semi-transparent and viscid after 45–60 days; reaction alkaline. 282 grows in all media more rapidly than the authentic strain.

Physiological characters.—Both strains utilize nitrate and ammonia well, although asparagine and peptone are superior. Nitrate is reduced to nitrite, strongly by the authentic strain, feebly by 282. The authentic strain produces no acid from sugars; 282 shows a faint acid-production in glycerine and mannite, and gives in old cultures a doubtful reaction in arabinose and dextrose. Optimal reaction, pH 6·8–7·2; 282 continues to grow at pH 4·3, and acidifies dextrose-NH_4Cl-solution to pH 3·8–3·9; the corresponding figures for the authentic strain are pH 5·3–5·6 and pH 4·2. Excellent growth at 37°C.

Dissociation.—A perrugose variant of 282 was obtained in great abundance by plating from 45-days-old culture in lithium-solution and from 80-days-old cultures in dextrose-peptone-solution of pH 4·3–4·6; only the original plane type was recovered from solutions of pH 6·8–7·2. This variant was culturally very much like the authentic strain, from which it differed only in a more rapid growth, a less strong acid-fastness, and some biochemical properties as stated above; like this it showed a distinct slipping growth (Text-fig. 2).

Subgenus *B.*—This group occurs more commonly in soil than the previous, from which it differs in its mode of cell division: the snapping growth is here predominant, and the slipping growth is little in evidence, sometimes not noticeable at all. Most organisms show a characteristic cytomorphosis: cells of the first generations after transfer to fresh medium ("embryonic forms", Henrici, 1928) are long, uneven-sided, sometimes branching rods which during the following stages of cell division gradually grow shorter ("mature forms"), until they finally appear as coccoid forms, often united in small clumps or short chains ("senescent forms"). *Myc. coeliacum* (Gray and Thornton, 1928; Jensen, 1931) may be regarded as the type-species of this group. It is worth noticing that this transformation from branched rods to cocci had been described previously by Ward (1898), who thought he was dealing with a minute fungus, and whose contribution seems to have been overlooked by subsequent workers. The acid-fastness is much weaker than in subgenus A, often noticeable only in milk-cultures, and it is not increased in subcultures from paraffine-cultures, as reported by Haag (1927). Cells of varying thickness and slender club-like forms are common, but typical cystites are rarely produced. Branches arise in precisely the same manner as in *Proactinomyces* (Jensen, 1932), and granules of aerial "mycelium" are common. Some strains utilize non-protein-nitrogen badly, and fail to utilize paraffine. Acid-production from sugars, although mostly weak, is stronger than in subgenus A.

MYCOBACTERIUM COELIACUM Gray and Thornton.

Synonym: *Flavobacterium coeliacum* (Gr. and Th.) Bergey (1930).

One authentic strain, and three isolated from soil: AI from lucerne soil, AIII from garden soil, 18 from grass soil.

Morphology.—All strains show after 18–24 hours on asparagine or nutrient agar a predominant snapping growth, on glycerine-agar also a certain amount of

slipping (Pl. i, figs. 3–4). The length varies from 2μ to 10μ, occasionally longer; the cells are shorter in protein media than in synthetic media (Pl. i, figs. 1–2). After 2 days the cells are shorter, 0·8–2·0μ, many quite coccoid (Pl. i, fig. 6). In older cultures only cocci are seen. Branching occurs sometimes in the early stages (cf. Jensen, 1931), particularly on glycerine-agar (Pl. i, fig. 3). Granules of aerial "mycelium" are common. No strain shows more than a trace of acid-fastness in synthetic or nutrient agars, but all exhibit a partial acid-fastness in milk after 3–10 days, particularly when decolorized for 15–30 seconds with 5% sulphuric acid. The strains agree well in morphological respect, except that strain 18 is somewhat thinner, 0·6–0·8μ against 0·7–1·0μ, and the authentic strain forms long filaments with cystite-like swellings in egg-media (Pl. i, fig. 7).

Cultural characters.—These differ more than the morphological ones. The original soil strains of the plane type did not resemble the authentic much, but the perrugose variants of two of them differ from this only in a less ready assimilation of non-protein-nitrogen, and a few minor points. The peculiar lobate growth in gelatine stabs, mentioned by Gray and Thornton (1928), was seen neither in the authentic nor in the soil strains. Apparently this character is easily lost, and moreover it must be remembered that Gray and Thornton based their description on one strain only. *Asparagine-agar*: authentic strain excellent growth, spreading, flat, opaque, edges undulate, surface folded, faintly glistening, cream-coloured, becoming greyish-yellow; soil strains only scant to fair growth (least in AIII), narrow, convex, smooth, glistening, semi-transparent, white becoming cream-coloured. *Dextrose-agar*: abundant growth; authentic strain like previous medium, colour more pinkish-orange, consistence crumbly; soil strains restricted, convex, edges even, surface smooth, glistening, at first moist and semi-transparent, white to cream-coloured, later dry and opaque with pinkish-orange tinge; consistence pasty. *Potato*: abundant growth, spreading, somewhat folded, dirty cream-coloured, later with orange tinge; authentic strain dry, dull and crumbly, soil strains moist, glistening and pasty. *Gelatine*: thin cream-coloured growth in stab, first granular, in old cultures finely arborescent; pinkish-cream-coloured spreading surface colony, flat, sometimes convex, while young, with lobate edges and radially wrinkled surface. No liquefaction. *Broth*: authentic strain produces at first a faint turbidity, with broken cream-coloured pellicle and granular sediment, later clearing; soil strains similar, with stronger turbidity. *Milk*: pinkish-cream-coloured flakes along the tube, later sediment and fragile pellicle of the same colour. Milk is slightly cleared after 3–4 weeks, semi-transparent and thickened after 45–60 days, reaction alkaline.

Physiological characters.—The strains differ mainly in their relation to non-protein-N, which is utilized well by the authentic strain, less readily by the soil strains, especially AIII. The authentic strain and AI reduce nitrate strongly to nitrite, the others feebly or not at all. The authentic strain utilizes paraffine readily with nitrate as a source of N, AI and AIII less readily unless provided with peptone, 18 apparently not at all. All strains produce acid from glycerine and mannite, 18 and AI also from levulose, AIII from saccharose. Optimal reaction, pH 6·2–7·2. Growth stops at pH 4·3–4·6. Dextrose-$\bar{N}H_4Cl$-solution is acidified to pH 3·5–3·7, by AIII only to pH 4·5–4·6. No growth, or only very scant, at 37°C.

Dissociation.—Strains AI and AIII gave perrugose variants, the former from the surface pellicle of an 18-days-old broth culture and from 205-days-old culture in lithium-solution, the latter from an 82-days-old culture in dextrose-peptone-

solution of pH 4·9; from solutions of pH 6·8–7·2 and from lithium-solution only the original plane type of this strain was recovered. The perrugose variants were morphologically like the original plane. Culturally they appeared, except for a more feeble growth on asparagine-agar, much like the authentic strain, producing on dextrose-agar a still more wrinkled, dry and dull, cream-coloured to greyish-yellow, crumbly growth, and leaving broth clear with thick fragile pellicle and flaky sediment. The authentic strain produced a plane variant after 130 days' cultivation in uranium-solution; this variant produced in agar media a smooth, glistening pinkish-orange growth, resembling the soil strains. This is the only instance I have observed of the perrugose type changing into the plane.

A number of previously described organisms, the true nature of which has not been realized, are probably closely related to or perhaps identical with *Myc. coeliacum*. These are: (1) the "false Bacterium" of Ward (1898); (2) *Bac. Berestnewii* Lepeschkin (1903). These two organisms seem to be longer and more branched in their young stages, and may come closer to *Proactinomyces*. (3) Bacillus No. 2 Bertani (1913); (4) *Actinococcus cyaneus* Beijerinck (1916); (5) *Nitrobacter opacus* Sack (1924; instructive microphotograph!); (6) nitrifying organism of Runow (1929).

MYCOBACTERIUM RUBROPERTINCTUM (Hefferan) Ford.

Synonyms: *Bacillus rubropertinctus* Hefferan (1904); *Serratia rubropertincta* (Grassberger) Bergey (1923–30).*

Two strains, from red soil from Griffith (279) and grass soil from Sydney (M).

Morphology.—This species shows an almost exclusive snapping growth on agar (Text-fig. 3). 18–24-hours-old cells are rod-shaped, 0·5–0·8μ × 1·5–5·0μ, in beautiful angular arrangement (Pl. i, fig. 8), after 2–3 days nearly coccoid, 0·6–0·8μ. The cocci are produced more rapidly in protein agar than in synthetic agar. Young colonies are often star- or burr-shaped, with projections of cells which remain rod-shaped longer than those in the interior. Branching does not occur in most media, but granules of aerial mycelium are sometimes seen (Text-fig. 3). On glycerine-agar there is, after 2–3 days, a tendency to formation of longer, club-shaped, sometimes branching cells around the edges of the colonies. No acid-fastness in agar-media after 1 day, sometimes a trace after 3–7 days. Cultures in milk are partially acid-fast after 3–7 days.

Cultural characters.—Asparagine-agar: good growth, restricted, convex, edges entire, surface smooth and glistening; growth opaque, pasty, first light coral-red, becoming very intense red. *Dextrose-agar*: abundant growth, narrow, convex, edges entire, surface smooth, glistening, opaque, orange-red, gradually becoming very intense scarlet. Strain M forms many small round white to pink secondary colonies after 3–4 weeks; 279 did the same immediately after its isolation. In sugar-free nutrient agar fair growth only, less intense red, with fewer secondary colonies. *Potato*: abundant growth, spreading, flat, somewhat granular, faintly glistening, first coral-red, then, after 6–8 days, dull orange, rather pale after 3 weeks. *Gelatine*: growth in stab at first thin, after 1–2 months quite heavy, granular to finely arborescent, yellow; small, convex, lobate, folded red surface colony; no liquefaction. *Broth*: faint uniform turbidity, later clear; small sediment and surface scales, first pink, becoming dull red. *Milk*: thick, fragile, dull coral-red pellicle and sediment; milk definitely cleared and somewhat viscid after 3–4

* The name *rubropertinctus* is due to Hefferan (1904), and not to Grassberger, who did not name the organism.

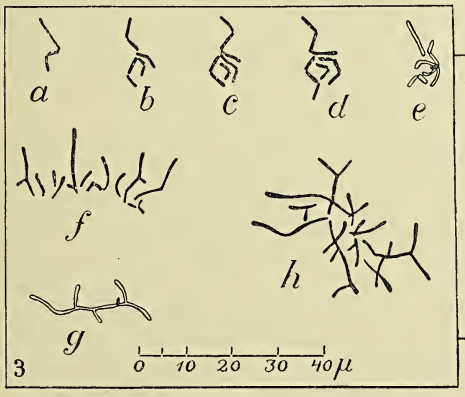
weeks; reaction alkaline. At 37°C. the milk is almost transparent after 4 weeks.

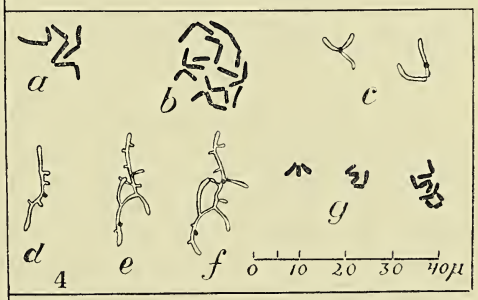
Physiological characters.—Nitrate is utilized readily, and ammonia and asparagine are almost as good sources of N as peptone. Nitrate is not reduced to nitrite. Paraffine is utilized very readily by 279, hardly at all by M. Acid is produced from saccharose and glycerine; 279 gives a doubtful reaction in dextrose and mannite. Optimal reaction, pH 6·8–7·2. Growth stops near pH 4·9. Dextrose-NH_4Cl-solution is acidified to pH 4·0–4·1 by 279, to pH 4·6–4·7 by M. Excellent growth at 37°C.

Dissociation.—Two separate phenomena of dissociation were observed.

i. *Perrugose variants.* Such a variant of 279 was obtained by plating from 2-months-old milk-culture and from 140-days-old culture in dextrose-peptone-solution of pH 6·8. In dextrose-agar cultures of M such a variant arose immediately after isolation as dull, flat outgrowths from the edge of the growth, and it was also obtained from 6-days-old culture in uranium-solution. These perrugose variants are morphologically like the plane, rather shorter in the rod-stage. In solid media they produce a flat, spreading, highly wrinkled, dry and dull, crumbly growth of a deep carmine-red colour, without secondary colonies, in broth a flaky cream-coloured sediment and coral-red scales on the surface, leaving the broth clear. They seem to correspond to the "dry" strains of Grassberger (1898).

ii. *Pink myceloid variants.* Plating from the white secondary colonies in single-cell cultures of M on dextrose-agar yielded a constantly pink variant of a plane type; a perrugose form of this was obtained by plating from a 10-weeks-old milk culture. A pink perrugose variant of 279 was obtained by plating from a 30-days-old single-cell culture in uranium-solution. These pink variants, plane as well as perrugose, differ morphologically from the red ancestral organisms. Their cells in asparagine- and dextrose-agar are longer, more frequently branching (Text-fig. 3), and produce cocci less rapidly. The most striking difference is





Text-figure 3.—*Myc. rubropertinctum.* Direct agar-microscopy. *a-d.* Successive stages in development, dextrose-agar, 22°C., 19-24 hours; *e.* Same, gelatine, 1 day, 20°C.; aerial "mycelium" heavily shaded; *f.* pink variant, dextrose-agar, edge of colony, 2 days, 25°C.; *g.* Same, glycerine-agar, 1 day, 25°C.; aerial "mycelium" heavily shaded; *h.* Same, 2 days, 25° C.

Text-figure 4.—*a-f. Myc. equi. a-b.* Successive stages of development, dextrose-agar, 25°C., 17 and 22 hours; *c.* Same, dextrose-agar, 26 hours, 20°C.; aerial "mycelium" heavily shaded; *d-f.* Perrugose type, dextrose-agar, 23°C.; 17-24 hours. *g. Myc. flavum,* casein-agar, 18 hours, 18°C.—All direct agar-microscopy.

seen in glycerine-agar, where after 1–3 days they produce actual small mycelia with numerous granules of aerial "mycelium" (Text-fig. 3), exactly as in certain species of *Proactinomyces* (Jensen, 1932). The mycelia divide into rods, and then cocci after 4–5 days. The M-variant is flesh-pink to pale coral-red in solid media, the 279-variant rose-pink in asparagine-agar, deep orange in dextrose-agar.

The red plane and perrugose types agree well with Hefferan's (1904) fairly good description of *Bac. rubropertinctum*, an organism isolated, but not named, by Grassberger (1898), and later, on account of its partial acid-fastness, transferred to the mycobacteria by Ford (1927). *Bact. rubrum* Migula (1900) may be identical, but is not sufficiently well defined to be identified with the present organism. Haag (1927) mentions a *Bact. rubrum* as capable of decomposing paraffine and otherwise appearing as a mycobacterium. *Myc. eos* Büttner (1926), although not very completely described (Haag, 1927), appears somewhat similar, but according to the statements of Haag, who recognized it as a variant of *Myc. lacticola*, it seems to exhibit the slipping growth of subgenus A. *Myc. rubrum* Söhngen (1913) is mentioned by Lehmann and Neumann (1927) as possibly identical with the weakly acid-fast *Myc. eos*, but according to Gray and Thornton (1928) *Myc. rubrum* is definitely acid-fast and thus hardly identical with the present organism either; maybe it is merely a strongly pigmented variety of *Myc. phlei.*

In connection with this species we may mention two strains which are closely related, but yet seem to be too aberrant to be included in the species-group.

Mycobacterium 272.

Isolated from red soil, Griffith. Morphologically and tinctorially it resembles *Myc. rubropertinctum*, still less acid-fast, and rather shorter and less branched in glycerine-agar. Its appearance in various media is also similar, but entirely devoid of red pigment, greyish-yellow to light ochre-yellow, like *Myc. lacticola*, from which it is otherwise quite different. It forms a perrugose variant like *Myc. rubropertinctum*, which it also resembles in physiological respect, differing from it in reducing nitrate to nitrite and in forming acid from dextrose and galactose. Paraffine is utilized fairly well. The organism is probably to be regarded as a non-pigmented variety of *Myc. rubropertinctum.*

Mycobacterium Bb.

From light sand soil under grass, Sydney. It is culturally and tinctorially somewhat similar to *Myc. rubropertinctum*, rather less acid-fast, and produces a less vigorous growth of a less intense red colour. Morphologically it differs in lacking the typical cytomorphosis with transformation from rods to cocci. It appears in nutrient agar at most ages as short rods with pointed ends, 0·5–0·6$\mu \times$ 3–4μ, with strong belt-staining and no branches. It reduces nitrate to nitrite, produces acid from dextrose and saccharose, and utilizes paraffine only with peptone as a source of N; no growth takes place at 37°C. A morphologically similar perrugose variant was obtained by plating from a 118-days-old culture in dextrose-peptone-solution of pH 5·3; it produces a rather pale coral-red to orange growth. This strain is somewhat suggestive of *Bact. latericeum* (Adametz), which is mentioned by Lehmann and Neumann (1927) as possibly a corynebacterium (cf. Kisskalt and Berend, 1918), but which is not sufficiently well defined to be identified with the present; moreover, the identity of *Bact. latericeum* seems dubious (Hefferan, 1904). We shall therefore regard this strain as a variety of *Myc. rubropertinctum.* The same may possibly be true of the badly defined *Bact. roseum* and *Bact. Winkleri* (Migula, 1900).

MYCOBACTERIUM EQUI (Magnusson), n. comb.

Synonyms: *Corynebacterium equi* Magnusson (1923); *Cor. (pyogenes) equi roseum* Lütje (1923). The *Cor. pyogenes (equi)* Miessner and Wetzel (1923), which Lehmann and Neumann (1927) identify with Magnusson's organism, is probably different, and seems to be a variety of the familiar *Cor. pyogenes* (cf. Brown and Orcutt, 1920).

Five strains were studied: one authentic, originally isolated by Dr. Bull (1924), two (N and A) isolated from garden soils, one (M) from grass soil, and one (125) from alluvial clay from Bathurst. The soil strains and the authentic strain are similar in every character studied, and agree well with the original descriptions by Magnusson and Bull. A *Bact. aurantium-roseum* Honing (1912) seems to bear a close resemblance to the present. Apparently the organism is a widespread soil saprophyte which under certain conditions acquires pathogenic properties. Its acid-fastness and particularly its very close relationship to *Myc. coeliacum* show that it has its place in the genus *Mycobacterium* rather than in *Corynebacterium*.

Morphology.—All strains produce in nutrient-agar after 16–24 hours at 20° to 30°C. long rods, mostly 0·8–1·0μ × 2–8μ, multiplying by typical snapping growth without any slipping; longer, branched rods with granules of aerial "mycelium" are occasionally seen (Text-fig. 4). After 2 days and in older cultures one sees only short, oval- to pear-shaped rods and cocci, 0·8–1·2μ × 1·0–1·5μ (Pl. i, fig. 9), often in short chains. A number of rods, some of them branching, may be found in broth and milk after 2–3 days. At 28–30°C. the rods in dextrose-agar are after 24 hours considerably shorter than at 20–22°C.; at 37°C. the cocci predominate already after one day (cf. Thomson and Thomson, 1926). The present is the most acid-fast species of subgenus B. In dextrose-agar and egg-medium numerous cells are partially acid-fast after 3–7 days, but not after one day. In milk there is after 3–7 days a quite strong acid-fastness, also towards 20% sulphuric acid: most cocci retain the stain completely, while the rods take the counterstain. The microscopical picture is very similar to that given by Martinaglia (1932).

Cultural characters.—*Asparagine-agar*: very scant growth; narrow, flat, thin, colourless streak, in old cultures sometimes becoming slightly yellowish and granular, in strain N with grey centre. *Dextrose-agar*: good and very characteristic growth, after 2–3 days narrow, convex, edges entire, surface smooth and glistening, very moist, semi-transparent, colourless or light cream-coloured with very pale pink tinge, after 5–6 days more dry and opaque, assuming a light pinkish-orange colour, and after 16–20 days quite firm and opaque, with finely rugose surface and finely myceloid edges. *Potato*: scant to fair growth, spreading, flat, thin, very moist, pink, gradually (7–14 days) growing more dry and opaque, granular, light dull orange. *Gelatine*: thin filiform to granular growth in stab, in old cultures becoming finely arborescent; small, round, convex, smooth, pinkish-cream-coloured surface colony; no liquefaction. *Broth*: faint uniform turbidity, small soft cream-coloured sediment. *Milk*: fine cream-coloured flakes along the tube, later cream-coloured to pink sediment. Milk is thickened, but only very slightly cleared, after 80–90 days; reaction faintly acid.

Physiological characters.—Non-protein sources of N are but very poorly utilized. Reduction of nitrate to nitrite is doubtful in strain M, faint in 125, strong in the others. Paraffine does not seem to be utilized even with peptone as a source of N, except perhaps in strain M. Only two strains (authentic and 125) show a faint production of acid from dextrose. Optimal reaction, pH 6·2–7·2.

Growth stops at pH 4·3–4·6; the authentic strain grows still at pH 4·3. The strains grow fairly well at 37°C., but apparently better at 28–30°C.

Dissociation.—Strains 125 and N yielded perrugose variants, the former from secondary colonies in old culture on dextrose-agar, the latter from a 112-days-old culture in dextrose-peptone-solution of pH 4·9. These variants produced on dextrose-agar a wrinkled, dull, warty growth of a rather hard, crumbly consistence, and in gelatine a flat, erose surface colony and a definitely arborescent growth in the stab. Morphologically they are distinguished by forming, after 1–2 days, long, curved, richly branching filaments which definitely approach a mycelium (Text-fig. 4) and carry numerous granules of aerial "mycelium". The young "mycelia" adhere firmly to the agar and show marked belt-staining; after 3–4 days they divide, like the plane type, into cocci which have a pronounced tendency to adhere together in chains.

In connection with this species we may mention the strain isolated at Glenfield Veterinary Research Station and identified as *Cor. equi*, which was studied for comparison. It resembles *Myc. equi* in a general way, but its rods in the young stage in dextrose-agar are considerably shorter ($0·8–1·0\mu \times 1·5–4·0\mu$), it is less acid-fast, grows hardly at all on potato (only a few small red granules after 3–4 weeks), and produces an intensely red growth on dextrose-agar, like *Myc. rubropertinctum*, which it also resembles in its growth in gelatine. Physiologically it resembles *Myc. equi*, but ceases to grow at pH 4·9–5·3, and shows a stronger acid-production in dextrose. It bears some resemblance to *Bact. erythromyxa* (Zopf) Migula (1900), but since this is not a well-defined species, the present strain cannot be identified with it, and must be left as an uncertain form which seems to occupy an intermediate position between *Myc. equi* and *Myc. rubropertinctum*.

MYCOBACTERIUM FLAVUM (Orla-Jensen), n. comb.?

Synonym: *Microbacterium flavum* Orla-Jensen (1919).

Morphology.—Cells in 18–24-hours-old cultures on dextrose-agar or Sabouraud's agar are rod-shaped or bluntly cuneate, $0·6–0·8\mu \times 1·5–3·5\mu$, multiplying by purely snapping growth (Text-fig. 5). Granules of aerial mycelium are sometimes visible. Contrary to the statements of Wittern (1933), I have always found this organism to exhibit a very typical angular arrangement in stained preparations, which is also demonstrated by Orla-Jensen's microphotographs (1919, Pl. 1). In older cultures there is no very typical formation of cocci, but the cells are always shorter and plumper, up to $1·0–1·2\mu$ thick, belt-staining or approaching a coccoid shape (Pl. i, fig. 10), in milk definitely club-shaped. This is the least acid-fast of all mycobacteria. In 2–3-days-old agar cultures some cells appear violet with red granules after staining with hot carbol-fuchsin, differentiation with 5% sulphuric acid, and counterstaining with aqueous methylene blue. In milk after 6–10 days many club-shaped cells appear deep violet, the rest as pure blue rods and cocci.

Cultural characters.—Asparagine-agar: trace of growth only; small isolated dewdrop-like colonies. *Dextrose-agar*: fair growth, narrow, convex, smooth, glistening, opaque, light ochre-yellow. *Sabouraud's agar*: similar appearance, more vigorous growth, crumbly consistence. *Potato*: fair growth, restricted, later spreading, slightly folded, glistening, opaque, bright ochre-yellow. *Gelatine*: thin granular growth in stab, gradually becoming quite thick, yellow; small raised and wrinkled, ochre-yellow surface colony; no liquefaction. *Broth*: faint uniform turbidity, clear after 4 weeks; small soft cream-coloured sediment, becoming viscid and yellow. *Milk*: small ochre-yellow sediment; milk remains unchanged.

Physiological characters.—Non-protein sources of N are hardly utilized at all. Nitrate is reduced to nitrite. Starch seems to be slightly hydrolyzed. Paraffine is not utilized. Acid is produced from dextrose, levulose, galactose, and glycerine; more detailed studies of the fermentative properties are due to Orla-Jensen (1919) and Wittern (1933). Optimal reaction, pH 5·6–6·8. Growth stops at pH 4·9–5·3. At 37°C. fair growth, but less than at 28–30°C.

The morphology of this bacterium shows conclusively that it belongs naturally with the genera *Mycobacterium* and *Corynebacterium*, and the fact that it produces lactic acid would hardly justify the placing of it in a special genus *Microbacterium* (Orla-Jensen, 1919). Actually the biochemistry of the acid-production by the real corynebacteria seems never to have been studied in detail, and they may, for all that we know, produce lactic acid also. Otherwise it is quite difficult to find a natural place for this organism. It is admittedly very different from the familiar mycobacteria of subgenus A, and appears less acid-fast than several true corynebacteria (Haag, 1927). The main reason why it has here—only tentatively—been included in *Mycobacterium* is that, in its general morphological and biological aspects, it seems to attach itself naturally to organisms like *Myc. coeliacum* and *Myc. equi*, and it seems to represent the extreme, corynebacterium-like end of a spectrum of mycobacteria with *Myc. tuberculosis* at the opposite end.

Common Properties of the Mycobacteria.

All mycobacteria of subgenus B, as well as A, are non-motile and grampositive. They do not invert saccharose, decompose cellulose, hydrolyze starch (with the possible exception of *Myc. flavum*), or produce indole, although they often give a positive Salkowski-reaction. Neither do they show any haemolytic or proteolytic effect. As mentioned in the introduction, most mycobacteria produce very little or no acid, and Merrill (1930) considers them incapable of any partial cleavage of sugars or other carbon compounds. This is doubtless true of the organisms studied by Merrill—all typical acid-fast representatives of subgenus A—but not of the organisms of subgenus B; also the results obtained here with *Myc. lacticola* and *Myc. phlei* seem to indicate that at least some strains of acid-fast bacteria will produce small amounts of acid (cf. Birch-Hirschfeld, 1932, and Thomson, 1932). There seems to exist a certain inverse correlation between acid-fastness and power of acid-production, as shown below:

Organism.	Acid-fastness.	Acid-production.
Myc. tuberculosis	Perfect.	None.
„ *lacticola*	Very good.	Faint in levulose.
„ *phlei*, authent.	Very good.	None.
„ „ 282	Good.	Faint in glycerine and mannite.
„ *equi*	Weak to fair.	Faint, or none, in dextrose.
„ Glenfield-Str.	Weak.	Strong in dextrose.
„ *coeliacum*	Weak.	Glycerine, mannite, some strains in levulose, saccharose.
„ *rubropertinctum* ...	Weak.	Saccharose and glycerine.
„ 272	Very weak.	Glycerine, dextrose, galactose.
„ Bb	Very weak.	Dextrose and saccharose.
„ *flavum*	Trace.	Dextrose, levulose, galactose and glycerine.

Most saprophytic mycobacteria of both subgenera show a characteristic behaviour in milk culture, where they produce a slow clearing without any real coagulation, but gradually rendering the milk semi-transparent, opalescent, viscid and in 2–3-months-old cultures even quite gelatinous.* This peculiar change, which

* This may be the "coagulation" referred to by Bertani (1913).

has been commented on by very few authors (e.g., Lehmann and Neumann, 1920, on *Myc. lacticola*), and which is also produced by the partially acid-fast proactinomycetes (Jensen, 1932), is not due to proteolytic action. Cleared milk is coagulated like normal when acidified, and formaldehyde-titration shows no significant increase in amino-N, but rather a decrease of sometimes significant proportions. The organisms seem to assimilate preferentially the free amino-groups of the casein-molecules. The results are seen in Table I. The clearing is probably due to some physical effect upon the casein.

TABLE I.

Action of Mycobacteria and Proactinomycetes in Milk. Inc. 28 days, 28°C.

Organism.	Formol-titrating N, mgm.		Organism.	Formol-titrating N, mgm.	
	Per 10 c.c.	Excess over Control.		Per 10 c.c.	Excess over Control.
Myc. tuberculosis[1]	2·9	(−0·2)	*Myc.* Bb.	2·8	(−0·3)
,, *lacticola*	3·3	(0·2)	,, *equi* aut.	2·8	(−0·3)
,, ,, 37°C.	2·3	−0·8	,, ,, 125	3·3	(0·2)
,, *phlei* aut.	3·2	(0·1)	,, ,, M	2·7	−0·4
,, ,, 282	3·1	0	,, ,, N	3·0	(0·1)
,, *coeliacum* aut.	3·1	0	Glenfield-strain	3·4	(0·3)
,, AI	3·4	(0·3)	*Myc. flavum*	2·8	(−0·3)
,, ,, AIII ..	3·2	(0·1)	*Proact. corallinus*	3·3	(0·2)
,, ,, 18	2·2	−0·9	,, *salmonicolor* ..	1·8	−1·3
,, *rubropertinctum* 279 ..	3·1	0	,, *erythropolis* ..	1·8	−1·3
,, ,, M ..	2·7	−0·4	,, *opacus*	1·9	−1·2
,, ,, 37°C. ..	2·5	−0·6	,, *paraffinae*	2·6	−0·5
,, 272	2·5	−0·6	,, *polychromogenes* ..	4·0	0·9
,,			,, *minimus*	4·6	1·5

All figures are averages of two parallel cultures. 14 titrations of sterile control tubes gave an average of 3·12 ± 0·20 mgm. formol-titrating N per 10 c.c. Differences not exceeding twice the standard deviation are regarded as insignificant, and are placed in brackets in the table.

[1] Incubated at 37°C.

The Genus Corynebacterium.

This genus is much more richly represented in the soil than the mycobacteria (Jensen, 1933). All the organisms studied here conform with the customary definition of the genus. They show constantly the snapping cell division without any slipping. The tendency to formation of branched cells, approaching a mycelium, is rather more pronounced than among the mycobacteria, from which they also differ in a generally much wider range of cell pleomorphism, stronger fermentation of sugars, and generally proteolytic action in milk and gelatine. Many of them invert saccharose and hydrolyze starch, but only one species (*Cor. fimi*) decomposes cellulose. Indole is not formed, although the Salkowski reaction is often positive. Haemolytic effect is very exceptional. All the strains studied here are strictly aerobic, non-motile and grampositive, and they show no acid-

fastness in agar or milk cultures (decolorized by 5% sulphuric acid in 10 seconds). Like Haag (1927), I have found them all incapable of utilizing paraffine, but I cannot confirm Haag's statement that the corynebacteria as a whole require protein as source of nitrogen.

CORYNEBACTERIUM HELVOLUM (Zimmermann) Kisskalt and Berend (1918).

Synonyms: *Bac. helvolus* Zimmermann, cit. after Lehmann and Neumann (1920); *Bact. helvolum* (Zimm.) Lehmann and Neumann (1896–1920); *Flavobacterium helvolum* (Zimm.) Bergey (1923–30). The following organisms are probably identical or closely related: *Bac. citreus* Frankland (1888); Bacterium No. III Düggeli (1904); *Bact. dimorphum* Troili-Petersson (1904); *Bact. Kirchneri* Löhnis (1905). Also the organisms which Greig-Smith (1911) took for rhizobia were probably mostly of this group (Jensen, 1933).

This species-group was the most common soil corynebacterium. Thirteen strains were isolated and studied: A1, A4, N1, N3 from garden soils, B, Bb, C, Ca1, Ca3 from grass soils, 163, 163S, 279 from red soils from Griffith, 121 from sand from Bathurst.

Morphology.—This large species-group shows a wide range of morphological variation. Generally it appears after 16–24 hours at temperatures from 18° to 32°C. as somewhat irregular rods in angular arrangements, occasionally branching; the thickness varies from 0·5 to 1·0μ, the length still more, from 1·0–1·2μ to 10–12μ, according to strain and medium. The rods are generally longer in dextrose-agar than in sugar-free nutrient agar and asparagine-agar, still longer and more branched in potato, especially strain C. The longest cells appear in strain N, the shortest in A1 and 163S. These cell-types are shown in Plate i, figures 11–15. In older cultures the picture becomes still more varied. The simplest cytomorphosis takes place in sugar-free nutrient agar, gelatine, potato and milk-agar, where the cells gradually grow shorter, after 3–4 days appearing largely as cocci of 0·8–1·0μ, in some cases looking exactly like a pure culture of true cocci (Pl. i, fig. 16). In dextrose-agar and asparagine-agar there is after 3–6 days at 28–30°C. (not so much at 18–22°C.) a pronounced tendency to formation of big cystites which in asparagine-agar and other protein-free media are approximately spherical, measuring from 0·8μ up to 3·5μ in diameter (Pl. i, fig. 17); similar cell-types arise in acid dextrose-peptone-solution. Strain C produces no cystites on asparagine-agar, but shows something resembling a division of the rods into cocci and subsequent lateral germination of these into new parallel rods, as described by Haag (1927), a phenomenon which I have not observed in other corynebacteria. In dextrose-agar the cystites are generally first club-shaped, resembling *Cor. diphtheriae*, after 5–6 days uniform thick rods (Pl. i, fig. 20), or spherical to lemon-shaped cells, up to 2·5μ thick. The relative frequency of these cells is variable; in some strains (121, N) they predominate entirely after 5–6 days, but mostly they account for roughly one-half, so that the microscopical picture gives the impression of a mixture of two different organisms (Pl. i, fig. 19); strain C produces no real cystites at 30°C. After 16–20 days the cystites seem gradually to disappear, and the picture is dominated by small cocci, 0·5–0·8μ, often imbedded in amorphous, granular masses. The sediment in milk and broth cultures contains mostly after 3–4 days numerous long, curved and branching rods sometimes resembling small mycelia. Some strains produce large cystites and other irregular cell types, often very long and branching, on dextrose-agar and particularly potato (Pl. i, figs. 22–23) at 37°C.

Similar cystites have been described in other corynebacteria by several authors, as mentioned in the introduction. They might be regarded as gonidangia according to the life-cycle theories of Löhnis (1922) and Enderlein (1925), an idea which is supported by their gradual disappearance and replacement by small cocci imbedded in amorphous masses, which latter might be construed either as remains of the gonidangia or as a symplasm in which gonidia are regenerated. But direct observation of such cystites transferred to various agar media (asparagine-, dextrose or Sabouraud's agar) by means of Ørskov's method (1923) for periods up to 6 days at temperatures from 18 to 30°C. gave different and quite consistent results. If the cystites are not too old, they germinate after one or two days with 1–2 "germ-tubes" and regenerate the slender rods which are characteristic of young cultures (Pl. i, fig. 21). In other cases, especially if the cystites are very big, they remain unchanged until they either seem to dissolve and disappear or are overgrown by neighbour colonies. I have never seen them reproducing their own cell type and thus stabilizing yeast-like forms as contended by de Negri (1916)* and Mellon (1926), but the initial stage of the "germ-tube" appears often as a pear-shaped bud attached with its pointed end to the cystite; this is probably the "budding-discs" of Bergstrand (1923). Neither have I seen any division into four ("tetrads"), as described by Mellon (1926) and Maver (1931); big cystites do, indeed, sometimes in nigrosin-smears, show an appearance suggestive of this, but the phenomenon is not seen in living specimens, and is probably an artefact due to a rupture of the big vacuolized cells during the process of drying. Ørskov (1923) found similar gigantic forms of *Cor. diphtheriae* sometimes capable and sometimes incapable of growth when transferred to fresh media. Several other workers (Stapp and Zycha, 1931; Klieneberger, 1930; Henneberg, 1932) have found such swollen cells in other bacteria incapable of growth when isolated, while the interpretation of these forms as gonidangia by another school of bacteriologists seems based entirely on the study of stained preparations. While not denying the possibility that the cystites examined here may under special conditions develop into gonidangia, we must also conclude that there is at present no positive evidence of this, and the cystites seem simply to represent the "senescent forms" (Henrici, 1928) of the organisms under the conditions at hand. Since not all cells in a culture develop into cystites, it seems likely that those cocci and small rods by which the cystites are gradually superseded, are the old viable "resting" forms of those cells which do not undergo swelling (cf. Klieneberger, 1930).

Cultural characters.—Asparagine-agar: rather scant to good growth, best in strains N and 163, poorest in 163S, restricted, convex, edges even to undulate, surface smooth, glistening, in strain C finely rugose, semi-opaque, soft-pasty, colour ranging from white and cream-coloured to lemon-yellow (in strains A1 and Ca3); strain Bb produces many big opaque secondary colonies after 2–3 weeks; some strains produce a faint dull pink soluble pigment. *Dextrose-agar*: good to abundant growth, slightly spreading, convex, edges even to undulate, surface smooth or slightly folded, glistening, opaque, soft-pasty, colour ranging from cream-coloured or light greyish-yellow to intense chrome-yellow (A1), pigment generally more intense at lower temperature; strain 279 was strongly yellow immediately after

* de Negri found that the big spherical cells generally regenerated the rod-stage when isolated in single-cell culture, until a stabilized "blastomycete" at length was obtained. It is a somewhat suspicious fact that this stabilization should take place only once, and then in a peptone-solution with 10% saccharose—a medium eminently selective for yeasts!

isolation, but lost the pigment after a few transfers. A pale yellowish-brown soluble pigment is often formed. Secondary colonies are common after 3–4 weeks; cultures obtained from these do not seem to differ from the mother culture. Sugar-free nutrient agar gives a similar growth, less vigorous, but often more strongly pigmented. *Sabouraud's agar*: very luxuriant but uncharacteristic growth; some strains (163, N3, Ca1) form a pink soluble pigment. *Potato*: good to abundant growth, somewhat spreading, convex, smooth and glistening, in C and 163 finely rugose during the first 3–6 days, soft-pasty, colour as on dextrose-agar. *Gelatine, plate*: deep colonies spherical with even edge, surface colonies round, convex, smooth, glistening, both finely granular, yellow to transmitted light, with sharply defined opaque central part. *Gelatine, tube*: thin filiform to granular growth in stab; surface colony round, smooth or flatly folded, first convex, later flat and spreading, cream-coloured to chrome-yellow. Liquefaction begins after 6 to 15 days, first saucer-shaped, after 4–6 weeks stratiform, slowest in strains 121 and 163, most rapid in Ca3 and A1. *Broth*: more or less strong uniform turbidity, soft to sticky cream-coloured sediment, occasionally a non-coherent cream-coloured to yellow surface pellicle. *Milk*: soft cream-coloured to yellow surface ring and pellicle, voluminous sediment of the same colour; no coagulation at 28–30°C., but gradual digestion in 2–5 weeks (most rapid in strains B, Ca1 and Ca3), with neutral to alkaline reaction. At 37°C. most strains produce a soft coagulation after 2–4 weeks. *Milk-agar*: growth fair to very abundant, white to pale yellow; some strains (Ca1, N3) form a pink pigment; proteolytic zones are very clear and broad (8–12 mm. after 4 days) in strains B and C, narrower in the others, but always present.

Physiological characters.—Nitrate, ammonia and asparagine are utilized (best by N3), although they are inferior to peptone. Nitrate is reduced to nitrite by most strains. All except A1 invert saccharose. All except B and 163S hydrolyze starch, 121, Bb and N3 strongly. All 13 strains produce acid from dextrose, glycerine and mannite, 12 from arabinose, 11 from saccharose, 9 from galactose, 7 from levulose, 6 from lactose, 3 from maltose, none from dulcite. The acid reaction is sometimes transient and changes to alkaline after 12–14 days. No correlation was noticed between vigour of growth and intensity of acid-production. All strains are proteolytic in milk, but to a different degree (Table 2). Optimal reaction is approximately pH 6·2–7·2; growth stops mostly at pH 4·3–4·6. Dextrose-NH_4Cl-solution is acidified to pH 3·9–4·6. Optimal temperature seems to be about 28–32°C.; most strains grow quite well at 37°C., some scantily.

Although the strains vary considerably, there is no discernible correlation between the variations, and no subgroups can be distinguished; we must therefore regard all 13 strains as one species-group.

Dissociation.—Two types of variants were produced.

i. "*Slimy variants*" were obtained of strain 121 from 102-days-old culture in dextrose-peptone-solution of pH 6·8, of Ca1 from 202-days-old culture in lithium-solution and 164-days-old culture in uranium-solution, and of N3 from 68-days-old culture in uranium-solution. These variants resembled generally the strains from which they had been derived, but differed in two respects. In 2–7-days-old cultures on solid substrata, especially potato and Sabouraud's agar, they produce a moist, somewhat transparent, extremely viscid growth of an almost glue-like consistence; older cultures are opaque and non-viscid, but become so on transfer. Morphologically they are shorter and plumper than the "parental" strains (the 121-variant almost coccoid), with less branching and less tendency to cystite

formation. The 121-variant reverted to a non-viscid type after 130 days' growth in broth; the reverted form remained shorter and plumper than the original. Strain 163 showed viscid colonies in platings from 90–110-days-old cultures in dextrose-peptone-solution of pH 4·6–7·2, but transfers from these colonies proved non-viscid in the first subculture.

ii. "*Myceloid variants*" were obtained of strain 163 from 150-days-old culture in lithium-solution, and of N3 and Bb respectively from 107- and 118-days-old broth cultures. These variants produce a somewhat spreading, flat, lobate and folded growth in agar media, and a finely and strongly wrinkled growth in potato after 2–5 days, later becoming smooth and glistening. Their cells in young agar cultures are longer and more richly branching than those of the "parental" strains, which they otherwise resemble, and show numerous granules of aerial "mycelium". On potato they, especially the N3-variant, produce actual mycelia after 1 day (Pl. i, figs. 24–25), with numerous branches arising as small lateral pear-shaped knobs or buds which gradually stretch into filaments, as in the actinomycetes (Jensen, 1932). With advancing age the mycelia divide into rods of varying length, and in dextrose-agar they often produce cystites of sometimes enormous dimensions (Pl. ii, fig. 27); these appear highly vacuolized, stain badly, and contain generally one or two refractive granules which show a lively Brownian movement (cf. Bergstrand, 1918). Such large cystites have regularly failed to grow when transferred to fresh agar. In old cultures they seem to disintegrate, and small short rods and cocci remain between their residues, thereby giving a picture which might well be interpreted as "liberation of gonidia" or "regeneration of cells from symplasm" (Pl. ii, fig. 28). The buds which represent the initial stages of the mycelial branches look exactly like the "regenerative bodies" of Löhnis (1922), and may conceivably function as such if detached from the parent cell, but there is no indication that this plays a special rôle as a mode of reproduction. The original strain C appears similar to the myceloid variants, to judge by its cultural appearance and its morphology in young potato cultures (Pl. i, fig. 15). Finally it is to be mentioned that the myceloid variants show little branching in sugar-free nutrient agar, where they appear like the original strains.

A variant of A4 was obtained from uranium-solution, showing a spreading, folded and wrinkled growth in agar media, but hardly any indication of mycelial growth. A somewhat similar form of 279 was obtained from lithium-solution.

CORYNEBACTERIUM CREMOIDES Lehmann and Neumann (1927)?

Synonym: *Bacterium cremoides* Lehmann and Neumann (1911–20). *Bact. cocciforme* Migula (1900) seems related.

Two strains, from garden soil (A) and grass soil (C). The strains are closely related to *Cor. helvolum*, and differ from Lehmann and Neumann's description in being slightly proteolytic.

Morphology.—Similar to *Cor. helvolum*, but shorter, 0·5–0·8μ × 2–3μ, and with less tendency to formation of cystites; both strains produce cocci of a diameter up to 2·5μ in asparagine-agar after 8–10 days, strain A also in dextrose-agar at 37°C. Strain C formed, immediately after its isolation, many big spherical cystites, up to 3·5μ in diameter, in broth culture. They failed to grow when transplanted to agar, and disappeared in the second subculture.

Cultural and physiological characters are mainly as in *Cor. helvolum*. The colour of the growth is creamy to greyish-yellow, never pure yellow. Liquefaction of gelatine and digestion of milk are definitely slower, not noticeable until after

4–5 weeks; milk is softly coagulated after 2–3 weeks at 37°C. Strain A reduces nitrate to nitrite and inverts saccharose. Both strains produce acid in dextrose, glycerine and mannite, A also in levulose, galactose and saccharose. This strain is capable of a faint growth at pH 4·3.

Dissociation.—A "slimy" variant of A was obtained from 235-days-old culture in lithium-solution; it was, like the slimy variants of *Cor. helvolum*, strongly viscid in young cultures, and morphologically somewhat shorter and plumper than the original strain.

CORYNEBACTERIUM INSIDIOSUM (McCulloch), n. comb.

Synonyms: *Aplanobacter insidiosum* McCulloch (see Jones and McCulloch, 1926); *Erwinia insidiosa* (McCulloch) Bergey (1930).

One strain, isolated from grass soil.

Morphology.—Almost identical with *Cor. helvolum*; in 1-day-old agar and potato cultures irregular rods in angular position, 0·5–0·7μ × 2–6μ. Beautiful club-shaped rods in dextrose-agar and milk-agar after 3–6 days, spherical cystites, 2·5–3·0μ, in asparagine-agar after 8 days. In sugar-free nutrient agar only small slender rods, 0·4–0·6μ × 0·8–1·5μ.

Cultural characters.—*Asparagine-agar*: good growth, restricted, convex, edges undulate, surface smooth, glistening, opaque, white, becoming cream-coloured. *Dextrose-agar*: abundant growth, restricted, convex, edges even, surface smooth, glistening, opaque, cream-coloured, becoming greyish-yellow. The organism showed after a few transfers an increasing production of a blue-violet insoluble pigment appearing as streaks in the growth, particularly near the edge. This pigment is formed most copiously at low temperatures (16–18°C.), and appears microscopically as roughly spherical, deep blue granules of 2–8μ diameter, exactly as described by Jones and McCulloch (1926). In sugar-free nutrient agar the growth is less vigorous, cream-coloured without blue pigment. *Potato*: good growth, spreading, convex, smoothly folded, opaque, greyish-yellow. *Gelatine*: thin filiform growth in stab; round, convex, smooth, cream-coloured surface colony; very slow saccate liquefaction, starting after 4–5 weeks. *Broth*: faint uniform turbidity, later clear with soft cream-coloured sediment. *Milk*: cream-coloured sediment and pellicle, slow digestion without coagulation; reaction neutral. *Milk-agar*: thin white growth, very slight proteolysis.

Physiological characters.—Nitrate, ammonia and peptone are readily utilized. Reduction of nitrate to nitrite, faint. Saccharose is inverted. Diastatic action faint. Acid is produced from arabinose, dextrose, levulose, saccharose, glycerine, mannite, and dulcite. Proteolytic action in milk weaker than that of *Cor. helvolum* (Table 2). Optimal reaction, pH 5·6–6·8; growth stops at pH 4·3–4·6. Dextrose-NH_4Cl-solution is acidified to pH 4·0–4·1. No growth, or only a trace, at 37°C.

Dissociation.—A "slimy" variant was isolated from 97-days-old culture in dextrose-peptone-solution of pH 7·2. It produces an abundant, moist and fluid, very viscid growth on agar and potato, and forms the characteristic blue pigment on dextrose-agar. Its cells are rather smaller and more slender than those of the original type, with no tendency to formation of cystites in dextrose-agar, where only short rods and small cocci are seen.

The slimy variant seems to agree better than the original type with Jones and McCulloch's description of their organism which was pathogenic to lucerne plants, produced a viscid growth in agar, and did not vary much in its morphology in different media. Their careful description and instructive microphotographs leave no doubt that the organism was really a corynebacterium. The present

strain seems to differ from it only in a few minor points: more vigorous growth, less definite yellow pigment in nutrient agar, no blue pigment on potato, no coagulation of milk, higher temperature maximum, and more resistance to acid reaction. An infection experiment did not show the organism to be pathogenic to lucerne.* We may therefore call this strain *Cor. insidiosum* var. *saprophyticum*.

CORYNEBACTERIUM FILAMENTOSUM, n. sp.

Five strains, 163, 272a, 272b, 276, 279, isolated from red soils from Griffith; the last strain died out during the work.

Morphology.—This characteristic species shows considerable variation according to the medium. 1–2-days-old cells in asparagine-agar are rod-shaped and typically curved, vibrio-like, mostly 0·5–0·8$\mu \times$ 2–7μ, sometimes longer and branched, always in very striking parallel bundles (Pl. ii, fig. 29). Living cells, which multiply by typical angular growth, exhibit alternating bands of more and less refractive parts of the protoplasm, which in connection with the angular and parallel arrangement of the cells give the quite young colonies on asparagine-agar a most characteristic patterned look when seen under a high-power dry lens, something like a pleat-work of straw; later the thin, flat colonies with their lobate edges look like ice-plants. The cells of most strains grow shorter (1·0–4·0μ) in this medium after 4–7 days; strain 279 showed many long branching cells after 5 days (Pl. ii, fig. 31), later belt-staining and ghost-forms. At 37°C. there are, in strain 272b after 3 days, only slender rods, in the others numerous fusiform to club-shaped cells up to 1·2μ thick. In dextrose-agar and Sabouraud's agar all strains produce, after 1–2 days, long, curved and wavy, often branched filaments 0·8–1·0μ thick (Pl. ii, fig. 30), which in older cultures either break up into shorter fragments or remain as long, thick, irregular, twisted filaments, badly staining or with marked belt-staining, 1·2–1·5μ thick. Similar forms arise in sugar-free nutrient agar, but the long filaments are less numerous here. In some cultures of this species, a few cells exhibit peculiar oscillatory or rotatory movements, but do not show any actual locomotion (cf. Jones and McCulloch, 1926).

Cultural characters.—*Asparagine-agar*: good and very characteristic growth, widely spreading, central part convex, smooth, glistening, white, sending raised dendritic projections into the broad marginal part, which is flat, dull, finely rugose, with lobate edges, white, bluish to transmitted light; strain 272a lacks this characteristic margin, and produces a restricted growth with even edges. Most strains (except 276) produce a light greenish-yellow soluble pigment. *Dextrose-agar*: growth much less vigorous than on previous, strain 163 no growth at all, the others scant to fair, 276 best, narrow, flat to slightly convex, edges undulate, surface smooth to slightly folded, cream-coloured to greyish-yellow, somewhat viscid. The growth in sugar-free nutrient agar and Sabouraud's agar is similar, rather weaker; strain 163 produces a faint growth in these media. *Potato*: scant growth, 163 none, narrow, flat, glistening, cream-coloured to greyish-yellow or almost grey, surrounded by a white halo, in 276 becoming raised and folded; consistence gum-like. *Gelatine*: plate colonies very small, spherical, edges smooth, interior finely granular with opaque centre. Tube: thin filiform white growth in stab; small, round to lobate, white to cream-coloured surface colony; liquefaction slow, starting in about a week, first funnel-shaped to saccate, later stratiform. *Broth*: faint uniform turbidity, small soft flaky cream-coloured sediment; strain

* My best thanks are due to Dr. W. L. Waterhouse, of the Faculty of Agriculture, University of Sydney, for assistance in carrying out this experiment.

163 does not grow. *Milk*: white to cream-coloured surface ring and sediment; no coagulation. Digestion in 2–4 weeks, most slowly by 163; reaction neutral to faintly acid. *Milk-agar*: abundant, opaque, spreading, white to cream-coloured growth, surrounded by clear proteolytic zones 10–12 mm. broad in 7 days.

Physiological characters.—Ammonia is utilized as readily as peptone, and asparagine still better; nitrate is not utilized by strains 272b and 279, readily by the others. Strains 163 and 272a reduce nitrate to nitrite. Saccharose is not inverted; starch is not hydrolyzed. Strain 276 produces acid from glycerine and, to a slight extent, arabinose; in all other cases there is a strong and rapid alkali-formation in the sugar-media. Proteolytic action in milk varies from weak to very strong (Table 2). Optimal reaction, pH 6·8–7·2; growth stops at pH 5·3–5·6. Dextrose-NH_4Cl-solution is acidified to pH 5·4–5·5, by 276 to pH 5·0–5·1. The group is more sensitive to acid reaction than most saprophytic corynebacteria. Excellent growth at 37°C.

Dissociation.—Strain 276 produced, after 124 days' growth in dextrose-peptone-solution of pH 6·8–7·2, a kind of "smooth" variant which had lost the characteristic flat dull fringe on asparagine-agar and appeared like strain 272*a*, from which it differed in a better growth in dextrose-agar and in not forming yellow soluble pigment. Morphologically it was like the original. In 90–100-days-old cultures it produced on dextrose-agar small opaque greenish-grey secondary colonies. Plating from these on asparagine-agar yielded two types of colonies: (*a*) like the mother-culture, and (*b*) much smaller, in subculture appearing as a dwarf-form of the variant. This was the only case in the whole investigation where a secondary variant was found. Its cells on asparagine-agar after 1 day are very small, slender, curved, 0·3–0·4μ × 1·2–2·5μ, in dextrose-agar straight, up to 4μ long, but after 3 days only 1·0–1·5μ. In Sabouraud's agar it forms after 3 days irregular curved and sometimes branching rods of varying thickness, 0·3–0·8μ × 1·0–7·0μ, some with club-like swellings. Culturally it is like the primary variant, but does not grow quite so vigorously, and produces yellow pigment in asparagine-agar, where its young colonies have the characteristic patterned appearance.

This species-group seems closely related to the "*Vibrio*" *linguale* (Weibel) Migula (1900), an organism which Bajardi (1905) considered a "streptothrix", as well as to *Bact. racemosum* Zettnow (1915), but according to the descriptions it is hardly identical with any of these. If this group of organisms is to be regarded as a separate genus, its name will be *Zettnowia* Enderlein (1925).

Corynebacterium simplex, n. sp.

Two strains, from grass soil (B) and from red soil from Griffith (282).

Morphology.—It appears after 1–2 days on asparagine-agar much like *Cor. filamentosum*, to which it is closely related. The rods are somewhat shorter and more slender, 0·4–0·5μ × 3–5μ, curved and in parallel bundles (Pl. ii, fig. 32). Young colonies on asparagine-agar show microscopically the characteristic patterned appearance. In older cultures no branching is seen, but the cells grow shorter, almost coccoid. The species is well distinguished from the previous by the absence of long branching filaments in dextrose-agar and Sabouraud's agar, where it appears after 1–4 days as straight, slender rods, 0·4–0·6μ × 2–4μ, in angular arrangement (Pl. ii, fig. 33). In sugar-free nutrient agar it produces after 5–10 days minute rods and cocci, 0·3–0·4μ × 0·5–1·5μ. Strain B produces in dextrose-agar at 37°C. some swollen cuneate rods and cocci up to 1·5μ thick; otherwise cystites are generally absent in this species.

Cultural characters.—*Asparagine-agar*: fair to good growth, very similar to *Cor. filamentosum*, with less broad marginal part, and becoming all moist and glistening with advancing age; no pigment. *Dextrose-agar*: abundant growth, spreading, slightly convex, edges even, surface smooth, glistening, cream-coloured to greyish-yellow, soft-pasty. Sugar-free nutrient agar similar, not so abundant growth, in strain B small opaque greenish-grey secondary colonies after 6 weeks. *Potato*: good growth, spreading, flat, smooth, very moist, greyish-white, 282 becoming greyish-brown; strain B slimy growth. *Gelatine*: plate colonies very small, spherical, with granular edge and interior. Tube: thin filiform growth in stab; small round smooth cream-coloured surface colony; liquefaction starts after 4 days, first saucer-shaped, later stratiform. *Broth*: uniform turbidity, small white sediment, later greyish-yellow and viscid. *Milk*: yellowish ring around surface, in B slimy white pellicle after 2 weeks. No coagulation; perfect digestion in 10–12 days; reaction neutral. *Milk-agar*: abundant white growth, becoming cream-coloured; clear proteolytic zones, 12–18 mm. broad in 7 days. Strain B produces much slime in various nutrient solutions.

Physiological characters.—Nitrate, ammonia and asparagine are readily utilized, the last as readily as peptone. Nitrate is reduced to nitrite. Strain 282 seems to invert saccharose. Starch is not hydrolyzed. Slight production of acid from saccharose in old cultures (14–20 days), else a rapid alkali-formation. This is the most proteolytic corynebacterium examined (Table 2). Optimal reaction, pH 6·8–7·2. Growth stops at pH 4·9–5·3. Dextrose-NH_4Cl-solution is acidified to pH 4·5–4·9. Excellent growth at 37°C.

Dissociation.—Plating from 142-days-old culture of strain B in lithium-solution yielded a dwarf-form appearing in two types: a "rough" and a "smooth". Both produced a scant white growth in asparagine-agar, narrow, dull and rugose in the "rough", more spreading, moist and glistening in the "smooth". In dextrose-agar good growth, flat, smooth, glistening, cream-coloured, the "smooth" more spreading. In broth uniform turbidity, the "rough" producing a coherent pellicle after 10–12 days. Microscopically the "smooth" type appears in asparagine-agar after one day as minute curved rods, 0·3–0·5μ × 1·0–1·5μ, in parallel bundles (Pl. ii, fig. 34), the "rough" more irregular, sometimes branching, straight, with many granules of aerial "mycelium", after 2 days producing burr-shaped colonies like the mycobacteria. After 6–18 days both types appear similar, as short, plump, almost coccoid rods, 0·6–0·8μ × 1·0–1·2μ. The colonies of both types have the characteristic ice-plant-like appearance. In dextrose-agar they are similar, after one day short, somewhat curved rods, 0·4–0·5μ × 1·5–2·5μ, gradually growing shorter and plumper, after 18 days almost coccoid, 0·6–0·8μ. This variant bears no small resemblance to the secondary variant of *Cor. filamentosum*, which by its lack of long filaments in dextrose-agar seems to stand as a kind of transition to *Cor. simplex*.

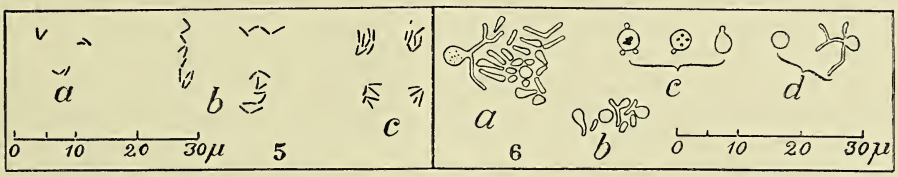
CORYNEBACTERIUM NUBILUM (Frankland), n. comb.

Synonyms: *Bacillus nubilus* Frankland, cit. after Bergey (1930); *Bacterium nubilum* (Fr.) Lehmann and Neumann (1911–27); *Flavobacterium nubilum* (Fr.) Bergey (1930).

The present single strain, isolated from garden soil, appears to be a small and feebly growing variety of the form which Lehmann and Neumann (1927) mention as possibly a corynebacterium. It forms no yellow pigment and has no connection with *Flavobacterium* as defined by Bergey. The name *Cor. nubilum* var. *nanum* might be suggested for this particular variety.

Morphology.—The organism has little in common with other corynebacteria. It appears as a minute rod, not much bigger than the influenza bacillus, mostly 0·3–0·4μ × 0·8–1·0μ, not varying much in different media or at different temperatures or ages. Longer rods, up to 5μ, may be seen in dextrose-agar and Sabouraud's agar, but branched and club-shaped cells do not occur. The cells stain badly and appear in typical V-figures and broad parallel bundles. A very distinct angular growth takes place in asparagine-agar (Text-fig. 5). This, in connection with its being non-motile, non-spore-forming and grampositive, is the main reason why it has been here included in *Corynebacterium.*

Cultural characters.—The organism grows slowly and feebly in all media; the growth became somewhat better and more rapid after prolonged cultivation. *Asparagine-agar*: scant growth, spreading, flat, thin, edges lobate, surface finely rugose, at first dry and dull, later moist and glistening, white, resembling *Cor. filamentosum* and *Cor. simplex. Dextrose-agar*: slow, but eventually fair growth, spreading, flat, dull, colourless with pink centre, after 3 weeks moist and glistening, pale pink. *Sabouraud's agar*: like previous, but better growth, dull red after 12 days. *Potato*: no growth. *Gelatine*: thin, granular, pink growth in stab; small red wrinkled surface colony; liquefaction very slow, at first saccate, after 3–4 months stratiform. *Broth*: faint uniform turbidity, becoming quite strong after 2 weeks; no pellicle or sediment. *Milk*: no growth.



Text-figure 5.—*Cor. nubilum.* Direct agar-microscopy, asparagine-agar, 15-16°C. *a*, 3 days; *b*, 6 days; *c*, 9 days.

Text-figure 6.—*Cor. tumescens.* *a-b.* Strain A, dextrose-agar, 3 days, 28-30°C.; *c.* Strain A, milk-agar, 10 days, 28°C.; *d.* Strain B, cystite from Sabouraud's agar, 10 days, 28°C., germinating after 4 days on same medium, 20-22°C.—*a, b, d,* direct agar-microscopy; *c,* unstained wet mount.

Physiological characters.—Ammonia and peptone are utilized feebly, asparagine slightly better, nitrate not at all; the compounds in meat-extract and Sabouraud's agar seem essential for a good growth. Nitrate is not reduced. Saccharose is not inverted. Starch is not hydrolyzed. No acid from carbohydrates. No proteolytic action in milk, but apparently in gelatine. Growth at 37°C. seems better than at 30°C.

Corynebacterium tumescens, n. sp.

Three strains: A from garden soil, B and 18 from grass soils.

Morphology.—This species shows a most characteristic cytomorphosis in dextrose-agar, Sabouraud's agar and milk-agar. Cells in dextrose-agar after 18–24 hours at 28–30°C. are curved, often branched, show angular arrangement (Pl. ii, fig. 36), 0·5–0·8μ × 2·5–6μ, in B shorter and less branched. After 2–3 days many spherical to club-shaped cystites, up to 3μ thick, arise as local swellings of the rods (Text-fig. 6). At first staining intensely, they gradually change into big, irregular, badly staining "ghost forms" which contain many deeply-staining belts and granules. Besides these one notices irregular, less swollen, intensely staining rods and small, intensely staining cocci, 0·4–0·5μ, which resemble the granules

present in the cystites. These cocci prove to be alive and capable of developing into rods when transferred to fresh media. In milk-agar the big coccoid cystites are often found in almost pure culture (Pl. ii, fig. 40); they have sometimes 2–4 small cocci attached to the outer cell wall, thereby giving a picture like that of a budding yeast cell (Text-fig. 6). When transferred to fresh agar, the cystites either fail to develop altogether, or (especially in strain B) germinate with the formation of one or two, occasionally three or even four slender sprouts which regenerate the rods present in young cultures (Pl. ii, fig. 41). This is the course of development when isolated cystites are observed. When cystite-material is put on fresh agar without "spreading" and examined after 16–24 hours, one finds a large number of small cocci which appear to sprout from the cystites (Pl. ii, fig. 39), and which resemble the cocci described above. It seems likely that those elements which regenerate the slender rods from isolated cystites, may in mass culture break off from the cystites as cocci, before developing into rods, and function as gonidia. This is the only species of corynebacteria studied by me which has shown some positive evidence of reproduction by gonidia. The cystites are formed most abundantly at 30–37°C.; at 16–18°C. they are sometimes not noticeable at all (Pl. ii, fig. 37). In old cultures on Sabouraud's agar they sometimes reach a diameter of 6–8μ (Pl. ii, fig. 38). They are also formed in nutrient agar, but in media poor in nutrients, such as the dextrose-casein-agar used for the isolation of the corynebacteria, no cystites are seen. The organism appears here after one day as long slender rods which rapidly grow shorter and after 3–4 days appear as cocci of 0·5–0·6μ diameter (Pl. ii, figs. 42–43).

Cultural characters.—*Asparagine-agar*: very scant growth, narrow, thin, flat, moist, colourless streak. *Dextrose-agar*: fair growth, restricted, convex, edges even, surface smooth, glistening, white to cream-coloured, semi-transparent. *Sabouraud's agar*: good growth, slightly spreading, convex, edges lobate, surface smooth, glistening, cream-coloured, in strain B greyish-pink; a pink soluble pigment is sometimes formed. *Potato*: slow, but eventually good growth, restricted, convex, smooth, glistening, greyish-white to dirty cream-coloured, in B greyish-orange; consistence strongly viscid. *Gelatine*: plate colonies very small, spherical, edges smooth, interior granular, opaque, yellow. In stab thin white filiform to granular growth, very small white surface colony; liquefaction very slow, starts after 3–4 weeks, funnel-shaped. *Broth*: faint uniform turbidity, after 2–3 weeks a soft white to cream-coloured sediment. *Milk*: thin white ring around the surface; soft coagulation after 18–20 days, later slow digestion; reaction faintly acid. *Milk-agar*: good growth, opaque, in 18 and A white, with 4–5 mm. broad proteolytic zones in 14 days, in B with pink tinge and very slight clearing.

Physiological characters.—Nitrate, ammonia and asparagine are but very slightly utilized. Nitrate is reduced to nitrite. Strain 18 inverts saccharose. Starch is hydrolyzed faintly by strain B. Acid is produced from arabinose, dextrose, galactose, maltose and glycerine by all strains, from saccharose by 18 and B, and from mannite by A and B. Weak proteolytic action in milk (Table 2). Strain B grows well at 37°C., the others more scantily than at 28–30°C. Optimal reaction, pH 6·2–6·8. Growth stops at pH 4·9–5·3.

Dissociation.—Strains 18 and B produced "slimy" variants after 172 days' growth in lithium-solution; B produced also such a variant after 3 passages on a similar agar-medium. The variants differ morphologically from the original strains in a less pronounced tendency (especially the 18-variant) to cystite-formation in dextrose-agar and Sabouraud's agar, where they appear after 3–6

days as irregular, curved, branching and club-shaped rods and filaments of varying length (Pl. ii, fig. 44). The growth on agar is, especially in the B-variant, of an extremely viscid consistence. Otherwise they resemble the original types, and the B-variant shows a still stronger production of pinkish-orange pigment.

CORYNEBACTERIUM MICHIGANENSE (Smith), n. comb.

Synonyms: *Aplanobacter michiganense* Smith (1914); *Erwinia michiganense* Bergey (1930); *Bacterium michiganense* (Sm.) Stapp (1930).

This species has been carefully examined by Stapp (1930), whose fine micro-photographs and generally good description leave no doubt that it is really a corynebacterium. The same is evidently true of the closely related *Bact. sepedonicum* (Stapp, 1930) and *Aplanobacter rathayi* (Smith, 1914).

The authentic culture was compared with a strain of very similar appearance, isolated from grass soil.

Morphology.—Both strains appear after one day at 28–30°C. in nutrient agar with or without dextrose, Sabouraud's agar, potato-extract agar and potato as small, straight, slender rods in typical arrangement, 0·4–0·6μ × 1·2–3·0μ; the authentic strain exceeds rarely 0·5μ in width and 2·0μ in length. Direct agar-microscopy shows distinct angular growth. The soil strain produces a few branching cells on Sabouraud's agar after 18 hours at 16°C., and the authentic strain becomes somewhat bigger and plumper, 0·5–1·0μ × 1·2–2·5μ, in Sabouraud's agar and dextrose-agar after 7 days at 28–30°C. This seems to be an instance of "mature forms" being bigger than "embryonic forms" (cf. Henrici, 1928), a phenomenon which I have not found generally true of the corynebacteria. The soil strain appears in dextrose-agar after one day at 37°C. as long, irregular, branching, club-shaped rods, exactly resembling *Cor. diphtheriae* (Pl. ii, fig. 35). These clubs develop after 3–5 days into spherical to pear-shaped cystites, 2·0–2·5μ thick. When transplanted to fresh agar, the real cystites constantly fail to grow, whereas less strongly swollen cells may multiply, in which case they regenerate the normal rods. The authentic strain produces no visible growth at 37°C., but the cells in the inoculum appear somewhat swollen and club-shaped after 18–24 hours at this temperature.

Cultural characters.—*Asparagine-agar*: trace of growth only; narrow, thin, colourless streak. *Dextrose-agar*: good growth, restricted, convex, edges even, surface smooth, glistening, white to cream-coloured, authentic strain with yellowish-brown centre after 2 weeks. In sugar-free nutrient agar the growth is fair only, somewhat folded, light ochre-yellow. *Sabouraud's agar*: abundant growth, authentic strain restricted, convex, with even edges and smooth surface, soil strain widely spreading, moist and fluid, both viscid, ochre-yellow, becoming almost sepia-brown after 2–3 weeks. *Potato*: abundant growth, spreading, flat, smooth, glistening, viscid, deep ochre-yellow; potato grey. *Gelatine*: granular yellow growth in stab; small wrinkled ochre-yellow surface colony; liquefaction very slow, saucer-shaped after 4–5 weeks. *Broth*: faint turbidity, after 2–4 weeks clear with small cream-coloured to light yellow sediment, sand-like in the authentic strain, slimy in the soil strain. *Milk*: small yellow sediment and surface ring; the soil strain coagulates the milk firmly after 10 days, the authentic more softly after 20 days. Slow digestion; reaction definitely acid. *Milk-agar*: dense ochre-yellow growth; the soil strain produces a fairly rapid clearing (4–6 mm. broad zones in 7 days), the authentic almost none.

Physiological characters.—Nitrate and ammonia are hardly utilized, asparagine very imperfectly. Nitrate is not reduced to nitrite. Saccharose is slightly inverted.

Diastatic action doubtful. Both strains produce acid from all the carbon-compounds tested, with the exception of dulcite, where the soil strain also gives a doubtful reaction; the acid-production is stronger and more rapid in this than in the authentic strain. The soil strain shows a faint haemolytic effect and is moderately proteolytic in milk. Its optimal reaction is pH 6·2–6·8, but it still continues to grow at pH 4·3. Scant growth at 37°C.

Since the soil strain seems to differ from the authentic only in its more rapid and moist growth, its higher temperature maximum and its stronger proteolytic activity, we may regard it as a *Cor. michiganense* var. *saprophyticum*.

The descriptions of *Bact. fulvum* (Zimmermann) by Migula (1900) and Lehmann and Neumann (1920) are not unlike the present soil strain. Haag (1927) mentions that the *Bact. fulvum* in the collection of the Hygienic Institute of Würzburg utilizes paraffine and appears like *Myc. phlei* in subculture herefrom; Lehmann and Neumann (1927) mention it as a corynebacterium. The form of *Bact. fulvum* examined here (from the Lister Institute) proved to be a simple, non-motile rod without any branching or club-formation, but growing in long chains without any indication of slipping or angular growth; paraffine was not utilized, nor did the organism show any other resemblance to the mycobacteria or corynebacteria. The London strain is thus obviously different from the Würzburg strain, and it seems hardly possible to see which of them is identical with Zimmermann's original organism.

CORYNEBACTERIUM FIMI (McBeth and Scales), n. comb.

Synonyms: *Bacterium fimi* McBeth and Scales (1913); *Cellulomonas fimi* (McB. and Sc.) Bergey (1923–30). Only the authentic strain examined here.

Morphology.—McBeth and Scales' microphotograph shows a certain "diphtheroid" appearance, and this was confirmed by direct agar-microscopy, which shows a typical angular growth. The organism appears on nutrient agar after 18–24 hours as a small straight rod, largely in V-figures, 0·4–0·5μ × 1·2–2·5μ, after 5–15 days (and at 37°C.) shorter, 1·0–1·5μ, otherwise not changing much. In dextrose-agar and Sabouraud's agar the cells are, after one day, longer, curved and of a striking "diphtheroid" type (Pl. ii, fig. 47). Many longer, irregular, curved, club-shaped and branching cells, up to 9μ long, are formed in these media as well as on potato after 5–21 days. The gram-reaction of the organism is variable; McBeth and Scales report it as gram-negative. It seems to be gram-labile like certain other corynebacteria, e.g., *Cor. pyogenes* (Brown and Orcutt, 1920).

Cultural characters.—*Asparagine-agar*: very scant growth, narrow, thin, glistening, white. *Nutrient agar*: restricted, convex, fair growth, smooth, glistening, opaque, lemon-yellow. On dextrose-agar and Sabouraud's agar the growth is more scant, cream-coloured. *Potato*: slow, but after 2–3 weeks good growth, raised, folded, glistening, chrome-yellow. *Gelatine*: granular yellow growth in stab; small round yellow surface colony, becoming lobate; liquefaction slow, saucer-shaped, starting after 10–14 days. *Broth*: uniform turbidity, strong after 3 weeks; small soft cream-coloured to yellow sediment. *Milk*: small yellow sediment; coagulation after 3 weeks at 37°C. (none at 28–30°C.); reaction acid.

Physiological characters.—Nitrate, ammonia and asparagine do not seem to be utilized. Nitrate is reduced to nitrite. Saccharose is not inverted. Diastatic action doubtful. Acid is produced from all the carbon-compounds tested, but only feebly from mannite and dulcite. Better growth at 37°C. than at 28–30°C. This

species alone of all the organisms examined here caused a rapid disintegration of cellulose supplied as filter paper in a 0·5% peptone-solution.

The morphology of the organism shows plainly that it belongs to the corynebacteria, and its ability to decompose cellulose would hardly be a valid reason to include it in the genus *Cellulomonas* together with morphologically different organisms. The same is probably true of the closely related *Bact. liquatum* McBeth and Scales (1913).

The Corynebacterium liquefaciens-Group

Type species: *Corynebacterium liquefaciens* (Orla-Jensen), n. comb. Synonym: *Microbacterium liquefaciens* Orla-Jensen (1919).

This group attaches itself closely to *Cor. fimi*. The strains, although similar to each other, are too different to be united into a single species, and since no two strains agree well, I have refrained from naming any new species. *Cor. flavum* and *Cor. pyogenes** Berend and Kisskalt (1918) and the serum-liquefying form isolated from oyster by Barratt (1924) are probably related to this group, as are also possibly some of the bacteria described by Townsend (1929), among which Group I appears to be corynebacteria.

The group is represented by 5 soil strains (B2, B3, 11, 18, 276) and *Micr. liquefaciens* Orla-Jensen. The last organism shows a distinct angular growth (as may also be seen from Orla-Jensen's microphotograph) and is in every other respect a true corynebacterium.

Morphology.—All strains are fairly uniform in 18–24-hours-old cultures on dextrose-agar, Sabouraud's agar and potato; slender, often curved and bent rods, mostly 0·4–0·6μ × 1·2–5·0μ, in typical angular arrangements (Pl. ii, fig. 45), all exhibiting angular growth by direct agar-microscopy. In older cultures the rods grow shorter, almost coccoid to pear-shaped (Pl. ii, fig. 46), sometimes increased in thickness to 0·7–0·8μ, but without typical cystites. Branching occurs in young stages, but not frequently. Strain 276 shows in Sabouraud's agar after 18–20 days remarkable long sinuous filaments, sometimes with terminal swellings 0·8–1·0μ thick, not unlike the "spirochaetoid" forms of diphtheroids described by Bergstrand (1919). Otherwise this group of corynebacteria, like *Cor. fimi*, shows less morphological differentiation than the others.

Cultural characters.—All strains produce a mere trace of growth in asparagine-agar. In dextrose-agar the growth is fair, soft and smooth, cream-coloured, in strain 11 quite scant, light yellow. A better growth takes place in Sabouraud's agar, often intense chrome-yellow to greenish-yellow. Strain 11 shows the remarkable property of growing well only in agar which has previously supported growth of acid-fast organisms (*Myc. lacticola, Myc. rubropertinctum, Proact. corallinus*) for 2–3 days and then been re-sterilized. Growth on potato is mostly scant to fair, cream-coloured to lemon-yellow, in strain B2 abundant, intense yellow. The growth in gelatine is mostly scant and not very characteristic, except in strain 18, which produces a thick, wrinkled, spreading, intensely chrome-yellow surface layer; all strains, with the exception of B2, liquefy the gelatine slowly. *Cor. liquefaciens*, B3 and 276 cause a soft coagulation of milk after 3–4 weeks; digestion is either very slow or not visible at all.

Physiological characters.—Non-protein N-compounds are not utilized to any significant extent. *Cor. liquefaciens* and 18 reduce nitrate to nitrite. B2, 11 and

* The latter name is hardly valid, since it appears to belong to another corynebacterium (Brown and Orcutt, 1920).

276 invert saccharose. B2 and 276 hydrolyze starch feebly. Acid-production is variable; the extremes are represented by 276, which produces acid from all carbon-compounds except lactose, and by B3 which ferments only dextrose and galactose. Proteolytic action in milk is weak or absent; strain B2 is the only one of the whole series which seems non-proteolytic both in milk and in gelatine. Optimum reaction appears to be about pH 6·2–6·8, but the resistance to acidity is quite variable; B2 grows still at pH 4·3, and 11 stops growth at pH 5·6. Strains 18 and B2 grow well at 37°C., the others scantily. No phenomena of dissociation have been observed in this group.

CORYNEBACTERIUM LACTICUM (Orla-Jensen), n. comb.

Synonym: *Microbacterium lacticum* Orla-Jensen (1919).

This organism proved to be a morphologically and biologically typical corynebacterium; this is also indicated by Orla-Jensen's instructive microphotographs. The genus *Microbacterium* cannot possibly stand as defined by Orla-Jensen, since of its four species, one is a true *Proactinomyces* (Jensen, 1932), one—*flavum*—an organism on the border-line between *Mycobacterium* and *Corynebacterium*, and *lacticum* and *liquefaciens* doubtless corynebacteria. As pointed out under *Myc. flavum*, their faculty of producing lactic acid does not make them a separate genus.

Cor. lacticum is in many respects, except for its acid-formation, studied in detail by Orla-Jensen (1919) and Wittern (1932), and its lower temperature-optimum, very similar to *Cor. pseudodiphtheriticum*. Orla-Jensen states that it will show some proteolysis in milk, whereas Wittern found it non-proteolytic. The present strain was non-proteolytic, but *Cor. pseudodiphtheriticum* appeared faintly proteolytic in milk (Table II). With this last organism we have arrived at the group of the real "diphtheroids", mainly non-proteolytic organisms, requiring protein, and chiefly occurring as parasites in warm-blooded animals.

A Tentative Scheme for the Identification of Saprophytic Corynebacteria.

I. Organisms with pronounced morphological differentiation; slimy or myceloid variants common (*Cor. diphtheriae* and the corynebacteria of de Negri, Bergstrand and Mellon are probably of this group).
  A. Good growth in protein-free media.
    1. Cystites big and numerous in dextrose-agar.
      a. Cream-coloured to chrome-yellow growth on agar ..... *Cor. helvolum.*
      b. Blue insoluble pigment in dextrose-agar ..... *Cor. insidiosum.*
    2. Cystites less typical. Weaker proteolytic than (1) ..... *Cor. cremoides.*
  B. Very scant growth in protein-free media. Characteristic cystites in dextrose-agar ..... *Cor. tumescens.*

II. Organisms with generally less morphological differentiation, and little tendency to formation of variants. (Most "diphtheroids", e.g., the *pseudodiphtheriticum-* and *xerosis*-types, seem to belong here.)
  A. Good growth in protein-free media. Characteristic curved cells on asparagine-agar. Strongly proteolytic.
    1. Long sinuous filaments in protein media ..... *Cor. filamentosum.*
    2. Short straight rods in protein media ..... *Cor. simplex.*
  B. Scant growth, or none, in protein-free media. Feebly proteolytic or non-proteolytic.
    1. Pink growth on agar ..... *Cor. nubilum.*
    2. White to yellow growth on agar.
      a. Cellulose decomposed ..... *Cor. fimi.*
      b. Cellulose not decomposed.
        x. Viscid, deep ochre-yellow growth on potato ... *Cor. michiganense.*
        xx. Pasty, white to lemon-yellow growth.
          a. Gelatine is liquefied (mostly) .....
          ..... *Cor. liquefaciens* and related group.

β. Gelatine is not liquefied .... *Cor. lacticum* and *pseudodiphtheriticum*-group. (Transition to "diphtheroids" proper.)

TABLE II.

Action of Corynebacteria in Milk. Incubation 28 days, 28°C.

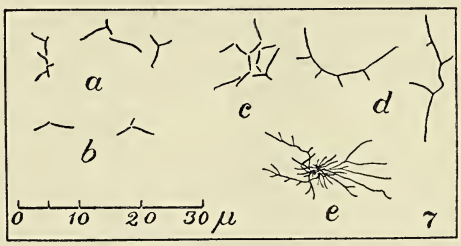
Organism.	Formol-titrating N, mgm.		Organism.	Formol-titrating N, mgm.	
	Per 10 c.c.	Excess over Control.		Per 10 c.c.	Excess over Control.
Cor. helvolum N3	16·7	13·6	*Cor. filamentosum* 163	5·7	2·6
,, ,, A1	17·0	13·9	,, ,, 272a ..	5·5	2·4
,, ,, A4	15·1	12·0	,, *simplex* 282	18·9	15·8
,, ,, N1	15·0	11·9	,, ,, B	12·8	9·4
,, ,, Ca3	14·9	11·8	,, *nubilum*	2·8	(−0·3)
,, ,, C	14·4	11·3	,, *tumescens* A	7·4	3·3
,, ,, 279	14·4	11·3	,, ,, 18	3·9	0·8
,, ,, 163S	14·3	11·2	,, *michiganense*, soil str. ..	9·0	5·9
,, ,, Ca1	14·1	11·0	,, *liquefaciens*	5·5	2·4
,, ,, Bb	13·7	10·6	*Liquef.*—group 276	3·5	0·4
,, ,, B	11·4	8·3	,, ,, 276, 8 w.[1] ..	8·0	4·9
,, ,, 163	11·1	8·0	,, ,, B2	3·2	(0·1)
,, ,, 121	7·2	4·1	,, ,, B2, 8 w.[1] ..	3·0	(−0·1)
,, *cremoides* C	5·8	2·7	,, ,, 11	3·3	(0·2)
,, ,, A	4·5	1·4	,, ,, 18	3·0	(−0·1)
,, *insidiosum*	6·2	3·1	,, ,, B3	4·0	0·9
,, *filamentosum* 279	15·7	12·6	*Cor. lacticum*	2·9	(−0·2)
,, ,, 272b	14·6	11·5	,, *pseudodiphtheriticum* I ..	4·6	1·5
,, ,, 276	13·5	10·4	,, ,, II ..	4·3	1·2

Control titrations as in Table I.
[1] Incubated for 8 weeks.

Organisms Uniting Corynebacteria and Proactinomycetes.

Two strains, A and M, isolated from garden soil and grass soil, respectively, were found to combine the characters of *Proactinomyces* and *Corynebacterium*. In dextrose-agar, Sabouraud's agar and potato they showed no extraordinary morphological features, appearing after one day at 18° to 30°C., both in stained preparations and by direct agar-microscopy, as fairly long, sometimes branching, slender rods in angular arrangement, mostly 0·3–0·5μ × 2–12μ (Pl. ii, fig. 48), A still thinner than M. No real mycelia are seen, and after 2–3 days they appear as short rods and minute cocci (Pl. ii, fig. 50). So far one would not hesitate to declare them corynebacteria. But in sugar-free nutrient agar they produce, after one day at low temperatures (17–18°C.) extensive, branching mycelia of a definite *Proactinomyces*-type (Text-fig. 7), although without any aerial growth. The mycelia remain for several days, but are so fragile as to be observable almost only by direct agar-microscopy; later they divide into rods and cocci. Strain M produces similar mycelia in dulcite-casein-agar and in milk-agar (Pl. ii, fig. 49); they divide rapidly into rods on the surface, but remain undivided for a considerable time in the depth of the agar. No mycelia are formed in liquid media. Strain A formed a "myceloid" variant after 208 days' growth in lithium-solution.

It appeared after one day at 28–30°C. as very long branching mycelia, in dextrose-agar changing into short rods and cocci after a few days, but in Sabouraud's agar remaining filamentous for several weeks, with oval to pear-shaped cystites of 1·0–1·2μ thickness.



Text-figure 7.—Organism between *Corynebacterium* and *Proactinomyces*, strain A. Direct agar-microscopy. *a-b*. Dextrose-agar, 20 hours, 28°C.; *c*. Twenty hours, 18°C.; *d*. Sugar-free nutrient agar, 20 hours, 17°C.; *e*. Two days; 17°C. (× 500).

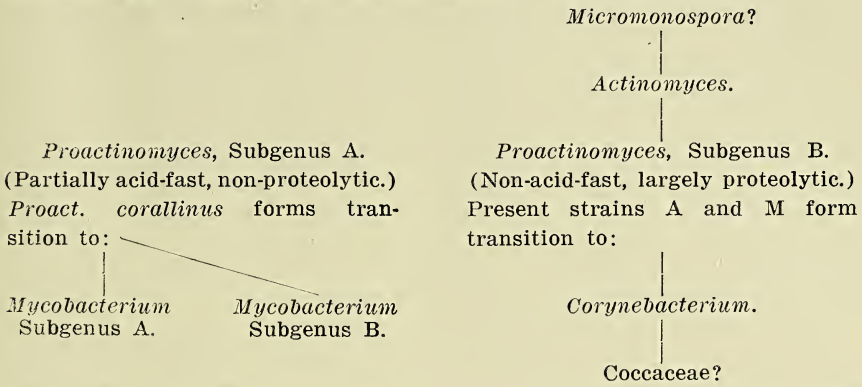
Culturally the two strains are somewhat similar to the *liquefaciens*-group: in asparagine-agar only very scant growth, in dextrose-agar and Sabouraud's agar fair to good growth, smooth and glistening, cream-coloured to chrome-yellow (especially strain A at 18–20°C.), in gelatine stab filiform to finely arborescent growth, very slow liquefaction. Gelatine-colonies of A are spherical and granular, but of M definitely myceloid. M coagulates milk and re-digests it slowly; A lost this faculty after a few transfers. M produces an abundant, dull yellow growth on milk-agar, the surface at first smooth and cartilaginous, after 4–8 days folded and soft, with strong clearing of the medium; the growth of A is slower, developing deep into the agar, with soft surface and hard deeper layer, very slow clearing. Non-protein sources of N are hardly utilized. M reduces nitrate to nitrite. A inverts saccharose. Diastatic action is good in M, faint in A. Both produce acid from arabinose, dextrose, levulose, galactose, maltose, saccharose, and lactose, M also from glycerine. Proteolytic action in milk is faint or absent. M is strongly haemolytic, and grows well at 37°C., A hardly at all. Optimal reaction pH 6·8–7·2. Growth stops at pH 5·3–5·6.

The two strains seem too dissimilar to be united into a single species, and have therefore been left unnamed. We have here a case where it is within the power of the experimenter to make the organisms appear either as typical corynebacteria or as typical proactinomycetes simply by altering the composition of the medium and/or the temperature of incubation. As to the question of their systematic position, one might be inclined to follow the principle of Enderlein (1925) according to which the stage of highest morphological differentiation (the "culminant") indicates the genus, and thus to regard them as members of *Proactinomyces*, closely related to *Proact. mesentericus* (Jensen, 1932; cf. also Wittern, 1932). But it is to be remembered that a logical adherence to this principle would entail the transferring to *Proactinomyces* of *Cor. helvolum* and indeed of any corynebacterium in which myceloid variants might be found.

Relation of Corynebacterium *and* Mycobacterium *to Other Groups of Microorganisms.*

The mycobacteria and the corynebacteria make two natural groups, which, however, are not sharply separated from each other. Subgenus B of the

mycobacteria stands, particularly as represented by *Myc. flavum*, closely midway, and each of the genera is closely connected with the genus *Proactinomyces*, from which both may be derived, as shown below:



Thus the genera *Mycobacterium*, *Corynebacterium*, *Proactinomyces*, *Actinomyces* and *Micromonospora* form a natural and consistent group of microorganisms—the order Actinomycetales—whose natural kinship is proved by the existence of transitional forms between all subgroups. Firstly, the mycobacteria of subgenus B are simply proactinomycetes of subgenus A, which have lost their mycelial growth, wholly or nearly; a certain "reversion" to this mode of growth is represented by the pink variants of *Myc. rubropertinctum*. The fact that such variants arise in single-cell cultures speaks for the correctness of the alleged existence of similar variants in *Myc. tuberculosis* (see introduction). This suggests a connection between *Mycobacterium*, subgenus A, and *Proactinomyces*, subgenus A, a point also supported by the ability of mycobacteria to assume an *Actinomyces*-like growth in the animal body (Schulze, 1899; Abbott and Gildersleeve, 1902, *et al.*). The relationship between *Mycobacterium* A and *Proactinomyces A* is further demonstrated by the mode of cell division (which has become more distinctly slipping in the former), the acid-fastness, the existence of rudimentary aerial "mycelium", and the biochemical similarities. Between the subgenera A and B of *Proactinomyces* the partially acid-fast *Proact. polychromogenus* and *minimus* seem in a certain way to form a connection, since they produce some proteolysis in milk (Table I). The connection between *Corynebacterium* and *Proactinomyces* subgenus B is obvious: the transition proceeds from the long-hyphed *Proact. flavescens* (which again forms the transition to *Actinomyces*; Jensen, 1932) over *Proact. actinomorphus* and *mesentericus* to the above-mentioned two strains A and M, which appear as either proactinomycetes or corynebacteria according to circumstances. An approach to the *Proactinomyces*-type from the other side is exemplified by the myceloid variants of *Cor. helvolum*, which lend some support to the allegation of actinomyces-like types of *Cor. diphtheriae*, as mentioned in the introduction. A variation in the opposite direction seems represented by a phenomenon reported by Wittern (1932): stabilization of a small rod-shaped to coccoid variant of *Proact. mesentericus*.*

There are certain other groups of microorganisms which doubtless stand in close relationship to the corynebacteria, such as the so-called propionic acid

* The strain in my possession has not shown this phenomenon.

bacteria ("*Propionibacter*"). Troili-Petersson (1909) first called attention to their morphological resemblance to the diphtheria bacillus, and van Niel (1928) classified them as a genus closely related to the corynebacteria, distinguished from these by their microaerophilic character and their obligate fermentative metabolism. It is to be remembered in this connection that microaerophilic corynebacteria have also been described (Eberson, 1918; Thomson and Thomson, 1926; Steck, 1932), but their metabolic properties have not been studied; such a study might possibly show that there is no sharp limit at all between *Corynebacterium* and *Propionibacter*. The lactic acid bacilli ("*Lactobacillus*" or "*Plocamobacter*") are considered close relations of the corynebacteria by Lehmann and Neumann (1927) and van Niel (1928). Among other microaerophilic and anaerobic bacteria which seem related to the corynebacteria, we might also mention the "*Bac.*" *cornutus* and "*Diplobac.*" *acuminatus* Distaso (1912) and an organism described by Davis and Mattick (1930).

While all these organisms seem naturally related, a more doubtful point confronts us in the relation between corynebacteria and true cocci. Stabilization of cocci from corynebacteria was alleged by Mellon (1917) and Kuschnarjew (1930). Novak and Henrici (1933) obtained from a typical chromogenic *Actinomyces* an organism which on plain agar appeared as a staphylococcus, but which in dextrose-agar formed rods and branching filaments (cf. *Cor. helvolum.*). Ohlmacher (1902), Kermogant (1922) and Mellon (1926) have mentioned a diphtheroid-like appearance of streptococci under certain conditions. Thomson and Thomson (1926), and Jensen and Morton (1931) describe organisms appearing either as diphtheroids or as streptococci, according to the medium. Prissick (1933) claims to have transformed a streptococcus into a diphtheroid and back again. Since, as Thomson and Thomson (1926) point out, delayed cell division may cause true cocci to appear like diphtheroids,* and since the warnings of Klieneberger (1932) ought also to be kept in mind, it would for the present seem advisable to regard the phylogenetic connection between corynebacteria and cocci as nothing more than a possibility, or, as Thomson and Thomson (1926, pp. 139–140) express it: "It is not beyond the range of possibility that there may be some organisms which form a connecting line between the streptococci and the diphtheroids. . . . It is just possible . . . that some of them may find a place in a separate genus."

The question which groups represent the ancestral and which the descendant forms can at present hardly be made the subject of more than hypothetical speculation, although one might be tempted to regard the formation of longer, branched cells in the young stages as evidence of descent from mycelial forms (cf. Henrici, 1928). This idea might suggest *Proactinomyces* as a primitive group, giving rise on one side by further differentiation to *Actinomyces* and *Micromonospora*, and on the other by reduction to *Mycobacterium* and *Corynebacterium*, and from the latter possibly to the true cocci. But here we are, as Henrici emphasizes, on purely hypothetical ground.

Finally we must mention Kuhn's *Pettenkoferia*-theory in its bearings upon the phenomena of variation in these organisms. According to this theory (Kuhn and Sternberg, 1931) all bacteria live in symbiosis with certain protozoa-like

* This may account for the diphtheroid-like appearance of certain micrococci in saline media (Matzuschita, 1900).

organisms, the "*Pettenkoferia*", possessing a definite life-cycle in which the bacteriophage represents a stage. Bacteria are supposed to occur only in two main forms, rods (without true branching) and cocci, and all so-called phenomena of pleomorphism are claimed to be due to the influence of parasitizing *Pettenkoferia*, which cause an abundant slime-production in cultures rich in them. Although I do not venture to pass judgment on the *Pettenkoferia*-theory generally, the phenomena observed in the mycobacteria and corynebacteria seem explicable without it, mainly on the basis of the cytomorphosis-theory of Henrici (1928). That true branching occurs in these organisms is easily seen by following the growth directly under the microscope, and the conclusion of Kuhn and Sternberg, that there is no relationship between the tubercle bacillus and the actinomycetes, cannot possibly be agreed to. Also the fact that swollen cystites (which according to Kuhn and Sternberg are infected with *Pettenkoferia*) may develop into apparently normal colonies (cf. Klieneberger, 1930), speaks against the theory, but not absolutely, since Kuhn and Sternberg say that the *Pettenkoferia* are often concealed and hard to detect. A stronger point against the theory is represented by the slimy variants of *Cor. helvolum* and related species; according to the theory these should be rich in *Pettenkoferia* and therefore likely to show phenomena of bacteriophagy, but no "taches vièrges" or other signs hereof have been observed. Neither did such phenomena appear in other cultures which had passed through lithium-chloride media (cf. Klieneberger, 1930).

Summary.

A morphological and biological study has been made of a number of soil mycobacteria and corynebacteria. The genus *Mycobacterium* is comparatively rare in soil. It has two subgenera, A and B. The former represents the mycobacteria proper, with *Myc. tuberculosis* as type-species. These organisms show a pronounced slipping growth, are strongly acid-fast, and produce little or no acid from carbon compounds. Subgenus B has *Myc. coeliacum* as type-species. These organisms show a characteristic cytomorphosis consisting in a transformation from long, often branching rods into cocci. They are only weakly acid-fast, and have more tendency to acid-production than those of subgenus A. The whole genus attaches itself closely to the partially acid-fast, non-proteolytic proactinomycetes. Most saprophytic mycobacteria are capable of decomposing paraffine, and all show a characteristic growth in milk, but no proteolytic or diastatic properties. A dissociation into "plane" and "perrugose" types is common among them, particularly under the influence of acid reaction.

The genus *Corynebacterium* is common in the soil. The saprophytic corynebacteria are not acid-fast, do not attack paraffine, but are mostly proteolytic, often diastatic, and generally capable of producing acid from numerous carbon compounds; they appear in no way sharply distinguished from the parasitic "diphtheroids". They show a wide range of morphological variation, and some of them produce variants with a strong slime formation, generally connected with a loss of formation of swollen cells, or "myceloid" variants which come near to the *Proactinomyces*-type. Such variants arise mainly in old cultures under the influence of lithium or uranium-salts. There is less evidence of "smooth" and "rough" variants. The phenomena of morphological variation seem more naturally explicable according to the cytomorphosis-theory of Henrici than according to the life-cycle theories of Löhnis and Enderlein. Only one species (*Cor. tumescens*)

showed some evidence of reproduction by gonidia. The *Pettenkoferia*-theory of Kuhn did not find any positive support in the results obtained with these organisms.

Numerous previously-described bacteria seem to belong to *Mycobacterium* subgenus B, or to *Corynebacterium*. Three new species (*Cor. tumescens, filamentosum*, and *simplex*) are described, as well as eight new combinations, with synonyms. Organisms have been found, which form a natural transition between *Corynebacterium* and the non-acid-fast, proteolytic group of *Proactinomyces*.

Cultures of the new species and other characteristic groups have been forwarded to The National Collection of Type Cultures, Lister Institute of Preventive Medicine, London.

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EXPLANATION OF PLATES I-II.

Photographs represent nigrosine-preparations, or films stained with dilute carbol-fuchsin, magnification × 750, unless otherwise stated.

Plate i.

Figs. 1-5.—*Myc. coeliacum*, AIII, living objects, × 350. 1-2, on dextrose-agar, 1 day, room temp., same organism with interval of 2 hours; 3-5, on glycerine-agar, 1 day, room temp., same organisms with intervals of 2 hours.

Fig. 6.—Same, asparagine-agar, 2 days, 28°C.

Fig. 7.—*Myc. coeliacum*, authentic, egg medium, 4 days, 28°C.

Fig. 8.—*Myc. rubropertinctum*, 279, asparagine-agar, 1 day, 28°C.

Fig. 9.—*Myc. equi*, M, dextrose-agar, 2 days, 28°C.

Fig. 10.—*Myc. flavum*, dextrose-agar, 3 days, 28°C.

Figs. 11-25.—*Cor. helvolum*. 11-13, strains Ca1, 163, and 279, dextrose-agar, 1 day, 28-30°C.; 14-15, strains A4 and C, potato, 1 day, 28°C.; 16, str. 163, nutrient agar, 3 days, 30°C.; 17, same, saccharose-nitrate-agar, 6 days, 28°C.; 18, str. C, asparagine agar, 2 days, 30°C.; 19, A4, dextrose-agar, 5 days, 28°C.; 20, N3, dextrose-agar, 6 days, 30°C.; 21, same, 6-days-old cystites germinating after 20 hours, room temp., on casein-agar; 22, 163, potato, 2 days, 37°C.; 23, C, potato, 4 days, 37°C.; 24, myceloid variant of N3, potato, 1 day, 30°C.; 25, myceloid variant of Bb, potato, 1 day, 30°C.

Plate ii.

Figs. 26-28.—*Cor. helvolum*, myceloid variant of str. 163, dextrose-agar. 26, 5 days, 28°C. (slope); 27, 6 days, 28°C. (condensation-water); 28, 16 days, 28-30°C. (slope).

Figs. 29-31.—*Cor. filamentosum*. 29, 272*b*, asparagine-agar, 2 days, 18°C.; 30, 276, dextrose-agar, 1 day, 28°C.; 31, 279, asparagine-agar, 5 days, 28°C.

Figs. 32-34.—*Cor. simplex*. 32, B, asparagine-agar, 1 day, 28°C.; 33, 282, dextrose-agar, 1 day, 28°C.; 34, B, dwarf-variant, asparagine-agar, 1 day, 28°C.

Fig. 35.—*Cor. michiganense*, soil strain, dextrose-agar, 1 day, 37°C.

Figs. 36-44.—*Cor. tumescens*. 36, A, dextrose-agar, 1 day, 28°C. (× 562); 37, B, Sabouraud's agar, 12 days, 16°C.; 38, B, Sabouraud's agar, 18 days, 28°C.; 39, A, transferred from dextrose-agar, 6 days, 28°C. to dextrose-agar, 20 hours, room temp., gonidia? (× 1125); 40, B, milk-agar, 8 days, 30°C.; 41, cystites from previous, germinating on Sabouraud's agar after 20 hours, 28°C.; 42, A, casein-agar, 1 day, 28°C. (× 562); 43, same, 3 days, 28°C. (× 562); 44, B, slimy variant, Sabouraud's agar, 5 days, 30°C.

Figs. 45-46.—*Cor. liquefaciens*-group, strain 276, dextrose-agar, 1 day and 3 days, 28°C.

Fig. 47.—*Cor. fimi*, dextrose-agar, 1 day, 28°C.

Fig. 48.—*Proactinomyces*-like organism, strain M, dextrose-agar, 1 day, 28°C.

Fig. 49.—Same, milk-agar, 1 day, 28°C.

Fig. 50.—Strain A, dextrose-agar, 2 days, 28°C.

NOTES ON SOME MONOCOTYLID TREMATODES.

By Professor T. Harvey Johnston, The University of Adelaide.

(Six Text-figures.)

[Read 18th April, 1934.]

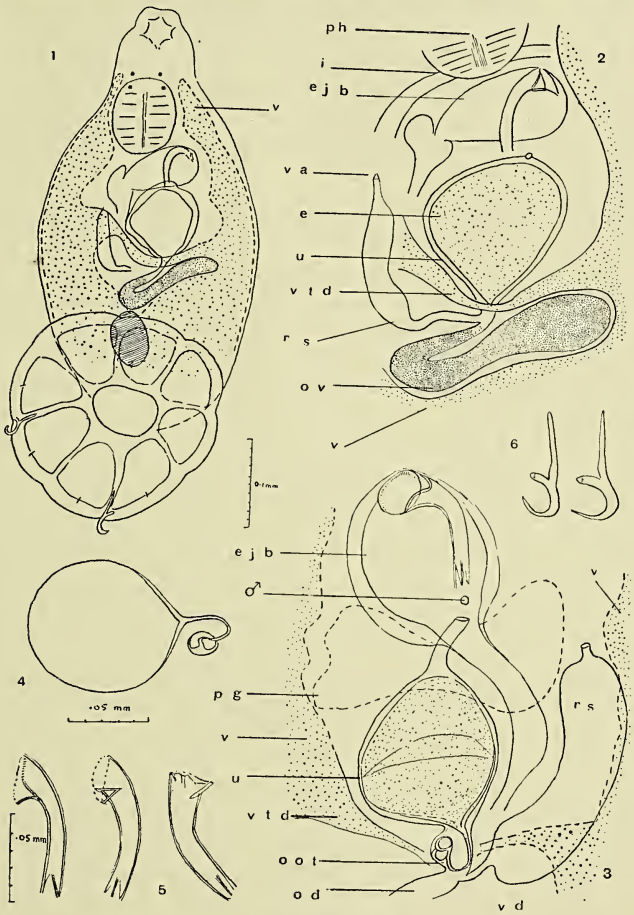
In 1922 a minute heterocotylean trematode from the gills of the common stringray of Sydney Harbour, *Urolophus testaceus* Mull. and Henle, was described briefly by Johnston and Tiegs as *Monocotyle robusta*. The accompanying text-figure indicates the general arrangements of the organs in dorsal view, though the relation of the cotylophore, as shown in it, suggests a ventral view.

As additional material has become available, though in a poor state of preservation and all of it somewhat distorted, a re-examination was decided upon. The Trustees of the Australian Museum, Sydney, kindly forwarded the type slide for re-study. The type is about 0·6 mm. long (including the cotylophore) by 0·24 mm. in maximum breadth, the widest portion being in the middle and posterior regions of the body, which narrows rapidly to join the sucker. The anterior end is broadly rounded. The mouth is surrounded by rather thin lip-like folds and is directed anteroventrally. In front of it, in some specimens, are to be seen low rounded head-lobes associated, no doubt, with cephalic organs as in other Gyrodactyloids. Dorsally are four eyes, the posterior pair slightly larger and more widely separated than the anterior pair. These organs are situated in the region just in front of the pharynx.

The cotylophore is about as wide as the broadest part of the body and its ventral surface is marked out into eight marginal loculi and a smaller, more or less rounded, central sucker, the last-named being the weakest in development. There is a delicate marginal fringe. The two major hooks lie one in each outer radius of the posterior loculi. Each hook has a long narrow straight rod-like root and a much shorter, thicker and slightly curved one, near whose free end is a ring-like thickening, probably for the insertion of muscle fibres. The longer dorsal root is rather wider near its junction with the other root and possesses a slight thickening in its inner (ventral) aspect. The free portion of the hook is strongly curved and terminates in a very sharp point. The length of each hook, excluding the curve, is about 0·062 mm., but if the curve be followed, then the length from the tip of the dorsal root to the free end of the hook is about 0·093 mm. The dorsal root measures 0·04 and the ventral 0·017 mm. long. The curves of the free portion are continuous with those of the ventral root. There is also a minute curved hooklet about 7μ long situated marginally in each interradius.

The wide ill-defined mouth narrows into a tubular portion succeeded by the comparatively large, transversely-marked, elliptical pharynx, about 0·08 mm. long. The latter is succeeded by the simple wide intestinal crura which are largely obscured by the vitelline glands.

There is a single, nearly median, testis lying behind the ovary and covered by the yolk glands. Its duct passes forwards on the right side alongside the vagina and receptaculum. It becomes swollen to form a vesicula, or more correctly, ejaculatory bulb, lying immediately behind the pharynx. The penis is a simple, slightly curved tube, 0·08 to 0·09 mm. long and 0·013 to 0·015 mm. in width. Its inner (and normally more or less anterior) end is slightly widened to form a kind of funnel, the walls being further strengthened by linear thickenings of the chitin, so that a V-shaped structure may appear when the organ is viewed from certain directions. The free end lies adjacent to the male pore and also has a marked longitudinal thickening near its tip. The prostate glands occupy a considerable region just above, and laterally from, the male pore. The glands



Text-figs. 1-6.

(1) *Monocotyloides robusta*—ventral; (2) reproductive system of type; (3) part of reproductive system, dorsal view; (4) egg; (5) penis; (6) major hooks.

Nos. 3 and 4 drawn to same scale; Nos. 5 and 6 to same scale.

Reference to lettering: *e*, egg; *ejb*, ejaculatory bulb; *i*, intestine; *od*, oviduct; *oot*, ootyp; *ov*, ovary; *ph*, pharynx; *pg*, prostate glands (outline of occupied area dotted); *rs*, receptaculum seminis; *u*, uterus; *v*, vitellarium; *va*, vaginal aperture; *vd*, vas deferens; *vtd*, vitelline duct.

extend laterally and may reach the vitellaria. They overlie the anterior part of the uterus. Their ducts enter the posterior end of the vesicula, whose walls may become considerably thickened.

The ovary lies transversely just in front of the testes and is sharply bent in itself. Its loop reaches the intestine, but the density of the yolk glands would not allow one to determine whether the organ crossed above and below the intestine, as has been described by Goto for *Monocotyle ijimae*. The ootyp is very short and the shell glands appear to be restricted to a very small adjacent area. The uterus, when devoid of an egg, is a narrow, nearly median, duct terminating at the uterine pore beside the male aperture. One or both of these apertures were found to be displaced from the mid-line in some specimens, but this may perhaps be due to the distortion of the parasites and to their imperfect state of preservation. The uterine walls, especially near the ootyp, are considerably thickened. The egg is more or less circular, 0·09 to 0·10 mm. in diameter, but usually collapses and becomes distorted during the process of clearing and mounting. Posteriorly it has a small knob to which is attached a short filament terminating in a swollen portion supported by a bifurcate thickening of the chitinous covering.

The yolk glands are very conspicuous on account of their size and coloration. They form a rather compact mass, very narrow anteriorly, but very wide posteriorly where those of opposite sides seem to fuse, this mass extending from the level of the anterior part of the pharynx to the posterior end of the body. They obscure the crura and testes, but do not cover the ovary. The narrow transverse yolk duct lies between the ovary and uterus and ventrally to the ootyp.

The vaginal aperture lies on the right of the mid-line, more or less on the same level as the male pore. It soon widens into an elongate, well-chitinized receptaculum seminis which, when full of sperms, occupies the region between the corresponding intestinal crus and the uterus and may partly underlie the former. In one specimen this organ was 0·16 mm. long. It narrows into a vaginal canal which travels inwardly above and just behind the transverse yolk duct to join the oviduct as the latter receives the very short common vitelline duct.

The systematic position assigned to the species does not seem quite satisfactory. The type of *Monocotyle*, *M. myliobatis* Taschb., 1878 (from *Myliobatis aquila* from Naples), has not been properly described, the original account being very short and incomplete. Parona and Perugia's figure of a specimen from Trieste (1890) is probably incorrect in many particulars. The generic diagnosis given by Taschenberg and by Braun (1890) would include our form except in regard to the position of the female ducts. Goto gave an excellent account of a new species, *M. ijimae*, from a Japanese ray, *Trygon pastinaca*, and formulated an amended and more detailed diagnosis of the genus. The Australian species differs in its body proportions, form of penis, receptaculum, position of female organs, presence (apparently) of only one testis, and of a definite central loculus in the cotylophore. The two latter features seem to be of generic value and are possessed also by two species described by MacCallum (1916) from *Trygon* (or *Dasybatis*) *pastinaca* from the United States of America, viz., *M. dasybatis* and *M. d. minimus* (=*M. minima* Johnston and Tiegs, 1922). These three forms may be grouped together under a new genus, *Monocotyloides*, which may be diagnosed thus: Monocotylinae, near *Monocotyle*, but differing in possessing a single testis and a cotylophore with a central loculus in addition to the eight marginals; hooks as in *Monocotyle*. Type

M. robusta (Johnston and Tiegs, 1922). Other species: *M. dasybatis* (MacCallum, 1916); *M. minima* (Johnston and Tiegs, 1922).

MacCallum (1916) also described another species of *Monocotyle*, *M. selachii*, from a hammer-head shark, *Sphyrna zygaena*, and from *Carcharias obscurus*, but its cotylophore and major hooks are quite distinct from those of the Mediterranean, Australian and Japanese species. It seems to belong to a new genus, near *Merizocotyle*. The name *Paramonocotyle* is suggested for it, and the following diagnosis is based on MacCallum's figure and account: Monocotylidae; cotylophore devoid of radial septa, but with ventral surface subdivided into numerous rounded loculi; two major hooks and numerous small marginal hooklets on disc; four groups of cephalic glands; mouth and digestive system as in *Monocotyle*; single testis (apparently); vagina apparently single and opening ventrally on the right of the mid-line; receptaculum seminis (?); other genital characters as in *Monocotyloides*. Type *P. selachii* (MacCallum, 1916). If it were shown that the vagina was double, then the genus would belong to the Merizocotylinae and would differ from *Merizocotyle* in very few features. Johnston and Tiegs (1922) placed the subfamily in the Gyrodactylidae, but mentioned (p. 115) that it formed an intermediate link between the latter family and the Monocotylidae. When Cerfontaine (1898) erected the genus *Merizocotyle*, he placed it in the Monocotylidae. Fuhrmann (1928) considers that it belongs to the Monocotylinae.

Summary.

An amended description of *Monocotyle robusta* Johnston and Tiegs is given. The parasite, together with two other species, *M. dasybatis* and *M. minima*, is assigned to a new genus *Monocotyloides*.

Monocotyle selachii MacCallum is placed in a new Merizocotyline genus, *Paramonocotyle*.

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REMARKS ON SOME AUSTRALIAN CESTODARIA.

By Professor T. Harvey Johnston, The University of Adelaide.

[Read 18th April, 1934.]

Order Amphilinidea.

In November, 1932, Ihle and Ihle-Landenberg described an Amphilinid cestode, *Kosterina kuiperi*, n.g., n.sp., from the lung cavity of an Australian tortoise, *Chelodina longicollis* (Shaw), from the Rotterdam Zoological Garden. They regarded it as the representative of a new subfamily, Kosterininae (Amphilinidae). Early in 1931 there was described *Austramphilina elongata* from the body cavity of the same species of tortoise from Lake Macquarie, New South Wales (Johnston, 1931). The parasite obviously belongs to the same species as Ihle's, so that *Kosterina* must be regarded as a synonym of *Austramphilina* and Kosterininae accordingly becomes Austramphilininae. I did not have material available for sectioning, but Ihle has published figures of several sections. The two accounts differ in very few particulars.

Ihle stated that the worms were taken from the lung cavity, whereas mine were obtained from the coelome in the vicinity of the ovary, the parasites in their rounded, greatly contracted, condition, being at first mistaken by Mr. Filmer, their discoverer, for eggs. All other known Amphilinids live normally in the body cavity of some fish, hence Ihle's material may have invaded the lung, perhaps damaged during the dissection. There is another possible explanation. *Amphilina* occurs in the body cavity of sturgeons and its eggs probably reach the exterior through the abdominal pores of the fish. In the case of *Gephyrolina paragonopora*, which infests the coelome of some Indian Siluroids (*Macrones* spp.), in which such pores are absent, Woodland (1923) has stated that the parasite is able by means of its rostellum and anterior boring apparatus, to make its way through the body wall and thus reach the exterior. Perhaps *Austramphilina*, with its weaker rostellum and less strongly developed glandular apparatus, can readily penetrate the thin-walled lungs and thus allow its eggs to escape through the rostellar cavity into the respiratory apparatus of the tortoise and reach the water, where, presumably, some crustacean serves as an intermediate host.

Ihle reported the absence of a rostellum and did not find frontal glands, but my material indicates the presence of the former, its appearance, when retracted, being figured in the original account and resembling that of other Amphilinids. In Ihle's specimens, judging from the figures, the rostellum is not retracted, and this would account for his statement that the uterus opens at the anterior end, whereas in my material it opens into the rostellar cavity, near its base. Large, finely granular cells were found scattered in the parenchyma in the anterior part of the parasite and were regarded as being frontal glands, though some of them

may have been giant subcuticular cells, similar to those figured by Fuhrmann (1930, fig. 182) for *Amphilina foliacea*. The small dorsal diverticulum at the junction of the receptaculum and vagina was not mentioned by Ihle. He emphasized the presence of a true receptaculum seminis, of relatively enormous size and developed as a widening of the vagina, this organ being absent in all other Amphilinids, its place being taken by an accessory receptaculum. The structures labelled as accessory receptacula in my figure (1931, fig. 9) are merely small swellings of the inner portion of the vagina and are not diverticula like the structures so named occurring in other Amphilinids. All the remaining features of this striking worm have been emphasized by both of us.

Poche had previously (1922) erected the family Schizochoeridae to include two subfamilies. Soon afterwards Woodland (1923) described *Amphilina paragonopora* from freshwater Siluroids from the Ganges basin, his species being made the representative of a new genus *Gephyrolina*, and subfamily Gephyrolininae, by Poche (1926*a*, 254–5; 1926*b*, 25). This Indian form was regarded as showing a number of characters intermediate between the Amphilinidae and Schizochoeridae and, as a consequence, Poche suppressed the latter and incorporated all four subfamilies—Amphilininae, Gigantolininae, Schizochoerinae, and Gephyrolininae—under Amphilinidae, and this arrangement has been accepted by Fuhrmann (1930). If the diagnosis of the order given by the latter (1930, 146–7) be accepted as that of the family, then the Austramphilininae would constitute a fifth subfamily which (apart from the disposition of its uterus) shows most affinity with the Gephyrolininae.

A. elongata possesses certain features similar to those of *Gephyrolina paragonopora* (Woodland, 1923), e.g., band-like form and terminal genital openings; but differs from it in the distribution and form of the testes; the presence of a true receptaculum in *Austramphilina* and its absence in the other, where it is replaced by an accessory receptaculum; and especially in the course of the uterus, a feature in which *Austramphilina* differs most widely from all other members of the order. In view of the outstanding features presented by this parasite, it seems advisable to retain the family rank—Austramphilinidae—assigned to it in 1931, and an amplification of the diagnosis is now made: Amphilinidea with band-like form; terminal limb of uterus median, posteriorly-directed limb lateral on the side opposite from the first ascending limb; testes scattered in a dorsal and a ventral layer above and below the uterus; male and vaginal apertures at the posterior end and opening into a short genital atrium; penis absent; very large receptaculum formed as a widening of the vagina.

As mentioned in the earlier accounts, the host relationship is noteworthy, since all the remaining known genera occur in bony fish, whereas *Austramphilina* is a parasite of a freshwater Chelonian.

Order Gyrocotylidea.

In their paper, Ihle and Ihle-Landenburg (1932, 316) stated that no Cestodaria, except *Kosterina*, were known from Australia. This is incorrect, since two species belonging to the Gyrocotylidae, viz., *Gyrocotyle rugosa* Dies. and *G. nigrosetosa* Haswell, have been recorded from our waters.

Gyrocotyle rugosa Dies.

This parasite was first recorded from the Commonwealth by Spencer (1889), who gave a detailed account under the name *Amphiptyches urna* Grube and Wagener, the host being the elephant fish, *Callorhynchus antarcticus* Lacep., from

Victorian waters. In 1902 Haswell referred to it as *G. rugosa* and gave a few figures, but did not mention any locality. He may have collected it at Dunedin, New Zealand, where the host is common and where he frequently spent his summer vacations. I have identified the species from the same host species in Tasmania, as well as from Encounter Bay, South Australia; the latter material having been collected by my colleague, Professor J. B. Cleland. This parasite is widely distributed in the Southern Ocean. It has been recorded by Monticelli (1889, 323; 1890, 327) from *C. antarcticus* from Dunedin; by Diesing (1850, 408) from Valparaiso, where it was said to have been found in a mollusc, *Mactra edulis* King (=*Mulinia edulis*, see Dollfus, 1923, 216 and fig. 1); and from Natal, where it was said to have been taken from a gazelle. The latter record is obviously incorrect and is no doubt due to a misplacing of labels; whereas that relating to the mollusc is probably based on a specimen which was voided by *Callorhynchus* and became accidentally enclosed by the *Mulinia*. Efforts to infect bivalves with embryos of *Gyrocotyle* have, so far, been unsuccessful. The record of the species from a South African sheep by Linstow in 1901 must also be a mistake due to incorrect labelling, as Dollfus and Fuhrmann have inferred.

In 1910, Hungerbuehler recorded the presence of the parasite in *C. antarcticus* from South Africa. In 1924, Linton described a new species, *Gyrocotyle plana*, from the same Chimaeroid from Table Bay. It is strikingly like *G. rugosa*, from which it was stated to differ in possessing a uterus with an axis and lateral diverticula and in having the genital apertures placed more like those of *G. urna*. The species was said to show little resemblance to *G. fimbriata*. The two latter are regarded by Dollfus (1923) as synonyms, though Fuhrmann (1930) retains them as distinct. It seems to me that *G. plana* is a synonym of *G. rugosa*, being based on a strongly contracted specimen.

The host is variously named in literature relating to Australasian fish, though *C. antarcticus* Lacep. is the term most commonly employed. Waite in his illustrated catalogue of the fishes of South Australia (*Rec. South Austr. Mus.*, 2 (1), 1921, 35) calls it *C. milii* Bory 1823, as also do Lord and Scott in their "Synopsis of the vertebrate animals of Tasmania" (1924, 30). McCulloch (Commonwealth Fisheries, Endeavour Reports, 1, 1911, 16) refers to it as *C. callorynchus* L., as also did Waite (*Rec. Canterbury Museum*, 1 (2), 1909, 23). Dollfus (1923, 228) states that *C. callorhynchus* L. is the same as *Chimaera monstrosa* L., and, if so, then the Linnaean name cannot apply to the southern Chimaeroid. McCulloch in his check-list (1929, 32) definitely identifies the fish as *C. milii* Bory, with *C. tasmanius* Richardson and *C. dasycaudatus* Colenso (from New Zealand) as synonyms. The remaining Australian Chimaeroids are *Chimaera ogilbyi* Waite from New South Wales and Tasmania, and *C. waitei* Fowler from Victoria.

Haswell (1902, 48) referred to the presence of *Gyrocotyle* "not only in the northern *Chimaera monstrosa*, but (also) in the southern *Callorhynchus antarcticus* and *C. argenteus*". Dollfus (1923, 228) pointed out that the latter name is a synonym of *Chimaera monstrosa*. Hutton in his "Index Faunae Novae-Zealandiae" (1904, 53) listed *C. antarcticus*, as well as *Chimaera monstrosa* var. *australis* Hector, as occurring in the waters of the Dominion, and *Gyrocotyle urna* (based on Spencer, 1889) is recorded (p. 310) among the cestodes. Phillips in his check-list of the fishes of New Zealand (*Jour. Pan-Pacific Research Institution*, 2 (1), 1927, p. 11) includes *Chimaera nova-zelandiae* Fowler (as a rare species) and *Callorhynchus milii*. It is probable, then, that Haswell's "*C. argenteus*" may

be the same as Hector's variety of *Chimaera monstrosa* or *Chimaera novaezelandiae*.*

GYROCOTYLE NIGROSETOSA Haswell.

This species was described by Haswell (1902) from *Chimaera ogilbyi* Waite, obtained at Manly, New South Wales. It was stated to be more nearly related to *G. urna* than to *G. rugosa*. A comparison of Haswell's figure with that recently published by Ruszkowski (1932, Pl. 41, f. 1) for *G. urna*, suggests that *G. nigrosetosa* is a synonym of the latter, which is known to be very variable in the form of its rosette and in the folding of its lateral margins. Ruszkowski's work appears to have settled the vexed question of the orientation of *Gyrocotyle*, as he found the larval hooklets lying at the end from which the rosette was developing. The rosette end is thus the posterior, as was believed to be the case by Haswell, Kofoid, Watson, Woodland (1923) and others, a view which was opposed by Spencer, Dollfus, Fuhrmann and other distinguished parasitologists.

GYROCOTYLE URNA Grube and Wagener.

It has been pointed out that Spencer's account of *Amphiptyches urna* from Victoria was based on *Gyrocotyle rugosa*. *G. urna* has not been recorded from Australian waters, but assuming my view regarding the synonymy of *G. nigrosetosa* to be correct, then *G. urna* occurs in *Chimaera ogilbyi*. I have identified a solitary specimen taken by Professor Cleland from *Callorhynchus* at Encounter Bay, South Australia, as *G. urna*. It closely resembles the figures published by Scott (1911), Watson (1911, as *G. fimbriata*), Dollfus (1923) and Fuhrmann (1930). Hungerbuehler recorded *G. urna* from *Callorhynchus* from South Africa in 1910.

The Cestodaria now known to occur in Australia are as follows:

Host.	*Parasite.*	*Locality.*
Chelodina longicollis	*Austramphilina elongata* Johnston.	New South Wales.
	(Syn. *Kosterina kuiperi* Ihle.)	Australia.
Chimaera ogilbyi	*Gyrocotyle urna* Gr. and Wag.	New South Wales.
	(Syn. *G. nigrosetosa* Haswell.)	
Callorhynchus milii	*Gyrocotyle rugosa* Dies.	Victoria, Tasmania, S. Australia.
	(Syn. *Amphiptyches urna* Spencer, *nec* Gr. and Wag.; *G. plana* Linton.)	
	Gyrocotyle urna Gr. and Wag. (*nec* Spencer, 1889).	S. Australia.

* Since this paper was submitted for publication, Mr. G. P. Whitley, Ichthyologist, Australian Museum, Sydney, in response to inquiries, has forwarded the following information. *Callorhynchus milii* Bory de St. Vincent is the correct name for the species inhabiting the Australian and New Zealand seas, with *C. antarcticus* Schinz 1822 as a synonym. Lacepede's description is based on a South American form, probably distinct. *Chimaera callorhynchus* L. 1758 is the South African species (= *Callorhynchus callorhynchus*), the name being wrongly applied by earlier authors to the Australasian

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"elephant fish". Dollfus' reference (1923) to the synonymy of *C. argenteus* is incorrect, the latter name being given by Philippi to a South American *Callorhynchus*. *Chimaera waitei* Fowler 1907 (= *Hydrolagus waitei*) is perhaps not distinct from *C. ogilbyi* Waite. Hutton's variety, *australis*, is a valid species, now known as *Phasmichthys novaezelandiae* (Fowler 1910), the former name being preoccupied.

A PRELIMINARY INVESTIGATION OF THE NATURAL HISTORY OF THE TIGER FLATHEAD (*NEOPLATYCEPHALUS MACRODON*) ON THE SOUTH-EASTERN AUSTRALIAN COAST. I.

DISTRIBUTION AND SUPPLY; LENGTH STATISTICS.

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(Nine Text-figures.)

[Read 18th April, 1934.]

Introduction.

Trawling in New South Wales waters has undergone many changes since its inception in the year 1915, but it is still one of the important industries of the State. Notwithstanding this fact, and the reasonable assumption that Australia offers conditions for an extension of trawling to the other States, practically nothing has been done in the way of organized scientific research on either the general or the special problems of deep sea fisheries, that is apart from the work of systematists (whose sphere is restricted in any case) and the pioneer researches of the ships '*Thetis*' and '*Endeavour*' prior to 1915.

Since 1915 a considerable amount of useful data has accumulated, mainly in the form of the records of the various companies, including the State Trawlers, and, although fragmentary in parts, could have proved of immediate practical value to those directly interested.

The scientific importance of such matters has often been urged, but neither detailed suggestive programmes of research, nor actual efforts to work out any problem have been made. In any case no money has been available, this naturally proving a rather serious deterrent. In 1927–28 the U.S.A. Government spent some £300,000 on its Bureau of Fisheries, whilst in the United Kingdom as much as £80,000 has been expended on a research vessel; in South Africa, too, £25,000 was made available for this purpose.

Early in 1930, Professor Dakin, of this Department, stressed the desirability of research in trawling problems in these waters, and suggested certain lines of inquiry and plans for investigation. The trawler companies were then complaining of a steady decline in the supply of fish in the trawling grounds.

The present investigations were initiated in 1930* and the trawling companies were approached for permission to send someone on their boats periodically with a view to making observations. Red Funnel Fisheries, Ltd., cordially invited us to make use of their ships, and our thanks are due to them for the kindness and courtesy extended throughout the work.

* The work was rendered possible by a grant from the Council for Scientific and Industrial Research, to whom separate acknowledgement must be made.

Thirteen cruises in all were made over a period of twelve months, the length of the trip varying from seven to nine days. Practically all of the present trawling grounds were visited at least once, and in some cases several visits were paid.

The tiger flathead (*Neoplatycephalus macrodon*) is by far the most important constituent of the catches, and certain aspects of its natural history constitute the subject of this paper.

During the course of the work, the writer has keenly felt the lack of time, other duties and certain additional circumstances preventing a more detailed treatment.

Acknowledgements.—I am deeply indebted to Professor Dakin, Head of this Department, who has suggested methods and lines of attack, and who has at all times maintained a keen and sympathetic interest in the work. He has, in addition, offered many helpful suggestions in the preparation of this paper; also to Captain Hales of the Red Funnel Company for making the trawlers available to us, and for assistance in many other ways. Thanks are also due to Captain C. R. Stuart and the crew of the Red Funnel Trawler '*Bar-ea-mul*' (upon which most of the cruises were made), for their ready co-operation at all times. They have been of material assistance in lessening the difficulty of working at sea. I am indebted to Captain S. Mills for indispensable assistance in the preparation of the maps of the trawling grounds, and for great help in other ways; this applies also to Mr. W. Howell, wireless operator on the '*Bar-ea-mul*'. Finally, to Mr. G. P. Whitley of the Australian Museum are my thanks due for the identification of certain fish specimens.

The N.S.W. Trawling Grounds. Text-figs. 1, 2, 2A.

Below are listed the principal areas which are worked by the N.S.W. trawlers. Brief information is given in the text and in the accompanying maps, as to the position, extent, depths, and nature of the bottom.

In addition to the grounds shown, there are minor areas to the north and south of the limits in the maps. Separate grounds are indicated by the Roman numerals, and it will be noticed that in some cases, one ground is merely a continuation of the one immediately contiguous thereto.

Nos. 1, 1a, and 2 are sometimes referred to collectively as the "Home grounds."

Grounds shown in Text-figs. 1 and 2.

I. *New Zealand Close Ground.*—Depth varies from 46–65 fathoms on the western margin to 86–95 fathoms on the eastern.

Ia. *Sydney Heads Wide.*—Depth 83–110 fathoms. This, and Nos. XVIII and XIX (Text-fig. 2A) are interesting in that they are comparatively new grounds, which are situated in deep water, and which were first tried for purely experimental purposes. For a time during 1933 they provided very good fishing, but the flathead soon disappeared.

II. *Botany-Wata Mooli.*—Depth 32–40 fathoms to 80–87 fathoms on the eastern side.

III. *Kiama Ground.*—Depth from 30 fathoms up to 85–99 fathoms on the eastern edge.

IV. *Jervis Bay Ground.*—Average depth about 74 fathoms.

V. *Tollgates-Moruya.*—Depth ranges from 22–40 fathoms along the western edge, to 75–82 fathoms towards the eastern margin.

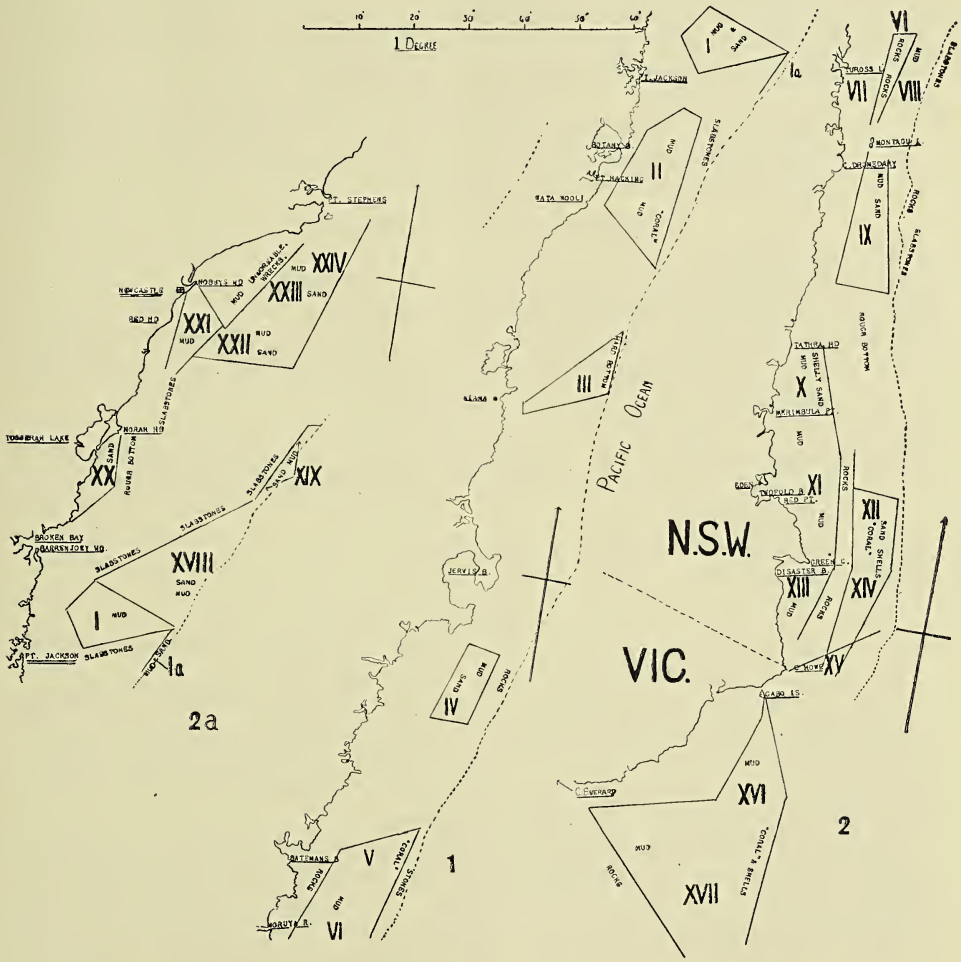
VI. *Pines Wide.*—A more or less direct continuation of the previous area. Depth 20–47 fathoms to 80–86 fathoms.

VII. *Pines Close.*—A comparatively small tract of sea bottom, off Tuross Lake. Depth 20–24 fathoms.

VIII. *North Montagu.*—Depth fairly uniform, ranging from 65 to 81 fathoms.

IX. *South Montagu.*—Depth from 29–40 fathoms to 68–81 fathoms.

X. *Tathra.*—Depth from 27 to 49 fathoms.



Text-fig. 1.—The grounds to the immediate south of Port Jackson. The lines marking the limits of the grounds are the actual bearings used by the trawling skippers. In this and the next two figures the dotted line to the right in the maps represents the edge of the continental shelf (100-fathom line).

Text-fig. 2.—The direct southerly continuation of Text-fig. 1. It will be noticed that the grounds actually encroach on Victorian waters.

Text-fig. 2A.—The direct northerly continuation of Text-fig. 1, showing the principal northern trawling areas.

XI. *Eden Close.*—Depth from about 30 to 49 fathoms. Separated from XII by a narrow belt of rocks.

XII. *Eden Wide.*—The centre of what was formerly an extremely prolific trawling area, but which has undergone considerable impoverishment during the last few years. Depth varies from 56 to 70 fathoms.

XIII. *Disaster Bay Close.*—Depth from 24 to 45 fathoms.

XIV. *Disaster Bay Wide.*—Separated from XIII by a belt of rocks. Depth 60–72 fathoms.

XV. *Gabo.*—Really a continuation of XIV. Bearings at this point evidently taken from Gabo Is. Depth 55–72 fathoms.

XVI. *Gabo North.*—The northern tip of a very extensive area of trawlable sea bottom. Depth varies from 54 to 68 fathoms.

XVII. *Everard North West.*—A ground which is comparatively new, and which still provides an occasional good cruise. The weather here is apt to be rather uncertain, and under such conditions trawling becomes dangerous. Depth varies from 53 to 68 fathoms.

Grounds shown in Text-fig. 2A.

I. & Ia. See above.

XVIII. *New Zealand Wide.*—Depth from 76 to 104 fathoms.

XIX. *Norah Head Wide.*—Depth from 88 to 106 fathoms.

XX. *Norah Head Close.*—A ground which is now seldom visited. Formerly a recognized leatherjacket locality, enormous quantities of this fish being caught there. Average depth 27 fathoms.

XXI. *Red Head.*—Depth from 16 to 51 fathoms.

XXII. *Newcastle South.*—The southern portion of a very extensive tract of trawlable sea bottom, which also includes Nos. XXIII and XXIV. Depth 65–70 fathoms.

XXIII. *Newcastle Close.*—Depth 41–60 fathoms.

XXIV. *Newcastle Wide.*—Depth 70–74 fathoms.

Section I.

The Variations in the Yield of Trawled Fish from S.E. Australian Grounds during the Years 1918–22 and 1930.

In this section it is proposed to discuss the question of supply, principally in connection with the Tiger Flathead (*Neoplatycephalus macrodon*), but with some mention of the other species as well. There are indications that a considerable change has occurred since 1915, both in the quantity of fish taken and in the relative proportions of the different species.

From the commercial viewpoint, the most serious factor has been an apparent absolute decrease in the available supply, and the trawlers are compelled to go further and further afield for their hauls. The Fishing Sheets of the State Trawling Undertaking for the years 1918–22 inclusive were available and have yielded interesting data concerning the conditions of fishing, the amount of fish caught, and the localities in which operations were carried out. It has accordingly been possible to make a direct comparison with present day results.

(*a*) *General Conditions in the Years 1918–1923.*

The State trawlers commenced operations on the 17th May, 1915, when the two recently purchased trawlers '*Brolga*' and '*Koraaga*' left the Sydney wharf, and proceeded to a point 10 miles NNE of South Head. The nets were "shot"

in depths ranging from 50 to 68 fathoms on a bottom of mud and sand, and the following species of fish taken in numbers: tiger flathead (*Neoplatycephalus macrodon*), sharp-beaked gurnard (*Pterygotrigla polyommata*), red gurnard (*Trigla kumu*), barracouta (*Thyrsites atun*), leatherjacket (*Cantherines ayraudi*), nannygai (*Beryx affinis*) and john dory (*Zeus faber*).

The records of this and succeeding cruises were unavailable to us, unfortunately, and our records do not commence until the year 1918, so that detailed information as to conditions during the previous two and a half years cannot be given. However, during this period the boats seem to have achieved extraordinarily good results, and many heavy catches were reported. (See Roughley, p. 224.)* At the same time considerable loss seems to have been suffered through damage to fishing gear by uncharted obstructions, but this is entirely to be expected in view of the newness of the grounds.

The area of coastline exploited in these years extended from Newcastle in the north to Cape Howe in the south, although only certain circumscribed stretches of sea bottom were "worked". The grounds north of Port Jackson seem to have been on the whole considerably less prolific than those lying to the south.

Truly amazing hauls were made on the "Home Ground" (see p. 79 and Text-fig. 1) almost from the beginning, the period of heavy fishing lasting from early September until approximately the beginning of December. Occasionally the fish would remain there until the end of the latter month. Nominally the length of the cruise was 4–6 days, but in the case of the "Home Ground", catches were so huge that often the boats would return to port long before the passage of this period in order to discharge their cargo.

The predominant form in these hauls was the tiger flathead, and it was so abundant that the crews were kept on deck many hours at a time, stowing away the fish and preparing for the next haul. These flathead were described as being "very large and bursting with roe", and their excessive abundance led to the period of heavy fishing being termed the "Botany Glut". This Botany Glut became a yearly expectation, the men knowing almost to the week when the flathead would appear, and being equally certain as to the time of the "take off"; when, in 1926 and succeeding years, the customary influx failed to materialize, the vessels were compelled to depend upon other grounds for their cargoes. The "Home Ground" is now practically useless for trawling purposes, and is usually visited by the boats towards the end of the trip only, when there is still time to fit in a few hauls before going in.

On the Southern grounds, too, remarkable catches were made, particularly in the Eden-Green Cape area, and in the neighbourhood of Montagu Island (see Text-fig. 2). At the former locality, leatherjacket (*Cantherines ayraudi*) figured prominently, sometimes to the almost total exclusion of the flathead, whilst gurnard were also taken in enormous quantities. It was quite a normal occurrence to get a sequence of hauls each of which exceeded ninety or a hundred baskets, the trawl in many cases being down for sixty minutes only.

A very interesting feature of these Southern grounds was that heavy fishing might last from January till July, great quantities of flathead often being taken in the winter months, an experience which is seldom if ever enjoyed by the present

* Roughley, T. C., 1916, The Fishes of Australia and Their Technology (pub. by the Govt. Printer, Sydney) contains a very good account, with photographs, of the trawling methods in N.S.W. waters.

trawling fleets. There is now not only a considerable decrease in the amount of flathead taken at any period during the year, but a corresponding reduction in the quantity of "mixed fish" (in leatherjacket, gurnard, john dory, morwong, etc.). This is one of the many changes which have occurred since the prosperous years 1915–26.

A more detailed summary can be given of the yield of fish in the years 1918–22, and this will be compared with the yield for 1930.

Year 1918. (See Text-fig. 3.)

The hourly catch in hundredweights for each month of this and the two succeeding years has been set forth as a curve, the numbers representing the average of the united efforts of all the boats. However, the record is incomplete in certain cases, for some of the trawlers were "held up" from time to time, for varying periods, so that the average given represents the efforts of the reduced number of ships.

The four trawlers, '*Goonambee*', '*Goorangi*', '*Dibbiu*' and '*Dureenbee*', did not commence to fish until late in 1919 (July, August, September and October respectively) so that the figures for the first six months are those of three trawlers only, the '*Brolga*', '*Gunundaal*' and '*Koraaga*'. Furthermore, the figures for the months January, February and March of 1918 are those of the '*Koraaga*' alone. In view of the latter fact, one is not surprised to find the hourly average for the first three months of 1918 very low (1·47, 1·28, and 1·54 cwt. respectively), and when, during the succeeding months, more vessels are engaged the figures undergo considerable increase.

Incidentally it is rather clearly evident from the fishing sheets that there was a marked difference in the ability of the respective crews of these boats, though all were fishing under similar conditions. During the months of April, May and June good fishing was obtained in the Southern Grounds (Merimbula–Green Cape), all three boats concentrating their efforts in this region; an occasional cruise to the "Home Ground" revealed an almost total absence of fish. Flathead was an important constituent of all the hauls, but there was also an abundance of gurnard, skate and barracouta. Good fishing continued on the Southern Grounds until the early part of July when a considerable falling off occurred. The hourly average for June was 3·81 cwt., while for July, August and September it was in the neighbourhood of 2 cwt.

In October, the fish began to come into the "Home Ground" and this is reflected in the curve, the latter giving a good indication of the Botany Glut, for the average jumps up to 4·61 cwt., finally dropping to 3·45 cwt. in December. Very heavy fishing was encountered during this period, the main constituent of the hauls being flathead; however, gurnard were also plentiful here as on the Southern Grounds earlier in the year.

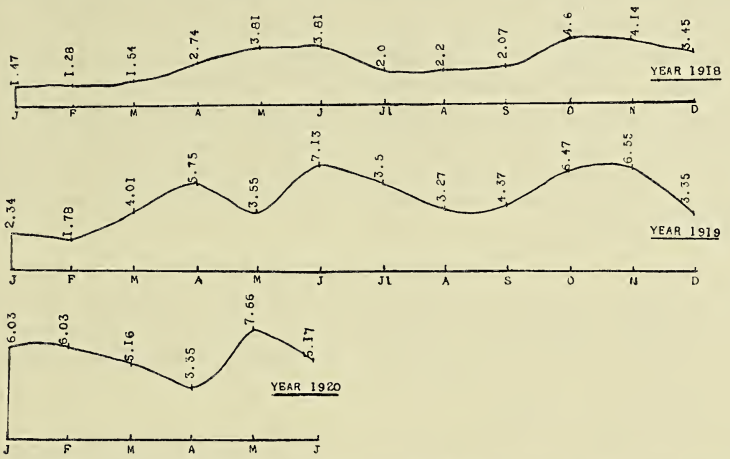
The log sheets of the '*Koraaga*' show that in one cruise (in November) hauls of 110 (2), 100 (2), 85, 70 and 60 baskets* were obtained, as well as several of fifty baskets; these figures should give some idea of the enormous amounts of fish taken during the period of the Botany Glut.

Year 1919. (Text-fig. 3.)

Conditions during this year were very similar to those of 1918. After the take off from the Botany area in December, 1918, the average shows a further

*Fifty baskets (70 lb. each) would be considered very good fishing under present conditions.

decrease for January and February of the new year (see Curve). Heavy fishing began in March and continued until the end of June. The unexpectedly low figure for May does not indicate a "take off" of fish from these grounds, but is due to the fact that the *'Brolga'* and the *'Gunundaal'* spent the greater part of the month in the "Home Grounds", where fish were decidedly scarce.



Text-fig. 3.—Curves showing the yield of flathead and other species, in cwt. per hour, for each month of the years 1918, 1919, 1920.

Once more extraordinarily large hauls were made on the Southern Grounds, a feature of interest being the fact that flathead were abundant right up till the end of June and the early part of July. Actually, however, over the whole period of heavy fishing gurnard and leatherjacket exceeded the flathead in quantity.

June, 1919, was a particularly prosperous one for the trawlers, the average hourly catch reaching the figure of 7·13 cwt. A large influx of gurnard seems to have been partly responsible, as many as 135 baskets per haul being taken. For July and August, the figures are low (see Curve), but in September and October the Botany Glut begins to manifest itself and once more the average undergoes a rapid increase. Just as in the previous year, the fish had disappeared from the Botany area by the end of November, so that for December the curve sinks to its previous low level.

Year 1920. (Text-fig. 3.)

This year must have been a very interesting one from the viewpoint of fishing, and it is most unfortunate that the records for the first half only of the year were available to us. Of great interest is the fact that during the first half of January there was apparently a secondary influx of flathead into the Botany area, for two of the boats at least (*'Brolga'* and *'Koraaga'*) obtained very heavy fishing here at this time, flathead being the predominant constituent of the hauls.

The hourly average for the month January, 1920, is 6·03 cwt., a marked contrast to the 3·35 cwt. of the previous month. In January also, heavy fishing commenced in the Southern Grounds and continued until the end of June at least, the available records only extending to this point. With the exception of

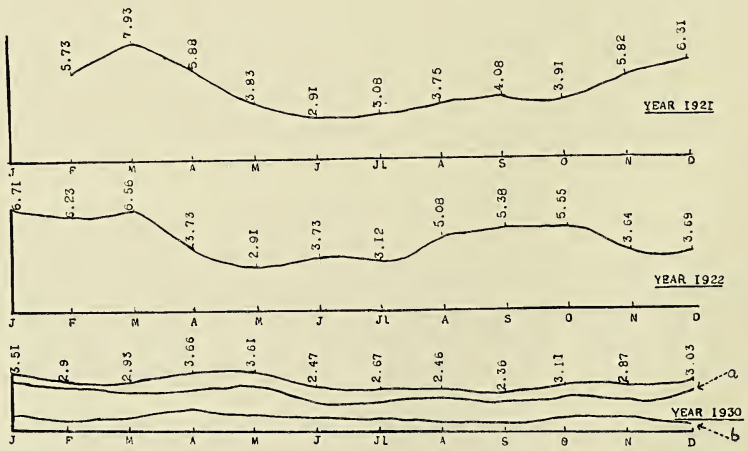
April (3·35 cwt.) the hourly average remains high, reaching no less than 7·66 cwt. in May. The low figure for April is due to two causes: (*a*) a temporary "take off" of the fish from the area of heavy fishing, and (*b*) most of the boats visited other grounds where fishing was very poor.

Another fact of significance which emerges from these records is that concerning the relative proportions of the three principal species taken (flathead, gurnard and leatherjacket) during the period of abundance. At the beginning of May (the "peak month" for 1920) leatherjacket was by far the most plentiful species present, but the numbers underwent a gradual decrease until flathead occupied first position. In the meantime, coincident with the decrease in leatherjacket, an influx of gurnard had been taking place, the latter eventually ousting the flathead from the first position, so that finally the original relations were completely reversed, gurnard being predominant, flathead next, and leatherjacket an insignificant third.

Year 1921. (Text-fig. 4.)

The log sheets of the trawlers '*Gunundaal*' and '*Koraaga*' for 1921 were unavailable, and in addition to this the writer was unable to get any record of the January hauls of any of the boats. The hourly averages for the months of 1921 are consequently based on the operations of five boats instead of seven, and data for January are lacking.

As in previous years, a great influx of fish occurred in the Southern Grounds, but this time the peak month is March, with the remarkable hourly return of 7·93 cwt. Flathead was by far the predominant constituent of the hauls, and it was during this "peak month" that the '*Brolga*', under the command of Captain C. R. Stuart, made what was claimed to be a world's record. Seventy-eight thousand one hundred pounds of fish were trawled in eight hauls of 1 hour 40 minutes duration each, or 14 hours in all. All the fishing was done off Green Cape, 90% of the catch was flathead and the hauls in succession were 150, 140, 142, 154, 137, 132, 125 and 124 baskets.



Text-fig. 4.—Curves showing the yield of flathead and other species, for the years 1921, 1922 and 1930. In addition the 1930 curves for flathead (*a*) and for the remaining species (*b*) are given separately.

After March, considerable decrease occurred in the amount of flathead, which was largely replaced by leatherjacket and gurnard. Of interest, too, is evidence of a considerable temporary influx of leatherjacket and gurnard into the Botany Area in May, this being a rather unusual happening. After April and May (5·88 cwt. and 3·83 cwt. respectively) the fish appear to have "taken off" from the Southern Grounds. In the latter part of July and during August, however, there appears to have been much flathead in the neighbourhood of Montagu Island, for certain of the trawlers, notably the *'Brolga'*, secured some very good catches. The hauls were not large, but remained consistently good.

This year the "Botany Glut" period was not nearly so pronounced as in previous years, and although rather large hauls were made, the averages for September, October and November were distinctly lower than those for the corresponding period of 1919. During the months of November and December some of the boats visited the Montagu Island area and experienced very heavy fishing. Flathead were so abundant that all the remaining species were dumped overboard, in order to conserve space. The *'Brolga'* in particular made several extraordinarily good cruises to this area, and the results are reflected in the high figures for November and December (5·82 and 6·31 cwt. respectively).

Year 1922. (Text-fig. 4.)

The record for this year is almost entirely complete, since all seven boats were engaged in active fishing operations, although log sheets are lacking for certain of the months in some cases.

The year 1922 is interesting chiefly because of the early influx of fish into the Southern area, this apparently having been well under way during the latter part of December, 1921. The period of heavy fishing shows a marked backward displacement as a whole, being restricted almost entirely to the first three months. The figures for these are accordingly high, being 6·71, 6·23 and 6·56 cwt. respectively. Although flathead were abundant, leatherjacket seem to have been the predominant form by far, numerous heavy hauls being secured.

After March, the averages are low until August, when the usual influx of flathead into the Montagu Island area seems to have occurred. The average hourly catch for August is 5·08 cwt. Towards the end of September, the period of the Botany Glut commenced, and this time, perhaps more than any other, extraordinarily heavy fishing prevailed. Thus in eight successive cruises to the "Home Ground" the *'Brolga'* caught 56,700, 82,300, 52,400, 62,700, 45,200, 46,000, 61,900 and 45,900 lb. of fish, the bulk of this being flathead. The greatest amount (82,300 lb.) was caught in 41 hours actual fishing time. In October the *'Brolga'* also paid one visit to the Montagu Island area with very profitable results, the return for 46 hours fishing being 47,500 lb. This was almost entirely composed of flathead. During November and December the fish seem to have moved away from the Botany area for the catches show a marked decrease.

This year, too, in late November and early December certain of the boats visited Montagu Island and experienced heavy fishing, large hauls of flathead being taken. It is difficult to state whether the influx of flathead into this area occurred in the latter part of November, or whether they had been in the locality since August, since during the intervening months fishing operations were concentrated on the grounds in the neighbourhood of Sydney. It is a significant fact that flathead were found in great quantity off Montagu Island in October (see Curve), and furthermore another trawler (the *'Dibbiu'*) had been experiencing

heavy fishing (flathead) in neighbouring areas up till the middle of September. It is possible that undue attention has been focussed on the occurrence of heavy fishing in the Botany area, and that the influx of fish into the latter may merely have been part of a general movement inwards towards a much larger tract of coast, extending as far south as Montagu Island at least. The trawlers would naturally find it much more convenient to confine their operations to local grounds, and thus would be created a false impression as to the amount of fish available in other parts.

Discussion of Results, 1919–1922.

A striking fact which emerges from the foregoing is the general high level maintained by the hauls throughout the greater part of the year. With the exception of about three months, there seems to have been a comparatively abundant supply of fish available during the year on the various grounds. During the months of September, October and November, the Botany Glut prevailed, and when this came to an end, the ships moved further south to the Merimbula–Green Cape area. In the latter locality heavy fishing was sometimes experienced up till the end of June, even flathead being taken in quantity at this late period. In August, flathead seems to have been abundant in the region of Montagu Island. The curves drawn for the years 1918–22 inclusive exhibit the results (Text-figs. 3 and 4).

TABLE I.

Year.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
1918	1·47	1·28	1·54	2·74	3·81	3·81	2·0	2·2	2·07	4·61	4·14	3·45
1919	2·34	1·78	4·01	5·75	3·55	7·13	3·5	3·27	4·37	6·47	6·55	3·35
1920	6·03	6·03	5·16	3·35	7·66	5·17						
1921	—	5·73	7·93	5·88	3·83	2·91	3·08	3·75	4·08	3·91	5·82	6·31
1922	6·71	6·23	6·56	3·73	2·91	3·73	3·12	5·08	5·38	5·55	3·64	3·69
1930—												
(*a*)	3·51	2·9	2·93	3·66	3·61	2·47	2·67	2·46	2·36	3·11	2·87	3·03
(*b*)	3·03	2·57	2·26	2·49	2·92	1·75	2·0	2·02	1·89	2·39	2·0	2·56

(*a*) All species included. (*b*) Flathead only.

Hourly catch of fish in cwt. for the years 1918–1922 and 1930. These figures were used for the construction of the curves in Text-figs. 3 and 4.

The curve for each year shows two fairly well defined maxima, corresponding respectively to the "Botany Glut" period (September-November), and to the period of heavy fishing in the Southern grounds. But when one compares the curves year for year, certain differences are at once evident. It is found that the fish do not always become abundant at exactly the same period each year, this being especially the case in the Southern grounds. With the latter, indeed, a considerable amount of variation seems to be the rule. Thus, in 1918, heavy fishing did not commence there until March, rose steadily until June, and then fell to its previous level in July, lasting for a period of about four months. In 1919, the period of heavy fishing extended from February to July, whilst in 1920, although records were only available for the first six months, there is indication that the period of abundance commenced in January, there being a considerable falling off at the end of June.

In 1921 a restriction is indicated to the months February-May inclusive, whilst in 1922 there is evidence that fish had become scarce after the first three months.

Taken together, then, these results show a tendency for a backward movement of the period of abundance towards the early part of the year. It is impossible to say whether this variation was a normal feature of the area or whether it was an expression of a change wrought by the continued intensive fishing operations, a change which has ultimately led to the present general scarcity.

A point of some importance, to be decided, is the degree of reliability of these fishing records. In other words, do they present a true picture of conditions prevailing on the sea bottom at the time? The actual state of affairs might be given an altogether different guise, by the interposition of such artificial factors as variable ability on the part of the respective skippers, and the number of cruises made to an area throughout the year. As a matter of fact, there seems to have been an extraordinary variation in the efficiency of the different crews or gear, some vessels regularly returning with much higher catches than certain of the others, even though all were working over the same ground. In addition, considerable loss seems to have been experienced through the use of faulty equipment and the inability of the crews in certain cases to restore the latter to efficient working order. But these factors would tend on the whole to decrease the total amount of fish captured during the year.

Now, regarding the other factor mentioned, viz., the number of cruises made to any particular ground throughout the year, there is much room for misconception. Thus, in the curve for 1919 there is a sudden drop from a high level in the month of May. On the face of it, this might be read as a sudden "take off" of fish from the Southern grounds at this time, whereas it is really nothing of the sort. An examination of the fishing records reveals the fact that during May, 1919, the boats confined most of their operations to the Home Grounds near Sydney, even though the fishing there was very poor. The few cruises which were made to the Southern Grounds during this month showed that the fish were just as abundant there as they had been during the previous month. A similar case is presented by the hourly average for April, 1920.

However, allowing for these factors where necessary, it is considered that the results give a reasonably reliable guide to the conditions actually prevailing. When one considers the hourly average for the whole year, all boats included, it is seen that there is a definite increase during the period 1918–22 (see Text-fig. 5). For 1918 the average is 2·9 cwt. and for 1919, 4·18 cwt. As the records for the first half only of 1920 were available, the figure 5·56 cwt. may be safely taken as being too high, the period covered being normally one of heavy fishing. For 1921 the average is 4·56 cwt., whilst in 1922 it rises to 4·68 cwt. At this point, unfortunately, the record ceases. It is not suggested that these figures are evidence for an actual increase of available supply, and probably do little else but indicate increased efficiency on the part of those engaged in trawling operations.

As stated elsewhere, the period of plentiful supply is reported to have ceased in 1926, and according to those engaged in trawling, the decrease has become more marked each year. The fishing records of one company for the year 1930 have been made available to us, and these will serve as a basis for comparison. Unfortunately the actual form of the fishing sheet has undergone considerable modification since 1923, and now contains far less useful information than did its predecessor, so that it is not possible to treat the results in the same full

manner. In any case it has been our experience that the skippers dislike filling in any but the barest essentials, and leave gaps elsewhere.

Year 1930. (Text-fig. 4.)

An outstanding feature of the 1930 results is the general small size of the hauls. The remarkable figures of 1918–23 are seldom, if ever, reproduced, and even forty baskets per three-hour tow is considered unusually good fishing.

The trawler '*Millimumul*' had two good cruises in January, returning with 692 and 675 baskets of flathead on these respective occasions. The bulk of the operations were conducted in the Eden-Green Cape area. But we find that the times taken to catch these quantities were considerably longer than would have been the case during 1918–23. Thus on the first cruise the actual fishing time was 114½ hours, whilst on the second it was 69½ hours.

A further fact of interest is the decrease in the relative quantities of flathead and "mixed fish" taken. For the year 1930, the proportion was 5·3 : 1, and, whilst no definite figures can be given for the years 1918–23 (since such information was not included in the fishing sheets), the relative amount of "mixed fish" (i.e., gurnard, leatherjacket, skate, morwong, etc.) seems to have been considerably greater. During the period of heavy fishing on the Southern grounds during these years, flathead quite frequently occupied a minor place in the hauls, the bulk being made up of leatherjacket and gurnard with smaller quantities of skate, john dory and barracouta. Nowadays the reverse is usually the case, and very seldom do these species exceed the flathead in point of number.

This falling off in the amount of "mixed" is not one of the least important changes which have occurred during the later years of the industry. The average hourly catch for the year 1930 was 2·97 cwt. only, a marked decrease compared with the figures for 1921 and 1922, viz., 4·56 and 4·68 cwt. respectively. It has already been seen that the average for 1918 was 2·9 cwt., but this only indicates that the topography of the grounds and the movements of the fish were still imperfectly known. The falling off in supply is even greater than the figures indicate, for present fishing operations are conducted with much increased efficiency, and an improved form of otter trawl is in use.

Text-fig. 4 gives the average hourly catch for each month of 1930. It takes a very different form as compared with corresponding curves for the years 1918–22. The hourly average for January is 3·51 cwt., but there is a decided fall in the next two months (2·9 and 2·93 cwt.). In April the maximum occurs (3·66 cwt. per hour), this figure being almost reached in May (3·61 cwt.). Thereafter the level remains generally low until October, when it again rises, reaching 3·11 cwt. In November a drop occurs to 2·87 cwt. and in December the average rises to 3·03 cwt. This curve represents the hourly catches of flathead and other species combined, and further information may be deduced by considering these separately.

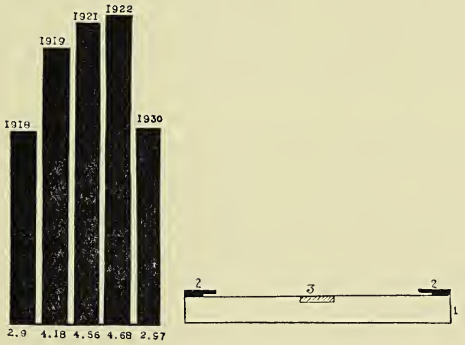
The flathead maximum occurs in January with 3·03 cwt. per hour. After this there is a general tendency (with, however, minor fluctuations) for a decline until the end of September (1·89 cwt.), when an increase once more manifests itself, the returns for the last three months of the year being 2·39, 2·00 and 2·56 cwt. per hour respectively. The curve for the remaining species, all grouped together as "mixed", is rather different in that it exhibits its maximum three months later than the flathead curve, and undergoes relatively large fluctuations throughout the year.

Perhaps the most striking feature of the 1930 curve for all species, flathead included, apart from the general low level of the catches, is its "flatness" when compared with corresponding curves for, say, 1921 or 1922. This is due to the almost entire disappearance of fish from the Botany area, and the considerable falling off in supply on the Southern grounds. On this account the well marked "peak" commencing about September has practically disappeared, whilst the other one for the January-June period has also become much decreased in magnitude. The small rise in October and November is due to the fairly good fishing obtained off Newcastle during these months, whilst the comparatively high figures for the first five months of the year are the result of successful operations conducted in the Southern grounds. Of the latter the comparatively new Cape Everard area bulks prominently in importance. It is possible that the January maximum in the curve for flathead only is closely connected with the breeding period of the fish in the Southern grounds. During the corresponding period of 1931 the writer had the good fortune to visit these grounds and most of the flathead taken were females with the ovaries in an advanced state of development.

Section II.

Length Statistics.

Length measurements of the flathead, as they occurred in the hauls, were conducted with several objects in view. Firstly, it is well known that if taken over a sufficiently long period at different seasons and without artificial selection of the samples they may present a picture of size classes which may be used for the determination of age. The distribution of size classes can be used for the discovery of migratory movements of the fish and, finally, comparative treatments of length measurements may give valuable information regarding overfishing. This is actually the first of our fishing investigations on the coast of Australia, and it must be regarded as a preliminary study.



Text-fig. 5.—Comparison of yields of flathead in cwt. per hour's fishing, for the years 1918, 1919, 1921, 1922 and 1930. For further information see text.

Text-fig. 6.—Section across measuring board. 1, board; 2, guides; 3, metre rule let into board.

The measurements of some 35,000 flathead were taken over a series of monthly cruises, the period ranging from March, 1930, to April, 1931, and over an area of coast extending from Port Stephens to Cape Everard (see map). Unfortunately it has not been possible to follow up the work at sea owing to other duties; consequently a comparison of any particular period with a corresponding period

during the following years cannot be made. The evidence obtained within the twelve months is again rather fragmentary in that the same fishing ground was seldom visited on two successive monthly cruises. There are, however, compensations, for had attention been focussed on one or two areas only, then the other grounds with their different conditions would not have been seen at all.

An extensive system of body proportion measurements had been planned, but owing to lack of time and the difficulty of working conditions, was not put into operation. It was here that the need for an assistant was most keenly felt, for the data obtained from such observations are of major importance in determining growth rates and racial differences. It must be recognized that the work was carried out whilst the author was really a guest on a commercial trawler. No interference with the working of the boat could therefore be thought of.

With the aid of suggestions from Professor Dakin, the actual length measurements were rendered extremely simple, the operations requiring the attention of one person only. The apparatus (which was based on a method suggested by Buchanan-Wollaston) cost considerably less than five shillings to construct, and has proved accurate and effective in practice. It consists of a rectangular piece of board 120 cm. in length and some 10 cm. in width, into the upper surface of which has been let an ordinary metre rule (graduated on one edge into centimetres and millimetres, and on the other into inches and tenths). At one end of the board, and corresponding exactly with the zero of the rule, a small piece of wood is screwed to act as a stop, whilst running along each side of the board throughout its length are two narrow celluloid strips slightly raised from the surface. These serve to hold in position the large strip of celluloid used for recording the actual measurements, the strip sliding in underneath (see Text-fig. 6). When making measurements the celluloid strip is placed in position, a flathead placed on top with its snout up against the wooden stop and the slightly concave margin of the caudal fin spread out. A mark is then made in the celluloid by means of a small awl at a point corresponding to the centre of the margin of the expanded tail. In this manner an accurate and indelible record of the length is made and after a time a remarkable speed can be attained by the operator. Such rapidity is achieved mainly by the elimination of waste movements, and exactness is not sacrificed.

Something like 800–1,000 lengths were recorded in one strip of celluloid, the difficulty of the awl going into the same hole twice being practically non-existent. Upon return to land, the measurements were read off comfortably in the laboratory, using another board similar to the one already described, but which lacked the side guides. The process of reading off also proved quite simple, it being possible to read and enter some three thousand measurements in a book in less than an hour and a half.

Readings were always taken to the nearest centimetre above, and were made by means of a metal slide having a slit exactly 1 cm. wide. This slide was moved from figure to figure along the scale (visible through the celluloid strip), the number of stabs between the slide gap being counted. Some 35,000 fish were measured during a series of thirteen cruises, the highest number for any individual cruise being more than 5,600, and the lowest somewhat more than 1,000.

The Relation of Length to Age.

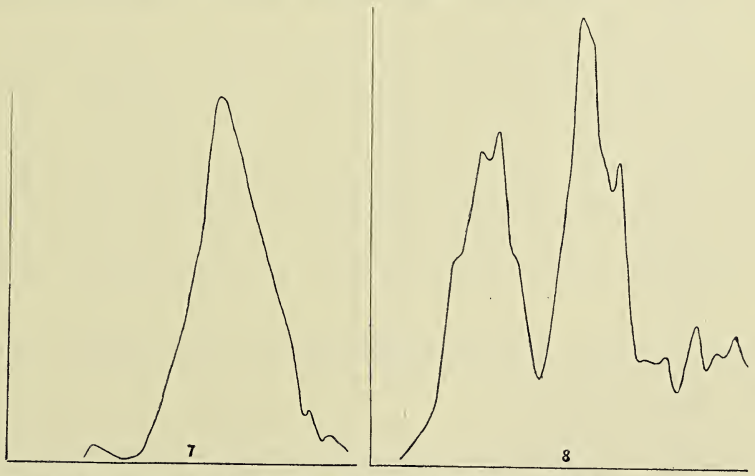
Investigators of fisheries problems in the Northern Hemisphere have been particularly fortunate where age determination of fish is concerned, for a variety

of methods is available. This fact is due in part to a marked discrepancy in the summer and winter growth rates of the fish, this difference finding expression in important structural details in such parts of the body as the scales, otoliths, opercular bones, and vertebrae. All these, when examined under suitable conditions, exhibit well marked growth bands of varying width according to the kind of season passed through, so that it has not only been possible to arrive at a very close correlation between these bands and the age of the fish, but also information has been adduced regarding the general conditions of the environment during preceding years. The length determinations constitute an important complement to these observations, since they not only provide a check for the age computations, but also furnish data regarding the distribution of sizes and the migratory movements of the fish.

This section of the work was approached by us with considerable interest, for apart from the newness of the field, the question of the applicability of the research methods of temperate waters to a sub-tropical region was one of much moment.

On the first cruise 1,230 flathead were measured. The smallness of this number was due to lack of familiarity with working conditions and lack of suitable apparatus. The type finally adopted, which is described elsewhere, was not constructed until after the writer's return from this initial cruise. Of the measurements, some 769 were made on the Cape Everard ground, 275 at Eden, and 186 at Wata Mooli. The curves based on the two latter series show considerable irregularity, presumably owing to the small number of specimens on which they are constructed, yet have points of resemblance to the curve drawn from the data obtained at Cape Everard. The latter curve exhibits a single decided "peak" at 42 cm., falling away steeply on either side of this point (see Text-fig. 7).

On the following cruise two more sets of measurements were made, at Eden and Cape Everard respectively, and each curve conformed to the type obtained in the first cruise, i.e., one with its maximum at 42 cm. The Eden curve, however, showed indications of a second smaller "peak" at 31 cm.



Text-fig. 7.—Curve based on measurements made at Cape Everard. Maximum at 42 cm.

Text-fig. 8.—Curve based on measurements made at Wata Mooli. Maxima at 24 and 32 cm.

The similarity of all these curves was very interesting, since it gave possible indications of the fact that the fish moved about in size groups, and that this particular one (in the 42 cm. group) predominated on the Eden and Everard grounds. At this stage it was not possible to say whether or not a definite segregation into age groups was indicated, although it seemed very probable that such was the case. Subsequent results have served to strengthen this conviction.

On succeeding cruises further curves were obtained with peaks at the 42 cm. mark, but showed in many cases equally well defined peaks at other definite points. These points were not exactly the same in every case, extending as they did over a range of some five centimetres, yet for any particular type of curve the maximum was sufficiently constant to justify the assumption that it really represented an age group. The complete results are set forth in tabular form in Table 2, and it is seen that there are four well defined size groups.

The first of these is represented by fish 24 cm. in length, and the second by fish of 30–36 cm. with a tendency to a predominance at 31–33 cm. The third group is very well defined, being represented mainly by fish of 42 cm., the range being 41–44 cm., whilst the fourth one is occupied by flathead of length 54 cm.

Of these four groups the first and the last are based each on one set of measurements only, but as the number of specimens measured in each case was reasonably large, 1,380 and 1,185 respectively, their true nature seems fairly well established. Of the other two groups, the second has occurred nine times and the third twelve times. On certain occasions a curve showing two peaks has been obtained, one embracing members of the second group and the other those of the third group. In the case of the Group I curve (see Text-fig. 8) there was also another even larger peak corresponding to Group II, and further signs of a third one at Group III (41–44 cm.), although the small number of specimens of larger sizes rendered the curve very irregular at this point. On same cruise a typical Group III curve also obtained. Now, from the viewpoint of age determination there are certain serious deficiencies in these results. Firstly, flathead less than 15 cm. in length were not taken in numbers whilst the writer was present, so that data regarding the sizes from 1 to 20 cm. are entirely lacking. This means that it will be very difficult indeed in our present state of knowledge to assign to Group I its true position in an age scheme. Some data may possibly be afforded by scale readings, but it is very essential to obtain some information as to the rate of growth of flathead during their young stages. Although in almost every case each curve has been based on measurements from one area only, different curves come from different localities, so that the question of racial distinction must be taken into account. It is quite conceivable that the growth rate would not be the same in any two given races, and a "lumping together" of all the results, regardless of this factor, might introduce considerable error.

Just how far the races (if present) differ in their growth rates it is impossible to say, for this line of research is as yet undeveloped, and incidentally is of the greatest importance.

Up to date our figures indicate that the tiger-flathead from the Green Cape area, for instance, are similar to those from, say, Botany, some 320 miles further north, insofar as body proportions are concerned. It is, of course, always possible that a length group from fish of an extreme northern locality might be of different age from those falling within the same group at another locality.

TABLE 2.

Locality.	No. of Specimens Measured.	Lengths in Cm.																					
		22–23	24	25–29	30	31	32	33	34	35	36	37–39	40	41	42	43	44	45	46	47	48–53	54	55–60
C. Everard	769												X—	—X									
Tathra–Eden ..	813														X								
C. Everard ..	2045														X								
Eden	2983														X								
Eden	1864						X							X									
Green Cape ..	506						X—	——	——	—X					X—	——	——	——	——	—X			
C. Everard ..	1617													X—	—X								
Moruya	5771							X						X									
Montagu	1008															X							
Wata Mooli ..	1380		X				X																
Newcastle	1185																					X	
Pt. Stephens ..	1198							X—	——	——	—X						X						
Pines–Montagu ..	1945									X					X								
Merimbula - Green Cape	2337					X—	——	——	——	——	—X				X—	——	—X						
Merimbula–Eden ..	1151					X																	
Jervis Bay ..	1142				X—	——	——	——	——	——	—X												
New Zealand Ground	1058																						

Particulars of the principal series of measurements, including locality, number of specimens, and point of the maximum of the curve in each case. The sign X indicates the position of the maximum, and when the latter extends over a range this is indicated by a crossbar, with an X at either end.

Bearing in mind these considerations, the following facts appear to be established. The curves when taken together to form a composite show four marked peaks (Text-fig. 9) and these conceivably correspond with four age groups. As already indicated, data regarding the 1–20 cm. flathead are lacking, and until this deficiency is remedied, one cannot go much further. It is an interesting fact that the intervals between the "peaks" are approximately equal,

Text-fig. 9.—Composite curve based on measurements from different localities, and showing the possible occurrence of age groups in the flathead. The maxima are at 24, 32, 42 and 54 cm. respectively.

being of the order of 8–10 cm. This constancy is of considerable significance and is conceivably evidence for a uniform growth rate and a uniform spacing of the breeding seasons. The latter seems more or less established already, but there is no certainty about the former.

The more abundant group throughout the whole period spent at sea has been the 42 cm. one. This could mean that the year in which they were hatched was a very favourable one for survival, and that the present abundance is a direct reflection of this. It is much to be regretted that length statistics were not continued for another year at least, for presumably such investigations would furnish data regarding the rate of growth.

Under present limitations we are debarred from utilizing an extremely useful method of attack for this problem, viz., liberating large numbers of marked fish and keeping a careful record of time and place of recapture, together with any increment in size which has occurred in the meantime. It would be impossible to conduct such operations unless arrangements for special cruises were made. The trawl would need to be used differently, and plenty of time would be necessary. At present the obvious aim of the trawler is to catch as much fish in the shortest possible time, and few, if any, of the flathead are in a suitable condition for reliberation after a three or four hour trawl.

There is some indication that certain age groups may remain in the same locality for long periods. Thus the curves based on measurements of Cape Everard flathead were always alike in character, exhibiting the single large "peak" at 42 cm., whilst measurements made in the shallow water (30–35 fathoms) off Eden showed a far higher proportion of smaller sizes than did corresponding series from deep water (60–65 fathoms) in the same locality. This tendency for a particular size of flathead to remain on the same ground for long periods has been known to the trawler men for years, and they described it to the author by saying, for instance, that "you get a different class of flathead at Eden from the one at Newcastle". Incidentally, in connection with the latter locality, the prevailing belief is that the flathead taken there are always very large. When the writer paid his one and only visit there in November, 1930, the average size was decidedly high, so much so that the curve showed its maximum at the 54 cm. mark. However, the Newcastle area is only visited for a few weeks towards the end of each year when the fishing becomes good, and it is impossible to say whether the average size remains high throughout the year.

Large flathead are also supposed to be the rule at Botany and on the New Zealand ground, but this is not always so. For instance, in September, 1930, there occurred an amazing influx of very small flathead into the Botany area. This is reflected in the curve (see Text-fig. 8) which has two peaks, one at 24 cm. and the other at 32 cm. Beyond the latter point, the curve "flattens out" considerably, indicating a relative scarcity of the larger sizes.

The length determination on another occasion provided important confirmation of a major migratory movement connected with the breeding season. In August 1930, a cruise was made to the Moruya-Tollgate area, where an extensive series (5,771) of measurements was made. The curve based on these confirmed the observation that small flathead, i.e., less than 40 cm., were in the majority, being present to the extent of 61% of the total. The larger flathead with developing ovaries were thus by no means plentiful. On the following cruise (late September), however, which was also made to this ground, a marked change was observed to have occurred. The curve showed that the average size had gone up very considerably, fish of less than 40 cm. now being present to the extent of 14% only of the total. Large numbers of females with ovaries in an advanced state of development were taken each haul, and it was obvious that oviposition would occur in a relatively short time. The increase in average size was such as would be noticed even by a casual observer, but it was interesting to obtain such exact and striking confirmation of the fact. Further mention of this event will be made in a paper on the breeding habits and food of the tiger flathead.

General Summary and Discussion.

Comparison of fishing statistics of the years 1918–23 with those of 1930 has revealed a considerable falling off in the hourly yield of flathead. This falling off has been particularly noticeable on the grounds near Sydney, and is also marked in the other areas exploited. The trawling industry has been considerably affected thereby.

Extensive length measurements of the tiger flathead have been made on trawlers over a period of twelve months, and from many localities. These measurements have served to demonstrate the possible occurrence of "age groups" in the flathead. A composite curve has been drawn and shows four well defined "peaks" separated by approximately equal intervals. The curve is incomplete in that data regarding flathead from 1–20 cm. length are lacking.

The minimum lawful size for marketable flathead is twelve inches, and our measurements show that the flathead caught by the trawlers belong to ages extending over a period of probably four years, as indicated by the four peaks on the composite curve. If the first peak corresponds to an age of 'x' years, then the ages of the succeeding groups of these commercially valuable fish are x + 1, x + 2 and x + 3 years respectively.

The importance of the results from the measurements lies in their use for purposes of comparison. The majority of flathead caught in 1930 fall into the 42 cm. group, but in future years it may be found that the group above or the one below is the predominant one. Such a situation would permit of certain definite deductions regarding migration or overfishing.

A series of curves taken at different times in the same locality reveal the tendency for an age group to remain on the same ground for long periods. The curves also reveal a tendency for the fish to shift about in age groups and have, in two cases, served to provide a pictorial record of important migratory movements, but owing to the shortness of the period investigated do not furnish immediately conclusive data regarding overfishing (see above). The latter has often been quoted as one of the prime causes for the present scarcity, and such a view may have some justification, seeing that we have been removing fish from our coastal waters at an enormous rate.

To quote Dakin (1931): "The present New South Wales grounds all added together are only equal to about two-thirds of the Irish Sea—the area of water between Ireland and England, and this from the point of view of steam trawling is nothing more than a huge lake. Discussions are frequent in Europe on the impoverishment of the Irish Sea and North Sea. Well, we have removed from our coastal area by trawling alone four times the catch that the Irish Sea has provided in the same time with its far more boats and men. In 1927, 10,763,600 lb. of fish were trawled from New South Wales waters, to say nothing of the huge estuarine catch."

If, however, overfishing has not been the prime cause and the tiger flathead have, for instance, moved to less disturbed localities, one is led to inquire where they may still be found. It has been suggested, in the face of considerable opposition, that the deeper waters off our coast, i.e., beyond the 100-fathom line, may prove of much importance in the future development of the industry. Unfortunately, evidence on this point is extremely meagre, but the few experiments which have been carried out have produced decidedly interesting results, and it is considered that further research along these lines is desirable. The field is a very extensive one, for apart from our comparative ignorance of the ocean currents, accurate information on the subjects of depths and the nature of the bottom is also lacking.

Experiments on the possibilities of the deeper waters have been very few on account of lack of adequate equipment and also of the necessary finance. In 1920 the Government trawler '*Gunundaal*', under the command of Captain J. Forder, made a few hauls in depths ranging from 100 to 170 fathoms at a station some 15–18 miles NW/W of South Head, on a sandy bottom. The net was drawn for a total period of 39¼ hours and 4,960 lb. of edible fish were taken. The principal species caught were the same as those which occur in shallower waters, viz., cucumber fish (*Chlorophthalmus nigripinnis*), sawfish (*Pristophorus cirratus*), skate, leatherjacket, john dory, morwong and "flathead". Apparently the term flathead applies in part at least to the deep sea flathead (*Hoplichthys haswelli*).

This beginning, though small, was at least promising, but the experiments were discontinued. Other isolated attempts in recent years have been made to test the possibilities of these deep sea grounds, and they too, although providing interesting results, were not followed up. In the year 1928 a few hauls were made in the deep water off Sydney Heads by one of the privately-owned trawlers. One "tow" of one hour's duration produced no less than one hundred baskets of cucumber fish (*Chlorophthalmus nigripinnis*), one of the choicest edible fish taken by the trawlers, yet usually discarded because of comparatively poor keeping qualities. Taken together, these results, meagre though they be, show that the deeper waters have distinct possibilities as trawling areas, and their fuller investigation should yield data of much importance in the future development of the industry.

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NOTES ON AUSTRALIAN ORCHIDS.

A REVIEW OF THE GENUS CYMBIDIUM IN AUSTRALIA. I.

By the Rev. H. M. R. Rupp, B.A.

(Four Text-figures.)

[Read 18th April, 1934.]

It was my purpose to attempt a review of one species only in this genus—the variable and perplexing *C. canaliculatum* R.Br.—but Dr. R. S. Rogers having suggested that all the known or alleged Australian forms of *Cymbidium* should be included, and having sent me valuable notes on the subject, I have endeavoured to comply. In addition to the assistance received from Dr. Rogers, I am greatly indebted to the following: The Government Botanists of Queensland and Victoria, the former for sending flowers of all forms represented in the Brisbane Herbarium, and the latter for the loan of all the specimens of *C. canaliculatum* in the Melbourne Herbarium; Mr. E. Nubling, Sydney, who went to a great deal of trouble to supply information from sources not accessible to me; Mr. W. F. Tierney, Cairns, who has forwarded generous supplies of living racemes of all North Queensland forms he could obtain; Mr. E. Cheel, Curator of the National Herbarium at Sydney, for useful notes; Messrs. W. H. Nicholls, F. A. Weinthal, Lieut.-Col. B. T. Goadby, and Mesdames C. A. Messmer and Edith Coleman. I must also mention Mr. C. Barrett, who brought to light what appears to be Mueller's *C. Hillii* when I had almost abandoned hope of any information about it.

For a long time past, difficulties have been encountered in connection with several Australian species. Of two of these, Fitzgerald's *C. gomphocarpum* and Klinge's *C. queenianum*, I have been unable up to the present to obtain any data whatever beyond the scanty information hitherto available. In regard to the supposed occurrence of *C. giganteum* Wall. in Australia (*Orchid Review*, Feb., 1928, p. 39, art. by E. Cooper), the evidence presented by the writer is that he had seen a plant of *C. giganteum* in flower in an English nursery, which had been "shipped from Sydney and so probably collected in Queensland." The above evidence is far from convincing in view of the fact that, so far as I can ascertain, no Australian botanist has ever recorded the occurrence within the Commonwealth of any member of the section Iridorchis to which *C. giganteum* belongs. In a fernery at Gosford, N.S.W., Mr. H. Cambourne has a Cymbidium which he secured from a collector who stated that it came from the Clarence River, N.S.W. This plant certainly belongs to no species hitherto recognized as Australian; and it may prove to be a member of the section Iridorchis, though I do not think it

is *C. giganteum*. Mr. Cambourne is endeavouring to trace its origin, and to ascertain whether or not it is really a native of the Clarence forests.*

Reference to early standard works on the Australian flora shows that the number of recognized species of *Cymbidium* has fluctuated. Robert Brown, in his Prodromus, described four—*C. canaliculatum*, *C. suave*, *C. reflexum*, and *C. pictum*. Lindley transferred the two last-named to the genera *Liparis* and *Geodorum* respectively. Brown alludes to a *C. squamatum* of Swartz, referring it to the genus *Dipodium*, of which it is a New Caledonian species. In 1839 Allan Cunningham (*Bot. Reg.*, 1839, Miscell. 34) described a species of *Cymbidium* from the Brisbane River, Queensland, under the name *C. iridifolium*. Now in 1832 Roxburgh (*Fl. Ind.*, 3, 458) had described an Indian orchid under this name, but it had been transferred by Lindley to his genus *Oberonia* (see Oakes Ames, "Orchidaceae", Fasc. I, 1905). *Oberonia iridifolia* is a small epiphyte recorded from India and Siam, through the Philippines, Malay Archipelago, and Australia, to Polynesia. It occurs in New South Wales. Cunningham's *Cymbidium iridifolium* is a very different plant, and his description is undoubtedly that of the species named by Mueller in 1859 *C. albuciflorum*. Why Cunningham's name was not recognized is not clear. In the year following his description, Lindley (*Bot. Reg.*, 1840, Miscell. 9) described a species under the name *C. madidum*, which appeared in publication as an East Indian plant. In 1889 R. A. Rolfe, wondering why it had never been recorded from the East Indies again during 50 years, examined Lindley's type and found it to be the Australian *C. albuciflorum* F.v.M. It seems strange that Lindley, who had transferred Roxburgh's *C. iridifolium* to the genus *Oberonia*, should have missed Cunningham's adoption of that name. It is clear, however, that Cunningham's description (which is quoted later in this review) is the earliest of the three which this *Cymbidium* received, and by the rule of priority we must abandon Mueller's name in favour of *C. iridifolium* Cunn.

Bentham (*Fl. Austr.*, vol. vi, 302) recognized only three Australian species—*C. canaliculatum* R.Br., *C. albuciflorum* F.v.M., and *C. suave* R.Br. Since then others have been described or reported, several of which have been reduced to varieties vaguely or not at all recognized. Two of the older species have proved so variable that identification has been rendered very difficult in view of their divergence from the original descriptions. In this review I have attempted to clear up the confusion which has resulted in regard to these forms.

Whatever may finally prove to be the number of valid species occurring in Australia, we may safely conclude that in future only such plants will be included as conform to the peculiar habit of life which we have come to associate with the genus *Cymbidium*. What is said on this point is based upon knowledge of Australian species only. Our Cymbidiums are commonly classed as epiphytes, but there is an important difference between their habit of life and that of our other epiphytes. Cymbidiums usually inhabit trees which from one cause or another have developed decay in the woody substance of trunk or branches.

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* Since the above was written, this plant has proved to be the Indian *C. loweanum*. Mr. Paine, of Exotic Nurseries, Ltd., of Dee Why, N.S.W., writes that he discovered it, with other plants, near Stockyard Creek, an affluent of the Clarence. There was, however, strong evidence that the orchid had originally escaped from the plant-house of an old homestead, long demolished. Mr. Paine, who was trained at Kew Gardens, is of the opinion that it is not indigenous; and other non-Australian plants, including two ferns, were found near by.

A Cymbidium seed lodges in a crack, or in the cavity left by a rotted branch, and germinates there. The roots, which are succulent, but also strongly fibrous, penetrate into the hollow formed by decay; and finding their nourishment—no doubt chiefly through the agency of mycorrhiza—in the humus composed of decayed wood, gradually follow the line of decay down the hollow trunk or branch. Roots have been reported more than 30 feet in length, and I have seen a hollow branch completely filled by them. Since the hollows of trees are capable of retaining moisture for a long time, we have here the probable explanation of the fact that *C. canaliculatum* is able to flourish in dry and arid regions where one would not expect epiphytes. The explanation, however, does not account for the fact that this species is equally at home in the rain-forests from which its fellow-species rarely stray for any distance.

With the exception of *Dendrobium speciosum* Sm., Cymbidium plants attain greater dimensions than any of our other orchids; "clumps" of *C. canaliculatum* not infrequently weigh more than a hundredweight. Some are most prolific bloomers. I estimated the number of individual flowers on a large plant of *C. canaliculatum* which bore 103 racemes, at 6,183. The number of fertilized seed-capsules is relatively very small, 81 being the maximum counted in my own experience. As the capsules are large and the seeds are extremely minute, the number of seeds produced by 81 capsules baffles calculation. I have not been able to discover by what agents fertilization is effected, but it is safe to assume that insects are mainly responsible. Wind is almost certainly the chief agency of distribution. In the Pilliga Scrub, on the north-west plains of New South Wales, I found two very large clumps of *C. canaliculatum*. In both cases younger plants were plentiful for some distance, in the direction of the prevailing winds only.

The range is imperfectly known. No Cymbidium has been found in Tasmania, Victoria, South Australia, or the southern half of Western Australia. The majority of species are restricted to the rain-forests of Eastern and Northern Australia, from Mount Dromedary on the South Coast of New South Wales, at least as far as Roebuck Bay in the north-west of Western Australia. One species extends upwards of 200 miles inland.

In addition to the two species mentioned above (*C. gomphocarpum* Fitzg. and *C. queenianum* Klinge) concerning which I have been unable to procure particulars, the following species are recognized as valid in this review: *C. canaliculatum* R.Br., *C. Hillii* F.v.M., *C. Leai* Rendle, *C. iridifolium* Cunn., *C. suave* R.Br.

These will now be considered in detail in the order given.

1. Cymbidium canaliculatum R.Br.

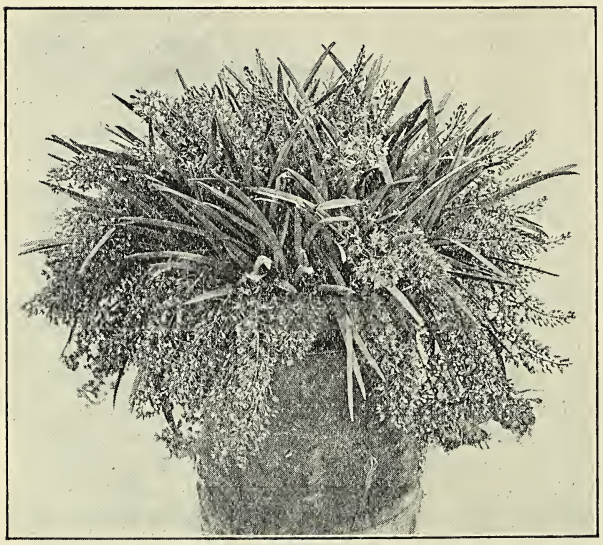
Prodr., 331; Lindl., *Gen. and Spec. Orch.*, 164; *Bot. Mag.*, t. 5851; Benth., *Fl. Austr.*, vi, 302; Bailey, *Q. Fl.*, 1547. (*C. Sparkesii* Rendle.)

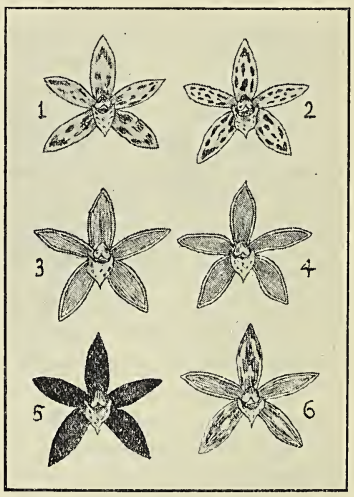
The protean character and remarkable distribution of this species make it of special interest among Australian orchids. It exhibits such striking variations in the colour-scheme of the flowers, and in the colours themselves, that in some instances one is extremely reluctant to deny specific distinction between flowers so dissimilar in appearance. This dissimilarity has undoubtedly been the cause of confusion and perplexity. With the exception of A. B. Rendle, no botanist appears to have ventured to isolate any of these variants. Rendle took a spectacular North Queensland form with flowers of such intensely deep maroon as to appear jet black in reflected light, and erected it into a species under the name *C. Sparkesii* (*Journ. Bot.*, xxxvi, 221; and xxxix, 197). After careful

examination of living racemes sent by Mr. W. F. Tierney, of Cairns, in 1932 and 1933, I conclude that Bailey (*Q. Fl.*, 1547) is right in absorbing *C. Sparkesii* in *C. canaliculatum*. I can find no structural feature justifying specific separation, but it certainly seems that a form of such strikingly distinctive appearance should receive varietal recognition, and I propose to restore Rendle's name to varietal rank. Bailey further includes in *C. canaliculatum*, Rendle's *C. Leai;* but here I cannot follow him. *C. Leai* will be discussed later on.

It has been widely assumed that Robert Brown's type form of *C. canaliculatum* is represented in the coloured plate of *Bot. Mag.*, t. 5851 (1870). This plate shows flowers with the perianth segments externally almost greyish, internally bright brown with a narrow marginal border of pale green. The plant was collected by John Veitch at or near Cape York. It is a form which, so far as I can ascertain, is restricted to the far north of the continent. Mr. Tierney has sent living specimens from Cairns which agree with the plate, except that the exterior of the flowers is rather pale brown than grey. But I can find no evidence that Robert Brown collected the species elsewhere than at Broad Sound (see Benth., *Fl. Austr.*, vi, 302), more than 400 miles south of Cairns and more than twice as far from Cape York. Some of the dried flowers sent to me from the Brisbane Herbarium came from the neighbourhood of Broad Sound; and they agree very well, not with Veitch's form, but with one which is very abundant in southern Queensland and over large areas of New South Wales. This I believe to be the type, and Veitch's form will be treated here as a variety.

At this stage it may be well to refer to a point of some difficulty in Brown's original description of the species. He uses the expression "apice trilobo" of the





Text-fig. I.—*Cymbidium canaliculatum* R.Br.—A plant with 103 flowering racemes. (G. E. Geggie, photo.)

Text-fig. II.—*Cymbidium canaliculatum* R.Br. Flowers from the front, to illustrate the classification proposed in this paper. 1, Type, forma *inconstans*; 2, Type, forma *aureolum*; 3, Var. *marginatum*, forma *fuscum*; 4, Var. *marginatum*, forma *purpurascens;* 5, Var. *Sparkesii;* 6, an intermediate between 1 and 3.

labellum. Hooker (commenting on the plate in *Bot. Mag.*) remarks that Veitch's plant apparently differs from Brown's in having the labellum lobed about the middle, not at the apex. Now if we regard the apex of the so-called mid-lobe as the apex of the labellum itself, not only is Hooker's distinction justified, but Brown's expression describes a form of labellum which—as far as I can ascertain—is unknown in this species to any present-day observer. But it seems to me more likely that Brown, accepting the definition of the labellum as "trilobate", regards the point where lobation begins as the apex of the labellum proper—the portion in front of that point being merely the mid-lobe. If this interpretation of "apice trilobo" be adopted, Hooker's distinction disappears and the difficulty is dissolved. I venture to question whether we ought not to revise our conception of the labellum found in several Cymbidiums and Caladenias as "trilobate". The recognition of a mid-lobe seems artificial and unnecessary. In a labellum such as that of *C. canaliculatum* the impression obtained by examination is that of a continuous lamina with a small lateral lobe on either side. However, grant trilobation, and Brown is correct in locating the apex of the labellum proper at the point which Hooker considered the middle.

With a view to attempting some satisfactory tabulation of the outstanding variations in *C. canaliculatum*, I have examined some hundreds of specimens, living and dried, from many districts in New South Wales and Queensland, the Northern Territory, and the north-west of Western Australia. The need for such tabulation lies in the fact that, despite structural identity, the chief variants differ from one another so greatly in appearance as to suggest specific distinction at once. I am aware that to make colour-scheme and colour itself the bases for tabulation, is to invite challenge; yet in the present case I am convinced that this course is amply justified, and will serve to simplify questions of identity. I propose, therefore, to subdivide the species thus:

C. canaliculatum R.Br.

1. TYPE.
   (*a*) Forma *inconstans*.
   (*b*) Forma *aureolum*.

2. Var. MARGINATUM, var. nov.
   (*a*) Forma *fuscum*.
   (*b*) Forma *purpurascens*.

3. Var. SPARKESII. (*C. Sparkesii* Rendle.)

Before discussing these groups those features are described which they all possess in common. *C. canaliculatum* forms large "clumps" on trees, the numerous stems being short, densely packed together, and covered by the fibrous remnants of the bases of old leaves. At its growing end the stem is concealed by the appressed sheathing bases of the living leaves, which form with it an ovate pseudobulb. The leaves (3 to 6) range in length from 20 to more than 60 cm., and in breadth from 2 to 5 cm. They are thick, rigid, tough and fibrous in texture, usually acute at the apex, and deeply channelled along the ventral surface. The racemes (1 to 4 on a stem) are borne between or below the living leaves; maximum length about 40 cm.; number of flowers from 20 to 100. Capsules 4½—6 cm. long, scarcely half as broad, crudely resembling small bananas. In New South Wales the seeds do not ripen for many months. Flowers 2½—3½ cm. from tip to tip of fully expanded segments, petals slightly smaller than sepals. All perianth segments (including labellum) acute or obtuse,

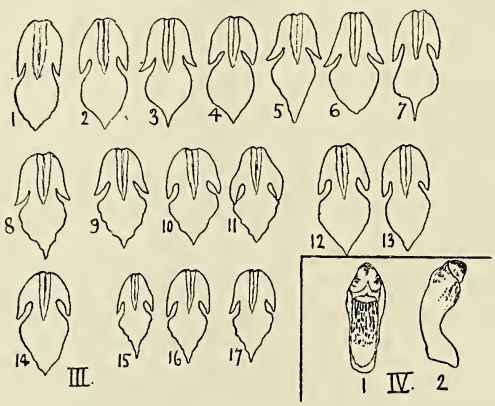
varying in this respect even on the same raceme. Labellum hardly as long as petals, consisting of a continuous lamina slightly dilated anteriorly (the "mid-lobe"), and with a small lateral lobe of varying contour on either side near the middle of the whole segment. Basal portion of lamina with 2 median longitudinal ridges, more or less ciliate in front, extending to the level of the lateral lobes. Column rather stout, usually loosely embraced by the lateral lobes of the labellum.

The slight variations from the above description are not sufficiently constant or important to merit notice. Only when we come to the distinctions of colour-scheme and colour itself, are we on safe ground in attempting to group the variants. It is in connection with the sepals and petals that these distinctions are most striking and most reliable. Certain forms have a colour-scheme quite different from that of others: within the unity of this scheme there may be diversity of actual colour. Except in var. *Sparkesii* the labella are not dissimilar to any great extent, and the exception is only one of colour.

1. The TYPE.—Sepals and petals outside brownish or green: inside, from dull to golden-yellowish-green, blotched, flaked, or spotted with brown or red. Labellum white with small purple or red markings: sometimes with suffusions of green.

(*a*) Forma INCONSTANS. This I believe to be the actual type as collected by Robert Brown.—Sepals and petals outside brown or green: inside dull to light green with heavy brown blotches or flakes. Labellum usually white with purplish dots. Sometimes the brown blotching has purple tints.

Range: Widely distributed from the Hunter River northward in New South Wales, from the coast to the western slopes (inclusive): spread over a corresponding area in Queensland at least as far north as Broad Sound. Possibly extending to the Northern Territory and the North-West; but while it is difficult



Text-fig. III.—*Cymbidium canaliculatum* R.Br. Outlines of labella to show variations. 1-7, Type, forma *inconstans*: 1, Cairns, Q.; 2, Rockhampton, Q.; 3, Brisbane River, Q.; 4, Tamworth, N.S.W.; 5–7, Hunter River, N.S.W.; 8, Type, forma *aureolum*, Pilliga, N.S.W.; 9–11, herbarium specimens referred to this form by the author: 9, Settlement Creek, Q.; 10, Roebuck Bay, W.A.; 11, Cambridge Gulf, W.A.; 12–13, Var. *marginatum*, f. *fuscum*, Cairns, Q.; 14, Var. *marginatum*, f. *purpurascens*, Brisbane River, Q.; 15-17, Var. *Sparkesii*: 15, Hughenden; 16, Mareeba; 17, Port Denison; all in Q.

Text-fig. IV.—*Cymbidium canaliculatum* R.Br. Column of Type. 1, Front; 2, Side.

to be sure of dried specimens, I am disposed to refer the Melbourne Herbarium flowers from those parts to the next following form.

(*b*) Forma AUREOLUM.—Sepals and petals outside almost bronze-hued; inside bright golden-yellowish-green with heavy red blotches or flakes, or red spots. Labellum purer white than in (*a*), with red dots or other marks. This form has a very distinctive appearance.

Habitat: Chiefly on the far western plains of New South Wales and Queensland; reported as far south as Forbes. Perhaps extending to the north-west of the continent: see under (*a*) above. Occasionally but rarely seen near the New South Wales coast.

2. Var. MARGINATUM, n. var.—Sepala petalaque extra fusca vel glauca, intra immaculata, cum marginibus viridibus. Sepals and petals outside brownish or glaucous: inside unicoloured, with a narrow marginal border of light green.

(*a*) Forma FUSCUM.—This is the Cape York form (*Bot. Mag.*). Sepals and petals outside as described above: inside clear brown with light green marginal border (occasionally wanting). Labellum whitish with green suffusions and red spots.

Habitat (so far as at present known): Cape York southward at least as far as Mt. Garnet, Queensland.

(*b*) Forma PURPURASCENS.—Sepals and petals outside somewhat glaucous: inside, bright or deep magenta with light green margins. Labellum whitish with red or purple spots. What I have called "magenta" is viewed by one correspondent as cerise, by another as purplish-red. For the elucidation of some mystery about this beautiful form I am indebted to Messrs. W. H. Nicholls and F. A. Weinthal. I had seen it once in cultivation, and heard of it several times, but could not trace its habitat. Mr. Nicholls sent a colour-sketch of a flower received from Mr. Weinthal, which I recognized at once. Mr. Weinthal informs me that he obtained plants from the head of the Brisbane River in Queensland. I have since received another definite record of it from Mr. K. Macpherson, Proserpine, North Queensland.

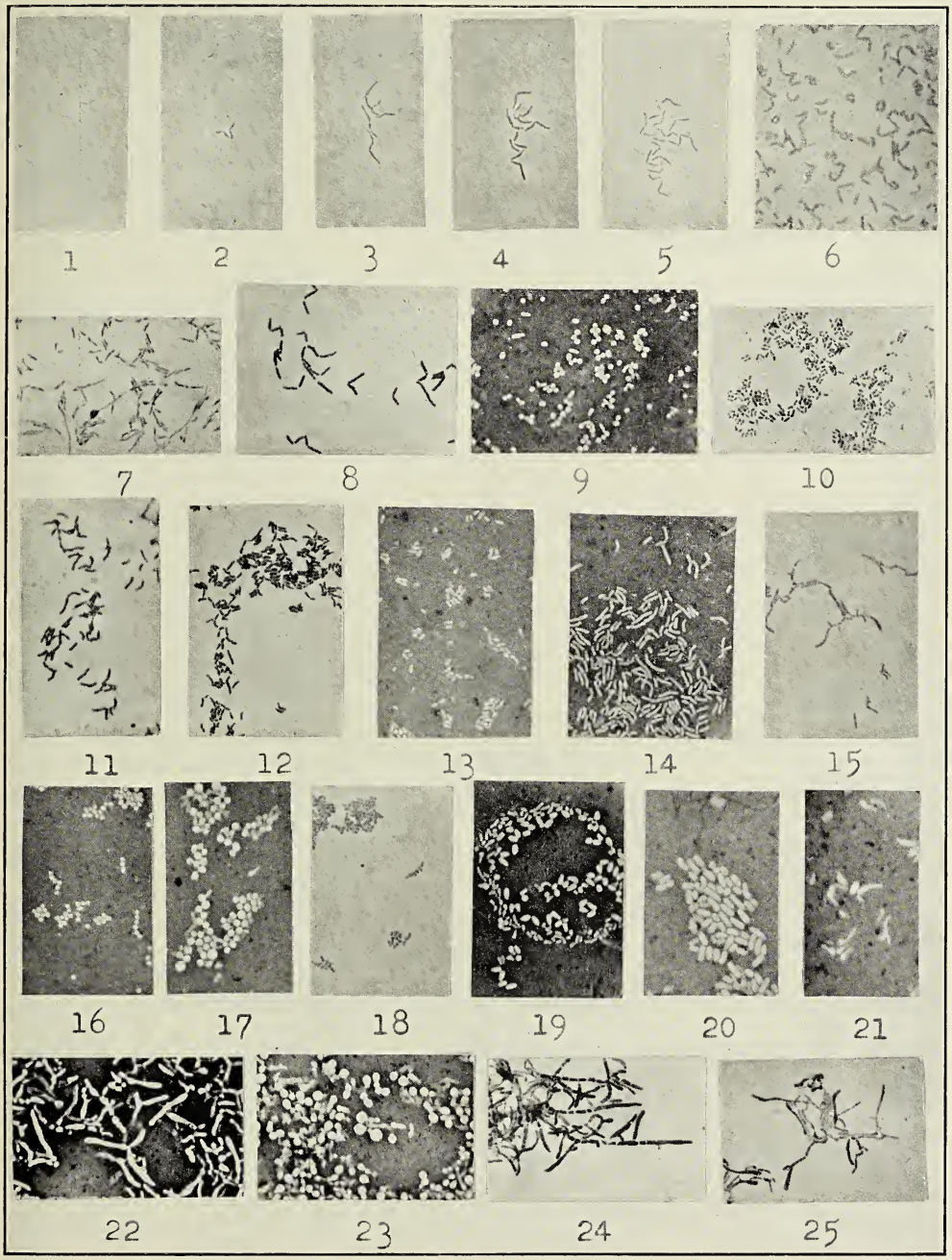
3. Var. SPARKESII (*C. Sparkesii* Rendle).—Sepals and petals wholly intensely-deep maroon, appearing black except when viewed by transmitted light. Labellum pink with a green base and crimson spots, or with heavy suffusions of dark red.

Habitat: Queensland coastal forests north of Townsville, and probably in some other areas of the tropics. Specimens sent to me by Mr. Tierney (Cairns) originally came from Mareeba. A Hughenden specimen in the Brisbane Herbarium seems to belong to this form, to which I am also disposed to refer flowers in the Melbourne Herbarium collected by G. F. Hill at Borroloola, N. Aust. Though not the most beautiful, this is the most striking form in the species, its jet-black appearance in reflected light giving it an almost uncanny aspect. Rendle remarks (*loc. cit.*) on the weird impression of its sombre hue in its habitat.

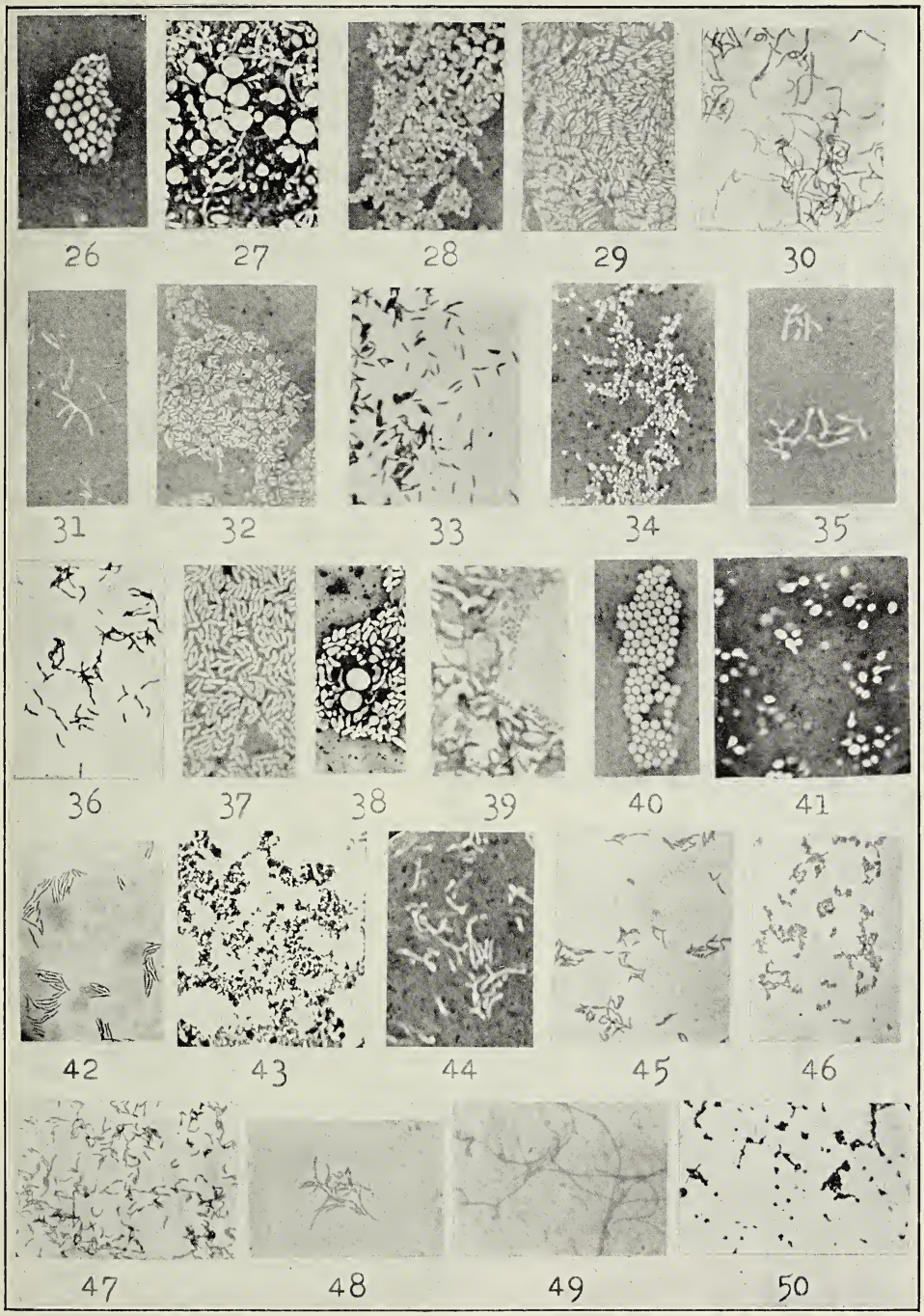
In the Sydney Herbarium there is a specimen from Lismore, New South Wales, labelled *C. canaliculatum*, which is rather puzzling. The general appearance of the raceme is typical, but the labellum suggests an approach to *C. iridifolium* Cunn., and the leaves are very similar to those of the latter. Living material of this plant is very desirable. A white-flowering form of *C. canaliculatum* has been reported from several districts: in one instance my informant had it growing and sold it. I have been unable to obtain any specimens, and can do no more than record the reports.

C. canaliculatum has a strong tendency to produce abnormal flowers; "double" flowers are frequently seen, and I have one which is really a compound of four. The four labella are all perfect. In these compound flowers a lateral sepal of one is often joined back-to-back with a similar segment of another.

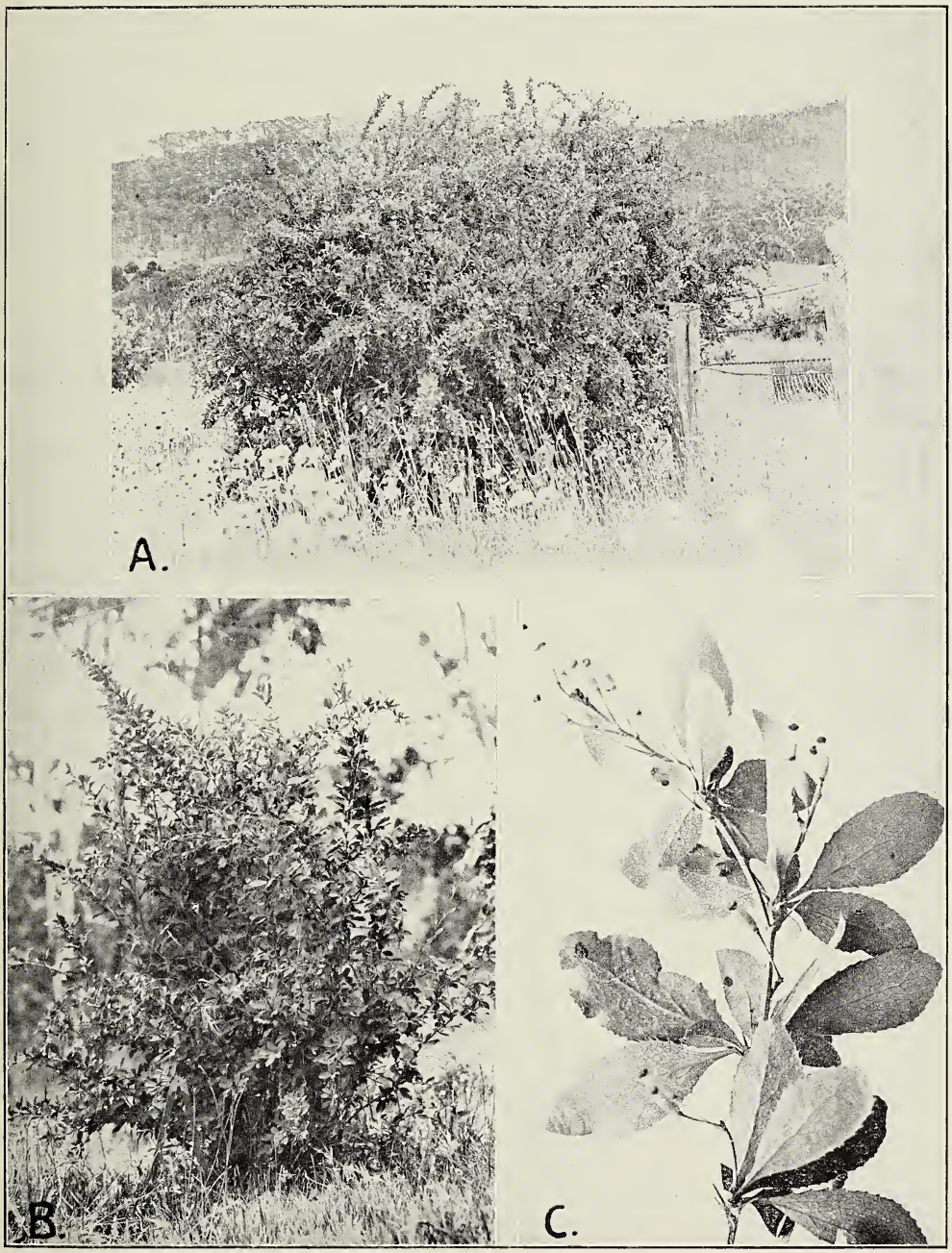
It must be understood that the varieties and forms named above are, at least in some instances and possibly in all, more or less connected by intermediates. Thus Mr. Tierney has sent a Cairns raceme which might be placed either in the form *inconstans* of the type, or in the form *fuscum* of var. *marginatum*: even in individual flowers, one or two segments suggest the latter, while the others agree better with the former. Similarly, the two forms of the type occasionally approach one another very closely.



Species of *Mycobacterium* (1-10) and *Corynebacterium* (11-25).



Species of *Corynebacterium* (26-47); and *Proactinomyces*-like Organism (48-50).



Barberries showing infection by Black Stem Rust.

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PROCEEDINGS, 1934, PARTS 1-2.

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Corrigendum (PROCEEDINGS, 1933, Parts 5–6.)

Page 468, lines 13, 17, for *Euchytra*, read *Enchytra*

(Issued 15th September, 1934.)

Vol. LIX.
Parts 3-4.

Nos. 253-254.

THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1934.

Parts III–IV (Pages 101–275.)

CONTAINING PAPERS READ IN MAY-AUGUST.

With four plates.

[Plates iv-vii.]

SYDNEY:
PRINTED AND PUBLISHED FOR THE SOCIETY BY
AUSTRALASIAN MEDICAL PUBLISHING CO., LTD.,
Seamer Street, Glebe, Sydney,
and
SOLD BY THE SOCIETY,
Science House, Gloucester and Essex Streets, Sydney.

1934.

PRICE 8/6.

Registered at the General Post Office, Sydney, for transmission by post as a periodical.

Agent in Europe:
Messrs. DULAU & Co., 32 Old Bond Street, London, W.1.

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CONTRIBUTIONS TO THE MICROBIOLOGY OF AUSTRALIAN SOILS. I.

NUMBERS OF MICROORGANISMS IN SOIL, AND THEIR RELATION TO CERTAIN EXTERNAL FACTORS.

By H. L. Jensen, Macleay Bacteriologist to the Society.

(Three Text-figures.)

[Read 30th May, 1934.]

Introduction and Methods.

Very little work has yet been devoted to a systematic study of the microflora of Australian soils, apart from the mainly physiological work by Greig-Smith (1910–18) on special groups of soil bacteria and protozoa, and two contributions by Dixon (1928–30) dealing almost only with the types of fungi occurring in Victorian soils. The present work represents an attempt to study the soil microflora on a broader basis, starting with an investigation of the numbers of bacteria, actinomycetes and fungi in soils of different types and in their relation to certain external factors, especially moisture and temperature.

Since it was desired to compare the numbers of microorganisms, the method of plate counting was used in spite of its serious limitations (especially the fact that its results represent only a fraction of the total soil microflora), because this method is the only one yet capable of giving numerical expressions for the soil fungi and actinomycetes. Bacteria and actinomycetes were counted on the following agar medium: dextrose 2·0 gm.; casein, dissolved in 0·1n NaOH, 0·2 gm.; K_2HPO_4 0·5 gm.; $MgSO_4$ 0·2 gm.; agar 20·0 gm.; H_2O 1,000 c.c.; pH 6·5–6·6. Dilutions of 1 : 50,000 to 1 : 250,000 were used, according to the character of the soil, and 4 to 5 parallel plates were incubated for 7–8 days at 28°C.* Fungi were counted on an agar medium of the following composition: dextrose 10·0 gm.; asparagine 1·0 gm.; KH_2PO_4 2·0 gm.; $MgSO_4$ 0·5 gm.; NaCl 0·5 gm.; agar 25·0 gm.; H_2O 1,000 c.c.; pH 4·6–4·8. Dilutions of 1 : 4,000 to 1 : 20,000 were used, and 4 to 5 parallel plates were incubated for 4–5 days at 28°C. The final dilutions for both platings were made up from the same soil suspension, prepared by shaking 20 grams of fresh soil for 4 minutes with 200 c.c. of sterile tap water. The total amount of data was tested for the χ^2 distribution, according to Fisher (1930): if the plate counts have given a reliable picture of the density of microorganisms counted, the index of dispersion, χ^2,† shall be distributed in a known manner, and if one, as here, is dealing with sets with a variable number of parallel plates,

* This somewhat high temperature of incubation was chosen because of the difficulty of keeping a lower constant temperature during the summer months.

† Calculated by the formula : $\chi^2 = \frac{S(x-\bar{x})^2}{\bar{x}}$, where x is the number of colonies counted on each plate, $\bar{x}$ the mean, $S(x-\bar{x})^2$ the sum of the squares of the deviations from $\bar{x}$.

the difference $2S(\chi^2) - 2S(n) - 1$ (where $S(\chi^2)$ is the sum-total of all the values of χ^2, n the number of parallel plates minus 1, and S(n) the sum-total of all the values of n) shall not materially exceed 2·0. The following results were found:

Bacteria.	Actinomycetes.	Fungi.
$S(\chi^2)$: 346·23	$S(\chi^2)$: 279·0	$S(\chi^2)$: 285·21
S(n) : 342	S(n) : 342	S(n) : 327
Difference : 0·18	Difference : − 2·51	Difference : − 1·67

While the result for the bacteria is entirely normal, there is, in the case of the actinomycetes, a tendency to subnormality (cf. Jensen, 1931*b*), but since the difference is not very great, we may be justified in regarding the majority of the actinomyces-counts as reliable. The difference for the fungi is within the permissible limits, and the technique must therefore be considered as giving a reliable index of the numbers of mycelial fragments and fungous spores capable of developing on the medium used.

The reaction of the soils was measured colorimetrically. Water content was determined by drying at 96–98°C. Organic matter was determined by ignition, and the water-holding capacity by the simple method described by Christensen (1923); neither of these two methods is very accurate, but their results may be used for comparative purposes, as was the main consideration in this case.

A. *Numbers of Microorganisms in Various Soils from New South Wales.*

The following 50 soils were examined:

1. Light sand soil, poor in humus, grass-covered, under bushes, Cooper Park, Sydney.
2. Heavy loam, rich in humus, flower-bed, Sydney University.
3.* Sand-mixed humus soil, Glen Innes, N.S.W.
4.* Red clay, poor in humus, Griffith, N.S.W.
5.* Red sandy loam, poor in humus, Cowra, N.S.W.
6.* Alluvial clay, fairly rich in humus, Bathurst, N.S.W.
7.* Red-brown loam, poor in humus, Griffith, N.S.W.
8. Heavy loam, rich in humus, flower-bed, Sydney University.
9.* Red loam, poor in humus, Griffith, N.S.W.
10.* Red loam, poor in humus, Griffith, N.S.W.
11. Heavy loam, very rich in humus, from pot experiments, School of Agriculture, Sydney University.
12.* Light sand soil, poor in humus, Goulburn, N.S.W.
13.* Sandy loam, very rich in humus, Scone, N.S.W.
14.* Red sandy loam, poor in organic matter, Temora, N.S.W.
15. Coarse, dark sand, very poor in humus, Rose Bay Heights, Sydney.
16.* Light sandy loam, poor in organic matter, Goulburn, N.S.W.
17.* Red loam, fairly rich in humus, Griffith, N.S.W.
18.* Light loam, fairly rich in humus, lucerne field.
19.* Light, coarse, gravelly sand, poor in humus, Bathurst, N.S.W.
20. Light loam, rich in humus, sheep pen, McMaster Laboratory, Sydney University.
21. White sand, very poor in humus, grass-covered, Bellevue Hill, Sydney.
22. Clay, rich in humus, almost bare, under trees, Sydney University.
23. Clay, very rich in humus, under trees, Sydney University.
24. Light loam (garden), fairly rich in humus, North Sydney.
25. Sand, very poor in humus, under bushes, Rose Bay Heights, Sydney.
26. Sand, rich in humus, grass-covered, Rose Bay Park, Sydney.
27. Heavy loam, rich in humus, wheat field, St. John's College, Sydney University.
28. Dark sand, fairly rich in humus, under casuarinas, Watson's Bay, Sydney.
29. Clay, poor in humus, Glenfield, N.S.W.
30. Clay, poor in humus, Glenfield, N.S.W.
31. Heavy loam (garden), rich in humus, Richmond, N.S.W.
32. Light loam, garden, very rich in humus, Richmond, N.S.W.
33. Sand, poor in humus, grass-covered, Bellevue Hill, Sydney.
34. Loam, rich in humus, from bush, Wahroonga, N.S.W.

35. Coarse sand, poor in humus, grass-covered, Centennial Park, Sydney.
36. Dark sand, poor in humus, grass-covered, Bronte, Sydney.
37. Dark sand, poor in humus, under casuarinas, Manly, N.S.W.
38. Sandy loam, poor in humus, St. Leonard's Park, North Sydney.
39. Red-brown loam, fairly rich in humus, pasture, Hinchinbrook, N.S.W.
40. Black loam, rich in humus, pasture, Hinchinbrook, N.S.W.
41. Coarse sand, rich in humus, under eucalypts, Ryde, N.S.W.
42. Light loam, rich in humus, grass-covered, Fivedock, Sydney.
43. Light sand, poor in humus, grass-covered, Coogee, Sydney.
44. Dark sand, poor in humus, under bushes, Cooper Park, Sydney.
45. Sand, poor in humus, under ferns, bush, Longueville, N.S.W.
46. Heavy loam, rich in humus, flower-bed, Victoria Park, Sydney.
47. Sand, very poor in humus, under thin grass, Maroubra, Sydney.
48. Heavy loam, very rich in humus, clover field, Ryde, N.S.W.
49. Coarse, dark sand, fairly rich in humus, under heavy grass, Centennial Park, Sydney.
50. Light sand, poor in humus, bush, Wahroonga, N.S.W.

The soils marked * were obtained from the collection of soil samples in the School of Agriculture, Sydney University, through the kindness of Mr. G. Wright, lecturer in agricultural chemistry; these samples were air-dry, and were therefore, prior to examination, kept moist in the laboratory for 15–20 days in order to enable the microflora to reach a certain equilibrium. The others were freshly taken samples from the upper 10 cm. of the soil.

The numbers of microorganisms, together with the pH-values and the contents of water and organic matter, are recorded in Table 1, and the various correlation coefficients which have been calculated from these data in Table 2.

The numbers of bacteria vary within wide limits, from 0·3 to 95 millions per gm. of soil, and are generally similar to those recorded from other parts of the world (Waksman, 1916, 1922; Cutler, Crump and Sandon, 1923; Smith and Worden, 1925; Jensen, 1931*a*). The numbers show a very good correlation with the content of organic matter in the soils; the correlation coefficient amounts to no less than 0·806 (Table 2), which value is not reduced very much when we eliminate the influences of hydrogen-ion concentration and moisture by calculating the corresponding partial correlation coefficients (Fisher, 1930). The bacterial numbers, on the other hand, do not show any significant correlation with the hydrogen-ion concentration,* or with the relative moisture content if the influence of organic matter is eliminated; it is to be noted, though, that this is true only when soils of different character are compared, since periodical counts of bacteria in one and the same soil have revealed a very definite correlation between moisture and bacterial numbers, as will be shown later. We must therefore conclude that the quantity of organic matter is the most important among the factors considered here in determining the numbers of bacteria which are able to develop on agar plates. The disagreement of this result with what was previously observed in Danish soils (Jensen, 1931*a*) is probably due to the fact that the latter series included several typical peat soils, poor in microorganisms but very rich in inert organic matter, a soil type that is not represented in the present investigation. A somewhat abnormal picture is shown by some coarse, acid sand soils, generally poor in humus, from the neighbourhood of Sydney, which all (Nos. 15, 25, 28, 37, 41, 47, 50) have shown bacterial numbers very much lower (0·3–4·2 mill. per gm.) than other soils with corresponding reaction and humus content. This paucity of organisms applies also to the actinomycetes, but not to the fungi. There do not seem to be any notable differences between bacterial numbers in cultivated

* It is of importance to note that the calculations are based on the actual hydrogen-ion concentration, and not on the pH-values.

TABLE 1.
Counts of Microorganisms in 50 Soils of Different Character.

No.	Moisture.		pH.	Organic Matter %.	Bact.[2]	Act.[2]	Fungi.[3]	Ratio A. : B.
	H_2O %.	Degree.[1]						
1	8·3	26·8	4·6	4·5	2·7	3·9	312	1·45
2	21·6	49·1	5·5	13·8	14·8	3·8	160	0·26
3	32·8	56·6	5·3	24·4	95·6	26·1	724	0·36
4	19·3	59·4	6·8	6·1	16·7	3·2	8	0·19
5	10·7	36·0	5·1	2·6	5·6	2·0	29	0·35
6	20·8	53·3	5·2	7·5	11·9	2·7	66	0·23
7	12·9	40·3	5·7	5·0	8·7	2·8	67	0·32
8	21·8	56·6	7·3	13·8	41·6	3·7	120	0·09
9	19·6	50·3	6·1	7·2	13·7	1·9	62	0·13
10	13·3	41·6	6·0	4·6	20·8	10·9	28	0·52
11	26·7	47·7	4·7	16·1	43·8	2·7	451	0·07
12	18·4	43·8	4·9	4·4	29·5	4·8	553	0·16
13	25·1	52·3	6·0	17·4	43·1	35·7	394	0·83
14	10·9	34·1	5·2	3·5	2·5	2·2	68	0·86
15	12·2	70·2	4·8	1·9	0·8	0·3	265	0·35
16	15·1	50·5	4·5	5·0	6·0	10·5	745	1·75
17	19·2	50·6	7·9	10·3	12·7	22·0	24	1·73
18	22·0	57·9	4·9	8·2	30·1	10·3	361	0·34
19	11·7	52·0	5·1	1·4	6·4	3·4	87	0·53
20	19·0	42·2	7·2	12·3	26·8	7·4	114	0·28
21	7·9	33·6	5·1	1·0	6·9	1·8	231	0·26
22	20·9	62·4	6·1	12·1	40·4	5·9	146	0·15
23	32·0	68·8	6·5	19·0	53·2	7·1	664	0·13
24	10·1	27·3	6·9	7·4	21·9	3·0	70	0·14
25	6·2	24·3	5·6	1·6	1·0	1·0	112	0·98
26	22·3	51·8	6·1	10·9	25·9	10·7	310	0·42
27	26·5	64·6	5·6	10·8	16·1	8·0	258	0·50
28	16·8	47·3	5·2	7·4	1·1	0·1	241	0·10
29	19·1	54·6	6·1	6·6	2·7	3·4	65	1·25
30	17·7	49·8	5·9	6·4	9·8	5·8	202	0·59
31	18·4	51·1	6·0	11·6	18·0	4·9	254	0·27
32	24·0	61·5	6·3	16·1	57·3	11·1	350	0·51
33	10·6	34·7	6·3	2·9	4·1	3·7	144	0·90
34	25·0	62·5	5·8	12·6	14·0	3·8	300	0·27
35	18·5	52·1	5·9	4·7	9·4	3·5	131	0·37
36	11·2	32·2	6·4	5·8	10·6	7·8	236	0·73
37	15·3	41·9	5·2	4·8	0·6	0·2	280	0·27
38	8·4	23·6	5·3	6·8	3·5	4·0	227	1·13
39	18·9	45·5	5·4	9·1	19·4	6·8	417	0·35
40	23·6	54·9	5·7	10·4	24·2	9·2	163	0·33
41	18·6	48·3	5·4	11·9	3·3	1·6	403	0·50
42	15·2	38·0	6·6	11·0	30·6	8·7	322	0·28
43	8·3	28·1	5·6	2·6	3·6	3·0	191	0·83
44	13·5	42·2	5·3	4·6	11·2	1·4	284	0·13
45	10·8	31·7	5·5	5·8	7·3	1·8	99	0·24
46	16·8	42·0	7·5	9·8	33·6	4·5	151	0·13
47	4·5	18·2	4·5	1·7	0·3	0·2	98	0·67
48	29·7	64·5	5·7	16·9	49·0	7·0	1088	0·14
49	36·6	89·3	6·0	8·5	55·1	1·1	179	0·02
50	10·6	32·1	5·5	5·8	1·5	0·3	469	0·22

[1] H_2O in % of water-holding capacity.
[2] Millions per gm. of air-dry soil.
[3] Thousands per gm. of air-dry soil.

TABLE 2.

Correlation Coefficients from Counts of Microorganisms in Table 1.

Correlation between	r*	n*	P*	Significance.
Bacteria and Organic Matter, total	0·806	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Hydrogen-Ion Concentration	0·795	47	<0·01	—
(*b*) Degree of Moisture	0·742	47	<0·01	—
(*a*) and (*b*)	0·794	46	<0·01	—
Bacteria and Hydrogen-Ion Concentration, total	−0·211	48	>0·1	Negative.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·054	47	>0·1	—
(*b*) Degree of Moisture	−0·115	47	>0·1	—
(*a*) and (*b*)	0·056	46	>0·1	—
Bacteria and Degree of Moisture, total	0·520	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·256	47	0·1–0·05	Negative.
(*b*) Hydrogen-Ion Concentration	0·496	47	<0·01	Positive.
(*a*) and (*b*)	−0·128	46	>0·1	Negative.
Actinomycetes and Organic Matter, total	0·585	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Hydrogen-Ion Concentration	0·576	47	<0·01	—
(*b*) Degree of Moisture	0·561	47	<0·01	—
(*a*) and (*b*)	0·556	46	<0·01	—
Actinomycetes and Hydrogen-Ion Concentration, total	−0·133	48	>0·1	Negative.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·041	47	>0·1	—
(*b*) Degree of Moisture	−0·095	47	>0·1	—
(*a*) and (*b*)	0·026	46	>0·1	—
Actinomycetes and Degree of Moisture, total	0·210	48	>0·1	Negative.
Same, partial, with elimination of:				
(*a*) Organic Matter	−0·100	47	>0·1	—
(*b*) Hydrogen-Ion Concentration	0·189	47	>0·1	—
(*a*) and (*b*)	−0·093	46	>0·1	—
Bacteria and Actinomycetes, total	0·563	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Organic matter	0·192	47	>0·1	Negative.
(*b*) Hydrogen-Ion Concentration	0·552	47	<0·01	Positive.
(*c*) Degree of Moisture	0·544	47	<0·01	—
(*a*) and (*b*)	0·195	46	>0·1	Negative.
(*a*) and (*c*)	0·218	46	>0·1	—
Fungi and Organic Matter, total	0·543	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Hydrogen-Ion Concentration	0·678	47	<0·01	—
(*b*) Degree of Moisture	0·488	47	<0·01	—
(*a*) and (*b*)	0·578	46	<0·01	—
Fungi and Hydrogen-Ion Concentration, total	0·199	48	>0·1	Negative.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·542	47	<0·01	Positive.
(*b*) Degree of Moisture	0·276	47	0·1–0·05	Negative.
(*a*) and (*b*)	0·440	46	<0·01	Positive.

TABLE 2.—*Continued.*

Correlation Coefficients from Counts of Microorganisms in Table 1.—Continued.

Correlation between	r*	n*	P*	Significance.
Fungi and Degree of Moisture, total	0·272	48	0·1–0·05	Negative.
Same, partial, with elimination of:				
(*a*) Organic Matter	−0·014	47	>0·1	—
(*b*) Hydrogen-Ion Concentration	0·331	47	0·05–0·02	Positive.
(*a*) and (*b*)	0·042	46	>0·1	Negative.
Bacteria and Fungi, total	0·525	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·175	47	>0·1	Negative.
(*b*) Hydrogen-Ion Concentration	0·581	47	<0·01	Positive.
(*a*) and (*b*)	0·094	46	>0·1	Negative.
Actinomycetes and Fungi, total	0·373	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·083	47	>0·1	Negative.
(*b*) Hydrogen-Ion Concentration	0·422	47	<0·01	Positive.
(*a*) and (*b*)	0·052	46	>0·1	Negative.
Ratio of Actinomycetes to Bacteria, and Organic Matter, total	−0·252	48	0·1–0·05	Negative.
Same, partial, with elimination of:				
(*a*) Hydrogen-Ion Concentration	−0·224	47	>0·1	—
(*b*) Degree of Moisture	−0·091	47	>0·1	—
(*a*) and (*b*)	−0·079	46	>0·1	—
Ratio A.: B. and Hydrogen-Ion Concentration, total	0·141	48	>0·1	Negative.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·075	47	>0·1	—
(*b*) Degree of Moisture	0·065	47	>0·1	—
(*a*) and (*b*)	0·047	46	>0·1	—
Ratio A.: B. and Degree of Moisture, total	−0·371	48	<0·01	Positive.
Same, partial, with elimination of:				
(*a*) Organic Matter	−0·295	47	0·05–0·02	—
(*b*) Hydrogen-Ion Concentration	−0·352	47	0·02–0·01	—
(*a*) and (*b*)	−0·271	46	0·1–0·05	Negative.
Ratio of Fungi to Bacteria plus Actinomycetes, and Organic Matter, total	−0·279	48	Near 0·05	Doubtful.
Same, partial, with elimination of:				
(*a*) Hydrogen-Ion Concentration	−0·202	47	>0·1	Negative.
(*b*) Degree of Moisture	−0·226	47	>0·1	—
(*a*) and (*b*)	−0·173	46	>0·1	—
Ratio F.: B.+A. and Hydrogen-Ion Concentration, total	0·345	48	0·02–0·01	Positive.
Same, partial, with elimination of:				
(*a*) Organic Matter	0·289	47	Near 0·05	Doubtful.
(*b*) Degree of Moisture	0·319	47	0·05–0·02	Positive.
(*a*) and (*b*)	0·286	46	Near 0·05	Doubtful.
Ratio F.: B.+A. and Degree of Moisture, total	−0·176	48	>0·1	Negative.
Same, partial, with elimination of:				
(*a*) Organic Matter	−0·049	47	>0·1	—
(*b*) Hydrogen-Ion Concentration	−0·108	47	>0·1	—
(*a*) and (*b*)	−0·018	46	>0·1	—

TABLE 2.—*Continued.*

Correlation Coefficients from Counts of Microorganisms in Table 1.—Continued.

Correlation between	r*	n*	P*	Significance.
Ratio F.: B.+A. and Organic Matter, 7 abnormal soils excluded, total	−0·304	41	Near 0·05	Doubtful.
Same, partial, with elimination of Hydrogen-Ion Concentration	−0·245	40	>0·1	Negative.
Ratio F.: B.+A. and Hydrogen-Ion Concentration, 7 soils excluded, total	0·607	41	<0·01	Positive.
Same, partial, with elimination of Organic Matter	0·587	40	<0·01	—
Organic Matter and Hydrogen-Ion Concentration, total	−0·282	48	Near 0·05	Doubtful.
Same, partial, with elimination of Degree of Moisture	−0·204	47	>0·1	Negative.
Organic Matter and Degree of Moisture, total	0·480	48	<0·01	Positive.
Same, partial, with elimination of Hydrogen-Ion Concentration	0·446	47	<0·01	—
Hydrogen-Ion Concentration and Degree of Moisture, total	−0·222	48	>0·1	Negative.
Same, partial, with elimination of Organic Matter	−0·092	47	>0·1	—
Organic Matter and Hydrogen-Ion Concentration, 7 abnormal soils excluded, total	−0·186	41	>0·1	Negative.

* r is the correlation coefficient, n the number of observations minus 2 and, in case of partial correlations, minus the number of eliminated variates, P (from Table V.A., Fisher, 1930) the probability of the corresponding correlation coefficient being due to random sampling from an uncorrelated population; if the value of P exceeds 0·05, the correlation is not to be regarded as significant. (Fisher, 1930.)

and uncultivated soils, except so far as the former are generally richer in organic matter.

The numbers of actinomycetes vary within equally wide limits, from 0·1 to 36 mill. per gm. Like the bacteria, their numbers show a definite positive correlation with the content of organic matter, although not so pronounced, the correlation coefficient amounting to 0·585; its value is not reduced materially by eliminating the influences of hydrogen-ion concentration and moisture, with which two factors the numbers of actinomycetes do not show any significant correlation. Neither is there, when organic matter is eliminated, any significant correlation between numbers of bacteria and of actinomycetes, so that these two groups of organisms do not, *per se*, seem to have any influence upon each other, at least when different soils are compared (cf. below).

The ratio of actinomycetes to bacteria varies widely, from 0·065 (No. 11) to 1·75 (No. 16), without showing any significant correlation with the organic matter or the hydrogen-ion concentration. There is some indication of a negative correlation with the moisture-degree, although the correlation coefficient is reduced below significance when organic matter and hydrogen-ion concentration are both eliminated; a larger number of observations might have shown a significant result, but still this factor does not seem very important. Countings from the same soil at different contents of moisture give a quite different result, as will be shown below.

The numbers of fungi vary within still wider limits (from 8,000 to 1,088,000 per gm.) and are generally somewhat higher than previously found with a similar

technique in Danish soils (Jensen, 1931*a*). Their correlation with the organic matter content is definitely significant ($r = 0{\cdot}543$), and remains so when hydrogen-ion concentration and moisture are eliminated. There is no significant correlation with the degree of moisture, but the correlation with hydrogen-ion concentration shows interesting relationships: the total correlation is insignificant, but the partial correlation coefficient with elimination of organic matter is highly significant, also if the influence of moisture is eliminated too. In other words, although increases in organic matter as well as increase in acidity tend to increase the numbers of fungi, the former factor seems to be the more important, to judge by the correlation coefficients. It is also noteworthy that, although there is no general correlation between degree of moisture and fungal numbers, some soils from districts with low annual rainfall (Nos. 4, 5, 9, 10, 14 and 17) have shown the lowest numbers of all.

No real analysis of the composition of the fungous flora has been attempted, but it was noted that the predominant forms were species of *Penicillium*, *Mucor*, *Aspergillus*, *Trichoderma*, and *Fusarium* (cf. Dixon, 1928–30)—organisms that represent the bulk of soil fungi in most geographical regions. The genus *Zygorhynchus*, which, according to Waksman (1932), has the widest geographical distribution of all soil fungi, was observed only in one soil (No. 30). Neither has it been recorded by Dixon (1928–30); since it is an easily recognizable organism, it does not seem to be common in Australian soils. The aspergilli were present in most samples, contrary to what was the case in Danish soils (Jensen, 1931*a*); this agrees with the well-known preference of these fungi for high temperatures. In one soil (No. 9) they accounted for no less than 85% of the total number of fungal colonies, otherwise their numbers were usually quite low.

The ratio of fungi to bacteria plus actinomycetes did not show any significant correlation with the organic matter or moisture, and the correlation with hydrogen-ion concentration was quite low or even doubtful, contrary to what was observed in Danish soils (Jensen, 1931*a*), but if we exclude the 7 soils with abnormally low numbers of bacteria and actinomycetes, referred to above, from the calculation, we find a correlation coefficient of high significance, viz., 0·607, and when organic matter is eliminated, 0·587. This correlation is not so marked as in the Danish soils, but the range of hydrogen-ion concentration is also considerably narrower here—pH 4·5 to 7·9 against pH 3·3 to 8·4. The reaction seems thus generally to be a very important factor in determining the balance between fungi and bacteria plus actinomycetes, rather than the actual numbers of organisms.

B. *Periodical Counts of Microorganisms.*

The data which we have just discussed suffer from the disadvantage that we are here comparing soils of different character, with different physical structure, and containing organic matter and other microbial food of probably widely differing quality, and moreover, since the observations cannot all be carried out simultaneously, seasonal changes in the microflora may take place. It is therefore of interest to compare them with periodical counts of microorganisms in one and the same soil, in order to get an idea of the changes which the microflora may undergo according to changes in moisture and temperature, and of the possible existence of seasonal changes or spontaneous fluctuations in the numbers of bacteria. For this purpose, a plot of uncultivated, grass-covered soil was selected on the grounds of Sydney University; the soil was a heavy loam, rich in organic matter, of pH 5·4–5·5. Fifty counts of bacteria and actinomycetes and 45 counts of fungi were carried out in two periods, with weekly or bi-weekly intervals. The samples

were taken from the upper 10 cm. of soil within an area of 4 m.², each sample being a composite of 6 individual samples, scattered as evenly as possible over the sampled area. Three parallel samples were examined in order to test the uniformity of the soil; the following results were obtained:

No.	Average number of colonies, and standard deviation.			H_2O %.
	Bacteria.	Actinomycetes.	Fungi.	
I	55·0±6·83	24·5±3·51	24·8±2·50	29·5
II	61·0±2·16	25·3±3·40	31·0±4·32	29·5
III	57·0±1·83	23·8±2·87	28·3±4·99	29·6

(Dilution: Fungi, 1 : 20,000. Bacteria and Actinomycetes, 1 : 200,000. 4 parallel plates.)

There are here significant differences between numbers of fungi in samples I and II, and of bacteria in samples II and III, but since they are only small, we may consider that the heterogeneity of the soil accounts for only a minor part of the changes in the numbers of microorganisms; it may, for instance, have something to do with the divergence of bacterial and fungal numbers at approximately equal degree of moisture, with which these numbers are as a whole closely correlated, as will be shown below.

All samples were not taken at the same hour of the day, and another experiment was therefore carried out to test whether the numbers of microorganisms, especially bacteria, on the medium employed here showed any spontaneous fluctuations within short intervals of time, as demonstrated by Cutler, Crump and Sandon (1923) and later by Thornton and Gray (1930). Platings from 4 samples taken at 2-hour intervals yielded the following result:

No.	Time.	Soil Temp.	H_2O %.	Average number of colonies, and standard deviation.	
				Bacteria.	Actinomycetes.
I	10 a.m.	24°C.	26·2	47·0±4·85	20·6±4·56
II	noon	26°C.	25·9	54·3±8·46	21·3±6·19
III	2 p.m.	26°C.	26·9	52·2±7·16	26·0±6·75
IV	4 p.m.	25°C.	27·2	52·3±3·40	22·5±2·38

(Dilution 1 : 200,000; 4 parallel plates.)

There are no significant changes in the numbers of either bacteria or actinomycetes from 10 a.m. to 4 p.m., between which hours all samples were taken. The reason is probably that the dextrose-casein-agar is less selective and gives higher counts than the mannite-asparagine-agar used by Thornton and Gray (Jensen, 1931*b*; cf. also Smith and Worden, 1925, and Thornton and Fisher, 1927). Since our medium thus does not show the spontaneous fluctuations, it would seem well adapted for studying the changes in the numbers of bacteria over longer periods in relation to external factors.

TABLE 3.

Periodical Counts of Microorganisms.

No.	Date.	Temp. °F.[1]	H_2O %[2].	Bact.[3]	Actinomyc.[3]	Fungi.[4]	Ratio A. : B.
1	20–10–31	59	17·4	5·6	3·6	305	0·64
2	27–10–31	68	17·7	7·2	4·5	338	0·62
3	2–11–31	64	23·9	13·2	7·9	494	0·60
4	10–11–31	65	31·4	24·5	9·6	834	0·39
5	17–11–31	77	22·1	15·9	8·6	488	0·53
6	20–11–31	60	25·2	19·6	9·4	829	0·48
7	24–11–31	66	21·6	12·7	8·4	806	0·67
8	30–11–31	64	18·5	10·1	5·4	422	0·54
9	7–12–31	68	22·8	15·5	10·0	907	0·64
10	15–12–31	64	21·1	10·1	4·0	781	0·39
11	22–12–31	67	17·6	6·4	3·4	485	0·53
12	29–12–31	73	24·1	14·0	7·2	712	0·51
13	6–1–32	77	18·5	9·5	7·4	682	0·78
14	12–1–32	82	17·1	7·9	7·5	772	0·95
15	20–1–32	78	15·8	5·9	6·2	532	1·04
16	28–1–32	80	15·5	7·6	7·2	582	0·96
17	2–2–32	81	16·3	7·6	6·7	516	0·89
18	9–2–32	73	24·4	15·0	7·8	798	0·52
19	17–2–32	66	29·5	18·5	12·4	817	0·68
20	14–9–32	63	31·9	21·1	12·0	667	0·57
21	14–7–33	57	39·5	16·0	7·0	526	0·44
22	24–7–33	53	38·4	14·9	6·0	1331	0·40
23	28–7–33	56	42·7	14·1	6·3	—	0·45
24	3–8–33	50	41·6	22·7	9·6	—	0·42
25	8–8–33	65	39·0	21·9	10·0	—	0·46
26	12–8–33	54	36·1	21·1	9·7	—	0·46
27	16–8–33	56	38·5	20·0	7·6	—	0·38
28	23–8–33	52	37·1	18·0	6·0	—	0·33
29	28–8–33	59	31·2	19·3	7·0	—	0·36
30	1–9–33	64	33·9	21·3	7·2	—	0·34
31	9–9–33	62	30·5	15·8	6·0	—	0·38
32	12–9–33	54	32·4	19·1	7·0	—	0·36
33	18–9–33	68	29·4	14·7	6·7	949	0·46
34	22–9–33	60	20·5	10·3	5·1	541	0·50
35	25–9–33	59	32·2	25·6	5·5	762	0·21
36	29–9–33	61	32·6	19·7	7·1	794	0·36
37	3–10–33	65	38·6	—	—	929	—
38	6–10–33	61	34·3	—	—	715	—
39	9–10–33	67	32·5	—	—	816	—
40	13–10–33	62	29·1	—	—	613	—
41	16–10–33	65	27·6	—	—	658	—
42	20–10–33	83	24·2	11·5	5·5	475	0·48
43	24–10–33	75	19·1	6·6	4·6	426	0·70
44	27–10–33	61	32·8	18·3	6·4	871	0·35
45	30–10–33	60	30·8	13·6	6·1	603	0·45
46	3–11–33	61	25·5	13·8	4·4	664	0·32
47	7–11–33	61	35·6	—	—	776	—
48	10–11–33	61	35·0	26·4	6·7	662	0·25
49	14–11–33	68	28·8	19·7	7·2	730	0·37
50	17–11–33	72	29·3	16·3	6·9	792	0·43
51	20–11–33	64	32·5	18·7	7·5	978	0·40
52	24–11–33	68	33·9	22·2	8·9	817	0·40
53	28–11–33	71	33·3	18·3	7·5	824	0·41
54	1–12–33	70	31·8	20·2	8·4	997	0·42
55	5–12–33	73	25·5	10·8	5·9	679	0·54
56	8–12–33	79	26·2	12·7	5·6	582	0·44

[1] Average temperature of the day.
[2] In dry soil.
[3] Millions per gm. of oven-dry soil.
[4] Thousands per gm. of oven-dry soil.

We have little definite knowledge concerning the influence of moisture and temperature on the numbers of soil microorganisms. Fabricius and v. Feilitzen (1905) found bacterial numbers in peat soil closely connected with the temperature, but gave few data. Engberding (1909) thought to have established a definite positive correlation between numbers of bacteria and moisture content of the soil; however, a calculation of the correlation coefficient from the data in his tables 5 and 6 shows $r = 0{\cdot}479$ and $0{\cdot}427$, respectively, which cannot be considered significant with only 16 observations (Fisher, 1930, Table V, A). The data of Waksman (1916) did not reveal any correlation of the bacterial numbers with either moisture or temperature. Another series of data published by Waksman (1922), representing 4 counts from each of 10 differently fertilized soil plots, shows in most cases a strong depression of bacterial numbers at low moisture content, but his data are too few for a statistical examination. The same applies to the data of Cobb (1932). Conn (1912) observed a striking parallelism between moisture and numbers of bacteria (including actinomycetes) in two soil plots, but since the samples were taken from two different parts of each plot and the uniformity of the distribution of the bacteria over the plots is unknown, we cannot calculate the correlation. Cutler, Crump and Sandon (1923) did not find the bacterial numbers correlated with either moisture or temperature, like Thornton and Gray (1930), who, however, in one series observed a definite correlation between rainfall and numbers of bacteria. Neither is any such correlation clearly observable in the counts of Smith and Worden (1925).

As to the influence of moisture on the numbers and activities of soil actinomycetes, it is sometimes alleged that these organisms are most active in comparatively dry soils, but very little experimental evidence is available, since the data on this point are but few. The data given by Conn (1912), Waksman (1922), and Cobb (1932) do not show any distinct preponderance, absolute or relative, of actinomycetes over bacteria at low degrees of moisture. Perhaps the strongest evidence for the preference of actinomycetes for dry soil is given by Dubos (1928), who found that cellulose-decomposing actinomycetes displayed their strongest activity at a degree of moisture considerably below the optimum for bacteria and fungi. There is some evidence that the actinomycetes as a whole are less tolerant towards low temperatures than many bacteria (Lochhead, 1926), but otherwise very little is known about their relation to temperature.

Neither do we possess much knowledge concerning the influence of moisture and temperature on soil fungi, so far as their numbers are concerned. Some data published by Waksman (1924) show no correlation whatever between soil moisture and fungal numbers. Cobb (1932) found a depression of fungi at periods of drought, but her results are too few for a statistical examination, and the same applies to the data of Dixon (1928–30), who found the fungal numbers correlated with temperature rather than with moisture.

The results of the present experiments are shown in Table 3, and the correlation coefficients calculated herefrom in Table 4.

Numbers of Bacteria.—As Text-figure 1 shows, there is a very definite correlation between moisture content and bacterial numbers, represented by a correlation coefficient of $0{\cdot}773$; this value still remains very high when the influences of temperature and of actinomycetes are eliminated, but the temperature shows no correlation at all with the bacterial numbers, when the influence of moisture is eliminated. The disagreement of this result with those of Cutler, Crump and Sandon (1923) and Thornton and Gray (1930) is probably due, partly to the less selective character of the counting medium which does not show the marked diurnal changes in the bacterial numbers, partly to the fact that the changes in

TABLE 4.

Correlation Coefficients from Periodical Counts.

Correlation between	r	n	P	Significance.
Bacteria and Moisture, total	0·773	48	<0·01	Positive.
Same, partial, with elimination of:				
Temperature	0·700	47	<0·01	—
Temperature and Actinomycetes	0·638	46	<0·01	—
Bacteria and Temperature, total	−0·493	48	<0·01	Positive.
Same, partial, with elimination of:				
Moisture	0·024	47	>0·1	Negative.
Moisture and Actinomycetes	−0·113	46	>0·1	—
Actinomycetes and Moisture, total	0·324	48	0·05–0·02	Positive.
Same, partial, with elimination of:				
Temperature	0·385	47	<0·01	—
Temperature and Bacteria	−0·075	46	>0·1	Negative.
Actinomycetes and Temperature, total	−0·051	48	>0·1	Negative.
Same, partial, with elimination of:				
Moisture	0·224	47	>0·1	—
Moisture and Bacteria	0·248	46	0·1–0·05	—
Bacteria and Actinomycetes, total	0·567	48	<0·01	Positive.
Same, partial, with elimination of:				
Moisture	0·528	47	<0·01	—
Temperature	0·624	47	<0·01	—
Moisture and Temperature	0·628	46	<0·01	—
Fungi and Moisture, total	0·588	44	<0·01	Positive.
Same, partial, with elimination of Temperature	0·577	43	<0·01	—
Fungi and Temperature, total	−0·208	44	>0·1	Negative.
Same, partial, with elimination of Moisture	0·158	43	>0·1	—
Bacteria and Fungi, total	0·527	38	<0·01	Positive.
Same, partial, with elimination of:				
Moisture	0·118	37	>0·1	Negative.
Temperature	0·500	37	<0·01	Positive.
Moisture and Temperature	0·113	36	>0·1	Negative.
Actinomycetes and Fungi, total	0·432	38	<0·01	Positive.
Same, partial, with elimination of:				
Moisture	0·317	37	Near 0·05	Doubtful.
Temperature	0·456	37	<0·01	Positive.
Moisture and Temperature	0·282	36	0·1–0·05	Negative.
Ratio Act.: Bact. and Moisture, total	−0·692	48	<0·01	Positive.
Same, partial, with elimination of Temperature	−0·492	47	<0·01	—
Ratio Act.: Bact. and Temperature, total	0·607	48	<0·01	Positive.
Same, partial, with elimination of Moisture	0·283	47	Near 0·05	Doubtful.
Moisture and Temperature, total, as applied to Bacteria and Actinomyctes	−0·653	48	<0·01	Positive.
Same, as applied to Fungi	−0·538	44	<0·01	Positive.
Same, as applied to Bacteria, Actinomycetes and Fungi	−0·534	38	<0·01	Positive.

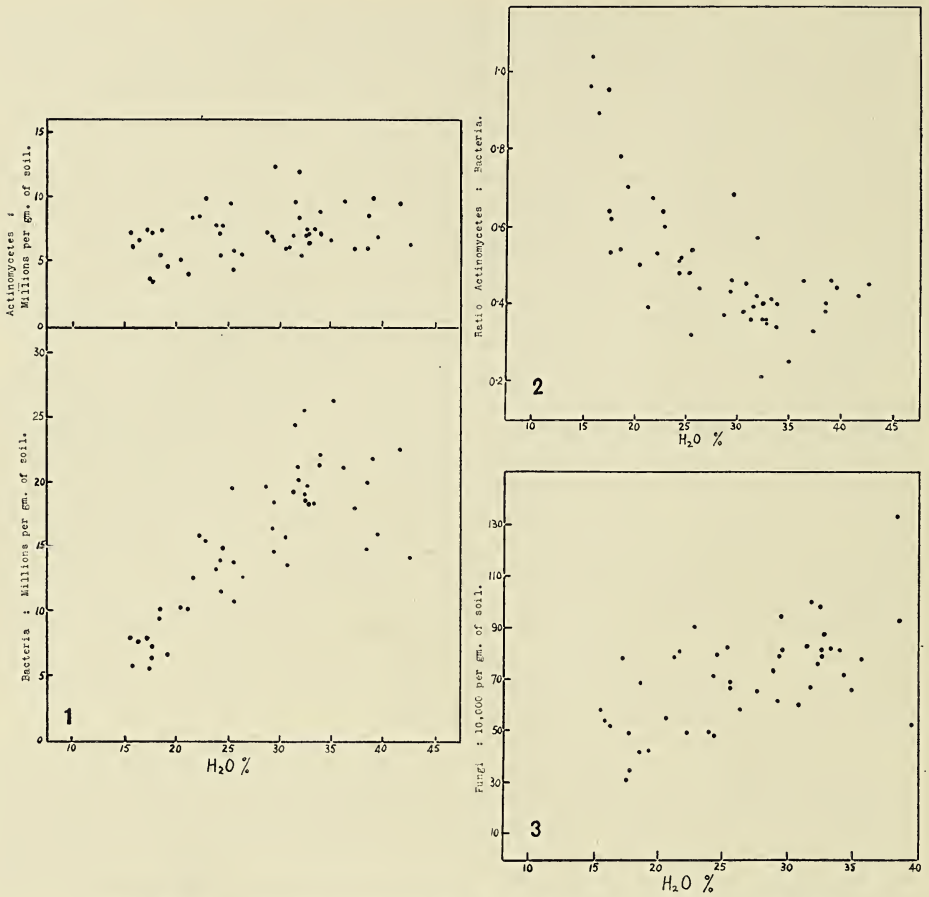
moisture here appear more drastic than in the English soils. The maximal numbers seem to occur at about 32–35% H_2O, which corresponds to 65–70% of the water-holding capacity of this soil, and the numbers seem to have a tendency to decrease at still higher degrees of moisture (40–42% H_2O), but the observations at these high degrees of moisture are too few to enable us to say definitely whether a real optimum exists at 32–35% H_2O, or whether the numbers of bacteria merely here show stronger fluctuations due to other causes. Indeed, if we calculate the correlation coefficient between bacteria and moisture up to 37·1% H_2O, which appears to mark the endpoint of the optimal zone, we find $r = 0{\cdot}882$, a value which is not significantly higher than the value $r = 0{\cdot}773$ applying to the whole range of moisture (Fisher, 1930, p. 170). Since thus the two samples show the same correlation, we cannot draw definite conclusions as to a decrease in bacterial numbers at the highest degrees of moisture observed here.

Numbers of Actinomycetes.—This group of organisms shows some interesting relationships. Their correlation with the moisture, total or with temperature eliminated, is significant, although low (cf. Text-figure 1), but when the influence of the bacteria is excluded, the correlation disappears altogether. Their correlation with the temperature is not significant, but they show a very definite correlation with the numbers of bacteria, particularly when moisture and temperature are eliminated. Whether this is due to an actual stimulation of the actinomycetes by the bacteria, or to some unknown factor that stimulates both groups of organisms simultaneously, remains an open question, but it is worth noticing that actinomycetes play an important role in the decomposition of dead microbial matter in the soil (Waksman and Skinner, 1926; Jensen, 1932), so that we might expect an increase in actinomycetes at periods when bacterial numbers run high and much bacterial protoplasm is being produced.

It should here be remarked that the term "actinomycetes", here as well as in the previous series of experiments, covers the genera *Actinomyces* and *Micromonospora* together with those forms of *Proactinomyces* that produce colonies of a visibly mycelial character. The distinction from the bacteria is thus somewhat arbitrary (the actinomycetes are, botanically speaking, a group of bacteria), but the genus *Actinomyces* accounts for an overwhelming majority of the soil "actinomycetes" (Jensen, 1931*c*).

As a natural consequence of the comparative independence of the actinomycetes on moisture, the ratio of actinomycetes to bacteria shows a strong negative correlation with the moisture content (see Text-figure 2), also if the influence of temperature is eliminated (Table 4). The correlation of this ratio to temperature seems to be positive, but only just on the verge of significance, when the influence of moisture is eliminated. This leads us to the conclusion that the relative abundance of actinomycetes, but not their actual numbers, is largely governed by the moisture supply, perhaps also by the temperature, the actinomycetes being most predominating under conditions of low moisture and high temperature.

Numbers of Fungi.—The correlation between moisture and numbers of fungi (Text-figure 3, and Table 4) is highly significant, although not so close as in the case of the bacteria, and it remains so when we eliminate the influence of temperature, which, on the other hand, shows no significant correlation with the fungal numbers. (It is true that the "numbers of fungi", as determined by plate counting, do not express the numbers of fungus-individuals as they exist in the soil, due to the breaking-up when the soil suspension is prepared, but still



Text-fig. 1.—Numbers of bacteria and of actinomycetes plotted against moisture-content of soil.

Text-fig. 2.—Ratio of actinomycetes to bacteria plotted against moisture-content of the soil.

Text-fig. 3.—Numbers of fungi plotted against moisture-content of the soil.

the fact that the plate-counted numbers are significantly correlated with such definite soil characters as reaction and contents of organic matter and moisture, indicates that they cannot be mere chance figures depending on the fortuitous disintegration of the mycelia and scattering of the spores, but must have a real bearing on the density of mycelia plus spores in the soil.) There is no correlation between fungal and bacterial numbers when the influence of moisture is excluded, and also the correlation between fungi and actinomycetes, with elimination of moisture and temperature, is too low to be considered significant. All in all, there is thus no evidence that these three groups of microorganisms, *per se*, exert any antagonistic influence upon each other, such as is the case with the bacteria and the protozoa, especially the free-living amoebae (Cutler, Crump and Sandon, 1923).

Finally, it is to be noted that no distinct seasonal changes in the numbers, apart from results from the changes in the moisture content, are noticeable in any of the groups of microorganisms. The disagreement of this result with observations made in some other geographical regions (see Thornton and Gray, 1930, and Waksman, 1932) is probably due to the climatic conditions being different from those obtaining in Europe and North America.

Conclusions.

We have now seen, firstly, that the numbers of all the three groups of microorganisms, and particularly the bacteria, increase markedly with increase in the content of organic matter, without being so much influenced by the reaction which, however, largely governs the ratio of fungi to bacteria plus actinomycetes, and secondly, that in a given soil the numbers of bacteria and fungi increase with increasing moisture without being influenced by the temperature (all, of course, within the limits of the present observations), and that the relative abundance of actinomycetes in proportion to bacteria increases strongly with decreasing moisture and probably also with increasing temperature. These results appear interesting in connection with certain aspects of the humus problem. It has been shown (Jenny, 1929–31, and several authors quoted by him) that climatic conditions exert a marked influence on both the quantity and the quality of soil organic matter, the quantity of which increases with decreasing temperature and with increasing humidity, while the carbon : nitrogen ratio becomes narrower with increasing temperature, i.e., the soil organic matter becomes richer in nitrogen, which facilitates the formation of nitrates (Waksman, 1932). The mother substances of soil "humus" are largely lignin and certain proteid compounds possibly derived from the dead bodies of microorganisms, particularly fungi. Actinomycetes are credited with the power of decomposing lignin, which is but very incompletely decomposed at low temperatures (Waksman and Gerretsen, 1931). Therefore we should indeed expect to find a more complete decomposition, i.e., less accumulation of humus with a higher nitrogen content (since lignin is a nitrogen-free compound) under conditions where actinomycetes preponderate over bacteria and fungi, namely, under conditions of low moisture and high temperature.

Summary.

Counts of microorganisms in 50 soils from New South Wales showed a definite correlation between the content of organic matter and the numbers of bacteria, actinomycetes and fungi. This correlation was most pronounced in the case of bacteria, least in the case of actinomycetes. The soil reaction had not in itself any influence on the numbers of bacteria and actinomycetes, but showed a significant correlation with the numbers of fungi, although its influence seemed less marked than that of the organic matter. The ratio of fungi to bacteria plus actinomycetes was distinctly correlated with the reaction, except in the case of certain soils abnormally poor in bacteria and actinomycetes. The moisture-content of the soil did not in this series of observations show any definite influence on any of the groups of microorganisms, but it was noted that several soils from dry districts were very poor in fungi.

Periodical counts of microorganisms in a soil from Sydney showed a strong positive correlation between moisture-content and numbers of bacteria, and a similar, although less pronounced, correlation between moisture and numbers of

fungi, whereas the numbers of actinomycetes did not seem actually to be influenced by changes in the moisture-content. None of the groups of organisms showed any actual correlation with the temperature, or any definite seasonal changes apart from those resulting from the changes in moisture. There was a definite positive correlation between the numbers of bacteria and actinomycetes, apart from the effects of moisture and temperature. The ratio of actinomycetes to bacteria became wider with increasing moisture, and there was also a certain evidence that this ratio becomes narrower with increasing temperature, i.e., the actinomycetes tend to predominate under conditions of low moisture-content and high temperature.

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THE HABITAT, CHARACTER, AND FLORAL STRUCTURE OF *CRYPTANTHEMIS SLATERI* RUPP (ORCHIDACEAE).

By the Rev. H. M. R. Rupp, B.A.

(Two Text-figures.)

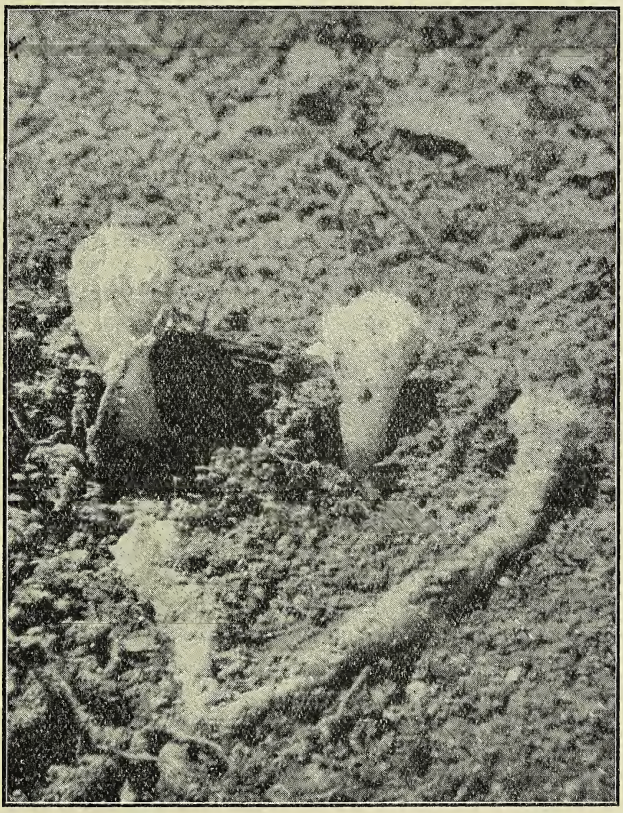
[Read 30th May, 1934.]

I have already described this orchid (These Proceedings, lvii, Parts 1–2, 1932; and lviii, Parts 3 and 4, 1933) from specimens sent from Bullahdelah, N.S.W., by Mr. E. Slater and Dr. H. Leighton Kesteven. These specimens were more or less fragmentary, and suffered a little damage in transit; moreover, with few exceptions, the flowers were well past maturity and their segments were withered. It was therefore difficult to give a satisfactory account of this strange plant, and many points of interest called for further investigation. A grant from the Australian and New Zealand Association for the Advancement of Science enabled me to pay a visit to Bullahdelah in October, 1933, and the orchid was studied *in situ*. I desire to express here my gratitude to Dr. Kesteven for his kind assistance during this visit; indeed, whatever credit may accrue from the investigations is mainly due to his enthusiastic and generous co-operation.

The site of the discovery of *Cryptanthemis* is a small and obscure water-channel, dry except during rain, when it discharges into a shallow gully a few yards on the south side of the old Alum Company's trolly line near the alum dump—on the lower western slope of the Alum Mountain, and I should say about 250 feet above sea-level. All plants of the orchid hitherto found—in number perhaps 12, but in view of the fragmentary character of the 1931–1932 specimens it is difficult to be sure—have been located within a radius of about eight yards from this spot. Dr. Kesteven pointed out to me, as a fact which may possibly have some bearing upon the occurrence of the plant here, that the surface soil near the old alum dump is almost certainly not the original surface. Years ago, fragments of alunite rock were dumped here by the thousand, and scattered about. A certain amount of soil would doubtless accompany them from higher levels; rain-storms would send down further supplies by erosion, and gradually the original surface would be covered. The ground is very stony, and there is little grass or undergrowth; it is a barren spot occupied chiefly by stringybark eucalypts, under which are carpets of fallen leaves and other debris. The lack of undergrowth serves to make conspicuous the numerous plants of *Dipodium punctatum* R.Br. which are found here. As all the earlier specimens of *Cryptanthemis* were discovered by disturbing the roots of *Dipodium*, it was conjectured that some definite association might exist between the two plants. Dr. J. P. Lindinger, of Hamburg, Germany, has expressed the opinion (*Vict. Nat.*, June, 1933) that *Cryptanthemis* was merely an abortive form of *Dipodium*. Even on the data then available, this hypothesis was untenable by anyone who had examined specimens, but the recent investigation by Dr. Kesteven and myself demonstrated beyond question, not only the validity of *Cryptanthemis Slateri*, but the fact that there

is no real association between it and *Dipodium* at all. Only one of the six plants we "unearthed" was in close proximity to a *Dipodium*.

The first two plants discovered by us had only withered capitula similar to those found in 1931 and 1932. Dr. Kesteven then exposed a white capitulum with all the flowers perfect, and this was found to belong to a plant with four branches, each with a perfect capitulum at its summit. The whole plant was completely subterranean, the top of the highest capitulum being about 2 cm. beneath the surface of the soil. The main rhizome curved slightly, and excavation for a photograph *in situ* was very difficult, as the plant is extremely brittle. One of the four branches broke off before we were ready for the camera, but the remainder of the plant was successfully photographed (Text-fig. A). Three more plants were



Text-fig. A.—*Cryptanthemis Slateri* Rupp.—Plant *in situ*, Bullahdelah, 10/10/1933. Soil excavated on one side. xxx, surface of soil.

found during the morning's search, the total number of capitula being ten, of which five were perfect and five more or less withered. One very small specimen, discovered at some distance from any other, may be a seedling plant.

Dr. Kesteven having suggested that seeds or plants might have been brought to this spot from higher levels in the old alum-mining days, we spent the greater part of an afternoon searching in the neighbourhood of the mine at the top of the

trolly-line, and from there along a zig-zag course down the western slope of the mountain on the north side of the dump. No trace of *Cryptanthemis* was seen, though numerous colonies of *Dipodium* were encountered. We "reconstructed" the largest plant while its form of growth was still clearly remembered; and further photographs were taken. A flower was then dissected and examined under a dissecting microscope. Miss Betsy Kesteven kindly assisted here by making two contour sketches of the labellum and column which were subsequently very useful.

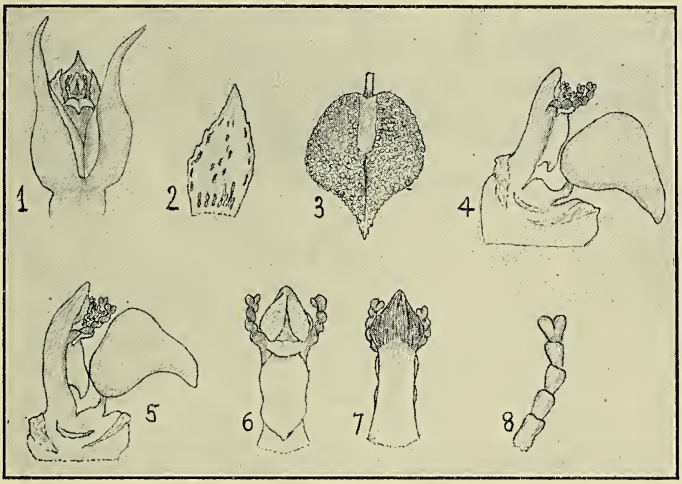
While our investigations had convinced us that the apparent association of *Cryptanthemis* with *Dipodium* in the case of previous specimens could not be deemed to involve any particular relation between the two, since the former was found to occur independently, we considered it likely that the mycorrhiza infesting both might be found to be identical. Dr. McLuckie's investigations of the mycorrhiza of *Cryptanthemis* will doubtless settle this point. If our conjecture is correct, further colonies of *Cryptanthemis* may be discovered by disturbing the soil in the vicinity of *Dipodium* plants, though this method of search was unsuccessful on the occasion just related above. I have already described the character of the ground at the only known habitat of *Cryptanthemis*, and it is of course possible that the plant is restricted to this kind of ground by circumstances not yet revealed: on the other hand, *Dipodium* is well known to occur in various soils of widely differing character.

There can no longer be any doubt that *Cryptanthemis* develops and matures its capitula of flowers beneath the actual surface of the soil. Nevertheless all the *withered* flower-heads found were just level with the surface underneath the debris of fallen leaves, etc. It would appear, therefore, that as the fertilized ovaries swell and mature, some slight elongation of the flowering branch must take place. One may fairly assume that the purpose of this is to facilitate the dispersion of seed by bringing the fruiting capitula to the surface. As they are still covered by debris, it is difficult to suggest how dispersion is effected except by rain-storms. In spite of the fact that large quantities of seeds are produced and ripened, the apparent scarcity of the plant suggests that successful germination is rare. We found evidence indicating a form of vegetative reproduction: in some instances it was obvious that a branch had been separated from the parent rhizome at the point of junction, and was established independently.

I am unable to record any direct evidence of the method of fertilization, which appears to be very effective. In a plant of so strange a habit, one is naturally disposed to postulate self-fertilization. Nevertheless, it appears to me quite possible that burrowing insects may be the agents. The pollen sacs are extremely fragile, and in many flowers even their remains were so difficult to see that only the discovery of some still intact convinced me of their existence. Pollen was lying loose on the rostellum and on the curving appendages of the column, which appeared to function as preventives of the pollen falling on to the stigma immediately below. I was not able to distinguish the number of pollinia in any of the flowers I dissected. The stigma is large and prominent, with a well-marked basal spur.

In the notes additional to the original description, which were based on the 1932 specimens, I stated that the curious appendages observed near the top of the column were straight, and not curved, as previously described. This is incorrect, and the straightening may have been due to the immersion in water mentioned in the notes. In the fresh flowers recently obtained the normal attitude of the appendages was clearly seen. They arise from the column, one

on either side, at the level of the rostellum, and are curved inward and forward, so that, at least in some of the flowers examined, they form with the rostellum a kind of platform or scaffolding holding the pollinia. Under the microscope each appendage has the appearance of a little chain of single cells, with two cells at the apex (see Text-figs. B, 4–8).



Text-fig. B.—Enlarged details of flower of *Cryptanthemis Slateri* Rupp.—1, A flower from the front. The labellum can be seen between the "flaps" of the large lateral sepals, with the petals flanking it, and behind it is the column protected by the dorsal sepal. 2, A petal, showing indented margins and (red) markings. 3, Labellum flattened out (upper surface). 4, Column and labellum from side, sepals and petals removed. (Outlines drawn by Miss Betsy Kesteven.) Near the top of the column is a remnant of the fractured anther sac. Pollen grains are in front of this, framed by the appendages and rostellum, under which is the large spurred stigma. 5, A similar sketch by the author from another flower. 6, Column from front. 7, Column from rear. 8, One of the column appendages.

The labellum varies in dimensions, but is never relatively as large as that of *Rhizanthella Gardneri* Rogers. It rests on a somewhat elastic-like claw attached to a very prominent projection at the base of the column. It is densely beset with unicellular papillæ, which are elongated at the labellum-margins, giving the appearance of a serrulate edge. Along the basal half of the upper surface is a smooth, shining median plate. The sepals and petals, though more or less overlapping, are quite free. They are thick and succulent in the young flower, but as maturity is reached they tend to become almost membranous. The petals are slightly and very irregularly denticulate, especially on the margin adjoining the dorsal sepal.

The colour of the whole plant, when in normal condition and while the flowers are young, is a waxy white, except where darker patches on the rhizome probably indicate the presence of the mycorrhiza. As the flowers mature, deep red splashes appear on the petals, and suffusions of the same colour become noticeable on the column and the basal half of the labellum. A few days after exposure to the light the whole flower darkens, this change being very

much slower than is recorded by Dr. Rogers to be the case with *Rhizanthella*. Branches are apparently developed by most plants, but here again the habit differs from that of *Rhizanthella*, for some of the branches were developing closely parallel to the parent stem. In the plant photographed *in situ* they were spreading.

Methods of fertilization and germination still await discovery, and it is to be hoped that new colonies of this remarkable orchid will be discovered in the spring of 1934.

AN INVESTIGATION OF THE SOOTY MOULDS OF NEW SOUTH WALES. II.

AN EXAMINATION OF THE CULTURAL BEHAVIOUR OF CERTAIN SOOTY MOULD FUNGI.

By Lilian Fraser, M.Sc., Linnean Macleay Fellow of the Society in Botany.

(Fifty-nine Text-figures.)

[Read 30th May, 1934.]

Introduction.

In a previous paper (Fraser, 1933) the composition of the sooty moulds of New South Wales was described. It was pointed out that the sooty mould forming fungi belong to three systematic divisions, the Capnodiaceae, the Atichiaceae and the Fungi Imperfecti. It is common to find several different fungi taking part in the formation of a single sooty mould. It was further shown that the fungi forming sooty moulds could be grouped according to their modes of occurrence into three divisions, perennials, ephemerals, and accidentals. The perennials, which include the Capnodiaceae and Atichiaceae, together with *Dematium pullulans* and *Cladosporium herbarum*, have a dark-brown or olive-green mycelium which is resistant to heat and desiccation. The ephemerals, which include members of the Fungi Imperfecti such as *Alternaria*, *Penicillium*, *Epicoccum* and *Asbolisia* spp., tide over adverse periods by means of their resistant spores. The accidentals, which include *Fusarium* spp., *Mucor* spp., bacteria, etc., disappear completely from the sooty mould during adverse weather conditions, and their reappearance is due to accidental infection.

Sooty moulds which appear on annual plants following attack by aphis are composed principally of *Cladosporium*, *Dematium* and a number of ephemerals. Similar sooty mould associations often develop on trees and shrubs attacked by scale insects, but usually they are replaced after a short time by associations in which one or more members of the Capnodiaceae are present.

As the commencement of an inquiry into the physiology of the members of the sooty mould flora, experiments have been made to investigate the ability of a selected number of these fungi to utilize a variety of nutrient compounds.

The composition of the honey dew on which sooty moulds grow (see Arnaud, 1911) is dextrin, gums, etc. In addition mineral material in the form of dust may be available to the sooty mould fungi. The natural medium, therefore, consists of complex carbohydrate and protein materials with various mineral salts.

It is noticeable that common saprophytes such as *Penicillium expansum* and *Cladosporium herbarum* occur to a greater or lesser degree in sooty mould formations. The highly specialized members of the Capnodiaceae on the other hand are not found elsewhere. Although they must possess the ability to utilize complex organic food materials, they are not found in competition with decay-causing fungi except on leaves covered with honey dew.

The sooty mould associations appear, therefore, to include fungi definitely adapted for the habitat in which they occur. It was with the object of finding out some of the physiological characteristics of the group that the experiments here reported were made. The fungi selected were grown on a variety of different food materials in order to find out if it were possible to group them according to their ability to utilize certain classes of organic and inorganic compounds. If this were possible it would indicate a basis for the interpretation of the distribution of these fungi.

The group of fungi chosen for this work includes representatives of all the classes of sooty mould fungi as defined in a previous paper (Fraser, 1933) as follows: *Botrytis cinerea* Pers., *Penicillium expansum* Thom., *Asbolisia* sp., *Cladosporium herbarum* Link., *Dematium pullulans* de Bary, *Caldariomyces* sp. (near *C. fumago* Woron.), *Capnodium* sp., 2 strains, *Microxyphium* sp. A, 2 strains, *Microxyphium* sp. B, *Microxyphium* sp. C.

Microxyphium, *Capnodium* and *Caldariomyces* are representatives of the permanent Capnodiaceae flora. The species of *Microxyphium* grow slowly in culture, *Capnodium* and *Caldariomyces* grow more quickly. *Dematium* and *Cladosporium* are important constituents of both perennial and annual moulds, *Cladosporium* being a widespread saprophyte. Both grow rapidly in culture. *Asbolisia* belongs to the ephemeral class of sooty mould fungi; it is fairly common and grows very rapidly in culture. *Penicillium* is a common saprophyte and a member of the ephemeral class of sooty mould fungi. It was included partly as a control, because of its cosmopolitan nature. *Botrytis* was also included as a control. It is a common saprophyte of decaying vegetable matter, but is not present in the sooty moulds of New South Wales.

Cultural Work.

The effects of the various types of food materials used in the investigations on the growth of the fungi were studied by measuring the amount of growth made on agar containing the different nutrients under investigation.

Sterilized Petri dishes of 9 cm. diameter were poured with 10 c.c. of agar of the appropriate composition, so that the resulting layer of agar was comparatively thin. The experiments were carried out in triplicate. All cultures were incubated in darkness at 25° C. throughout the investigation, so that as far as possible conditions would be comparable between the different sets of experiments. The dishes were inoculated with the fungus to be examined, and the diameter of the colony measured three times weekly. The hydrogen-ion concentration of the media was adjusted to pH 5·5 throughout.

There are a number of objections to the method of determining the growth of fungi in culture by the measurement of the diameter of the colonies. For example, growth on one medium may be rapid, but the resulting colony thin and straggling, whereas on a different medium the increase in diameter may be slower, but the growth is more efficient as shown by the production of spores. It has been maintained, therefore, that the measurement of dry weight gives more reliable results.

In the present investigation allowances have been made, as far as possible, in the statement of conclusions, for the different types of growth. The method of examination of growth by measurement of the diameter of the colony was used because, as well as the final comparison of growth on different types of agars, the growth rate of a fungus on any one agar could also be studied. Indications of staling phenomena, should they occur, could thus be detected.

Growth on Carbohydrate Media.

Waksman's peptone agar was used throughout, with a 2% concentration of the carbohydrate to be tested. It was made up as follows: peptone 0·5%, potassium dihydrogen phosphate 0·1%, magnesium sulphate 0·05%, carbohydrate 2%, agar 1·5%.

The following carbohydrates were used:

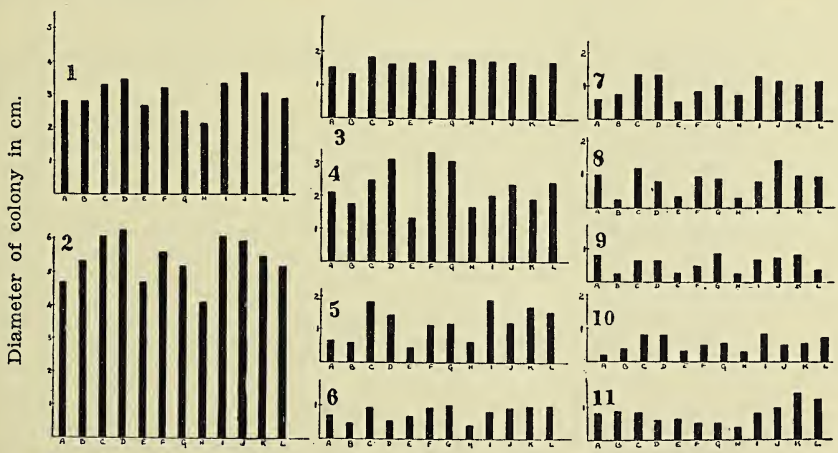
(i) Sugars.—(*a*) Monosaccharides. Pentoses ($C_5H_{10}O_5$): arabinose, xylose; hexoses ($C_6H_{12}O_6$): dextrose, levulose, mannose.
(*b*) Disaccharides ($C_{12}H_{22}O_{11}$): sucrose, maltose, lactose.
(*c*) Trisaccharide: raffinose.

(ii) Polysaccharides: inulin, dextrin, starch.

(i) *Sugars.*—The comparative amounts of growth made on the different agars by the selected fungi are shown in Text-figures 1–11. Except in the cases of *Microxyphium* spp. A and B, the text-figures show the diameters of the colonies 7 days after inoculation. The species of *Microxyphium* have a very slow growth rate, the colony 7 days after inoculation being very small. It was therefore found advisable in this case to give the amount of growth after 21 days. No text-figures are included to show the amount of growth made by *Botrytis cinerea* since, after 7 days, the fungus colony usually covered the whole area of the Petri dish.

A summary of the results obtained, with special regard to the types of growth and amount of spore production, is given in Table 1.

It appears from this table that there are a number of differences between the two strains of *Capnodium* sp., as shown by their reactions on similar media. The chief difference is that strain 1 grows poorly on dextrose agar, whereas strain 2 grows well. The growth rate of strain 2 on all media is slightly higher than that of strain 1 (Text-figs. 6–7).



Text-figs. 1-11.—Tables to show the amount of growth made on different carbohydrate media by sooty mould fungi. (A, arabinose; B, xylose; C, levulose; D, dextrose; E, mannose; F, sucrose; G, maltose; H, lactose; I, raffinose; J, inulin; K, starch; L, dextrin.) 1. *Penicillium expansum*; 2. *Asbolisia* sp.; 3. *Cladosporium herbarum*; 4. *Dematium pullulans*; 5. *Caldariomyces* sp.; 6, 7. *Capnodium* sp.; 8. *Microxyphium* sp. A, strain 1; 9. *Microxyphium* sp. A, strain 2; 10. *Microxyphium* sp. C; 11. *Microxyphium* sp. B.

TABLE 1.

Fungus.	Monosaccharides.			
	Pentoses.		Hexoses.	
	Arabinose.	Xylose.	Dextrose.	Levulose.
Botrytis cinerea ..	Growth and spore production poor.		Growth and spore production very good.	
Penicillium expansum	Growth and spore production medium.		Growth and spore production very good.	
Asbolisia sp. ..	Growth medium, pycnidium production poor.		Growth and pycnidium production very good.	
Cladosporium herbarum ..	Growth and spore production medium.		Growth and spore production good.	Growth and spore production very good.
Dematium pullulans	Growth medium, colony thin, olive-green.	Growth medium, colony dark, slimy due to numerous conidia.	Growth good, colony olive-green.	Growth medium, colony olive-green.
Caldariomyces sp...	Growth very poor, spore production medium.		Growth and spore production very good.	Growth and spore production good.
Capnodium sp. strain 1.. ..	Growth and pycnidium production medium.		Growth and pycnidium production poor.	Growth and pycnidium production very good.
Capnodium sp. strain 2.. ..	Growth and pycnidium production poor.	Growth and pycnidium production poor.	Growth and pycnidium production good.	
Microxyphium sp. A, strain 1.. ..	Growth and pycnidium production medium.	Growth and pycnidium production very poor.	Growth and pycnidium production medium.	Growth and pycnidium production good.
Microxyphium sp. A, strain 2.. ..	Growth and pycnidium production medium.	Growth and pycnidium production very poor.	Growth and pycnidium production medium.	Growth and pycnidium production good.
Microxyphium sp. B	Growth good.	Growth good.	Growth medium.	Growth good.
Microxyphium sp. C.	Growth and pycnidium production poor.	Growth and pycnidium production very poor.	Growth and pycnidium production good.	

TABLE 1.

Mannose.	Disaccharides. Sucrose.	Maltose.	Lactose.	Trisaccharide. Raffinose.	Text-fig.
Growth and spore production very good	Growth and spore production very good.		Growth and spore production poor.	Growth and spore production poor.	
Growth and spore production medium.	Growth and spore production good.	Growth and spore production medium.	Growth and spore production poor.	Growth and spore production good.	1
Growth and pycnidium production medium.	Growth and pycnidium production good.	Growth and pycnidium production medium.	Growth and pycnidium production poor.	Growth and pycnidium production very good.	2
Growth and spore production good.	Growth and spore production very good.	Growth and spore production good.	Growth and spore production very good.	Growth and spore production very good.	3
Growth very poor, colony white.	Growth very good, colony olive-green.	Growth medium, colony olive-green.	Growth poor, colony white.	Growth rather poor, colony white.	4
Growth and spore production medium.	Growth and spore production medium.		Growth poor, spore production good.	Growth and spore production very good.	5
Growth and pycnidium production rather poor.	Growth and pycnidium production good.		Growth and pycnidium production medium.	Growth and pycnidium production good.	6
Growth and pycnidium production poor.	Growth and pycnidium production medium.			Growth and pycnidium production good.	7
Growth and pycnidium production poor.	Growth and pycnidium production good.		Growth and pycnidium production poor.	Growth and pycnidium production fairly good.	8
Growth and pycnidium production poor.	Growth and pycnidium production medium.	Growth and pycnidium production good.	Growth and pycnidium production poor.	Growth and pycnidium production fairly good.	9
Growth poor.	Growth medium.		Growth poor.	Growth good.	11
Growth and pycnidium production medium.	Growth and pycnidium production good.		Growth poor, pycnidium production medium.	Growth and pycnidium production good.	10

The differences in reaction to similar culture media between strains 1 and 2 of *Microxyphium* sp. A (Text-figs. 8–9) are only of minor importance, the chief being the greater growth rate of strain 1.

All the sugars used in this experiment are utilized to a greater or lesser degree by the fungi under investigation. On the whole the pentoses are not so satisfactory for the maintenance of growth and reproduction as are the hexoses. Of the hexoses, mannose is generally poorly utilized, whereas dextrose and levulose are uniformly very satisfactory. Of the disaccharides, sucrose and maltose are moderately satisfactory, and lactose poor. The trisaccharide raffinose is unsatisfactory for *Dematium pullulans* (Text-fig. 4) and *Botrytis cinerea*, but is otherwise well utilized, especially by the members of the Capnodiaceae.

The growth reactions of the Capnodiaceae to the various sugars are strikingly similar (Text-figs. 5–11). It is noticeable that the two widespread saprophytes, *Penicillium expansum* (Text-fig. 1) and *Cladosporium herbarum* (Text-fig. 3) show less difference in growth on the different sugars than do the other fungi. This ability to utilize a wide range of food materials is no doubt responsible for their cosmopolitan distribution. On the other hand the growth reactions of *Dematium pullulans* (Text-fig. 4), which is also a widespread saprophyte, are in striking contrast with those of *Penicillium* and *Cladosporium*. In the case of *Dematium*, and to a lesser extent in the Capnodiaceae, the growth on the various media used shows a great variation. Instead of a more or less uniform growth on all the media, growth on some of the sugars may be very good, whilst other sugars may scarcely be utilized at all, as with *Dematium* on mannose.

On the whole the growth of the members of the Capnodiaceae is very slow compared with that of the other fungi investigated.

The mould *Botrytis cinerea* shows the least ability to utilize the range of carbohydrates, which is contrary to what would be expected when its widespread occurrence is considered.

The growth rates of *Penicillium* and *Caldariomyces* on a representative number of the agars used are shown in Text-figures 12 and 13. They are typical of the fast and slow growing fungi respectively.

Brown (1923) has pointed out that in culture media the growth of a fungus is at first slow, but increases until a maximum is reached, at which it remains steady, or from which it subsequently declines. A declining growth rate is due to staling of the medium by materials produced by the growth of the fungus.

Text-figure 12 shows that there is no evidence of staling by *Penicillium* during the period in which the fungus was under investigation, even in the case of sugars which were not very satisfactory for growth, such as lactose and mannose.

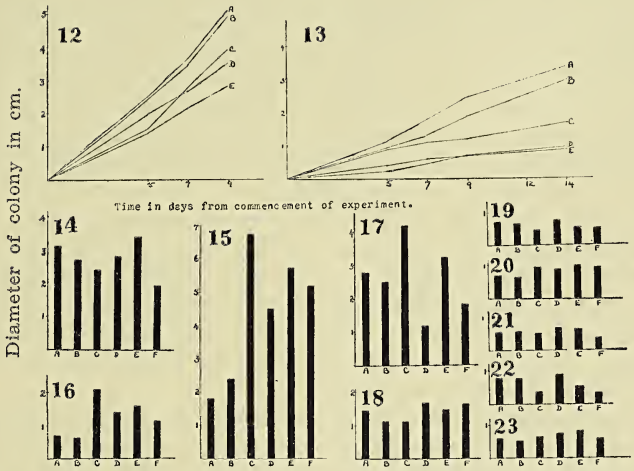
The slight flattening of the curves of *Caldariomyces* shown in Text-figure 13 indicates slight staling, especially in the cases of xylose and mannose.

(ii) *Polysaccharides.*—The amount of growth made on polysaccharide media is shown in the preceding figures. In all cases good growth was made, comparable with or better than that made on the sugar media. Inulin is found to be slightly less favourable than starch or dextrin for the growth of members of the Capnodiaceae, but for the other fungi it is quite satisfactory. The growth rates of all the fungi are uniform on the polysaccharide media, and there is no evidence of staling during the period when the cultures were under investigation.

From the above results it is not possible to find any definite relationship between the distribution of sooty mould fungi and their ability to utilize various

carbohydrates as a source of food. The two most widespread mould fungi, *Penicillium* and *Cladosporium*, show the greatest ability to utilize a wide range of carbohydrates.

Farries and Bell (1930), working with *Nematospora* and allied fungi, found that growth on media containing the pentoses arabinose and xylose was negligible. Glucose, fructose and mannose, on the other hand, were very favourable. Sucrose and maltose were favourable, but growth on lactose was negligible. One species of *Nematospora* made good growth on starch, the others making slight but quite



Text-fig. 12.—Graph to show the growth rate of *Penicillium expansum* on a number of carbohydrate media. (A, inulin; B, dextrose; C, arabinose; D, mannose; E, xylose.)

Text-fig. 13.—Graph to show the growth rate of *Caldariomyces* sp. on a number of carbohydrate media. (A, levulose; B, raffinose; C, inulin; D, mannose; E, xylose.)

Text-figs. 14-23.—Tables to show the amounts of growth made on different nitrogen compounds by sooty mould fungi. (A, ammonium sulphate; B, ammonium nitrate; C, potassium nitrate; D, sodium nitrate; E, peptone; F, asparagin.) 14. *Penicillium expansum*; 15. *Asbolisia* sp.; 16. *Cladosporium herbarum*; 17. *Dematium pullulans*; 18. *Caldariomyces* sp.; 19, 20. *Capnodium* sp.; 21. *Microxyphium* sp. A, strain 1; 22. *M.* sp. B; 23. *M.* sp. C.

definite growth, indicating the presence of diastase. Norman (1930) found that certain soil fungi showed greater ability to utilize hexose than pentose sugars.

It is apparent that the sooty mould fungi investigated in the present work have a greater ability to utilize a wide range of carbohydrate materials than have parasitic species such as *Nematospora*.

Growth on Nitrogen Media.

In order to investigate the ability of the sooty mould fungi to utilize various nitrogen compounds the following inorganic and organic sources of nitrogen were used. Inorganic: ammonium sulphate, ammonium nitrate, potassium nitrate, sodium nitrate. Organic: peptone, asparagin.

Agars were made up according to the formula of Farries and Bell (1930) as follows: agar 2%, dextrose 2%, potassium dihydrogen phosphate 0·5%, magnesium sulphate 0·25% and the nitrogen compound in sufficient quantity to yield 0·3% nitrogen.

The amount of growth made by each fungus on the different nitrogen compounds is shown in Text-figures 14–21. Except in the case of *Microxyphium* spp. A and B, for which the figures indicate growth after 21 days, the diameter of the fungal colony after 7 days is given. Curves to show the individual growth rates of a representative set of fungi, *Asbolisia*, *Penicillium*, *Cladosporium*, *Dematium* and *Caldariomyces*, are also shown. From these figures it can be seen that there is a great variety of reactions to the different compounds.

Botrytis cinerea.—Growth is feeble on the ammonium compounds and on KNO_3, moderately good on $NaNO_3$, and good on peptone and asparagin.

Penicillium expansum (Text-fig. 14).—Growth is satisfactory on all compounds except asparagin. Peptone and NH_4SO_3 give the best results. Although at first growth on asparagin is not much less than on other media (Text-fig. 24), the growth rate falls off rapidly and ceases altogether by the ninth day (as shown by the flattening of the curve for asparagin in Text-fig. 24). Staling is therefore indicated. Slight staling is also indicated by the declining rate of increase shown by the curve for NH_4NO_3. Very rapid growth in diameter takes place on KNO_3, but the colony is thin and the conidia sparse.

Asbolisia sp. (Text-fig. 15).—Growth is poor on ammonium salts. On KNO_3 growth is rapid but thin. On asparagin, though the growth is rapid, the colony is pale and uneven, and no pycnidia are produced. Peptone and $NaNO_3$ are very satisfactory. From a study of the growth rate of the fungus on the different media (Text-fig. 25), it is apparent that staling takes place on asparagin and ammonium salts. As is the case with *Penicillium*, the growth rate on KNO_3 is very fast, but the resulting colony is very thin.

Cladosporium herbarum (Text-fig. 16).—Growth is poor on ammonium salts, medium on asparagin, very good on KNO_3, and good on $NaNO_3$ and peptone. Text-figure 26 shows the growth rates on the various media. The curves for ammonium salts and for asparagin indicate that staling is strongly marked on these media.

Dematium pullulans (Text-fig. 17).—Growth is good on KNO_3 and peptone, and medium on the other compounds. $NaNO_3$ is rather unsatisfactory. The growth curve for asparagin (Text-fig. 27) indicates pronounced staling. Slight staling is also indicated by the curves representing growth on ammonium salts, peptone and $NaNO_3$.

Caldariomyces sp. (Text-fig. 18).—Growth and spore production are satisfactory on all media except asparagin, $NaNO_3$ being the most favourable. As shown in Text-figure 28, growth on asparagin is at first good, but staling becomes very pronounced. Staling is also indicated on KNO_3 and NH_4NO_3.

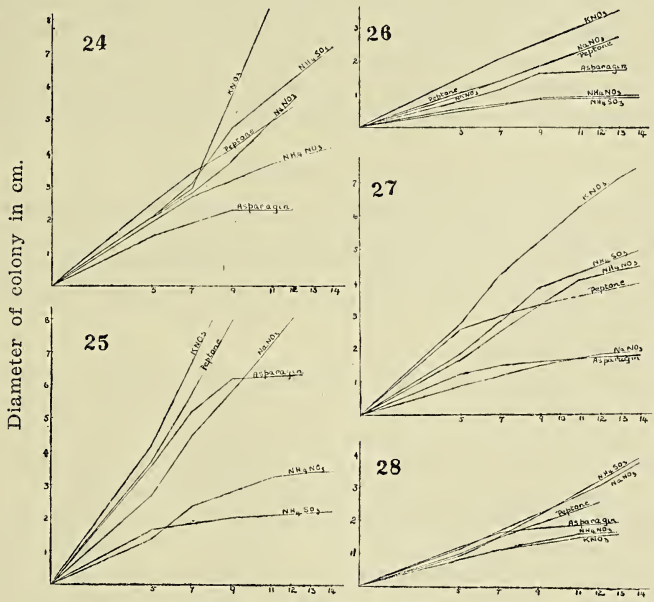
Capnodium sp. (strain 1, Text-fig. 19; strain 2, Text-fig. 20).—On the whole, growth is faster in strain 2 than in strain 1. Growth and spore production are best on $NaNO_3$ and peptone, but all media are fairly satisfactory. Staling is marked on asparagin.

Microxyphium sp. A (strain 1, Text-fig. 21).—Both strains react similarly. Growth and pycnidium production are best on $NaNO_3$ and peptone, medium on ammonium salts and KNO_3 and poor on asparagin. Staling is not shown because of the slow rate of growth.

Microxyphium sp. B (Text-fig. 22).—Growth is best on $NaNO_3$ and ammonium salts, poor on KNO_3 and asparagin, and medium on peptone. Staling is not shown.

Microxyphium sp. C (Text-fig. 23).—Growth is good on $NaNO_3$ and peptone, and rather poor on ammonium salts, KNO_3 and asparagin. Staling takes place on asparagin.

It will be apparent at once that the results obtained for growth on nitrogen compounds differ from those obtained for growth on carbohydrates. Growth on unfavourable nitrogen compounds is accompanied, especially in the case of the fast-growing fungi, by pronounced staling. On unfavourable carbohydrates, on the other hand, growth is slow, but staling, if shown at all, is not pronounced.



Text-figs. 24-28.—Graphs to show growth rates on different nitrogen compounds: 24. *Penicillium expansum*; 25. *Asbolisia* sp.; 26. *Cladosporium herbarum*; 27. *Dematium pullulans*; 28. *Caldariomyces* sp.

From this it may be concluded that certain carbohydrates are unsatisfactory because they cannot readily be utilized by the fungus, whereas, in the case of unfavourable nitrogen compounds, materials are produced as the result of the metabolism of the fungus which are inimical to further growth, and so cause staling.

Asparagin is unsatisfactory as a source of nitrogen for all fungi except *Botrytis cinerea*, and growth on this medium is accompanied by pronounced staling in all cases but that of *Botrytis*. The fact that *Botrytis* grows very quickly and is a non-staling type of fungus (Brown, 1923) may account for its good growth on asparagin, since staling is not shown by other fungi till after about 7 days, and by that time the growth of *Botrytis* has covered the area of the Petri dish.

Ammonium salts are unsatisfactory for *Cladosporium*, *Dematium* and *Asbolisia*, but are utilized moderately well by the Capnodiaceae, and very well by *Penicillium*.

The growth of the fungi on KNO_3 is generally thin. Peptone and $NaNO_3$ are the most universally satisfactory nitrogen compounds. $NaNO_3$ is very satisfactory for the Capnodiaceae, rather more so than peptone, but is very unsuitable for *Dematium pullulans*.

Penicillium has the ability to utilize the greatest range of nitrogen compounds, growing equally well on organic and inorganic media. *Cladosporium herbarum*, which, like *Penicillium*, has the ability to utilize a wide range of carbohydrate materials, is, on the other hand, fairly restricted in its growth on nitrogen compounds. It grows well only on $NaNO_3$, peptone and KNO_3. *Dematium pullulans* is also unable to utilize satisfactorily a wide range of nitrogen compounds.

Farries and Bell (1930) have found that peptone and, to a less degree, asparagin are utilized by *Nematospora*, but that KNO_3 and ammonium salts are of little value. On the whole, the sooty mould fungi show a considerably greater ability to utilize inorganic as well as organic nitrogen compounds than the parasitic *Nematospora*, but are less omnivorous than the widespread mould *Penicillium*.

The Carbohydrate-Nitrogen Ratio.

This section of the inquiry commenced with a study of the effects of increased concentrations of sugar on the growth and reproduction of the fungi under investigation. Since these were found to give suggestive results, the inquiry was extended to include other variations in the relative concentrations of carbohydrates and nitrogen.

The work falls into three sections:

(i). *Media of varying sugar concentration.*—Agar was made up in the manner described in the previous section, but the sugar concentration varied as follows: (*a*) low concentration 0·5%, (*b*) medium concentration 2%, (*c*) high concentration 10%. The nitrogen constituent was constant throughout, so that the media were of low, medium and high carbohydrate-nitrogen ratio respectively.

(ii). *Media of varying nitrogen concentration.*—Four sets of experiments were made: (*a*) with peptone dextrose agar, (*b*) with peptone maltose agar, (*c*) with $NaNO_3$ dextrose agar, (*d*) with $NaNO_3$ maltose agar. The sugar concentration was 2% throughout, and other constituents as before. The concentration of nitrogen varied as follows: (*a*) low concentration, nitrogen constituent to give 0·08% N, (*b*) medium concentration, nitrogen constituent to give 0·3% N, (*c*) high concentration, nitrogen constituent to give 1·2% N. Media were thus obtained with high, medium and low carbohydate-nitrogen ratios, differing in concentration from those in the previous section.

(iii). *Media of varying concentration of both nitrogen and sugar.*—Two sets of experiments were made, one in which peptone and the other in which $NaNO_3$ was the source of nitrogen. The agar was made up as previously, except that the concentrations of nitrogen and sugar were varied as follows: (*a*) low concentration, dextrose 0·5%, N compound to give 0·08% N, (*b*) medium concentration, dextrose 2%, N compound to give 0·3% N, (*c*) high concentration, dextrose 10%, N compound to give 1·2% N. In these media the carbohydrate-nitrogen ratio was therefore constant throughout.

All these experiments were not carried out simultaneously owing to lack of space, but since each set contained one identical group, viz., that in which the concentration of nitrogen and sugar was medium, it was possible to check them to see if comparable results were being obtained. It was found that the results for these groups were very close in each set, and therefore comparisons could be made.

(i) *Varying sugar concentration.*

In general, colonies on media of low sugar concentration (i.e., low carbohydrate-nitrogen ratio) grow fairly rapidly and fruit abundantly. Growth is thinner, however, than on media of medium concentration. Spore production is on the

whole slightly less than on media of medium concentration. On media of high sugar concentration spore production is slightly depressed, especially when peptone is the source of nitrogen.

The growth curve of *Cladosporium* on $NaNO_3$ agar is shown in Text-figure 29. This type of curve is also representative of *Penicillium*, *Capnodium* and *Microxyphium* sp. C. It is apparent that growth is most rapid on medium and slowest on concentrated media, but there is no sign of staling.

Text-figure 30 shows the growth curve of *Dematium pullulans* on peptone agar. This type of curve also illustrates the growth of *Asbolisia* sp. Growth on media with high concentration of sugar is extremely rapid, and more so on medium than on low concentrations. Text-figure 31 shows the growth curve for *Caldariomyces*. This is of the same general type as that of *Dematium pullulans*, but the contrast between the growth on the different concentrations is not so marked. Text-figure 32 shows the growth curve for *Microxyphium* sp. B. *Microxyphium* sp. A also exhibits this type of growth. Staling is indicated at high sugar concentration, and best growth takes place at medium concentration.

It appears from these results that the optimum sugar concentration for growth differs for each species. The majority of fungi grow and fruit best at medium concentration. *Botrytis*, *Dematium*, *Asbolisia* and, to a less extent, *Caldariomyces* are able to utilize to advantage much higher concentrations. Staling as a rule is not shown; it was noticed only with *Microxyphium* spp. A and B on media of high sugar concentration.

(ii) *Media of varying nitrogen concentration, and* (iii) *Media of varying concentration of both nitrogen and sugar.*

It will be convenient to deal with the results of the experiments carried out under sections (ii) and (iii) together. Curves indicating the growth rates of the fungi are given in the accompanying figures. The data concerning growth and spore production are summarized in Table 2. In some cases the growth curves for both maltose and dextrose agars are given. In other cases where the growth on the two sugars is very similar, one set of growth curves only is given. In the case of *Microxyphium* sp. A, the final amount of growth made after 21 days is given, since the growth rate of this fungus is very slow, and the growth curve does not show any points of special interest.

Botrytis cinerea.—At low concentrations of nitrogen, and in media in which the concentrations of nitrogen and sugar are both low, growth is thinner than at medium concentrations, and spore production is rather poorer. At high concentrations of nitrogen and sugar and of nitrogen alone growth is very rapid and spore production heavy, the resulting colonies being thicker and more darkly coloured than at lower concentrations.

Penicillium expansum.—Best growth is made on agars with medium concentrations of sugar and nitrogen. Growth is rather thin and spore production less on media of low concentration, especially when sugar as well as nitrogen is low. From an examination of Text-figure 33, which represents growth rates on dextrose and maltose $NaNO_3$ agars, it can be seen that there are indications of staling on maltose agar at high concentrations of $NaNO_3$. At this concentration spore production is quite normal. No staling is indicated at high concentrations of dextrose, but spore production is poor, and the growth rate is slower than at lower concentrations.

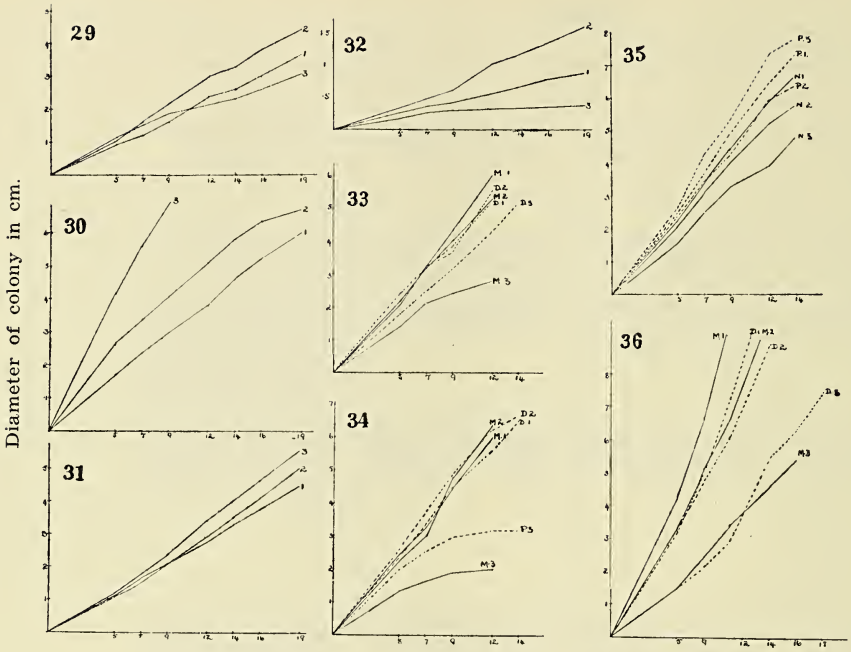
Staling is much more marked at high concentrations of peptone than of $NaNO_3$ (Text-fig. 34), and more so with maltose than with dextrose. If Text-figures 33

TABLE 2.

Fungus.	Carbohydrate-Nitrogen Ratio Medium.		
	Concentration low.	Concentration medium.	Concentration high.
Botrytis cinerea	Growth thin, spore production depressed.	Growth and spore production good.	Growth and spore production good.
Penicillium expansum ..	Growth thin, spore production medium.	Growth and spore production good.	Growth rate high, no staling, spore production depressed.
Asbolisia sp...	Growth thin, pycnidium production medium.	Growth and pycnidium production good.	Growth rate depressed on $NaNO_3$ agar, medium on peptone agar, no staling, pycnidium production poor on $NaNO_3$ agar, medium on peptone agar.
Cladosporium herbarum ..	Growth thin, spore production good.	Growth and spore production good.	Growth rate high, no staling, spore production good on $NaNO_3$ agar, poor on peptone agar.
Dematium pullulans ..	Growth thin and white on $NaNO_3$, slow and dark on peptone agar.	Growth good, colony greyish green on peptone, white on $NaNO_3$ agar.	Growth rapid on peptone, slow on $NaNO_3$ agar, colony greyish on peptone, white on $NaNO_3$ agar.
Caldariomyces sp.	Growth thin, spore production good.	Growth and spore production good.	Growth rate and spore production depressed, no staling.
Capnodium sp.	Growth thin, pycnidium production good.	Growth and pycnidium production good.	Growth rate and pycnidium production depressed, staling.
Microxyphium sp. A ..	Growth and pycnidium production good.		Growth rate depressed, pycnidium production prevented.
Microxyphium sp. B	Growth rate slightly depressed.	Growth good.	Growth rate depressed.
Microxyphium sp. C ..	Growth and pycnidium production good.		Growth rate depressed, staling, pycnidium production prevented.

TABLE 2.

Carbohydrate-Nitrogen Ratio High.		Carbohydrate-Nitrogen Ratio Low.	
Carbohydrate medium, Nitrogen low.	Carbohydrate high, Nitrogen medium.	Carbohydrate low, Nitrogen medium.	Carbohydrate medium, Nitrogen high.
Growth thin, spore production medium.	Growth and spore production good.	Growth thin, spore production medium.	Growth and spore production good.
Growth thin, spore production good.	Growth rate slightly retarded, spore production good, no staling.	Growth thin, spore production good.	Growth rate slow, spore production poor on dextrose $NaNO_3$ agar, staling on peptone and maltose $NaNO_3$ agars.
Growth thin, pycnidium production poor.	Growth very rapid, pycnidium production good, no staling.	Growth thin, pycnidium production poor.	Growth slow, pycnidium production depressed, staling on peptone agar.
Growth thin, spore production medium.	Growth slow, no staling, spore production good.	Growth thin, spore production good.	Growth rate and spore production depressed.
Growth thin, colony white.	Growth very rapid, especially on peptone agar, no staling, colony white.	Growth thin, colony white.	Growth slow, staling marked, especially on peptone agar, colony white.
Growth thin, spore production good.	Growth good, spore production slightly depressed, no staling.	Growth thin, spore production good.	Growth medium, spore production depressed, staling on peptone agar.
Growth thin, pycnidium production good.	Growth good, pycnidium production slightly depressed, no staling.	Growth thin, pycnidium production good.	Growth slow, pycnidium production depressed, staling on peptone agar.
Growth thin, pycnidium production good.	Growth good, pycnidium production depressed.	Growth thin, pycnidium production good.	Growth good, pycnidium production depressed, staling.
Growth rate depressed, no staling.		Growth medium.	Growth rate depressed.
Growth and pycnidium production good.	Growth rate depressed, pycnidium production prevented, no staling.	Growth and pycnidium production good.	Growth rate depressed pycnidium production prevented, staling.



Text-figs. 29-36.—Graphs to show growth rates.

29.—*Cladosporium herbarum* on sodium nitrate agar with different concentrations of sugar. Sugar concentration low (1), medium (2), high (3).

30.—*Dematium pullulans* on peptone agar with different concentrations of sugar. Sugar concentration low (1), medium (2), high (3).

31.—*Caldariomyces* sp. on sodium nitrate agar with different concentrations of sugar. Sugar concentration low (1), medium (2), high (3).

32.—*Microxyphium* sp. B on sodium nitrate agar with different concentrations of sugar. Sugar concentration low (1), medium (2), high (3).

33.—*Penicillium expansum* on dextrose (D) and maltose (M) agars of varying sodium nitrate concentration. Nitrogen concentration low (1), medium (2), high (3).

34.—*Penicillium expansum* on dextrose (D) and maltose (M) agars with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3).

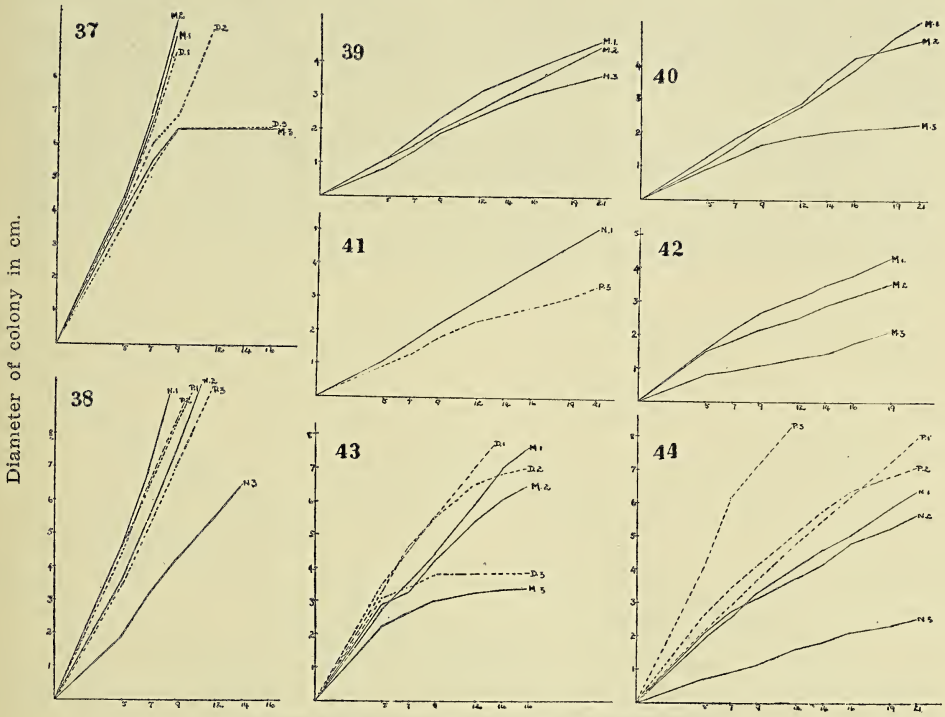
35.—*Penicillium expansum* on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentration low (1), medium (2), high (3).

36.—*Asbolisia* sp. on dextrose (D) and maltose (M) agars of varying sodium nitrate concentration. $NaNO_3$ concentration low (1), medium (2), high (3).

and 34 are compared with Text-figure 35 it can be seen that, although staling is marked at high concentrations of nitrogen when the sugar concentration is medium, no staling occurs in media in which the concentration of sugar as well as that of nitrogen is high. The growth rate is greatly increased in media of high peptone, high sugar concentration, but the spore production is much reduced. Spore production is good on media of high sugar, high $NaNO_3$ concentration.

Asbolisia sp.—The results obtained with this fungus resemble those obtained for *Penicillium*. Growth and pycnidium production are best at moderate concentrations. The actual diameter of the colony may be greater on media of low

concentrations, but the growth is thinner and the pycnidia fewer. On $NaNO_3$ agars growth at high concentrations is slow and no pycnidia are produced. No definite staling, however, is indicated (Text-fig. 36). Staling at high concentrations of peptone is very marked (Text-fig. 37). Pycnidia are produced on dextrose agar but not on maltose agar. As in the case of *Penicillium*, when the concentrations of both peptone and sugar are high no staling takes place, and pycnidium production



Text-figs. 37-44.—Graphs to show growth rates.

37.—*Asbolisia* sp. on dextrose (D) and maltose (M) agars of varying peptone concentration. Peptone concentration low (1), medium (2), high (3).

38.—*Asbolisia* sp. on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentration low (1), medium (2), high (3).

39.—*Cladosporium herbarum* on maltose agar with different concentrations of sodium nitrate. $NaNO_3$ concentration low (1), medium (2), high (3).

40.—*Cladosporium herbarum* on maltose agar with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3).

41.—*Cladosporium herbarum* on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentrations low (1), medium (2), high (3). The curves representing growth on media of low, medium and high $NaNO_3$ concentration, and of high and medium peptone concentration, are similar. Accordingly only the curves for low dextrin, low $NaNO_3$ and high peptone concentration are given.

42.—*Dematium pullulans* on maltose agar with different concentrations of sodium nitrate. $NaNO_3$ concentration low (1), medium (2), high (3).

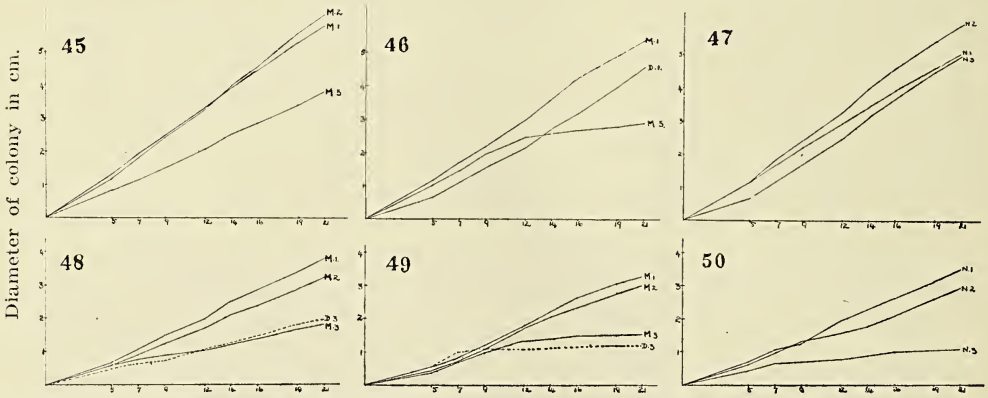
43.—*Dematium pullulans* on dextrose (D) and maltose (M) agars with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3).

44.—*Dematium pullulans* on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentration low (1), medium (2), high (3).

is satisfactory. In the corresponding experiment with high $NaNO_3$ and sugar concentrations, the growth rate is slow and pycnidia are not produced (Text-fig. 38).

Cladosporium herbarum.—Text-figures 39, 40 and 41 indicate results similar to those obtained for *Penicillium*. Growth and spore production are best on media of medium concentration. Fruiting is inhibited at high concentrations of peptone and is poor at high concentrations of $NaNO_3$ on both dextrose and maltose media. Staling is marked at high concentrations of peptone (Text-fig. 40), but is less marked at high concentrations of $NaNO_3$ (Text-fig. 39). The growth rate is high and there is no evidence of staling when the concentrations of sugar and nitrogen are both high (Text-fig. 41). Spore production is depressed especially on peptone agar.

Dematium pullulans.—Results were similar to those obtained for *Cladosporium*. Staling takes place at high concentrations of peptone (Text-fig. 43), but growth is rapid and no staling is shown when the sugar concentration, as well as the peptone concentration, is high (Text-fig. 44). At high concentrations of $NaNO_3$ growth is slow, but staling is not shown (Text-fig. 42).



Text-figs. 45-50.—Graphs to show growth rates.

45.—*Caldariomyces* sp. on maltose agar with different concentrations of sodium nitrate. $NaNO_3$ concentration low (1), medium (2), high (3).

46.—*Caldariomyces* sp. on dextrose (D) and maltose (M) agars with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3). The curve representing growth on maltose agar of medium concentration of $NaNO_3$ is similar to that on maltose agar of low $NaNO_3$ concentration. The curve representing growth on dextrose agar of low $NaNO_3$ concentration is similar to that on dextrose agar of medium $NaNO_3$ concentration. The curve representing growth on maltose agar of high $NaNO_3$ concentration is similar to that on dextrose agar of high $NaNO_3$ concentration.

47.—*Caldariomyces* sp. on sodium nitrate agar with different concentrations of sodium nitrate and sugar. Concentration low (1), medium (2), high (3).

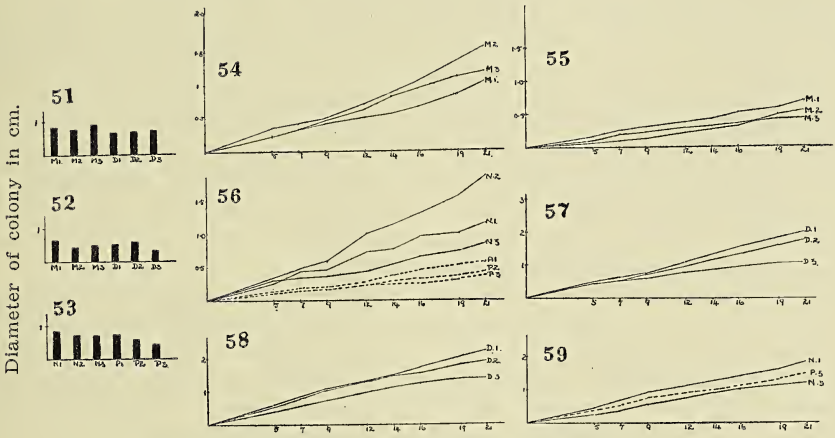
48.—*Capnodium* sp., strain 2, on dextrose (D) and maltose (M) agars with different concentrations of sodium nitrate. $NaNO_3$ concentration low (1), medium (2), high (3).

49.—*Capnodium* sp., strain 2, on dextrose (D) and maltose (M) agars with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3).

50.—*Capnodium* sp., strain 2, on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentration low (1), medium (2), high (3).

Caldariomyces sp.—Spore production is poor at high concentrations of peptone and of $NaNO_3$. Staling takes place at high concentrations of peptone (Text-fig. 46) and the fungal colonies are thick and irregular. No staling takes place at high concentrations of $NaNO_3$ (Text-fig. 45). No staling takes place when the concentrations of sugar and of nitrogen are high (Text-fig. 47), but spore production is poor. At low concentrations of nitrogen, and of sugar and nitrogen, growth is thin and spore production very good.

Capnodium sp.—The reactions of both strains are similar. Growth is slow at high concentrations of $NaNO_3$ (Text-fig. 48) and peptone (Text-fig. 49) and pycnidia are not produced. Staling is pronounced, especially on peptone. Staling is also indicated when the concentrations of sugar and nitrogen are both high (Text-fig. 50), and no pycnidia are produced. Growth at low concentrations is thin but satisfactory, and pycnidium production is good.



Text-figs. 51-53.—Graphs to show amount of growth made after 21 days.

51.—By *Microxyphium* sp. A, strain 1, on dextrose (D) and maltose (M) agars with different concentrations of sodium nitrate. $NaNO_3$ concentration low (1), medium (2), high (3).

52.—By *Microxyphium* sp. A, strain 1, on dextrose (D) and maltose (M) agars with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3).

53.—By *Microxyphium* sp. A, strain 1, on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentration low (1), medium (2), high (3).

Text-figs. 54-59.—Graphs to show growth rates.

54.—*Microxyphium* sp. B on maltose agar with different concentrations of sodium nitrate. $NaNO_3$ concentration low (1), medium (2), high (3).

55.—*Microxyphium* sp. B on maltose agar with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3).

56.—*Microxyphium* sp. B on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentration low (1), medium (2), high (3).

57.—*Microxyphium* sp. C on dextrose agar with different concentrations of sodium nitrate. $NaNO_3$ concentration low (1), medium (2), high (3).

58.—*Microxyphium* sp. C on dextrose agar with different concentrations of peptone. Peptone concentration low (1), medium (2), high (3).

59.—*Microxyphium* sp. C on peptone (P) and sodium nitrate (N) agars with different concentrations of sugar and nitrogen. Concentration low (1), medium (2), high (3).

Microxyphium sp. A.—Staling was not apparent during the course of the experiment on any of the media used. Growth at high concentrations is thick and irregular, but the ultimate diameter of the colonies is much the same at all concentrations (Text-figs. 51, 52, 53). Pycnidia are produced at high concentrations of $NaNO_3$, but not at high concentrations of peptone, nor when the concentrations of sugar and nitrogen are both high. Pycnidia are produced abundantly at low and medium concentrations.

Microxyphium sp. B.—No staling is shown on any of the media (Text-figs. 54, 55, 56). Best growth takes place on media of medium concentration.

Microxyphium sp. C.—Staling is indicated at high concentrations of peptone (Text-fig. 58) and of $NaNO_3$ (Text-fig. 57), but not when the concentration of sugar is high as well as that of the nitrogen (Text-fig. 59). The growth rate at all high concentrations is slow, and no pycnidia are produced. Growth and pycnidium production are good at medium and low concentrations.

From an examination of the above results it is apparent that a low carbohydrate-nitrogen ratio obtained by combining a high concentration of nitrogen with a medium amount of sugar depressed or entirely prevented spore formation in most cases. This effect was more marked with peptone than with $NaNO_3$. The results when a low carbohydrate-nitrogen ratio was obtained by combining a medium concentration of nitrogen with a low concentration of sugar differ from these strongly, and resemble much more closely the results obtained at low concentrations of sugar and nitrogen. It would appear that the reduction in size of the colony and the amount of spore production was due to starvation rather than to the unbalanced carbohydrate-nitrogen ratio.

At high concentrations of peptone and medium concentrations of sugar, staling phenomena are very strongly shown except by the fast growing *Botrytis* and the very slow growing *Microxyphium* spp. A and B. Staling is less marked at high concentrations of $NaNO_3$. Although staling is marked at high nitrogen concentrations, it does not often occur when the concentrations of sugar and nitrogen are both high, i.e., at a balanced ratio of carbohydrate and nitrogen.

A high ratio, due to high concentration of sugar, somewhat depresses the growth rate in all but *Asbolisia*, *Dematium*, *Botrytis* and *Caldariomyces*, and also slightly depresses the spore production. At a high ratio due to low concentration of nitrogen the growth is sparse and the fruiting less in most cases. This again may be due to starvation rather than to an unbalanced ratio of carbohydrate and nitrogen.

Staling of the medium and reduction in the amount of spore production appear to be related to some extent. Staling appears to be a function of the nitrogen compound. This has also been found to be the case by Brown and Horne (1924) and Brown (1925) in the case of species and strains of *Fusarium*.

Both the concentration and the type of compound are of importance, as it has been found that $NaNO_3$ is not so conducive to staling at high concentrations as peptone, and unfavourable nitrogen compounds such as ammonium salts cause staling at low concentrations. Brown and Horne (1924) conclude that staling is also dependent on the concentration of the medium, and that the effects of concentration can be removed by dilution of the media. In the present investigation the effect of staling at high concentrations of the culture medium is strongly marked only in the case of *Capnodium* sp. Its effect was not observed in other cases, possibly because the concentration of the medium was not sufficiently great. It was apparent, however, that a concentration of nitrogen

sufficient to cause serious staling is not effective if the concentration of sugar is increased to balance it.

In agreement with the observations of Horne and Mitter (1927) it was found that high and low concentrations retard the growth rate. It is also apparent that each species has a different optimum concentration and a different range of concentrations suitable for growth. In the Capnodiaceae best growth takes place on media of low and medium concentration, whereas *Dematium* and *Asbolisia* respond to high concentrations of peptone, and *Cladosporium* and *Penicillium* grow more or less satisfactorily on media of high and low concentrations.

In the higher plants it has been shown (Knight, 1924/5; Kraus, 1925) that the relation between the amount of vegetative growth and the amount of reproductive growth made by a plant is determined by the relative amounts of carbohydrate and nitrogenous materials available within it. Efficient growth and reproduction are dependent on a balanced carbohydrate-nitrogen ratio. A low ratio caused by an increase in the amount of nitrogen results in vegetative growth; and a high ratio caused by excess of carbohydrates reduces vegetative growth without inducing fruitfulness.

It appears from the present investigation that much the same relationship holds for the fungi. Spore production is slowed down or prevented by a low ratio due to excess of nitrogenous material, and by an unduly high ratio. Maximum fruitfulness and most efficient vegetative growth take place when the amounts of carbohydrate and nitrogen are balanced and of moderate concentration.

Summary.

1. Experiments have been made to ascertain culturally whether there are any appreciable differences between sooty mould fungi and other moulds in their ability to utilize different classes of food materials.

2. For this purpose representatives of all types of sooty mould fungi, with *Penicillium expansum* and *Botrytis cinerea* as controls, have been grown on agar media containing a variety of different food materials.

3. *Penicillium expansum* and *Cladosporium herbarum* were able to utilize a wide range of carbohydrates. The other fungi utilized the pentoses and mannose and lactose rather less well. Only *Dematium pullulans* and *Botrytis cinerea* were unable to make good growth on the trisaccharide raffinose.

4. All the fungi grew well on the polysaccharides inulin, dextrin and starch.

5. *Penicillium* was able to use the widest range of nitrogenous compounds. *Cladosporium* was able to grow satisfactorily on peptone, KNO_3 and $NaNO_3$ only. Asparagin was generally unsatisfactory and caused pronounced staling. Members of the Capnodiaceae grew moderately well on all the media tested.

6. By varying the amount of nitrogenous and carbohydrate food material in the agar media the reactions of the fungi to changes of the carbohydrate-nitrogen ratio have been studied. It appears that the fungi resemble the higher plants to a certain extent in that fruiting is poor at low ratios when nitrogen is present in high concentration.

7. Staling was pronounced in agars of moderate sugar and high peptone concentration, but much less so in agars with moderate concentration of sugar and high $NaNO_3$. In most cases staling was not shown when the concentration of both sugar and nitrogen was high.

8. Staling and decrease in spore production appear to be related to some extent.

9. Each fungus has a different optimum concentration of carbohydrate and nitrogen, some being able to utilize higher concentrations than others.

In conclusion, the writer wishes to thank Professor T. G. B. Osborn, in whose laboratory this work was carried out, for his interest and helpful criticism.

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FURTHER ADDITIONS TO THE FLORA OF THE COMBOYNE PLATEAU.

By E. C. Chisholm, M.B., Ch.M.

[Read 27th June, 1934.]

In These Proceedings (1925, p. 284, and 1927, p. 378) the writer has previously recorded the Flora found on the Comboyne Plateau, with notes on the species. The present paper is a continuation of his observations, bringing the record up to date.

Cryptogamae vasculares.

Filicales (Ferns).

Hymenophyllaceae.

Trichomanes venosum.—A delicate feathery climbing fern found on trunks of brush trees and fairly plentiful.

Cyatheaceae.

Dicksonia antarctica.—A fairly common tree fern often found near water, and in the less dense brushes; in fact, it flourishes quite out in the open exposed to the sun's rays.

Alsophila australis.—The hill tree fern. This species seems to prefer the mountainous country and is an inhabitant of the brushes, especially the less dense ones, and found often on creek banks. About the commonest tree fern here.

Alsophila Cooperi.—This and *A. australis* are very much alike in appearance. In *A. Cooperi* the fracture at the base of the dead main rhachis where it joins the stem is clean, leaving more or less of a pit, whereas in all the others the proximal remains of the old rhachis are left attached to the stem. This is an inhabitant of the more open forest hardwood country.

Alsophila Leichhardtiana.—Prickly tree fern. A tall tree fern with a slender stem. As the name implies, the rhachis is covered with sharp spines more thickly at its base. This is a common species inhabiting the dense brushes. The hairy scales in its crown are very pale, almost white in contrast with the other two species of *Alsophila* in which the scales are of much the same elongated flattened shape, but dark reddish-brown in colour.

Polypodiaceae.

Dryopteris decomposita.—A common inhabitant of the brushes, preferring the sombre light and the dampness and forming a dense carpet on the brush forest floor.

Dryopteris acuminata.—Very like the last, and preferring the same kind of situations, very often one brush containing one of these and another brush the other form, the two species being seldom seen together.

Dryopteris punctata.—This species is found commonly in open low-lying ground in the neighbourhood of creeks and often quite plentiful on their banks.

Dryopteris rugulosa.—A softer fern and more hairy than the last, but otherwise much resembling it; the two species are frequently found growing in association, preferring the same sort of locality. They are both plentiful.

Dryopteris parasitica.—A much less common fern, being found as a rule close to water and often in rocky situations. This is a graceful, handsome fern.

Arthropteris obliterata.—This and the two following species are climbers. Found on trunks of brush trees growing in dense clusters. The fronds are small in this species.

Arthropteris Beckleri.—Much like the last and growing in the dense brushes attached to tree trunks.

Arthropteris tenella.—A very beautiful species with large pinnae; it follows the trunks of the brush trees, to which it attaches itself, to a height of perhaps 20 feet. The frond is of a delicate structure.

Davallia pyxidata.—Hare's foot fern. A fairly plentiful species found along creeks and sometimes in rocky situations. Its structure resembles that of a stunted tree fern; it has a broad low trunk from which several stems arise.

Davallia dubia.—A much smaller, softer fern of a light yellowish-green, growing mostly on the banks of running water in the open. This is found fairly plentifully in patches and often in association with other species.

Athyrium umbrosum.—A soft fern of pretty form, growing in isolated clumps in the open, sometimes near running water, sometimes not, and fairly plentiful when searched for. It may attain a height of 5 feet.

Athyrium umbrosum var. *semidivisum*, n. var.—This fern in general form resembles the type of *A. umbrosum*, but differs in some essential features. It has only been found by the writer so far in one area in the centre of the Plateau along the course of a creek in dense brush and here it is plentiful over a small area. In height it may reach 5 feet, which is about equal to that attained by the type. In those specimens of larger growth here and there one sees a gradation towards the type, especially in the complete division of the larger pinnules towards the base of the plant, particularly with a tendency to spacing between the pinnules and a more decided crenation of their edges. In typical *A. umbrosum* there is not only complete division of the pinnules, but there is wide spacing between them of from ¼ to ½ inch and the crenation is so decided that the pinnule is divided into lobes. The method of sporulation of both ferns is similar, the sori being elongated and placed with their long axes arranged diagonally following the course of the venation, though the shape and size of the sori in each case differ somewhat. This variety has not previously been described.

The differences between typical *Athyrium umbrosum* and this variety are as follows:

	Athyrium umbrosum.	*A. umbrosum* var. *semidivisum.*
1.	A fern of finer texture and more elaborate in formation of pinnules.	Coarser texture and less finely finished pinnules.
2.	Rhachis light coloured.	Rhachis dark coloured.
3.	Pinnae closer and more numerous.	Pinnae wider apart and less numerous.
4.	Pinnules divided to base with space of ¼ to ½ inch between them at junction with base.	Pinnules usually divided from each other about half-way to base.
5.	Margins of pinnules distinctly crenate.	Smooth or only slightly crenate.
6.	Sori shorter and wider, 1·8-2·5 × 1·4 mm.	Sori longer and narrower, 2·0-4·5 × 1·0 mm.
7.	Secondary pinnae distinctly alternate throughout.	Secondary pinnae in some specimens opposite.

Athyrium umbrosum.	*A. umbrosum* var. *semidivisum.*
8. Pinnules sometimes as much as one-third of their length longer than those of variety.	Pinnules two-thirds the length of those of type.
9. Secondary pinnae not so acuminate, becoming wider at base and more deltoid.	Secondary pinnae acuminate, rather narrow at base and less deltoid.
10. Scales on under side of rhachis wanting or extremely few.	Numerous scales in this situation.
11. Found in open grass lands away from water sometimes.	Found in brush in vicinity of running water.

When all these facts have been considered and the points of departure from the type of *Athyrium umbrosum* recognized, it would appear that this form is entitled to at least varietal rank. In allusion to the pinnules in the main being only partially divided from each other and not being distinctly separate as in the type, and this being an important feature, I propose for the variety the name of *Athyrium umbrosum* var. *semidivisum.*

ATHYRIUM UMBROSUM var. SEMIDIVISUM, n. var.

Filix centimetra xc–cl alta, in area circumscripta inventa, prope aquam in sylva densa. Pinnae remotae. Pinnae secundariae plerumque alternae aliquando oppositae, exemplis fortuitis. Pinnulae ad basem indivisae ut plurimum semidivisae plus minus praeter prope bases pinnarum magnarum ubi disjunctio perfecta absolutaque sit, etiam cum interstitio parvo, margines pinnularum plerumque intactae praeter in frondibus magnis prope basem plantae ubi leviter serratae sint.

A fern 90–150 cm. (3–5 ft.) high, found in restricted area near water in brush. Pinnae far apart. Secondary pinnae mostly alternate, sometimes opposite in odd specimens. Pinnules undivided to base usually divided more or less for half their depth except near base of large pinnae where the division may be complete even with small interspaces. The edges of pinnules mostly entire, except in the large fronds near the base of the plant where the edges may be crenate.

I want here especially to thank Miss Lilian Fraser and Miss Joyce Vickery for the interest they have taken in this new fern and for their great help in working out its affinities.

Asplenium nidus.—Bird's nest fern. This is an epiphyte on the trunks of numerous brush trees and is very plentiful. It covers a large area with its wide and long fronds. It is quite often that one sees a tree trunk almost covered with them, situated one below the other.

Asplenium flabellifolium.—One of the smallest climbers of the family, each pinna shaped like a miniature fan. This grows mostly in rocky situations, especially in damp places, but not necessarily in the brushes. It seems to prefer the open. It is fairly plentiful in these situations.

Asplenium adiantoides.—An extremely pretty climbing fern growing in great profusion in certain brushes and being entirely absent in others. Not very common.

Blechnum cartilagineum.—This, like all the genus, grows in clumps and often in association with different members of the genus. It is rather stiff and smooth, and common in certain damp situations, as, for example, along the banks of creeks.

Blechnum serrulatum.—As its name implies, it has a markedly serrated edge to fronds; is generally of a light green; the commonest species and found most often at the water's edge and often in association with *B. discolor.*

Blechnum Patersoni.—This is a species with a dark green frond. It is not as plentiful as the other species and seems to prefer damp rocky situations such as would be found in close proximity to waterfalls.

Blechnum discolor.—This species is one of the commonest, and is found in profusion about the banks of creeks close to the water's edge. This species and *B. cartilagineum* are very likely to be confused on account of their similarity, the fertile fronds being the only certain means of distinguishing them, and this confusion is aggravated when they are growing in company.

Blechnum capense.—This prefers the floor of the brushes and is of a dark green colour. The rhachis is generally covered with numerous coarse scales. Not as common as the other forms here.

Doodia aspera.—This fern is found in rocky and hilly country out in the open forest, often away from water, but sometimes in close proximity to it. It is a harsh, rough species, showing beautiful pink tints in its young fronds. It is plentiful.

Pellaea paradoxa.—An unusual looking species with cordate fronds growing in clumps, often in rocky situations far up hillsides and again on the floor under brush trees. It is met with frequently in these situations.

Pellaea falcata.—The habitat of this varies; sometimes it is found near running water in rocky situations, at others on the higher elevations away from water. It is a handsome species, commonly called herring-bone fern. May be found in the brushes or in hardwood country and quite plentiful.

Pellaea falcata var. *nana.*—Very like the last, but a smaller form in its general growth and also in its pinnae. It is found in the same sort of situations as the last and often in close association with it, especially near water in rocky localities.

Notholaena distans.—Found in dry and rocky situations and often at high elevations in open forest country. It is not commonly an inhabitant of the basalt. It is uncommon here.

Adiantum aethiopicum.—Common maiden hair. This is an extremely rare form here, probably due to the elevation of the Plateau. In the writer's experience this form grows mostly below the 2,000-foot level and is quite rare above. It likes moist situations in shady spots. I know of only one locality on the Plateau where it occurs, and that is an area of perhaps half an acre covering a spring at the edge of a brush.

Adiantum formosum.—A very handsome fern growing mostly in rocky situations and often quite a distance from water. It is plentiful in certain localities.

Adiantum affine.—A handsome species resembling *A. formosum* in some ways, but the individual pinnules are not incised into lobes to the same extent. It is taller and more attenuated and does not branch so widely. It is a common inhabitant of the brush floor, preferring the dense vegetation and gloom and liking the moist atmosphere. It is common.

Adiantum hispidulum.—This species much resembles the last, differing in the under surface of the fronds and the rhachides being covered profusely with hairs which extend over the sori. In its mode of branching it approaches most closely to *A. formosum.* In the arrangement of the sori it also differs from *A. affine.* It seems to prefer rocky places in close proximity to water, especially that associated with falls where it is continually bathed in sprays. Not so abundant as *A. affine* and not often noticed.

Pteris tremula.—Very like bracken at first sight and often growing in association with it, but its fronds are softer and finer. Found growing in mountainous situations, sometimes on steep slopes well away from water, and frequently growing under and about logs lying on the ground. Fairly plentiful in these situations. It is not an inhabitant of the brushes, preferring open hardwood country.

Histiopteris incisa.—A pretty soft fern of a fairly high growth, often found growing on the banks of running water and moderately plentiful here. It seems to vary a good deal in the arrangement of its pinnules, which are of large size.

Pteridium aquilinum.—This is plentiful everywhere in the open, but does not grow in the brushes. This is the common Bracken.

Polypodium australe.—A small fern appearing to prefer rocky moist situations amongst moss, such as in close proximity to waterfalls where there is a continuous spray. Not often noticed.

Polypodium Brownii.—A dark green species with long narrow fronds. A climber found in rocky situations near water and also in the denser brushes associated with clumps of moss on the trunks of brush trees. Plentiful.

Polypodium diversifolium.—As its name implies, this is very variable in the shape of its fronds, some fronds being simple, as in *P. Brownii*, and others being pinnatifid and of varying shapes. Found in the brushes ascending the trunks of trees and associated with decaying vegetation. It is common in the denser brushes.

Cyclophorus serpens.—This is another climber seen frequently growing on rocks near water and also in the brushes, often in association with species of other genera on the trunks and branches of trees. One of its special favourites is *Sambucus xanthocarpa* (Elderberry), on the trunks of which it is frequently found.

Cyclophorus confluens.—Very like the last, the fronds in this species being more elongated than those of *C. serpens*, which are shorter and more rounded. This grows in the same situations and often in association with the latter. Both are plentiful.

Platycerium bifurcatum (*P. alcicorne*).—Elk horn. This is the commoner species of the genus here, though it is not so very plentiful. It grows as an epiphyte on the brush tree trunks and branches and is a typical brush growth and often in association with *Asplenium nidus* (Bird's nest fern). The fronds are very divided.

Platycerium grande.—Staghorn. Quite a rare form here and noticed more particularly on the western side of the Plateau. More common in the brushes nearer sea-level. It grows as an epiphyte on the trunks and branches of brush trees in the same manner as *P. bifurcatum*. The fronds in this are broader and less divided; it is easily distinguished by its broad green expanded frond enveloping the base and the veins are more distinctly marked.

GLEICHENIACEAE.

Gleichenia circinata.—Commonly found near water, especially springs or on the banks of creeks, but not in the brushes. It is a pretty species, but not very plentiful.

Gleichenia flabellata.—The Umbrella fern. Found fairly plentifully on the banks of creeks and generally in association with other species. It does not inhabit the brushes.

OSMUNDACEAE.

Todea barbara.—King fern. This is always associated with water and found in the brushes following the course of creeks. It possesses a short, stunted, thick trunk from which the fronds, which are wide and finely crenate, arise. It is quite common.

ANGIOSPERMAE.

MONOCOTYLEDONEAE.

CYPERACEAE.

Carex brunnea.—Plentiful on cleared land.

FLAGELLARIACEAE.

Flagellaria indica.—Lawyer cane, sometimes called "Vine-reed cane", is found festooning high trees in the brushes, but is not plentiful. It is sometimes called Lawyer Vine, but this is usually applied to a thorny climber as *Smilax australis*. *F. indica* is not thorny.

COMMELINACEAE.

Commelina cyanea.—This differs from the coastal species in the flower being a pale blue in contrast to that on the immediate coast line, which is a vivid Prussian blue in colour, the difference being probably due to elevation, with its different climate or soil, or perhaps both factors are at work.

LILIACEAE.

Dianella caerulea.—Fairly common in rocky situations.

Drymophila Moorei.—This grows plentifully on the floor of some of the brushes.

ORCHIDACEAE.

Diuris maculata.—This has been only noticed once here, and that was in an open grass paddock on basalt formation.

DICOTYLEDONEAE.

CASUARINEAE.

Casuarina suberosa Ott. & Dietr.—Not common and only found in a small area on south-eastern side.

ULMACEAE.

Trema aspera.—Peach-leaf Poison Bush. As its name implies, this is dangerous to stock. It grows fairly abundantly in the brushes in certain parts, but never seems to attain to large growth.

URTICACEAE.

Australina pusilla.—Found in moist rocky places enjoying the spray of waterfalls.

PROTEACEAE.

Persoonia (*mollis* R.Br., var.? or near it).—A geebung only found in restricted area on the northern side of the Plateau on a mixed soil. This has large leaves. It is under investigation.

Persoonia sp.—Has long narrow leaves and is uncommon.

Lomatia Fraseri.—This appears to differ from the type in some characters. It grows as a small tree along the banks of watercourses and is plentiful. The timber has a very pretty grain and is pink in colour.

Banksia collina R.Br.—Only found in restricted area in south-east.

CHENOPODIACEAE.

Chenopodium triangulare.—A climber and fairly plentiful. At first sight this, *Rumex scutatus* (an introduced plant) and *Melothria Cunninghamii* are easily confused, as their leaves are very similar, and they are all climbers and grow in the same kind of places. *Rumex* has stem-clasping stipules in the leaf axils and *Melothria* has tendrils in this situation.

RANUNCULACEAE.

Ranunculus rivularis.—This is not a very common species here, and is found on banks of creeks close to the water's edge. It has a much smaller flower than *R. lappaceus* (common Buttercup).

MONIMIACEAE.

Daphnandra micrantha.—Called sometimes "Satin Wood", from the silky sheen of the timber. It grows mostly at the western side of the Plateau. The timber is yellowish and very like that of *D. tenuipes.*

LAURACEAE.

Cryptocarya patentinervis.—The timber of this is of a reddish colour and should be useful, but does not seem to be passed through the mills to any extent. The only use to which it is put here is for making whip handles from the sapling wood on account of its resiliency. It is fairly plentiful.

Cryptocarya obovata.—This Laurel is remarkable for its large coarse leaf with prominent veins on the underside. It is not plentiful in the brushes which are still standing. The timber does not seem to be used in the mills here, though it should be useful.

Cryptocarya erythroxylon.—Not a common species here now. Its leaves have a close resemblance to those of *E. patentinervis*, as have also the trees in general appearance, though the timber differs considerably. When the green wood of this species is first cut, it is whitish, becoming yellowish in different shades as it dries, and this may take place within an hour of its being cut. It is called here "Marble Wood" on this account. The freshly-cut timber has a strong aromatic scent. It is always welcomed at the mills.

Endiandra (*virens*?).—This has a whitish timber and is very hard, hence it gets the name "Steel Wood". There is a little doubt about the species. It is fairly plentiful as a tall brush tree.

Endiandra Muelleri.—A very shapely laurel with fine canopy and close foliage, making a good shade tree and an ornament to any plantation. It is distinctly rare.

Cassytha melantha R.Br.—Only found in restricted area in the south-east.

CAPPARIDACEAE.

Capparis nobilis.—This caper grows to a height of at least 25 feet, with a diameter of more than a foot at the butt. The writer has never seen it at the top of the Plateau, but only on the lower slopes near the base. It is distinctly uncommon.

SAXIFRAGACEAE.

Cuttsia viburnea.—This is more a shrub than a tree, not very common, and grows in the brushes on basalt.

Quintinia verdonii.—A brush tree with a loquat-like leaf. It is fairly plentiful, the timber being yellowish-red with rather a pretty grain. Sometimes called "Red Beech".

Polyosma Cunninghamii.—"Feather Wood." Not often seen. The fruit has eight longitudinal ribs and is blue-black.

PITTOSPORACEAE.

Bursaria incana.—Only found in a very restricted area outside the brushes. This is a Black Thorn.

LEGUMINOSAE.

Acacia Cunninghamii var. *longispicata.*—This wattle grows mostly on the southern side outside the brushes and attains a fair size, in contrast with the same species seen about the mouth of the Camden Haven River near Laurieton, about 20 miles away, growing on sand near the beach, where it has acquired a running habit, growing only to the height of two feet or so, but spreading out over a large area.

Hardenbergia monophylla.—The writer has stated in a previous paper that this species does not occur here, but, since that was written in 1925, it has been seen only once, so that it is decidedly rare.

Glycine clandestina.—Plentiful climbing over small plants.

Jacksonia scoparia R.Br.—Restricted to small area in south-east.

RUTACEAE.

Pleiococca Wilcoxiana F.v.M.—Very rare; only seen once on the eastern side.

Phebalium elatius Benth.—Only found on south-east side.

EUPHORBIACEAE.

Croton verreauxii.—Only found growing at the western side of the Plateau and apparently not very abundant. Only a small tree or shrub. The timber is yellowish in colour. It is called "Native Cascarilla".

CELASTRACEAE.

Elaeodendron australe.—A brush tree, not plentiful. It possesses a stiff leaf and the fruit, when ripe, is olive-shaped and bright red.

ICACINACEAE.

Pennantia Cunninghamii.—A tall tree, growing in the brushes, with a diameter at the butt of up to two feet. Not plentiful.

Chariessa Moorei.—Called here "Corduroy Beech". A large brush tree and fairly plentiful.

RHAMNACEAE.

Alphitonia excelsa.—Red Ash. It is a valuable timber, but is not very plentiful. It grows to about 50 feet high, with a diameter at the butt of two feet. The timber is pink in colour, getting darker with age. It is durable and close-grained and used for indoor work and coopers' staves. It grows in the brushes.

ELAEOCARPACEAE.

Sloanea australis.—Maiden's Blush, called so from the delicate pinkish tint of the timber, which, however, is inclined to turn brownish with age. This is a fairly plentiful tree in the brushes, where it may attain the height of 100 feet. Used for cabinet and ornamental purposes, as it possesses a pretty grain.

Sloanea Woollsii var.—This closely resembles typical *S. Woollsii* as a standing tree, though the timber differs a good deal, especially in the colour. In the case of typical *S. Woollsii*, the dark heart wood is deep down in the centre of the log and of very small proportions, the bulk of the timber being white. In *S. Woollsii* var. there is only a narrow rim of white wood externally, the bulk being dark,

extending from the centre to a few inches from the bark. This matter is under investigation by the writer.

MYRTACEAE.

Rhodamnia trinervia.—Sometimes called "Brush Turpentine" on the North Coast. This is a tree growing to 80 feet in the brushes. The leaf is 3-veined, and the veins are prominent on the underside. It does not appear to be of any value as a timber, especially for large work, as the larger trees are mostly hollow.

Eucalyptus altior Maid. & Cambage (*E. oreades* Baker).—Only found in small area of two or three acres on south-east of the Plateau.

Eucalyptus paniculata.—Grey Iron Bark. A little clump grows in a small area just below the top of the Plateau on the northern side, off the basalt.

Eucalyptus Shiressii.—A grey gum with narrow-leaved sucker found on the northern slope a little way from the top. Not seen anywhere else. This makes the sixteenth Eucalypt found on this Plateau.

Kunzea sp.—This is a rare form here and only lately discovered. Its habitat is a small area along the course of a creek in cleared land. It is under investigation.

Leptospermum flavescens var. *grandiflorum.*—This is a tree reaching 40 or 50 feet in height and only found on the southern side bordering a brush. It has a flaky bark, not plentiful.

Melaleuca styphelioides.—Rare, only a few trees found.

OENOTHERACEAE.

Epilobium glabellum var. *Billardierianum.*—This grows in damp places. It has a larger leaf and is of taller growth than typical *E. glabellum.*

UMBELLIFERAE.

Hydrocotyle tripartita.—Very common, growing in damp places forming a dense carpet on the ground.

CORNACEAE.

Marlea vitiensis.—Musk Tree. It is not plentiful and grows to only a medium height of 20 to 30 feet. The timber is yellow, with a black heart, and having a musk-like scent. It is used for cabinet work. The wood is close-grained.

EPACRIDACEAE.

Monotoca sp.—Not common.

Leucopogon juniperinus (*Styphelia juniperina*).—An Epacrid found on Mount Bulli and mentioned, though the species not determined, in These PROCEEDINGS, Vol. 1, Part 3, p. 297 (1925).

MYRSINACEAE.

Rapanea variabilis.—Fairly plentiful.

OLEACEAE.

Notelaea venosa.—A tree growing to about 15 feet. It is comparatively rare here, and only seen by the writer at the northern side of the Plateau on mixed strata. The timber is close-grained and very hard, a fact which has earned for it the name of "Axe-breaker" tree. It bears an olive-shaped fruit.

LABIATAE.

Mentha saturejoides.—This mint, with *M. gracilis*, shares the name of Native Pennyroyal. It does not seem to be plentifully distributed, but grows in patches here and there. It has medicinal properties.

Ajuga australis.—Not very plentiful.

SOLANACEAE.

Solanum nigrum.—This is a low-growing plant with black fruit, in contrast to *S. opacum* which it rather resembles, which has green fruit.

Solanum stelligerum.—A low-growing, prickly species only noticed growing on the western side of the Plateau.

SCROPHULARIACEAE.

Gratiola peruviana.—A small plant found growing at the edge of running water and actually immersed in it.

GOODENIACEAE.

Goodenia Chisholmi.—This species was mentioned in These PROCEEDINGS (Vol. lii, Part 3, 1927, p. 379) as being probably new. The matter of its affinities was then being investigated at the National Herbarium, Botanic Gardens, Sydney. The result of the investigation established it as a hitherto undescribed species.

On studying the Flora recorded for this Plateau, it will be noticed that the grasses are omitted and that about two-fifths or 40% of the plants are trees or tall shrubs—of the trees, about three-fourths or 75% are brush woods, the remaining 25% are hardwoods. In this connection it might be stated that the writer has in his possession 145 samples of different species of timber native to the Comboyne Plateau, more than 100 of which are brush woods, the remainder hardwoods.

My thanks are due to Mr. W. F. Blakely of the National Herbarium, Botanic Gardens, Sydney, for identification of species and for general information.

I take this opportunity of recording my appreciation of two enjoyable and profitable days—January 20th and 21st, 1934—spent in the field at Comboyne in the company of Miss Joyce Vickery, M.Sc., and Miss Lilian Fraser, M.Sc., when some interesting botanical work was done, and I wish to thank them for determination of specimens and helpful information given both at the time and later.

Corrigenda.

These PROCEEDINGS, Vol. l, 1925, Part 3:

Page 295, for *Dicksonia Youngiae* C. Moore, read *Dicksonia antarctica* Labill.

Page 296, for *Lomatia ilicifolia* R.Br., read *Lomatia Fraseri* R.Br.

Pages 288 and 296, for *Cryptocarya australis* Benth., read *Cryptocarya Meissneri* F.v.M.

Pages 288 and 296, for *Acacia elongata* D.C., read *Acacia Cunninghamii* Hook. var. *longispicata* Benth., and delete *Acacia longifolia* Willd.

Page 295, for *Cheilanthes tenuifolia* var. *Sieberi* Benth., read *Notholaena distans* R.Br.

Page 296, for *Bursaria spinosa* Cav., read *Bursaria incana* Cav.

These PROCEEDINGS, Vol. lii, 1927:

Page 379, for *Cryptocarya* sp., read *Chariessa Moorei* Engler.

REVISED LIST OF THE PLANTS OF THE COMBOYNE PLATEAU, 1934.

THALLOPHYTA.

Fungi: *Polyporus* (*Ovinus*) *mylittae* Cooke.
Muscineae: *Dawsonia superba* Grev.

CRYPTOGAMAE VASCULARES.

FILICALES.

Hymenophyllaceae: *Trichomanes venosum* R.Br.

Cyatheaceae: *Dicksonia antarctica* Labill.; *Alsophila australis* R.Br.; *A. Cooperi* F.v.M.; *A. Leichhardtiana* F.v.M.

Polypodiaceae: *Dryopteris decomposita* R.Br.; *D. acuminata* Lowe; *D. punctata* Thunb.; *D. rugulosa* Copeland; *D. parasitica* (L.) O. Kuntze; *Arthropteris obliterata* (R.Br.) J. Sm. (*Aspidium ramosum* Palis); *A. Beckleri* Mett.; *A. tenella* Forst.; *Davallia pyxidata* Cav.; *D. dubia* R.Br.; *Athyrium umbrosum* Ait.; *A. umbrosum* Ait. var. *semidivisum*, n. var.; *Asplenium nidus* L.; *A. flabellifolium* Cav.; *A. adiantoides* L.; *Blechnum cartilagineum* Sw.; *B. serrulatum* Rich.; *B. Patersoni* R.Br.; *B. discolor* Forst.; *B. capense* (L.) Schlecht.; *Doodia aspera* R.Br.; *Pellaea paradoxa* (R.Br.) Hook.; *P. falcata* (R.Br.) Fée; *P. falcata* (R.Br.) Fée var. *nana* Bailey; *Notholaena distans* R.Br.; *Adiantum aethiopicum* L.; *A. formosum* R.Br.; *A. affine* Willd.; *A. hispidulum* Sw.; *Pteris tremula* R.Br.; *Histiopteris incisa* (Thunb.) J. Sm.; *Pteridium aquilinum* L.; *Polypodium australe* R.Br.; *P. Brownii* Wickstr.; *P. diversifolium* Willd.; *Cyclophorus serpens* (Forst.) C. Chr.; *C. confluens* (R.Br.) C. Chr.; *Platycerium bifurcatum* (Cav.) C. Chr. (*P. alcicorne* Desv.); *P. grande* (A. Cunn) J. Sm.

Gleicheniaceae: *Gleichenia circinata* Sw.; *G. flabellata* R.Br.

Osmundaceae: *Todea barbara* (L.) Moore.

PHANEROGAMAE-GYMNOSPERMAE.

CYCADALES.

Cycadaceae: *Macrozamia Perowskiana* Miq.

CONIFERAE.

Taxaceae: *Podocarpus elata* R.Br.

Pinaceae: *Callitris Macleayana* F.v.M.

ANGIOSPERMAE-MONOCOTYLEDONEAE.

Typhaceae: *Typha angustifolia* Linn.

Potamogetonaceae: *Potamogeton tricarinatus* F.v.M.

Cyperaceae: *Lepidosperma concavum* R.Br.; *Gahnia aspera* Spreng.; *G. psittacorum* Labill.; *Carex brunnea* Thunb.

Palmae: *Linospadix monostachyus* Wendl. & Drude; *Archontophoenix Cunninghamiana* Wendl. & Drude.

Araceae: *Typhonium Brownii* Schott.; *Colocasia macrorrhiza* Schott.; *Gymnostachys anceps* R.Br.; *Pothos longipes* Schott.

Flagellariaceae: *Flagellaria indica* L.

Commelinaceae: *Commelina cyanea* R.Br.

Philydraceae: *Philydrum lanuginosum* Banks.

Liliaceae: *Kreyssigia multiflora* Reichb.; *Stypandra glauca* R.Br.; *Dianella coerulea* Sims; *Xerotes longifolia* R.Br.; *Xanthorrhoea resinosa* Pers.; *Cordyline stricta* Endl.; *Drymophila Moorei* Baker; *Geitonoplesium cymosum* A. Cunn.; *Eustrephus latifolius* R.Br.; *Rhipogonum album* R.Br.; *Smilax glycyphylla* Sm.; *S. australis* R.Br.

Iridaceae: *Libertia paniculata* Spreng.

Orchidaceae: *Dendrobium speciosum* Smith; *D. Kingianum* Bidw.; *D. gracilicaule* F.v.M.; *D. pugioniforme* A. Cunn.; *D. teretifolium* R.Br.; *Bulbophyllum Shepherdi* F.v.M.; *Dipodium punctatum* R.Br.; *Spiranthes australis* Lindl.; *Diuris maculata* Sm.; *Microtis porrifolia* R.Br.

DICOTYLEDONEAE.

Casuarineae: *Casuarina suberosa* Ott. & Dietr.; *C. torulosa* Ait.

Fagaceae: *Fagus Moorei* F.v.M.

Ulmaceae: *Trema aspera* Blume (*T. cannabina* Lour.).

Moraceae: *Cudrania javanensis* Trèc.; *Ficus Henneana* Miq.; *F. eugenioides* F.v.M.; *Ficus rubiginosa* Desf.; *F. macrophylla* Desf.; *F. stephanocarpa* Warb.

Urticaceae: *Urtica incisa* Poir.; *Laportea gigas* Wedd.; *Australina pusilla* Gaud.

Proteaceae: *Persoonia media* R.Br.; *P. linearis* Andr.; *P.* sp.; *P. mollis* R.Br. var.?; *Helicia glabriflora* F.v.M.; *Orites excelsa* R.Br.; *Hakea saligna* R.Br.; *Lomatia Fraseri* R.Br.; *Stenocarpus salignus* R.Br.; *Banksia collina* R.Br.

Santalaceae: *Exocarpus cupressiformis* Labill.

Loranthaceae: *Phrygilanthus celastroides* Eichl. (*Loranthus celastroides* Sieb.); *Loranthus dictyophlebus* F.v.M.; *L. pendulus* Sieb.

Polygonaceae: *Polygonum hydropiper* L.

Chenopodiaceae: *Chenopodium triangulare* R.Br.
Phytolaccaceae: *Codonocarpus attenuatus* Hook.
Ranunculaceae: *Clematis aristata* R.Br.; *C. glycinoides* DC.; *Ranunculus lappaceus* Sm.; *R. rivularis* Banks & Solander.
Menispermaceae: *Legnephora Moorei* Miers.
Magnoliaceae: *Drimys dipetala* F.v.M.
Anonaceae: *Eupomatia laurina* R.Br.
Monimiaceae: *Piptocalyx Moorei* Oliv.; *Wilkiea macrophylla* A. DC.; *Palmeria scandens* F.v.M.; *Daphnandra micrantha* Benth.; *D. tenuipes* Perk.; *Doryphora sassafras* Endl.
Lauraceae: *Cinnamomum Oliveri* Bailey; *C. virens* R. T. Baker; *Litsea dealbata* Nees; *L. reticulata* Benth.; *Cryptocarya patentinervis* F.v.M.; *C. obovata* R.Br.; *C. glaucescens* R.Br.; *C. erythroxylon* Maiden & Betche; *C. Meissneri* F.v.M.; *Endiandra* (*virens* F.v.M.?); *E. Muelleri* Meissn.; *Cassytha melantha* R.Br.
Capparidaceae: *Capparis nobilis* F.v.M.
Saxifragaceae: *Cuttsia viburnea* F.v.M.; *Quintinia Sieberi* A. DC.; *Q. Verdonii* F.v.M.; *Polyosma Cunninghamii* J. J. Benn.; *Anopterus Macleayanus* F.v.M.
Pittosporaceae: *Pittosporum undulatum* Andr.; *P. revolutum* Ait.; *Hymenosporum flavum* F.v.M.; *Bursaria spinosa* Cav. var. *incana* Benth.; *Billardiera scandens* Sm.; *Citriobatus multiflorus* A. Cunn.
Cunoniaceae: *Aphanopetalum resinosum* Endl.; *Geissois Benthami* F.v.M.; *Ackama Muelleri* Benth.; *Schizomeria ovata* D. Don.; *Ceratopetalum apetalum* D. Don.; *Weinmannia rubifolia* Benth.; *Callicoma serratifolia* Andr.
Rosaceae: *Rubus moluccanus* L.; *R. parvifolius* L.; *R. rosaefolius* Sm.; *R. Moorei* F.v.M.; *Acaena ovina* A. Cunn.
Leguminosae: *Acacia juniperina* Willd.; *A. melanoxylon* R.Br.; *A. binervata* DC.; *A. floribunda* Sieb.; *A. Cunninghamii* Hook. var. *longispicata* Benth.; *A. intertexta* Sieb.; *A. mollissima* Willd.; *Cassia Sophera* L.; *Oxylobium trilobatum* Benth.; *Jacksonia scoparia* R.Br.; *Daviesia corymbosa* Sm. var. *arborea* Maiden; *Gastrolobium Boormani* Maiden & Betche; *Goodia lotifolia* Salisb.; *Indigofera australis* Willd.; *Swainsona coronillifolia* Salisb.; *Glycine clandestina* Wendl.; *Kennedya rubicunda* Vent.; *Hardenbergia monophylla* Vent.
Geraniaceae: *Geranium dissectum* L.; *Pelargonium inodorum* Willd.
Oxalidaceae: *Oxalis corniculata* L.
Rutaceae: *Bosistoa euodiformis* F.v.M.; *Pleiococca Wilcoxiana* F.v.M.; *Geijera salicifolia* Schott.; *Evodia micrococca* F.v.M.; *Zieria Smithii* Andr.; *Phebalium elatius* Benth.; *Acronychia laevis* R. & G. Forst.; *A. Baueri* Schott.
Meliaceae: *Cedrela australis* F.v.M.; *Melia Azedarach* L.; *Dysoxylum Fraseranum* Benth.; *D. rufum* Benth.; *Synoum glandulosum* A. Juss.
Tremandraceae: *Tetratheca thymifolia* Sm.
Polygalaceae: *Comesperma ericinum* DC.
Euphorbiaceae: *Breynia oblongifolia* J. Muell.; *Croton Verreauxii* Baill.; *Clayoxylon australe* Baill.; *Baloghia lucida* Endl.; *Homalanthus populifolius* Grah.
Celastraceae: *Celastrus australis* Harv. & F.v.M.; *Denhamia pittosporoides* F.v.M.; *Elaeodendron australe* Vent.
Icacinaceae: *Pennantia Cunninghamii* Miers; *Chariessa Moorei* Engler.
Sapindaceae: *Guioa semiglauca* Radlk.; *Diploglottis Cunninghamii* Hook.; *Sarcopteryx stipitata* Radlk.; *Nephelium leiocarpum* F.v.M.; *Dodonaea triquetra* Wendl.
Akaniaceae: *Akania Hillii* Hook.
Rhamnaceae: *Emmenospermum alphitonioides* F.v.M.; *Alphitonia excelsa* Reiss.
Vitaceae: *Vitis Baudiniana* F.v.M. (*V. antarctica* Benth.); *V. hypoglauca* F.v.M.
Elaeocarpaceae: *Elaeocarpus reticulatus* Sm.; *Sloanea australis* F.v.M.; *S. Woollsii* F.v.M.; *S. Woollsii* var. *N.*
Malvaceae: *Sida rhombifolia* L.; *Hibiscus heterophyllus* Vent.
Sterculiaceae: *Brachychiton acerifolius* F.v.M.; *B. populneus* R.Br.; *Tarretia actinophylla* Bailey; *Commerconia Fraseri* J. Gay.
Dilleniaceae: *Hibbertia volubilis* Andr.; *H. dentata* R.Br.
Violaceae: *Viola betonicifolia* Sm.; *V. hederacea* Labill.
Flacourtiaceae: *Streptothamnus Beckleri* F.v.M.
Passifloraceae: *Passiflora alba* Link. & Otto.
Thymeleaceae: *Pimelia ligustrina* Labill.

Myrtaceae: *Rhodamnia trinervia* Blume; *Myrtus Beckleri* F.v.M.; *Eugenia Smithii* Poir.; *E. corynantha* F.v.M.; *E. australis* Wendl. (*E. myrtifolia* Sims.); *E. cyanocarpa* F.v.M.; *E. coolminiana* C. Moore; *Syncarpia laurifolia* Ten.; *Backhousea myrtifolia* Hook. & Harv.; *Tristania conferta* R.Br.; *T. laurina* R.Br.; *Eucalyptus Andrewsi* Maiden; *E. pilularis* Sm.; *E. acmenioides* Schau.; *E. altior* Maid. & Cambage (*E. oreades* Baker); *E. microcorys* F.v.M.; *E. paniculata* Sm.; *E. quadrangulata* Deane & Maiden; *E. saligna* Sm.; *E. grandis* Maiden; *E. propinqua* Deane & Maiden; *E. punctata* DC.; *E. Shiressii* Maid. & Blakely; *E. canaliculata* Maiden; *E. tereticornis* Sm.; *E. amplifolia* Naudin; *E. corymbosa* Sm.; *Leptospermum flavescens* Sm.; *L. flavescens* Sm. var. *grandiflorum* Benth.; *Kunzea* sp.; *Callistemon lanceolatus* DC. var.; *Melaleuca leucadendron* L.; *M. styphelioides* Sm.

Oenotheraceae: *Epilobium glabellum* G. Forst.; *E. glabellum* G. Forst. var. *Billardierianum* F.v.M.

Halorrhagaceae: *Halorrhagis* (*tetragyna* (Labill.) Hook.).

Araliaceae: *Tieghemopanax Murrayi* R. Viguier; *T. sambucifolius* R. Viguier.

Umbelliferae: *Hydrocotyle tripartita* R.Br.; *H. asiatica* L.

Cornaceae: *Marlea vitiensis* Benth.

Epacridaceae: *Styphelia juniperina* Spreng. (*Leucopogon juniperinus* R.Br.); *Monotoca* sp.?; *Trochocarpa laurina* R.Br.

Myrsinaceae: *Rapanea variabilis* Mez.

Sapotaceae: *Sideroxylon australe* Benth. & Hook.

Ebenaceae: *Diospyros cargillia* F.v.M.

Oleaceae: *Notelaea venosa* F.v.M.

Gentianaceae: *Erythraea australis* R.Br.

Apocynaceae: *Chilocarpus australis* F.v.M.; *Alyxia ruscifolia* R.Br.; *Lyonsia straminea* R.Br.; *L. largiflorens* F.v.M.

Asclepiadaceae: *Marsdenia rostrata* R.Br.

Borraginaceae: *Ehretia acuminata* R.Br.

Verbenaceae: *Clerodendron tomentosum* R.Br.; *Gmelina Leichhardtii* F.v.M.

Labiatae: *Plectranthus parviflorus* Henck.; *Mentha saturejoides* R.Br.; *Brunella vulgaris* DC.; *Prostanthera ovalifolia* R.Br. var. *latifolia* Benth.; *Ajuga australis* R.Br.

Solanaceae: *Solanum nigrum* L.; *S. opacum* A. Br.; *S. aviculare* G. Forst.; *S. simile* F.v.M.; *S. verbascifolium* L. var. *auriculatum* Ait.; *S. pseudo-capsicum* L. (Introd.); *S. stelligerum* Sm.; *S. pungetium* R.Br.; *Duboisia myoporoides* R.Br.

Scrophulariaceae: *Gratiola peruviana* L.

Bignoniaceae: *Tecoma australis* R.Br.

Acanthaceae: *Eranthemum variabile* R.Br.

Myoporaceae: *Myoporum acuminatum* R.Br.

Plantaginaceae: *Plantago varia* R.Br.

Rubiaceae: *Morinda jasminoides* A. Cunn.; *Psychotria loniceroides* Sieb.

Caprifoliaceae: *Sambucus xanthocarpa* F.v.M.

Cucurbitaceae: *Melothria Cunninghamii* Benth.

Campanulaceae: *Lobelia trigonocaulis* F.v.M.; *Wahlenbergia gracilis* A. DC.

Goodeniaceae: *Goodenia Chisholmi* Blakely.

Compositae: *Olearia dentata* Moench.; *O. ramulosa* Benth.; *Cassinia longifolia* R.Br.; *Helichrysum bracteatum* Willd.; *H. elatum* A. Cunn.; *H. Beckleri* F.v.M.; *H. diosmifolium* Don; *H. ferrugineum* Less.; *Gnaphalium japonicum* Thunb.; *G. purpureum* L.; *Erechites prenanthoides* DC.; *Senecio dryadeus* Sieb.

THE GASTEROMYCETES OF AUSTRALASIA. XVI.

HYMENOGASTRACEAE, PART I: THE GENERA RHIZOPOGON, MELANOGASTER AND HYMENOGASTER.

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(Plate iv; twenty-seven Text-figures.)

[Read 27th June, 1934.]

The family Hymenogastraceae, as defined herein, is held to contain commonly non-stipitate and tuberiform plants which are composed of a (usually) well-developed peridium enclosing a permanent gleba of tramal plates anastomosed to enclose numerous lacunae. Most of the species are hypogaean, and all are indehiscent; and because of this and their comparatively simple structure and development, members of the family are usually regarded as being the most primitive Gasteromycetes.

In most taxonomic treatments, genera are usually placed under two families: the Hymenogastraceae, in which the tramal plates are said to arise from the peridium; and the Hysterangiaceae, in which these structures are said to arise from a radial, basal sterile tissue. The developmental details given below show that this arrangement cannot be maintained; for it is now possible to arrange many genera in a developmental sequence which does not allow of this dissociation. It is likewise impracticable to maintain these families on morphological grounds, since there are no clear-cut features by which separation may be effected. Notwithstanding this, Dodge (1928, p. 468 *et seq.*) and Fischer (1933, pp. 7–32) have each arranged the genera under four families; the former recognizing the Rhizopogonaceae, Hydnangiaceae, Hymenogastraceae and Hysterangiaceae; the latter replacing the first by the Melanogastraceae, but considering the other three as valid.

General Morphology.

The indehiscent peridium is composed of hyphae either intertwined to form a felt-like tissue, or modified to form a pseudoparenchyma. In most species it consists of a single layer (the so-called simplex peridium of Zeller and Dodge, 1918); but in a few species it is formed of two or more distinct layers (the duplex peridium of Zeller and Dodge, 1918). In *Octaviania* and *Gautieria* occur a few species in which the peridium may be wanting at maturity, or reduced to a tenuous layer of loosely woven hyphae. In most genera the plants are attached to the substratum by one or several radicate strands, which may be produced into a rudimentary stem-like base (as in a few species of *Hysterangium*), or compacted to form a definite stem (as in certain collections of *Phallogaster*); but in *Rhizopogon*, *Melanogaster* and *Sclerogaster* the radicate strands are replaced by many or few strands which arise laterally and basally from the exterior of the peridium.

In all species included in the family the gleba is composed of numerous tramal plates anastomosed to enclose subglobose or labyrinthiform cavities. The plates are composed of intertwined hyphae or of pseudoparenchyma, may be fleshy or cartilaginous, and are lined with the hymenium, which in most genera is composed of basidia compacted into a close palisade. In *Melanogaster*, however, the hymenium is formed of a relatively broad zone of loosely intertwined hyphae among which the basidia are scattered. In the majority of species the gleba remains unaltered, but in a few (especially in *Hysterangium*) as maturity is approached there is a tendency for basidia and frequently the tramal plates (usually in large specimens) to become gelatinized, and in extreme cases to collapse and leave the central portions of the plant hollow. In the peculiar genus *Phallogaster*, partial gelatinization of areas of the gleba is followed by rupture of corresponding portions of the peridium; consequently in the mature plant the spores become exposed, embedded in a fetid gelatinous matrix. In several genera (as *Phallogaster*, *Dendrogaster*, *Gautieria* and *Hysterangium*) the gleba is partially or completely traversed by a simple or freely branched columella, usually arising from a sterile base. This structure may be conspicuous, scanty, or rudimentary in different species of the same genus, being often difficult to detect in herbarium specimens.

Basidia are usually cylindrical, less frequently subclavate, and bear from 1 to 8 spores on short or long sterigmata. The number of spores which the basidia bear cannot be used in generic delimitation, since in different species of *Hysterangium* (for example) the basidia may carry 2, 4, 6 or 8 spores. The spores may be globose or elliptical, hyaline or coloured, smooth or variously sculptured, and serve as admirable specific and generic characters.

Economic Significance.

At present little is known as to the economic role played by members of the family. Recent investigations have shown that a few species aid in the establishment of forest trees; for in New Zealand it has been demonstrated experimentally that *Rhizopogon rubescens* readily forms a mycorrhiza with *Pinus radiata*; and elsewhere *R. luteolus* has been found to perform a similar function. A few species have been reported as being edible, provided they are consumed before the gleba has become coloured. In this region many are sought for and devoured by marsupials and rodents, since partially eaten plants are often secured in the vicinity of scrapings made by these animals. Possibly the penetrating odour given off by several aid these animals in locating edible species.

Development.

As relatively few species have been studied ontogenetically, it is not possible to give a complete account of the developmental sequence of the family. Available particulars suggest the possibility of two or more phylogenetic series.

Rhizopogon is generally conceded to be the most primitive genus in the family, consequently details of the development of *R. rubescens* will serve as an introduction to the manner in which arise the essential structures as peridium and gleba. The development of this species was first studied by Rehsteiner (1892), and the following account is based partly on his work, partly on a recent study I have made from New Zealand collections.

The rudimentary plant arises from a small subclavate body upon the dorsal surface of a mycelial strand, usually in proximity to a maturing plant. Sections

show that it is composed of loosely interwoven hyphae of a type similar to that forming the mycelial strand from which it arises, there being no differentiation into cortical and medullary tissues, as with more complex species described below. As the plant enlarges, the interior hyphae become compacted, and in the central region appear a few large and irregular primary glebal cavities which are formed schizogenetically, and enclosed by somewhat compacted knots of hyphae which represent the primary tramal plates. As development proceeds, these plates become more compacted, increase in size, branch, and anastomose freely, so that the primary glebal cavities become divided into numerous smaller areas. Then further cavities and tramal plates arise peripherally to these first formed ones, and in this manner the interior tissues are shortly converted into the chambered gleba, the outer area being compacted ultimately to form the simple peridium. Additionally, further cavities form in the tramal plates, especially at the gussets and other regions where space permits. When plants are about 5 mm. diameter, the plates become lined with a definite palisade of closely compacted basidia, and then follows a period of intense spore production. Thus with this species glebal development commences in the centre of the plant and progresses centrifugally, and the peridium is formed from peripheral hyphae unused during development.

In *Octaviania tasmanica* development proceeds in the same general manner, for glebal cavities and tramal plates are formed first in the central portion of the plant, and subsequently are laid down centrifugally. But development differs from that of the preceding species in that the cavities and tramal plates are at first formed in small groups, separated by relatively wide regions of undifferentiated hyphal tissues (trabeculae), which foreshadow the dendroid columella of higher genera. Although these trabeculae are conspicuous in the developing plant, they become much thinner as glebal formation progresses, and in the mature plant are evident only as slightly thickened tramal plates. The peridium is formed in a manner similar to that described for *Rhizopogon*. The first formed basidia are not compacted into a palisade, but are somewhat irregularly inserted, suggesting affinities with *Scleroderma*, with which genus it agrees also in the manner of development. But as development progresses the basidia become more compacted and assume finally a palisade arrangement similar to that of other members of the genus. As particulars are not available as to the method of development of other species, it is not possible to indicate more fully the relationship of *Octaviania* to *Rhizopogon*.

Hysterangium sclerodermum is significant in that it tends to link the developmental characteristics of *Rhizopogon* (and possibly *Octaviania*) with those of the more complex species and genera possessing a well developed and permanent columella. As I have shown elsewhere (1924), differentiation of the primordium into cortical and clavate medullary regions commences at an early stage. Between these tissues appears a dome-shaped zone of cavities, and between each cavity passes a branch of the columella. As the plant enlarges, these branches elongate by peripheral growth, and produce numerous lateral branches, which become further branched to produce tramal plates. These in turn elongate, branch, and anastomose to enclose the cavities of the gleba. Additional cavities and plates are produced centrifugally, and where space permits, from earlier formed plates or even branches of the columella, so that as maturity is approached these become tenuous and much branched. The cortical tissue becomes compacted gradually to

form the pseudoparenchymatous peridium. When plants have attained a diameter of about 15 mm., tramal plates and branches of the columella become strongly gelatinized, after which increase in glebal tissue occurs apparently only in the peripheral region. Then follows considerable increase in diameter owing to the expansion of the gelatinized plates. In large plants most of the plates become tenuous and deliquesce, so that the interior becomes hollow save for a few persistent main branches of the columella, and the spores become embedded in a tenuous gelatinous matrix lining these and the inner surface of the peridium.

Gautieria novaezelandiae would appear to possess a similar development, for with this species, too, the tramal plates of the gleba are formed from the branches of the columella, and are also laid down centrifugally. In large specimens development continues until the branches of the columella are largely converted into sporogenous tissue, and in consequence are barely perceptible in mature plants.

Both *Hysterangium sclerodermum* and *Gautieria novaezelandiae* serve as intermediaries by which plants with a development similar to that of *Rhizopogon* may be linked with *Hysterangium lobatum* and *H. tunicatum*, and, as is shown below, these in turn are directly associated with the highest members of the series.

In *Hysterangium lobatum* the first cavities are laid down in a dome-shaped zone between cortical and medullary tissues, as in *H. sclerodermum* (the sterile lobes of the former developing at a considerably later period); but development proceeds in such a manner that small isolated blocks of glebal cavities and corresponding plates are formed, each block being separated from its fellow by one of the conspicuous branches of the columella. This results in the formation of isolated but completely differentiated areas of the gleba at quite an early period. Subsequently additional plates and cavities are formed at the peripheral margin of each, but the process is so gradual that these blocks retain their individuality until the plant approaches maturity. When glebal development is practically completed, there arise from the dorsal surface of the medullary or potentially sporogenous tissue, clavate or subglobose sterile lobes, which are often of a size as great as that of the sporogenous tissue. These structures are at first composed of woven hyphae, but ultimately become strongly gelatinized; although their function is unknown, their origin suggests that they are merely undifferentiated sporiferous tissue.

In *Hysterangium tunicatum* the usual dome-shaped zone of primary glebal cavities is formed beneath the cortical layer. These cavities arise from the periphery of the medulla and are separated from one another by the primary branches of the columella. The species differs from those discussed above in that further development is confined to centrifugal growth of the primary and subsequently formed branches of the columella (which arise through dichotomous branching of the first-formed branches). As these branches increase in length they carry outwards the tissues of the cortical layer, which ultimately become compacted to form the pseudoparenchymatous peridium. In consequence of this type of development, the cavities are radially arranged, and greatly elongated. According to Fitzpatrick (1913), a similar type of development occurs in *Hysterangium clathroides*, and the close relationship of these two species is further strengthened in that the spores of both are at maturity covered with a delicate gelatinous tunic, which, delicately wrinkled in *H. clathroides*, is considerably inflated in *H. tunicatum*.

From the details given by Fitzpatrick (1913), it would appear that *Phallogaster saccatus* and *Gautieria graveolens* show the final stage of this series; for in these plants the primary cavities appear immediately beneath the cortex, and further development would appear to be due entirely to peripheral development of tramal plates, the rudimentary columella remaining practically unaltered through the period of development.

Hymenogaster would appear to belong to a different developmental series, if particulars given by Rehsteiner (1892) of the development of *H. Rehsteineri* are typical of the genus. For in this species there arises in the apical portion of the central region a large irregular cavity, and into this, from the roof of this cavity, several tramal plates grow vertically downwards. These plates elongate, branch, and anastomose to form the chambered gleba, and finally fuse with the basal portion of the as yet undifferentiated gleba.

Taxonomy.

During the preparation of this and the following papers on the Hymenogastraceae, numerous difficulties have been encountered in the arrangement of species and genera. In several genera it was found that the characters upon which they were erected were untenable, with the result that emendation of a few and suppression of others became necessary. Additional difficulties have been introduced owing to the divergent views held by different workers as to the limits of the family. Thus certain workers consider that *Melanogaster* is a member of the Sclerodermaceae; *Phallogaster* a member of the Phallales; and others would place under the Hymenogastraceae unrelated genera, as *Secotium* and *Podaxon*. That there exists considerable difficulty in differentiating between genera of the Hymenogastraceae and the Phallales is evidenced by the fact that several instances are known where Phalloid "eggs" have been described as species of this family. Examples in point are *Rhizopogon Rodwayi* McAlp., *Hysterangium burburianum* Rodw., *Phallogaster globosus* Lloyd, *Protubera africana* Lloyd and *Kupsura sphaerocephala* Lloyd.

In the delimitation of species, similar difficulties have been encountered. Owing to the scanty descriptions given by many earlier workers and to the fact that in many cases no types are extant, it has been practically impossible to ascertain the identity of many of the older species. In many cases, species were described from single plants which, although in existence, are often too fragmentary to permit of their being identified with certainty. Many records are based on misdeterminations, and in such cases, unless the actual plants are available, it is seldom possible to ascertain to what species the collection should be referred.

As the object of any taxonomic revision is to present genera and species in such a manner that they may be recognized by subsequent workers, I have considered it advisable to indicate the characters, both generic and specific, which are least liable to be affected in consequence of the preparation of specimens for the herbarium. For the taxonomist is usually placed in the unfortunate position of being compelled to work with dried material. Thus the size, colour, and markings of the spores, the structure of the peridium and tramal plates, and the number of spores carried by the basidia, are specific characters which may be used with safety. Whereas the colour of the peridium (and often of the gleba), shape of the plant, and nature of its exterior, are of little, if any, practical specific value, since these factors are usually altered in drying. The thickness of the peridium and tramal plates has little comparable value, since this feature

depends upon the age of the plants at the time of collection, and upon the manner in which the specimens were preserved. The presence or absence of a sterile base is likewise of little value, since this feature varies in different plants of the same collection. As generic features, the position of the organs of attachment, whether lateral (as in *Rhizopogon* and *Melanogaster*), or basal, as in the majority of genera; the presence or absence of a columella (if clearly seen in dried plants); the shape and occasionally the colour of the spores may be considered of value. The presence of lactiferous ducts cannot be used with safety, since these structures may be seen in dried plants, as a rule, only when thin sections are treated with special reagents; and appear to be present or absent in different collections of plants agreeing in all other particulars. For this reason *Arcangeliella* is considered as a synonym of *Hydnangium*. It is likewise apparent that ontogenetic differences, not apparent in mature plants, cannot be used taxonomically.

Acknowledgements.

I am indebted to Dr. J. B. Cleland, The University, Adelaide, Mr. L. Rodway, Government Botanist, and Mrs. L. Rodway, Keeper of the Herbarium, Hobart, Tasmania, for the very generous manner in which they have made available their abundant collections for examination; and to Sir Arthur Hill, Director, and Miss E. M. Wakefield, Royal Herbarium, Kew, England; the late Abbé J. Bresadola, Italy; the late Dr. N. Patouillard, France; Prof. W. C. Coker, University of North Carolina, and Dr. S. M. Zeller, Corvallis, Oregon, United States of America; Mr. W. Carne, Department of Agriculture, Western Australia, and Mr. C. C. Brittlebank, late of the Department of Agriculture, Victoria, Australia, for donations or loan of specimens. Mr. H. Drake, of this Station, has kindly provided the photographs of specimens and line drawings reproduced.

HYMENOGASTRACEAE (including the Hysterangiaceae).

Plants hypogaean or epigaean, tuberiform, subglobose, or pyriform, without a distinct stem, but attached to the substratum by lateral or basal rhizomorphs. Peridium of one or two indehiscent layers. Gleba of permanent, anastomosed, fleshy or gelatinized tramal plates, enclosing cellular or labyrinthiform cavities lined with the hymenium. Basidia cylindrical or subclavate, bearing apically on short or long sterigmata from 1 to 8 spores. Spores globose or elliptical, coloured or hyaline, smooth or variously sculptured.

About 45 genera have been described in literature, but it is doubtful if more than about 18 are valid, of which the following 8 are known to occur with certainty in this region.

Artificial Key to the Genera.

Peridium with lateral and basal mycelial strands.
- Spores elliptical and smooth.
  - Spores hyaline or tinted only ..... 1. *Rhizopogon.*
  - Spores deeply coloured ..... 2. *Melanogaster.*
- Spores globose and verrucose ..... *(*Sclerogaster*).

Peridium with radicate mycelial strands.
- Spores globose.
  - Gleba traversed with an evident simple or dendroid columella .. 5. *Hydnangium.*
  - Gleba without a columella ..... 4. *Octaviania.*
- Spores elliptical.
  - Gleba without a columella ..... 3. *Hymenogaster.*

* A genus which may be present in this region.

Gleba traversed with an evident simple or dendroid columella
Spores smooth ..... 7. *Hysterangium.*
Spores verrucose or areolate ..... 6. *Dendrogaster.*
Spores longitudinally ribbed ..... 8. *Gautieria.*

Section I: Peridium with lateral rhizomorphs (mycelial strands), without a columella; spores elliptical and smooth.

1. Rhizopogon Fries and Nordholm.

Symb. Gast., i, 1817, p. 5; *emend.* Tul., *Giorn. Bot. Ital.*, ii, 1844, p. 56.—*Hysteromyces* Vitt., *Not. nat. civ. sulla Lombardia*, i, 1844, p. 340.

Plants subglobose or tuberiform, without a definite sterile base, epigaean or hypogaean. Peridium tough and membranous, of stupose, sometimes gelatinized hyphae arranged in one or two layers; exteriorly covered with many or few adherent anastomosing dark-coloured fibrils which are united below to form mycelial strands or rhizomorphs. Gleba of permanent tramal plates anastomosed to form subglobose or labyrinthiform cavities. Spores hyaline or tinted, smooth, elliptical or less commonly obovate. Basidia subclavate or cylindrical, usually soon collapsing, bearing 2–8 spores on short sterigmata.

Type species.—*Rhizopogon luteolus* Fr. et Nordh.

Distribution.—Practically world-wide.

Habitat.—Growing in or upon the ground, usually in sandy areas rich in humus.

The genus is characterized by the smooth, pallid, usually elliptical spores, and the mycelial strands which arise from different parts of the peridium. The latter may be copiously developed (*R. luteolus*) or scanty (*R. rubescens*), and may be simple, anastomosed to form a network upon the exterior of the peridium, or aggregated into conspicuous rhizomorphs. Its nearest relative apparently is *Melanogaster*, since both possess these lateral rhizomorphs, and in addition similar elliptical smooth spores, and comparable glebal tissues. Separation may be effected by the deeply coloured spores and different hymenium of *Melanogaster*.

About 30 species have been described, but it is doubtful if more than about half this number are valid. In this region, but three species are known to occur with certainty, two having a wide distribution, the third being endemic to Australia.

Key to the Species.

Peridium of two distinct layers, spores obovate ..... 1. *R. clelandi* G. H. Cunn.
Peridium of a single layer, spores elliptical.
Gleba strongly gelatinized and indurated ..... 3. *R. luteolus* Fr. et Nordh.
Gleba fleshy, firm though soft ..... 2. *R. rubescens* Tul.

1. Rhizopogon clelandi, n. sp. Text-figs. 3, 6.

Plants subglobose, to 3·5 cm. diameter, pallid-cream colour, drying lemon-yellow or tawny-brown. Peridium 400–800μ thick, of two layers; the outer of partly gelatinized hyphae, peeling away in shreds and exposing the inner layer, which likewise is of partly gelatinized hyphae but more firmly compacted. Fibrils few, adnate, absent above, rhizoid-like below, sometimes wanting. Gleba cream-coloured, becoming tawny, fleshy, not at all indurated; cells subglobose, empty; tramal plates 70–100μ thick, scissile, of woven hyphae, not at all gelatinized. Spores hyaline, obovate or less commonly subglobose, 7–8·5 × 4·5–6μ (rarely to 10μ long), shortly pedicellate, smooth. Basidia persistent, 2–4-spored.

Distribution.—Australia. South Australia: Second Valley, Forest Reserve, 6/30, J. B. Cleland* (3 collections, type locality).

* An asterisk denotes that the collection in question is in the herbarium of Dr. J. B. Cleland, The University, Adelaide.

The double-layered peridium, obovate spores and persistent basidia are the characters of the species. The double peridium associates this with four species described by Zeller and Dodge (1918) from the Western region of the United States; but the spores and basidia show it to be distinct from any of these. Basidia and spores are not typical of the genus, so that were it not for the lateral fibrils, the species would be better considered under *Hymenogaster*. Although the plant is apparently without smell when fresh (according to the collection notes of Dr. Cleland), herbarium specimens have a strongly aromatic odour as of aniseed.

2. Rhizopogon rubescens Tulasne. Pl. iv, figs. 1, 2; Text-figs. 2, 5.

Giorn. Bot. Ital., ii, 1844, p. 58.—*Hysterangium rubescens* Tul., *Ann. Sci. Nat.*, ser. 2, xix, 1843, p. 375.—*Melanogaster berkeleyianus* Br., *Ann. Mag. Nat. Hist.*, xv, 1845, p. 41.—*Rhizopogon lapponicus* Karst., *Finska Bidr. Nat. Folk.*, xlviii, 1889, p. 19.

Plants gregarious, sometimes caespitose, irregularly globose or tuberiform, to 6 cm. diameter, at first white, then lemon-yellow, drying bay-brown or ferruginous, often with a reddish tint, and tinged red where bruised or cut. Fibrils usually scanty above, more prominent below, though not infrequently almost wanting, appressed, dark brown or black. Peridium 150–300μ thick, of a single layer of loosely woven but firm hyphae, tawny or yellowish-brown in section, mixed with numerous amorphous globules of orange pigment. Gleba from tawny to ferruginous-brown, firm but soft and readily sectioned; cells subglobose, empty of spores; tramal plates 35–60μ thick, rarely more, slightly scissile, of loosely woven hyphae not at all gelatinized. Spores smooth, tinted, elongate-elliptical, ends rounded, 6–9 × 2·8–3·5μ. Basidia cylindrical, 6–8-spored.

Type locality.—Europe.

Distribution.—Europe; Asia; North and South America; Australia; Tasmania; New Zealand.

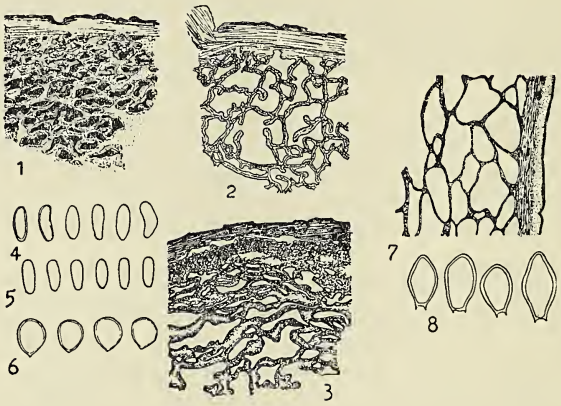
New South Wales: Milson Island, Hawkesbury River, 6/13, J.B.C.* (Det. by Dodge as *R. occidentalis*); Canobolas, 10/16, J.B.C.*; Blayney, 12/17, J.B.C.*; Mittagong, 7/19, J.B.C.*; Leura, 10/14, J.B.C.*.—Western Australia: Narrogin, W. Carne, 8/25; Perth, H. Elliott, 5/27; Mundaring Weir, 6/26, W. E. Campion (Collections ex Dept. Agric. W. Aust.).—Tasmania: Hobart, L. Rodway (ex herb. L. Rodway).—New Zealand: Auckland, Te Aroha, 6/23, G.H.C. (Det. by Dodge as *R. roseolus*); Hawkes Bay, Lake Tutira, 11/27, G.H.C.; Wellington, Tangimoana, 11/30, 10/31, 11/32, 2/33, E. E. Chamberlain; Canterbury, Ashburton, 8/25, D. W. McKenzie (Det. by Dodge as *R. roseolus*).

This species appears to be abundant in areas where *Pinus radiata* is growing, and forms a mycorrhiza with this plant, as has been demonstrated at this Station by Mr. T. C. Birch. As in Australia and New Zealand, it has been found only in proximity to pines, it is probably an introduced species, since the genus *Pinus* is not indigenous to this region.

The species is characterized by the fleshy nature of the gleba, which in herbarium specimens may be sectioned readily. The tramal plates are not gelatinized, a feature which separates the species from the following and explains why the plant does not become indurated when dried. I have compared our collections with specimens of *R. rubescens* from Europe (ex herb. Bresadola) and found them to agree in all essentials.

3. RHIZOPOGON LUTEOLUS Fries and Nordholm. Text-figs. 1, 4.

Symb. Gast., i, 1817, p. 5; *emend.* Tul., *Giorn. Bot. Ital.*, ii, 1844, p. 57.—*Rhizopogon induratus* Cke., *Grev.*, viii, 1879, p. 59.—*Melanogaster wilsonii* Lloyd, *Myc. Notes*, 1923, p. 1176.



Text-figs. 1-8.

1.—*Rhizopogon luteolus.* Drawing of section showing the indurated nature of the gleba. × 7. Original.

2.—*Rhizopogon rubescens.* Drawing of a section showing the nature of the tramal plates. × 7. Original.

3.—*Rhizopogon clelandi.* Sectional drawing showing the double peridium and scissile tramal plates. × 7. Original.

4.—Spores of *Rhizopogon luteolus.* × 570. Original.

5.—Spores of *Rhizopogon rubescens.* × 570. Original.

6.—Spores of *Rhizopogon clelandi.* × 570. Original.

7.—*Melanogaster ambiguus,* × 7. Section showing the compact peridium and tenuous tramal plates. (The cells are filled with spores, a feature not shown in the drawing.) Original.

8.—*Melanogaster ambiguus,* spores, × 570. Original.

Plants subglobose, oblong or tuberiform, to 3 cm. diameter, bay-brown or tawny-brown, often distinctly yellowish. Fibrils well developed, dark brown or black, appressed, rhizoid-like basally. Peridium 250–350μ thick, of strongly gelatinized woven hyphae, ochraceous or tawny in section. Gleba firm and indurated, at first white, becoming yellowish-brown, finally almost black in areas; cavities labyrinthiform, filled with spores; tramal plates 70–90μ thick, strongly scissile, of gelatinized hyphae. Spores tinted yellow, elliptical or occasionally irregular, 6–9 × 2·8–3·5μ, sometimes shortly pedicellate. Basidia subclavate, bearing 6–8 spores.

Type locality.—Europe.

Distribution.—Europe; Asia; Africa; North America; Australia; New Zealand.

New South Wales: Willoughby, 8/15, J.B.C.*.—South Australia: Mt. Lofty, 5/28, J.B.C.*; same locality, 4/24, J.B.C.* (Det. by Dodge as *R. roseolus*); Kuitpo, 5/21, 6/28, J.B.C.*; Kalangadoo, 5/28, J.B.C.*.—Tasmania: Hobart, L. Rodway (ex herb. L. Rodway).—New Zealand: Auckland, Rotorua, 2/27, G.H.C.; Blockhouse Bay, 3/32, M. Hodgkins; Canterbury, Banks Peninsula, Berggren, 1879 (Herb. Kew, No. 403, type of *R. induratus*).

Herbarium specimens may be recognized readily by their indurated nature, due to the tramal plates and peridium being strongly gelatinized, and the cavities of small diameter and filled with spores. Our collections agree well with European specimens (ex herb. Bresadola), and with the description given by Coker and Couch (1928, p. 33) of a plant so named by von Hoehnel from Europe; but differ considerably from the description given under this name by Zeller and Dodge (1918, p. 10). Through the courtesy of the Director of the Royal Botanic Gardens, Kew, and Miss E. Wakefield, I have been enabled to examine a slide prepared from the type of *R. induratus* Cke. and find this to be based on a specimen of *R. luteolus*. Examination of part of the type (kindly loaned by Dr. Shear) shows that *Melanogaster wilsonii* Lloyd (Lloyd herb. No. 53361) was also based on a specimen of this species.

Doubtful and Excluded Species.

(*a*). *Rhizopogon induratus* Cke = *R. luteolus* Fr. et Nordh.

(*b*). *R. occidentalis* Z. et D.—A collection from Milson Island, in the possession of Dr. Cleland, has been identified by Dr. Dodge as this species. I have examined these specimens and consider they belong to *R. rubescens*.

(*c*). *R. pachyphloeus* Z. et D.—According to Zeller and Dodge (1918, p. 10), a collection of this species is in the Lloyd herbarium (Sydney, R. T. Baker, No. 03957). I have not seen specimens from this region.

(*d*). *R. rodwayi* McAlp., *Agr. Gaz. N.S.W.*, vi, 1895, p. 755.—The original description and illustrations show that this species was erected upon the "egg" of some phalloid.

(*e*). *R. roseolus* (Cda.) Hollos.—In the text are listed three collections which have been identified by Dr. Dodge as belonging to this species. I have been unable to ascertain to what species this name refers, as the original description is too scanty to permit of accurate diagnosis; and the matter is further complicated: whereas Zeller and Dodge (1918) described and illustrated a plant which appears to be a form of *R. luteolus*, Coker and Couch (1928) consider under this name a plant which is close to, if not identical with, *R. rubescens*. Examination of the three collections referred to has shown that two belong to *R. rubescens*, and one to *R. luteolus*, which further illustrates the fact that *R. roseolus* has no character by which it may be recognized.

(*f*). *R. violaceus* Cke. et Mass. = *Hysterangium sclerodermum* (Cke.) G. H. Cunn.

2. Melanogaster Corda.

Sturm., *Deutsch. Crypt. Fl.*, iii, 1831, p. 1.—*Uperhiza* Bosc., *Mag. Ges. nat. Freunde Berlin*, v, 1811, p. 88.—*Bullardia* Jungh., *Linnaea*, v, 1830, p. 408.—*Argylium* Wallr., *Fl. Crypt. Germ.*, ii, 1833, p. 874.

Plants subglobose or irregularly tuberiform, with branched fibrils arising from the exterior of the peridium, more numerous basally, hypogaean. Peridium of a simple tough layer of woven gelatinized hyphae, continuous with the tramal plates. Gleba of tramal plates anastomosed to form numerous polygonal or subglobose cavities, which are usually larger towards the centre and are at maturity filled with spores; hymenium of clavate, 2–8-spored basidia (commonly 2–4), which are not arranged in a definite palisade, but irregularly distributed through a broad hyphal zone lining the cavities. Spores borne on short sterigmata, elliptical or lemon-shaped, deeply coloured, smooth, shortly pedicellate.

Type species.—Melanogaster variegatus (Vitt.) Tul.

Distribution.—Europe; North America; Africa; New Zealand.

The genus appears to be closely related to *Rhizopogon*, from which it is separated by the deeply coloured spores and different arrangement of the hymenium. The basidia are not crowded into a compact palisade, as is usual in members of the family, but are irregularly distributed through a relatively broad zone of loosely woven hyphae which lines the cavities. (This feature is not apparent in mature plants.) On this account the genus was considered by Fischer (1900, p. 334) to be a member of the Sclerodermaceae. In his recent treatment, however, Fischer (1933, p. 9) placed it under the family Melanogastraceae. As is shown by the synonymy, the genus possesses two prior names; but as it has been almost universally known as *Melanogaster*, and as this last name has been proposed by R. Maire (*Rec. Synop. V. Congrès internat. Bot.*, 1930, p. 120) as a *nomen conservandum*, I have thought it advisable to use it herein.

Although several species have been described, it is probable that there are not more than four or five, the many others listed being synonyms of these or of species of *Rhizopogon* or *Hymenogaster*. The genus does not appear to occur naturally in this region, for the six collections examined were taken from flower beds, to which they had been apparently introduced with exotic cultigens.

1. Melanogaster ambiguus (Vittadini) Tulasne. Text-figs. 7, 8.

Fungi Hypogaei, 1851, p. 94.—*Octaviania ambiguua* Vitt., *Mon. Tuberacearum*, 1831, p. 18.

Plants tuberiform, to 2·5 cm. diameter, wrinkled exteriorly, black or almost so. Peridium 400–500μ thick, simple, of woven gelatinized hyphae, white internally, coloured deeply peripherally; fibrils numerous, laterally arranged, simple or aggregated below into prominent rhizomorphs. Gleba black, mottled with isabelline or white tramal plates, which are from 50 to 200μ thick, composed of firmly woven gelatinized hyphae; cavities irregularly subglobose, varying in size from 1 to 4 mm., larger towards the centre, filled with spores. Spores citriform, 11–15 × 7–10μ, almost black, smooth, apex somewhat acuminate, base shortly pedicellate.

Type locality.—Europe.

Distribution.—Europe; North America; New Zealand.

New Zealand: Wellington, Botanic Gardens, 6/25, G.H.C. (2 collections); Canterbury, Oxford, 10/21, G. Archey (3 collections); Otago, Dunedin, 5/22, Miss H. K. Dalrymple.

The species is separated from others of the genus by the large, lemon-shaped, almost black spores.

Excluded Species.

Melanogaster wilsonii Lloyd, *Myc. Notes*, 1923, p. 1176 = *Rhizopogon luteolus.*

Section II: Peridium with a radicate base; without a columella; spores elliptical, smooth or variously sculptured.

3. Hymenogaster Vittadini.

Mon. Tuberacearum, 1831, p. 20.—*Hymenangium* Cda., *Icon. Fung.*, v, 1842, p. 28.—*Hysterogaster* Z. et D., ex Dodge, in *Comp. Morph. Fungi*, 1928, p. 488. *Nomen nudum.*

Plants subglobose, pyriform or occasionally tuberiform, attached to the substratum by a radicate base or strands, lateral rhizomorphs being absent. Peridium of one or two layers, composed of stupose or pseudoparenchymatous hyphae. Gleba of tramal plates anastomosed to enclose numerous subglobose

cavities lined with the palisade hymenium; columella absent. Spores elliptical, coloured, smooth or more often covered with a firm, wrinkled or otherwise roughened gelatinous membrane; basidia persistent, cylindrical, bearing 2–4 spores on short stout sterigmata.

Habitat.—Growing superficially or partially submerged in soils rich in vegetable debris.

Distribution.—Practically world-wide.

Type species.—None indicated, but possibly *H. citrinus* Vitt.

The genus is separated from the two preceding ones by the absence of lateral rhizomorphs, the plants being attached to the substratum by one or several radicate strands; from *Octaviania* by the elliptical spores; and from the remaining genera present in this region by the absence of a columella.

In the genus there are two groups of species, characterized by the spores. In the first group these are quite smooth (apparently the basis of *Hysterogaster* Z. et D.); and in the second the spores are covered with a gelatinous utricle which appears delicately wrinkled, areolated or reticulated. Owing to the usual confusion which exists in literature, it is not possible to indicate, even approximately, the number of species in the genus. In this region I have been enabled to recognize ten, all save one of which would appear to be endemic.

Key to the Species.

Spores perfectly smooth.
- Spores 7-10μ long ..... 1. *H. Maideni* Rodw.
- Spores 13-16μ long.
  - Peridium reddish-brown ..... 2. *H. tasmanicus* G. H. Cunn.
  - Peridium golden yellow ..... 3. *H. aureus* Rodw.
- Spores 18-22μ long ..... 4. *H. fusisporus* (M. et R.) G. H. Cunn.

Spores covered with a membrane which in mature plants is rugulose-areolate or verrucose.
- Peridium of two distinct layers ..... 5. *H. luteus* (Mass.) G. H. Cunn.
- Peridium of a single layer.
  - Spores 12-16μ long.
    - Spores elliptical; 4 on each basidium ..... 6. *H. nanus* Mass. et Rodw.
    - Spores fusiform; 2 on each basidium ..... 7. *H. albellus* Mass. et Rodw.
  - Spores 16-22μ long ..... 8. *H. zeylanicus* Petch.

Spores with a strongly reticulated membrane.
- Endospore markedly thickened ..... 9. *H. macrosporus* G. H. Cunn.
- Endospore thin ..... 10. *H. reticulatus* G. H. Cunn.

1. Hymenogaster Maideni Rodway. Text-figs. 11, 18.

Proc. Roy. Soc. Tas., 1921, p. 157.

Plants irregularly globose or oblong, to 4 cm. diameter, dull white, becoming dingy brown when dried. Peridium 50–200μ thick, of closely woven gelatinized hyphae, hyaline. Gleba pallid buff or pallid cinnamon-brown, cells empty, subglobose, 1-2 mm.; tramal plates 50–100μ thick, of densely woven gelatinized hyphae; basidia 4-spored. Spores broadly elliptical or slightly obovate, pallid ferruginous, 7–10 × 4·5–6μ, perfectly smooth, shortly pedicellate.

Type locality.—Near Hobart, Tasmania.

Distribution.—Australia; Tasmania.

South Australia: Encounter Bay, 5/26, J.B.C.*; Second Valley, Forest Reserve, 6/30, J.B.C.* (2 collections); Stirling, w., 7/27, J.B.C.*; Upper Tunkalilla Creek, 6/30, J.B.C.*

This is separated from other species with smooth spores by the thin white peridium, and small size of the spores. The collections listed agree well with

the description of *H. Maideni*, and are included therein, although I have not had an opportunity of examining the type.

2. Hymenogaster tasmanicus, n. sp. Text-figs. 10, 19.

Plants firm, subglobose, to 2·5 cm. diameter, reddish-brown and delicately tomentose. Peridium 150–200μ thick, of densely woven gelatinized hyphae, the outer layer becoming arranged with the hyphae radially disposed, much inflated and firmly compacted. Gleba olivaceous, firm and indurated, cells lenticular or less frequently subglobose, about 1 mm. long; tramal plates 60–80μ thick, of loosely woven hyphae embedded in a gelatinous matrix, scissile, tending to break down in the centre; basidia 2-spored. Spores broadly fusiform, tinted yellowish-brown, 11–15 × 4·5–6μ (occasionally to 20μ long), perfectly smooth, shortly pedicellate.

Distribution.—Tasmania: National Park, 1/28, L. Rodway (type collection in herb. Cleland).

The prominent vesiculose hyphae of the exterior of the peridium, olivaceous and firm gleba, and smooth tinted spores are the characters of the species. It resembles *Hysterangium* in the colour and firm context of the gleba; but as the basidia are typically those of *Hymenogaster*, and as no columella is present, it is evident the species belongs to this genus.

3. Hymenogaster aureus Rodway. Text-fig. 23.

Proc. Roy. Soc. Tas., 1923 (1924), p. 152.

Plants subglobose, 1–2 cm. diameter, exteriorly bright golden-yellow, drying yellow or some shade of yellowish-brown. Peridium 200–600μ thick, of a single layer of parallel interwoven hyphae. Gleba ferruginous, cells somewhat compressed, or lenticular, 3–4 mm.; tramal plates 24–40μ thick, of woven hyaline hyphae, somewhat scissile at the gussets; basidia chiefly 2-spored. Spores tinted yellow, smooth, fusiform, some allantoid or irregular, 12–16 × 5–7μ, apex acuminate, base pedicellate.

Distribution.—Tasmania: Wellington Falls, 2/02, L. Rodway (type collection); Mt. Nelson, 7/19, L. Rodway (Det. by Rodway as *Hysterangium membranaceum*).

This is separated from the preceding species by the differently coloured peridium and gleba, and different context of the tramal plates; and from *H. fusisporus* principally by the smaller spores.

4. Hymenogaster fusisporus (Massee and Rodway), n. comb. Text-figs. 9, 20.

Hysterangium fusisporum Mass. et Rodw., *Kew Bull.*, 1898, p. 127.—*Hymenogaster barnardi* Rodw., *Proc. Roy. Soc. Tas.*, 1918 (1920), p. 157.—*Hysterogaster fusisporum* (M. et R.) Z. et D., Dodge in *Comp. Morph. Fungi*, 1928, p. 488.

Plants irregularly globose, 1–2 cm. diameter, smooth, yellowish, becoming brown when dried. Peridium 200–350μ thick, white in section, of closely woven, gelatinized hyphae. Gleba at first white, drying ferruginous or yellowish-brown, of minute cells, 3–4 mm., empty; tramal plates 20–35μ thick, of densely woven gelatinized hyphae, not scissile, brittle when old; basidia 2-spored. Spores elongate-fusiform, 14–22 × 6–8μ, pallid yellowish-brown, perfectly smooth, apex sharply acuminate, base shortly pedicellate.

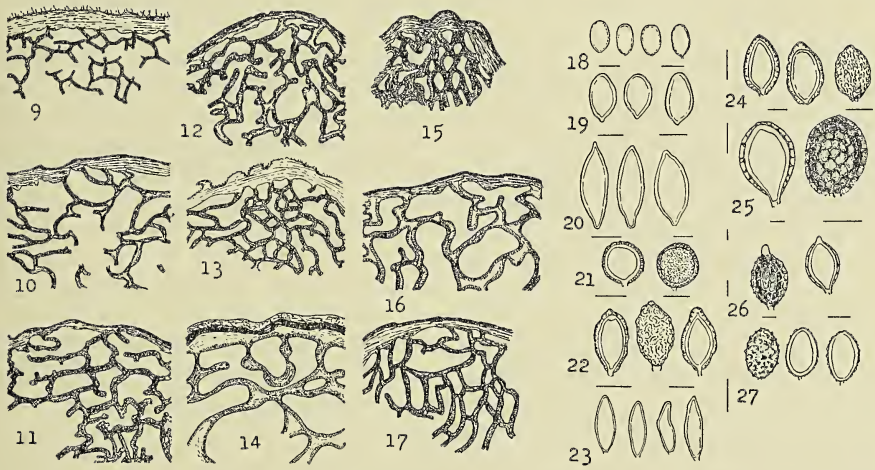
Distribution.—Tasmania: Unknown locality, L. Rodway (type collection, in herb. Rodway).

This is separated from the preceding species by the larger spores, which not infrequently attain a length of 22μ. The description has been drawn from part of the type collection, kindly loaned by Mrs. Rodway; and from this it will be seen that the plant cannot be considered under *Hysterangium*.

5. Hymenogaster luteus (Massee), n. comb. Text-figs. 14, 21.

Protoglossum luteum Mass., *Grev.*, xix, 1891, p. 97.—*Hysterangium viscidum* Mass. et Rodw., *Kew Bull.*, 1898, p. 127.

Plants irregularly globose, subglobose or pyriform, to 3 cm. in diameter, yellowish-ochre to ochraceous-tawny when fresh, and viscid, drying bay-brown. Peridium 250–400μ thick, of two definite layers, an inner coloured one of pseudoparenchyma, and an outer layer arising from this, of loose hyphae arranged radially and embedded in a thick gelatinous matrix. Gleba dark umber brown, firm, cells subglobose, about 1 or 2 mm. in diameter, empty; tramal plates 50–150μ thick, of woven strongly gelatinized hyphae, scissile, tinted; frequently with a rudimentary sterile base; basidia 2–4-spored. Spores broadly elliptical or slightly obovate, occasionally subglobose, golden-brown, 11–15 × 9–11μ, shortly pedicellate, covered with a gelatinous membrane which is 2·5μ thick and markedly areolate.



Text-figs. 9-17.—Sections of 9, *Hymenogaster fusisporus*; 10, *Hymenogaster tasmanicus*; 11, *Hymenogaster Maideni*; 12, *Hymenogaster zeylanicus*; 13, *Hymenogaster albellus*; 14, *Hymenogaster luteus*; 15, *Hymenogaster reticulatus*; 16, *Hymenogaster macrosporus*; 17, *Hymenogaster nanus*. All × 7. Original.

Text-figs. 18-27.—Spores of 18, *Hymenogaster Maideni*; 19, *Hymenogaster tasmanicus*; 20, *Hymenogaster fusisporus*; 21, *Hymenogaster luteus*; 22, *Hymenogaster albellus*; 23, *Hymenogaster aureus*; 24, *Hymenogaster zeylanicus*; 25, *Hymenogaster macrosporus*; 26, *Hymenogaster reticulatus*; 27, *Hymenogaster nanus*. All × 570. Original.

Type locality.—Victoria, Australia.

Distribution.—Australia; Tasmania, New Zealand.

New South Wales: Unknown locality, J.B.C.* (Det. by Rodway as *H. viscidum*).—South Australia: Mt. Lofty, 6/21, J.B.C.* (Det. by Rodway as *H. viscidum*); National Park, 7/25, J.B.C.* (Det. by Dodge as *H. nanus*); Stirling, W., 7/27, J.B.C.*—Victoria: Clarendon (Herb. Kew, No. 859, type of *Protoglossum luteum* Mass).—Tasmania: Unknown locality, L. Rodway (Herb. L. Rodway).—New Zealand: Wellington, Rimutaka Mts., 1/23, J. S. Yeates.

The viscid exterior (of fresh plants) and peculiar nature of the double peridium separates this from other species of the genus present in this region. The spores (save in shape) show relationships with several other species

described below, and show, too, that the plant cannot be considered under *Hysterangium*. When fresh the peridium may be as much as 2 mm. in thickness, due to the swelling of the gelatinous exterior, but in dried plants it is but 0·25 to 0·5 mm.

An examination of slides prepared from the type of *Protoglossum luteum* (kindly forwarded by Miss Wakefield, Royal Herbarium, Kew), has shown that this species possesses the spores and peridium of plants identified by L. Rodway as *Hysterangium viscidum*. In the original diagnosis of *P. luteum* it was stated that a well developed columella was present; but Miss Wakefield found that such was not the case, there being no trace of a columella in the type specimen. It is evident, therefore, that *Protoglossum luteum* is a *Hymenogaster*, and co-specific with *Hysterangium viscidum*; and as the former name has priority the species should be known as *Hymenogaster luteus*.

6. Hymenogaster nanus Massee and Rodway. Text-figs. 17, 27.

Kew Bull., 1899, p. 180.

Plants subglobose, to 15 mm. diameter, pallid-brown when dry, smooth. Peridium 100–200μ thick, of loosely arranged pseudoparenchyma, hyaline. Gleba with a well developed sterile base, ferruginous, cells 1–2 mm., subglobose, empty; tramal plates 35–60μ thick, of partly gelatinized pseudoparenchyma, hyaline, occasionally scissile at the gussets; basidia 4-spored. Spores broadly elliptical, ferruginous, 11–16 × 7–10μ, shortly pedicellate, covered with a gelatinous membrane which is arranged in the form of coarse irregular warts.

Type locality.—Hobart, Tasmania.

Distribution.—Tasmania: Hobart, Newtown Track, 6/25, L. Rodway (Herb. L. Rodway).

Although I have not seen the type, the collection from which the description has been drawn, identified by L. Rodway as being *H. nanus*, agrees well with the original diagnosis; and differs from the preceding (which Dodge identified as *H. nanus*) in the smaller cells of the gleba, different spores, and especially in the different peridium. The spores most closely resemble those of *H. albellus*, but differ in being elliptical and verrucose, not fusiform and areolate. The basidia, too, differ, being 2-spored in *H. albellus*, whereas in *H. nanus* they are 4-spored. Even when the spores are displaced from the basidia they retain their tetrasporous arrangement, being compacted into groups through adhesion of their gelatinized walls.

7. Hymenogaster albellus Massee and Rodway. Text-figs. 13, 22.

Kew Bull., 1898, p. 126.

Plants subglobose to shortly pyriform, 1–3 cm. diameter, commonly 15 mm., pallid-yellow to bay-brown when dry. Peridium 100–250μ thick, of densely compacted, partly gelatinized hyphae, externally tapering off into separate threads and appearing somewhat tomentose. Gleba ochraceous to ferruginous, cells small, 3–4 mm., subglobose, filled with spores; tramal plates 35–50μ thick, of densely woven, partly gelatinized hyphae, sometimes scissile at the gussets; basidia 2-spored. Spores broadly fusiform or acuminate-elliptical, golden-brown, 12–16 × 8–10μ, covered with a gelatinous membrane which appears prominently areolate, 2·5μ thick, apex bluntly acuminate, base shortly pedicellate.

Type locality.—Hobart, Tasmania.

Distribution.—Australia; Tasmania.

New South Wales: Parramatta, 7/12, J.B.C.* (Det. by Rodway as *H. albellus*); Mosman, 7/15, J.B.C.*—Tasmania: Unknown locality, L. Rodway; Waterworks, Hobart, L. Rodway (Type collection, herb. L. Rodway).

From *H. nanus* this species is separated by the different spores and basidia; and from *H. zeylanicus* by the different peridium and smaller spores.

8. Hymenogaster zeylanicus Petch. Text-figs. 12, 24.

Ann. Roy. Bot. Gard. Peradeniya, vi, 1917, p. 207.

Plants irregularly subglobose or pyriform, to 20 mm. diameter, ochraceous or ferruginous brown. Peridium 100–125μ thick, pseudoparenchymatous, covered exteriorly with scattered hyphae arranged in a radial manner. Gleba umber brown, cells subglobose, 1–2 mm., filled with spores; tramal plates 45–70μ thick, of woven, partly gelatinized hyphae, strongly scissile; basidia 2-spored. Spores broadly fusiform or citriform, apex acuminate, base shortly pedicellate, deep chestnut-brown, 15–22 × 9–12μ, coarsely areolate.

Type locality.—Hokgala, Ceylon.

Distribution.—Ceylon; New Zealand.

New Zealand: Wellington, Palmerston North, 5/23, G.H.C. (Det. by Dodge as *H. zeylanicus*).

The large areolated spores separate this from all save the following species; from this it is separated by the different peridium and different shape and markings of the spores. The species was identified for me by Dr. Dodge; and his diagnosis has been confirmed by comparison with part of the type (kindly loaned by Dr. Shear) forwarded by Petch to Lloyd (No. 37975).

Our plant differs in several minor details from the original description, but examination of the type specimens has shown that they agree too closely to allow of separation. The basidia are typically 2-spored, not monosporous as stated, and the spores and tramal plates are of the dimensions given above.

9. Hymenogaster macrosporus, n. sp. Text-figs. 16, 25.

Plants irregularly globose, to 2 cm. diameter, ochraceous or dull cream colour. Peridium 80–200μ thick, of partly gelatinized, parallel hyphae. Gleba dark ferruginous, or chocolate-brown, cells empty, subglobose, 1–2 mm.; tramal plates 40–160μ thick, of densely woven gelatinized hyphae, hyaline, usually scissile; basidia 2–4-spored. Spores elliptical or obovate, golden-brown, 18–24 × 12–17μ, distinctly reticulated, wings of reticulations to 2μ tall, endospore 2μ thick and deeply coloured.

Distribution.—Tasmania: Cradle Mountain, 11/25, G. Weindorfer (Type collection, in herb. L. Rodway).

The species is characterized by the reticulated epispore and thick, coloured endospore.

10. Hymenogaster reticulatus, n. sp. Text-figs. 15, 26.

Plants subglobose, to 15 mm. diameter, bright ochraceous or yellowish-brown. Peridium 120–300μ thick, of densely woven hyphae which exteriorly are more loosely arranged, not gelatinized. Gleba ferruginous, cells subglobose, minute, 5–6 mm., empty; tramal plates 50–80μ thick, of woven, strongly gelatinized hyphae, scissile at the gussets; basidia apparently 2-spored. Spores fusiform, both ends acuminate, or spindle-shaped, clear fuscous brown, 18–22 × 11–15μ (including spindle and reticulations), strongly and coarsely reticulated, wings to 3μ tall, endospore thin, 1μ thick.

Distribution.—Australia; Tasmania.

South Australia: National Park, 4/24, J.B.C.*—Tasmania: Hobart, L. Rodway (Type collection, herb. L. Rodway).

The species is separated from the preceding by the spindle-shaped spores, the greater degree of reticulation, thin endospore, and smaller cells of the gleba.

Doubtful and Excluded Species.

(*a*). *Hymenogaster albidus* Mass. et Rodw. = *Gautieria albida* (M. et R.) G. H. Cunn.

(*b*). *H. barnardi* Rodw. = *Hymenogaster fusisporus* (M. et R.) G. H. Cunn.

(*c*). *H. fulvus* Rodw. = *Dendrogaster fulvus* (Rodw.) G. H. Cunn.

(*d*). *H. klotschii* Tul.—Recorded by Cooke (1892, p. 247) from Western Australia. I have not seen specimens, and it is not possible from the description to ascertain the identity of the plant so listed.

(*e*). *H. lycoperdineus* Vitt.—This has been recorded by Cooke (1892, p. 247) from Western Australia. Unfortunately the description is so scanty that it is not possible to refer the collection to any species known to occur in this region.

(*f*). *H. moselei* Berk. et Br., *Trans. Linn. Soc.*, ii, 1882, p. 40.—The species was recorded as being collected in New South Wales. The description is too scanty to permit of identification; the citrine colour suggests that the species may be the same as *H. aureus* Rodw., and this is supported by the fact that the spores are fusiform, smooth, and 11–14 × 7μ. This I have been able to ascertain through examination of a slide prepared by Miss Wakefield from the type at Kew; but as the sections were such that it was not possible to ascertain the nature of the tramal plates, gleba and peridium, the identity of the species is still uncertain.

(*g*). *H. rodwayi* Mass. = *Gautieria rodwayi* (Mass.) Z. et D.

(*h*). *H. violaceus* Mass. et Rodw. = *Dendrogaster violaceus* (M. et R.) G. H. Cunn.

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EXPLANATION OF PLATE IV.

Fig. 1.—*Rhizopogon rubescens*, × $\frac{2}{3}$. Photograph of the fresh plant showing rhizomorphs. Photo H. Drake.

Fig. 2.—*Rhizopogon rubescens*, × 3. Section through developing plant showing the cellular structure of the gleba. Original.

MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. II.

By G. H. Hardy, late Walter and Eliza Hall Fellow in Economic Biology, Queensland University, Brisbane.

(Five Text-figures.)

[Read 27th June, 1934.]

Subfamily Empidinae.

The described Empidinae in Australia fall into two main biological units, the *Empis* and the *Hilara-Hilarempis* complexes. To these must be added the genus *Apalocnemis*, making a third unit that has the general features of the second complex, but without the water-breeding habits. Originally described from South America, this genus was later recorded by Collin from New Zealand, and now it has been found in Australia. The following key will enable it to be recognized:

1. With metapleural hairs or bristles. With a long outstanding bristle on the costa near the base ..... *Empis*
   Without metapleural hairs or bristles. Without a long outstanding bristle on costa 2
2. Proboscis of male directed forwards and much shorter than that on the female which is directed downwards. Bush-frequenting ..... *Apalocnemis*
   Proboscis in both sexes directed downwards and usually equal in length. Water frequenting and breeding ..... *Hilara-Hilarempis* complex

This key contains characters additional to those in my earlier one (*Aust. Zool.*, vi, 1930, 241) which was based on that of Collin. The presence of a long outstanding bristle on the costa might apply to the *Empis*-complex throughout the World—apparently its importance has been overlooked, although it has often been shown in drawings.

Apalocnemis sanguineus, n. sp. Text-fig. 5.

A black species with a grey pulverulent covering, except the abdomen, which is bright blood-red with a silvery pulverulent covering. The proboscis on the male is rather short and projects forwards, that of the female is as long as the depth of the head and projects downwards.

♂. The frons of the male is somewhat narrower than that of the female, and uniformly diverges towards the antennae, being at the ocellar tubercle about as wide as the anterior ocellus, and at the antennae as wide as the ocellar tubercle. At the base of the antennae there is a V-shaped indentation of the eye-margin, after which the eye-margin proceeds parallel down each side of the face. At one-third above the antennae, the frons has a small median depression and bordering the eyes is a row of very small and obscure bristly hairs. The face is bare and somewhat undulating, being prominent at one-third its length, and again more strongly so at the oral margin. The basal segment of the antennae is twice as long as the very short second segment, the third very long, being

more than four times as long as the two basal ones united, and beyond this is a very small fourth cylindrical segment that terminates in a depression containing a minute spine. The length of the fourth segment is about half the width of the third. The black proboscis is little longer than the length of the face, and the palpi are about as long as the oral opening, yellowish, cylindrical, but broadening at the apex into a rounded knob. The bristles of the palpi are rather long and strong, and those behind the head, below the weak postocular bristles, though irregularly placed, definitely form two further postocular rows.

On the thorax, three black stripes contain about two rows each of short bristly hairs, whilst the grey stripes between them are mainly bare. There is a strong bristle each side of the pronotum, a pair above each wing-insertion, one on each postocular callus, and three marginal pairs on the scutellum, and a weaker pair outside these; elsewhere the bristles are small and weak, increasing in length towards the scutellum, and at least a pair of intraalar bristles may be picked out. The pleura is bare.

The abdomen is entirely blood-red, but may fade somewhat, and it has very few hairs, except laterally on the two basal segments. From there onwards the abdomen has a silvery pulverulent overlay that depends upon the incidence of light to obscure the ground-colour. The black hypopygium is turned to lie with its apex pointing upwards and is rather long.

The legs are black, thickly covered with rather uniform short bristly pubescence and without bristles. The anterior metatarsus is swollen, as long as, but twice as thick as, the intermediate metatarsus.

The venation is normal, with the incomplete costal vein and the fourth radial vein rather straight. At the base, the wings are strongly suffused with black-brown; this colour fades out well before the apical margin.

♀. Very similar to the male but the frons is more parallel-sided, the upper part near the anterior ocellus being almost as wide as the ocellar tubercle, and at this area the bristles tend to form rows. There are four pairs of strong marginal scutellar bristles and the anterior metatarsus is not swollen.

Hab.—Queensland: Brisbane, 11 ♂, 8 ♀ taken in tea-tree country at Sunnybank and Broadwater, September, 1927 to 1933; it is not uncommon, but very few are seen in any season.

A closely allied species is represented by one male from Ringwood, Victoria, November, 1931, in the collection of Mr. F. E. Wilson. This specimen has the antennae longer and the wings suffused intensely over a larger area.

Genus Empis.

Only two species have been described from the mainland and four from Tasmania, but the genus is abundantly represented in collections. Two of the species described below are the only ones known from Sydney, and they are not related to the described Tasmanian species, all of which I have examined.

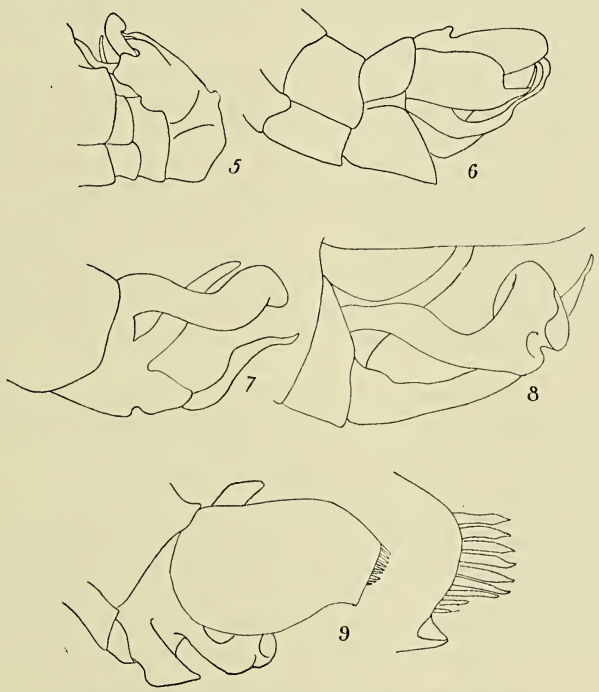
Empis xanthopyga Schiner. Text-fig. 6.

Schiner, Reise Novara Dipt., 1868, 204 (male only).

A black-brown species looking very much like *E. tenuirostris* Thomson, the female of which Schiner had confused with it, many characters being common to both. It may be distinguished from *E. tenuirostris* by the male having the first two segments of the hind tibiae swollen and by the hypopygium, whilst the female has some soft hairs on the face, a character missing in Thomson's species.

On the male there are two strong ocellar bristles and two rows of postorbital bristles, a pair on the pronotum and a pair on the prosternum; also 6 dorsocentrals, 2 or 3 humeral, 2 posthumeral, 5 notopleural, 1 presutural, 2 intraalar, 1 postalar and 2 marginal scutellar, each side of the median line; also a row of two or three long and a row of three weak metapleurals, five pairs of submarginals on the first abdominal segment and four on the others, and two pairs on the last four sternites; these are all more or less in conformity with those of *E. tenuirostris*. On the anterior femora, one row of bristles each on the anterior dorsal and ventral surfaces; similar rows on the intermediate femora, but a second ventral row is present; and on the posterior femora an anterior and ventral row and two subapical posterior bristles. The three pairs of tibiae have consecutively 2, 3 and 4 rows, whilst the posterior tarsi have the two basal segments swollen, with a few bristles and abundant long hairs.

The hypopygium is of the shape illustrated in Text-figure 6, and it has not been analysed for the purpose of determining the constituent parts, nevertheless it is of a shape not met with on any other of the species before me.



Text-fig. 5.—*Apalocnemis sanguineus*, n. sp.; lateral view of hypopygium.
Text-fig. 6.—*Empis xanthopyga* Schiner; lateral view of hypopygium.
Text-fig. 7.—*Empis tenuirostris* Thomson; lower portion of hypopygium showing clasper and spine.
Text-fig. 8.—*Empis alata*, n. sp.; lower portion of hypopygium showing clasper and spine.
Text-fig. 9.—*Empis waterhousei*, n. sp.; lateral view of hypopygium, and an enlarged view of the apical spines that occur at the apex of the upper forceps on all species in the *tenuirostris*-group.

In colour this is a black species with a pulverulent greyish overlay and a thin obscure abdominal margin, the venter, the legs and the hypopygium fulvous. The median marks of the thorax form three black stripes similar to those of *E. tenuirostris*, but closer together, and all reach the pronotum and, outside these, a brown presutural and a postsutural spot may occur. The wings are yellowish with fulvous veins.

The female is similar but the posterior tarsi are normal and there are short soft white hairs on the face.

Hab.—New South Wales: Sydney, 2 ♂, 2 ♀, August, 1932, in the vicinity of French's Forest. It is evidently a winter and early spring species, and has been overlooked by me when previously collecting owing to its early occurrence.

As the female described by Schiner under the name *xanthopyga* is *E. tenuirostris*, the females described here are marked as allotype and paratype. Schiner's male specimen is regarded as being the holotype.

Empis tenuirostris group.

This group is to be recognized by the upper forceps of the hypopygium terminating in a row of broad, flattened bristles, six being well formed, and others somewhat reduced in size and shape.

The four species described here have in common a few bristly hairs on the frons, hardly or not perceptible on the male, a pair of large bristles on the ocellar tubercle, two widely separated postocular rows, a pair of bristles on the pronotum, two to four on the prosternum; also 5 to 9 dorsocentrals, 2 or 3 humerals, 2 or 3 posthumerals, 5 notopleurals, 1 presutural, 1 or 2 intraalars, 1 postalar, and 2 marginal scutellar on each side of the median line; together with four metapleural bristles in a row and sometimes another weak row. Occasionally one or two pairs of presutural acrostichal bristles are to be detected, but on one species there are five pairs, all small. Also a strong pair of cruciate presutural acrostichal bristles occur on one specimen, but this is probably incidental.

The abdomen has five pairs of submarginal bristles on all tergites, but one species has this number increased on the two basal segments. Also the sternites have a well formed median pair of bristles and a pair of outer weaker bristles may also occur. Dorsally some discal bristles are to be seen.

The coxae usually have a row of bristles, or the traces of a row. The rows on the femora are variable, being, at the maximum, one anterior, one dorsal, one posterior and two ventral. The tibiae and tarsi have up to four rows each. The wings are slightly tinged yellowish and the veins fulvous.

The variations that seem to mark specific limits are recorded below under the descriptions; the most consistent and easy to observe are used in the key.

Key to the males of the E. tenuirostris *group.*

1. With a conspicuous row of anterior acrostichal bristles. Anterior tibiae and tarsi unusually hairy, the hairs being about as long as the bristles, much longer than on the other legs ..... *tibialis*, n. sp.
   Without acrostichal bristles, or at most with one or two occasional pairs. Hairs of tibiae and tarsi uniformly short on all legs 2
2. Ten pairs of dorsocentral bristles ..... *waterhousei*, n. sp.
   Only five or six pairs of dorsocentral bristles 3
3. Abdomen fulvous or mainly so ..... *alata*, n. sp.
   Abdomen fuscous or mainly so ..... *tenuirostris* Thomson

EMPIS TENUIROSTRIS Thomson. Text-fig. 7.

Syn.—*Empis xanthopyga* Schiner, females only.

The bristles of the thorax include two pairs on the prosternum, and only one row of metapleural. On the dorsum are 5 dorsocentrals, 2 humeral, 2 posthumeral, 1 presutural, 2 intraalar each side of the median line. On the legs, those on the intermediate coxae are missing; on the anterior femora, anteriorly there are two intermediate bristles and one subapical only. On the intermediate femora, anteriorly there is a row of bristles, but posteriorly only a subapical bristle. On the posterior femora the dorsal row is missing. In other respects the bristles on the legs are normal.

The hypopygium has a rather sinuous ventral spine and the width of the claspers rather uniform throughout, otherwise it conforms to that of *E. waterhousei*.

In colour the male has the head black, only part of the proboscis and the palpi being fulvous, and it is mainly covered with a pulverulent grey. A similar grey covers the black thorax but leaves three central stripes, the outer of which may be very broad, and in addition, there may be an elongate black presutural spot placed more laterally. The three central stripes reach about two-thirds the length of the thorax and only the central one approaches the head. There is also a tinge of yellow on the grey colour and this extends on to the scutellum. A similar pulverulent grey on the abdomen, extending from the base to half the second segment and on all incisions, leaves the abdomen black elsewhere and rather shining dorsally; this grey may extend over the venter which otherwise varies from black to fulvous; the hypopygium is also fulvous, tinged fuscous in part. The legs are fulvous and the hind femora are but slightly longer than the intermediate ones.

The female is similar, but the basal segments of the antennae are usually fulvous, which colour may also be more extensive on the abdomen.

Hab.—New South Wales: Sydney, 1 ♂, August, 1932, and Blackheath, 11 ♂, 15 ♀, November, 1919.

As Thomson described this species from the female only, the above males are labelled allotype and paratypes.

EMPIS ALATA, n. sp. Text-fig. 8.

The thorax contains three prosternal bristles and an extra row of weak metapleurals, also 6 dorsocentral and 3 posthumeral; in other ways the bristles conform to the normal, except that the male has a pair of presutural acrostichal that are cruciate and perhaps not consistent. On the anterior femora, one anterior row of bristles, and one posterior row; on intermediate femora, one each anterior and posterior and two ventral rows; on posterior femora, one each anterior, posterior and ventral. The tibiae have three rows on the anterior and four on the others.

The hypopygium is very like the others, but the claspers are provided with a strongly turned flange at apex and near this is a deep incision that is very marked and readily perceived from any angle. Also the spine is straight and long.

In colour the whole insect is fulvous, except the third segment of the antennae, the eyes, the bristles and certain dorsal marks of the thorax, all these being black, and the apices of the tarsi are fuscous. The thoracic markings are identical with those of *E. tenuirostris*, and there is a silvery-white sheen over

the abdomen and slightly on the legs, and the incidence of light might cause it to hide the ground colour.

The female is similar, but fuscous areas occur behind the eyes, on the scutellum and adjacent to it; on the abdomen a large dark spot occurs on each side of the second to fifth segments.

Hab.—New South Wales: Blackheath, 1 ♂, 1 ♀, November, 1919.

EMPIS WATERHOUSEI, n. sp. Text-fig. 9.

The bristles of the thorax are three prosternal, and an extra row of weak metapleural bristles. Those dorsally vary from the normal by having 10 dorsocentrals, 3 posthumeral, 2 or 3 small extra pronotal, and up to 4 postsutural bristles. There are nine or more pairs of submarginal bristles on the first abdominal segment and six or seven pairs on the second. The anterior femora have one row each anteriorly, posteriorly and ventrally, and the posterior tibiae have three rows; elsewhere the bristles are normal.

The hypopygium is normal, but the claspers are rather like those of *E. alata*, and they can be easily distinguished by the entire absence of the deep indentation, or at most a very slight one may occur in the same region. There is no sign of a ventral spine, but this may possibly have broken away, leaving no trace.

The head and thorax are black, mainly covered with a pulverulent brown, but grey on pleura, sides of dorsum and scutellum. The black dorsal stripes correspond to those of preceding species. The abdomen is rich fulvous, slightly shining and covered with a slight pulverulent grey, more intensely so at the base and ventrally. The legs are fulvous, with the femora slightly fuscous above.

The female is similar but the stripes of the thorax are rather obscure and have a deeper pair of very thin short stripes superimposed on the faint but unusually broad central stripe. The fuscous of the femora is confined to the anterior pair.

Hab.—New South Wales: Mt. Kosciusko, 1 ♂, 3 ♀, December, 1921. Collected by Dr. G. A. Waterhouse, after whom the species is named.

EMPIS TIBIALIS, n. sp.

The bristles of the thorax include four prosternals and two strong metapleurals and a row of weak ones. There are 5 presutural acrostichals, 7 or 8 dorsocentrals, 3 posthumeral each side of the median line. The anterior femora have a row of mainly weak bristles on anterior, dorsal and posterior sides, but there are outstanding bristles that occur in conformity with those on *E. tenuirostris*. The intermediate femora have one row each anteriorly and ventrally, and one subapical posterior bristle. The posterior femora have one row each on the anterior, dorsal and posterior sides. The anterior tibiae have three rows of bristles and, like the tarsi, are very hairy, the hairs being as long as the bristles. The intermediate and posterior tibiae have four rows of bristles, other characters being normal. The anterior metatarsus is slightly swollen.

The hypopygium has the forceps much as in other species but relatively smaller, and the claspers are rather simple, slender, with a simple broadened rounded apex. The ventral spine is represented by a pair of very bristle-like long filaments in no way comparable with that of other species.

The insect is almost entirely black with a pulverulent grey that gives place to brown on the dorsum of thorax where the stripes are hardly discernible. The legs are fulvous.

Hab.—Tasmania: Cradle Mt., 5 ♂, January, 1917.

NOTES ON THE AUSTRALIAN SPECIES OF *MOLOPHILUS* [TIPULIDAE, DIPTERA]. II.

By Charles P. Alexander, Amherst, Massachusetts.
(*Contribution from the Entomological Laboratory, Massachusetts State College.*)
(*Communicated by I. M. Mackerras, M.B., Ch.M.*)

(Text-figures 1–12.)

[Read 27th June, 1934.]

The preceding paper under this general title appeared in this journal in 1929 (Proc. Linn. Soc. N.S.W., 54, 137–144). It considered eleven species of this vast genus that were described by Skuse in 1889. The present report considers twelve further members of the group, the majority being taken by my good friend and co-worker on the Tipulidae, Mr. F. Erasmus Wilson, in New South Wales, Victoria and Tasmania, the types being preserved in the Wilson Collection. A smaller number from the Dorrigo of northern New South Wales were taken by Mr. William Heron, who has collected numerous Tipulidae in this very interesting region. These specimens are retained in my own collection.

Molophilus fusiformis, n. sp.

Belongs to the *plagiatus* group; allied to *longicornis*; general coloration dark plumbeous grey; antennae of ♂ elongate, the segments fusiform; wings greyish, the veins conspicuous, narrowly seamed with dusky; terminalia of ♂ with the apical beak of basistyle blackened but irregular in outline; basal dististyle a black, nearly straight rod, relatively stout, the outer third gradually narrowed to a spinous point; phallosomic structure a pale, oval, setuliferous cushion.

♂. Length about 3·5 mm.; wing 4 mm.; antenna about 4 mm.

Rostrum and palpi dark brown. Antennae of ♂ black throughout, somewhat longer than the entire body; flagellar segments fusiform, the apical narrowed portion longer and more slender than the basal. Head dark brownish-grey.

Mesonotum dark plumbeous grey, without stripes. Pleura dark grey. Halteres pale, the knobs weakly darkened. Legs with the coxae yellowish testaceous; trochanters yellow; remainder of legs broken. Wings greyish, the veins conspicuous, pale brown, narrowly seamed with dusky. Venation: R_2 lying a short distance beyond level of r-m; m-cu about one-third the petiole of cell M_3; vein 2nd A relatively short, ending some distance before m-cu.

Abdomen black throughout. Male hypopygium (Text-fig. 1) with the apical beak of basistyle (*vb*) blackened and irregular in outline, not forming a smooth structure as usual in the group. Outer dististyle (*od*) with the outer arm truncated and microscopically toothed at apex. Basal dististyle (*bd*) a black, nearly straight to slightly arcuate rod of moderate stoutness, on distal third gradually narrowed into a spinous point; surface of style with a few microscopic punctures. Phallosomic structure (*p*) a pale oval cushion, clothed with delicate setulae.

Hab.—New South Wales.

Holotype, ♂, Dorrigo, Eastern Dorrigo, altitude about 2,000 feet, 12th February, 1933 (W. Heron).

Molophilus fusiformis is amply distinct from *M. longicornis* Skuse, in the general dark grey coloration and details of structure of the male terminalia, especially the apical beak of basistyle and the conformation of the basal dististyle. The flagellar segments are more fusiform than in several other allied members of the *plagiatus* group.

MOLOPHILUS PARVISERRATUS, n. sp.

Belongs to the *plagiatus* group; allied to *perdistinctus*; general coloration of thorax pale brownish-yellow; antennae of ♂ nearly as long as body, the flagellar segments fusiform; ♂ terminalia with the phallosome appearing as a conspicuous blackened lyriform plate, the inner margins of the arms microscopically serrate.

♂. Length about 4–4·5 mm.; wing 4·8–5·5 mm.; antenna about 4–4·2 mm.

Rostrum yellowish-brown; palpi brown. Antennae of ♂ elongate, nearly as long as the body; scape and pedicel yellowish-brown; flagellum brownish-black; flagellar segments elongate-fusiform, with long outspreading verticils on the swellings. Head brownish-grey.

Thorax almost uniformly pale brownish-yellow, the dorsum a trifle darker. Halteres dusky, the base of stem pale yellow. Legs with the coxae and trochanters yellowish testaceous; remainder of legs yellow, the colour more or less obscured by dark setae; outer tarsal segments more uniformly darkened; fore tibiae of ♂ not darkened subbasally. Wings greyish; veins pale brown; macrotrichia darker brown. Venation: R_2 lying slightly distad of level of r-m; petiole of cell M_3 relatively long, exceeding three times m-cu; vein 2nd A long, ending shortly beyond m-cu.

Abdomen dark brown, the terminalia brownish-yellow. ♂ terminalia (Text-fig. 2) with the beak of ventral lobe (*vb*) of basistyle slender but heavily blackened. Outer dististyle (*od*) bifid, the outer arm larger and more flattened. Basal dististyle (*bd*) shorter than outer, slender, a little sinuous at outer end and here provided with small tubercles. Phallosome (*p*) conspicuous, appearing as a blackened lyriform plate, the arms narrowed into slender, acute, gently incurved spines, the inner margins of these arms with small acute teeth.

Hab.—Tasmania.

Holotype, ♂, National Park, 11th–15th January, 1933 (F. E. Wilson). *Paratopotype*, ♂; *paratypes*, ♂, Mount Wellington, 10th January, 1933 (F. E. Wilson).

Molophilus parviserratus is most nearly allied to *M. perdistinctus* Alexander and *M. distinctissimus* Alexander, being readily told from all other described species of the genus by the structure of the phallosome of the male hypopygium. This more resembles in conformation the corresponding organ in *M. lyratus* Alexander and allies, which, however, fall in a different group (*gracilis, ruficollis* subgroup) of the genus. In the present collection, the species was associated in nature with a group of other Molophili, several of which likewise had elongate antennae in the male sex (including *M. duplex* Alexander, *M. parvistylus* Alexander, *M. perdistinctus* Alexander, *M. variistylus* Alexander, and others).

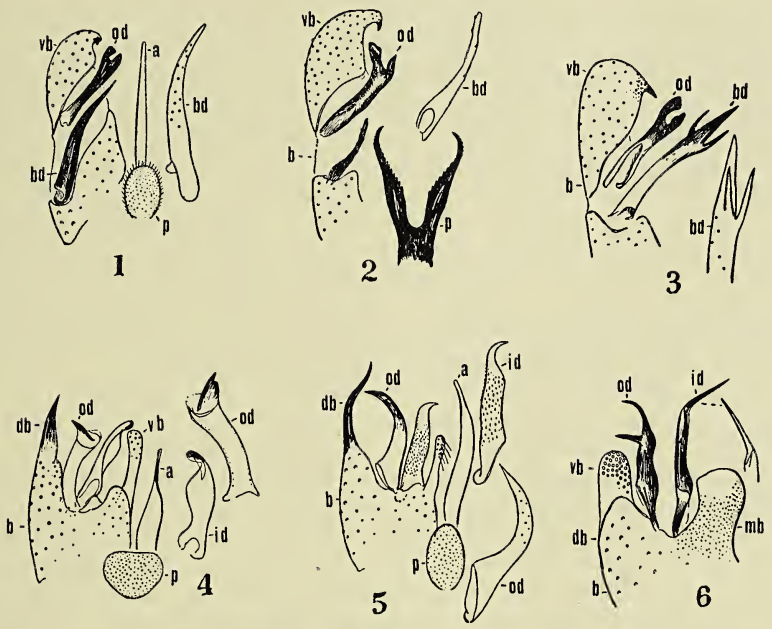
MOLOPHILUS TERNATUS, n. sp.

Belongs to the *plagiatus* group; allied to *bucerus*; general coloration of entire body pale yellow; male terminalia with the axis of basal dististyle terminating in a stout acute spine that is subtended by two more slender spines.

♂. Length about 3·2–3·4 mm.; wing 4–4·2 mm. ♀. Length about 4 mm.; wing 4·5 mm.

Body, including head, thorax, abdomen, legs, and wings, entirely light yellow; palpi dark brown; outer segments of antennae weakly darkened; eyes black.

Antennae of ♂ of moderate length, if bent backward extending about to base of halteres; verticils long and conspicuous. Darkened ring on fore tibia of ♂ pale and relatively inconspicuous. Wings with the veins pale yellow. Venation: R_2 lying just distad of level of r-m; vein 2nd A ending shortly beyond origin of



Text-figs. 1-6.—Male terminalia.

1, *Molophilus fusiformis*, n. sp.; 2, *M. parviserratus*, n. sp.; 3, *M. ternatus*, n. sp.; 4, *M. megacanthus*, n. sp.; 5, *M. drepanostylus*, n. sp.; 6, *M. tetracanthus*, n. sp. (Symbols: *a*, aedeagus; *b*, basistyle; *bd*, basal dististyle; *db*, dorsal lobe of basistyle; *id*, inner dististyle; *mb*, mesal lobe of basistyle; *od*, outer dististyle; *p*, phallosome; *vb*, ventral lobe of basistyle.)

petiole of cell M_3. Male hypopygium (Text-fig. 3) with the beak of the ventral lobe (*vb*) of basistyle relatively slender. Basal dististyle (*bd*) stouter than in *bucerus*, the axis terminating in a stout spine that is subtended by two more slender spines.

Hab.—Victoria.

Holotype, ♂, Beech Forest, Turton's Pass, Otway Peninsula, 11th–19th January, 1932 (F. E. Wilson). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, 4 ♂, ♀.

The trispinous apex of the basal dististyle of the male terminalia readily separates this fly from the allied *Molophilus bucerus* Alexander (Victoria).

Molophilus megacanthus, n. sp.

Belongs to the *gracilis* group and subgroup; general coloration dark grey, including the scutellum, the latter sometimes a trifle brightened; knobs of halteres

dark or only vaguely brightened; wings with a blackish suffusion; male terminalia with the dorsal lobe of basistyle an unusually short and stout black spine; ventral lobe a slender club; outer dististyle a nearly straight rod, at apex produced laterad into an acute black spine.

♂. Length about 3·5–3·8 mm.; wing 4·2–4·6 mm. ♀. Length about 5 mm.; wing 4·8–5 mm.

Rostrum greyish-black; palpi black. Antennae black throughout, in ♂ of moderate length, if bent backward extending nearly to the root of wings; flagellar segments long-oval, with long outspreading setae and verticils on the basal five or six segments that slightly exceed the segments in length. Head dark grey.

Anterior lateral pretergites restrictedly light yellow. Mesonotal praescutum dark brown, grey on sides; posterior sclerites of mesonotum, including the scutellum, dark grey; in cases, the scutellum slightly brightened. Pleura dark plumbeous grey. Halteres dark brown, the extreme base of stem yellow; in cases, the knobs vaguely brightened. Legs with the coxae dark grey; trochanters testaceous brown; remainder of legs brownish-black; the usual subbasal ring on fore tibia of ♂ is lacking or scarcely evident. Wings relatively narrow, with a blackish suffusion; stigma and vague clouds along cord and some of the longitudinal veins darker; macrotrichia dark; veins dark brown. Venation: R_2 in alignment with r-m; petiole of cell M_3 variable, in cases unusually long, exceeding vein M_4 and fully five times as long as m-cu; in other cases only about three times m-cu; vein 2nd A ending shortly beyond m-cu.

Abdomen, including terminalia, brownish-black. Male terminalia (Text-fig. 4) with the basistyle (*b*) short and stout; dorsal lobe (*db*) unusually stout, terminating in a broad flattened black spine; mesal lobe extended into a small, finger-like setiferous lobule; ventral lobe (*vb*) slender, as in *tenuiclavus* and allied forms. Outer dististyle (*od*) a straight to gently curved rod, at apex produced laterad into a long blackened spine; apex of style at insertion of the terminal spine in cases with white membranous tissue; in type, lacking this white membrane and produced into a few microscopic spinulae. Inner dististyle (*id*) subequal in length, appearing as a flattened scoop-like blade. Aedeagus (*a*) relatively short, the apex slender, the basal portion subtended by wide flanges.

Hab.—New South Wales.

Holotype, ♂, Wentworth Falls, Blue Mts., altitude 2,840 feet, 20th–30th October, 1930 (F. E. Wilson). *Allotopotype*, ♀. *Paratopotypes*, 1 ♂, 1 ♀; *paratypes*, 1 ♂, 1 ♀, Blackheath, Blue Mts., altitude 3,495 feet, 20th–30th October, 1930 (F. E. Wilson).

Molophilus megacanthus is well distinguished from all other members of the *gracilis* subgroup by the details of the male terminalia, including the unusually broad spine of the dorsal lobe of basistyle and other details of the organ.

Molophilus drepanostylus, n. sp.

Belongs to the *gracilis* group and subgroup; allied to *setulistylus*; general coloration dark brownish-grey, the scutellum obscure yellow; male terminalia with the ventral lobe of basistyle small; outer dististyle a strongly curved sickle-shaped rod; inner dististyle with abundant microscopic setulae.

♂. Length about 4–4·2 mm.; wing 5–5·2 mm.

Rostrum and palpi black. Antennae of moderate length, if bent backward extending about to wing-root, brown throughout. Head chiefly greyish-brown, the front and orbits narrowly yellowish.

Pronotum and mesonotum dark brownish-grey, variegated by the yellow anterior lateral pretergites and the obscure yellow scutellum. Pleura dark greyish-brown. Halteres light yellow. Legs with the fore coxae dark brown, the remaining coxae somewhat paler; trochanters yellow; remainder of legs chiefly dark brown, the femoral bases obscure yellow; tibial enlargement of ♂ present. Wings with a faint brownish tinge, the veins a little darker; trichia dark brown. Venation: R_2 lying some distance beyond level of r-m, R_{2+3} being from two to nearly three times R_{4+5}; petiole of cell M_3 varying from one-half longer to nearly twice m-cu; vein 2nd A ending about opposite midlength m-cu.

Abdomen, including terminalia, dark brown. Male terminalia (Text-fig. 5) with the dorsal spine (*db*) of basistyle long and slender, gently curved; ventral lobe of basistyle slender but much smaller than in *aequistylus*, *setulistylus* or *tenuiclavus*. Outer dististyle (*od*) a strongly curved rod that is roughly sickle-shaped, the tip acute, the surface with a few scattered punctures. Inner dististyle (*id*) of nearly the same length, relatively slender, the surface, except at base and apex, with microscopic setulae.

Hab.—New South Wales.

Holotype, ♂, Dorrigo, East Dorrigo, altitude about 2,000 feet, 12th April, 1931 (W. Heron). *Paratopotype*, ♂, 20th April, 1931.

The nearest ally of the present species is *Molophilus setulistylus* Alexander, which has the ventral lobe of basistyle much larger, being longer than the dorsal spine; the shapes of the dististyles are similarly distinct.

Molophilus tetracanthus, n. sp.

Belongs to the *gracilis* group and subgroup; size small (wing about 3·5 mm.); mesonotum chiefly yellowish, the pleura and mediotergite more plumbeous; legs chiefly pale; fore tibiae (♂) without differentiated basal ring; male terminalia without spines on any lobes of basistyle; both dististyles bifid, the outer with very long branches.

♂. Length about 2·5–2·6 mm.; wing 3·4–3·5 mm.

Rostrum brown; palpi black. Antennae of ♂ short, testaceous brown; flagellar verticils long. Head brownish-grey.

Mesonotum almost uniform reddish-yellow, the postnotal mediotergite more plumbeous. Pleura plumbeous to somewhat more testaceous. Halteres with the stem testaceous, the knobs light yellow. Legs with the coxae and trochanters yellowish-testaceous; remainder of legs chiefly pale, the outer tarsal segments more darkened; trichia of legs dark; no modified annulus on fore tibia (♂). Wings faintly greyish subhyaline, the prearcular and costal portions somewhat more luteous; veins pale, macrotrichia slightly darker. Venation: R_2 opposite or just beyond level of r-m; petiole of cell M_3 from two to two and one-half times m-cu; vein 2nd A ending about opposite one-fourth the length of the petiole of cell M_3.

Abdomen dark brown, the terminalia obscure yellow. Male terminalia (Text-fig. 6) with the dorsal lobe (*db*) of basistyle weakly developed and obtuse at apex; ventral lobe (*vb*) of moderate size, with the usual retrorse setae of the group; mesal lobe (*mb*) very extensive, with delicate setulae. Both dististyles heavily blackened, the outer style (*od*) with two very long spines, the axial spine gently curved, the lateral spine straight and somewhat more powerful, leaving the axis at about a right angle at near two-thirds the length of the style; inner dististyle (*id*) long and slender, narrowed to a long apical spine, at near two-thirds the

length bearing a small acute lateral spine; surface of inner style with about fifteen microscopic punctures.

Hab.—Victoria.

Holotype, ♂, Mount Donna Buang, above Warburton, altitude 3,000–4,000 feet, April, 1931 (F. E. Wilson). *Paratopotype*, ♂. *Paratype*, 1 ♂, Mount Dandenong, 24th January, 1931 (F. E. Wilson).

Molophilus tetracanthus has no close described relatives in the Australian fauna. It approaches species such as *M. aphanta* Alexander and *M. forceps* Alexander, yet is very different in the details of structure of the male terminalia.

MOLOPHILUS DORRIGANUS, n. sp.

Belongs to the *gracilis* group, *ruficollis* subgroup; most nearly allied to *variistylus* and *macleayanus*; antennae of ♂ a little longer than the body, strongly nodulose; knobs of halteres darkened; male terminalia with the basal dististyle a strongly curved blackened hook from a dilated base, without a basal tail-like extension, as is the case in *variistylus*.

♂. Length about 3·2 mm.; wing 4 mm.; antenna about 3·5 mm.

Rostrum and palpi light brown. Antennae of ♂ elongate, slightly exceeding the body in length, black throughout; flagellar segments strongly nodulose, rounded-fusiform, the apical necks slender. Head brown.

Thorax light brown, the dorsopleural region somewhat darker. Halteres pale, the knobs dark brown. Legs with the coxae and trochanters testaceous; remainder of legs broken. Wings greyish-subhyaline; veins pale; macrotrichia long, brown. Venation: R_2 in alignment with r-m; petiole of cell M_3 exceeding twice m-cu; vein 2nd A relatively short, ending some distance before m-cu.

Abdomen, including terminalia, dark brown. Male terminalia (Text-fig. 7) with the ventral lobe (*vb*) of basistyle obtuse at apex. Outer dististyle (*od*) slender, sinuous, near apex splitting into two short blackened arms. Basal dististyle (*bd*) with a flattened base that narrows into a long slender curved black spine, with a few setae at point of curvature; no pale tail-like extension at base, as is the case in *variistylus*. Phallosome (*p*) broadly ovate, the apex narrowed, the surface glabrous.

Hab.—New South Wales.

Holotype, ♂, Dorrigo, East Dorrigo, altitude 2,300 feet, 20th March, 1931 (W. Heron).

Molophilus dorriganus is most closely allied to *M. macleayanus* Alexander (New South Wales, Victoria) and *M. variistylus* Alexander (Tasmania), agreeing in the elongate nodulose antennae of the male, differing in the structure of the male terminalia.

MOLOPHILUS PICTOR, n. sp.

Belongs to the *gracilis* group, *ruficollis* subgroup; most nearly allied to *permutatus*; mesothorax chiefly obscure orange, contrasting with the dark grey head and black abdomen; antennae short in both sexes; knobs of halteres light yellow; legs black; wings with a strong blackish tinge, the prearcular region abruptly yellow; male terminalia with the basal dististyle appearing as a slender, gently curved spine, the outer face a little roughened.

♂. Length about 4·3–4·5 mm.; wing 5·2–5·5 mm. ♀. Length about 5·5 mm.; wing 6–6·2 mm.

Rostrum light brown; palpi black. Antennae short in both sexes, black throughout; flagellar segments sub-oval, the ends of the more basal ones trun-

cated; verticils exceeding the segments. Head dark grey, the anterior vertex more buffy-grey.

Pronotum obscure orange, slightly infuscated on sides; anterior lateral pretergites light yellow. Mesonotum dull orange. Pleura obscure orange, very sparsely variegated with brown on the sternopleurite and meral region, the anepisternum and propleura more extensively darkened; dorsopleural region dusky. Halteres with base of stem yellow, the remainder of stem dusky, the knobs light yellow. Legs with the coxae brownish-yellow, the fore coxae darker; trochanters yellow; remainder of legs black. Wings with a strong blackish tinge, the prearcular region abruptly yellow; veins conspicuous, brownish-black, brighter at wing-base. Venation: R_{2+3+4} nearly twice the basal section of R_5; petiole of cell M_3 about one-third longer than m-cu; vein 2nd A relatively long, ending about opposite, or in cases, to opposite one-third the length of the petiole of cell M_3.

Abdomen black, terminalia dark brown. Genital segment of female obscure orange; valves of ovipositor very long and slender, gently upcurved. Male terminalia (Text-fig. 8) of the general structure of *immutatus* and *permutatus*; mesal lobe (*mb*) of basistyle not produced into a spine, as is the case in *immutatus*. Outer dististyle (*od*) long and slender, the apex a slender curved hook. Basal dististyle (*bd*) more slender than in *permutatus*, appearing as a gently curved black spine, the outer surface microscopically roughened. Phallosomic structure (*p*), with the lateral spines simple, the crown broad, with numerous setae.

Hab.—Victoria.

Holotype, ♂, Warburton, on and near rock faces at river level, altitude 500 feet, April, 1931 (F. E. Wilson). *Allotopotype*, ♀. *Paratopotypes*, 1 ♂, 2 ♀.

The only closely allied species are *Molophilus immutatus* Alexander and *M. permutatus* Alexander, both likewise from Victoria. The former species differs notably in the coloration and in the structure of the male terminalia, especially the long conspicuous spine on the mesal lobe of the basistyle and the lateral spine on the basal dististyle. *M. permutatus* is much smaller, almost entirely black, including the thorax, and with the details of the terminalia distinct, especially the stouter basal dististyle and the weakly bidentate lateral spines of the phallosome.

Molophilus neolyratus, n. sp.

Belongs to the *gracilis* group, *ruficollis* subgroup; allied to *lyratus*; general coloration of mesonotum light reddish-brown, the pleura darker brown; legs brownish-black; wings yellowish, the veins slightly darker; male terminalia with the basal dististyle a simple, gently curved rod, narrowed to an acute blackened point, at apex with a few long setae; arms of the lyriform phallosomic structure smooth.

♂. Length about 5·2 mm.; wing 5·8 mm.

Rostrum brown, palpi black. Antennae of ♂ brown, of moderate length, if bent backward extending about to the wing-root; flagellar segments long-oval, the verticils exceeding the segments. Head light buffy-brown.

Lateral pretergites restrictedly whitish. Mesonotum light reddish-brown, without distinct markings; mediotergite restrictedly darker medially. Pleura slightly darker brown than the notum; posterior edge of pteropleurite with a group of conspicuous setae. Halteres pale, the knobs obscure yellow. Legs with the coxae yellowish testaceous; trochanters obscure yellow; remainder of legs

brownish-black; fore tibia of ♂ with a slightly enlarged, more blackish, subbasal ring. Wings broad, the ground-colour yellowish; veins slightly darker yellow; macrotrichia dark brown, the costal fringe conspicuous. Venation: R_2 lying slightly beyond r-m; petiole of cell M_3 a little less than two times m-cu; vein 2nd A elongate, extending to about opposite one-third the length of the petiole of cell M_3.

Abdomen brown, the terminalia more yellowish. Male terminalia (Text-fig. 9) with the ventral lobe of basistyle (*vb*) relatively slender, terminating on mesal face in a small blunt lobe directed cephalad. Outer dististyle (*od*) bifid, the lateral arm stout and straight, the shorter inner or mesal arm black, gently curved, its tip obtuse. Basal dististyle (*bd*) a simple, gently curved rod, gradually narrowed to the acute blackened tip, at extreme base a little expanded but not bearing a spine, as is the case in *lyratus*; just before apex of style on inner face a few long setae; style slender, without a lateral flange, as in *sublyratus*. Phallosomic structure (*p*) lyriform, as in the subgroup; arms long and slender, entirely smooth.

Hab.—New South Wales.

Holotype, ♂, Wentworth Falls, Blue Mts., altitude 2,840 feet, 20th–30th October, 1930 (F. E. Wilson).

Molophilus neolyratus differs from *M. lyratus* Alexander (Tasmania) in the very different structure of the basal dististyle of the male terminalia, and from *M. sublyratus* Alexander (Victoria) in the smooth, untoothed arms of the phallosomic structure.

MOLOPHILUS EQUISETOSUS, n. sp.

Belongs to the *gracilis* group, *ruficollis* subgroup; general coloration of thorax reddish-brown, the praescutum only vaguely lined with darker; antennae of ♂ elongate, nodulose; male terminalia with the outer dististyle a simple blackened horn; basal dististyle a long slender sinuous rod, dilated on basal fourth, thence narrowed into a slender spine, at point of narrowing with a score or more of long setae that resemble to some degree a horse's tail; phallosome a blackened depressed plate that bears spines and protuberances.

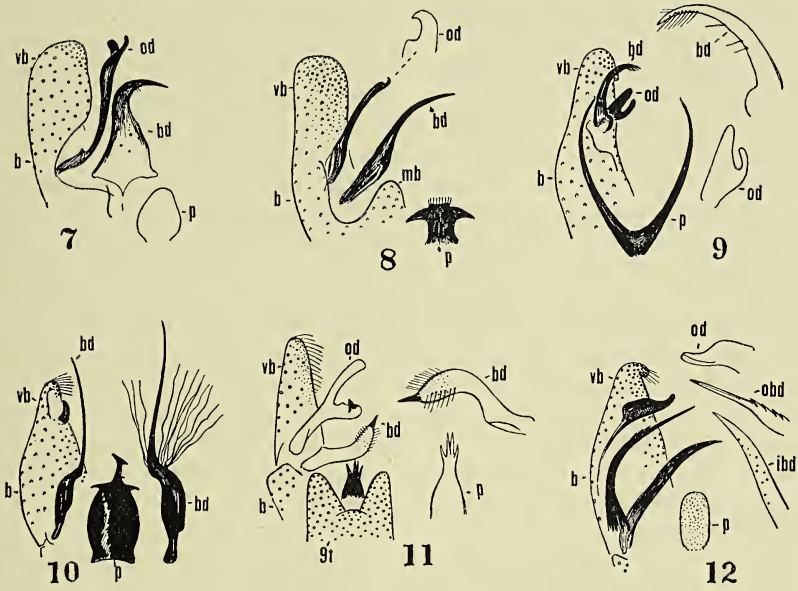
♂. Length about 5 mm.; wing 6 × 1·8 mm.; antenna about 4 mm. ♀. Length about 5·5 mm.; wing 6·5 mm.

Rostrum brown; palpi darker. Antennae of ♂ elongate, as shown by the measurements, dark brown throughout; flagellar segments fusiform, broadest on basal half, narrowed to tips, with conspicuous outspreading setae. Head dark brown.

Mesonotum reddish-brown, the praescutum with vague indications of a darker median vitta. Pleura reddish-brown, the dorsal region not or scarcely darker in colour. Halteres yellow basally, the knobs broken. Legs obscure yellow, the outer tarsal segments darker. Wings broad, tinged with greyish-brown; trichia abundant, dark brown; veins pale brown. Costal fringe long and conspicuous. Venation: R_2 lying beyond level of r-m; petiole of cell M_3 about twice m-cu; vein 2nd A long, extending to near one-third the length of the petiole of cell M_3.

Abdomen dark brown. Male terminalia (Text-fig. 10) with the apex of ventral lobe (*vb*) of basistyle relatively narrow, with numerous coarse setae. Outer dististyle (*od*) a small simple blackened horn. Basal dististyle (*bd*) a long slender spine, in a position of rest extending caudad beyond the extreme level of the basistyle; basal fourth more expanded, thence suddenly sinuous and

narrowed into the very long, nearly straight, apical spine; at point of narrowing, a group (exceeding a score) of long reddish setae, somewhat suggesting a horse's tail, these setae exceeding in length one-half the length of the terminal spine. Phallosome (*p*) a blackened depressed plate, near outer end on either



Text-figs. 7-12.—Male terminalia.

7, *Molophilus dorriganus*, n. sp.; 8, *M. pictor*, n. sp.; 9, *M. neolyratus*, n. sp.; 10, *M. equisetosus*, n. sp.; 11, *M. extensicornis*, n. sp.; 12, *M. trifasciolatus*, n. sp. (Symbols: *a*, aedeagus; *b*, basistyle; *bd*, basal dististyle; *ibd*, inner basal dististyle; *mb*, mesal lobe of basistyle; *obd*, outer basal dististyle; *od*, outer dististyle; *p*, phallosome; *t*, tergite; *vb*, ventral lobe of basistyle.)

side produced laterad into an acute spine; the median area of plate extends further caudad into a straight black rod, at apex terminating in two blackened spines that lie in a straight angle to one another.

Hab.—New South Wales.

Holotype, ♂, Mount Victoria, Blue Mts., altitude 3,425 feet, 20th–30th October, 1930 (F. E. Wilson). *Allotopotype*, ♀, 13th November, 1933 (V. C. Retford). *Paratopotype*, ♂, 12th November, 1933 (V. C. Retford).

The nearest allies of this remarkable species are *Molophilus tasioceroides* Alexander and *M. wilsoni* Alexander, both of which have elongate antennae in the male sex, and with a variously modified blackened phallosome, but in all other respects are entirely different flies. The present species and *M. wilsoni* are the largest members of this particular subgroup of the genus.

Molophilus extensicornis, n. sp.

Belongs to the *gracilis* group, *ruficollis* subgroup; allied to *wilsoni*; antennae of ♂ approximately as long as body, the flagellar segments not nodulose; wings grey, without brown suffusion; male terminalia with inner arm of outer dististyle bearing a blackened tooth before apex; basal dististyle shorter than the

outer, appearing as a strongly curved rod that terminates in an acute black spine.

♂. Length about 5 mm.; wing 6·5 mm.; antenna about 4·8 mm.

Rostrum and palpi dark brown. Antennae of ♂ elongate, approximately as long as the body, dark brown throughout; flagellar segments elongate-cylindrical, not nodulose, with long, outspreading setae. Head dark brown.

Thorax almost uniformly dark brown; setae of praescutal interspaces long and conspicuous. Halteres dusky. Legs with the coxae and trochanters testaceous; remainder of legs brown, the colour chiefly produced by dark setae. Wings tinged with grey, the veins slightly darker; macrotrichia dark brown. Venation: Petiole of cell M_3 relatively short, about twice m-cu.

Abdomen, including the terminalia, dark brown. Male terminalia (Text-fig. 11) with the ventral lobe (*vb*) of basistyle elongate, narrowed to the obtuse tip, the mesal face with long, very delicate setae. Outer dististyle (*od*) bifid, the two arms long and divergent, the outer longer, a little expanded at tip; inner arm with an erect blackened tooth before apex. Basal dististyle (*bd*) shorter than the outer, appearing as a strongly curved rod that terminates in an acute black spine; outer half of style with abundant delicate setae, especially on lateral face and surrounding the apical spine. Phallosome (*p*) black, narrowed at apex into a group of four black spines that are arranged more or less in pairs, the apical pair lying about in a line with the axis of the structure and not divergent. Ninth tergite (*9t*) large and conspicuous, as in this restricted section, profoundly emarginate, the lobes with coarse black setae.

Hab.—Victoria.

Holotype, ♂, Yarram, South Gippsland, 2nd July, 1933 (F. E. Wilson).

Molophilus extensicornis is similar in general appearance and size to *M. wilsoni* Alexander (Victoria) which may be considered as being the nearest ally. The structure of the styli of the male terminalia, especially the basal dististyle, readily distinguishes the species. The various members of this section of the subgroup have the male antennae greatly lengthened, differing from the other species of the genus in the Australian fauna by the simple cylindrical flagellar segments of the antennae, which much resemble those of the genus *Tasiocera*.

Molophilus trifasciolatus, n. sp.

Belongs to the *pervagatus* group; mesonotum light reddish-brown, the mediotergite and dorsal pleurites blackened, the ventral sternopleurite paling to reddish-brown; halteres yellow; femora yellow, the tips narrowly but conspicuously blackened; wings cream-yellow, with three grey areas that appear as more or less complete crossbands; male terminalia with the outer dististyle a simple structure, the apex narrow and obtuse; both dististyles acute at apices.

♂. Length about 3·8–4 mm.; wing 4·6–4·8 mm.

Rostrum and palpi brownish-black. Antennae with scape yellow, the pedicel yellowish-brown; flagellum dark brown, with long verticils that much exceed the segments. Head obscure yellow, the centre of the vertex extensively brownish-grey.

Pronotum obscure yellow above, dark brown laterally. Anterior lateral pretergites light sulphur-yellow. Mesonotal praescutum and scutum light reddish or reddish-brown, the former a little darker medially, especially in front; scutellum obscure yellow, the parascutella darker; mediotergite brownish-black,

more reddish-brown laterally. Pleura brownish-black to plumbeous, the ventral sternopleurite and dorsal meral region paling to reddish-brown; ventral meron again darkened. Halteres light yellow. Legs with the coxae and trochanters yellow; femora yellow, the tips narrowly but conspicuously blackened; tibiae and basitarsi obscure yellow; terminal tarsal segments brownish-black; fore tibia with a narrow but very conspicuous jet-black subbasal ring. Wings with the ground-colour cream-yellow, trifasciate with brownish-grey, the broadest area including the wing-apex; a narrower but almost complete crossband at cord, extending from R_2 to the margin along vein Cu_1; the most basal band incomplete, occupying the cubital and anal fields only; veins yellow, darker in the clouded areas. Venation: R_2 and r-m in approximate transverse alignment; vein 2nd A ending about opposite the caudal end of m-cu.

Abdomen dark brown to brownish-black, the terminalia only a trifle brighter. Male terminalia (Text-fig. 12) with the outer dististyle (*od*) a simple blackened structure, the distal half narrowed to a somewhat obtuse blunt lobe, not at all bifid or trifid. Outer basal dististyle (*obd*) a long slender acute rod, near its outer end with appressed spines. Inner basal dististyle (*ibd*) a little shorter but broader, appearing as a blade of moderate width, gradually narrowed to the acute tip.

Hab.—New South Wales.

Holotype, ♂, Megalong Valley, Blue Mts., 20th–30th October, 1930 (F. E. Wilson). *Paratopotype*, ♂.

The present species is very similar in its general appearance to *Molophilus pervagatus* Skuse, differing in the larger size and quite distinct structure of the male terminalia, especially the unlobed nature of the outer dististyle. The male terminalia are most like that of *M. acutistylus* Alexander, which differs especially in the pattern of the legs, and less evidently in that of the wings.

THE EARLY STAGES OF *ACTINA INCISURALIS* [DIPTERA, STRATIOMYIIDAE].

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(Nine Text-figures.)

[Read 25th July, 1934.]

Introduction.

The first reference in Australian literature to *Actina incisuralis* Macq. was by White (1914), when he described both sexes and gave the distribution of the species as Tasmania, Victoria and N. S. Wales. Two years later (White, 1916) he stated that *A. incisuralis* ranges from Tasmania to Queensland and is one of the commonest and most widely distributed of Australian Stratiomyiidae. Hardy (1931) described three new species of *Actina* and pointed out the variability in coloration of *A. incisuralis*.

This species belongs to the subfamily Beridinae, to which the larvae described in the present paper also run in Malloch's key to Dipterous larvae (1917). The adults bred from the same series have the normal coloration and agree with the descriptions of typical *A. incisuralis*.

The work of White and of Hardy is purely taxonomic. The only published work on the early stages of Australian Stratiomyiidae is that of Irwin-Smith (1920-23) on *Metoponia rubriceps* Macq., a brief note by J. G. Myers (1920) on *Neoexaireta spiniger* Sch., and a short description by Froggatt (1896) of a species of *Ophiodesma* from grass-tree. Nothing has been written on the life-histories of Australian species of *Actina*.

Observations on Habits of Larvae.

During the course of carrion insect investigations in August, 1932, larvae of *Actina incisuralis* were found in abundance on the under-surface of a sheep carcase, which had been lying in the same place for seven months. Larvae of all sizes were numerous on the moist, slimy surface of the bones, and, when disturbed, moved slowly away into crevices. They were also present in large numbers amongst the wet wool, and on the remains of the skin.

The following month, when searching for earthworms, quantities of *A. incisuralis* larvae were found on the earth under masses of rotting grass. They were also present in the soil amongst the roots of growing grasses and at the bases of the stems. In all these situations moisture was plentiful. Apparently the food of these larvae is not specific, as they are found associated with decaying plant and animal matter as well as with living plants, but moisture seems to be essential.

Larvae from the carcase and from grass were placed in two separate jars provided with damp soil and wool or grass. Nothing was added to the jars except a little water from time to time. The larvae did not appear to grow after being placed in the jars but many pupated. There was no change in external appearance, the larva simply becoming immobile and the skin hardening. After a period of from 7 to 8 months from the time of collecting, adults of *A. incisuralis* emerged in numbers from both jars.

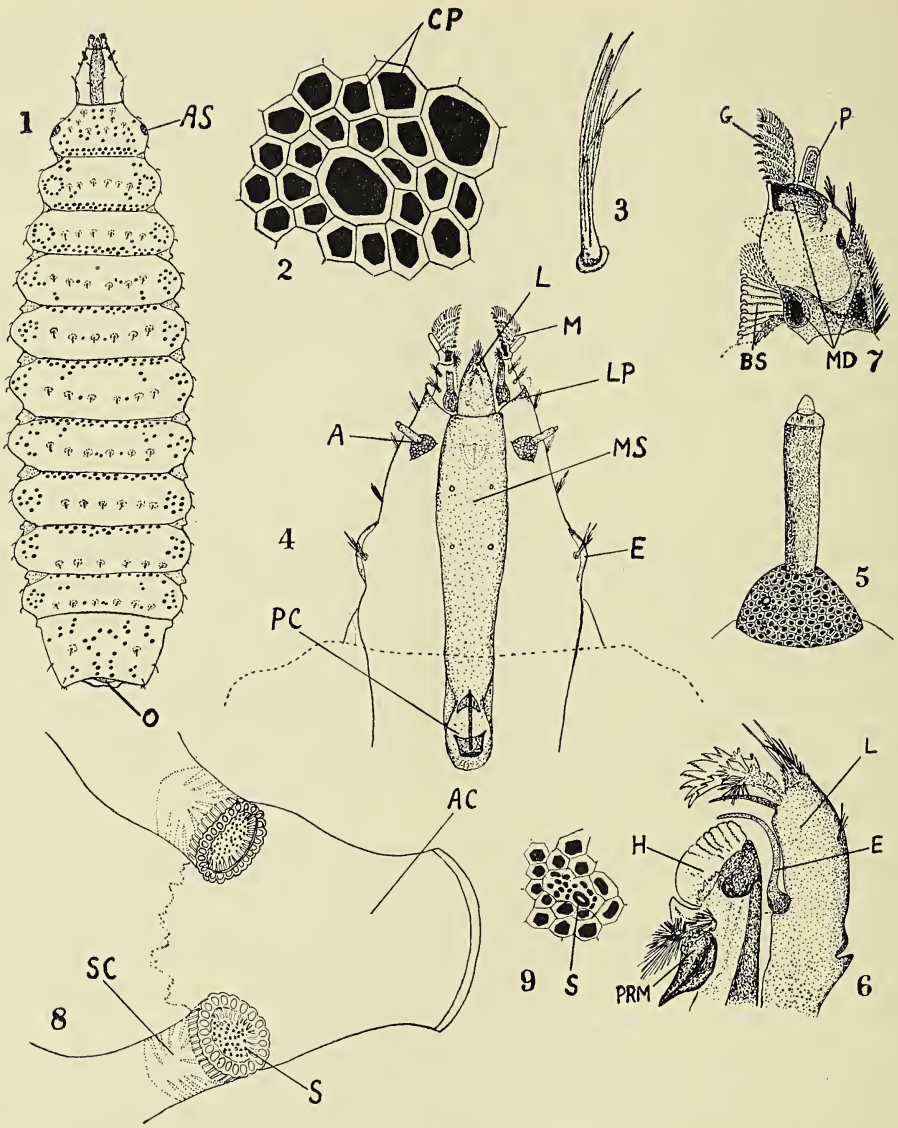
Description of Larva.

The length of the larvae taken in the field varied from 4 to 9 mm. They were evidently full-grown at 9 mm., as all of that size pupated and the flies that emerged were of the same size as captured specimens. The colour changed with age, the smaller larvae being a dirty whitish shade, becoming greyish-brown and finally brown.

The body (Text-fig. 1) is somewhat flattened dorso-ventrally, although the younger larvae are more cylindrical in form. The dorsal and ventral surfaces are convex and the lateral edges produced into a ridge. In the younger larvae the arrangement of body bristles and structure of the head and mouth parts seem to be similar to that of the mature larvae. It was not determined when or how often ecdysis takes place. There are eleven body segments and a head. The body is strongly constricted between the segments, giving the larva a scalloped appearance along the sides. Dorso-laterally the integument between each abdominal segment, and between the third thoracic and first abdominal, is produced into a small papilla projecting outwards. The thoracic segments become broader passing from the head, whilst the abdominal segments are of uniform width and length, with the exception of the eighth, which is narrower and longer than the others, more flattened and produced into two blunt projections at the posterior corners. All the body segments are much broader than long. The head is elongated, narrow and pointed.

The larva is lighter in colour on the ventral surface. The colour is due to the presence of a close armour of small, hexagonal plates which occur all over the surface (Text-fig. 2). These vary from light to dark brown, causing the difference in colour on the two surfaces and in young and old larvae. On the lateral edges also the skin is lighter in colour. The plates are calcareous, and the skin bubbles freely when hydrochloric acid is applied, a test suggested by Lundbeck (1907). Certain of the plates are much enlarged, more roughly circular in outline and more densely coloured, standing out as conspicuous spots. These spots are arranged in a definite pattern. Both dorsally and ventrally there is a double row at the junction of each segment, except at the fore border of the first thoracic, and dorsally between the seventh and eighth abdominal segments, where there is only a single row. A group occurs on both surfaces near the lateral edges of each segment, arranged in the segments nearer the head in a rough circle. There are a few other spots scattered about on the dorsal surface, being most numerous on the first and last segments (Text-fig. 1).

Bristles and hairs are present on the body and are arranged as follows: On the dorsal surface of each segment, except the last, near the middle are six lighter coloured areas where the hexagonal plates are smaller and less pigmented. These occur in a row across the segment three each side of the centre except on the first segment where they form two triangular groups. From each of these areas



Text-figs. 1-9. *Actina incisuralis.*

1.—Full-grown larva. × 7·5. *as*, anterior spiracle; *o*, opening of air chamber.
2.—Larval integument. × 280. *cp*, calcareous plates.
3.—Branched dorsal bristle. × 190.
4.—Head of larva viewed dorsally. × 45. *a*, antenna; *e*, eye rudiment; *l*, labrum; *lp*, lateral plate; *m*, maxilla; *ms*, median sclerite; *pc*, pharyngeal chamber.
5.—Antenna. × 190.
6.—Labrum and hypopharynx. × 100. *e*, epipharynx; *h*, hypopharynx; *l*, labrum; *prm*, prementum.
7.—Maxilla, inner surface. × 100. *bs*, banded segment; *g*, galea; *md*, mandible; *p*, palp.
8.—Posterior spiracles. × 180. *ac*, air chamber; *s*, spiracle; *sc*, sieve chamber.
9.—Abdominal spiracle. × 280. *s*, spiracle.

arises a large branched bristle accompanied by a number of smaller ones (Text-fig. 3). These bristles are blunt and curved at the upper extremity. They project straight up and then bend slightly in towards the centre; they are a pale yellow colour. In many individuals the bristles curve posteriorly instead of medially. On the last segment there are only two of these groups of bristles, one each side of the middle. The first segment has some extra bristles on the dorsal surface anteriorly.

On the lateral edges of each segment are two pairs of blunt bristles curved backwards, one pair being dorsal and one ventral. The more posterior member of each pair is larger than the other. On the last segment there is only one bristle laterally and a tuft on the dorsal and ventral surfaces of the projections at the posterior corners. On the ventral surface, across each segment is a wide band of fine colourless hairs curved backwards. This band does not extend to the lateral edges of the segment but occupies the central third only. The hairs are numerous and closely set. On the last segment they surround the anal groove.

On the ventral surface of the eighth segment, there is a short transverse fold in the skin near the anterior border of the segment. At right angles to this fold and running from it longitudinally down the middle of the segment a little more than half-way to the posterior edge is the anal slit. The lips are armed on the inner edge with a series of strong, inwardly and backwardly directed teeth which interlock when the slit is closed. The rest of each lip is covered with fine hairs directed in the same way. From the end of the anal slit to the posterior border of the segment is a deep narrow groove. There is also a postero-dorsal groove on the last segment running transversely and protecting the opening to the air cavity into which the posterior spiracles open.

The Head (Text-fig. 4).—The head is elongated and somewhat conical in shape. On the dorsal surface there is a strongly chitinized brown sclerite running down the centre for the whole length, being a little less than a third the width of the head. This is constricted towards the anterior end and then slopes to a point forming the labrum. The rest of the integument of the head is thinner and pale yellow in colour. The "lateral plates" of Irwin-Smith occur each side of the labrum near its base and articulate with the maxillae. The maxillae lie slightly below and on each side of the labrum, in front of which they extend. They are complicated in structure. The antennae (Text-fig. 5) are situated a short distance behind the junction of the maxillae with the side lobes, occupying a dorsal position close to, and on each side of, the middle sclerite. Each consists of a large mound-like basal segment, closely covered with small brown plates which are darker and more conspicuous than those on the rest of the head. On the inner side half-way to the apex is one bristle. From the apex of the basal segment arises an elongated strongly chitinized stout segment, whilst the apical segment is small and dome-shaped. The antennae are large and conspicuous features of the head.

A little behind the middle of the head are a pair of lateral swellings representing rudimentary eyes. On the dorsal surface, and near the outer edge of each eye-swelling, there is a small concavity from which a branched hair with a large swollen base arises. Two other branched hairs arising from small depressions occur on each side of the head between the eye rudiment and the maxilla. On the median dorsal sclerite are a number of bristles arranged in two rows down the sides.

Mouth Parts.—A lateral view of the head shows the labrum arising from the dorsal sclerite and curving between the two maxillae, so that its plume-like appendage is ventral. The maxillae lie each side of the labrum and their palps and spinose galeas are the most anterior of the mouth parts. The mandibles are fused to the inner faces of the maxillae. The hypopharynx is close against the ventral face of the labrum. The labium is situated behind and below all these parts. It consists of a small prementum in the form of a spade-shaped chitinous sclerite attached to the ventral face of the hypopharynx near its base and covered with tufts of hairs and spines, a mentum made up of two lobes of thin membranous chitin densely covered with fine hairs, and a submentum consisting of a hairy membranous plate and a turned back part of very delicate chitin with long fine hairs on its edge. The mentum overlies ventrally the basal half of the maxillae.

The side-lobes of the head, called by Irwin-Smith "lateral plates", and by Bischoff (1925) "lateralia", are not pointed at the apex as in *Beris* and *Metoponia*, but are truncated or blunt, and project forwards over the base of the maxillae; that is, the maxillae arise from the head at a point before the termination of the lateral lobes and are sheathed by them at the sides. The mentum is joined to the lower edges of the lateral lobes and passes across the ventral surface of the head forming a lower lip.

The labrum (Text-fig. 6) consists of a strong boat-shaped sclerite, being the apical termination of the dorsal head plate. It narrows at the apex and is curved towards the ventral surface. At the apex is a tuft of spines, among which are two longer ones. Below and behind this is a large plumose structure strongly recurved ventrally. It is trifid, having a large central, and two smaller side lobes. Each lobe is doubly serrated, and the whole is of delicate membranous chitin. Closely associated with this structure is a chitinous rod, which arises a little behind it. Behind this there is a wide slit along the ventral surface, where the lower edges of the boat-shaped sclerite do not meet. This open part is protected by a strong chitinous structure, which is connected at its base with the postero-ventral edge of the labrum and extends forward lying along the ventral surface as a curved chitinous plate. Its position indicates that it represents the epipharynx. The hypopharynx lies below the labrum against the epipharynx, and consists of a sclerite with a chitinous strut along its inner edge and a curved dissected apical end. The prementum is attached on the ventral surface and behind the curved apex, so that the hypopharynx lies between the labrum and labium.

The maxilla (Text-fig. 7) is very complex in structure, having the mandible fused with its inner face. It is slightly convex on the outer surface, from which two large plumose hairs arise towards the top edge. Also on the outer surface, just behind the palp, is a chitinous knob bearing a tuft of spines spreading fan-wise. The palp arises from the outer surface just behind the apex, which is occupied by the galea, a fan-shaped structure bearing rows or combs of fine, closely set hairs, hooked at the ends. The dorsal edge of the maxilla is fringed with some rows of bristles directed forwards. The posterior half of the ventral edge is occupied by Bischoff's "banded segment" supplemented in front by a small area densely covered with hooked spines. The inner face of the maxilla shows the closely appressed mandible. Bischoff's terminology is being used for these

parts for the sake of uniformity and convenience, but without necessarily agreeing as to their homology. At the base of the mandible is a very densely chitinized mass lying just above the banded segment. It is rounded and narrows anteriorly. Above this is a more lightly chitinized band running up to the dorsal edge of the maxilla. It continues along the dorsal edge with stronger chitinization, and then becomes thin again just before the knob bearing the spreading spines, ending in a strong chitinous piece close to the apex of the maxilla at the base of the galea. In this feature it closely resembles many of the Stratiomyiid larvae illustrated by Bischoff.

The pharynx runs back to the middle of the first segment, and at its posterior end is a mechanism which, from the dorsal surface, has the appearance of a pump. There is a slight constriction in the wall of the pharynx at the anterior end of the structure and a bell-shaped mass fits into this narrow part. Below this is a broadly oval chamber which is filled by a piston-like mass of chitin, with a central rod connecting with the anterior portion. The posterior end of the chamber opens into the oesophagus. Viewed from the side the structure loses its piston-like appearance, and the central mass of chitin is seen to be composed of two parts, one forming the dorsal wall of the pharynx and curving towards the ventral side at the posterior end, the other a similarly curved piece lying parallel with it and connected with the part at the anterior end. The whole mechanism appears to be valvular in function and corresponds to Irwin-Smith's masticatory apparatus, the chitinous piston probably being her "wing-bearer".

The Spiracles.—On the dorsal surface of the eighth segment just before the posterior edge is a transverse fold, of which the ventral lip projects furthest. At the bottom of the fold centrally, there is an elliptical opening with strongly chitinized lips. On the inner edge of the lips are several bristles. The opening is the entrance to a large chamber, which extends back under the dorsal surface nearly as far as the posterior end of the anus (Text-fig. 8). The posterior spiracles are not visible externally, but open into this chamber near its base. In cleared specimens the spiracles may be seen through the skin. A large tracheal trunk runs into each side of the air cavity near its base and ends in a special modified section called by Irwin-Smith the "sieve chamber", in which a number of strong, short chitinous hairs project inwards from the wall. The sieve chamber ends in the spiracle, which opens into the air cavity. The spiracle is circular in outline, with a large opening in the middle surrounded by a thick raised rim, which is strengthened by a series of chitinous bars forming a ring-like pattern similar to the border of the slits in Calliphorid spiracles.

The anterior spiracles are situated on the prothorax laterally about the middle of the segment. They are larger than the posterior spiracles and consist of a mound of chitin raised above the surface of the integument. This is roughly circular in outline and is somewhat crater shaped, that is, the rim is raised and the centre sunken. Towards the anterior edge it is more elevated, and here the two spiracular slits open. They are oval and close together, but diverging at the top end. The chitinous mound slopes down from here to a roughened portion with a small gap, representing the stigmatic scar. The slits are the openings of the felt chamber, which is at the end of the tracheal trunk and lies inside the chitinous mound.

There is a pair of very minute spiracles present on the metathorax and on each of the abdominal segments except the last. They occur dorso-laterally and

appear as small black spots. Each lies between the two bristles on the lateral edges but nearer to the centre. The spiracle (Text-fig. 9) consists of an irregular opening surrounded by a strong chitinous rim projecting slightly above the surface. The surrounding area is composed of calcareous plates many times smaller than those of the general integument and more rounded in shape. There is one row of these small plates on the inside of the spiracle and several rows on the outer edge. No head spiracles were observed as noted in *Metoponia* by Irwin-Smith.

The Puparium.—Pupation takes place inside the old larval skin which, apart from becoming hard and rigid, does not change in appearance. When emergence of the fly occurs, the second segment splits right around in a circle near the anterior border, so that the whole of the first segment and head come off as a cap. A longitudinal split forms in the middle of the dorsal surface, extending from the free edge of the second segment to a point behind the anterior border of the fourth, where it meets another transverse split running right across the dorsal surface.

Just prior to emergence the chitin of the puparium becomes sufficiently transparent to show the outlines of the fly inside.

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A NOTE ON THE OCCURRENCE OF SEEDLING LESIONS CAUSED BY CEREAL SMUTS.

By J. G. Churchward, University of Sydney.

(Plate v.)

[Read 27th June, 1934.]

Introduction.

The cereal smuts annually cause heavy losses in Australia. Losses due to flag smut caused by *Urocystis tritici* (Koern.) have been estimated to amount to approximately £400,000 per annum.*

In Australia, preventive measures are not only costly, but often ineffective. The development of immune or resistant varieties offers the most promising solution of the problem. In such work, the determination of resistance or susceptibility in the seedling stages is of great practical value to the plant breeder.

Angell† has shown that, under certain conditions, wheat seedlings become distorted when infected by *Urocystis tritici*. Dr. W. L. Waterhouse, of the Sydney University, and the writer repeated the experiments and obtained additional information relating to infection of seedlings by certain cereal smuts. The results are recorded here.

Methods and Results.

Flag Smut.

The methods described by Angell were closely followed. Four varieties of wheat, viz., Federation, Dundee, Nabawa, and Hope, were heavily inoculated with spores of flag smut which had been presoaked in water for three days. The grain was sown half an inch deep in 4-inch pots in a sterilized loam soil moistened to 40% of its moisture holding capacity, and maintained at a temperature of 20°C. in a dark cellar. The control plants were inoculated with a suspension of spores previously killed by boiling.

An examination of the plants ten days after sowing showed some distortion of all varieties which had been inoculated. But, what was more striking, white opaque patches, varying in size from minute spots to areas 0·5 × 1·5 cm., were observed on the coleoptile and leaves of inoculated plants (Plate v, figs. 1–4). Occasionally spots became confluent, producing a continuous white patch along the entire length of the coleoptile, which, because of the swellings accompanying the spots, often assumed an irregular or blistered appearance.

A microscopic examination of stained sections cut through these spots showed the presence of the smut fungus (Plate v, figs. 5–6). Two very distinct types of mycelium were seen in different parts of the plant tissue. The first,

* Seventh Ann. Report of Council Sci. and Indust. Research, 1933.

† *Journ. Council Sci. Indust. Research*, 7, 1934, 110-112.

which was deeply stained and associated with the vascular tissue, was more abundant and more easily discernible than the second type, which did not stain so deeply. Further, the latter, which apparently originates from the first, grew out towards the periphery at right angles to the length of the coleoptile. The nuclei of the deeply stained mycelium were in the dikaryophase, but none was seen in the second type.

These white spots were produced also on seedlings which had not been confined to darkness during the first ten days of their growth. Light, however, in causing an elongation of the coleoptile made the infection spots more easily discernible and provided a greater area over which the fungus could operate.

The spots appeared on the resistant varieties, Hope, Nabawa, Dundee, as abundantly as on Federation, which is notably susceptible.

Bunt.

Sterilized grain of four varieties of wheat, Federation, Canberra, Nabawa and Florence, was heavily inoculated with a known physiologic form of *Tilletia tritici* (Bjerk.) Winter, which causes bunt of wheat, and grown under the same conditions as described for flag smut.

No distortion occurred; in fact, the inoculated seedlings showed more vigorous growth than the controls, appearing to be stimulated by the presence of the smut. White opaque spots occurred on several plants of Canberra and Federation. Examination of stained sections of these spots showed the presence of a smut mycelium very similar in appearance to that of flag smut.

Grain of the same varieties, inoculated with a mixture of bunt and flag smut, germinated poorly, and the seedlings, which were distorted, were heavily covered with white opaque spots.

Oat Smut.

Two varieties of Oats, Fulghum and Algerian, were dehulled and the grain inoculated with spores of *Ustilago avenae* (Pers.) Jens., which causes the loose smut of oats. These were sown and germinated under the conditions described above. The inoculated pots of Algerian oats showed striking distortion (Plate v, fig. 4) with white opaque spots. Microscopic examination of sections through these showed the presence of smut mycelium. Distortion was not so striking in Fulghum, but the germination was poorer and the growth of the plants less vigorous.

Summary and Conclusions.

Grain of reputedly resistant and susceptible varieties of wheat and oats was inoculated with spores of several cereal smuts and grown under conditions approximating to those set down by Angell. Well defined white opaque spots developed on the coleoptile and first leaf of resistant and susceptible varieties alike, and, in the case of Algerian oats infected by loose smut, distortion was also very marked. An examination of stained microscopic sections through these spots showed the presence of an abundance of smut mycelium of two kinds. The nuclei, which were seen only in the deeply stained mycelium, were in the dikaryophase.

The advantages of being able to detect resistance or susceptibility in the seedling stage are obvious. Under the conditions of the present experiment, white infection spots occurred on both resistant and susceptible varieties, and therefore this symptom, like the distortion of seedlings described by Angell,

cannot be used as a criterion of resistance or susceptibility. These white leprous spots, however, are better indicators of infection than the reported distortion, for, while all the plants in several varieties were spotted, by no means were all distorted.

It is probable that conditions may be found under which field-resistant varieties will not show these infection spots in the seedling stage, having prevented the establishment of the fungus in their tissues. Under the same conditions susceptible varieties may become infected.

There may be, also, further factors for resistance which operate later in the development of the plant. Further experiments on the nature of resistance to cereal smuts are in progress.

Acknowledgment.

It is desired to acknowledge the helpful advice of Dr. W. L. Waterhouse, University of Sydney, at whose suggestion the work was commenced.

EXPLANATION OF PLATE V.

1.—The wheat seedling leaves showing white infection spots caused by *Urocystis tritici*. × ¾.

2, 3.—White opaque infection spots caused by *Urocystis tritici* on the coleoptile of wheat seedlings. 2, × 1½; 3, × ¾.

4.—Distorted plants of Algerian oats showing white opaque infection spots caused by *Ustilago avenae*.

5, 6.—Photomicrograph of sections through infection spots on 5, coleoptile; and 6, the leaf of wheat seedlings showing smut mycelium. × 600.

CONTRIBUTIONS TO THE MICROBIOLOGY OF AUSTRALIAN SOILS. II.

A COMPARISON OF THE ROSSI-CHOLODNY METHOD AND THE PLATE METHOD FOR STUDYING THE SOIL MICROFLORA.

By H. L. Jensen, Macleay Bacteriologist to the Society.

(Plate vi.)

[Read 25th July, 1934.]

Introduction.

Direct microscopical methods for the observation and enumeration of soil microorganisms have received considerable attention during recent years. A useful technique for this purpose was first developed by Conn (1918) and later modified by Winogradsky (1925). These methods have shown that soils contain bacteria in numbers many times as high as those obtained by the current plate or dilution methods. The figures, however, are often very erratic, as shown by Kühlmorgen-Hille (1928), and the same would presumably apply to the essentially similar methods of Vande Velde and Verbelen (1930) and Fehér (1932). More reliable results may be obtained by means of an improved technique devised by Gray and Thornton (1928). Another method, specially adapted to the study of soil protozoa, has been developed by Koffmann (1928-31). A common feature of these methods is that the microorganisms are made visible by staining of a soil suspension, either in wet mounts, as in one of the modifications of the method of Koffmann, or else in dried films. Although adequate for the study of bacteria and protozoa, such methods are less suitable for the actinomycetes and fungi, which organisms consist of mycelia that may be broken up and scattered by the preparation of the soil suspension (this is also one of the main disadvantages of the usual plate methods); indeed, fungus mycelium may be altogether absent from the microscopical picture (Conn, 1918). The first attempt to find an adequate method for the microscopical study of fungi and actinomycetes in soil was made by Conn (1922), but this method does not seem to have been widely used, and may not always lead to reliable results (McLennan, 1928). A more promising way of attacking the problem appears to have been found by Cholodny (1930) and Rossi (1928, cit. after Cholodny) who, independently of each other, devised a simple method consisting in placing microscopic slides in the undisturbed soil for a certain interval of time, and fixing and staining the microorganisms growing upon and adhering to them. Conn (1932) has shown how this method may be applied to laboratory experiments with soil. Beautiful pictures of the soil microflora and -fauna, obtained by the same method, have been published by Demeter and Mossel (1933), who also discuss the limitations of the method, particularly the facts that it is only very roughly quantitative,* and that, like

* In view of the irregular distribution of the organisms and the fact that the coarser soil particles are washed off the slides, it would appear highly doubtful whether the combined counting and weighing of the slides, as attempted by Verplancke (1932), could give reliable quantitative results.

the other microscopical methods, it does not supply any cultures of the organisms observed. It must also be realized that when the slides are left in the soil for periods of several weeks, we do not obtain a picture of the soil population at any given moment (such as found by the other microscopical methods and the culture methods), but one resulting from a shorter or longer process of growth of organisms on the slides. On the other hand, the Rossi-Cholodny method shows the fungi and the actinomycetes in their actual, undisturbed state and, like the other microscopical methods, it reveals the presence of organisms not amenable to study by plate or dilution methods. It would, therefore, seem very interesting to compare the results obtained by means of these two methods; an attempt hereat is presented in this contribution.

Methods.

Various kinds of organic matter were added to soils in the laboratory, and the resulting changes in the microflora were followed both by the plate method and by the Rossi-Cholodny method as recommended by Conn (1932). Two different soils were used: one (*A*) a loam, rich in organic matter and lime, of pH 7·3, from a flower bed, the other (*B*) a heavy loam, very rich in organic matter, of pH 5·4, from uncultivated grass land. The samples had been air-dried, ground and sieved before use. Portions of about 500 gm. of moist soil (moisture adjusted to approximately 70% of the water-holding capacity of each soil) were placed in big Petri dishes (internal diameter 18·5 cm., depth 4·5 cm.), forming a layer about 3 cm. deep, and a number of microscopic slides were placed vertically in the soil, with their long sides against the bottom of the dish. Previous to use, the slides had been carefully cleaned by boiling with potassium bichromate and sulphuric acid, washing with water, and storing in alcohol which was removed by flaming. After various periods of time, one or two slides were taken out for microscopical examination, and at the same time samples (8-10 gm.) of the surrounding soil were taken out for plate counts and moisture determinations. The dishes with soil were kept at room temperature (21–26°C.), and only small changes in the moisture content took place during the course of the experiments. The following series of experiments were run:

A. (Alkaline garden soil.)

First series: *a.*—Control soil (no addition); *b.*—Soil + 1·0% mannite; *c.*—Soil + 0·5% dry milk; *d.*—Soil + 0·5% keratin.

Second series: *a.*—Control soil; *b.*—Soil + 1·0% cellulose + 0·05% $NaNO_3$; *c.*—Soil + 1·0% liquid paraffine + 0·05% $NaNO_3$.

B. (Acid grass soil.)

First series: *a.*—Control soil; *b.*—Soil + 1·0% cellulose + 0·1% $(NH_4)_2SO_4$.

Second series: *a.*—Control soil; *b.*—Soil + 1·0% mannite; *c.*—Soil + 0·5% dry milk.

Besides these, some experiments were carried out on various soils without addition of organic matter. Since no large quantities of these soils were available, they were kept in smaller glass containers as used by Conn (1932). The media and the technique of plate counting were the same as used in a previous series of experiments (Jensen, 1934), except that the plates were incubated at room temperature. The mannite-asparagine-agar devised by Thornton (1922) was also used for counting bacteria and actinomycetes in the alkaline soil with mannite. In the first series of experiments with the acid soil, as well as in some of the soils without additions, counts of fungus spores were made according to

the method of McLennan (1928): drying of the soil *in vacuo* for 3 days, which kills the vegetative mycelia while leaving the spores intact. A modification was introduced in the staining of the preparations for microscopical examination, instead of simple staining with Rose bengale (Conn, 1918) or erythrosine (Winogradsky, 1925). Preliminary experiments showed that a differentiation of the soil microflora could be obtained by staining according to the Gram method; the soil colloids are decolourized by the alcohol treatment, and are not re-stained when erythrosine or Rose bengale* is used as a counterstain for the Gram-negative soil organisms. Barthel (1918, 1919) has previously shown that good pictures of Gram-positive organisms may be obtained by Gram-staining of smears from cultures in sterilized soil. Also Demeter and Mossel (1933), whose paper appeared while the present work was in progress, suggest Gram-staining, but apparently without yet having used it for soil. In my experiments the following technique has been used:

1. After air-drying and removal of sand-grains, the slide is passed through a Bunsen flame to fix the microorganisms.—2. Staining 2–3 minutes with Crystal-violet-ammonium oxalate-solution (Gram-Hucker).—After washing, treatment for 1–2 minutes with Lugol's iodine.—3. Washing, drying, and differentiation 4–5 minutes with absolute alcohol which is renewed 3–4 times.—4. Drying, and counter-staining 10–12 minutes on water bath at 60–70°C. with Rose bengale solution after Conn (1932).

In some cases a search was made for acid-fast organisms by staining with hot carbol-fuchsin and differentiation 30–60 seconds with 5% sulphuric acid.

Experimental Results.

The results of the plate counts in the first series of experiments with soil A are shown in Table 1.

TABLE 1.[1]

Numbers of Bacteria and Actinomycetes in Alkaline Garden Soil. Series I.

Time.	Control.		Mannite.				Milk.		Keratin.	
			Casein Agar.		Mann. Agar.					
	Bact.	Act.	Bact.	Act.	Bact.	Act.	Bact.	Act.	Bact.	Act.
Start ..	50·9	3·2	50·9	3·2	—	—	50·9	3·2	50·9	3·2
3 days	44·4	4·5	112·9	1·6	—	—	1529·0	45·5	—	—
7 ,,	26·7	4·5	412·9	2·0	423·8	4·3	489·0	17·9	206·5	25·6
11 ,,	25·1	4·1	—	—	294·9	1·9	408·7	26·9	196·5	31·6
16 ,,	31·4	4·3	301·9	3·1	350·0	8·0	342·9	23·7	265·4	20·2
22 ,,	18·2	3·5	253·3	2·3	238·7	3·1	377·5	18·3	208·3	17·9

[1] In this, as well as the following tables, bacteria and actinomycetes are expressed as millions, and fungi as thousands per gm. of dry soil.

* Of the batches of dyes at my disposal, Rose bengale gave rather better results than erythrosine.

The examination of the slides gave the following results:

a. Control soil.—The majority of the bacteria in this soil is represented by small Gram-negative rods, occurring singly, in short chains, or in colonies of greatly varying size. The rest of the bacterial flora is made up of (1) small short Gram-positive rods, mostly in pairs or small clusters, showing the characteristic angular arrangement of the corynebacteria, (2) big Gram-negative cocci, 1·0–1·4μ, (3) long, unbranched, Gram-negative filaments, 0·8–1·0μ thick, often, especially after 16–22 days, occurring in characteristic spools, very much resembling the Fig. 11*a* of Demeter and Mossel (1933), an object which these authors interpret as an actinomyces. Vegetative mycelia of actinomycetes are generally scarce, often Gram-negative; a strong development in isolated patches was seen after 11 days. Chains of Gram-positive actinomyces-spores are constantly seen, although not in very large numbers; a single, very extensive system of mycelium producing aerial spores was seen after 16 days. Fungus mycelium was constantly present, but not very abundant; the hyphae frequently appeared decayed and badly staining, with Gram-negative rods or long Gram-negative filaments clinging to them (cf. Conn, 1932, and Demeter and Mossel, 1933). Fungus spores could not be observed with certainty.

b. Soil + Mannite.—This soil showed throughout the whole course of the experiment a strong development of typical *Azotobacter*-organisms: big oval to spherical cells, 2·0–3·0 × 2·5–4·5μ, mostly in big, scattered colonies, with markedly granular cytoplasm, nearly all Gram-negative, some with Gram-positive granules, a few partially or almost wholly Gram-positive (Pl. vi, fig. 8). This strong multiplication of *Azotobacter* is clearly reflected in the counts on the agar plates, where a great rise in the numbers of colonies sets in, reaches its maximum by the 7th day, and then recedes somewhat. This increase is for the very largest part due to *Az. chroococcum*, whose colonies account for some 80–90% of the total numbers of colonies on both media, which do not differ significantly from each other. Petersen (1925) has previously shown that *Az. chroococcum* will develop on dextrose-casein-agar by direct plating from soil with addition of mannite. Besides *Azotobacter*, there was, during the whole experiment, a number of small Gram-positive rods, sometimes branched, resembling corynebacteria (Pl. vi, fig. 11). The small Gram-negative rods and the long Gram-negative filaments were rare, especially during the first 3–11 days. Actinomyces-mycelia (largely Gram-negative) and -spores were present, but not more conspicuous than in the control soil; in agreement herewith, we observe no very considerable changes in the numbers of actinomyces-colonies on the agar plates. The fungus flora did not seem to undergo any distinct change as compared with the control soil, except that a number of spindle-shaped fungal spores (*Fusarium*?) were seen after 16 days.

c. Soil + Milk.—The slides from this soil showed, after 3 days, a huge development of small, Gram-negative, rod-shaped bacteria, which from the 7th day to the end of the experiment appeared somewhat less abundant. The other types of bacteria (small Gram-positive rods, big Gram-negative cocci, and long Gram-negative filaments) were very scarce after 3 days, later somewhat more prominent, although still forming only a small fraction of the flora. Contrary to expectation, no vegetative cells of spore-forming bacteria were observed, although some bacterial spores were seen after 3 days. The actinomycetes showed a most impressive development; their vegetative mycelia were remarkably

scarce, often Gram-negative, but throughout the whole experiment there was an abundance of Gram-positive actinomyces-spores, mostly 1·0 × 1·2–1·6μ, in fine, long, fairly straight chains (Pl. vi, fig. 5), with some tendency to break up and scatter after 16–22 days. It was very striking that these spore-chains were nearly always situated in those regions of the slides that were free from soil colloids. The counts on agar plates (Table 1) show a rapid increase and a slow decrease in bacteria (small rods) and actinomycetes, like the microscopical examination. The fungus mycelia did not show any considerable development on the slides, although some hyphae of *Mucor*-type were seen. From the 7th day to the end of the experiment, a considerable number of amoebae were seen; they were generally 12–20μ in diameter, Gram-negative, and contained numerous Gram-positive actinomyces-spores (Pl. vi, fig. 7).*

d. Soil + Keratin.—There was here, after 3 days, a considerable increase in small Gram-negative rods, although not so impressive as in the soil with milk. Later, small and middle-sized Gram-positive rods resembling corynebacteria (Pl. vi, fig. 10) became quite numerous, together with the big Gram-negative cocci and the long Gram-negative filaments. The actinomycetes developed strongly after 3 and 7 days, showing vegetative mycelia (Pl. vi, fig. 4) as well as chains of spores (Pl. vi, fig. 6), the latter sometimes forming spirals. The vegetative mycelia became less conspicuous after 11 days, but the spores remained abundant all through the experiment. Fungal hyphae of a *Mucor*-type were quite numerous after 3–7 days, later disappearing. In this soil, too, a considerable number of amoebae containing actinomyces-spores were observed. The figures in Table 1 show, corresponding to the microscopical picture, an increase in bacteria as well as actinomycetes, but less than in the soil with milk, in agreement with the less abundant development of organisms on the slides. A large number of corynebacteria appeared on the plates.

Table 2 shows the results of the plate counts from the second series of experiments with this soil.

TABLE 2.

Numbers of Bacteria and Actinomycetes in Alkaline Garden Soil. Series II.

Time.	Control.		Cellulose.		Paraffine.	
	Bact.	Act.	Bact.	Act.	Bact.	Act.
Start	37·8	5·3	37·8	5·3	37·8	5·3
5 days	43·1	5·5	53·1	6·3	68·0	12·6
10 „	50·4	6·2	101·4	5·0	65·9	13·1
15 „	36·7	4·4	52·5	3·6	47·2	14·6

The microscopical examination gave the following results:

a. Control soil.—The microscopical picture was in no way different from that of the first series. Staining for acid-fast organisms showed that small rods of this character were present, but very rare.

* Severtzova (1928) found amoebae unable to feed on actinomycetes in agar culture, where they could probably only get into contact with the vegetative mycelium, but no information seems available as to the power of amoebae to ingest the aerial spores of actinomycetes.

b. Soil + Cellulose.—The bacterial flora in this soil underwent little visible change after 5 days; after 10 and 15 days there was a notable development of big oval Gram-negative organisms, 1·0 × 1·5–2·0μ, mostly in clumps around the fibres of cellulose, and of some quite small, thin, curved threads resembling the cellulose-decomposing *Spirochaeta cytophaga.* Numerous small Gram-positive rods were also seen, and the long Gram-negative filaments produced very fine "spools" in this soil (Pl. vi, fig. 9). Fungus mycelia appeared in considerable amounts after 15 days, but the actinomycetes showed no change in comparison with the control soil. In agreement herewith, the numbers of actinomycetes remained virtually unchanged in the plate counts, and the bacteria showed only a moderate increase by the 10th day. An attempt was made to determine the approximate number of cellulose-decomposing bacteria in this and the control soil by the dilution method: inoculation from increasing dilutions of soil suspension in test-tubes with a strip of filter paper and a mineral nutrient solution containing $NaNO_3$ as a source of nitrogen. *Spirochaeta cytophaga* developed from the soil with cellulose in dilutions up to 1:4,000, but from the control soil only in the dilution of 1:10.

Soil + Paraffine.—The slides from this soil showed some development of short, plump, almost coccoid, Gram-negative or Gram-variable rods in large clusters. Small Gram-positive rods were also quite numerous. There was a considerable growth of vegetative actinomyces-mycelia, some of them richly branching, Gram-negative, with marked belt-staining, others chiefly Gram-positive, divided into segments of irregular size and shape, suggesting a *Proactinomyces*-type. Very few actinomyces-spores and fungus mycelia were seen. Staining for acid-fast organisms revealed, after 10 and 15 days, a small number of minute acid-fast rods, mostly in angular or parallel clusters (Pl. vi, fig. 13) and clumps of small acid-fast cocci. The plate counts show only a small increase in bacteria, but a quite definite multiplication of actinomyces-colonies. About 25% of these were represented by pink colonies of a partially acid-fast organism which, after isolation, proved to be a form closely resembling *Proact. polychromogenes*, an organism that has previously been found multiplying in soil with addition of paraffine (Jensen, 1931). This may have been identical with the acid-fast organisms observed on the slides.

The results of the plate counts from the acid soil B are shown in Table 3.

The first series of experiments gave the following results:

a. Control Soil.—This was quite rich in bacteria, mostly small, nearly coccoid, Gram-negative rods; also small Gram-positive rods resembling corynebacteria, and big Gram-negative cocci. A few small, short, irregular, acid-fast rods were found. Some extensive vegetative actinomyces-mycelia were present, although not abundantly, largely Gram-negative; chains of actinomyces-spores were seen here and there. A fair amount of fungus mycelium was seen, especially after 7 days; later, most of the hyphae appeared badly staining and decayed, often surrounded by Gram-negative bacteria which sometimes formed actual sheaths around them. Some fungal spores, apparently *Fusarium*, were seen after 30 days, and a few nematode-larvae were observed in this, as well as in the next soil.

b. Soil + Cellulose.—The bacterial flora did not undergo any considerable change, compared with the control soil; some beautiful pictures of Gram-positive, corynebacterium-like rods were seen (Pl. vi, fig. 12). Also the actinomycetes were little influenced; their mycelia were sometimes seen to form distinct spirals. The

TABLE 3.

Numbers of Bacteria, Actinomycetes and Fungi in Acid Grass Soil.

I. Soil with Addition of Cellulose.

Time.	Control Soil.				Soil+Cellulose.			
	Bact.	Act.	Fungi.		Bact.	Act.	Fungi.	
			1,000 per gm.	Spores %.			1,000 per gm.	Spores. %.
Start ..	11·7	6·5	603	40·5	11·7	6·5	603	40·5
7 days ..	47·4	4·2	759	26·6	53·2	4·4	1462	37·5
15 „ ..	30·5	5·7	597	40·5	38·2	4·0	1473	43·8
22 „ ..	—	—	454	40·1	—	—	999	55·1
30 „ ..	19·1	6·0	523	56·4	36·3	4·1	1217	(lost)

II. Soil with Addition of Mannite and Milk, after 3 days.

	Bacteria.	Actinomycetes.	Fungi.
Control Soil	25·8	3·5	606
Soil + Mannite	154·8	4·0	447
Soil + Milk	173·4	2·6	1440

fungi were entirely different: after 7 days the slides showed an abundant growth of fungus mycelia of mycomycetous type, with distinctly septate hyphae (Pl. vi, fig. 1). After 15–30 days the mycelia became much less abundant, largely Gram-negative and decaying, but fungal spores, which were few after 7 days, became quite numerous from the 15th day. They were partly spherical, measuring 2·0–2·5μ, resembling those of the ordinary Penicillia and Trichodermae, partly lemon-shaped, in fine long chains (Pl. vi, fig. 2). A pink *Penicillium* (*lilacinum*?) with spores of this characteristic shape appeared on the agar plates. These results are in good agreement with the plate counts, which show no very considerable change in the numbers of bacteria and actinomycetes as compared with the control soil, but by the 7th day a distinct increase in the numbers of fungi (chiefly *Trichoderma* and *Penicillium*), which remain quite high, owing to increasing spore production, as shown by both the microscopic and the plate method. The increase in fungi on the agar plates by the 7th day is somewhat less striking than one would expect after having seen the abundance of mycelium revealed by the microscopic method. The reason is probably that the mycelia at this period, being young and virile, are not easily broken up by the preparation of the soil suspension, so that they give rise to a comparatively small number of colonies, whereas the chains of spores, produced at a later period, are easily scattered.

In the second series of experiments, the control soil appeared microscopically quite like the previous.

b. Soil + Mannite.—This soil showed a considerable increase in bacteria (as also shown by the plate count), chiefly small Gram-positive rods, whereas the Gram-negative organisms did not increase much. *Azotobacter* was totally absent. Numerous small vegetative mycelia of actinomycetes were seen, but very few spores. Fungus mycelia were scarce; to judge by the plate count, the fungi seem actually depressed by the addition of mannite.

c. Soil + Milk.—A big increase in numbers of bacteria was shown both by the microscopic and the plate method. Nearly all bacteria on the slides were small or middle-sized, plump, Gram-negative rods. Vegetative actinomyces-mycelia were present, but largely Gram-negative; very few spores. On the agar plates the number of actinomycetes appeared definitely depressed. The slides showed a very strong development of fungus mycelium: mainly thick, non-septate, profusely branching hyphae of the *Mucor*-type. A corresponding increase in fungi was seen on the agar plates, chiefly represented by Mucoraceae.

The plate counts from the soils without additions are reproduced in Table 4. These soils were samples that had previously been used for microbiological analyses (Jensen, 1934); their character has been described under the corresponding numbers in Table 1 in the paper referred to. The air-dried samples (with the exception of No. 23, which was a freshly taken sample) were remoistened to 60–70% of their water-holding capacity and incubated for 7–14 days at room temperature.

TABLE 4.

Numbers of Microorganisms in Soils without Additions.

Soil No.	Incubation.	Bacteria.		Actinomycetes. Mill. per gm.	Fungi.	
		Mill. per gm.	Corynebact. %.		1,000 per gm.	Spores %.
15	10 days	(none)	—	(none)	373	53
25	14 ,,	1·4	18	1·3	90	—
6	10 ,,	3·5	22	0·2	17	—
16	14 ,,	10·2	4	0·2	359	84
4	12 ,,	23·0	38	1·1	13	—
9	14 ,,	24·4	46	0·9	43	—
3	7 ,,	47·8	50	11·2	425	37
23	12 ,,	58·8	41	11·1	498	22

Microscopical examination gave the following results:

No. 15.—Extremely poor in bacteria, nearly all Gram-negative rods, some of them quite big, club-shaped, containing spores, apparently clostridia; some free spores are also seen. A few Gram-negative actinomyces-mycelia are seen, but no actinomyces-spores. Bacteria and actinomycetes failed altogether to develop on agar. There was a fair amount of fungal hyphae, but mainly Gram-negative and decayed-looking, and a considerable amount of fungal spores, some lemon-shaped, others spherical, of *Penicillium*-type. In agreement herewith, the flora on agar was found to consist almost entirely of Penicillia, and a large fraction was represented by spores.

No. 25.—Poor in bacteria, although richer than the previous. Mainly small or middle-sized Gram-negative rods, some of the latter in long chains. A few small Gram-positive rods and big Gram-negative cocci. Fair amount of vegetative actinomyces-mycelia, partly Gram-negative, but very few spores. Large amount of fungal hyphae, partially Gram-negative and surrounded by bacteria; a few spores of *Penicillium*-type.

No. 6.—No mycelia of fungi or actinomycetes could be detected. The examination for bacteria was difficult owing to the fact that the colloids of this soil retained the Gram-stain quite tenaciously, but no large number of bacteria appeared to be present.

No. 16.—Very poor in bacteria, practically only small Gram-negative rods, some of them in chains and filaments. Fair amount of vegetative actinomyces-mycelia, but no spores. Fungal hyphae scant, Gram-negative or nearly unstained.

No. 4.—Poor in bacteria, almost exclusively plump, medium-sized, Gram-negative rods, mainly in big irregular colonies. No fungi or actinomycetes could be detected at all.

No. 9.—Rather poor in bacteria; mainly small Gram-negative rods in irregular colonies, also a number of small Gram-positive rods in pairs or small clusters. Some fungus mycelia are present, but no fungal spores or actinomyces-mycelia, and only few actinomyces-spores.

No. 3.—Rather poor in bacteria, which mostly occur in regions with much colloidal material. Small short Gram-positive rods and cocci are most common, whereas Gram-negative organisms are rare. Vegetative mycelia of actinomycetes are not visible, but some spores are seen. Fair amount of fungus mycelium. It is to be noted that this soil, owing to its high humus content, was of a very coarse-crumbly structure, so that a close contact with the slide may not have been established.

No. 23.—Rich in bacteria, still more so than the control soils A and B of the previous series. The majority of the bacteria are small, slender, Gram-negative rods, mostly in colonies of varying size; some plump Gram-negative rods were also common. Small Gram-positive rods, big Gram-negative cocci and long Gram-negative filaments are present in smaller numbers. Some of the Gram-negative rods show the same angular arrangement as the corynebacteria. Vegetative actinomyces-mycelia (largely Gram-negative) and actinomyces-spores are found, but not very frequently. Large amount of fungus mycelium, but the hyphae are mostly Gram-negative, often surrounded by clumps of bacteria. Very few fungal spores are seen.

There is thus in this series a rough parallelism between the apparent density of bacteria on the slides and their numbers in the plate counts, and the percentages of fungal spores as shown by the plate method coincide to some extent with the amount of mycelium on the slides, soil No. 16 with its high proportion of spores being very poor in mycelia, and No. 23 with its low spore-percentage being rich herein.

Discussion.

The decomposition experiments just described have shown that changes in the soil microflora, quantitative as well as qualitative, are revealed both by the Rossi-Cholodny method and the plate method, the results of which are largely in agreement with each other. So far, the results of the microscopic method might

also have been obtained by a judicious application of the plate and dilution methods, which, moreover, have the advantages of leading to quantitative results and of showing the state of the microflora (or, more correctly, a part of it) at a definite moment. The weakness of the microscopic method (apart from the facts that it does not give cultures of the organisms observed, and that most organisms cannot be identified simply by their morphology) is, firstly that we cannot tell whether the picture seen on the slides has been produced soon after the slide was placed in the soil, or just before it was removed (this is especially of importance when the slides have been left in the soil for several weeks), and secondly, that the distribution of the organisms on the slides is always too irregular to admit of a reliable counting. On the other side it has its advantages where the plate method falls short. It is able to inform us whether organisms not amenable to the study by cultural methods are active in the soil, and it shows the configuration of bacteria in colonies and their location around organic matter represented, for instance, by decaying fungal hyphae. If organisms of a characteristic morphology appear in great abundance on agar plates, it may also show whether or not these organisms make out a significant part of the total soil flora (cf. *Azotobacter* in soil plus mannite). It is also interesting to note that the microscopic method shows the bulk of the soil bacteria usually to be represented by small rods, as also found by Conn (1918), Kühlmorgen-Hille (1928), Cholodny (1930), and Demeter and Mossel (1933). The cocci, which Winogradsky (1925) and Koffmann (1931) found most numerous, are generally present, but in much smaller numbers. The majority of the bacteria are seen in nearly all cases to be Gram-negative, but Gram-positive rods, which seem to be corynebacteria, are also represented. Their relative abundance seems much smaller than shown by the plate method (cf. Table 4, and a previous paper—Jensen, 1933); it is to be remembered, however, that a certain proportion of the Gram-negative bacteria are doubtless cells that have been dead for a long time, among which there may be numerous corynebacteria no longer stainable by the Gram method. The microscopic method gives instructive pictures of the actinomycetes, showing their presence both as mycelium and as spores, which cannot as yet be distinguished from each other by any cultural method. It is noteworthy that the chains of actinomyces-spores are almost entirely confined to those parts of the slides that are free from soil colloids—evidently because the formation of the spores takes place in the air-filled pores of the soil (cf. Kubiena, 1932). The sporulation is seen sometimes to occur very rapidly, as in soil A with dry milk. These results sound a note of warning against an uncritical interpretation of microscopic counts of bacteria in soils where a rich sporulation of actinomycetes takes place; the spore-chains are very easily broken up and scattered when a soil suspension is prepared, in which case the spores will almost inevitably be counted as bacteria (cf. the remarks of Koffmann, 1931), since it is almost impossible to distinguish microscopically between bacteria and detached actinomyces-spores. There is also a possibility that the microscopic method may not always give an unbiassed picture of the actinomyces-flora: it is conceivable that where air-spaces are in contact with the slide, aerial hyphae of actinomycetes may grow out from the soil and adhere to the glass, where they appear as chains of spores, while the vegetative mycelia, from which these hyphae are produced, may remain in the soil. The growth of fungi in the soil, too, is finely demonstrated by the microscopic method, as also pointed out by Cholodny

(1930) and Conn (1932), and it seems to show the presence of young vegetative mycelia rather better than the plate method. Both methods agree in demonstrating the existence of fungal spores, sometimes in large numbers, in soils both with and without additions of organic matter; it seems, therefore, that the conclusion of McLennan (1928), according to whom the fungi exist almost entirely as mycelia in the soil, cannot be valid in general, at least as far as soils incubated in the laboratory are concerned. Finally, it is noteworthy that the existence of free-living amoebae in the soil can also be demonstrated by the microscopic method. The forms seen here (especially in soil A with milk and keratin) were quite large organisms which Koffmann (1931) considers aquatic forms, and therefore only active in soil under conditions of excessive moisture (soil suspensions which are allowed to stand). The present results seem to suggest that they may also become active under certain other circumstances.

The general impression is thus, that the Rossi-Cholodny method and plate method (supplemented by the dilution method, if desired) compensate each other's disadvantages to a large degree, and when combined they may yield very valuable information on the changes in the micropopulation of the soil in decomposition experiments with organic matter. Direct counts of microorganisms, especially by the method of Gray and Thornton (1928), may of course be used together with them, and may prove a still further aid in such studies.

Summary.

The Rossi-Cholodny method for direct microscopical examination of the soil micropopulation was compared with the plate method in decomposition experiments with organic compounds in soils of different character.

The results of the two methods were found generally to agree with each other, and since they largely compensate each other's disadvantages and serve as a control upon each other, their combined use seems very much to be recommended for the study of the soil microflora.

A differentiation between Gram-positive and Gram-negative soil organisms may be obtained by staining according to the Gram method and using Rose bengale or erythrosine as a counterstain.

The method may also be adapted to the study of acid-fast microorganisms in the soil.

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EXPLANATION OF PLATE VI.

Staining with Gram plus Rose bengale, magnification × 750, unless otherwise stated. 1.—Fungal mycelium. Soil B + cellulose, 7 d. 2.—Fungal spores. Same, 15 d. 3.—*Actinomyces*-mycelium. Same, 7 d. 4.—*Actinomyces*-mycelium. Soil A + keratin, 7 d. 5.—*Actinomyces*-spores. Soil A + milk, 3 d. 6.—*Actinomyces*-spores. Soil A + keratin, 3 d. 7.—Amoeba containing actinomyces-spores. Soil A + milk, 11 d. 8.—*Azotobacter.* Soil A + mannite, 11 d. 9.—Gram-negative filaments, forming "spools". Soil A + cellulose, 10 d. 10-12.—Gram-positive rods (corynebacteria?). 10: Soil A + keratin, 7 d. 11: Soil A + mannite, 16 d. 12: Soil B + cellulose. 13.—Acid-fast rods, stained with carbol-fuchsin, decolourized with 5% sulphuric acid. Soil A + paraffine, 10 d. Nos. 3, 4, 6, 7, 11, 12 and 13 have been retouched in order to make the organisms clearly visible among the soil colloids.

STUDIES IN THE GENUS *UROMYCLADIUM* (UREDINEAE). I.

GENERAL INTRODUCTION, THE ANATOMY OF THE GALLS, AND THE CYTOLOGY OF THE VEGETATIVE MYCELIUM AND PYCNIA OF UROMYCLADIUM TEPPERIANUM (SACC.) MCALP. ON ACACIA STRICTA WILLD.

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(Twenty-four Text-figures.)

[Read 25th July, 1934.]

Introduction.

In Australia, work on the rusts has been more or less limited to species of economic importance—principally *Puccinia graminis*—and to systematic problems. The cytological details of almost all our indigenous rusts are unknown. This fact, coupled with the interest stimulated by recent research on the functions of the pycnium in rusts, led to the present study of a common and essentially Australian genus.

The genus *Uromycladium* (McAlpine, 1905) consists of seven species, *Ur. simplex* McAlp., *Ur. Robinsoni* McAlp., *Ur. maritimum* McAlp., *Ur. alpinum* McAlp., *Ur. notabile* (Ludw.) McAlp., and *Ur. Tepperianum* (Sacc.) McAlp., of which *Ur. simplex* is the type species for the genus. Arthur (1906) divided the above into two genera, calling his new genus *Macalpinia* and taking *Ur. Tepperianum* as the type. He retained the name *Uromycladium* for the other. Clements and Shear (1931) do not recognize the validity of this division, and most mycologists agree.

Six species are endemic to Australia and the seventh, *Ur. Tepperianum*, is reported to extend to Java (Magnus, 1892). The six endemic species, so far as is known at present, are restricted to the genus *Acacia*, but *Ur. Tepperianum* occurs on *Albizzia montana* as well (Magnus, 1892). Two species, *Ur. Tepperianum* and *Ur. notabile*, are of particular interest because they form large galls on the branches and phyllodes of their hosts.

The systematic position of the genus *Uromycladium* is in the Raveneliae section of the family Pucciniaceae (Arthur, 1929, p. 144). The genus forms a well-marked group characterized by the presence of a pedicellate, depressed globose teleutospore, and the occurrence of more than one spore on the same stalk. Apparently all the species are microcyclic with the possible exception of *Ur. bisporum*, which is incompletely known, the teleutosporic stage being the only one so far recorded.

Ur. simplex and *Ur. Robinsoni* (Gaumann and Dodge, 1928) are considered to be closely allied to Uromyces, but are distinguished by the presence of the characteristic depressed globose teleutospore and the cyst. In *Ur. bisporum* two teleutospores occur, but the cyst is absent. *Ur. maritimum* and *Ur. alpinum* have

two teleutospores and a cyst. The two remaining species, *Ur. notabile* and *Ur. Tepperianum*, lack the cyst but have three teleutospores in a head.

The cyst when present is usually derived from the basal cell and is generally considered as being comparable with the cyst of *Ravenelia* (Gaumann & Dodge, 1928, p. 579). From a study of the segmentation of the spore groups in various species, it appears evident that the cyst is not a special structure, but is morphologically a teleutospore. This conclusion is supported by the occasional occurrence of a perfect spore in the place of the cyst (*vide* McAlpine, 1906, Plate xxi, fig. 179).

In *Ur. Tepperianum* the three teleutospores are formed in the manner indicated in Figure 1, *e* and *f*. This figure also illustrates the method of segmentation of the two spores and the cyst in *Ur. maritimum* (Fig. 1, *a–d*). The nature of the divisions suggests that *Ur. maritimum* is derived from a type such as *Ur. Tepperianum*, at least so far as the teleutospore structure is concerned. A similar suggestion may be advanced regarding *Ur. bisporum* (Fig. 1, *g* and *h*) and *Ur. simplex* (see Fig. 1, *g* and *i*). From a consideration of the known facts, the derivation of a Uromycladium from a Uromyces type might have proceeded along some such lines as these: the first step would be the duplication of the teleutospore giving rise to the condition met in *Ur. bisporum*. Specialization of one of the spores might lead to the formation of a cyst and produce the *Ur. simplex* type. If, instead of forming two spores in the head, three were developed, a similar modification of a spore to a cyst would give the *Ur. maritimum* type from the *Ur. Tepperianum* type (cf. Fig. 2).

Ravenelia may be considered as the climax of such a series. The spore head of *Ravenelia* could be interpreted as a fascicle of *Uromycladium* teleutospores each with a cyst attached. The fusion of the individual portions to form the head is secondary.

Although originally the species of *Uromycladium* were limited to Australia and Java, some have attained a much wider range. Introduction of a host plant (*Acacia decurrens*) into South Africa and New Zealand has resulted in the spread of *Uromycladium Tepperianum* in both countries. During a stay in New Zealand in December and January, 1932-33, specimens were collected from numerous localities. In every place visited in which trees of *Acacia decurrens* were growing, some were found to be infected with *Ur. Tepperianum*. At Nelson and at Auckland the infections were heavy. In South Africa the disease has spread to many of the Wattle Bark plantations and, as in Victoria, causes severe damage to the trees.

Ur. Tepperianum has by far the most extensive host range of the genus. McAlpine, in 1906, recorded it from nineteen species of *Acacia*. Since then the knowledge of the host range has been considerably extended and now includes the following forty-nine species:

aneura F.v.M., *armata* R.Br., *auriculaeformis* A. Cunn., *Baileyana* F.v.M., *binervata* D.C., *bynoeana* Benth., *calamifolia* Sweet, *dallachiana* F.v.M., *dealbata* F.v.M., *decurrens* Willd. and vars., *diffusa* Edw., *elata* A. Cunn., *erioclada* Benth., *fasciculifera* F.v.M., *glaucoptera* Benth., *glaucescens* Willd., *hakeoides* Cunn., *holosericea* A. Cunn., *homalophylla* A. Cunn., *implexa* Benth., *juniperina* Willd. and vars., *linifolia* Willd., *linophylla* Fitz., *ligulata* A. Cunn., *longifolia* Willd., *Maideni* F.v.M., *melanoxylon* R.Br., *microbotrya* Benth., *montana* Benth., *myrtifolia* Willd., *neriifolia* A. Cunn., *notabilis* F.v.M., *obliqua* A. Cunn., *Oswaldi* F.v.M.,

penninervis A. Cunn., *pruinosa* A. Cunn., *pycnantha* Benth., *retinoides* Schlecht., *rigens* A. Cunn., *salicina* Lindl., *siculaeformis* A. Cunn., *spinescens* Benth., *stricta* Willd., *tetragonophylla* F.v.M., *trinervata* Sieb., *trineura* F.v.M., *verniciflua* A. Cunn., *verticillata* Willd., *vomeriformis* A. Cunn.

So wide a host range as this, including as it does species from all sections of the genus *Acacia*, naturally raises the question as to whether *Uromycladium Tepperianum* is only one species or a group of closely related physiological strains. The latter idea seems more acceptable. Samuel (1924) states that "This great range of infection of *Ur. Tepperianum* cannot but raise doubts as to the physiological homogeneity of this species. Field observations of the fungus only increase these doubts." Before making the above comment Samuel had remarked on the wide divergence of gall types and the occurrence in some cases of witches' brooms, varying forms being associated with different species of hosts. At Ooldea (S. Australia) Samuel (1924) states that *Acacia ligulata* and *A. linophylla* are to be found growing together in many places. In one definite area *A. ligulata* was heavily infected and *A. linophylla* free, while in another area the reverse was the case. To quote further from Samuel, "This cannot but suggest that the fungus affecting one is not cross-inoculable to the other, although morphologically the two fungi are identical in every respect, and referred to the one species *Uromycladium Tepperianum*." He finds a similar state of things between plants of *A. armata* and *A. pycnantha*.

These observations are borne out by those made by the present writer, in New South Wales. At Pennant Hills (N.S.W.) clumps of *Acacia stricta* have been seen growing together with *A. Maideni*.

The former species was heavily infected and the latter quite free of disease. About half a mile away the reverse was the case. Similar observations have been made of *A. stricta* and *A. juniperina*, and *A. stricta* and *A. myrtifolia*.

So far as is known at present, all the species of *Uromycladium* are microcyclic. In the three species examined, *Ur. Tepperanium*, *Ur. notabile* and *Ur. maritimum*, the vegetative mycelium is uninucleate and gives rise to pycnia. The binucleate mycelium is not extensive and is limited to the spore-producing layer. This forms uredospores and then teleutospores or, in the more reduced forms, only teleutospores. Subsequent reinfection is by uredospores or sporidia. The origin of the binucleate condition is still in doubt. Definite examples of nuclear migration have been found in the hyphae which form the developing sorus, but the paucity of examples suggests that the method may not be the chief means of the initiation of the diploid phase. During a study of the pycnial stage, hyphae have been observed projecting from the hymenial layer, and in some cases these have been shown to be binucleate. Further, it is possible to follow a line of hyphae which stain more readily with saffranin from some old pycnia to the developing teleutosorus. In a few cases the teleutosorus has been shown to develop at the base of the pycnium. The matter is still being investigated.

Gall Structure.

Although the ability of fungi to cause the formation of galls is not rare, it is, nevertheless, limited to comparatively few genera which are widely separated systematically. Among the rusts, *Gymnosporangium* (Sandford, 1888) and *Cronartium* (Dodge and Adams, 1918) are well known examples of gall-forming fungi, and some species of *Puccinia* (e.g., *P. rubigo vera* on *Clematis*) possess the same capacity. None of these, however, produces galls comparable in size to

those caused by *Uromycladium Tepperianum*. McAlpine has recorded galls on *Acacia implexa* weighing as much as three pounds, and the writer has observed some, not far short of this weight, on the same species at Canberra (F.C.T.).

Infection by *Uromycladium* causes different results on different hosts and occasionally the reaction of the same host species may vary in different habitats. At National Park (N.S.W.) plants of *Acacia myrtifolia* were found infected with *Ur. Tepperianum*. This had led to the formation of galls about 1–2 cm. in diameter. The conditions under which the host plants were growing were favourable—well-drained soil and ample water supply. Specimens of the same host infected with the same fungus but collected from Central Australia (Macdonnell Ranges) showed no gall formation. The fungus caused the bark to be ruptured and filled the opening with a dense layer of teleutospores. Apparently the more severe conditions of the Central Australian habitat prevented the usual hyperplasy of the stem tissue.

Of the two gall-forming species of *Uromycladium*, *Ur. Tepperianum* is more widespread and shows a greater variety of gall forms than does *Ur. notabile*.

When the infection by *Ur. Tepperianum* is confined to the phyllode, the gall is small, seldom more than 0·5 cm. in diameter. It is on stems that the greatest distortion occurs. On *Acacia juniperina* the stem galls are spindle-shaped, tending to be irregular and from 1 to 5 cm. long. Usually they are not more than 0·75 cm. wide. Normally on this species the gall is annual, but now and then odd perennial galls are found. The galls on *A. stricta* are larger than those on *A. juniperina* and may be as much as 8 or 9 cm. in length and 3–4 cm. in breadth. The gall is normally annual, but the evidence seems to indicate that there is a tendency for the mycelium to perennate in the stem tissues. The foregoing species of *Acacia* are shrubs; when trees become infected, as in *A. implexa* or *A. glaucescens*, the galls are usually perennial and may have a life as long as eight or ten years. The continued growth produces the large galls referred to earlier in the paper. In most cases these perennial galls do not produce spores continually, but undergo a resting period, usually in the dry months of the year. This resting period is by no means well defined and different galls vary considerably in their activity.

As material of *Acacia stricta* infected with *Ur. Tepperianum* was available in large quantities near Sydney, the galls on this species were used for the anatomical study.

The host plant is a shrub or sometimes a small tree which grows to about 15 feet in height. True leaves are absent in the adult plant, their place being taken by phyllodes which are vertically flattened. The inflorescence is axillary, the flower heads being either solitary or in pairs on short peduncles.

As *A. stricta* frequently occurs in almost pure societies in the field, infection spreads readily. No part of the plant above the ground is immune from infection. Phyllodes, stems and branches, inflorescence and pods may all be diseased. The axillary shoot is particularly susceptible—probably because spores can lodge in the axil and are thus more or less protected.

The first evidence of infection is visible, as a rule, in February or March. If a young inflorescence shoot is concerned it may become completely distorted and hypertrophied in a few weeks. Infection on stems or phyllodes does not lead to such rapid distortion. On the stem the swelling of the tissue causes an early bursting of the epidermis or bark, according to the age of the organ concerned. The gall tissue which swells through the fissure is fairly smooth on

the outer surface. At this stage pycnia are formed most abundantly. Towards the end of March teleutospores make their appearance in large numbers. Growth of the galls is rapid and by April or May they are about 3–4 cm. long and 1–2 cm. in diameter. The confluence of the developing teleutosori soon covers the whole gall with a rusty mass of spores. Spore production is continued throughout most of the winter. Towards August the galls begin to die and spore production ceases. When the galls are on thick branches they are perennial occasionally, and in the following year produce warty out-growths which bear pycnia and teleutosori as before.

Anatomy.

The stems of *Acacia stricta* are ribbed, partly owing to the tendency for the phyllodes to be decurrent. Normally there are about five ribs. A section of a stem is represented diagrammatically in Figure 3. The young stems are bounded by an epidermis (*a*) which is very slightly papillate. The cuticle is very thick and tends to emphasize the slightly papillate nature of the epidermis. Beneath the epidermis is a layer of collenchyma (*b*) several cells in thickness. The cortex is very narrow. Pericyclic fibres (*c*) are well developed and may form a complete ring. The phloem area (*e*) is extensive for a stem and contains numerous islands of fibres (*d*). The cambial zone (*f*) is very narrow and poorly defined, and frequently indented: these indentations do not, however, coincide with the grooves on the stem. Secondary wood (*g*) is extensive and shows annual rings. Vessels (*k*) are few in number—fibres and tracheids composing the greater part of the xylem. There is little wood parenchyma. Medullary rays (*h*) are well marked and are simple. Starch is present in the xylem fibres surrounding the vessels and in the pith cells (*i*), these latter being simple pitted parenchymatous units.

Infection occurs generally before cork formation has begun, but in a few cases the fungus may force an entry through the cork-bound stem. Abnormalities in the stem are first visible in the phloem where the cells enlarge and resemble parenchyma. Small patches of cells become meristematic and rapidly cause distortion of the outer cells, and eventually rupture of the cortex and epidermis. At this stage few hyphae and haustoria are visible. About the same time as the epidermis breaks, the cambium, and with it the young xylem, are infected. During this period large numbers of haustoria appear in the phloem region. In the early stage of xylem disturbance the fungus is not much in evidence, but it alters the physiology of the plant sufficiently to prevent lignification of the newly-formed xylem elements. At the same time large quantities of plastic substances, which appear to be of the nature of tannins, are deposited in the outer cells of the developing gall. When the fungus is well developed and has produced haustoria in most of the unthickened cells no more plastic substances are deposited. Subsequent development of the fungus causes the throwing off of the outer layers (see p. 218 and fig. 5) so that only little tannin may be present in a well developed gall.

In view of Wood's (1932) work on the correlation of the disappearance of tannins with the increase of lignification, it is tempting to suggest that the tannic material would normally go to the lignification of the xylem, but owing to the disturbance of the normal physiological conditions of the cell has been diverted. As the fungus at this stage is not developed extensively, the amount of food material is in excess of its requirements, and this excess is deposited

in the outer cells. When the fungus is fully developed, and sporing freely, most of the available food material is used, and little or no tannin occurs.

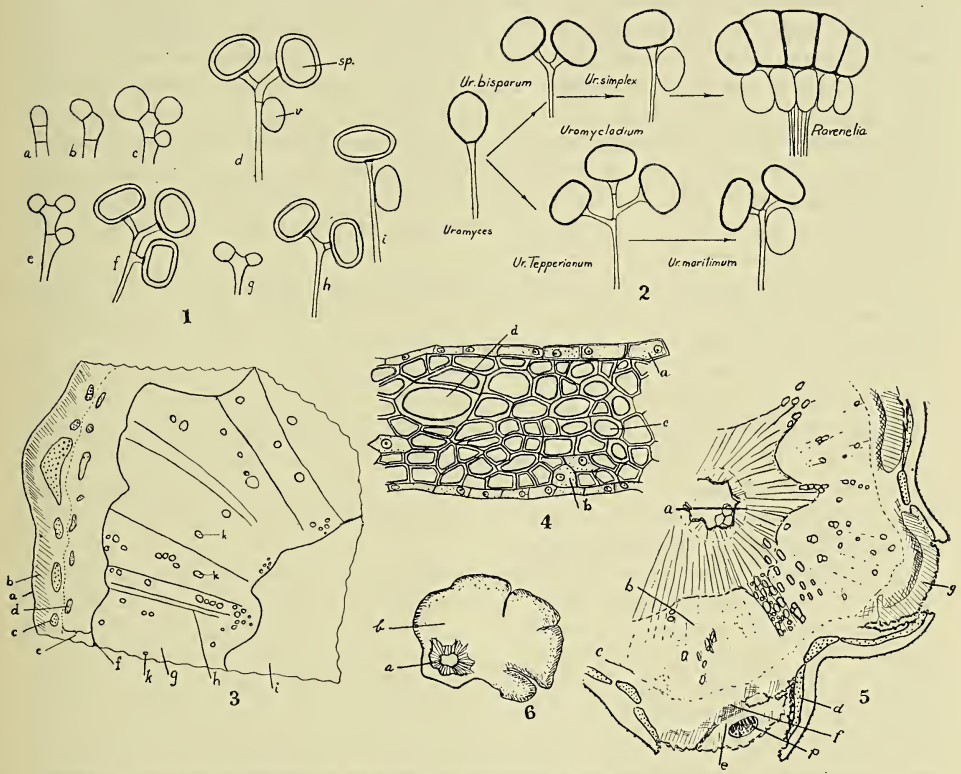

Fig. 1.—*a-d*, segmentation of the teleutcspores of *Uromycladium maritimum*; *e-f*, *Ur. Tepperianum*; *g-h*, *Ur. bisporum*; *g* and *i*, *Ur. simplex*; *sp*, spore; *v*, vesicle. All diagrammatic.

Fig. 2.—Diagram showing suggested lines of evolution.

Fig. 3.—Camera lucida drawing of a portion of a normal stem of *Acacia stricta* in cross section. *a*, epidermis; *b*, collenchyma; *c*, pericyclic fibres; *d*, phloem fibres; *e*, phloem region; *f*, cambial zone; *i*, pith; *k*, vessel. × 17.

Fig. 4.—Normal xylem from *Acacia stricta* stem. *a*, cell of medullary ray; *b*, wood parenchyma; *c*, fibre; *d*, vessel. × 333.

Fig. 5.—Diagrammatic section of a young gall caused by *Uromycladium Tepperianum* on *Acacia stricta*. *a*, normal xylem; *b*, affected xylem; *c*, position of the cambium; *d*, pericyclic fibres; *e*, portion of gall being exfoliated by *f*, developing teleutosorus; *g*, exposed hyperplasied phloem; *p*, old pycnium being thrown off by developing teleutosorus. × 10.

Fig. 6.—Cross-section of an old gall on *Acacia stricta*. *a*, normal xylem; *b*, gall tissue. × 1.

In the phloem regions the disturbance caused by the fungus is due to an increase in size of the cells and a return to the active conditions. A similar state of affairs occurs in the xylem. Even in young galls it is very difficult or even impossible to locate the cambium. The normal radial arrangement of the xylem is recognizable in the young galls, the cell rows being continuous with those formed prior to hyperplasy, but in the older galls irregular division of the

still active xylem elements makes the identification of tissues extremely difficult. The occurrence of a few tracheids here and there helps somewhat, but, as Butler (1930) points out in his study of the morbid anatomy of plant galls, most cells have the capacity to develop in any direction, and perfect tracheids may be formed from cortex or other tissues. Figures 3–8 illustrate the structure of the uninfected and infected tissue. Figure 3 is a camera lucida outline drawing of a portion of a normal stem of *Acacia stricta*. The details of the xylem are shown in Figure 4. In Figure 5 the structure of the young gall is shown diagrammatically. At *g* (Fig. 5) the epidermis and cortex have been ruptured by the hyperplasia of the phloem which is extruding through the break. The exfoliation of the outer layer at (*e*) is due to a developing teleutosorus (*f*). This also causes the old pycnia (*p*) to be shed.

In an old gall the outer surface is irregular, owing to the activity of isolated meristematic zones (see Figure 8) in place of the normal continuous cambium. Figure 6 is a drawing of a cross-section of an old gall.

Mention has been already made of the failure of the greater part of the affected xylem to lignify. In the earlier stages (Fig. 7) the structure of the xylem is abnormal only in the lack of thickened lignified walls on the cells. Medullary rays can still be detected (*a*, Fig. 7), and well-formed vessels or tracheids are present. As the gall continues to grow, isolated patches of cells become meristematic (Fig. 8), and by their growth they crush and eventually cause exfoliation of the outer layers.

The length of life of the cells forming the gall is variable. Usually the fungus does not seem to cause rapid death. At the time when the cells of the gall are dividing rapidly, intercellular mycelium is very scarce and haustoria are almost absent. The intensity of the stimulus of the rust is shown by the marked activity of the host in comparison with the small amount of parasitic growth. Usually in August or September weather conditions limit the further growth of the fungus, and with it the gall. Following the death of the parasite many of the gall cells become lignified to form short tracheids or sclereids, and the remaining cells of the gall die. In most old galls insects are common, and these secondary invaders frequently terminate the life of the gall earlier than might have otherwise been the case.

In addition to insect invaders, other fungi are frequently present. Some of these are definitely parasitic, others appear to be saprophytes or weak parasites. *Darluca filum*, which attacks the *Uromycladium*, may frequently reduce a spore output to half, or less than half of the usual number. Other types appear to be parasitic on the gall tissues, such as *Pestolozzia* sp., *Macrosporium* sp., and an undetermined Ascomycete belonging to the Sphaeriales. The pycnial fluid, especially in moist weather, provides a medium for the development of *Cladosporium* and *Penicillium*. Odd members of the Imperfectae appear from time to time, but are never important.

Comparison with other Galls.

Butler (1930), in his study of the morbid anatomy of plants, divided the various kinds of galls into groups according to the various regions hypertrophied. He classes the Acacia rust-gall as one involving both the cortex and the vascular cylinder. The Acacia gall examined by Butler was caused by *Ur. notabile* on *Acacia decurrens*. On this species, the fungus usually attacks the rachis of the bipinnate leaf; but, apart from this difference, there appears to be little variation

between the sequence of tissues attacked in both this species and *A. stricta*, with perhaps one notable difference. Butler records that phloem hypertrophy is extensive and that xylem hypertrophy may not keep pace with it and may come to an end fairly soon. In the galls on *A. stricta* the reverse appears to be the case, for nearly all the gall tissue is made up of deformed xylem. Where fungus galls are formed from the vascular cylinder they are usually woody, as in *Gymnosporangium* (Harshberger, 1902), and there is little or no trace of delignification. Sometimes in *Gymnosporangium* arcs or sectors of the wood consist of parenchyma—representing unlignified xylem (Wornle, 1894). There are, however, fungal galls which show similar features to those of *Uromycladium Tepperianum* on *Acacia stricta*. For example, in the witches' broom of Cocoa (*Marasmis perniceosis*) the gall is composed of all the stem tissues (Went, 1904) and hypertrophy exists in the xylem, the affected cells of which are largely parenchymatous. In the bacterial galls of *Rubus occidentalis* the gall wood is sharply differentiated from the normal wood by the scarcity of fibres, and the thinner walls and larger lumina of the cells. Isolated patches of tracheids are also present (Butler, 1930, p. 192). Thus the prevention of lignification is by no means confined to the galls of *Ur. Tepperianum*, being possessed in varying degrees by other organisms. The occurrence of well-formed tracheids in the centre of parenchyma is seen in *Gymnosporangium* (Stewart, 1915).

In many types of fungal infection there is an attempt on the part of the host to isolate the infected region by bark formation. Apparently the balance between the host and parasite in the *Uromycladium* gall is very delicate, as is the case in most rusts, and the reaction of the host is such that no cork formation is initiated in the region of fungal infection.

Morphology and Cytology of Uromycladium Tepperianum.

As in the case of the examination of the gall structure, *Acacia stricta* infected with *Uromycladium Tepperianum* was the most convenient source of material for the study of the morphology and cytology of the fungus.

Most of the work was done by means of microtomed sections. Various fixatives were used, including Carnoy, Bouins, Formal-Acetic-Alcohol, Chrom-acetic and Flemming's Special Fixative. Of these Flemming's Special Fixative and Chrom-acetic Fixative gave the best results. Sections of varying thickness were cut; for studying nuclear details of the pycnia 2μ sections were preferred, but for haustoria, sections cut at 10μ were better. Most of the sections were cut at 4μ.

When staining, Iron Alum Haematoxylin, Flemming's Triple stain and Newton's Gentian Violet were used most frequently. The haematoxylin gave the best preparations of nuclear division in the pycnia, but Flemming's Triple was much to be preferred when working with the teleutosorus and teleutospores. Wherever possible results obtained with Iron Alum Haematoxylin were checked by a comparison of material stained with a transparent stain such as Flemming's Triple or Newton's Gentian Violet. For a general study of the distribution of the mycelium Thionin and Orange G proved useful, and for staining fresh material, Acid Fuchsin was employed. Congo Red was found to be an excellent stain for the fungal cell walls, but in thick sections it tended to obscure detail.

The Vegetative Mycelium.

The entrance of the sporidial germ tube and the early stages of infection have not yet been observed. Apparently no part of the host plant above ground is

immune. Frequently each shoot on a branch is infected, including the developing inflorescences. In such a case the great extent of infection may have been due either to a heavy dusting of spores or to progressive infection of the branch, starting from a single infection. This latter view seems the less likely. Careful staining seldom reveals hyphae at any great distance from the galls, indicating that *Uromycladium*, like most rusts, has a fairly limited mycelium which is localized at the seat of infection. The period of incubation is not yet known, but evidently it may be as long as months. Spore shedding is at a maximum in May, June and July, but the new crop of galls seldom appears before February. Once the galls have commenced growth, weather conditions appear to have little effect on them except that when they are mature, dry weather may completely check spore formation.

In the youngest cases of infection examined, the haustoria and most of the mycelium are confined to the cortex and phloem. Mycelium and haustoria do not appear in the wood to any marked extent, until fairly large areas of modified xylem are to be found.

The mycelium is intercellular but forms intracellular haustoria. Generally the hyphae are about 3μ in diameter, although occasional examples may reach 5μ. Frequently several strands lie in the same intercellular cavity, which becomes greatly extended by the growth of the fungus. Septa are frequent throughout the mycelium, giving the individual cells the short stumpy appearance generally associated with rust mycelia. The thin hyphal walls conform to the shape of the host cell-walls bounding the intercellular spaces, so that the rust cells are often slightly irregular in outline. Each cell contains a single nucleus, finely granular cytoplasm and usually one or more vacuoles. The number of vacuoles found varies. In actively-growing hyphae none or only small ones are present. In the hyphae distant from the sorus at the time of sporing the number of vacuoles increases, and the individuals themselves enlarge. Towards the end of the sporing period most of the mycelium is extensively vacuolated. Usually small granules can be detected in the hyphae but the nature of these is unknown. In living material oil drops have been seen in the hyphae but their occurrence is not extensive. The nuclei are comparatively large and usually centrally placed in the cell. There is a definite nuclear membrane, a single nucleolus and chromatin material which is in the form of an irregular network lining about one-half to two-thirds of the nuclear membrane. In most nuclei there is a darker staining body in the centre of the network, and this may correspond to a centrosome. A similar arrangement of chromatin material in the rust nucleus is recorded by Colley (1918), Olive (1908), and others.

Haustoria are produced during the early stages of formation of the gall. Magnus (1900), however, records that in *Puccinia leucosperma* the haustoria arise late, and considers that the main nourishment is obtained by the osmotic activity of the intercellular mycelium. The early occurrence and the number of the haustoria in *Uromycladium* seem to indicate that the amount of food material absorbed through the host wall is probably small. Any part of a hypha may produce a haustorium. The young haustorium seems to penetrate the host cell wall without difficulty and there is no attempt on the part of the host to thicken the wall at the point of entry, although there is always a definite constriction of the hypha as it enters the host cell. Once having penetrated the cell wall, the hypha comes in contact with the primordial utricle. The subsequent

development in other rusts has been variously interpreted, but the general consensus of opinion is summed up by Arthur (1929, p. 117): "The plasma membrane of the host cell is not at first penetrated by the haustorium, but on the contrary appears to be merely invaginated and pushed inwards by the growing tip. It is probable that in no instance does the haustorium come into organic contact with the protoplasm of the host cell."

Young haustoria have been examined in *Uromycladium* but no evidence of invagination of the primordial utricle has been found. Colley (1918), in describing the haustoria of *Cronartium*, states that no invagination occurs; also,

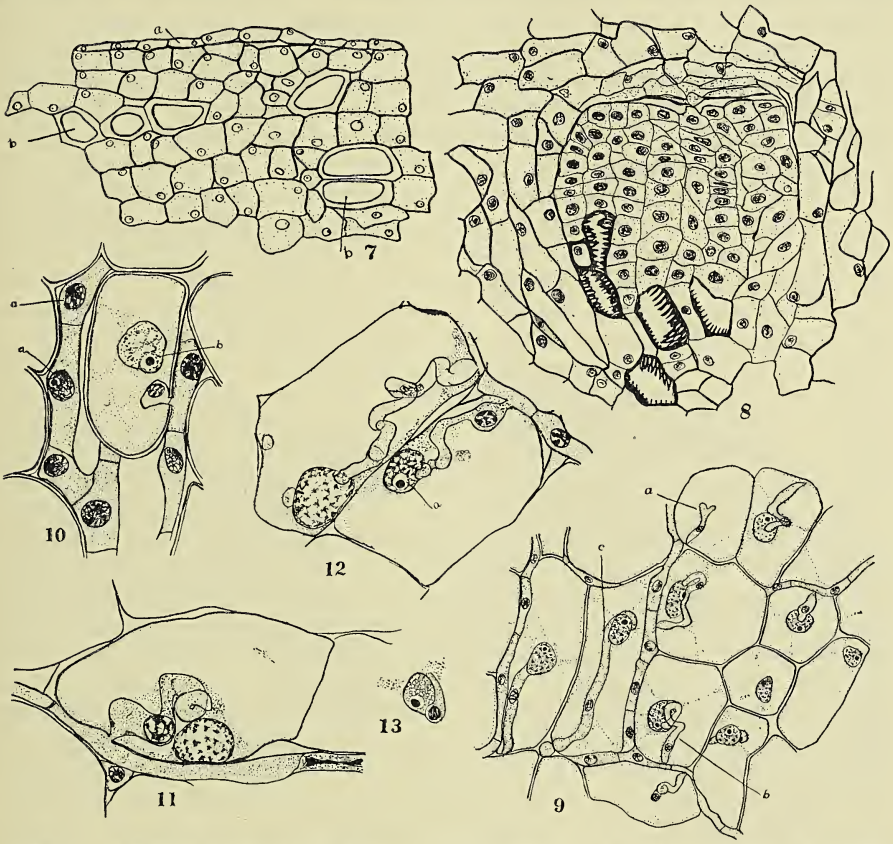

Fig. 7.—Affected xylem from gall on *Acacia stricta*. *a*, medullary ray; *b*, vessel; *c*, fibre or tracheid. × 333.

Fig. 8.—Isolated meristematic zone in gall of *Acacia stricta*; note tracheids. × 333.

Fig. 9.—Vegetative mycelium and haustoria. *a*, haustorium showing suggestion of lobing; *b*, coiled haustorium; *c*, haustorium becoming vacuolate. × 400.

Fig. 10.—*a*, vegetative nuclei of the fungus showing nucleolus and polarization of the chromatin; *b*, host nucleus, showing clear region round the nucleolus. × 1,000.

Fig. 11.—Coiled haustorium and host nucleus, the latter shows the chromatin as irregular clumps. × 1,000.

Fig. 12.—Coiled haustoria in contact with the host nucleus. *a*, contraction of chromatin away from the nucleolus. × 1,000.

Fig. 13.—Host nucleus showing the chromatin in the reticulate condition, partly enwrapped by a haustorium. × 1,000.

"that it is certain that the plasma membrane of the host cell is not broken or pierced by the haustorium; it must be pushed in as the tip of the haustorium grows". Allen (1923) takes the same view in connection with the wheat rust; Robinson (1913) draws attention to the fact that many figures of past workers do not show clearly whether the haustoria in *Puccinia malvacearum* lie in the cell vacuole or in the cytoplasm. As the result of his investigations of this rust on *Althea rosea*, he described the hyphae as entering the cytoplasm and growing along strands to the nucleus. It is to be regretted that previous workers have used the term "cell membrane" in connection with this problem. Whether the primordial utricle is considered to be the "cell membrane" or whether the ectoplast is meant, is uncertain. If ectoplast is meant, it is immaterial whether it is broken or not, since the physical nature of protoplasm is such that an ectoplast will immediately form between the main body of the cytoplasm and a foreign object, in this case the haustorium. If the primordial utricle is meant a definite problem is involved. In *Uromycladium* the haustoria are in close contact with the cytoplasm of the host cell and in most cases cytoplasm can be detected around the infecting hypha. In a few cases this is doubtful, and the writer is inclined to believe that the haustoria sometimes penetrate the primordial utricle and enter the vacuole. Figures 15 and 16 are drawn from material which was slightly plasmolyzed in sugar solution and then fixed in Chromacetic. Figure 16 strongly suggests that the primordial utricle has been penetrated and that most of the haustorium lies in the vacuole. Figure 15 also shows that the haustoria may possibly enter the vacuole of the host cell. It is hoped at a later date to investigate this matter in more detail. As a rule, only one haustorium is found in a cell, although sections showing two or more entering from different sides are sometimes seen. In most cells, but not in all, the hyphae grow in the direction of the nucleus and may touch, or partly enfold, it. This may lead to distortion of the nuclear membrane, though lobed or greatly hypertrophied nuclei are very rare. The haustoria are simple in most cases, only occasional indication of lobing being seen (*a*, Fig. 9). They may be straight or coiled in varying degrees (see Figs. 9, 11 and 12). Throughout its life, the walls of the haustorium are thin and never show any thickening comparable to the sheath found in *Cronartium* (Colley, 1918). Frequently the haustoria are swollen at their base; this swelling commonly contains the nucleus (Figs. 12, 14 and 16). The cytoplasm of the haustorium is dense and finely granular at first, but later becomes vacuolate. The vacuoles at first appear some distance from the tip, leaving dense cytoplasm at the base and apex of the haustorium. Still later vacuolation occurs throughout the hypha, which begins to collapse, its function at this stage being, apparently, over. The nucleus of the haustorium varies little from the normal vegetative nucleus. It is more difficult to recognize a nucleolus and radiating chromatin material, but in favourable preparations this is possible. During the final vacuolation of the haustorium the nucleus tends to collapse and retains stains very tenaciously, making it impossible to get an accurate picture of the details at this stage. One other feature of interest in connection with haustoria is the position of the septum which cuts off the haustorial element. In some cases (*c*, Fig. 14) it is right at the base; here, however, it seems that the hypha is terminated by a haustorium. Where this organ is lateral there frequently appears to be no segmentation of a specialized cell, but merely an outgrowth which penetrates the host cell wall and later receives the nucleus of the mother cell (Figs. 12 and 11).

Apart from the stimulation already referred to (page 218), there is the effect of the parasite on the host nucleus. The normal nucleus in *Acacia stricta* contains a single nucleolus or rarely two nucleoli, and the chromatin material is in the form of a fine reticulum. Under the influence of the fungus the nucleus enlarges and the chromatin material becomes aggregated into irregular masses at points which probably represent the joins in the original reticulum (Figs. 14, 10, 16, 12, and 15, in order). The occurrence of several of the above stages in a uniformly stained preparation, indicates that the difference is not due to variations of technique. As the nucleus enlarges, the chromatin material appears to pull away from the nucleolus. In the earlier stages of the investigation it was thought

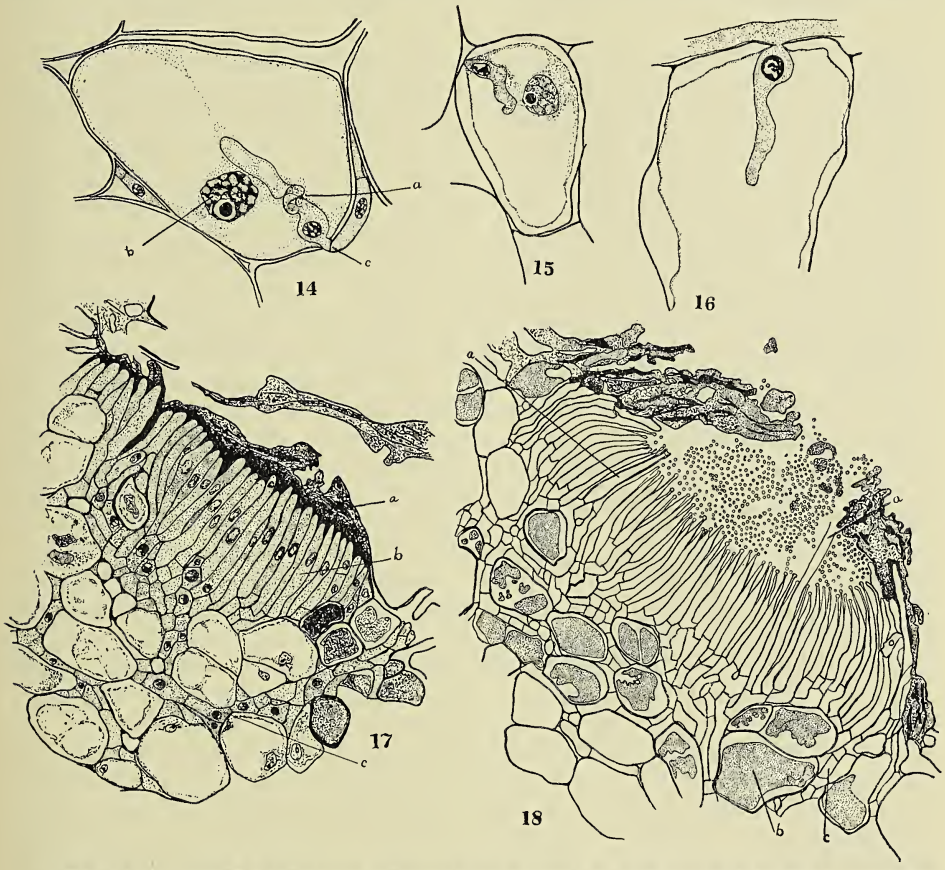

Fig. 14.—*a*, coiled haustorium becoming vacuolate; *b*, host nucleus showing clumping of the chromatin; *c*, wall separating haustorium from main mycelium. × 1,000.

Fig. 15.—From material plasmolysed in sugar solution and then fixed. Note contraction of the primordial utricle away from the wall except at the point of entry of the haustorium. × 1,000.

Fig. 16.—From the same material as fig. 15, note again the contraction of the primordial utricle away from the wall but not away from the haustorium. × 1,000.

Fig. 17.—Developing pycnium. *a*, crushed cells; *b*, young sporophores; *c*, contributing hyphae. × 533.

Fig. 18.—Adult pycnium. *a*, intrahymenial paraphyse; *b*, host cells containing plastic substances; *c*, contributing hyphae. × 390.

that this was due to faulty fixation, but variation of the fixative fails to produce a corresponding variation in the nuclear structure. Rice (1927) figures a similar condition in the host nucleus due to rust influence, but Allen (1923*b*), dealing with wheat infected with *Puccinia graminis tritici*, shows no indication of this phenomenon. In the wheat plant the nucleus does not possess such a marked reticulum, and the chromatin tends to collect on one side of the nucleus. Swelling of the nucleus in the acacia rust gall may cause an increase to twice the normal diameter. When vacuolation starts in the haustorium, the host nucleus usually begins to collapse (Fig. 15) and is more retentive of stains; this collapse continues and in the dead cells of the gall the nucleus is represented as an undifferentiated mass slightly larger than the unaffected nuclei.

The Pycnia.

As is usual in the rusts, the pycnia are the first spore-producing organs formed. In *Uromycladium Tepperianum* they are typically flask-shaped, and subcortical in origin. McAlpine (1906) states that the pycnia are produced under the cuticle, and Clements and Shears (1931), evidently following McAlpine, also describe them as subcuticular; this, however, is incorrect. The error could easily occur if the examinations were made of hand-sections, because the cells above the developing pycnia are greatly crushed and stain in some cases as a uniform mass resembling a very much thickened cuticle. In some cases the pycnia may underlie seven or eight layers of cells. There is a slight variation in size of the pycnia—the average being about 150μ in diameter. They are reddish-brown when young but soon appear blackish; in transmitted light they are brown. The hyphae which go to form the pycnia aggregate between the cells of the cortex and gradually push the host cells apart. In this mass of hyphae a pseudo-parenchymatous region is differentiated, which in its turn produces the young sporophores. The sporophores elongate parallel to each other and crush the cells external to the young pycnium (Fig. 17). A few of the outer cells remain sterile and form a very poorly defined band of periphyses, which are never sufficiently developed to project as hairs (Fig. 18). The sporophores then commence to bud off pycnospores and the pressure caused by the increasing mass of spores soon ruptures the overlying tissue and an ostiole is formed. This ostiolate and almost nonperiphysate pycnium may be compared with that of *Milesia marginalis* (Hunter, 1927), which lacks periphyses yet possesses a definite ostiole. The pycnia of *Uromycladium* are more indefinite than those of *Milesia*. There is a tendency, at times, for the outer tissue to be cast off, leaving an exposed hymenial layer. Lateral fusion of the pycnia sometimes occurs. At the base of the pseudo-parenchymatous layer are radiating cells which Colley (1918) in describing *Cronartium* has termed "contributing hyphae". These are in communication with the main mass of intercellular mycelium and serve as a means of transport for the food materials. In the young and even in the well-developed pycnia these hyphae have fairly dense cytoplasm and usually a number of small darkly-staining granules. Towards the end of the life of the pycnium vacuoles appear and increase in size, till eventually most of the basal hyphae are almost devoid of contents but for a small residuum of darkly staining protoplasm, probably representing the nucleus. At that stage the pycnia cease to produce spores.

The hymenial layer of the pycnium (Fig. 19) consists of parallel hyphae about 30μ to 40μ long and 2μ to 3μ in diameter. They are usually swollen slightly

in the centre and taper towards the apex. The nucleus is situated about the centre but moves somewhat during division. In the resting stage it varies little from the vegetative nucleus except in size, 3μ to 4μ by 3μ, as compared with 2μ to 3μ by 2μ in the vegetative hyphae, and chromatin content. In the vegetative nucleus the polarization of the chromatin is usually observable, but in the nuclei of the sporophores the polarization is not so definite and frequently difficult to demonstrate; the chromatin material is distributed round the nuclear membrane in the form of small irregular lumps. The nuclear membrane in very active nuclei is indistinct and, apparently, occasionally absent (cf. Blackman, 1904, fig. 49). A prominent nucleolus is invariably present. The cytoplasm of the sporophore is very finely granular, slightly vacuolate at the base and denser towards the apex.

The division of the sporophore nucleus has been examined with a fair degree of detail,, principally from preparations stained with Iron Alum Haematoxylin, the observations, wherever possible, being checked by comparison with material stained in Flemming's Triple or Newton's Gentian Violet. Immediately prior to division of the nucleus the chromatin ceases to show even the polarization phenomenon recorded above and collects into irregular lumps scattered over the nuclear membrane. There may be as many as twenty of these chromatin masses, so they do not appear to bear any direct relationship to the chromosomes (1, Fig. 20). At this stage there is a slight indication that the centrosome has divided (see 2, Fig. 20), but this has not been definitely established. The nucleus then elongates and the membrane becomes indistinct (4, Fig. 20) and at the same time the chromatin material collects and forms a smaller number of deeply staining masses which are here interpreted as chromosomes (6, Fig. 20). There appear to be five or six of these. No definite metaphase condition, nor any evidence of a spindle, has been seen. Centrosomes are inconspicuous or absent, although some preparations (as in 9, Fig. 20) show bodies which may be interpreted as such. These, however, may only be chromosomes or portions of chromosomes slightly separated from the main group. Anaphase figures are the most frequent found in sections. Figure 20 (5) is difficult to interpret. It is probably an early anaphase, indicating a longitudinal division of the chromatin comparable to that figured by Blackman (1904, fig. 57) in *Gymnosporangium*. The process of separation of the chromosomes is irregular and individuals appear to lag behind (cf. 7, 8, 9, Fig. 20). In the majority of cases observed it is possible to distinguish some material joining the two groups of chromosomes towards the end of anaphase. This material is more retentive of stains than the general cytoplasm and appears to envelop the chromosomes. During these changes the dividing nucleus moves towards the apex of the sporophore. Telophase is indistinct. As the pycnospore nucleus commences to move into the pycnospore, traces of chromosome structure are still visible, but nearly all this detail becomes obscured when the nucleus passes through the slight constriction of the sporophore (10, Fig. 20), owing to the strong affinity of the chromatin for stains, at this stage. The sporophore nucleus begins to reorganize and continues to do so rapidly. If divisions are following each other quickly, the nuclear membrane may not be formed, and the next division commences before the spore is abstricted (6, Fig. 20). After reaching the apex of the sporophore the pycnospore nucleus contracts and stains less heavily. No nucleolus is discernible and the chromatin is scattered over the nuclear membrane (Fig. 21). The spores are freed partly

by abstriction and partly by septation. No indication of a collar such as Blackman described for *Gymnosporangium clavariaeforme* was seen, although numerous stains, including Congo Red, were used in an attempt to detect such a structure. The staining reactions shown by the upper end of the sporophore indicate that it differs from the lower part; saffranin readily stains the lower region, but not the apical part.

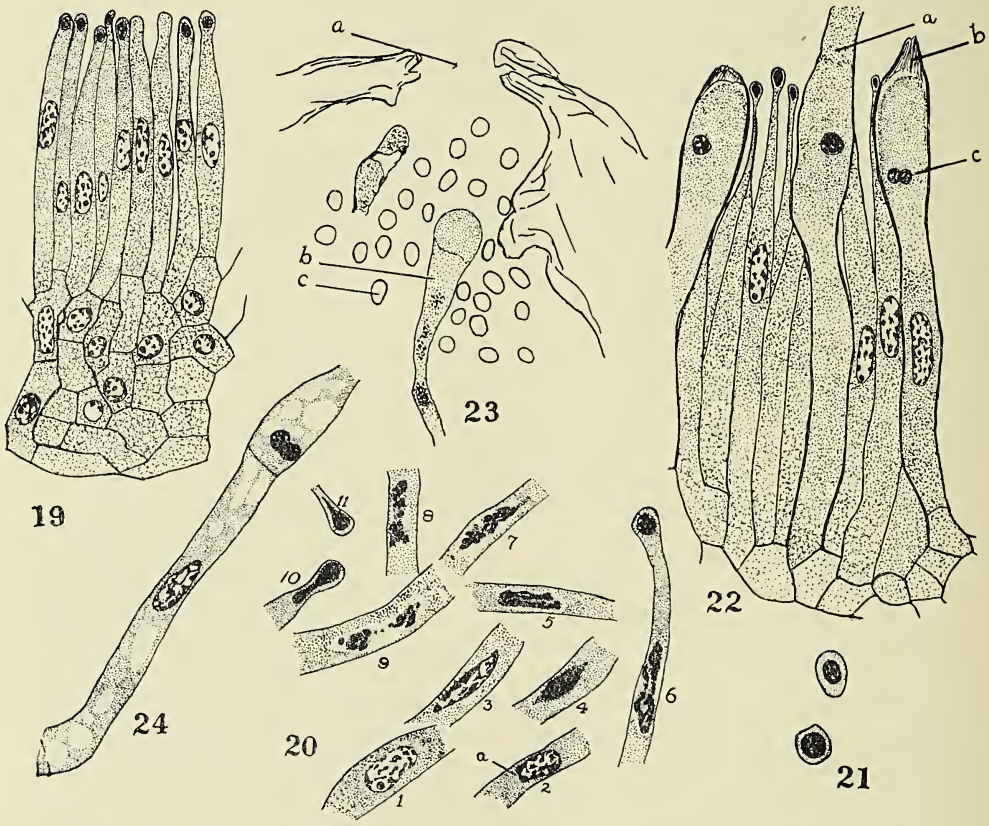

Fig. 19.—Hymenium of pycnium. × 1,500.

Fig. 20.—Nuclear division of the sporophore. 1-4, prophase; 5-9, anaphase; 10-11, telophase. At *a*, 2, note possible division of centrosome. × 1,500.

Fig. 21.—Pycnospores. × 1,500.

Fig. 22.—Hymenium of old pycnium. *a*, paraphyses; *b*, paraphyse wall cut obliquely; *c*, paired nuclei. × 1,500.

Fig. 23.—Mouth of pycnium showing apex of paraphyse. *a*, ostiole; *b*, apex of sporophore; *c*, pycnospore. × 1,500.

Fig. 24.—Paraphyse showing vacuolate condition of the cytoplasm and paired nuclei in the upper part, which is cut off by a septum. × 1,500.

Scattered throughout the hymenium are cells which are best termed intrahymenial paraphyses (Figs. 22, 23, and 24). These become evident in the mature pycnia. They arise in the position of sporophores, but differ from them in having a swollen apex which is usually vacuolated, and may be cut off from

the remainder by a septum (Fig. 24). When the pycnium is older these paraphyses grow out and some reach the mouth of the pycnium (Fig. 23). Colley (1918) mentions that in the pycnium of *Cronartium* hyphae grow out from the hymenium, but he does not figure, or discuss them. In *Uromycladium Tepperianum* they are a constant feature of the adult pycnium. In old pycnia binucleate examples of these paraphyses have been found and the possible significance of this will be discussed later. It was thought that these hyphae might secrete the pycnial fluid, but the evidence is against this view. The pycnial fluid is most abundant during the early life of the pycnia when these paraphyses are absent. They may function as dispersing organs, their upward growth forcing the spores out through the ostiole. A third suggestion is that they may be concerned with the formation of the binucleate stage in the life history of the fungus (cf. Craigie, 1933).

Acknowledgments.

The thanks of the writer are due to Mr. G. Samuel of South Australia, Mr. Geach of Canberra, and Mr. Cheel of Sydney, for supplying information regarding the collections in their charge and for permission to examine some of the specimens; to Mr. C. C. Brittlebank of Victoria for information bearing on the life of the galls; to Professor T. G. B. Osborn, Professor J. McLuckie, and Miss L. Fraser, M.Sc., of the Department of Botany, Sydney University, for suggestions and helpful criticism throughout the course of the work.

Summary.

1. The paper is the first of a series dealing with the Australian genus of gall-forming rusts, *Uromycladium*.

2. An evolutionary arrangement of the species is suggested.

3. The host range of *Uromycladium Tepperianum* is discussed, and possible physiological specialization indicated.

4. The genus *Uromycladium* is composed of microcyclic species.

5. The galls formed by *Uromycladium Tepperianum* on *Acacia stricta* are described in detail. Most of the gall is composed of xylem tissue which is unlignified.

6. It is suggested that the fungus utilizes the material which would normally produce lignification.

7. The galls are usually annual but may be perennial.

8. The vegetative mycelium is described, beginning at the stage when the gall is first discernible. The mycelium is localized at the seat of infection. The cells of the mycelium are uninucleate, the nuclei possessing a nucleolus, and a polarized chromatin network, possibly with a centrosome.

9. The haustoria may arise at any point along a hypha, and it is suggested that in some cases they may lie in the cell vacuole.

10. Changes in the host nucleus are described.

11. The pycnia are subcortical, non-periphysate, and imperfectly ostiolate. They may tend to become indefinite by lateral fusion.

12. Stages in the division of the pycnospore nucleus are recorded. Structures which were interpreted as chromosomes were seen. These are five or six in number.

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THE DIPTERA OF THE TERRITORY OF NEW GUINEA. I.

FAMILY CULICIDAE.

By Frank H. Taylor.
School of Public Health and Tropical Medicine, The University of Sydney.

(One Text-figure.)

[Read 29th August, 1934.]

The present paper contains part of the results of two expeditions to the Territory of New Guinea, when between three and four thousand specimens were either bred from larvae and pupae or collected in the field.

One species is described as new and notes are given on twenty-four others. Ten species are new to the Territory of New Guinea, while the distribution of seven others is considerably extended within the Territory.

When the entire collection is worked up many species, not previously recorded, will be added to the total of twenty-nine species and two varieties at present listed for the Territory.

The numerals preceding the names of some of the species refer to the catalogue number of the species in my recently published Check List of the Culicidae of the Australian Region. This has obviated the necessity of referring to important literature, only that of the author of each species being quoted.

Among interesting discoveries made to date are the description of a new species of *Bironella* subgenus *Brugella* (tribe Anophelini); *Anopheles longirostris* Brug, *Ficalbia* (*Etorleptiomyia*) *elegans* Taylor, and *Culex* (*Culex*) *brevipalpis* Giles.

The type of the new species is in the collection of the School of Public Health and Tropical Medicine.

Unless otherwise stated the specimens have been taken by myself.

My personal thanks are due to the Administrator, General T. Griffiths, for granting transport facilities, to Dr. E. T. Brennan, Director, Public Health Department, for considerable assistance in many directions, and Drs. Clive Backhouse, E. A. Holland, H. Champion Hosking and Mr. S. V. Bayley, of the same Department for the gift of much material, also to Mr. G. H. Murray, Director of Agriculture, for his kindness in supplying the photograph of the *Pandanus* sp. (Text-fig. 1).

Bironella (Brugella) hollandi, n. sp.

♂. Head clothed with thin narrow-curved black upright-forked scales except on the vertex, where they are silvery-white, and some silvery-white hairs overhang the eyes in the centre; palpi less than one-fourth the length of the proboscis, jet black; antennae not plumed, segments brownish-black, except the bases which are orange, more conspicuously so on the basal segments; proboscis black, labella brownish-black.

Thorax chocolate-brown, covered with numerous short brown hairs, the anterior third broadly pale yellow from the anterior margin to half-way to the wing-bases, from there to the wing-base the pale yellow is confined to the lateral margin; scutellum pale yellow except the middle third, which is pale brown with its posterior margin pale yellow, posterior bristles long, brown; bristles on thorax brown, well developed; pleurae chocolate-brown.

Wings: vein scales black, fringe dusky brown; fork-cells about equal in length, stem of the first slightly longer than its cell, that of the second about the length of its cell, base of the second fork-cell nearer the base of the wing than that of the first; the angle formed by the junction of the first and second veins quite shallow, base of the second vein about level with the base of the third fork-cell, base of the third vein slightly nearer the base of the wing than that of the second vein; stem of the second fork-cell with a comparatively sharp downward bend, about its middle, towards its base; anterior branch of the third fork-cell with a slight downward curve from about its centre to the cross-vein m-cu, cross-vein r-m longer than m-cu, parallel and about half its length from m-cu; basal half of the halteres pale, remainder black.

Legs: coxae and trochanters pale, femora, tibiae and tarsal segments dusky-brown except tarsals two to five of the hind legs, which are pale brown; ungues apparently all equal and simple.

Abdomen deep chocolate-brown, covered with moderately dense brown hairs, venter similar; coxite about twice as long as broad, tapering very slightly apically, with eight moderately long spines on raised tubercles close together at the base of the coxite, style with the basal third broader than in *B. travestitus*, curved inwards from about the base of the apical half, apical third about the same width throughout, spine apical, short, broad and blunt.

♀. Head: palpi, antennae and proboscis similar to the ♂; the silvery-white hairs on the vertex overhanging the eyes are more pronounced than in the ♂, and the silvery-white upright scales on the vertex extend on to the occiput.

Thorax chocolate-brown, narrowly pale brown laterally, more densely covered with brown hairs than in the ♂, the longer hairs arranged in rows, those along the acrostichal row of bristles being the most prominent; scutellum chocolate-brown. Wings as in the ♂.

Abdomen and legs as in the ♂.

Length, 3·5 mm.

Habitat.—Kavieng, New Ireland.

Bred from a mixed batch of larvae and pupae taken in a native village well, about three feet deep, situated on the east coast road about three miles from Kavieng.

Differs from *B. travestitus* Brug in having dark pleurae, the curvature of the stem of the second fork-cell less pronounced and that of the basal portion of the anterior branch of the third fork-cell more conspicuous; darker legs, and the coxite of the ♂ terminalia having eight spines at its base, instead of four as in *B. travestitus* Brug.

This is the first occurrence of the subgenus *Brugella* in the Territory of New Guinea, and it is possible that this species may be the same as *B. walchi* Soesilo, which was described from the larva only from Dutch New Guinea.

It affords me much pleasure to name this species after Dr. E. A. Holland, who has collected in New Ireland much valuable and interesting material for the

School of Public Health and Tropical Medicine. Grateful acknowledgement of the gift of various species of *Bironella* and of its subgenus *Brugella* is made to Col. S. L. Brug and Dr. R. Soesilo.

35. Anopheles (Myzomyia) longirostris Brug.

Geneesk. Tijd. Ned.-Ind., lxviii, 1928, 278.

The proboscis with the basal half black, apical half deep yellow with a faint brown patch of scales beneath at the base of the labella; palpi with segments one and two black scaled, first segment with a narrow apical ring of white scales, second with a broad white apical band, third with a narrow basal black band, rest white scaled, apical with a narrow black basal band, the rest yellow.

Abdomen typical; halteres pale creamy, apical half more white than creamy. Wings typical.

Legs black scaled, the speckling of the femora, tibiae and first tarsals distinctly yellow and not creamy as in typical specimens.

Habitat.—Kavieng district, New Ireland.

A single specimen differs in the above details from typical specimens generously presented to the School by Col. S. L. Brug. It can, at most, be regarded as a colour variation, not deserving a varietal name in the absence of a series of specimens. New to the Territory of New Guinea.

39. Anopheles (Myzomyia) punctulatus Donitz.

Insekten-Borse, xviii, 1901, 372.

This species is found, though not commonly in the writer's experience, on low-lying ground, preferring localities of a few hundred feet altitude to mountainous country. It is common in the Wau (3,500 feet), Bulolo (2,200 feet) and Upper Watut districts. The latter has about the same altitude as Bulolo. Wau is about 35 miles from Salamaua, Upper Watut approximately 20 miles from Bulolo, the latter about 50 miles from Salamaua, the port of entry for the Morobe goldfield district.

This species is probably widely distributed in more or less elevated localities in the Territory of New Guinea. It occurs sparingly in the Rabaul District, and is abundant at Toma (1,000 feet *circa*), New Britain.

Var. moluccensis Swellengrebel and Sw. de Graaf.

Bull. Ent. Res., xi, 1920, 78.

To a great extent this variety supplants the typical form in coastal localities. I have not found either larvae or adults in mountainous country in the Territory of New Guinea, and I doubt very much if it occurs in such localities.

This variety has been taken by the writer at Keravat, Kokopo and throughout the district between the outskirts of Rabaul and Keravat on the north coast road, and Kokopo in New Britain. It has also been found by the writer in New Ireland in various localities on the east coast road, breeding in the wells of native villages, in open swamps, backwaters of rivers and creeks. It was also found in the Namatanai district, New Ireland, breeding in similar situations to the above.

It was particularly abundant at Pondo, on the North Coast of New Britain, about 120 miles from Rabaul, when the writer was there in November, 1933.

44. Megarhinus inornatus Walker.

Proc. Linn. Soc., viii, 1865, 102.

Breeding in an old stump of a sago palm, Kavieng, New Ireland.

49. Tripteroides (Rachisoura) filipes Walker.

Proc. Linn. Soc., v, 1861, 229.

The larvae breed in rot holes in trees.

Habitat.—Rabaul, New Britain.

62. Tripteroides (Tripteroides) bimaculipes Theobald.

Ann. Mus. Nat. Hung., iii, 1905, 114.

Originally described from the Madang District of New Guinea, this species has been bred in some numbers from larvae found in the cut ends of bamboos.

Habitat.—Rabaul, New Britain (S. V. Bayley; F. H. Taylor).

68. Tripteroides (Tripteroides) quasiornata Taylor.

Proc. Linn. Soc. N. S. Wales, xl, 1915, 177.

A comparatively common species the larvae of which have been frequently taken by the writer in the water held by the axils of banana leaves and of *Colocasia* spp.; also found in rot holes of trees.

Habitat.—Rabaul, New Britain; Bulolo, New Guinea; Kavieng, New Ireland.

69. Hodgesia cairnsensis Taylor.

Proc. Linn. Soc. N. S. Wales, xliii, 1918 (1919), 842.

Habitat.—Kavieng, New Ireland.

74. Uranotaenia argyrotarsis Leicester.

Cul. Malaya, 1908, 214.

Larvae breed in small collections of casual ground water, not fully exposed to sunlight.

Recorded definitely for the first time from the Territory of New Guinea, though Hill (*Proc. Roy. Soc. Victoria*, xxxvii (n.s.), 1925, 67) doubtfully recorded it from Rabaul, New Britain and Kavieng, New Ireland.

My thanks are due to Dr. F. W. Edwards for the determination of this species.

Habitat.—Pondo (F. H. Taylor), Rabaul (G. F. Hill, F. H. Taylor), New Britain; Kavieng, New Ireland (G. F. Hill).

75. Uranotaenia atra Theobald.

Ann. Mus. Nat. Hung., iii, 1905, 114.

Originally described from Muina, New Guinea, it now extends from Queensland through the Territory of New Guinea to India.

Habitat.—Alenaua Is., New Ireland (Lincoln Bell). Muina or Muima is a native village near Madang, New Guinea.

77. Uranotaenia nigerrima Taylor.

Trans. Ent. Soc. London, 1914, 203.

Larvae of this species were found in water held by a large leaf of a forest tree.

Habitat.—Salamaua, Bulolo, New Guinea. Previously known only from Papua.

81. Uranotaenia quadrimaculata Edwards.

Bull. Ent. Res., xx, 1929, 313.

The larvae of this species are commonly found in water held by fallen banana leaves.

Habitat.—Rabaul, New Britain; Bulolo, Salamaua, New Guinea. Not previously recorded from New Guinea.

89. Ficalbia (Etorleptiomyia) elegans Taylor.

Trans. Ent. Soc. London, 1913, 703 [1914 (*Dixomyia*)].

A ♂ bred from a pupa, found in a small hole in the ground, agrees perfectly with the type from Townsville, Queensland.

This is the first recorded species from the Territory of New Guinea of a species of *Ficalbia*.

Habitat.—Rabaul, New Britain.

90. Mansonia (Coquillettidia) crassipes v. d. Wulp.

Bijd. Fauna Midden Sumatra, Dipt., 9, 1892.

Habitat.—Upper Ramu, New Guinea (Dr. G. A. M. Heydon). Not previously recorded from the Territory of New Guinea.

101. Aëdes (Mucidus) aurantius Theobald var. nigrescens Edwards.

Bull. Ent. Res., xx, 1929, 314.

Bred from larvae found in a shady pool in a sago palm swamp. Not previously recorded from the Territory of New Guinea.

Habitat.—Kavieng, New Ireland (Dr. E. A. Holland).

136. Aëdes (Finlaya) kochi Donitz.

Insekten-Borse, v, 1901, 38.

Hill (*Proc. Roy. Soc. Victoria*, xxxvii (n.s.), 1925, 72) states that the larvae of this species were taken in half coconut shells on many occasions. The writer has bred many thousands of mosquitoes from larvae found in half coconut shells in various parts of the Territory of New Guinea and has so far never bred any species of *Finlaya* from such a breeding place.

It is exceptional, in my experience in the Territory of New Guinea, to find larvae of species other than *Armigeres lacuum* Edwards, *Tripteroides* (*Rachisoura*) *filipes* Walker, *Aëdes* (*Stegomyia*) *scutellaris* Walker, breeding in such a situation.

Finlaya spp. breed in rot holes in trees, the leaf axils of trees and of taro (*Colocasia* spp.). The larvae of both *Finlaya kochi* Donitz, and *F. wallacei* Edwards breed almost exclusively in the leaf axils of *Pandanus* spp., the former being found also in the leaf axils of the various species of taro (*Colocasia* spp.).

Habitat.—Kavieng, New Ireland (Miss P. Holland, biting indoors at night); Bulwa, New Guinea (larvae in axils of *Colocasia* sp.).

140. Aëdes (Finlaya) notoscriptus Skuse.

Proc. Linn. Soc. N.S.W., xiii, 1888 (1889), 1738 (*Culex*).

♂. Abdomen with a small median basal spot of white scales on tergites four and five and the apical segment entirely white-scaled, and with basal white lateral spots except on the first tergite. ♀ with tergites entirely black, the lateral basal spots on segments three to seven.

Thorax of ♀ with the white lyre-shaped stripe and the median white line only; in the ♂ there are two very narrow short white stripes, one on either side of the median line, and about half the length of these lines in the typical form in which they are golden.

The coxite and style appear to be essentially the same as in the typical form from Sydney.

Habitat.—Rabaul, New Britain.

Until further material comes to hand I refrain from giving the above a varietal name.

150. Aëdes (Finlaya) wallacei Edwards.

Bull. Ent. Res., xvii, 1926, 105.

This species was common in Kavieng, New Ireland, January to February, 1934; enters houses to bite and is a troublesome species at night time, the bite being painful. It appears to breed exclusively in the axils of the leaves of the various species of *Pandanus*.

Habitat.—Kavieng, New Ireland (Dr. E. A. and Miss P. Holland).

Text-fig. 1.—*Pandanus* sp.
Finlaya kochi and *Finlaya wallacei* breed in water held in the axils of the leaves of *Pandanus*.

151. Aëdes (Macleaya) tremula Theobald.

Entomologist, xxxvi, 1903, 154.

Habitat.—Rabaul, New Britain (S. V. Bayley, F. H. Taylor). Several specimens, one of which was identified by Dr. F. W. Edwards. Not previously recorded from the Territory of New Guinea.

166. Aëdes (Geoskusia) fimbripes Edwards.

Bull. Ent. Res., xiv, 1924, 390.

A long series of both sexes of this species was taken from crab-holes on the foreshores of Rabaul Harbour. Their association with crab-holes is somewhat of a mystery, for in no case was water found in numbers of the crab-holes which were dug up after capturing the adults. The sand at the bottom of the holes was perfectly dry in every case investigated. Both sexes were always taken at the same time in these holes. Adults were bred from larvae found in ground water pools by the writer.

171. Aëdes (Stegomyia) albolineatus Theobald.

Entomologist, xxxvii, 1904, 77.

This species seems to breed exclusively in rot holes in trees.

Habitat.—Rabaul, New Britain (Dr. Backhouse, S. V. Bayley); Kavieng, New Ireland (Dr. E. A. Holland).

174. Aëdes (Stegomyia) scutellaris Walker.

Proc. Linn. Soc., iii, 1859, 77.

This species seems to breed almost exclusively in half coconut shells and rot holes in trees containing water. It is, however, becoming a "domestic" species as the larvae were frequently found in tin water-containers in the native village, and in two house tanks belonging to a house in the course of construction at Salamaua, also in beached canoes near habitations.

Habitat.—Wau (3,500 ft. alt.), Bulolo (2,200 ft.), Bulwa, Salamaua, New Guinea; and throughout the Territory of New Guinea, especially where there are coconut plantations.

Var. *A.*—Two female specimens, bred from larvae, show a marked variation in the abdominal markings, although constant in other respects. Tergites one to four with lateral spots only, median on one to three, submedian on four, small on one and two, easily in dorsal view on three and four, tergites five to seven with submedian white banding, less prominent on the fifth, sternites one and two with a broad white line of scales, sloping from the lateral spots to the centre at base of sternites, rest black-scaled, third sternite with a broad median white band, prolonged in the centre to base of sternite, fourth sternite similar but the median basal prolongation broader and with a black narrow line of scales about half its depth in its centre, the broad part of the wedge posterior, fifth sternite similar to that of the fourth but the black line in the centre about three times as wide, sixth sternite with the basal half all white except a small lateral patch basally which is black, seventh sternite black with a small lateral white patch.

Habitat.—Rabaul, New Britain.

In the absence of males I do not consider it wise to give these specimens varietal names. It is unfortunate that these specimens were not bred singly so that their larval and pupal skins could have been preserved.

Var. *B.*—A ♂ which has typical terminalia shows abdominal tergites one to four inclusive unbanded with median lateral spots increasing in size, that of the fourth appearing as a dorsal band with the middle two-thirds missing, tergites five and six with submedian white bands, seventh with median lateral spots, eighth entirely pure white, sternites one to six normal, seventh and eighth black.

Habitat.—Rabaul, New Britain.

182. Aëdes (Aëdes) funereus Theobald var. ornatus Theobald.

Ann. Mus. Nat. Hung., iii, 1905, 79.

Through a printer's error, Hill (*Proc. Roy. Soc., Victoria*, xxxvii (n.s.), 1925, 73) records the varietal name as "*rnatus*".

This variety seems to be confined to coastal regions. I did not find it at Wau, Bulolo or Bulwa in New Guinea. The larvae seem to be confined to partly shaded ground water.

Culex brevipalpis Giles.

Handb. Gnats, 2nd Ed., 1902, 384 (*Stegomyia*); Barraud, *Ind. Jnl. Med. Res.*, xi, 1924, 1277; *op. cit.*, xii, 1924, 432; Brug, *Bull. Ent. Res.*, xiv, 1924, 440.

Habitat.—Rabaul, New Britain; Alenaua Is., New Ireland (L. Bell).

Previously known from India, Malay States and East Borneo. Recorded for the first time from the Australian Region. I am indebted to Dr. F. W. Edwards for the determination.

212. Culex (Culex) mimulus Edwards.

Bull. Ent. Res., v, 1915, 284.

Taken in considerable numbers. Recorded for the first time from New Guinea.

Habitat.—Wau, Bulolo, New Guinea.

STUDIES IN THE AUSTRALIAN ACACIAS. III.

SUPPLEMENTARY OBSERVATIONS ON THE HABIT, CARPEL, SPORE PRODUCTION AND CHROMOSOMES OF ACACIA BAILEYANA F.V.M.

By I. V. Newman, M.Sc., Ph.D., F.L.S.,
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(*From the Botanical Laboratories, University of Sydney.*)

(Plate vii; thirty-three Text-figures.)

[Read 25th July, 1934.]

The first part of this enquiry (Newman, 1933) described the ecology, habit, floral structures, reproductive processes as far as the production of the spores, and the haploid chromosome number. As the material for that paper was collected late in the season, it did not show some of the earlier stages of development. Good material became subsequently available, so missing stages can now be presented, with further discussion and with additional observations on the chromosomes.

Annotations for the figures have been standardised and will be found in the "Notes on the Illustrations".

Most of the material used for this part of the work was collected by Mr. J. Stewart from trees in cultivation at Strathfield, Sydney. The writer expresses his thanks for good service rendered.

Methods and fixatives were described in the previous paper (p. 146). The alcoholic fixatives were more suitable from the point of view of sectioning as they seemed to make the air more easily extracted from the spaces within the flower heads.

HABIT.

On page 150 of Part I, it was stated that there seemed to be two sections of the species, one with mostly three and one with mostly four pairs of pinnae. A slight statistical examination was made of eight trees in 1932. Though it showed the possibility of a third section with mostly five or six pairs of pinnae, the distribution of the numbers among the samples indicated that there may be a significant variation from year to year, due rather to fluctuations of vigour than to genetical differences. Kelly (1912, p. 120) gives equally wide variations for the size and outline of the phyllodes of other unsplit species of *Acacia*. It is significant, however, that Clos (1929), describing *A. Baileyana* as cultivated in Argentina, refers only to two or three pairs of pinnae. The inference is that the original plant or plants introduced there possessed such a *genetical* character. Before any valid division of the species into sections based on these characters could be made, an accurate statistical examination would have to be undertaken. A similar situation arises with the occurrence of the racemes singly or in pairs.

At the beginning of anthesis the style (contorted in the bud) emerges between the separating tips of the petals. A flower head may have all its styles extended, without any sign of the stamens. The stamens are extended by the lengthening and uncoiling of the filaments, and the tip of the style projects beyond them (Plate vii, fig. 1).

As described in Part I, p. 153, and below, the legume is a folded foliar structure, with an elongated tip of which the stigma is the slightly opened end. The stigma appears as a shallow cup (Plate vii, figs. 2, 3). Note that the heavy cuticle (with wavy surface) on the epidermis of the top of the style does not extend on to the stigmatic surface (Plate vii, fig. 3, *ct.*).

The Morphology of the Legume.

The youngest fertile legumes described in Part I were at the stage of the primary megasporogenous cell. Sections of legumes at a stage earlier than that are shown here in Plate vii, figs. 9–12. The two epidermes of the appressed margins of the folded foliar structure are clearly visible on one side of the carpel, while absence of such features and the presence of the midrib primordium are equally visible on the other side. In *A. Baileyana* the carpel definitely arises as a single folded (foliar) structure.

By the theory of Carpel Polymorphism, Saunders (1925, p. 142) interprets the legume as composed of two carpels and gives *A. suaveolens* and *A. longifolia* as examples (1929, pp. 225–8, 258). After examining microtome sections of the developmental stages of the legume from its initiation to the time of fertilization, it is hard to understand how such an interpretation could be made. This question was discussed in Part I (p. 155); but in view of the additional evidence now available further comment will be made here.

Almost every author who has occasion to describe or figure the legume before post-fertilization development represents it as a single folded structure at whose appressed margins the ovules arise, e.g., Reeves (1930*b*, fig. 2) shows the appressed epidermes in *Medicago sativa*; Taubert (1894, pp. 84–6) figures the single folded structure for the legume in general, as does Thompson (1931) for species of all sections of the Leguminosae; and Bugnon (1925*a*) shows the legume of *Lathyrus vernus*, *Trifolium pratense* and *Lupinus perennis* to be open on one side in the early stages. For comparison, we could note that Brough (1933, pp. 37, 41) describes an almost identical form for the gynoecium of *Grevillea robusta* (Proteaceae). Bugnon undertook his enquiry on account of Grégoire's (1924) statement that the legume in the Papilionaceae is not a folded structure because its primordium is annular and it dehisces along two sides, figuring *Lathyrus*. Grégoire's figures are unconvincing because, though they show tissue structure, their ovules are of such a size and outline that one expects to see differentiation of sporogenous tissue, but does not see it. Moreover, as Bugnon points out, the carpels shown are too old for reference to primordia. It is on account of neglecting truly primordial stages, and emphasizing adult stages, secondary developments and external contour that the misinterpretation of the legume has been possible.

Post-fertilization development of the legume of *Acacia Baileyana* rapidly masks the single and folded nature of its primary morphological structure. It has been seen to have the form of a single folded foliar organ, with appressed epidermes of the margins, with two marginal vascular bundles "adaxially" and the single midrib "abaxially". The carpel is so undeveloped by the time of

fertilization that the vascular bundles are scarcely more than primordial. On the marginal side, the side of the insertion of the ovules, secondary growth produces a narrow zone of parenchyma along the line of the appressed epidermes (*pce.* in Plate vii, figs. 4, 5). On the midrib side secondary growth produces a zone of parenchyma (*pcm.* in Plate vii, figs. 4, 6) from the edge of the loculus to the outer epidermis, dividing the midrib. There is no difficulty in accepting this division of the midrib which, before the secondary growth began, was almost primordial. Between the seeds, the walls of the loculus are pressed together and its epidermal cells become much enlarged and pithy. Along the broad axis (A to B in Plate vii, fig. 4) of the legume, there is a line of weakness composed of parenchyma cells which, except at one end (the midrib end), are mainly cells of two appressed epidermes. There is nothing in this secondary development to refute the previous conclusion that this legume is a single carpel. This investigation emphasizes the necessity of the study of primordial stages in the interpretation of floral structure.

Except where passing between the hard tissues of the vascular bundles, the line of weakness (parenchyma) described above has on either side a zone of collenchyma cells produced by the secondary growth (*cc.* in Plate vii, figs. 4–6). Dehiscence is brought about by the differential contraction of these tissues, and is in no way an indication of the fundamental structure of the legume.

The disputed theory with regard to the legume rests largely on the relative prominence of the secondary vascular systems arising from what are usually regarded as the marginal bundles. Bugnon (1925*b*) contests the application of the theory of Carpel Polymorphism to the legume, objecting to interpretations based on the adult gynoecium without taking into account ontogeny or comparative foliar morphology. He points out that in some Monocotyledons the marginal veins of some floral leaves give off secondary veins while the midrib remains simple. And Arber (1933, p. 235) says that "the predominance of the marginal regions in the carpel as compared with the foliage leaf . . . is not an absolute change, but merely a *variation in relative emphasis*;". She also (p. 233) attacks the assumption in the theory that a vascular system can remain as a survival of an organ of which no external trace exists, holding that the vascular system is rudimentary to the same degree as or more than the rudimentary external form. The case of *Acacia Baileyana* gives general support to this objection in that the marginal bundles receive emphasis only in accordance with the need they serve; for in the fertile carpel they do not pass into the style (i.e., beyond the ovules they supply), and in the sterile carpel without even rudimentary ovules they are entirely absent.

Sporangial Structures.

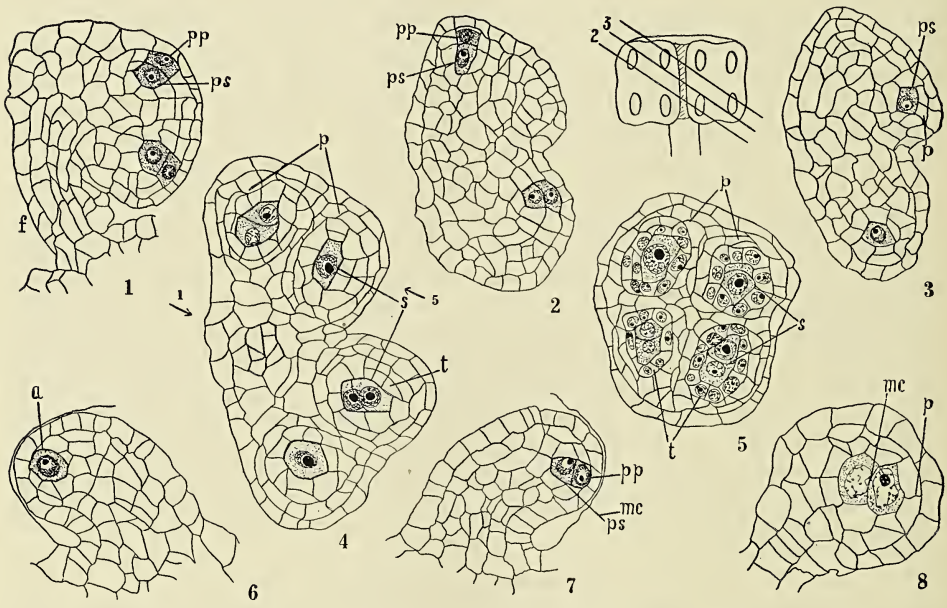
Sporangial structures are considered only up to the shedding of the pollen in the one case and to the time of fertilization in the other case. The sporogenous tissue after the archesporium is considered under "Sporogenesis".

Microsporangial.

The disposition of the eight groups of sporogenous cells in the anther has been described already in Part I, p. 157. Judging from the clear cases of the immediate products of its division (Text-figs. 1, 2), the archesporium is regarded as a single hypodermal cell for each sporogenous tissue (microsporangium). Text-figures 1 and 2 may suggest that the functional archesporium is

selected from a group of archesporial cells. But in view of the smallness of the anther it is considered that there is difficulty in distinguishing somatic meristem from sporangial meristem. The anther is, therefore, held to contain eight morphologically superficial sporangia derived from eight separate archesporia. The whole of each sporangium is shed as a unit, the pollinium. (See also section on "Sporogenesis" below and in Part I, p. 159.)

Albizzia lebbek, in another genus of the Mimoseae, is described by Maheshwari (1931, p. 244) as having a deep-seated archesporium, i.e., with a morphologically embedded sporangium. He says that the archesporium consists of a row of two cells. After comparing his figures with the account given below, it would seem that what he identifies as a row of two archesporial cells is the two cells resulting from the division of the primary sporogenous cell. Compare his figures 4 and 5 with Text-figures 3–5 of this paper. Probably in both *Acacia Baileyana* and *Albizzia lebbek* the early stages are passed through very quickly. In *Asclepias cornuti*, another plant that forms a pollinium, but with many grains in it, the archesporium is a transverse row of cells (Gager, 1902, p. 129).



Text-figures 1-5.—Stages in the formation of the microspore mother cells. × 390. 1, longitudinal section of a young stamen. 2 and 3, consecutive oblique sections of a young anther (with primary sporogenous cells) as in the diagram between the figures. In two cases the primary parietal cell has divided. 4, transverse section of an anther showing parts of four bi-cellular sporogenous tissues, each surrounded by its tapetum. The arrows indicate the plane of sections 1 and 5. 5, longitudinal section of a lobe of an anther showing parts of four bi-cellular sporogenous tissues.

Text-figures 6 and 7.—Longitudinal sections of two young ovules showing the initiation of the sporangium. × 390.

Text-figure 8.—Oblique longitudinal section of a young ovule showing two mother cells in synapsis, possibly derived from one archesporium. × 540.

There are three layers of anther tissue vertically, and four or five layers horizontally between the dividing primary sporogenous cells in *Acacia Baileyana* (Text-figs. 1, 4, 5). From these and the parietal tissue, the tapetum is organized as a (usually) single layer of uninucleate cells for each sporangium, leaving one layer vertically and two or three layers horizontally of non-tapetal cells between the sporangia (Text-figs. 4, 5).

Schürhoff (1926, p. 239) derives the tapetum on the outer side from the primary sporogenous layer (the inner layer resulting from the division of the hypodermal layer). But in *Acacia Baileyana* it is derived from the primary parietal cell. A similar origin for the tapetum has been found in other Leguminosae by Reeves (1930*a*, p. 30) in *Medicago sativa*, Weinstein (1926, p. 250) in *Phaseolus vulgaris*, Maheshwari (1931, Figs. 4, 5)—judging by his figures—in *Albizzia lebbek*, and by Sethi (1930, p. 128) in *Cassia didymobotrya*; in another pollinium-forming genus by Gager (1902, p. 129) in *Asclepias cornuti*; in two other Australian Angiosperms by Brough in *Dampiera stricta* (1927, p. 478) and *Grevillea robusta* (1933, p. 49).

After examining 43 species from 24 families of Angiosperms, Cooper (1933, p. 359) says that they can be divided into three slightly overlapping groups having the following tapetal conditions: 1, uni-nucleate cells; 2, bi-nucleate cells; 3, pluri-nucleate cells. Among the Leguminosae he listed 4 species of *Medicago*, and 2 species of *Melilotus* in group 1, to which can be added *Albizzia lebbek* (Maheshwari, 1933, p. 245) and *Acacia Baileyana*. *Cassia didymobotrya* (Sethi, 1930) can be placed in group 3, as also a pollinium-forming plant from another family—*Asclepias cornuti* (Gager, 1902, p. 130). It is interesting to find that species of the Papilionaceae and Mimoseae are associated in group 1, while a Caesalpineous species is in group 3, otherwise than might be expected in view of the floral forms of these sub-families.

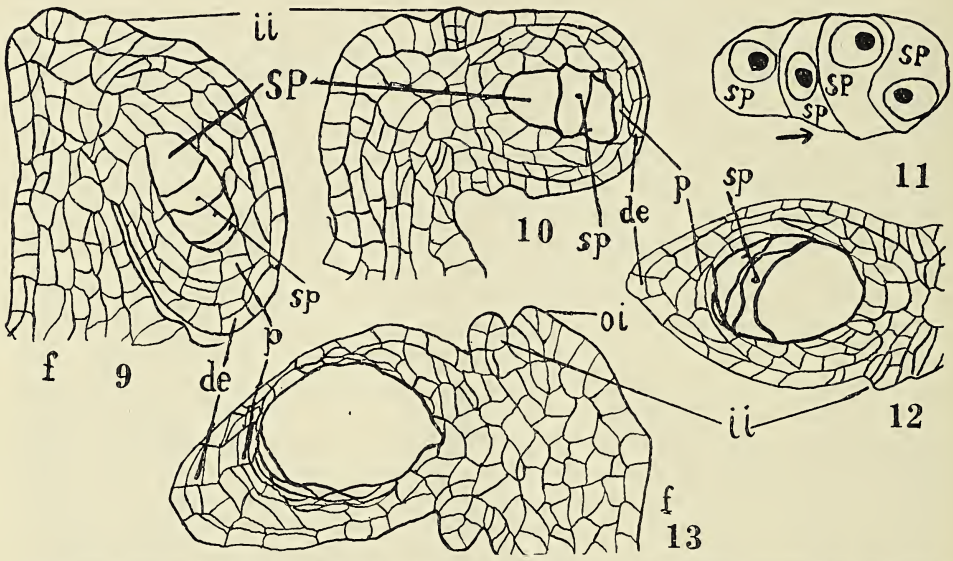
Megasporangial.

In describing the ovule, the term "sporangium" will be used only of the products of the archesporial cell. These comprise the parietal tissue (if any) and the sporogenous tissue (usually one cell only). The sporangium is borne on a receptacle (nucellus) at the margin of the carpel. The term "nucellus" itself will be used only where the whole of the structure above the stalk (funiculus) of the receptacle is referred to, irrespective of the internal differentiations. (For explanation of the use of these terms see Newman, 1928, pp. 515, 522).

From the transverse section shown in Plate vii, fig. 9, it will be seen that the young carpel before the initiation of the ovule consists of three layers of cells surrounded by an epidermis and containing a midrib primordium. Figure 10 on the same plate shows that there are still only three layers within the epidermis, except at the margins, when the ovule primordia appear by multiplication of the hypodermal layer. Though the primordia appear to be on the inner (adaxial) surface, from the curve of the cell layers they can be interpreted as on the morphologically outer (abaxial) surface of the carpel. This depends on whether the margin of the carpel is at B or A in Plate vii, fig. 10. The latter condition was demonstrated by the writer in the case of *Doryanthes excelsa* (Newman, 1928, p. 507).

The megasporangium is derived from a hypodermal archesporial cell (Text-fig. 6) that gives rise to the primary parietal cell and the primary sporogenous cell (Text-fig. 7) whose further development has been described in Part I (p. 162).

The ovule is more or less anatropous, and is naked until after fertilization, the integuments being only primordial collars till then. The inner integument is the first to appear about the time of megaspore formation (Text-figs. 9, 10, 12, 13). The development of the integuments will be described in connection with the development of the seed in a subsequent paper.



Text-figures 9, 10, 12, and 13.—Longitudinal sections of young ovules at various stages. The chalazal megaspore is functioning. × 455. 9, four spores. 10, three spores. 12, two-nucleate sac. 13, organization of cells in the sac.

Text-figure 11.—Row of four megaspores with the two distal spores functioning. × 880.

In Part I, p. 159, it was said that there is no multiplication of the epidermis of the ovule. This is true only until the formation of the spores. After that time periclinal divisions occur in the epidermis over the parietal tissue (Text-figs. 9, 10, 12) till, by the time of fertilization, it is several layers thick (Text-fig. 13, Plate vii, fig. 13).

The epidermis of the chalazal region is continuous with several layers of cells in the distal region of the ovule. By the time of fertilization or very soon after, the only tissue left above and beside the embryo sac is of epidermal origin. This is a correction of the previous statement of absence of crushing of the parietal tissue (loc. cit.).

Starch is plentiful in the nucellus at the time of fertilization. The refringent bodies shown in Plate vii, fig. 13, are the starch grains.

The origin of the ovule from the hypodermal layer appears to be normal (Coulter and Chamberlain, 1903, p. 53). Guignard (1881, p. 28) describes the ovule of the Acacias as completely anatropous at the time of fertilization (based chiefly on *A. retinoides*), and says that the ovules of the Caesalpineae are less anatropous than those of the Mimoseae (p. 45). If this be so, there is again a character common to the Papilionaceae and Mimoseae differing from that possessed by the Caesalpineae which manifest the more primitive condition

(Coulter and Chamberlain, 1903, p. 56). But *Acacia Baileyana* appears to be indefinite in this respect.

The position of the archesporial cell is as generally found in other Leguminosae. Guignard (1881, p. 22 et seq.) described it and its division to primary parietal and sporogenous cells in a number of species of *Acacia*, as did Maheshwari (1933, p. 246), in *Albizzia lebbek*. Among some Papilionaceae, there is a tendency to have a multi-cellular archesporium. Reeves (1930*b*, p. 240) and Martin (1914, p. 160) found mostly two or more archesporial cells in *Medicago sativa*, though Guignard (1881, p. 119) found only one in *M. arborea*. Martin found that sometimes the archesporial cell functioned as the mother cell. In *Trifolium pratense* he also found (p. 156) more than one archesporial cell to be usual. Saxton (1907, p. 1) was not able to recognize an archesporial cell in *Cassia tomentosa*, stating that the mother cell is differentiated deeply. A multicellular archesporium can be considered primitive and is characteristic of the Rosaceae (Coulter and Chamberlain, 1903, pp. 58–61). Here again the Papilionaceae manifest the primitive condition; but in this case the Mimoseae (see also Guignard, 1881, pp. 22, 46) are not associated with them and manifest the advanced condition, in association with the Caesalpineae.

Among the Leguminosae there is considerable variation in the degree of development of the parietal tissue. Interpretation is complicated by the frequent multiplication of the epidermis covering it, from about the time of spore formation. Warming (1878, p. 228) and Vesque (1879, p. 277) have described this multiple epidermis for a number of Angiosperms distributed mostly among the Archychlamydae, but also among the Metachlamydae and the Monocotyledons. Guignard (1881, p. 23) records the multiple epidermis over the parietal tissue as common in the Leguminosae, and Péchoutre (1902, p. 154) does the same for the Rosaceae.

The last three authors are agreed that the multiple epidermis persists usually for a long time, even though all the underlying parietal tissue may be destroyed by the enlarging embryo sac. Martin (1914, figs. 8–12) shows few divisions in the epidermis for *Trifolium pratense*, but this epidermis may even be crushed by the mature embryo sac. Vesque (1879, p. 279) points out that when a more or less massive parietal tissue has a multiple epidermis, destruction of tissue stops short of that epidermis.

Sporogenesis.

Relative Size of Spores.

The question of the relative size of the megaspores and microspores was raised by Gates in a letter to *Nature* (1932*a*). A few measurements in *A. Baileyana* suggest that its megaspore is the smaller. In such a question the spores must be measured at comparable stages. In this case the measurement was made just after the spores were formed.

Microspore.

The eight single hypodermal archesporial cells give rise to the eight single primary sporogenous cells. Two of these, with the primary parietal cells, are shown in Text-figure 1, representing a longitudinal section of a young stamen. Text-figures 2 and 3 represent oblique transverse sections of an anther showing the same and slightly later stages. The primary sporogenous cells are slightly larger and more densely cytoplasmic than the surrounding cells whose meri-

stematic condition makes difficult the identification of the young primary sporogenous cells. But they can be identified by following back to them from the unmistakable condition shown in Text-figures 4 and 5, where can be seen the products of their division both resting and preparing for the second division. This produces the four mother cells in each sporangium. From this stage the account in Part I began.

The occurrence of only four mother cells in the microsporangium makes *A. Baileyana* (and probably all Acacias) suitable material for testing the recent theory of Huskins (1932) that meiosis is initiated by the suppression or retarding of the split in the chromosomes during the last pre-meiotic mitosis. This theory was discussed in a letter to *Nature* (Newman, 1932) in which it was pointed out that an explanation would be needed as to why meiosis did not occur in the primary parietal cells of plants whose primary sporogenous cells functioned as mother cells. For in the anther of *A. Baileyana*, both cells formed by the last pre-meiotic mitosis undergo meiosis. But in ovules such as that of *A. Baileyana* and in anthers such as that of *Grevillea robusta* (Brough, 1933, p. 49) where the primary sporogenous cells function as mother cells, only one of any two nuclei formed by the last pre-meiotic mitosis undergoes meiosis. Huskins (1932, p. 26) reports that he has observed pairing of chromosomes in the parietal tissue in the ovule of *Matthiola incana*. If sometimes, why not always?

Though tetrad formation is not considered here, it is worth noting that Kanda (1920, p. 60) records two types of tetrad formation in *Verbena*: 1, some peripheral cytoplasm of the microspore mother cell remains to form a temporary common wall for the tetrad; 2, all the cytoplasm of the microspore mother cell is used up within the spores. It seems possible that type 1 is a step towards the evolution of pollinia such as occur in the Acacias.

Megaspore.

Megaspore formation has now been found to be succedaneous. Plate vii, figure 15, of the homotypic division, shows that a wall had been formed at the end of the heterotypic division. It is also to be noted that the spindles of the homotypic division are sometimes inclined to one another, which may account for the occasional attempts by two spores to function in the one ovule (Plate vii, fig. 15).

An unusual case of two mother cells in synapsis in one ovule was found (Text-fig. 8). This differs from the case described in Part I, p. 158, in that there is here no tissue between the mother cells, which suggests the possibility of their origin by division of a primary sporogenous cell, a different condition from that of the multicellular archesporium of the Rosaceae.

The functional spore may be proximal (Text-figs. 9, 10, 12) or distal (Plate vii, fig. 14, and Text-fig. 11), but it is difficult to say which is the more frequent. The functioning of the second or third spore is rare.

Several cases of more than one mother cell in an ovule and even more than one sac in an ovule have been seen in *A. Baileyana*, and Guignard (1881, p. 37) records examples of two sacs in an ovule in several species of *Acacia*. No example has been seen in this species of more than one tetrad in an ovule. Therefore, the occasional occurrence of more than one functional spore or sac in an ovule would appear to be due to development of more than one spore of a tetrad. Reeves (1930*b*, p. 241) records that more than one tetrad in an ovule may be formed in *Medicago sativa*, but only one megaspore develops to a complete

embryo sac. The same author (p. 241) records vertical division of the upper daughter cell of the heterotypic division as in the figure given here (Plate vii, fig. 15).

Guignard (1881, pp. 136–7) records, in the Leguminosae, most of the possible variations in the numbers of megaspores formed from one mother cell, namely: the mother cell functioning as spore, two, three unequal, three equal, four equal spores. He listed Mimoseae and Caesalpineae in only the last two groups. Schürhoff (1926, p. 574), summarizing work on the Leguminosae, says there are three or four spores of which the lowest or second lowest functions. Martin (1914, p. 160) records occasional functioning of the third megaspore in *Trifolium repens*. *A. Baileyana*, therefore, with the approximately equal functioning of the chalazal or distal megaspore, seems to occupy a unique position among the Leguminosae. In another Australian Dicotyledon, *Styphelia longifolia* (Epacridaceae), it is the distal megaspore that functions (Brough, 1924, p. 168). According to Saxton (1907, p. 2) the non-functioning of the proximal megaspore among the Dicotyledons is almost confined to the Rosaceae and the Leguminosae.

Sterility.

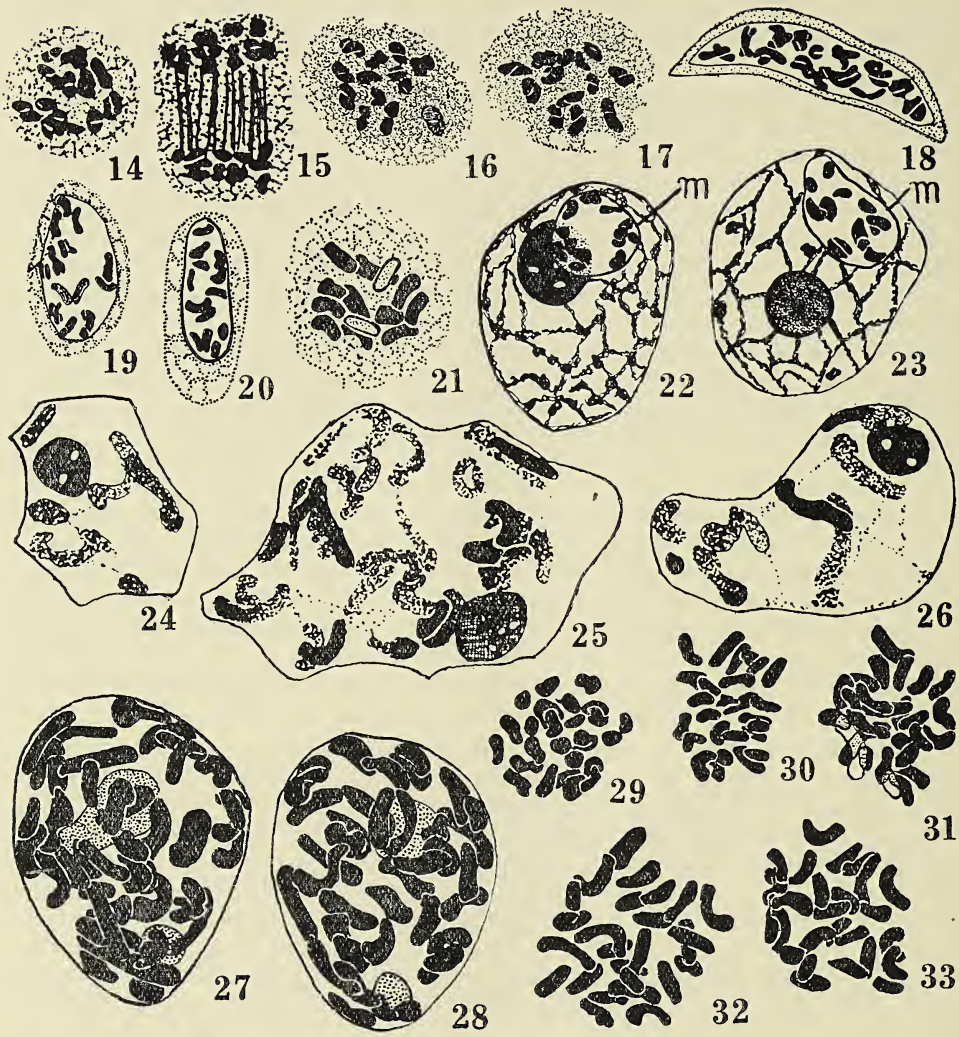
Sterility in the female organs seems to be influenced considerably by geographical position. For, at Hill Top, about 90 Km. south-west from Sydney and at an altitude of 600 m., the setting of the seed is abundant, while at Strathfield, Sydney (at altitudes up to 50 m.) it is difficult to get material giving preparations of fertile ovules in the few fully developed legumes produced (Plate vii, figs. 7, 8). Note that the ovules shown in Figure 8 had attained full size before degenerating. In contrast to the above, copious germination was obtained in culture of pollen collected at Strathfield.

Maheshwari (1931, pp. 251, 260) describes degenerations in *Albizzia lebbek* only after formation of the microspores in the anther, and in the ovule only from the prophase of meiosis onwards—mostly after the formation of tetrads—and concludes that it represents "an inherent tendency towards the elimination of one or both of the sex organs on some flowers". In *Trifolium pratense*, Martin (1914, p. 159) finds that sterility occurs before the formation of mother cells, as none of these were found in synapsis in sterile ovules. The general and indefinite sterility in *A. Baileyana* seems in a different category from these types referred to, nor is it a Mendelian character such as described for pollen sterility (confined to mother cells) in some races of *Lathyrus odoratus* by Gregory (1905, p. 154).

Chromosomes (*Number, Form and Behaviour*).

Shimotomai (1933, p. 4), working with the genus *Chrysanthemum* in which there is much polyploidy, avoids the difficulty of confusing the "haploid" and "diploid" numbers of different species by reserving the letter "n" for the basic number of chromosomes for the genus, using "ϕ" for the gametic number and "2ϕ" for the zygotic number. This convention will be used in the study of the Acacias from now on.

The gametic number, $\phi = 13$, was counted previously for *Acacia Baileyana* in meiosis in the anther (Newman, 1933, p. 166). This number has now been confirmed by counts in microspore division, the generative nucleus, the male nuclei within the embryo sac, the homotypic division in the ovule and the second and third divisions in the embryo sac (Text-figs. 14–23; Plate vii, figs. 15–17*b*').



Text-figures 14 to 33.—Chromosome numbers and forms. In these figures the presence or absence of trabants is disregarded. × 3250.

Text-figures 14-23.—The gametic complement of chromosomes, ϕ = 13, in various situations. Note the size differences and the frequent visibility of the split at anaphase and telophase. 14 and 15, metaphase and anaphase of microspore division. 16 and 17, polar view of the two groups of an anaphase of microspore division; note the corresponding positions of the chromosomes in the two groups; the lighter chromosome was on the next section. 18, young generative cell with telophase chromosomes. 19 and 20, generative cell in the pollen grain and tube respectively. 21, metaphase of the third division in the embryo sac, polar view. 22 and 23, male nuclei (m) in contact with egg and polar nuclei respectively.

Text-figures 24-28.—Endosperm nuclei in prophase. Showing approximately 3ϕ = 39. Note the size differences in the chromosomes. 24-5-6, consecutive sections of a primary endosperm nucleus distorted by starch grains. 27-8, daughter nuclei of the primary endosperm nucleus.

The zygotic number, $2\phi = 26$, has now been counted in the following tissues (Text-figs. 29–33): filament, microsporogenous tissue, inner and outer epidermis of the pod, and the testa of a young seed. In these zygotic counts trabants and constrictions were disregarded.

The endosperm number, $3\phi = 39$, has been observed, approximately, in the primary endosperm nucleus and its daughter nuclei (Text-figs. 24–28).

Hedayetullah (1931) in *Narcissus*, and Koshy (1933, p. 304) in *Allium* have described the anaphase chromosomes as showing the split for the next mitotic division. This split is very clearly shown in some of the anaphase and telophase figures given in this paper (Text-figs. 15–18; Plate vii, figs. 15, 17*a*-*b*′). The split for the current division is shown in prophase nuclei of gametophytic tissue (Text-fig. 19; Plate vii, fig. 16, *a*, *b*).

In Plate vii, figures 16*a*-17*b*′, of prophase and telophase of the second and third divisions respectively in the embryo sac, there are shown structures that strongly suggest trabants (see Part I, pp. 160 and 166).

There are marked differences in chromosome size. I am of the opinion that in the gametic complement there is one chromosome definitely larger, and three chromosomes definitely smaller than the others. One or both of these features are to be seen in most of the figures showing chromosomes. It is remarkable that such a feature should be observable, not only in divisions in the formation of the embryo sac, but also in the generative nucleus and the male nuclei. The same differences with the numbers doubled are discernible in the figures from zygotic tissue (Text-figs. 29–33).

A detailed study of the cytology of *Acacia Baileyana* and other species will be made at a later date; but certain points may be mentioned now. It was pointed out in Part I (p. 167) that 13 was a recent discovery for the gametic chromosome number among Leguminosae, the usual numbers being low multiples of 6, 7, and 8. Evidence is accumulating that a number such as 13 may be a secondary polyploid number based on a simple number such as 6, 7, or 8 with duplication of one chromosome or fusion of one or more pairs of chromosomes. For instance, in *Cassia occidentalis*, $\phi = 13$, Muto (1929, p. 270) figures two, possibly 3, distinctly large chromosomes and in *C. didymobotrya*, $\phi = 14$, Sethi (1930) finds no very large chromosomes. Other plants with 13 as a basic number for the chromosome complement are *Epacris impressa* (Samuelsson, 1913) and species of *Gossypium* (Denham, 1924; Banerji, 1929; Davie, 1933; Skovsted, 1933). All four authors agree in finding two races of *Gossypium*, the Asiatic species with $\phi = 13$ and the New World and Egyptian species with $\phi = 26$. Compare the similar difference between Australian and extra-Australian species of *Acacia* (Ghimpu, 1929, *a*, *b*). Skovsted (pp. 243–4) and Davie (pp. 44–45) discuss the possibility of these species of *Gossypium* being secondary polyploids based on lower numbers with duplication or fusion of chromosomes, Skovsted also considering the possibility of polyploidy based on the numbers 7 and 6. If fusions are the case, then Davie finds the appropriate number of large chromosomes to be present. Gates (1932*b*, p. 10) has quoted records of end to end fusion of two chromosomes to form a

Text-figures 29-33.—Polar view of zygotic chromosome complements showing $2\phi = 26$. Note the size differences of the chromosomes. 29, anaphase group from the filament of a stamen. 30, anaphase group from the division of a primary sporogenous cell. 31, metaphase from the epidermis of the loculus of a young pod; the two chromosomes in outline were on the next section. 32, metaphase from the outer epidermis of a young pod. 33, metaphase in the testa of a young seed.

single body. If the basic number, n = 13, for the Acacias is derived by the fusion of two chromosomes to form one large one, then the appropriate numbers of large chromosomes are considered to be present in *Acacia Baileyana*, and there is an approach to these numbers in the illustrations given by Ghimpu (1930, p. 192, 198) for mitosis in *A. cyanophylla* and *A. scorpioides* var. *adstringens*. It seems reasonable to suggest that the number ϕ = 13 for *A. Baileyana* is secondary polyploidy based on duplication of the number 7 with fusion of a pair of chromosomes to form one large one. The investigation of the cytological details of *Acacia Baileyana* will soon be undertaken.

Summary and Conclusion.

This paper presents supplementary observations and discussion on vegetative features, spore production and chromosomes of *Acacia Baileyana*.

After slight examination, it is concluded that extensive statistical inquiry would be necessary before splitting the species into sections based on the numbers of pinnae.

Anthesis with proterogyny is described.

The primordia of the legume are described and discussed in refutation of the application of the theory of Carpel Polymorphism to the legume. The post-fertilization development of the pod is shown not to support that theory.

In the anther, there are 8 separate unicellular archesporia. The tapetum is derived from the primary parietal cell; and its cells are uninucleate, being associated therein with the Papilionaceae and not with *Cassia didymobotrya* (Caesalpineae).

The ovules arise from the hypodermal layer at the margins of the folded legume, and are possibly morphologically abaxial. They are more or less anatropous, being intermediate between the Caesalpineae and the Mimoseae and Papilionaceae. They are naked at fertilization.

In the ovule there is one hypodermal archesporial cell as in the Mimoseae and Caesalpineae. The parietal tissue is early destroyed. The epidermis over the parietal tissue is multiple by the time of fertilization, and is persistent.

The megaspore is possibly smaller than the microspore.

In the anther, the single primary sporogenous cell from the division of each archesporial cell divides twice to form the four microspore mother cells, in each sporangium.

In the ovule, the primary sporogenous cell functions as the megaspore mother cell. Megaspore formation is succedaneous.

There is discussion of the significance of the small number of mother cells in connection with the theory that pairing of chromosomes at meiosis is due to delayed split in the pre-meiotic mitosis.

The approximately equal choice of the distal or proximal megaspore for functioning is unique among the Leguminosae.

The general and indefinite sterility is influenced by climate to different degrees in the stamens and legumes.

The symbols "ϕ" and "2ϕ" are adopted for the chromosome numbers of any species, "n" being reserved for the basic number of the genus. The number ϕ = 13 is confirmed, and counts are made of 2ϕ = 26. There are size differences in the chromosomes some of which may have trabants. The anaphase split in mitosis is clearly shown. The possibility that the species is a secondary polyploid is discussed.

The general conclusion will be reserved till the completion of the inquiry in a paper now almost ready for publication.

I would express my thanks to Professor T. G. B. Osborn for the facilities provided in this Department and for his interest in the work.

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Notes on the Illustrations.

All text-figures have been prepared from camea-lucida drawings. Of the figures on Plate vii, numbers 3 and 13-17*b'* are from camera-lucida drawings, the remainder being from photographs. All photography is the work of the writer except the enlarged print for figure 1 on the Plate (Mr. H. G. Gooch).

Annotations have been standardized throughout the Text-figures and the Plate-figures. A few special letterings are given in the legends and explanations. The following are the standard letterings:

a, archesporium; *ae*, appressed epidermes; *de*, multiple epidermis; *f*, filament (stamen), funiculus (ovule); *ii*, inner integument; *mb*, marginal bundles; *mc*, mother cell; *mr*, midrib; *oi*, outer integument; *p*, parietal tissue or layer(s); *pp*, primary parietal cell; *ps*, primary sporogenous cell; *s*, sporogenous cell(s); *SP*, functional spore; *sp*, non-functional spore; *t*, tapetum.

All magnifications were obtained by measurement.

EXPLANATION OF PLATE VII.

1.—Raceme at anthesis, showing proterogyny and exsertion of the styles. About natural size.

2.—Tip of a style with two pollinia projecting from the shallow stigmatic cup. × 380 (approx.).

3.—Tip of style with germinating pollinium and tubes from a second pollinium. Note shallow cup of stigma, and the thick cuticle (*ct.*) not in the cup. × 380 (approx.).

4.—Transverse section of a young pod between the seeds. The thickening on the collenchyma is not yet laid down. The midrib (lower end of figure) is beginning to be divided by parenchyma. *pce,* secondary parenchyma along epidermal line at the marginal side; *pcm,* secondary parenchyma dividing the midrib; *cc,* collenchyma cells; *l.* edge of loculus. × 410.

5 and 6.—Transverse sections of marginal and midrib edges of a full size pod. Collenchyma fully formed. Lettering as in Fig. 4. × 410.

7.—Longitudinal section of a young legume showing sterility in ovules about stage of formation of megaspores. × 158.

8.—Oblique transverse section of a young legume showing sterility in ovules that had attained nearly full size. × 150.

9.—Transverse section of a young legume before appearance of ovule primordia. × 220.

10.—Transverse section of a young legume showing the ovule primordia (*ov*) arising in the hypodermal layer. A and B, possible positions of the margins of the legume. × 220.

11 and 12.—Longitudinal sections of the marginal (adaxial) and midrib (abaxial) sides of a young legume showing the presence and absence respectively of appressed epidermes. About the age of the legume shown in Figure 9. × 220.

13.—Longitudinal section of a nucellus just before fertilization, showing starch (refringent) in the nucellar cells, and the multiple epidermis. × 540.

14.—Oblique longitudinal section of a young ovule with the nucleus of the functional spore (distal) in prophase. × 440.

15.—Anaphase of the homotypic division in the ovule. The distal spindle is horizontal, an exceptional case. In the distal cell only one group of chromosomes is shown in polar view with the anaphase split visible. × 2130.

16*a, b.*—Prophase nuclei of the two-nucleate stage of an embryo sac, showing 13 chromosomes each. The split and trabants are visible in some cases. Note the difference in the size of the chromosomes. Starch grains are in the cytoplasm. × 1060.

17*a, b, b'*.—Telophase nuclei of the third division in an embryo sac. Split and trabants visible in some chromosomes. 17*a* is the distal end in which the two darker nuclei are incomplete, three and one chromosomes belonging to the right and left nuclei being on the next section. Otherwise there are 13 chromosomes in each of the eight nuclei. Note the incipient wall formation between the left hand pair of nuclei in both groups. *b'* is the fourth nucleus from 17*b*. Starch grains present. × 2030.

AUSTRALIAN AND NEW GUINEA COLEOPTERA.

NOTES AND NEW SPECIES. NO. III.

By H. J. Carter, B.A., F.R.E.S.

(Five Text-figures.)

[Read 29th August, 1934.]

Fam. Buprestidae.

Diadoxus erythrurus White, var. septentrionalis, new var. (or sp.).

Mr. F. E. Wilson has sent, for diagnosis, two examples (♀) of a *Diadoxus* from North Queensland that varies from the typical form as follows: Orange-red markings at the latero-basal area of pronotum in place of the usual testaceous maculae, the post medial pair of subfasciate maculae tinged on the outside with orange-red. The green markings at the base of elytra are continuous to the sides, and the dark area on the apical half is much greater, the testaceous subfasciae being considerably wider apart. The ventral segments are a darker brown than in 10 examples of *D. erythrurus* now before me. I can find no structural or sculpture distinction. There are faint signs of the red elytral markings on some examples of *erythrurus*. Type returned to Mr. Wilson.

Note.—Under the description of *D. jungi* Blackb. the author states that "in *erythrurus* the apical ventral segment is trispinose in both sexes". This is not so. In all undoubted ♂ examples before me the apical segment is truncate, the external corners are more or less dentate, not spinose.

Melobasis radiola, n. sp.

Elongate-oval. Head golden and glabrous, prothorax golden copper with wide green vitta on each side of middle. Scutellum and the suture for short distance behind it golden. Elytra peacock-green, darker on sides and apex, with curved, pale golden vitta radiating from the shoulder, narrowing and obsolescent on apical third, following line of subsutural carina. Underside and femora metallic gold, glabrous, antennae, tibiae and tarsi blue.

Head densely minutely punctate, eyes a little prominent. *Prothorax* at apex slightly narrower than head, apex and base lightly bisinuate; widest at base, sides nearly straight, very lightly, arcuately narrowed to apex, medial line indicated near base, disc very finely and densely punctate, punctures slightly larger and less dense at sides, with very fine transverse strioles on postmedial area. *Scutellum* transversely ovate, very minutely punctate and longitudinally bisected by fine sulcus. *Elytra* subparallel to apical third, thence narrowed and separately rounded at apex, margins of apical third clearly denticulate; finely striate-punctate, intervals densely set with smaller punctures than those in striae, a defined subsutural depression limited by a lightly defined costa. Underside closely punctate, the punctures on metasternum coarser than those on prosternum,

those on abdomen fine and subelongate, except on apical segments, here round and larger. Apex of abdomen with subcircular excision, limited by strong spines. *Dim.*, 10 × 4 mm.

Hab.—South Queensland: Fletcher (E. Sutton).

A single example, probably ♀, can only be confused with *M. iridicolor mihi.* Mr. Wilson has compared it with the type of *iridicolor* in the National Museum and finds abundant distinctions as follows:

iridicolor	*radiola*
Form narrower	more robust
Head pubescent	glabrous
Pronotum with smooth medial line	medial line indistinct except near base
Scutellum minute and longitudinal	much larger and transverse
Elytra clearly seriate-punctate	seriate punctures scarcely distinct from interstitial

Colour differences as stated in descriptions. Holotype in Coll. Wilson.

Stigmodera (Castiarina) broomensis, n. sp. Text-fig. 1.

Oblong-ovate; head, prothorax, scutellum, underside and legs peacock blue, prothorax with wide orange border, the elytra orange-yellow, with the following markings dark blue: a triangular patch surrounding the scutellum, and produced along the suture, terminating at basal third in an enlarged oval, a nearly straight postmedial fascia widened at suture, not extending to sides, an apical patch narrowly connected along suture with the fascia.

Head deeply excavate and channelled; punctate. *Prothorax* widest considerably behind middle, thence abruptly narrowed to base and gradually to the apex, a well marked basal fovea connected with a clearly cut medial line on basal third, surface rather irregularly punctured. *Elytra* perceptibly enlarged at shoulders, feebly so behind middle, apices lunate and bispinose, subapical margins strongly denticulate; striate-punctate, strial punctures well marked, intervals convex throughout, strongly so towards apex, and themselves closely punctate. Underside very lightly pubescent and punctate. *Dim.*, 10–11 × 4 mm.

Hab.—Western Australia: Broome (H. W. Brown).

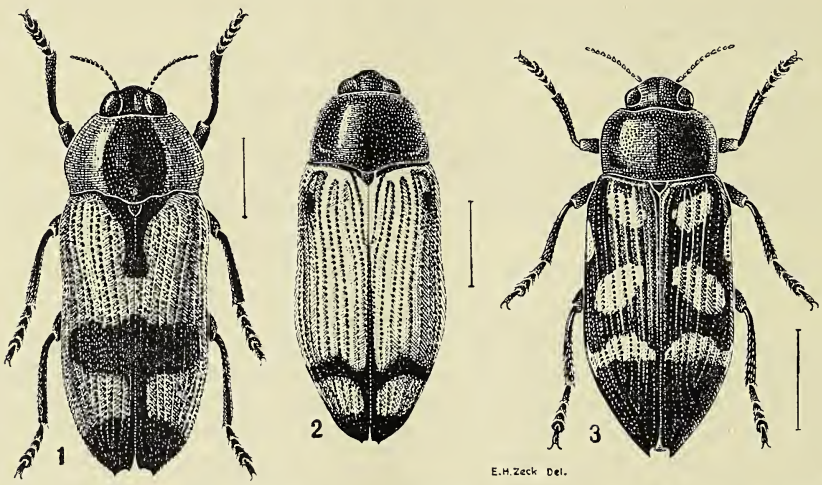
A species first diagnosed as a variety of *S. gibbicollis* Saund., but further comparison with a series of the latter shows the following, apparently constant, differences: (1) More cylindric form, (2) wider lateral band to prothorax (the light and dark colours forming three vittae of subequal width), (3) narrow scutellary mark instead of a wide basal band, (4) short and narrow postmedial fascia (leaving at least two clear intervals at sides), (5) different elytral sculpture, apical teeth more developed. (In *gibbicollis* intervals flat, except at apex.) Holotype in Coll. Carter.

Stigmodera (Castiarina) eborica, n. sp. Text-fig. 2.

Oblong-ovate; head, prothorax, underside, appendages and elytral markings green, the first three tending to golden, the last two to olive. Elytra testaceous, with wide basal border, shoulder mark (extending from base to behind shoulder) narrow, zig-zag, preapical fascia extending to, and widened at, sides and suture, narrow, straight apical mark, scutellar region and suture itself narrowly, dark green.

Head excavate and channelled, finely, densely punctate. *Prothorax*: apex and base bisinuate, anterior angles acute, posterior rectangular, widest at middle,

sides lightly arcuate, disc closely and finely punctate, medial line defined throughout, with a terminal fovea behind and a foveate depression near each hind angle. *Elytra* subparallel, very lightly enlarged at shoulder, little compressed behind them, apices with a moderately wide lunation, the sutural angle scarcely defined:



Text-fig. 1.—*Stigmodera* (*Castiarina*) *broomensis*, n. sp. Text-fig. 2.—*Stigmodera* (*Castiarina*) *eborica*, n. sp. Text-fig. 3.—*Stigmodera* (*Castiarina*) *insculpta*, n. sp.

margins entire, striate-punctate, the seriate punctures distinct, intervals laevigate, alternate intervals clearly raised and convex. Underside glabrous, finely and closely punctate. *Dim.*, 11–11·5 × 4–4·2 mm.

Hab.—N. S. Wales: Ebor (F. E. Wilson).

Mr. Wilson captured two examples in December, 1933. It is clearly distinct from, though, in colour, near *S. domina* Cart., from which it differs markedly in its smaller size, narrower and more parallel form, and the subcostate and laevigate alternate intervals of elytra. Holotype in Coll. Wilson.

Note.—Mr. C. F. Deuquet writes that he has taken several of this species at Ebor and considers it a variety of *S. rotundata* Saund. But the following differences are apparent, besides the distinctions of colour and pattern: *Pronotum*: Discal punctures larger and more widely separated. The base less strongly bisinuate. *Scutellum* larger.

Stigmodera (Castiarina) laevinotata, n. sp.

Elongate-oblong; head, prothorax, antennae and scutellum bronzy-black, elytra red with the suture (wholly or in part) and extreme apex black, underside blue-black, legs blue.

Head deeply excavate and channelled, lightly punctate. *Prothorax*: apex lightly arcuate, anterior angles produced and deflected, base bisinuate, posterior angles subacute, widest at base, sides converging to front with very slight curvature; surface strongly and rather closely rugose-punctate with a wide medial line and a transverse line a little in front of middle forming a raised laevigate cross. *Elytra* forming an obtuse angle at junction with prothorax, subparallel for the greater part, apices with shallow bidentation, a little divergent

near apex, margins everywhere entire, striate-punctate, alternate intervals costate, seriate punctures large, costae sublaevigate. *Prosternum* finely and sparsely, *metasternum* more coarsely, punctate. *Dim.*, 15 × 4·7 mm.

Hab.—N. S. Wales: Bogan River (J. Armstrong).

Three examples (2 ♂, 1 ♀) have lately been sent by this keen young entomologist, the two males taken on Wilga (*Geijera parviflora*) flowers, the female on Eucalyptus flower. It is an ally of *S. impressicollis* Macl. and *S. latipes* Cart. in the elongate form, red and costate elytra, but has not the uneven deeply impressed pronotum of these species, the disc being nearly flat except for the punctures and the embossed laevigate cross, which easily distinguish the species in Sect. A of my tabulation of 1931 (*Austr. Zool.*). There are some colour differences also in the three species mentioned, the suture being more or less black (wholly so in one example), as also the extreme tip of apices. The figure of *latipes* (These Proc., 1924, p. 22, f. 3) would almost serve for this, save for the pronotal impressions, the wide tibiae and the absence of dark suture. Holotype in Coll. Carter.

Stigmodera pratensis, n. sp.

Oblong-oval, rather flat; head, prothorax, underside, legs and ground colour of elytra metallic green, the mouth and disc of pronotum golden-green, underside dark green, somewhat obscured—especially on prosternum—by dense silvery pubescence; elytra dark clear green with yellow markings as follows: a round spot near middle of each elytron, a short, narrow, undulate, transverse line on apical fourth, extending neither to suture nor sides, and a minute spot on side at the posthumeral swelling, extending over epipleura (on the right-hand elytron this spot only on the epipleura).

Head with shallow excavation and channel, closely and finely punctate. *Prothorax* widest slightly behind middle, apex lightly bisinuate, little advanced in middle, base also feebly bisinuate, all angles obtuse, sides nearly straight behind, arcuately narrowed to apex; disc rather flat, subexplanate towards sides, medial line indicated by shallow, irregular depression, only clearly defined near base; latero-basal foveae unusually large; surface closely, not densely punctate, the punctures larger at sides and base. *Scutellum* triangular, longitudinally depressed and channelled. *Elytra* as wide as prothorax at base, widened at shoulder, sides nearly straight, entire throughout, apices with wide, shallow bidenticulation; striate-punctate, intervals impunctate and rather sharply carinate except in the region of the medial yellow spot, the two lateral carinae subcrenulate; underside densely pubescent. *Dim.*, 19 × 7 mm.

Hab.—Tasmania: National Park (D. McBurney).

A unique example, probably female, in the Australian Museum, taken in February, 1933, is the only one I have seen, and is a notable addition to the Tasmanian Buprestidae. It seems clearly distinguished from its nearest ally, *S. virginea* Erichs., by the following tabulation (under *S. insculpta*), besides different elytral markings.

Holotype, K.66904, in the Australian Museum.

Stigmodera (Castiarina) insculpta, n. sp. Text-fig. 3.

Elongate-ovate; head, prothorax, underside and legs bright metallic green, elytra green, with the following markings yellow; two oval, postbasal spots, two latero-subhumeral spots, two oval medial spots and an arcuate postmedial fascia,

interrupted at suture and slightly extended at margins; glabrous above and below (traces of pubescence only at sides of prosternum).

Head canaliculate and lightly excavate between eyes, finely, closely punctate. *Prothorax* sub-convex, apex rather strongly bisinuate, and produced in middle, anterior angles depressed and wide, base nearly straight, excisions scarcely evident, hind angles subrectangular, widest a little in front of middle, sides arcuately (but little) narrowed to apex, almost straight to the base; a little explanate laterally, with rather large, deep depressions near hind angles; disc finely, evenly punctate, medial sulcus well defined near apex and on basal half, with smooth line terminating in a small basal fovea. *Scutellum* small, triangular, laevigate. *Elytra* obliquely widening to shoulder, lightly compressed behind it, apices with wide oval lunation bounded by strong external and short internal spines, margins entire; striate-punctate, strial punctures regular and well defined, intervals sharply carinate, the first four close and uniform, 5th and 6th more strongly raised and wider apart, between these an almost obsolete interval arising behind middle, the wider interstices irregularly punctate, elsewhere the intervals laevigate. *Pro-* and *metasternum* rather strongly and evenly punctate, abdomen very finely so. *Dim.*, 12 × 4½ mm.

Hab.—Tasmania: Great Lake district (Critchley Parker).

Another unique having for its nearest ally *S. virginea* Erich., but clearly separated by (1) the six sharper raised intervals (in *virginea* only four, and these less prominent), (2) the wider and more strongly punctate prothorax, (3) the wider and bispinose apical lunation. Holotype in British Museum.

N.B.—In These Proceedings, 1919, pp. 137–139, I enumerated the fourteen species of this genus known from Tasmania and tabulated the five species with metallic green coloration, likely to be confused. The present paper adds three to the total, of which two belong to this group. The three having carinate intervals may be separated as follows:

1. Elytra with alternate intervals raised ..... *virginea* Erich.
   Elytra with all intervals carinate 2
2. Size large, 19 × 7 mm., underside pubescent ..... *pratensis*, n. sp.
   Size small, 12 × 4½ mm., underside glabrous ..... *insculpta*, n. sp.

Stigmodera (Castiarina) rudis, n. sp.

Oblong-obovate; head, pronotum, abdomen, legs and scutellum dark blue—the pronotum almost black—prosternum with subtriangular basal area violaceous, its remaining part red; elytra brick-red, having basal margin, suture near scutellum, and each with two narrow elongate spots black, these placed en echelon behind the shoulder, the first, rather undefined, on inside of 3rd costa, the 2nd behind this, between 3rd and 4th costae.

Head rather flat, canaliculate but not excavate in middle, closely and rather coarsely punctate, with sparse, upright, silvery hair. *Prothorax*: apex arcuate, anterior angles acute and produced, base feebly bisinuate, the usual excisions minute, hind angles rectangular, widest near middle, sides thence nearly straight (feebly sinuate) to base, arcuately narrowed to apex; disc lightly convex, depressed and explanate laterally, an ill-defined but distinct medial sulcus traceable throughout; surface densely and coarsely punctate, subrugose at sides and base, the punctures forming sharply crenulate margins; sparse, long, upright hairs over greater part of surface. *Scutellum* transverse, longitudinally depressed in middle, laevigate. *Elytra* slightly widened at shoulders, widest behind middle,

a little divagate at apex, with oblique lunation each terminating in a single tooth, apical margins entire, each with four strong, smooth costae, besides a narrower, short scutellary costa, continuous with lightly raised suture; intercostal spaces with three rows of large, somewhat irregular punctures (sometimes coalescing), surface glabrous. *Prosternum* and *metasternum* with moderately large, close punctures, abdomen sublaevigate, glabrous and nitid. *Dim.*, 18 × 7½ mm.

Hab.—Tasmania: Great Lake (Critchley Parker).

A single female example, sent from the British Museum, has the following attached note by its captor: "This beetle provides a lot of food for the trout. It flies about at dusk and alights on the water. Taken Great Lake, Jan., 1934." It is strikingly distinct by colour, clothing and sculpture from any recorded species, though nearest in form to *S. decipiens* Westw. The latter, however, has only three elytral costae, besides the scutellar, while the intercostal area is without the large punctures of *rudis*. The long hair on head and pronotum, with glabrous underside, and the bicoloured prosternum are peculiar features. The faint indications of black along suture suggest that other examples may have this to a more marked extent. It adds another interesting species to the Coleoptera of Tasmania. Holotype in British Museum.

Stigmodera (Castiarina) erythroptera Boisd. subsp. nigroterminata (? n. sp.).

Differs from the widely distributed *erythroptera* by (1) the apex narrowly covered with black marking, instead of the usual short preapical fascia; (2) narrower form, especially of the prothorax, this very lightly rounded; (3) elytral costae less raised; and (4) underside much less strongly punctate.

I have been in doubt as to considering this a distinct species. It is, at least, a good example of a constant geographical variety, i.e., subspecies. Fourteen examples are before me, of which eleven are from the Bogan River, taken by Mr. J. Armstrong, on *Geijera parviflora*, the other three taken by myself in the Coonabarabran district, N.S.W., on *Leptospermum*. Type in Coll. Carter.

Stigmodera (Themognatha) pictipes Blkb.—Mr. Clark has recently sent me, for examination, examples of this, including one labelled type, besides a variety with blue elytra. This type shows the following discrepancies from the author's description: (1) dimensions in description are "Long. 14 l., lat. 5½ l." (31 × 12 mm. as measured by Blair); dimensions of National Mus. type, 35 × 15 mm.; (2) type as described is "Mas", whereas the Melbourne type is ♀.

In Mr. Lea's useful paper on the Blackburn types, that of *S. pictipes* is said to be in the British Museum. This is possibly the male said to have been presented to him (Blackburn), the female being returned to Mr. French. The variety with blue elytra is another case of the variation noted in my Revision of the genus (*Trans. Roy. Soc. S. Aust.*, 1916, p. 81, also Proc. Linn. Soc. N.S.W., 1932, p. 104). I propose the name *pictipes* var. *pavo* for this.

S. spencei L. and G.—A ♂ in the National Museum, from Rockhampton, Q., has the pronotum a golden bronze, the elytra without the usual premedial dark fascia, but is, I am confident, conspecific with a wider ♀ from Condamine, Q., and those with the typical darker pronotum from northern N.S.W. (Trial Bay and Wardell). The sexual coloration noted above is found in many other species, e.g., *duboulayi*, *conspicillata*, *imperialis*, *vitticollis* and others.

TORRESITA CUPRIFERA Kirby var. LIMBATA, n. var.

An example from Forest Reefs, N.S.W., in the National Museum shows striking differences of colour and size from the other named varieties, though without distinction of form or sculpture. The head, prothorax and a wide lateral band around the elytra are a fiery copper, the medial area of elytra, underside and legs are blue. *Dim.*, 17 × 7 mm. Unique, in the National Museum, Melbourne.

Cisseis prasina Cart.—Mr. Armstrong has sent this, taken in fair quantity, associated with *C. marmorata* L. and G., on the Myall acacia in the Bogan River district. All the examples of *prasina* are male, while all the *marmorata* are female. I find this to be the case in a long series of the latter, so have little doubt that *prasina* Cart. is the ♂ and *marmorata* L. and G. the ♀ of the same species. This provides an extension of a common sexual coloration in the genus.

CISSEIS AUROCYANEA, n. sp.

Oval; head, prothorax and underside coppery-bronze, elytra golden, with post-scutellary lozenge, the suture widely, postmedial fascia and apex cyaneous, the last fiery coppery at sides; appendages dark bronze.

Head convex (seen from above), a small depression near clypeus, finely punctate. *Prothorax*: apex lightly, base strongly bisinuate, sides lightly, arcuately narrowed to apex, widest about middle, posterior angles subrectangular, lateral carinae rather widely separated and subparallel for the greater part, meeting at base; disc finely strigulose, with slight depression on each side near base. *Scutellum* transversely ovate. *Elytra* (5 × 3 mm.) lightly convex, sides sinuate, widest a little behind middle, lightly compressed behind shoulders, apical margins very minutely serrulate, surface finely scalose-punctate. *Underside* finely strigulose, front margin of prosternum bisinuate, hind tibiae fringed with a single row of fine bristles (not in fascicles). *Dim.*, 7 × 3 mm.

Hab.—South Queensland: Fletcher (E. Sutton).

A single example sent by this keen collector is unlike any recorded *Cisseis* in pattern, which is somewhat as in *Neospades lateralis* Blkb., but without the white maculae and with larger postscutellar lozenge; the form and sculpture are widely different from that species. The figure of *C. pulchella* (These PROC., 1923, p. 169) comes near it in shape. Holotype in Coll. Carter.

CISSEIS BROWNI, n. sp.

Oblong-ovate, violet bronze above and below; head and parts of underside coppery; pubescent with defined white maculae and scattered fascicles above, rather close silvery pubescence beneath.

Head lightly canaliculate, closely punctate. *Prothorax*: apex and base strongly bisinuate, sides nearly straight, narrow lateral vitta of pubescence at sides, two large foveate depressions near middle, more or less filled with pubescence; disc punctate on apical half, transversely strigose on basal half. *Elytra* with maculae and fascicles as below. Tibiae narrow and straight, hind tibiae without marginal spinules.

Hab.—Western Australia: Dedari (H. W. Brown).

Three examples sent by the above indefatigable naturalist are clearly differentiated from its nearest ally *C. duodecimmaculata* F. by the following detailed comparison.

duodecimmaculata F.	*browni*, n. sp.
Form ovate obliquely attenuate towards apex.	elongate, subparallel, gradually narrowed behind.
Colour blue, often coppery on head and raised parts of underside.	violet copper, head and pronotum coppery, elytra tending to cyaneous at sides and apex, underside fiery coppery.
Head subglabrous, clearly channelled.	closely pubescent, lightly channelled.
Prothorax: form wider, sides rounded, pubescence limited to lateral vitta, this wide and widening to base, discal foveae vague.	narrower and longer, sides nearly straight; pubescence besides forming narrow lateral vitta also in two wide lines extending obliquely from near basal excisions towards middle, terminating in two foveate depressions, half-way between sides and centre.
Elytra: pubescence limited to 14 spots, more or less round and clearly defined, 12 discal, 2 posthumeral (the 2 subapical spots more oval than the rest).	pubescence on 12 defined spots; of these 8 more or less round, the 2 posthumeral spots replaced by small lateral fascicles throughout the length, with similar fascicles scattered over greater part of elytra (2 subapical spots vaguely linear).
Hind tibiae curved and thickened, with 4 or 5 bunches of spinules on exterior margin.	straight and narrow, without spinules.
Underside subglabrous, very short pubescence scarcely perceptible, except for defined spots at sides of ventral segments, a spot on edge of prosternum and a large spot on metasternal margin extending to hind coxae.	silvery pubescent over whole, large spots on sides of ventral segments, and one on side of metasternum not extending to hind coxae.
Dim., 7-11 × 3-5 mm.	9-10 × 3 mm.
Examples from Q'land, N.S.W., Victoria and Western Australia.	Dedari, W.A.
Holotype in Coll. Carter.	

N.B.—Hope's name *quatuordecimmaculata* is more appropriate than that of the earlier name by Fabricius.

Cisseis heroni, n. sp.

Blue-black, with coppery gleams on head, shoulders, suture and apex, lightly concave between eyes, pubescent on epistoma, minutely striolate on forehead.

Prothorax: base bisinuate, sides from above almost straightly converging from near base to apex, with hind angle widely rounded off; lateral carinae evenly arcuate for the greater part, widely diverging from junction at base, bent upward near apex: disc with saddle-like convexity, causing a medial production at apex, minutely transversely strigose. *Elytra* widened at shoulders, convex behind scutellum, apices finely denticulate, with fine pale pubescence more or less arranged in close transverse lines, a wide arcuate, subfasciate, preapical patch more noticeable than the rest. *Dim.*, 5–8 × 2·5–3·5 mm.

Hab.—N. S. Wales: Dorrigo (W. Heron).

Seven examples were sent some time ago by Mr. Heron, who has collected this district so thoroughly. It is nearest *C. pygmaeus* Blkb. in colour and size. The following comparison will distinguish them:

pygmaeus Blkb.	*heroni*, n. sp.
Dim., 4-5 mm. long.	5-8 mm. long.
Head rather strongly concave.	lightly so.
Prothorax: sides (seen from above) well rounded, lateral carinae constricted near middle.	converging obliquely to apex, bent upward near apex.

pygmaeus Blkb.	*heroni*, n. sp.
Elytra: pubescence irregular, with 2 parallel, preapical fasciae.	more or less in transverse lines, with one wide fasciate patch.

Holotype and Allotype in Coll. Carter.

Cisseis myallae, n. sp.

Narrowly ovate, attenuate behind; bronze, with minute adpressed pubescence on base, wide medial and preapical areas of elytra, with coppery gleams on head and some tendency to cyaneous colour on elytra.

Head closely punctate, sulcate in middle. *Prothorax* gradually narrowing from base to apex, base strongly sinuate, lateral carinae sinuate, intercarinal area widest near base, then rather abruptly narrowed; disc subglabrous, sparse short hair scarcely evident, covered with the usual undulate striolae. *Elytra* of same width as prothorax at base, very lightly compressed behind shoulders, attenuate at apex, apical margins minutely denticulate. Underside nitid coppery, evenly clothed with fine short hairs. *Dim.*, 4·6 × 1·5 mm.

Hab.—N. S. Wales: Bogan River (J. Armstrong).

The fine veil of pubescence is characteristic. The preapical fascia is widened at suture into an oval patch produced backwards. Five examples sent by my friend are in size and form somewhat near *C. subbifascialis* Cart., but differ in colour and in the absence of the long white pubescence of that species, as well as in the form of the lateral carinae, its smaller size and less parallel outline. Mr. Armstrong writes that *C. bifascialis* occurs on the River Wilga (*Acacia stenophylla*), while the above species frequents the Myall (*Acacia pendula*). Holotype in Coll. Carter.

Cisseis nitidiventris, n. sp.

Elongate-ovate; nitid coppery bronze above and below, with silvery pubescence at sides of prothorax, sparse on elytra, beneath only at lateral margins of pro- and metasternum and of ventral segments. Without sexual coloration.

Head glabrous and finely punctate, sulcate but scarcely concave in middle. *Prothorax*: apex lightly, base strongly, bisinuate, sides subparallel on basal half, thence lightly, arcuately narrowed to apex, the lateral carinae subparallel, closer together than in *C. acuducta* Kirby, disc very nitid and glabrous, with fine transverse striolae. *Elytra* enlarged at shoulders, compressed behind them, lightly attenuate to apex, apical margins finely denticulate, disc coppery, with atroviolaceous shading and scattered pubescence on basal two-thirds, on apical third forming a straight, rather wide fascia continuous to sides, a second short fascia close to apex not extending to sides. Underside very nitid coppery, pubescence limited to margins; prosternum with large, not close, punctures, metasternum almost impunctate, abdomen closely and finely punctate. *Dim.*, 7–8 × 3 mm.

Hab.—N. S. Wales: Gosford (N. MacGregor).

Ten examples were in the collection of Mr. W. Duboulay, of which he has kindly given me four. It is clearly separated from *C. acuducta* Kirby and *C. cupripennis* Guér., with which it is most nearly allied: from *acuducta* by the glabrous and nitid underside (everywhere clad with short pubescence in *acuducta*) besides its flatter elytra and more parallel form; *cupripennis* has the head and prothorax of ♂ green, with more cylindric form and more strongly punctured surface. Holotype in Coll. Carter.

ETHON ROEI L. & G. var. OBSCURUM, n. var.

I have been puzzled by three examples of an *Ethon* taken by Miss M. Duboulay at Albany, W.A. These differ from normal forms of *roei*, but I do not feel justified in describing them as specifically distinct without seeing a longer series. The following comparison shows the main differences:

E. roei.	var. *obscurum.*
Head and prothorax bright coppery, little obscured by hair.	Darker bronze, obscured by long hairy pubescence.
Elytra violet-bronze, pubescence sparse with tendency to concentration in a preapical fascia.	Brown-bronze, pubescence more marked.
Sculpture fine, with linear punctures and carinulae.	Showing a tendency to striation.

The lateral carinae of prothorax and the clothing of the underside are similar to those of typical *roei*. *Dim.*, 11 × 4·5 mm. Type in Coll. Carter.

Family DRYOPIDAE.

Simsonia purpurea Cart. = *S. deanei* Cart. and Zeck.—The acquisition of further material from Tambourine Mountain, Q'land, shows the latter species to be too close to the former for specific distinction and the name must be sunk as a synonym.

Onthophagus carteri Blkb.—An interesting fact of distribution is in my possession in an example of this Sydney species being given me from Nauru (Ocean) Island.

Family TENEBRIONIDAE.

ORCOPAGIA ANGUSTATA, n. sp.

Narrowly subcylindric; opaque reddish-brown.

Head convex with raised margins, a vertical horn on clypeus, this rounded at its apex, a round tubercle at inside of each eye, antennae with two apical segments forming a club. *Prothorax* having the discal region strongly raised, divided throughout by deep medial channel and produced over the head with a forked apex, as in certain Poropterus weevils, the margins of this discal region irregularly raised by successive rounded tubercles, forming an elongate ellipse with anterior and posterior extensions, the extreme margins on a much lower plane forming a somewhat S-shaped curve, wide on the anterior half, with about four irregular crenulations, the concave posterior half with a single tubercle at margin; hind angles subrectangular. *Elytra* wider than prothorax at base, the surface irregularly covered with elongate tubercles, culminating in larger rounded knobs at apical declivity, lineate punctures visible in places, margins unseen from above, the visible outline showing small tubercles, the apex rather sharply serrated. Under-surface concealed by squamose derm. Front tibiae strongly widened, hooked at apex beneath, mid-tibiae slightly widened, all tibiae crenulated on outside by small tubercles. *Dim.*, 8–12 × 2·8–4 mm.

Hab.—New Britain: Rabaul (F. H. Taylor).

♀. Without clypeal horn.

Several examples taken by my friend, of which seven are before me, the larger examples being females. A specimen sent to Herr Gebien was diagnosed as clearly distinct from *O. sepidioides* Geb. by (1) narrower form, (2) sides of head not bidentate before the eyes, (3) front tibiae hooked.

N.B.—The sexual distinction (clypeal horn in ♂) will probably be found

also in *sepidioides* with the examination of more material. Holotype and Allotype in Coll. Carter.

PTEROHELAEUS CELLULOSUS, n. sp.

Oblong-ovate; nitid black, antennae and tarsi piceous.

Head sparsely punctate, antennae unusually slender, except for the enlarged four apical segments, of these 8 is subtriangular, 9–11 round. *Prothorax*: apex deeply arcuate, front angles produced and rather sharply rounded, base lightly bisinuate, posterior angles acute and sub-falcate, foliate margins thin and subtransparent, rather strongly concave and recurved, disc with close, moderately strong punctures (more strongly punctate than in *P. vicarius* Pasc.), medial line finely impressed, two basal foveae. *Elytra* parallel for the greater part, horizontal margins rather narrow but of uniform width throughout, striate-punctate, the punctures large and close, the striae also close, intervals narrow and slightly raised in places, a row of large punctures at junction with margins. Underside finely and densely strigose. *Dim.*, 14 × 6 mm.

Hab.—W. A.: Kalgoorlie (From Mr. W. Duboulay).

A single example given to me by Mr. Duboulay is nearest in sculpture to *P. persculptus* Cart., *punctipennis* Macl. and *vicarius* Pasc. The first of these is larger (17 × 8 mm.) with a differently shaped prothorax, the "extreme border moderately thick and reflexed", the same being exceptionally thin and wafery in *cellulosus*. *P. punctipennis* Macl. is a small species from North Queensland, of more convex form with narrower foliation. *P. vicarius* is also more convex and ovate, the elytral sculpture is more irregular and less uniform. Holotype in Coll. Carter.

N.B.—An example of *P. persculptus* is in the collection of Mr. F. E. Wilson, taken at You-yang, Victoria. The type had no locality label.

ONOSTERRHUS COSTATUS, n. sp.

Convex, ovate; nitid black, antennae opaque black.

Head: labrum prominent, clypeus straight in front, rounded at sides, forming an angle with the wide, flat antennal orbits, antennal segment 3 as long as 4–5 combined, 4–8 successively shorter and wider, 8–10 transversely ovate, 11 ovate, forehead uneven with three depressions bordered by longitudinal ridges, the exterior of these, near eye, costate, the middle two wide. *Prothorax* (7 × 12 mm.) widest at middle, apex arcuate-emarginate, anterior angles widely rounded and directed downwards, base bisinuate, posterior angles subacute and overlapping elytra, sides widely rounded, nowhere sinuate, extreme border very thick, little raised above but seen sideways widely rounded, margins widely foliate and concave; disc scarcely perceptibly punctate with clearly impressed medial sulcus terminated near base by short transverse sulcus. *Elytra* (18 × 14·2 mm.) lightly obovate, wider than prothorax at base, shoulders rounded, a narrow horizontal border with a line of punctures within it; each with four defined, smooth costae, besides the suture itself, more narrowly but sharply raised throughout and limiting the postscutellary triangular depression, the fourth costa near margins less raised than the others, intervals impunctate, vaguely uneven, with the suggestion of longitudinal convexity midway between costae. Underside glabrous with a few ventral strigae. Hind tibiae with a line of tomentum on inside, mid tibiae rather strongly curved, mid and hind tibiae enlarged at apex,

with very short spines. Submentum with a triangular tooth directed forwards, prosternal process sulcate. *Dim.*, 26 × 14 mm.

Hab.—Queensland (in the British Museum of Natural History).

A single example, sent for inspection by Mr. Blair, is the largest species of the genus. It is easily distinguished by the combination of nitid, almost impunctate surface and its 4-costate elytra. Holotype in the British Museum.

ONOSTERRHUS ROBERTUS, n. sp.

Convex, widely ovate; subopaque black above, more nitid beneath, antennae piceous.

Head: labrum prominent, clypeus straight in front, sinuate at sides, antennal orbits not much raised, surface very minutely punctulate, antennal segment 3 rather shorter than 4–5 combined, 4–7 subtriangular, 8–10 rounded, 11 oval. *Prothorax* (6 × 10 mm.) widest behind middle, apex arcuate-emarginate, with narrow border widening towards angles, these acute, base bisinuate, posterior angles produced, roundly blunted at tip, sides well rounded, subsinuate behind (in one example of three, feebly so behind front angles), extreme border round and thick, gradually narrowing to the front and widened at the hind angles, concave and sulcate within this border; disc microscopically punctulate, in one example a fine medial line shown on front half. *Scutellum* transversely triangular. *Elytra* (16 × 13 mm.) wider than prothorax at base, shoulders obliquely rounded, widest near middle, a narrow laminate border and a row of large punctures in the sulcus within this, each with three distinct and equidistant costae, the suture also raised for the greater part and bordering the triangular depression behind scutellum to form a feeble fourth costa; on each side of costae an irregular line of small punctures, especially evident near suture, the intervals also irregularly punctate and rugose. *Underside* glabrous, submentum with bluntly rounded but vertical tooth, ventral segments with a few longitudinal strigae, tibiae without tomentum save at extreme apex. *Dim.*, 21–23 × 13–14 mm.

Hab.—N. S. Wales: Coonabarabran and Mullaley district (J. Armstrong, Bob Anderson, and H. J. Carter).

Two complete examples and fragments of two others, one having the thorax, elytra and part of legs. I found an elytron near Coonabarabran in 1923; Mr. Armstrong found an uninjured example and fragments of another near Mullaley in November, 1933; a month later the 8-year-old son of Mr. Anderson, of Garrawilla Station (after whom I name it), found another example (the holotype). The species is nearest *O. sloanei* Blackb., from which it differs in its wider prothorax with much more strongly thickened border and more acute anterior angles, also the more clearly defined elytral costae. Holotype in Coll. Carter, paratype in Coll. Armstrong. One example was sent to the British Museum for comparison with the type of *sculpturatus* Blackb. Mr. Blair has kindly returned this with the note "Your *Onosterrhus* is certainly not *sculpturatus* Blackb., which is smaller and smoother, subnitid, with the costae scarcely indicated, etc.".

HYPAULAX UNDULATICOSTIS, n. sp.

Elongate-obovate; glabrous, dull black above, nitid black beneath, antennae (towards apex) and tarsi reddish.

Head: clypeus truncate in front, at sides making an angle with the antennal orbit, surface impunctate. *Prothorax* lightly arcuate at apex, anterior angles widely rounded off, base bisinuate, posterior angles dentate, obliquely pointing

outwards, widest near front, narrowed at base, sides with a few crenulations behind middle, abruptly, sinuately narrowed towards base, disc impunctate, with a finely impressed medial line and two small foveae on each side of this near middle, basal border wide, lateral border narrowing on front half. *Elytra* little wider than prothorax at base, widest behind middle, each with nine wide sulci containing close foveate punctures and limited by seven sharp zig-zag costae, the suture forming an extra, but straight costa, the 4–5 and the 6–7 rows of foveae being geminate, i.e., not separated by sharp costae. Prosternum bisulcate and carinate, ventral segments striolate at base, pro- and mid-tibiae bent inwards at apex. *Dim.*, 25–20 × 10–8·2 mm.

Hab.—South-western Queensland: Morven (F. Sullivan).

Two examples (♂, ♀) in Mr. W. Duboulay's collection, which he has generously given me for description, are strikingly distinct from its nearest ally, *H. spenceri* Cart., by the very different form of the prothorax (widest behind in *spenceri*), besides many evident details of sculpture as specified. Holotype in Coll. Carter.

Apasis distortipes, n. sp.

Oblong-ovate; head, prothorax and underside black, elytra and legs brownish-bronze, tibiae and tarsi clothed on inside with red tomentum, antennae and tarsi brown, the former largely opaque.

Head as in *Adelium*, but the eyes less transverse (rounded towards inside), antennae submoniliform, segment 3 only slightly longer than 4, 4–5 cupuliform, 6–10 increasingly widened and transversely oval, 11 as wide as and little longer than 10. *Prothorax* transverse and rather flat, apex arcuate-emarginate, front angles rounded, base subtruncate, hind angles well defined (about 110°), sides evenly rounded, widest at middle, with distinct sinuation near base, extreme border narrowly raised, shallow horizontal foliation separated by short, curved sulcus from disc, the latter uniformly and finely punctate, two shallow depressions near middle, without any sign of medial line. *Scutellum* widely triangular, finely punctate. *Elytra* slightly wider than prothorax at base and more than twice as long, subparallel for the greater part, shoulders rounded, apex rather widely so; striate (without sign of seriate punctures), intervals lightly convex, 3rd and 5th wider than the rest, minutely and indistinctly punctate. *Prosternum* transversely striolate, notched on the convex area, rest of underside sublaevigate, post-intercoxal process rounded. *Hind tibiae* widely angulate before the middle, widened and strongly incurved to apex, mid tibiae also sinuately widened but less strongly than the post. Hind tarsi short, with basal segment not quite as long as the rest combined. *Dim.*, 15 × 5½ mm.

Hab.—Victoria: Yarram, S. Gippsland (F. E. Wilson).

A single male example was found by Mr. Wilson in the small reserved area (Bulga Park) of what was formerly a densely forested region. It has some affinity with *Cardiothorax* in the lateral foliation of the prothorax and the tibial characters, but I think it more properly may be associated with *Apasis* through the more rounded eyes, the widely truncate base of prothorax, the form of antennae and tarsi. Holotype in Coll. Wilson.

Female latet.

Daedrosis rufipes, n. sp.

Oblong-ovate; subnitid, head and prothorax brownish-bronze, elytra and underside subcastaneous, antennae and legs red.

Head densely punctate, clypeus rounded in front, eyes large and prominent, antennae extending to basal third of prothorax, segment 1 slightly wider than 2, 2 shortly ovate, 3, 4, 5 subequal in length, 5 widening at apex, 6 subconic, 7–10 asymmetrical and increasingly transverse, the exterior half of segments more sharply produced, 11 globose, its diameter as wide as and twice as long as 10. *Prothorax*: apex and base bisinuate, median apical area convex and somewhat produced over head, anterior angles rounded off; widest in front of middle, sides with raised border, well rounded, sinuate behind, posterior angle obtuse (not widely so), disc densely and coarsely punctate, the punctures at apex and middle as on head, much coarser towards sides and hind angles. *Scutellum* triangular, nitid and impunctate. *Elytra* wider than prothorax at base, epipleural fold forming a wide tooth at shoulders; striate-punctate, striae well marked, a little irregular in definition, punctures elongate and ill-defined, 3rd interval containing minute pustules, intervals wide, lightly convex and transversely rugulose, the sutural interval wide and flat with transverse wrinkles. Sternal regions punctate, abdomen strongly strigulose. *Dim.*, 7 × 2·5 mm.

Hab.—Victoria: Lower Terwin (G. F. Hill).

A single specimen sent by Mr. Clark is very distinct from *D. crenatostriata* Bates by its smaller, flatter form and more strongly and densely punctate prothorax, red appendages and different antennae. Holotype in the National Museum.

LICINOMA PUTEOLATA, n. sp.

Elongate-ovate; nitid bronze-black, antennae and legs red.

Head coarsely, unevenly punctate, with a smooth, nitid, raised area behind each antennal orbit, antennae unusually stout, its segments lineate-ovate and setose, 3 only slightly longer than 4, 5–10 successively more widely ovate, 9–10 subspherical, 11 largest of all, piriform. *Prothorax*: apex subtruncate, lightly advanced at angles, these wide and rounded, base truncate; moderately convex, lateral margins deflexed, widest at middle, thence gently, evenly narrowed each way, hind angles obtuse; disc irregularly pitted with round, deep, setiferous punctures, besides having a closer, more regular system of smaller punctures, a row of setiferous punctures on each narrow, lateral margin. *Elytra*: shoulders obliquely rounded, striate-punctate, the strial punctures strongly crenulating the sides of the convex intervals, the lateral striae bearing larger, irregular, setiferous punctures, more sparsely found on other intervals. Hind tarsi having basal segment as long as apical, slightly longer than 2nd and 3rd combined. *Dim.*, ♂, 11 × 3·6 mm.; ♀, 13 × 4 mm.

Hab.—Queensland: Stanthorpe district, two taken by F. E. Wilson and E. Sutton, one previously sent by Mr. E. Sutton.

A strikingly distinct species. The sculpture of the pronotum is suggestive of certain *Seirotrana* species in having the dual system of punctures, while the setae springing from large punctures on the upper surface are unusual in the genus. Holotype in Coll. Carter, allotype in Coll. Wilson.

In 1930 I examined Macleay's types of *Amarygmus* from the Fly River when working out the large number of Tenebrionidae collected by Mr. McNamara and others for the South Australian Museum, but omitted to publish the following synonymy.

Amarygmus inornatus Macl. = *A. morio* F.—This adds another to the long list of names given to this much described species. The type was very dirty.

When cleaned the colour came out a clear bronze, though described as "black". See also my note (*Trans. Roy. Soc. S. Aust.*, 1913, p. 34) that Mr. Blair had a similar experience with the type of *A. morio* F. from the Banks Collection.

A. convexiusculus Macl.—Macleay used this name twice: (1) for a Gayndah species in 1871; (2) for a New Guinea species in 1887. In the Junk Catalogue, Gebien supplied a new name "niger" for (2). This name is unfortunate, since, again, when cleaned the type has a clear, rather dark bronze colour. The description gives "black", but Macleay notes "a slight purplish gloss on thorax". This is a common species in New Guinea that I have from Mt. Lamington, N.E. Papua and Bulolo.

Gonocephalum subcostatum Cart.—This is a *Cestrinus* and is synonymous with *C. carbo* Cart. The type is in the Queensland Museum and escaped my notice when describing *carbo*. It must therefore now be known as *Cestrinus subcostatus* Cart.

Menephilus colydioides Er. var. *armstrongi* Cart.—A comparison of the type of *armstrongi* with that of *parvulus* Macl. (= *colydioides* Er.) shows too close affinities of structure for specific distinction, and can only rank as a variety.

Family Cistelidae.

Nocar funereus, n. sp.

Widely ovate, convex; black, rather nitid, above and beneath, subglabrous, with inconspicuous pubescence on pronotum and sides of elytra.

Head finely punctate, eyes separated by a space of the diameter of one, antennae rather slender. *Prothorax* strongly narrowed to front, apex at middle slightly compressed and hood-like, base widely bisinuate, its angles acute. Disc with fine, shallow punctures and two small basal foveae. *Elytra* striate-punctate, the striae very fine, the strial punctures small and regular, intervals quite flat and very finely punctate; the two lateral striae more strongly impressed, giving a quasi-rounded aspect to the lateral intervals. Underside glabrous, almost impunctate. *Dim.*, 6 × 4 mm.

Hab.—South Queensland: Fletcher (E. Sutton).

Three examples have been sent by Mr. J. Armstrong, taken by Mr. Sutton. It is an exceptionally wide species, distinguished from other concolorous species by its black colour, this extending to antennae, legs and tarsi. (I described *N. rugosus* as black, but a longer series since acquired shows a brownish tint to prevail, with its appendages reddish). The sculpture of *N. funereus* is finer than that of any other. Holotype in Coll. Carter.

Family Cerambycidae.

Aridaeus princeps, n. sp.

♂. Black, sparsely pubescent; head, palpi, scutellum and two linear marks on each elytron red.

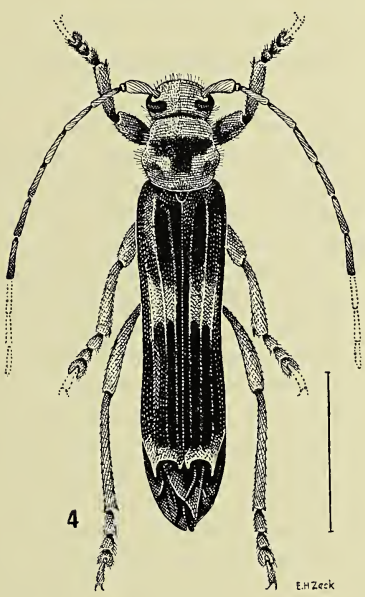
Head as in *A. heros* Pasc., antennae much stouter and longer than in that species and tapering to a very fine apex. 3–5 spinose, subequal in length, 6–11 unarmed, 6–10 equal in length, 11 longer than 10. *Prothorax* ovate, widest at middle, strongly constricted near base; disc velvety, with short medial costa behind the two basal protuberances, sparsely clad with upright white hairs. *Scutellum* triangular, pubescent. *Elytra* widest at shoulders, there rather squarely rounded, sides nearly straight for the greater part, apices widely truncate, the exterior angle subdentate. Black, except for a short curved mark behind the

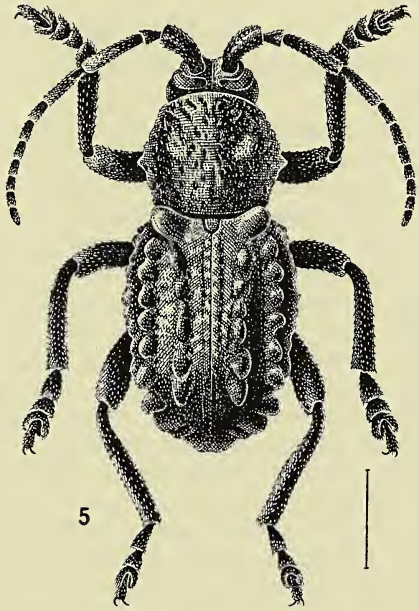
shoulders and a curved fascia extending backwards from the suture near middle, but not reaching sides; surface cellulose-punctate on basal two-thirds, the punctures more distant on yellow fascia, behind this the surface becoming asperate and finely pustulose. Legs very long, femora stout, hind tibiae with long spine at apex. *Dim.*, 21 × 6 mm.

Hab.—N. Queensland: Cooktown (C. Olive).

A single ♂ in my collection is larger than any example of *Aridaeus* that I have seen, with longer antennae (nearly twice as long as body), and distinguished by its finely tapering apex with its unusually long apical segment. Every part of the insect is a dull velvety-black, except for the red parts specified above. Holotype in Coll. Carter.

N.B.—*A. heros* Pasc.—In the note under the description the author states that the antennae are "without apical spines in the ♂". In two males before me the apical spines are well developed on segments 3–5 as in *A. thoracicus* Don. The species has a wide distribution in Queensland.





Text-fig. 4.—*Tragocerus cylindricus*, n. sp. Text-fig. 5.—*Microtragus tuberculatus*, n. sp.

TRAGOCERUS CYLINDRICUS, n. sp. Text-fig. 4.

Elongate, cylindric; head, seven basal segments of antennae, and legs red, prothorax red with large T-shaped black macula (not extending to sides or base), elytra chiefly black, reddish at sides, with medial and apical fasciae testaceous, the former not quite extending to suture, the latter narrow, with longitudinal extension between third costa and margin, underside red with base of coxae and front margins of ventral segments black.

Head pubescent, lightly channelled between eyes, antennae more slender and lineate than in other species, segments successively diminishing in length from third outwards, 6–7 slightly darkened at apex, 8 almost wholly black, 9–11 wanting. *Prothorax* widest near base, surface rather uneven, depressed at apex, constricted and hollowed at base, slightly raised at middle, with oblique, rounded, postero-lateral hump on each side. *Scutellum* large, rounded behind, closely punctate, surrounding area excavated. *Elytra* little wider than prothorax and $4\frac{1}{2}$ times as long, bispinose and considerably abbreviated at apex, with three well marked costae, besides similarly raised suture and lateral margins, intercostal area finely rugose and punctate. Abdomen glabrous, the rest of underside with fine upright hair. *Dim.*, 22 × 4 mm.

Hab.—S. Queensland: Milmerran, Darling Downs (J. Macqueen).

A single example (? ♀) given by its captor is strikingly distinct in its genus by uneven pronotum, elongate form and abbreviated elytra. The uncovered part is about 3 mm. long. The apical spines are longer than in *T. formosus* Pasc. and rendered more distinct by the absence of pubescence on the elytra. Holotype in Coll. Carter.

MICROTRAGUS TUBERCULATUS, n. sp. Text-fig. 5.

Concolorous dark brown, squamose, with short, recumbent pale setae on head and elsewhere.

Head without apparent punctures, antennae, also eyes, approximate, a transverse row of small tubercles near junction with thorax, antennae extending to apical third of elytra, segment 1 very stout, 2 nodulose, 3 and 4 elongate, 3 longer than 4, 5–11 subequal, much shorter than preceding. *Prothorax* oval, rather wider than long (4 mm.), convex, apex subtruncate, base lightly bisinuate, widest slightly behind middle, surface uneven, rugose and tuberculate, with coarse, more or less longitudinal ridges near middle, ridges and tubercles somewhat confused laterally, two lateral triangular tubercles at widest part and two large rounded, flattish tubercles near middle of disc. *Scutellum* oval, subvertically raised. *Elytra* considerably wider than prothorax at base, convex, abruptly declivous at apex, the usual humeral spines replaced by large tubercles having a blunt triangular outline, as seen sideways; with three longitudinal rows of tubercles on each, the first rather closely placed curving inwards from humeral tubercle and terminating in a large tubercle on apical declivity, and second starting just below humeral tubercle and terminating behind and below the end of the first row in a crest of three subjoined tubercles, the third row at sides just visible from above, of smaller tubercles than those of the second row; interspaces of rows with large punctures, a single row of these on each side of suture. Underside smooth. *Dim.*, 13 × 5 mm.

Hab.—South Queensland: Wyberba district (E. Sutton); and N. S. Wales: Armidale (C. F. Deuquet).

Three examples examined appear to be of the same sex, since the palpi have their terminal segments sublinear. The Armidale specimen was erroneously placed amongst my series of *M. luctuosus* Shuck., but with three examples before me I have no hesitation in considering it as a distinct species from the following comparison:

tuberculatus.	*luctuosus.*
Size smaller, 13 mm. long.	larger, 16-18 mm. long.
Excrescences non spinose.	chiefly spinose.
Elytra with 3 rows of tubercles.	with 2 rows of spinose tubercles.
The antennae have segments 5-11 much shorter than in *luctuosus.*	

It is not near any other of the genus. Holotype in Coll. Carter.

NOTES ON AUSTRALIAN CHENOPODIACEAE.

By R. H. Anderson, B.Sc.Agr., Senior Assistant Botanist, National Herbarium, Sydney.

(Four Text-figures.)

[Read 29th August, 1934.]

Kochia Cheelii, n. sp.

Fruticulus, ramis albo-tomentosis nonnunquam glabrescentibus, foliis linearisubteretibus glabris vix acutis 6–10 mm. longis, perianthio fructifero valde depresso tomentoso circiter 5 mm. diametro 5 aliis horizontalibus rigidis crassiusculis plus minusve cuneatis comprehensis, tubo breviter convexo 1·5–2 mm. lato infra alas ipsas 10 costis prominentibus instructis.

Zara, E. Officer, 12, 1913.

This species is a dwarf shrub, the branches at first white tomentose but sometimes becoming almost glabrous in age. The leaves are narrow linear, somewhat terete, glabrous or almost so, and 6–10 mm. long.

The fruiting perianth is more or less covered with a rather loose woolly tomentum, and including the wings is about 5 mm. in diameter. The five wings are quite distinct, rather thick and hardened, broadly cuneate and contracting into a fairly broad stipes. The shortly convex tube is marked by 10 prominent radiating ribs, which extend to the wings.

This species resembles *Kochia brevifolia* R.Br. in having 5 equal and separate horizontal wings, and in the tube of the fruiting perianth being ribbed. It differs, however, in the hardened and thickened nature of the wings (which are membraneous in *Kochia brevifolia* R.Br.), in the woolly tomentum covering the fruiting perianth and in the leaf characters. The fruiting perianth of *K. brevifolia* R.Br. is glabrous or slightly pubescent.

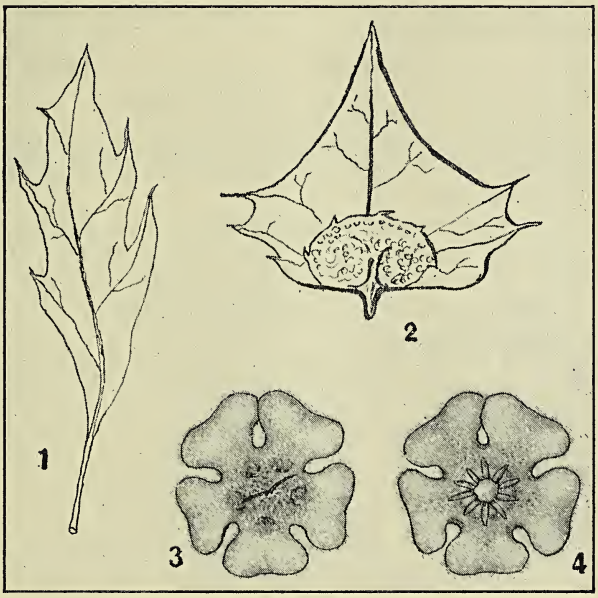
In the thickened character of the wings the species shows affinities with *Kochia scleroptera* J. M. Black, but in the latter species the fruiting perianth is completely concealed under a dense woolly tomentum, the leaves are silky villous, and the tube of the fruiting perianth is not ribbed.

The species is named in honour of Edwin Cheel, Government Botanist and Curator of the National Herbarium, Sydney, who first drew attention to the distinctive character of this species, and in recognition of his many contributions to the advancement of botany in this State.

Atriplex acutilobum, n. sp.

Herba annua plus minusve cano-farinosa, foliis ad 6 cm. longis ovato-lanceolatis sinuato-dentatis lobis acutis ad basim attenuatis, floribus glomeratis, bracteolis fructiferis late-triangularibus circiter 5 mm. latis marginibus

denticulatis appendicibus plus minusve spongiosis instructis, semine orbiculari fusco, radicula supera.



Text-figs. 1-4.
1.—Leaf of *Atriplex acutilobum.*
2.—Fruiting perianth of *Atriplex acutilobum.*
3.—Fruiting perianth of *Kochia Cheelii* (upper surface).
4.—Fruiting perianth of *Kochia Cheelii* (lower surface).

Stephen's Creek, near Quandong Hotel, 30 miles east of Broken Hill, A. Morris, No. 2732, 25.10.1931.

This species is a fairly stout erect annual about 45 cm. high, the young branches, undersurface of leaves, flowers and fruiting bracteoles being more or less scaly tomentose. The mature leaves are ovate-lanceolate, up to 6 cm. long, sinuate toothed, the lobes generally very acute or drawn out into a fine point, glabrous above, scaly tomentose on the undersurface and tapering at the base into a fairly long petiole.

The fruiting bracteoles are broadly triangular, about 5 mm. long and as broad or somewhat broader than long. The margins are variously toothed, the teeth often somewhat drawn out into a fine point and each bracteole bears a distinct slightly spongy appendage at the base, the appendage being often slightly toothed and occasionally 2-lobed.

In some respects this species resembles *Atriplex velutinellum* F.v.M., but it differs from that species in having petiolate leaves and in the character of the fruiting bracteoles. The fruiting bracteole of *A. velutinellum* is triangular lanceolate, being usually much longer than broad, and is entire or with irregular teeth at the base. Like other species of the genus, *A. velutinellum* varies a good deal in the character of the appendage at the base of the bracteole. In most cases this is absent or very inconspicuous, but occasionally a fairly well developed

appendage is found on one or both bracteoles. This appendage is often toothed, but in no case is it so conspicuous or well developed as in *A. acutilobum.*

The general shape of the fruiting bracteoles and the presence of the conspicuous appendages, apart from the petiolate leaves, readily distinguish the proposed species from *A. velutinellum.*

So far the species has been recorded only from the locality given above.

Bassia convexula R. H. Anders.

This species is now recorded from Queensland, a specimen having been collected at Yanna, near Charleville, by G. D. Hutchison (March, 1934). This is the typical form of the species.

Apart from this locality an interesting form has been collected by John Mann near Roma (March, 1934). This differs rather markedly from the typical form of the species. The fruiting perianth is much smaller, the spines considerably reduced, often to mere protuberances, the top of the tube is much flatter, and the habit of growth is generally weaker.

In the majority of fruiting perianths examined the longest spine was barely 1 mm. long, while the other spines were shorter or reduced to points or blunt protuberances. The bifid spine found in the typical form of the species was in most cases reduced to a blunt protuberance or had only one of the points slightly developed. The apex of the tube of the fruiting perianth was flatter than is usual in the species. The seed was placed horizontally as in the species.

In some respects this form approaches *Bassia parviflora* R. H. Anders., but differs in the number and nature of the spines and in the character of the general vestiture.

It is possible that the variations in characters shown by this form are due to retarded development or abnormal growth conditions. If subsequent investigation shows that the differences are constant, then the form might be accorded varietal or specific rank.

Chenopodium carinatum R.Br. var. melanocarpum J. M. Black.

Hitherto this variety has been recorded in New South Wales only from the Broken Hill district, but it has now been collected at Bogan Gate by E. H. Ising (Collector's No. 2107).

The variety is a well defined one, the segments of the fruiting perianth being prominently keeled and completely covering the seed. The perianth also turns black on maturing.

Chenopodium carinatum R.Br. is a most widely distributed species in New South Wales, but the var. *melanocarpum* appears to be rare.

Bassia tricuspis (F.v.M.) R. H. Anders.

The fruiting perianth of this species is usually three-spined, although very occasionally a fourth spine is present, the spines being all more or less equal, and regularly spaced.

A specimen, however, from Chinchilla, Queensland, collected by J. Mann, has all the fruiting perianths furnished with four spines. The collector makes the following note: "The species grows quite freely in the Chinchilla district, and is mostly found on black soil country."

NOTE ON *CAMPANULARIA INTEGRA* AND *ORTHOPYXIS CALICULATA*.

By W. M. Bale.

[Read 29th August, 1934.]

The question of the identity or otherwise of *Campanularia integra* MacG. with *Orthopyxis caliculata* (Hincks) has been much debated, some competent observers maintaining that they are distinct species; others, equally competent, claim that they are only forms of one species, and that they occur abundantly together, even in the same colony, and with all intermediate gradations. In dealing with the Australian species, and in the absence of specimens of *C. integra*, I have treated *O. caliculata* as distinct, because my specimens agreed completely with Hincks' account of that species, but did not at all correspond with the descriptions of *C. integra*. Moreover, it is to be noted that while *O. caliculata* appears to be cosmopolitan, *C. integra* is a strictly northern form, which does not appear to have been recorded from the southern hemisphere at all, those hydroids which have been referred to the species from Patagonia, Chili, Natal, Australia, and New Zealand being in all cases admittedly *O. caliculata*, while none of the observers refer to any intermediate forms.

I have had the opportunity of examining typical specimens of *C. integra* (for which I have to thank Dr. Broch), and I find that the hydrothecae agree absolutely in form with those of *O. caliculata* (though differing greatly in size). That is to say, that they have precisely the characters of the genus *Orthopyxis*, a fact which I think observers have not noted. I pointed out in 1914 that *O. caliculata* was the type of a group of species distinguished by having the lower part of the hydrotheca laterally compressed, so that there are at this part two broader and two narrower sides, and the "floor" of the theca is elliptic; and further, that the perisarc of the narrower sides is thickened, sometimes slightly, often very considerably, even in the same species. From the compressed condition of the lower part of the thecae it naturally results that they present a very different appearance according to the aspect in which they are viewed; seen broadside they have a bell-shape, seen in the narrower aspect they are more funnel-shaped, and this difference is greatly accentuated when the thickening of the perisarc is pronounced. This, as I have previously noted, is the explanation of the descriptions by various observers of two different forms of thecae (with intermediate gradations) being found growing on the same hydrorhiza. Thus Hincks (1868, Plate xxxi, fig. 2*b*) shows two thecae of *O. caliculata* which he supposed to have been differently formed, but which really represent two aspects of the same theca. Other instances of the kind are *O. compressa* (Clarke), *O. everta* (Clarke), *O. crenata* (Hartlaub), *O. pacifica* Stechow, *Campanularia* (?) *intermedia* Stechow. The hydrothecae are therefore intermediate between those of the typical Campanularians and those of the genus *Silicularia*, in which the compressed condition is much more marked.

Northern observers recognize a "*C. integra* forma *calyculata*" which they consider identical with *O. caliculata*. It is said to differ from the type *C. integra* only in having the theca laterally compressed at the margin, and in having the perisarc thickened. The latter feature, however, is common to the type form, so that the elliptic margin is the sole distinction. It is immaterial; it may be expected that where the lower half of the theca is compressed the condition may sometimes extend to the margin. I have noted such instances in *O. macrogona*, and probably careful search would discover them in other species. While observers are unquestionably right in associating this form with the type, it is not apparent why they have associated it with *O. caliculata*, which has not been described as possessing and which does not possess, this character.

Although the hydrothecae of *O. caliculata* agree with those of *O. integra* in form, they are easily distinguished by their far smaller size. This character seems to have been generally overlooked, yet it is specially stressed by Hincks, who, after giving several figures "highly magnified", adds a much smaller figure "drawn to the author's scale, for comparison with other species". This figure shows the theca not much more than half the length of that of *C. integra*, with the other dimensions in the same proportion. I have measured a series of thecae of *O. integra*, which range between 0·65 and 0·82 mm. in length, most of them averaging about 0·72. A similar number of thecae of *O. caliculata* show extreme measurements of 0·33 and 0·50, with the majority averaging about 0·38. The relative proportions of the two species therefore agree fairly with the figures of Hincks.

While, however, the hydrothecae of the two species differ from each other only in size, it is quite otherwise with the gonangia, which are unlike in every particular. Those of *O. integra* differ from those of most species in not being compressed, so that a transverse section is circular. They are very long, and deeply furrowed in a continuous spiral throughout their length, the edges of the furrow being so sharply angular that they are sometimes described as carinated. (It has been pointed out, however, by Levinsen and other observers, that in many cases the furrow is much less pronounced, being only a slight spiral depression. Whether the difference is developmental, sexual or abnormal is not stated.) Fully developed specimens are mostly from 2·2 to 2·5 mm. in height, and so far as I have seen they have thin perisarc, almost colourless.

The gonothecae of *O. caliculata* differ from these so completely that I cannot suppose that any observer having the two species before him would think of uniting them. They are 1·2 to 1·25 mm. in length, slightly compressed, oblong or ovate when regularly formed, but in all the colonies which I have seen there are but few of regular form, the great majority being more or less distorted and irregular. Sometimes they have two slight inflations, corresponding to the two contained zooids, as shown by Hincks, or the position of the second zooid may be indicated by an awkward-looking angular prominence. Occasionally the sides exhibit a few scarcely noticeable undulations, but I have never seen any distinct annulations, nor any trace of spiral markings. In my account of the species I have given outlines of several individuals, which embrace some of the variations which I have met with. In the few fertile colonies which I have examined the gonothecae are numerous, equalling or surpassing in number the hydrothecae. They are fairly thick-walled and rather deeply coloured.

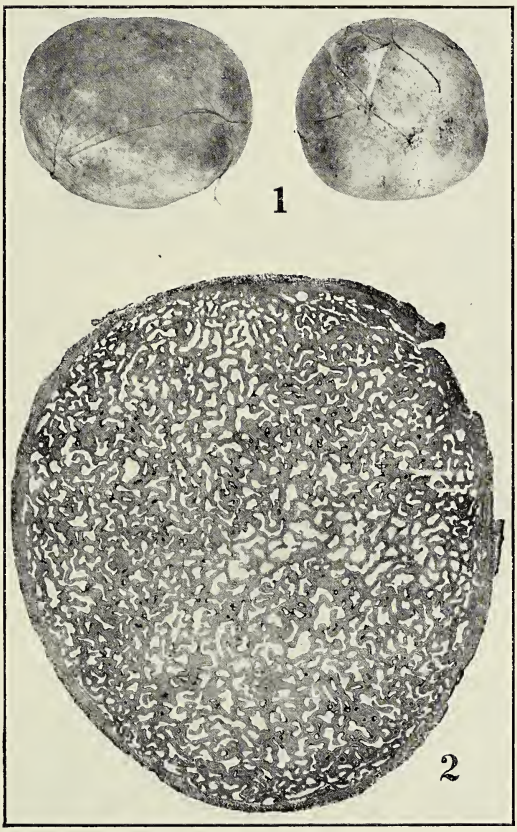
A most important character of the genus *Orthopyxis* is the structure of the hydranth, which has the hypostome formed in its lower half by the union of

the basal parts of the tentacles in a calyx, and in the distal half by a free dome-like extension of the edge of the calyx; a structure shown by Jickeli in a section of *O. caliculata*, and by Broch in *Bonneviella*. The hydranths of my specimens of *O. integra* are not in a condition to enable me to verify the structure, but presumably it agrees with that of *O. caliculata*. A hydranth fully retracted, seen from above, appears elliptical; this, however, is due merely to the form of the lower part of the hydrotheca, in which it is closely packed. In an empty theca, seen from above, the "floor" measured 0·25 mm. in the longer diameter by 0·20 in the narrower, and this seems to be about the usual proportion. Of course the proportionate diameter of the outside of the theca will vary according to the amount of perisarcal thickening of the narrower sides.

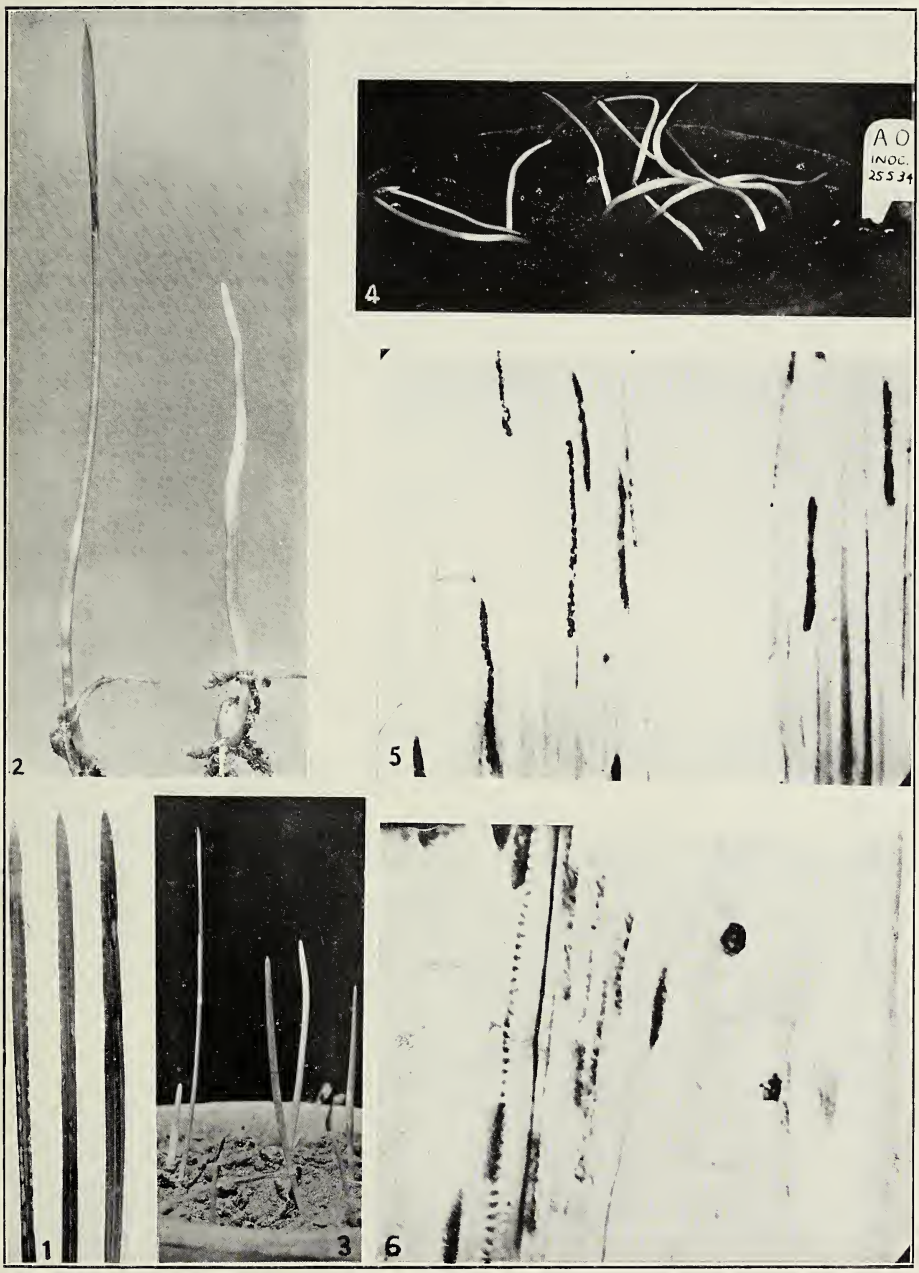
O. caliculata then is distinguished from *O. integra* forma *calyculata* by the far smaller hydrothecae and gonothecae, and by the totally different form of the latter. Not all the hydroids which have been referred to *O. caliculata* really belong to that species. A specimen assigned to it by Nutting is said to have the hydrothecae larger even than those of *O. integra*; this can hardly be a correct identification. *O. compressa* (Clarke), which is sometimes classed among the synonyms of *O. integra*, is easily distinguished by the smooth thick pedicels, which are never waved or twisted, even in the absence of the very distinct much flattened gonothecae, characters emphasized by Clarke, Nutting, Vanhoffen, and Linko. The "*C. caliculata*" of Calkins and Fraser is *O. pacifica* Stechow, a species with large hydrothecae and very distinctive female gonothecae, large (about 2·2 mm. in height and 1·2 in width), regular in form and widening up to the top, and sometimes faintly corrugated transversely. The few male gonothecae which I have seen were much shorter, and wider at the base. *O. crenata* (Hartlaub) and *O. everta* (Clarke) have large hydrothecae with crenate margins (often indistinct); the latter species is readily distinguished by the small oblong gonothecae.

The *Tubularia clytioides* of Lamouroux is classed by Nutting as an *Orthopyxis*, but its position in the genus is doubtful. All the known species have the pedicels formed like those either of *O. compressa* or *O. integra*, the former straight, smooth (though often with a few well-defined separate joints near the top); and the latter with more or less loosely disposed spiral undulations. The pedicels of *T. clytioides* are unlike either of these, having a series of distinct annulations at the top and bottom, or throughout, just like those of an *Obelia*.

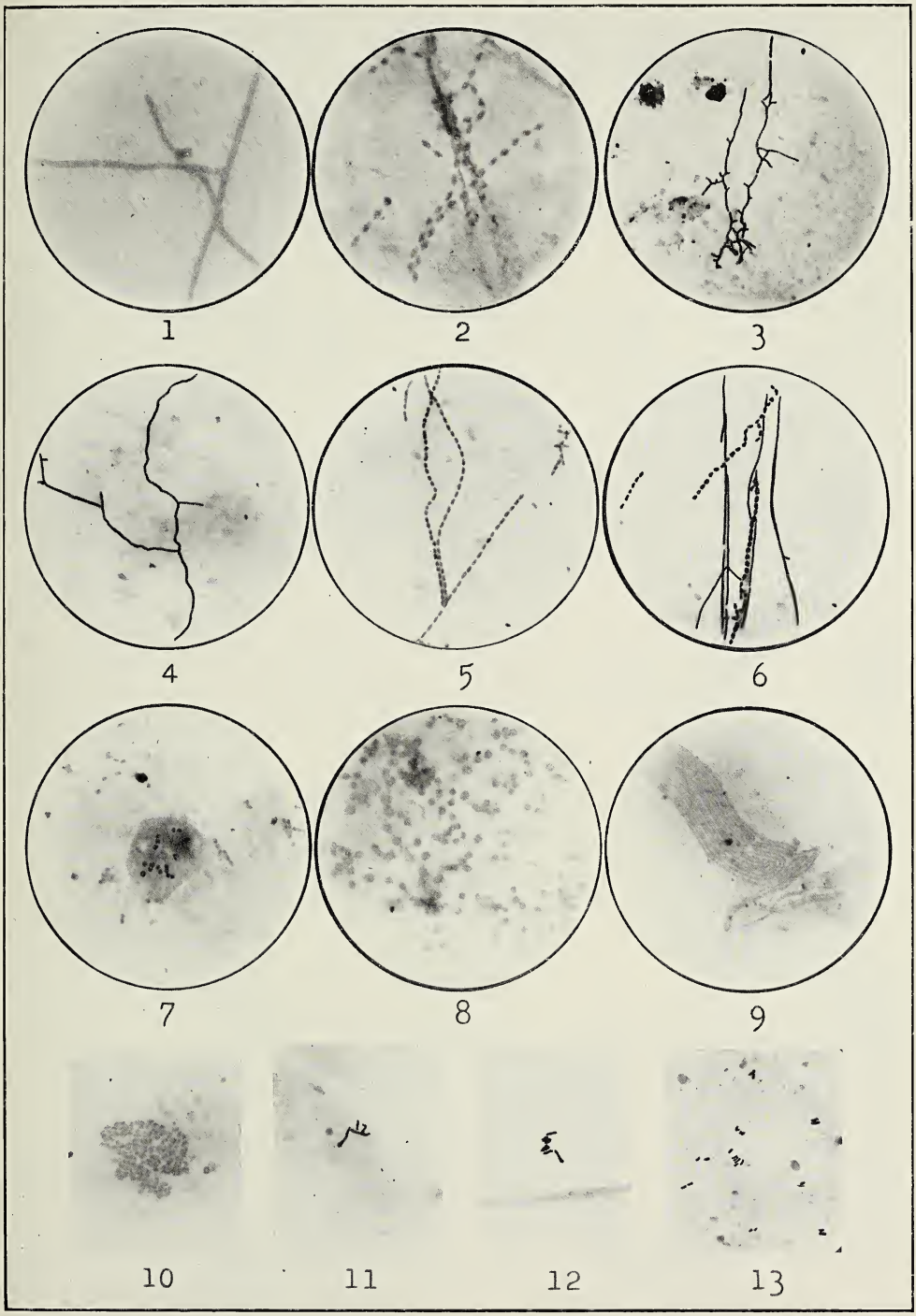
Of the five Australian species which I have observed, *O. caliculata* agrees fully with Hincks' account. *O. macrogona* has the hydrothecae more compressed and wider at the base, and the band of thickened perisarc surrounding the upper half is distinctive. The gonothecae are like those of *O. caliculata*, and equally irregular in form, but are very much larger. The other three species have very similar hydrothecae. *O. angulata* differs from all the rest in having smooth pedicels like those of *O. compressa*. *O. platycarpa* has oblong compressed gonothecae, while those of *O. wilsoni* are large, sub-cylindrical, tapering at the base, not compressed, with a number of irregular longitudinal folds.



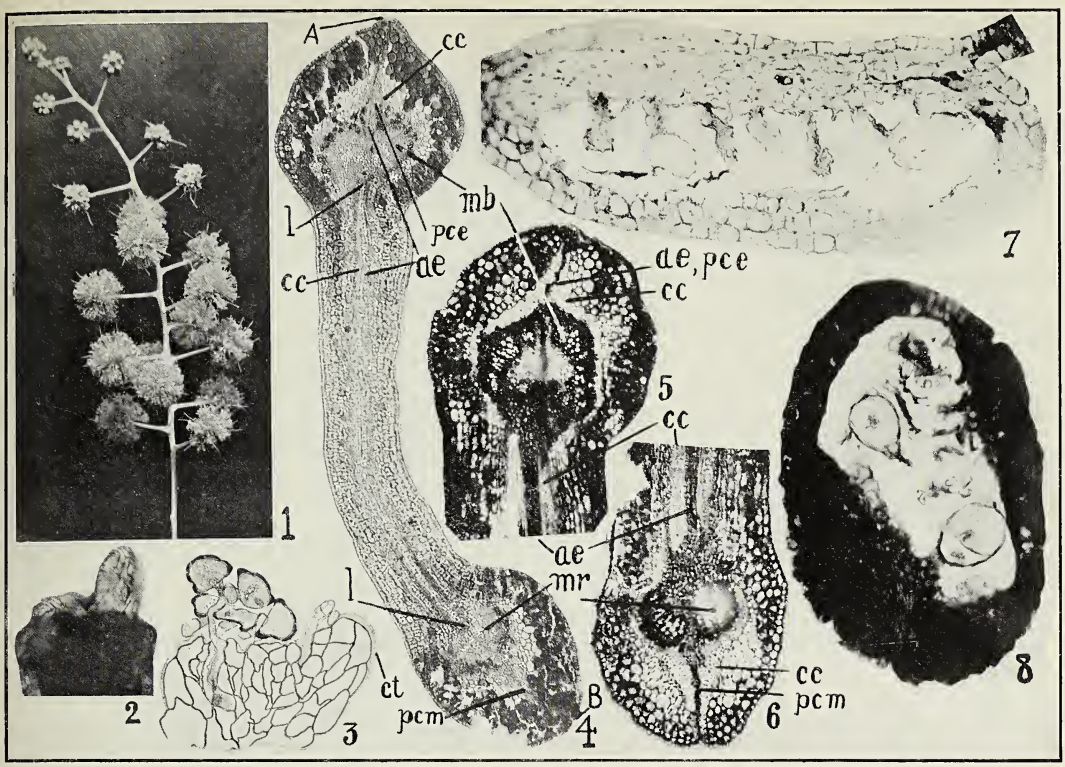
Rhizopogon rubescens.

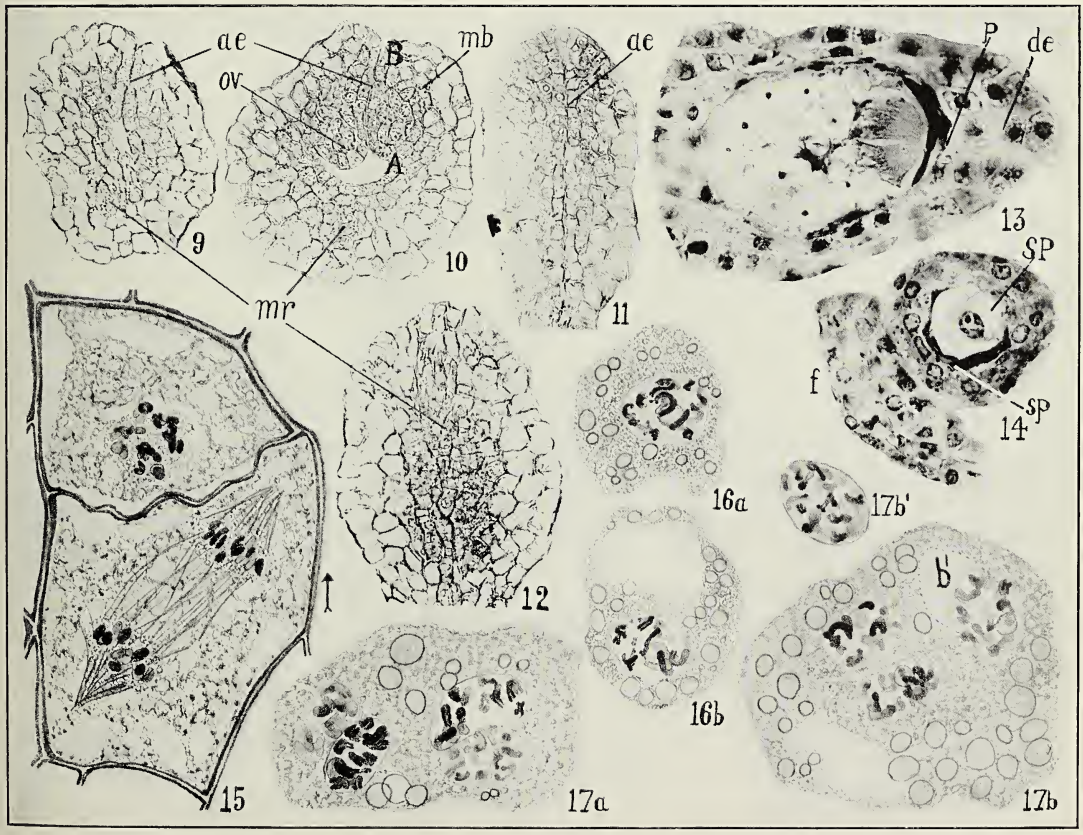


Seedlings of wheat and oats showing white infection spots.



Soil microflora.





Acacia Baileyana F.v.M.

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OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1934.

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SYDNEY:
PRINTED AND PUBLISHED FOR THE SOCIETY BY
AUSTRALASIAN MEDICAL PUBLISHING CO., LTD.,
Seamer Street, Glebe, Sydney,
and
SOLD BY THE SOCIETY,
Science House, Gloucester and Essex Streets, Sydney.

1934.

PRICE 10/9.

Registered at the General Post Office, Sydney, for transmission by post as a periodical.

Agent in Europe:
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STUDIES IN THE AUSTRALIAN ACACIAS. IV.

THE LIFE HISTORY OF ACACIA BAILEYANA F.V.M.

Part 2. Gametophytes, Fertilization, Seed Production and Germination, and General Conclusion.

By I. V. Newman, M.Sc., Ph.D., F.L.S., Linnean Macleay Fellow of the Society in Botany.
(*From the Botanical Laboratories, University of Sydney.*)

(Plate viii; and sixty-six Text-figures.)

[Read 26th September, 1934.]

Introduction.

The first two papers of this enquiry (Newman, 1933*b* and 1934) described the ecology, habit, floral structures, reproductive processes as far as the production of the spores, and the chromosome numbers. The present paper completes the description of the reproductive processes.

The statement and correlation of times for the various stages of development will be reserved generally for a special section at the end of the paper. Annotations for the figures have been standardized and will be found, except for certain special cases, in the section "Notes on the Illustrations" (p. 312).

The material on which the study of the gametophytes is based was collected from trees in cultivation at Strathfield, Sydney; that for the fertilization and post-fertilization stages was collected from trees in cultivation at Hill Top,* except that the stages about the formation of cotyledons were in material from Pennant Hills, Sydney, and full-sized seeds were from Canberra, F.C.T. The illustrations of the germination of the microspore and three of those of the germination of the megaspore were made from slides that had been prepared when the writer was a post-graduate student at King's College, London, under Professor R. R. Gates, F.R.S.

The material collected at Hill Top and Pennant Hills was subjected to a certain degree of mutilation to facilitate the penetration of the fixing fluids. It was found that alcoholic fluids were more satisfactory from the point of view of sectioning. Material for non-alcoholic fluids was first rinsed in 90% alcohol and then water.

The following fixatives were used:

A. 1–2% Chromo-Acetic acid with 2 c.c. of 1% Osmic acid.
B. 4–5–5–50% Mercuric chloride–Acetic acid–Formalin–Alcohol at 38°C.
D. 6–50% Formalin–Alcohol.
E. 6% Formalin in Absolute Alcohol.

* I would express my thanks to Mr. E. Cheel, Government Botanist, for permission to collect this material on his property.

Of these fluids A and D were used the most, D being especially serviceable.

The stains used were Haidenhain's Iron Alum Haematoxylin differentiated with Acid Alcohol, and Safranin combined variously with two of Orange G, Light Green, and Gentian Violet in water or Clove Oil solution. Good results were obtained by differentiating Safranin with 0·02% Light Green in 95% Alcohol.

The Gametophytes.

male.

Germination of the Spore.

In examining the illustrations of microspores it must be remembered that their shape is determined by their position in the pollinium, and that the thickened extine is deposited on only one face of the spore—that towards the outside of the pollinium. In the fully formed microspore the cytoplasm is evenly and loosely vacuolate, and the chromatin of the nucleus is in a loose reticulum (Text-fig. 1). The thickened extine is sculptured by a rectangular groove (Text-figs. 2, 3; Plate viii, fig. 3), which has no connection with the emergence of the pollen tube. There is a thickening of the intine at the corners of the spore (Text-figs. 1–4), which has no apparent connection with germination.

The microspore germinates in the anther. The first sign is the appearance of large vacuoles against the walls of the spore except the outer wall (Text-fig. 2A), causing the spindle to be perpendicular and nearer to that wall. The division of the nucleus, thus orientated, takes place quite normally (Text-fig. 2, from A to F) ending with the formation of the small generative cell against the outer wall of the spore. The cytoplasm becomes uniformly and finely vacuolate and the generative cell is freed from the wall. The spore can now be regarded as the pollen grain (Text-fig. 3). The tube nucleus has a coarse reticulate chromatin, and the generative nucleus has the chromosomes organized and showing the split for the next division—probably the telophase condition.

The ripe pollen contains the spindle-shaped generative cell, whose nucleus shows chromosomes, and the tube nucleus which is usually partly disorganized and sometimes unidentifiable (Text-figs. 4–7, 5–9; Plate viii, fig. 2). The stains are taken so deeply by the pollen grains that it is very difficult to examine the generative cell for the presence of a definite membrane. The nucleus is certainly surrounded by an area of lighter cytoplasm, but it has not always been possible to demonstrate a membrane satisfactorily (cf. Text-fig. 4). The generative nucleus is undivided at the time of dehiscence of the anther.

Attention has already been called to the initiation of germination of the microspore by the formation of large vacuoles which orientate the spindle, and to the somewhat similar criterion of germination of the megaspore established by Rutgers in 1923 (Rutgers, 1923, p. 21, and Newman, 1929, p. 417). Sax and Edmonds (1933, p. 158) describe this phenomenon in detail in *Tradescantia*. Where adequate figures are shown in the literature, this vacuolation can usually be observed, even if it is not referred to. Among cases where it is to be observed may be mentioned, *Albizzia lebbek* (Maheshwari, 1931, Figs. 7–8), *Grevillea robusta* (Brough, 1933, Text-fig. 54), *Myricaria germanica* (Frisendahl, 1912, Figs. 38–44). After recording different phases of spindle formation in the division of the microspore of *Myricaria germanica*, Frisendahl (loc. cit., p. 27) suggests the evolution of the broad (non-converging) from the pointed spindle. In this direction then, *A. Baileyana* is constant with broad-ended spindles and is not primitive. In another pollinium-forming plant, *Asclepias cornuti*, Finn

(1925, Pl. 1, fig. 6) shows the anaphase split of the chromosomes in the division of the generative cell (so clearly shown in *Acacia Baileyana* in the division of the microspore nucleus), but interprets it as a peculiar form of the chromosome (loc. cit., p. 9).

There is considerable difference of opinion on the question of the presence or absence of a membrane enclosing a generative *cell.* A definite cell is recorded by Welsford (1914, p. 266) in *Lilium auratum,* and by Frisendahl (1912, p. 29) in *Myricaria germanica.* In *Asclepias cornuti,* Gager (1902, p. 137) describes a generative cell, and Finn (1925, p. 8) describes only a variably staining layer of pollen grain cytoplasm round the generative nucleus. In *Albizzia lebbek* (Maheshwari, 1931, p. 246) and *Cypripedium* (Pace, 1907, p. 358) a wall is formed but later disappears, the nuclei lying free in the pollen grain. Reeves (1930*a*, p. 36) describes a differentiated layer of cytoplasm round the generative nucleus in *Medicago sativa. Acacia Baileyana* agrees with the majority of plants described, in the spindle shape of the generative nucleus and associated cytoplasm. But it differs from many, such as *Lilium auratum* (Welsford, 1914, p. 265), in that the cytoplasm around the generative nucleus is less dense than that of the pollen grain.

Pollination.

Functional proterogyny has not been demonstrated, though the manner of anthesis suggests it (Newman, 1934, Plate vii, fig. 1). The opinion was formed after culture experiments that the pollen is at its best for germination about three or four days after anthesis. This might make proterogyny effective for any one flower-head, but would not serve in respect of any one tree in view of the great mass of flowers and the length of time during which anthesis is occurring on the tree. And, moreover, self pollination has been successfully carried out to produce a normal degree of pod formation, with the raising of normal seedlings. The mode of pollination is probably not specialized. In the nearly related *Albizzia lebbek,* Maheshwari (1931, p. 249) found no precise mechanism for pollination.

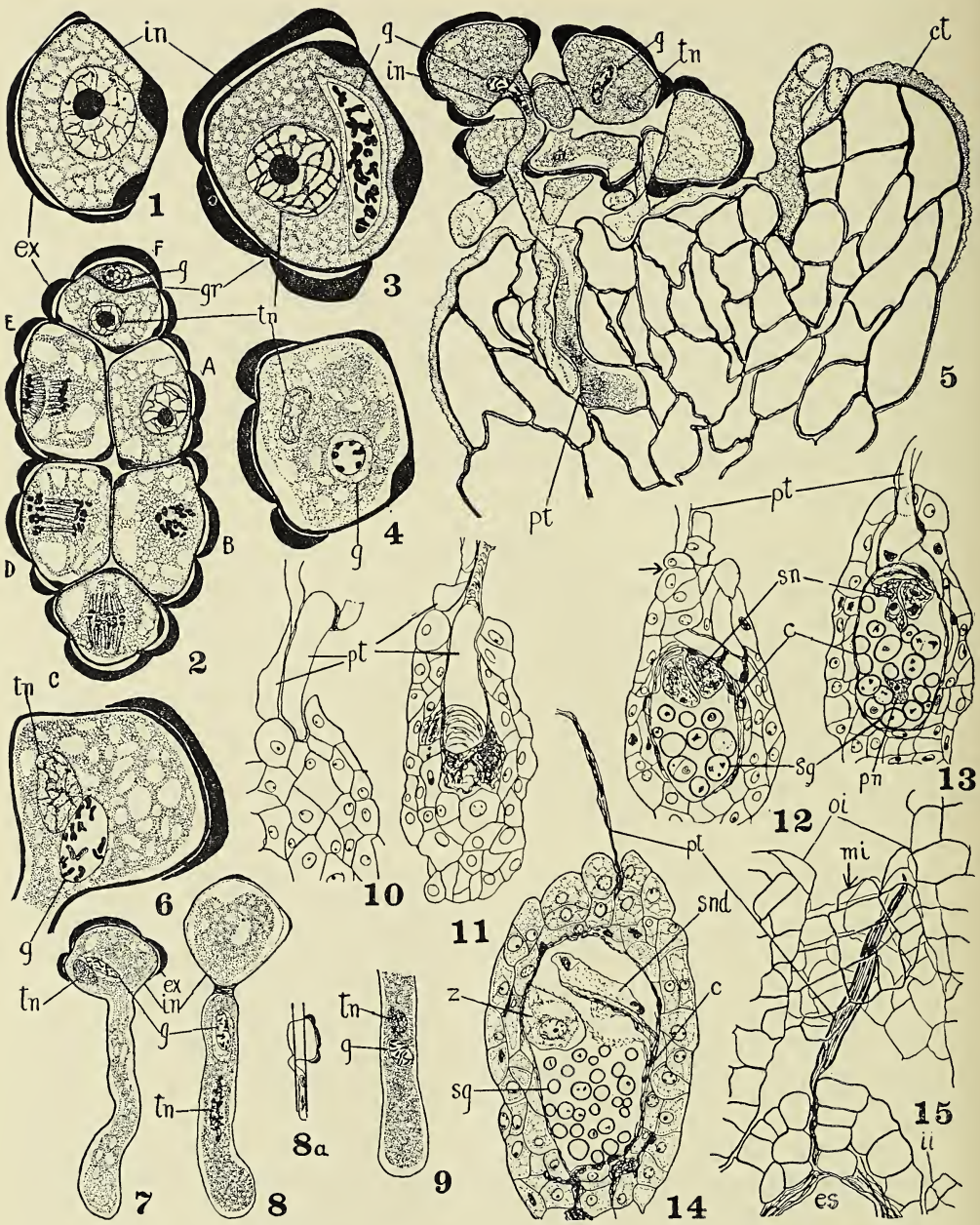
The pollinium lodges in the cup of the stigma. It must be held there by some adhesive substance; for there is no friction against hairs to overcome the reaction to the force required for the penetrating of the stigma by the many pollen tubes. In several instances two pollinia were seen on one stigma (Text-fig. 5 and Plate viii, fig. 3), and in one instance there were three.

The period of pollination and fertilization is marked by heavy frosts and cold winds, especially at Hill Top and Canberra. On many days, however, there would be bright sunshine. Seasonally this period is the depth of winter! And the writer has seen trees of another species of *Acacia* in full flower covered with snow!

Normally the style does not wither after pollination. In a number of cases fungi have been seen on withered and even unwithered stigmas. Withering of the stigma is therefore considered to be due to fungal infection.

Germination of the pollen.

General.—The germination of the pollen has been studied by examination of killed and fixed carpels, of living material both on the plant and in culture, and of killed and fixed material from cultures. In all cases the pollen grains germinated towards the *inside* of the pollinium, causing it to split along the



Text-figures 1-3.—Sections showing germination of the Microspore. 1, The adult spore with resting nucleus and evenly vacuolate cytoplasm; × 2,115. 2, Representation of a transverse section of a pollinium, compounded from drawings of different stages of the germination of the microspore. A, Prophase and beginning of large peripheral vacuolation. B, Early metaphase. C, Beginning of anaphase. D, Late anaphase. E, Early telophase with phragmoplast beginning to cut off the generative cell against

original mother-cell wall; and through the one or more slits the pollen tubes crowd out (Plate viii, figs. 2, 5). This is in marked contrast to the pollinium of *Asclepias cornuti* where the germination of the pollen is through the "outer" wall (Gager, 1902, p. 138). In nature, the tubes emerge from the pollinium through a slit next the stigma, whose tissues they penetrate almost simultaneously (Plate viii, figs. 1, 4, and Text-fig. 5). It is a curious fact that stigmas placed among germinating pollinia in culture seemed to have no attraction for the tubes, some of which grew past the stigmatic surface without deviating from their original direction. Probably the chemotactic power of the culture medium was greater than that of the stigma.

The wall of the pollen tube is a continuation of the intine (Plate viii, figs. 2, 4, and Text-figs. 5, 6, 7). In the germinating pollen grains, on account of the great attraction the cytoplasm has for stains, it is sometimes impossible to determine whether the tube nucleus is present or not. Usually the generative cell precedes the tube nucleus into the tube (Plate viii, fig. 2; Text-figs. 5, 6, 7, 9). Occasionally the tube nucleus enters first (Text-figs. 5, left hand pollen grain, and 8). The disorganization of the tube nucleus is shown in Text-figures 5–9. The tube entirely drains the grain of cytoplasm (Plate viii, fig. 4).

The contents of the pollen tube could not be recognized in the carpel till after the embryo sac was penetrated. Between the stigma and the embryo sac the generative nucleus had divided and given rise to two slightly elliptical male nuclei of equal size which were first seen, one inside the egg cell and the other in contact with a polar nucleus. The size of the male nuclei is not much larger than that of the nucleoli of the egg and polar nuclei. The 13 chromosomes are clearly visible, probably being in the telophase condition (Text-figs. 30*a*–31). No cytoplasmic sheath was observed in connection with the male nucleus; this is not to deny the existence of one. In several instances a body was observed which is interpreted as the remains of the tube nucleus (Text-figs. 30*b*, 35*b*).

Coulter and Chamberlain (1903, pp. 135–6) point out that the time of division of the generative nucleus has no relation to the great plant groups

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the outer wall of the spore. F, Generative cell completed, large vacuoles disappearing. × 1,250. 3, Germination completed, now the pollen grain, with the generative cell free from the wall; × 2,115. In these figures note the thickening at the corners of the intine.

Text-figures 4-9.—Sections showing germination of the pollen. 4, Tube not yet formed, tube nucleus disintegrating, generative cell cut transversely showing a membrane; × 2,030. 5, One pollinium and two tubes from a second pollinium on one stigma; examination of adjacent sections showed absence of a tube nucleus from the upper left pollen grain. *ct*, cuticle. × 1,040. 6, Generative cell leading the tube nucleus into the tube; × 2,030. 7, As 6, the tube nucleus much disintegrated; × 950. 8, Generative cell in the tube behind the now formless tube nucleus; × 950. 8*a*, Diagram to show the plane of section of the germinating grain shown in Figure 8. 9, End of pollen tube showing the generative cell leading the disintegrating tube nucleus; × 950.

Text-figures 10-13.—Consecutive, slightly oblique L.Ss. through a nucellus, showing the penetration of two pollen tubes to one embryo sac. In Figure 12 the portion above the arrow had been moved away slightly during the making of the preparation. These sections include only half of the thickness of the nucellus. × 475.

Text-figure 14.—L.S., Nucellus showing distortion in the contents of the sac after entry of the pollen tube, and showing the zygote and the projecting remains of the pollen tube. This ovule is shown in Text-fig. 45. × 475.

Text-figure 15.—L.S. of tip of a nucellus (multiple epidermis) and the micropyle with the projecting remains of the pollen tube within it. The section includes the upper and lower inner faces of the micropyle. This is from the ovule shown in Text-fig. 46. × 475.

and may even be variable in a species. An example of the latter case is *Myricaria germanica* (Frisendahl, 1912, p. 30). From the few references in the literature of the Leguminosae, it seems general that the generative nucleus does not divide in the anther. This is the condition in *Albizzia lebbek* (Maheshwari, 1931, p. 246) as well as *Acacia Baileyana*. The condition of the male nuclei in the latter species suggests that the division takes place only just before the tube reaches the sac, as is thought to be the case in *Theobroma cacao* by Cheesman (1927, p. 112). The generative cell divided in the unshed pollinium of *Asclepias cornuti* (Gager, 1902, p. 137, and Finn, 1925, p. 5).

No general statement can be made as to the fate of the tube nucleus and the order of precedence into the tube. Weinstein (1926, Figs. 15, 16, 37) shows the tube nucleus leading the generative nucleus in *Phaseolus vulgaris*, and Frisendahl (1912, pp. 30, 45) says that the tube nucleus may degenerate in the grain or upper part of the style of *Myricaria germanica*.

A study of the literature referring to the male gametophyte of Angiosperms gives the impression that the formation of male *cells* is the more frequent, "cells" being taken to mean at least the definite association of a mass of cytoplasm with the male nucleus. In some cases a definite membrane has been recorded. It appears to be almost universal that before (Welsford, 1914, p. 267, for *Lilium auratum*) or soon after the liberation of the male gamete from the pollen tube the nucleus escapes from the "cell" (Guignard, 1899, p. 867, for *Lilium martagon*; Ishikawa, 1918, p. 291, for *Oenothera*), though Wylie (1923, p. 194) for *Valisneria spiralis* considers it probable that some cytoplasm enters the egg. The structure and behaviour of the male gametes of *Acacia Baileyana* will be reported on in detail in a future communication, as there are some important phenomena requiring detailed investigation in the fertilization processes of this species.

Culture.—The general method for procuring pollen germination was used successfully by Brough (1927, pp. 481–2) with *Dampiera stricta*, a plant that flowers all the year round and has a stigma with glandular hairs. He dusted the pollen on to a 5% cane-sugar solution; and germination took place rapidly, the tubes being about five times the diameter of the grain after $2\frac{3}{4}$ hours. Unsuccessful attempts were made with the pollen of *Acacia Baileyana* on the surface of cane-sugar solutions of various concentrations. Cheesman (1927, p. 111) found the best germination of the pollen of *Theobroma cacao* to take place on agar films on glass slides, the medium being 1·5–2% agar and 5% cane-sugar. Bamford and Gershoy (1930, p. 7), using 1% agar and 12% cane-sugar, were successful with the pollen of violets. In view of these successes, the agar method was used for the pollen of *Acacia Baileyana*; different concentrations of agar and sugar were tried. The successful one was 1% agar and 20% cane-sugar (cf. Plate viii, fig. 5). The ratio of sugar to agar required by these three plants is $3\frac{1}{3}$, 12 and 20 to 1 respectively. The success of the experiment requires not merely the germination of the grain (emergence of the tube), but also sustained growth of the tube. The wide difference between the conditions for sustained growth of the tube is in support of Brink's (1925, p. 161) conclusion that in Nature the conditions required for germination of pollen are less exacting than those for the growth of the tube. This is also suggested by the experiments outlined below.

For germination of the pollen of *Acacia Baileyana*, the following agars were tried as plates in petri dishes:

		Ratio $\frac{\text{Sugar}}{\text{Agar, etc.}}$
I. 2% Glucose	1% Agar, 20% Potato	0·095 : 1
II. 2% Glucose	2% Agar, 2% Peptone, ½% Pot. dihyd. Phosphate, ½% Mag. Sulphate	0·4 : 1
III. 25% Cane-sugar	5% Agar	5 : 1
IV. 12% Cane-sugar	2% Agar	6 : 1
V. 20% Cane-sugar	2% Agar	10 : 1
VI. 30% Cane-sugar	2% Agar	15 : 1
VII. 20% Cane-sugar	1% Agar	20 : 1

The lids were kept on the dishes which were left on the laboratory table (winter time). Agars V and VII were also tried as smears on slides inverted over water in a glass vessel with a loose lid. By both methods, agar VII was found to be very satisfactory; for pollinia germinated readily in contact with the medium, whether they occurred singly or in groups. Thus the medium with the greatest sugar-agar ratio, 20 : 1 (VII), gave the best results. Though fair results were given by ratios of 6 : 1 (IV) and 10 : 1 (V), the ratios 5 : 1 (III) and 15 : 1 (VI) were unsatisfactory. The failure of the media with the latter pair of ratios which are close to or within the range of those of the more successful media is probably due to a too high sugar concentration, viz., 25% (III) and 30% (VI), the highest of the series.

In good germinations the tubes attained a length of about 7 or 8 times the diameter of the pollen grain in 2½ hours after inoculation.

Pollen from flowers freshly opened on the day of inoculation never germinated readily. Pollen from the flowers of a cut shoot that had been standing in water for seven days before the inoculation still germinated well. It is concluded that the pollen is at its best from about 3 to 7 days after anthesis.

Path of the Pollen Tube.

Other than the tubes from the germinating pollinia in the tip of the style shown in Plate viii, figure 1, and Text-figure 5, the only trace of the tubes seen clearly in the style has been the cavity caused by them. This cavity is soon repaired by further growth of the style tissue. The cavity has been traced from the stigma to the ovary. This path of the tubes is through no specialized conducting tissue, and the style is so small in cross section that it is difficult to say that the path of the sixteen pollen tubes is in any particular region of it.

In the ovary the tubes pass along the floor among the thick-walled hairs which are mostly destroyed, and come into direct contact with the tips of the naked anatropous ovules (Text-fig. 22). As might be expected from the excess number of pollen tubes available (16 from one pollinium for 12 ovules) and the naked condition of the ovule, two pollen tubes are found occasionally attacking one ovule, and even entering the embryo sac (Text-figs. 10–13). These figures show that the pollen tube makes a very large wound in the tip of the ovule; but this is quickly healed and the tissue appears as vigorous as ever (Text-figs. 14, 15, and Plate viii, figs. 9, 12, 14). The pollen tube at the time of fertilization is a very delicate structure, and is easily destroyed in the making of the preparations. It is therefore very difficult to find many clear examples of it soon after fertilization when the gap in the tip of the ovule has closed up. But later on, the walls of the tube seem to harden, so that it is easily and frequently seen projecting from the tip of the nucellus in preparations made of stages up to embryos of about twelve cells in pods about 50 mm. long (length at fertilization,

0·5 mm.) (see Text-figs. 14, 15). In fact, instead of the pollen tube passing down the micropyle, the micropyle is formed round the pollen tube.

On the entry of the pollen tube there is a considerable, though variable, disturbance of the upper contents of the embryo sac (Text-figs. 13, 14), which may push the egg laterally and clear the starch grains away from above the polar nuclei. This latter would be a very useful effect in making easy the approach of the second male nucleus to the polar nuclei. On the other hand, the pollen tube may cause very little damage to the synergids (Text-fig. 33). Whatever be the disturbance, it is soon repaired and the zygote becomes attached to the distal wall of the embryo sac (Text-figs. 36, 37; Plate viii, fig. 12).

That the pollen tubes in culture ignored the presence of stigmas is in line with the findings of Martin (1913, p. 123) for the pollen of *Trifolium pratense*. He found that the stigma exerted no influence on the direction of growth of the pollen tubes, and concludes: "The behaviour of the stigma in the experiments at least indicates that its function in the germination of the pollen is to regulate the water supply; and the nature of the pollen necessitates no other function". If this is a general condition, then pollen germination in Nature must be very promiscuous, and it is chemical and physical factors such as those investigated by Brink (1925) which inhibit the growth of the foreign tubes in the stigma.

There is every indication that some at least of the excess pollen tubes of *Acacia Baileyana* enter ovules already attacked. Weinstein (1926, p. 255) describes the excess tubes of *Phaseolus vulgaris* growing to the base of the ovary and then disintegrating. The exact behaviour of the two pollen tubes on their entry to the sac has not been observed in *A. Baileyana*. In *Valisneria spiralis*, Wylie (1923, p. 195) describes them entering a synergid each.

The entry of more than one tube into one embryo sac requires a revision of the ideas of chemotaxis and that fertilization causes a reversal of chemotropism. Compton (1912*a*) describes in a *Lychnis* hybrid an ovule with two sacs which had been penetrated by two tubes right up to the sacs, and another with one sac which had been penetrated by two tubes of which one had died half-way across the parietal tissue. He makes the rather daring conclusion that these facts "seem to indicate a quantitative relation between embryo-sac and pollen tube in the matter of chemotaxis, two embryo-sacs excreting sufficient of the chemotropic substance to attract two pollen-tubes". The situation in *A. Baileyana* definitely negates this idea. There have been a number of records of more than two pollen tubes penetrating one ovule and even discharging into one embryo sac. From the following examples it would appear to be a phenomenon of the less advanced Angiosperms, though one is from the Monocotyledons. Shattuck (1905) found two tubes to one embryo sac in *Ulmus americana*; Frisendahl (1912, p. 49) says that very often more than one tube discharges into the sac of *Myricaria germanica*; Nawaschin and Finn (1913, p. 19) found in *Juglans nigra* as many as five tubes to one ovule and four discharging into one sac, three tubes arriving some time after the first tube; other cases are found in *Xyris indica* (Weinzieher, 1914), *Myosurus minimus* (Tchernoyarow, 1915) and *Oenothera* (Ishikawa, 1918, p. 295). It is significant that in *Gnetum*, where there are several eggs available for fertilization, several tubes attack the one embryo sac (Lotzy, 1899, p. 96).

FEMALE.

Germination of the Spore.

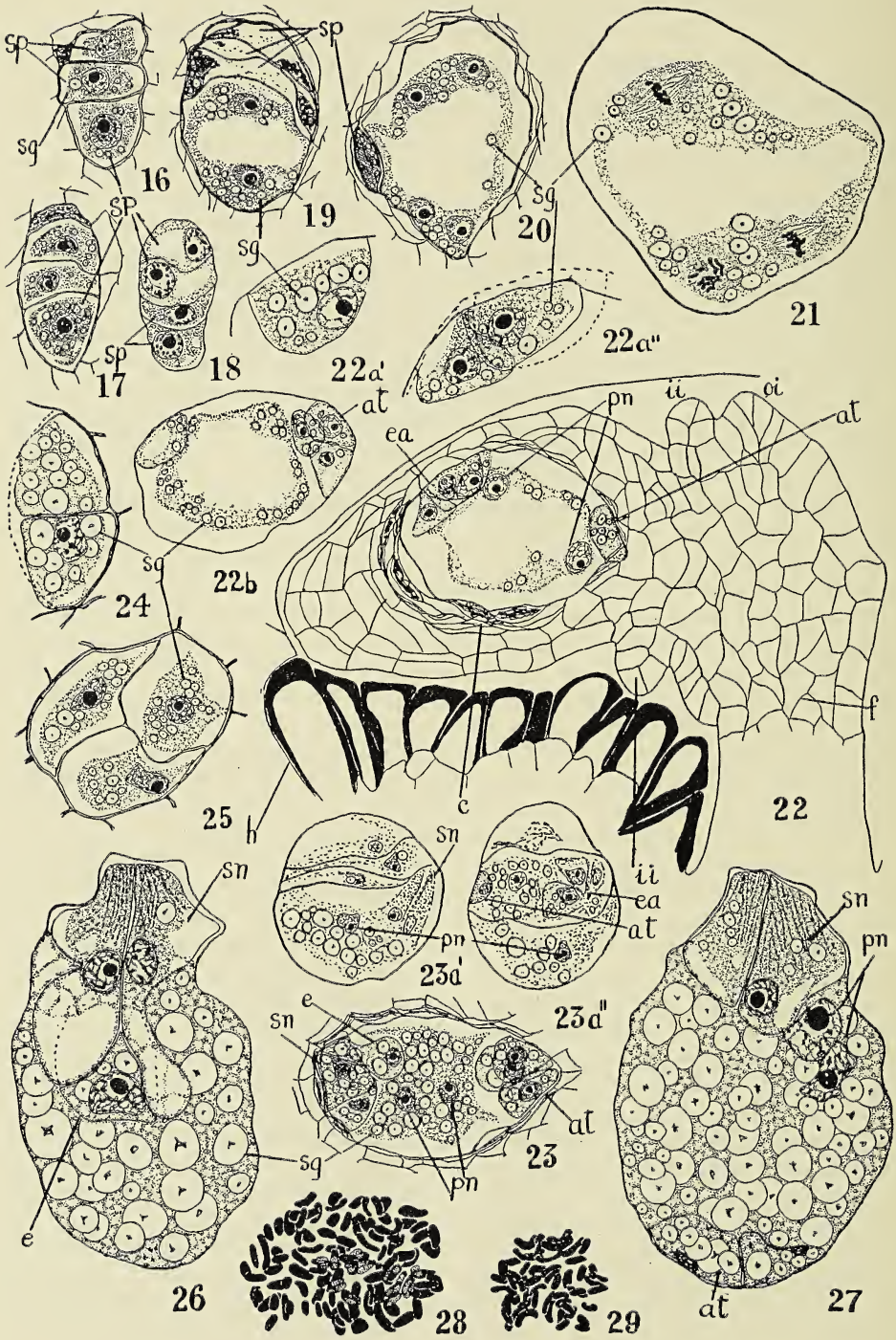
As with the microspore, the first sign of germination is the formation of vacuoles in the cytoplasm (cf. Text-fig. 16 with 17). These coalesce to form one large central vacuole about the time of the division of the nucleus, shown in Text-figure 18 and Plate viii, figure 6; the former shows two functional distal megaspores, and the latter shows a functional distal megaspore with chromosomes in the nucleus and whose central vacuole has contracted in the preparation. The nuclei resulting from the division pass to the aggregations of cytoplasm at opposite ends of the sac (Text-fig. 19). These nuclei undergo division to four (Text-fig. 20) which divide simultaneously (Text-fig. 21) to form the eight nuclei of the adult embryo sac. In the telophase of this third division, the beginning of wall formation can be discerned (Newman, 1934, Plate vii, figs. 17*a–b*, left-hand pairs of nuclei). Whether this is evanescent or is completed was not determined.

There is little evidence upon which to determine the sisterhood of the cells of the egg apparatus and upper polar nucleus. But from the direction of the spindles and from nuclear sizes and disposition in the early adult stages, it could be argued that the egg and upper polar nuclei are sisters.

Starch is formed early in the megaspores, especially in the functional ones, and is abundant in the peripheral cytoplasm, particularly in the neighbourhood of the nuclei, while the embryo sac is being completed (Text-figs. 16–21).

A. Baileyana falls clearly within Rutgers' (1923, p. 21) distinction between the formation and development (germination) of megaspores, by beginning the germination with vacuolation of the cytoplasm. The central vacuole is recorded by Saxton (1907, Figs. 6–9) for *Cassia tomentosa*, Maheshwari (1931, Figs. 22–25) for *Albizzia lebbek* and Reeves (1930*b*, p. 242) for *Medicago sativa*, in which case it becomes filled with starch from the 2-nucleate stage till the divisions are completed. This last is a similar condition to that described by Guignard (1881, p. 25) for *Acacia farnesiana*. In *A. Baileyana*, the starch develops early and remains over a long course of the development. The discussion of it will be reserved till the consideration of the situation in the definitive sac.

The separation of the polar nuclei from the distal and proximal groups of three nuclei has been observed in *Doryanthes excelsa* (Newman, 1929, p. 415), and in *Medicago sativa* (Reeves, 1930*b*, p. 242). In the former case, as in *A. Baileyana*, it was inferred that the egg and upper polar nuclei are sisters. Frisendahl (1912, p. 37, and Taf. III, fig. 87), in *Myricaria germanica*, shows the egg and upper polar nuclei being cut off from one another at the simultaneous cell formation in the egg apparatus. He also shows a definite T orientation of the spindles in his figures of the third division in the sac (p. 36), though he says (p. 37) that they have no definite orientation to one another and the long axis of the sac. Porsch (1907) says that the upper polar nucleus is sister to the egg and represents the ventral canal nucleus, the synergids being sisters. Nawaschin (1898, pp. 381–2) held that the second male nucleus fused with the sister of the egg; but he seemed to interpret the upper polar as a second egg, regarding the endosperm as a second embryo; and made comparison with the several proembryos in the sac of *Gnetum*. This question is important for the homologies of the endosperm. Schürhoff (1928), after a careful analysis of the findings of many authors, is of the opinion that neither the direction of the spindles in the last division in the embryo sac nor the orientation of the four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free micropylar nuclei are valid criteria for the determination of the sisterhood within the egg apparatus (pp. 565–6). In considering the wall formation, he could only find one significant figure in the literature, that of Frisendahl (1912, Taf. III, fig. 87) for *Myricaria germanica*; but as that shows a simultaneous cell formation, he says there is no criterion in the phragmoplast. He then considers cases of abnormal embryo sacs and the Gymnosperms, concluding that the sisterhood is synergid–egg, synergid–polar, each pair representing an archegonium, so that "double fertilization" is right in the truest sense of the word (p. 572).

Definitive Embryo Sac.

Occasionally in *Acacia Baileyana* two embryo sacs have been seen in one ovule. This is not surprising in view of the occasional occurrences of more than one mother cell or germinating megaspore in an ovule. The two embryo sacs have always been degenerate (Text-fig. 23*a*′, *a*″). The enlargement of the embryo sac destroys almost all the parietal tissue except the multiple epidermis (Text-fig. 22).

Soon after the third division in the embryo sac, the organization of cells in the egg apparatus and antipodal groups takes place, starch grains being enclosed with the nuclei (Text-figs. 22–22*b*, 24 and 25). The central vacuole becomes filled with cytoplasm containing numerous starch grains, the polar nuclei begin to approach one another and the cells of the egg apparatus to elongate (Text-fig. 23). The starch is so abundant that the spherical grains seem to be in contact at every possible point (Plate viii, fig. 8). In many cases they nearly fill the vacuolate regions of the egg and synergids and the whole of the antipodals, so that the limits of these cells are difficult to determine (Text-figs. 24, 26, 27; Plate viii, fig. 8). The starch persists in the egg during fertilization and is so packed in the sac that the polar nuclei are distorted even up to the completion of fusion with the second male nucleus (Text-figs. 30*a*–43, 58).

The enlargement of the embryo sac does not obliterate all the nucellar tissue by the time of fertilization in the Acacias as recorded by Guignard (1881, p. 28),

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Text-figures 16-20.—Development from the functional megaspore to the four-nucleate sac; × 586. 16, The functional spore proximal of three. 17, Germination beginning in the proximal spore of four. Vacuolation beginning. 18, Two distal spores germinating, note large vacuole. 19, Two-nucleate sac with central vacuole. 20, Four-nucleate sac with central vacuole.

Text-figure 21.—Embryo sac showing three spindles of the third division. 13 chromosomes visible in one of the metaphase plates. × 1,100.

Text-figures 22-22*b*.—From an ovule soon after the formation of the cells in the embryo sac. 22, L.S. of the whole ovule showing the egg apparatus, polars and part of an antipodal, also the hairs (*h*) on the floor of the ovary; × 586. 22*a*′, the egg; × 1,100. 22*a*″, the synergids (position of egg in outline); × 1,100. 22*b*, From the section adjacent to that shown in 22; part of the egg and three antipodals are shown; × 586.

Text-figure 23.—L.S., Embryo sac showing the approach to the definitive condition and the obliteration of the central vacuole; × 586.

Text-figures 23*a*′, 23*a*″.—Consecutive L.Ss. showing in the one ovule non-functional megaspores and part of two degenerating embryo sacs that had become nearly definitive; × 514.

Text-figures 24, 25.—L.S. and T.S. of the base of embryo sacs showing the antipodals as cells; × 1,100.

Text-figures 26, 27.—Consecutive L.Ss. of a definitive embryo sac. Part of two antipodals only are shown, and the upper part of the egg is in outline. × 1,100.

Text-figures 28, 29.—Metaphase plates from two abnormal endosperms. For explanation, see text in sub-section Multiple Fusion of section Fertilization. × 1,680.

and in *Albizzia lebbek* as figured by Maheshwari (1931, fig. 26). In two Papilionaceous genera there is what might be considered an advanced tendency: In *Medicago sativa* (Reeves, 1930*b*, p. 243) the sac has enlarged to obliterate all the nucellar tissue and comes in contact with the integuments except at the base; in *Trifolium* (Martin, 1914, p. 164) the sac becomes long by resorption of the chalaza. In *Trifolium* the central vacuolation remains; in *Vicia* and *Medicago* it becomes filled with cytoplasm (loc. cit.).

Starch.—The starch grains vary considerably, from the size of the smaller nucleoli of the sac to one-quarter of the width of the sac. In permanent preparations the grains appear under the microscope as spherical refringent bodies with the hylum as a black or bright area according to the focus (see in Plate viii, fig. 8). The starch does not seem to be of a typical nature, for though staining blue with iodine, it could not be removed from the sac in sections of fixed material by the usual means, such as prolonged hydrolysis with dilute sulphuric and hydrochloric acids, diastase, saliva, and acetone followed by saliva. If in any case the starch was removed, so were the whole sections that had been fixed to the slide with egg albumen. These tests were made on sections of both *Acacia Baileyana* and *A. discolor*. Before fertilization the starch takes no stain with Haidenhain's Iron Alum Haematoxylin or with Safranin. After fertilization it takes a purplish stain with the Haematoxylin and a dull red stain with Safranin.

The presence of starch in the embryo sac seems to be of wide and variable occurrence; and frequently the form of it is not normal. Cheesman (1927, p. 108) refers to starch grains, "if the term is used in its wide sense", in the embryo sac of *Theobroma cacao*; and describes how they do not take stains before fertilization, but do so afterwards, as has been described for *A. Baileyana*. Dahlgren (1927), reviewing the records up to about 1927 of the appearance of starch in the embryo sac, gives lists where, as here, the starch obscures the structures of the sac (p. 374), and appears in the egg apparatus and antipodals (p. 375). Is it possible that the centrosomes figured by some authors as occurring in the egg are small starch grains, as for instance, by Schaffner (1897) in *Sagittaria variabilis*? Dahlgren (1927) lists the first appearance of starch in different species at times ranging from the megaspore mother cell stage to the fusion of the polar nuclei (p. 375), and says that it reaches its maximum just before fertilization, and then is more or less rapidly consumed (p. 376). Its occurrence may even vary within a species (p. 374).

Starch in the embryo sac seems to be of wide occurrence in the Leguminosae. Guignard (1881, p. 25) records it in the functional megaspore of *Acacia farnesiana*, as it is here in *A. Baileyana*; Maheshwari (1931, p. 248) never finds it before the 8-nucleate stage in *Albizzia lebbek* where it persists, as here, even to the stage of the free-nucleate endosperm. Among the Papilionaceae it is found by Reeves (1930*b*, pp. 242–3) from the stage of the two-nucleate sac to maturity in the neighbourhood of the egg apparatus and polar nuclei in *Medicago sativa*; by Martin (1914, p. 164) it is described in the micropylar end of the nucellus only of *Trifolium* and *Vicia*, and filling the sac in *Medicago*; in *Arachis hypogea*, it fills the sac before fertilization (Reed, 1924, p. 380). Dahlgren (1927, p. 380) lists starch grains in the embryo sacs of species from five families of the Rosales other than the Leguminosae and Rosaceae, there being only one species of the latter—*Spiraea lindleyana* in which Péchoutre (1902, p. 92) describes the sac filled with starch before fertilization.

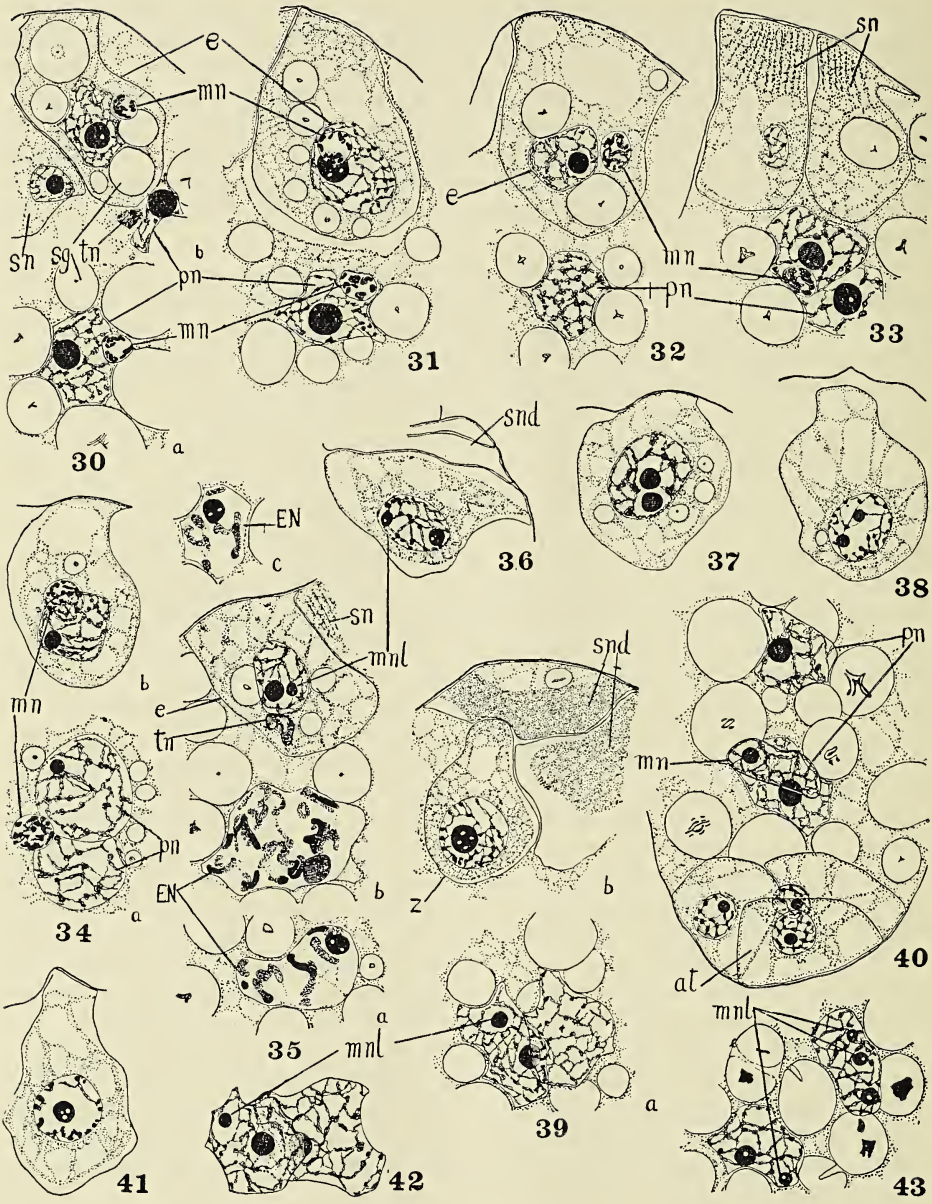
Juel (1911, p. 9), examining *Hippuris vulgaris*, considers starch formation in the embryo sac to be a consequence of delayed fertilization, a possibility concluded by Maheshwari (1931, p. 249) from observations on *Albizzia lebbek*. But in *Verbena*, Kanda (1920, p. 63) describes the starch as occurring "not only a little before fertilization, but more especially after fertilization has occurred", a condition that is contradictory of the conclusion just mentioned. And in such cases as *Acacia Baileyana* and others mentioned above where starch appears in the early stages of germination of the megaspore, it cannot be due to delayed fertilization.

Egg Apparatus.—Though variable in their arrangement, the cells of the egg apparatus are not unusual in form. The synergids are largely vacuolated at the base, with a dense mass of striated cytoplasm in the upper part and the nucleus at the junction of the two zones, while just below the dense cytoplasm there is a hook or notch in their contour, which does not appear to be due to plasmolysis (Text-figs. 26, 27, 33, and Plate viii, fig. 8). The egg, as usual, has the nucleus in the lower part and large vacuoles in the upper part (Text-figs. 23, 26, 31, 32).

The variations of arrangement are in the position of the egg, which may be below or beside the synergids. In case it is below them their great length causes the egg to be half-way down the sac, sometimes even below the polar nuclei (Text-figs. 26, 27). A case in which it was level with the synergids is shown in Text-figures 32 and 33, which are consecutive sections. Cases where the egg had been below the synergids before fertilization are shown in Text-figures 36 and 39*b*. The egg is considered to be drawn up to the top of the sac after fertilization by adhesion to the synergids that are being resorbed. When the egg is level with the synergids it is attached to the embryo sac wall at the top or just below the top (Text-figs. 23, 32, 33, 58, 59; Plate viii, fig. 9).

The egg apparatus as described above is generally in line with that described by Guignard (1881, p. 28) for several species of *Acacia*. Weinstein (1926, p. 254) recorded the disappearance of the synergids before fertilization in *Phaseolus vulgaris*. Saxton (1907) makes no reference to cell formation in the egg apparatus of *Cassia tomentosa*, and figures only nuclei (Fig. 10). Dahlgren (1928) has reviewed the records of the presence of a hook or notch on the synergid. In a list of plants in which it had been recorded up to about 1928 (pp. 434–7) he mentions no Leguminosae. *Acacia Baileyana* must now be added to the list. Of the Rosales, he only mentions those recorded by Pace (1912), namely: *Parnassia palustris*, *Saxifraga cordifolia*, *Heuchera brixoides* and *Drosera rotundifolia*; and by Himmelbaur (1911, fig. 19), *Ribes pallidum*. He concludes that the notch is generally a true structure and not due to plasmolysis (pp. 437–8), arising through the mechanics of development ("dürfte ihr Entstehen allein von entwicklungs-mechanischen Ursachen bedingt sein"), that it may or may not appear in one plant, and that certain families more than others are liable to manifest the phenomenon (p. 441).

Polar Nuclei.—The antipodal polar nucleus migrates towards the egg near which it and the upper polar nucleus remain associated (Text-figs. 23, 26, 27; Plate viii, fig. 8). They are so distorted by the starch grains that it is impossible to determine whether they differ in size. Their limits are so obscured by the starch grains that sometimes the only clear indications of them are the two large nucleoli (Plate viii, fig. 8). Their distortion and unfused condition up to and during fertilization can be seen in Text-figures 26, 27, 32, 33, 40 and 42.



Text-figures 30*a*-43.—Stages of fertilization; × 1,300. 30*a*, *b*, In the one embryo sac, the male nuclei against a polar and the egg nucleus respectively. Chromosomes definite (13). 31, Male nuclei enlarging against the egg and polar nuclei, chromosomes still definite (13). 32, 33 (consecutive sections), Male nuclei with chromosomes losing definition, against the egg and polar nuclei. 34*a*, *b*, Male nuclei approaching the resting condition against the polar nuclei and egg nucleus. 35*a*, *b*, *c*, Three consecutive sections showing the primary endosperm nucleus with three nucleoli and about thirty-nine spongy prophase chromosomes, while the zygote shows a large and a small nucleolus in the resting nucleus. The tube nucleus, *tn*, is outside the zygote. 36-38, 41, The zygote,

In *Lilium martagon*, Guignard (1899, p. 865) described the upper polar nucleus to be larger than the egg nucleus, as is recorded here; but it could not be determined whether *Acacia Baileyana* agrees in the larger size of the lower polar nucleus. The time of fusion of the polar nuclei seems to be indefinitely distributed among the Leguminosae. In the Papilionaceae, fusion is either (1) before fertilization, (2) during fertilization, or (3) variable in time. Records of (1) are a statement of its general occurrence by Guignard (1881, p. 142) and for *Crotalaria sagittalis* by Cook (1924, p. 440); of (2) are a statement of its occurrence in some Vicieae by Guignard (loc. cit.) and in five species from among *Trifolium*, *Vicia*, and *Medicago* by Martin (1914, p. 163); of (3) are statements of its occurrence in *Phaseolus vulgaris* by Weinstein (1926, pp. 254–5) and in *Medicago sativa* by Reeves (1930*b*, p. 243). In the Caesalpineae, Guignard (1881, p. 142) says polar fusion is before fertilization; confirmed by Saxton (1907, p. 4) for *Cassia tomentosa*. In the Mimoseae, Guignard (1881, pp. 28 and 142) describes the fusion before fertilization, but in *Albizzia lebbek* (Maheshwari, 1931, p. 248) and *Acacia Baileyana* it is not before fertilization. Thus the rarer occurrence, the late fusion, seems to be shared by some Mimoseae and some Papilionaceae. In *Myricaria germanica*, Frisendahl (1912, p. 54) records the fusion of the polar nuclei very late, after the division of the zygote, and connects it with the reduced endosperm formation. There is a suggestion in this that the late fusion is an advanced condition. But in some Australian plants recently examined, the more advanced types show fusion before fertilization (*Styphelia longifolia* and *Dampiera stricta*—Brough, 1924, p. 171 and 1927, p. 487; *Doryanthes excelsa*—Newman, 1929, p. 416), and the less advanced during fertilization (*Grevillea robusta*—Brough, 1933, p. 55; and *Acacia Baileyana*).

Antipodals.—The antipodals are cells (Text-figs. 24, 25) and are still strongly organized at the time of the formation of the primary endosperm nucleus (Text-fig. 40), but disintegrate soon afterwards.

Guignard (1881, p. 141) describes the antipodals in the Papilionaceae as generally having a delicate membrane and degenerating before fertilization, confirmed by the work of Martin (1914), Cook (1924, p. 441), and Weinstein (1926, p. 254); while in the Caesalpineae and Mimoseae they are more robust and persist till about or after fertilization as described by Saxton (1907, p. 3) for *Cassia tomentosa* and by Maheshwari (1931, p. 248) for *Albizzia lebbek* respectively, and above for *Acacia Baileyana*. The last two sub-orders possess the primitive feature in common, as would be expected. *Grevillea robusta*, an Australian Protead, also has persistent antipodals (Brough, 1933, p. 55).

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showing the nucleus passing from the resting condition to just before the organization of the prophase chromosomes, and the two unequal nucleoli becoming equal and finally appearing to have fused. 39*a*, The two polar nuclei after the second male nucleus has fused with one of them. The small male nucleolus is in the polar nucleus lying below the second polar nucleus, whose nucleolus is not shown. 39*b*, From the same sac as 39*a*, showing the zygote with the nucleus having passed back from prophase to the resting condition. 40, Base of sac, earlier than 39*a*, *b*, showing the enlarged resting male nucleus lying against one polar. Note the different sizes of the nucleoli; also the antipodal cells. 41, See above. 42, The two polar nuclei after the fusion of the male nucleus with one of them. One polar nucleus, with the small male nucleolus in it, is lying above the other polar nucleus. 43, Two polar nuclei containing one and two small nucleoli representing probably three male nuclei.

In all these figures note the starch which disappears from the later zygotes, and in the sac finally shows signs of corrosion (43).

Fertilization.

The Nuclei at the Time of Contact.

Both male nuclei at the time of contact show 13 deeply-staining chromosomes. At the same time the egg and polar nuclei have coarsely reticulate chromatin with a large nucleolus (Text-figs. 30*a*–31). The shape of the male nuclei is very slightly elongated with occasionally a slight curve, or they may be sometimes apparently spherical.

It seems general among the Angiosperms that when the male gamete discharged into the sac is a cell with or without a membrane, it is finally the naked nucleus that makes contact with the egg or polar nucleus. In *Valisneria spiralis*, however, Wylie (1923, p. 196) describes a cell in contact with the egg and says that some or all of the male cytoplasm enters the egg.

The male nucleus of *Acacia Baileyana* is definitely not vermiform, being only very slightly elongated if not spherical. In a recent text-book of Plant Cytology, Guilliermond, Mangenot and Plantefol (1933, p. 788) say that the male nucleus is as a rule ("suivant la règle générale") vermiform and spiral. From the literature available to me certain considerations arise that may modify this statement. The following are records of vermiform male nuclei: *Lilium martagon* and *Fritillaria tenella* (Nawaschin, 1898, p. 378), *Lilium martagon* (Guignard, 1899, p. 867), *Caltha palustris* (Thomas, 1900*a*, p. 318), *Lilium martagon* and *L. auratum* (Blackman and Welsford, 1913, p. 112, and Welsford, 1914, p. 267), *Trillium grandiflorum* and *Lilium martagon* (Nothangel, 1918, pp. 147–9) and *Triticum durum hordeiforme* Hort. var. *cubanka* (Sax, 1918, p. 315). These plants belong to the Monocotyledons or Ranales. The following are records of elliptical or spherical male nuclei and the plants belong to the Dicotyledons other than the Ranales: *Myricaria germanica* (Frisendahl, 1912, p. 52), *Asclepias cornuti* (Finn, 1925, p. 19), *Phaseolus vulgaris* (Weinstein, 1926, p. 255), *Theobroma cacao* (Cheesman, 1927, fig. 10), *Viola odorata* var. *praecox* (Madge, 1929, p. 567), *Grevillea robusta* (Brough, 1933, Text-fig. 69), and now *Acacia Baileyana*. This apparent difference of distribution must be regarded with caution as the numbers are small. It may also be noted that the vermiform nuclei are described in the earlier records.

From the literature quoted in the last paragraph with the addition of a further paper on *Caltha palustris* (Thomas, 1900*b*, p. 531), it appears that *Acacia Baileyana* follows the general rule in the greater increase in size of the male nucleus that fuses with the polars. This is probably to be correlated with the longer period during which it is free in the embryo sac. The male nuclei usually attain a spherical form before or after contact, but this is prevented for the enlarging second male nucleus in *Acacia Baileyana* by the starch grains.

Cases recorded other than that of *Acacia Baileyana* where the male nuclei on contact are not in a typical resting condition are *Fritillaria pudica* (Sax, 1918, p. 313), with a dark staining network; *Myricaria germanica* (Frisendahl, 1912, p. 52) with a kind of telophase condition not showing definite chromosomes; and *Lilium martagon* and *L. auratum* (Welsford, 1914, p. 268) with a spireme. The complete resting condition has been described in many plants, for records of which reference should be made to the literature quoted in the two preceding paragraphs with the addition of *Cypripedium* (Pace, 1907, p. 359), *Oenothera* (Ishikawa, 1918, p. 294) and *Valisneria spiralis* (Wylie, 1923, p. 196 and Fig. 8). The resting condition at the time of contact of the male nuclei is characteristic of the

Coniferales (Guilliermond, etc., 1933, pp. 784–5) and of *Bowenia* and some other Cycadales (Lawson, 1926, p. 377). Thus the distribution among the Phanerogams of the condition of the male chromatin at the time of contact appears to be indefinite.

The Course of Fusion.

The earliest stage of fertilization seen was when one male nucleus was within the egg cell and the other was closely adjacent to one of the polar nuclei (Text-figs. 30*a*–31). There does not seem to be any uniform direction of approach of the male nucleus to the egg nucleus.

The chromatin changes are similar in both male nuclei during fertilization. Fusion with the egg takes place in advance of that with the polar nucleus, though the times are variable. In triple fusion, about the middle of the sac, the second male nucleus fuses with one polar nucleus, the product then fusing with the other polar nucleus. The chromatin of the egg and polar nuclei undergoes no apparent change during fertilization.

As fusion approaches, the male nuclei enlarge, their chromosomes become less definitely organized (Text-figs. 31–34*b*), and probably in both cases they attain the resting condition with a nucleolus and coarse reticulum as observed in the second male nucleus (Text-fig. 40). With the disappearance of the male nucleus from outside the egg and polar nuclei, the latter two each acquire an extra nucleolus which is small and of similar size to that of the resting male nucleus seen in contact with the polar nucleus (Text-figs. 36, 39*a*, 42). The fusion therefore takes place in the resting condition, the male nuclei having just passed through telophase. In the zygote, the nucleoli become equal in size and ultimately fuse (Text-figs. 37, 38, 39*b*, 41). About the time of fusion of the nucleoli the chromatin of the zygote appears to enter on a spireme stage preparatory for division (Text-figs. 38, 41), but as chromosomes are about to be organized at the periphery, the nucleus returns to the resting condition which it maintains for a long time (Text-figs. 39*b*, 59). In the polar position there are visible normally the two large nucleoli representing the polar nuclei and one small nucleolus representing the male nucleus (Text-figs. 39*a* and 42). Only one example of the primary endosperm nucleus was seen, and that was in prophase of division with about 39 rather spongy chromosomes and three nucleoli (Text-figs. 35*a-c*). It seems that the polar and male nucleoli may not fuse on account of the rapid onset of division of the primary endosperm nucleus.

As well as the positive evidence of fertilization and triple fusion given above, there is the indirect evidence of chromosome number. The number of chromosomes found in the last division in the embryo sac (and therefore in the egg) and in the sperm nucleus is half that found in various sporophytic tissues (Newman, 1934). The number of chromosomes found in the sperm and polar nuclei, similarly, is one-third the number found in the division of the primary endosperm nucleus and of its two daughter nuclei (loc. cit.).

There seems to be no definite distribution among the Angiosperms of the chromatin changes during fertilization. In general, the nuclei taking part may be in the resting condition or prophase at the actual time of fusion (Guilliermond, etc., 1933, pp. 788–9). If the male nuclei undergo change of phase after they enter the sac, obviously the nucleus that fuses later will have proceeded further in its change than the other one. For instance, here in *Acacia Baileyana*, the male

nucleus that fuses with the polar nucleus proceeds further into the resting condition than that fusing with the egg; and in *Triticum durum hordeiforme* in the triple fusion the second male nucleus (also the polar nuclei) passes on to the metaphase before fusing, while the first male nucleus and the egg nucleus fuse earlier, in the spireme condition (Sax, 1918, pp. 316–7). In *Fritillaria pudica* the male nuclei usually pass into the resting condition for fusion, but sometimes they pass beyond that into a spireme (op. cit., pp. 313–5). Fusion with the male nuclei at the very end of telophase, as in *Acacia Baileyana*, is found in *Myricaria germanica* by Frisendahl (1912, p. 49). In *Phaseolus vulgaris*, Weinstein (1926, p. 255) has described all the nuclei in the resting condition at the time of fusion.

The relative times of the two fertilizations and the order of the triple fusion in *Acacia Baileyana* present no unusual features (see Guilliermond, etc., 1933, pp. 788–9), the order of the triple fusion (male with one polar, then with the other polar) being of a less general type.

In view of a later discussion, attention is called to the appearance of the nucleoli in the fusion nuclei, whether endosperm or zygote. As described above, after fusion there is to be seen a smaller additional nucleolus in the fusion nucleus. Cheesman (1927, p. 114) in *Theobroma cacao* has described two and three nucleoli in the fertilized egg and polar nuclei respectively. The smaller size of the additional nucleolus is recorded in both cases for *Oenothera* by Ishikawa (1918, p. 294) and in the primary endosperm nucleus of *Viola odorata* var. *praecox* by Madge (1929, p. 570).

MULTIPLE FUSION (POLYSPERMY).

Direct Evidence.

Several cases were observed where at the polar position there were two nuclei (after fertilization of the egg) that together had more than three nucleoli between them—mostly 5 nucleoli (Text-fig. 43). This would not attract much attention, but for the fact that two of them (not in the one nucleus) were always much larger than the others and of a size similar to that of the nucleoli of the polar nuclei before fertilization, and that the others were of a size similar to that of the additional nucleolus in the zygote and of the nucleolus in the resting male nucleus (Text-fig. 43; cf. Text-figs. 35*b*, 36, 40, 42). The immediate inference is that these nucleoli are evidence of additional sperms. The presence of the starch grains made it impossible to observe whether any of these small nucleoli were in separate nuclei. There were two possible cases of four sperms in the sac at the time of contact with egg and polar nuclei. Other direct evidence, that is to say, phenomena that are capable of being in the line of causation (not results), is given below.

Passing backwards in time: Two pollen tubes have been seen to penetrate to one embryo sac in several cases, though the difficulties of preparation have prevented a correlation of this occurrence with the presence of extra nucleoli at the polar position. The naked ovule is a suitable object for the attack of more than one pollen tube. One fully germinated pollinium (the unit of pollination) provides 16 tubes for the 12 ovules in the carpel; so that there are 4 surplus pollen tubes. Two pollinia have been seen germinated on one stigma in several cases, whence the 32 pollen tubes would provide two for each ovule and eight surplus. In the one case where three pollinia were seen on one stigma there would be four tubes for each ovule.

In view of the foregoing, one would be surprised, not at the occurrence of polyspermy, but at its absence. There was never any suggestion in the preparations of additional male nuclei associated with the egg.

Indirect Evidence.

As polyspermy is only suggested in connection with endosperm formation, the phenomena considered here can be little more than chromosome numbers. The normal number of chromosomes in the endosperm is 39; and in most endosperms none of the division figures seen suggested any deviation from this number. Two aberrant endosperms were found.

In one endosperm the division figures showed an enormous number of chromosomes and the metaphase plates frequently appeared branched in side view (Plate viii, fig. 7). The examination of such a plate in polar view is complicated by the presence of the vertical arm, on which the chromosomes would appear as paired halves. Text-figure 28 shows a plate of this kind. Allowing for the vertical arm, there are considered to be approximately 104 chromosomes represented; but if certain paired structures are pairs of half chromosomes at the inclined edges of the plate (cf. Plate viii, fig. 7), the number is reduced to approximately 91. These numbers are 8ϕ and 7ϕ respectively, and would be attained if 6 or 5 sperms took part in endosperm formation. All plates in this endosperm appeared of similar size.

In another endosperm, the chromosome plates of the division figures show definite differencees of number. One metaphase was observed in polar view to have 52 (4ϕ) chromosomes (Text-fig. 29), a nucleus in prophase was estimated to have 13 (ϕ) chromosomes, and another in anaphase had 13 (ϕ) chromosomes in each group. Such a condition could arise if three sperms fused with one polar nucleus and the second polar nucleus divided without fusion, or if two sperms and two polar nuclei fused while the third sperm divided without fusion.

It may be objected that it is well known that nuclear fusions and abnormalities of nuclear division are often found in endosperm tissues. But it is difficult to derive the numbers found here from nuclear fusions or failures of cell division (some of the latter have been observed) based on the normal endosperm number of 39. In view of evidence of polyspermy in other plants, a case has been made out for further investigation.

Discussion of Polyspermy.

Even if the above interpretation of polyspermy in endosperm formation be not proved by further work, it will have served a purpose in directing attention to the presence of extra sperms in the embryo sac of Angiosperms; for in three recent text-books of a morphological-cytological nature by Sharp (1921), Schürhoff (1926) and Guilliermond, Mangenot and Plantefol (1933) there is only slight reference to polyspermy, and then it is considered only in association with embryo formation. This association is the only one entertained in the literature that has come under my notice.

It may be objected that the phenomenon that drew attention to the possibility of polyspermy—the extra nucleoli after polar fusion—is not a valid criterion. This objection was made by Ernst (1902) when describing double fertilization in *Paris quadrifolia* and *Trillium grandiflorum*; Nothangel (1918, p. 150), in *Lilium martagon* and *T. grandiflorum*, described the male nucleus without a nucleolus before fusion and the zygote nucleus with various nucleoli after the

fusion. Sax (1918, p. 313) describes the zygote of *Fritillaria pudica* as having several extra nucleoli. On the other hand, Campbell (1911, p. 783) describes the polar fusion nucleus of *Pandanus coronatus* as showing the nucleoli of the component nuclei—2–6 nuclei being concerned. Doubtless, by itself, increase in the number of nucleoli would be of little value for determining polyspermy, but when the increase appears as an occasional feature in a definite manner, and is associated with other phenomena pointing to the same possibility, it must be allowed to bear some weight.

It is not unreasonable to suggest a multiple fusion of nuclei available in the embryo sac, for there is the example of *Pandanus coronatus* quoted above, and the multiple fusions in the formation of the primary endosperm nucleus of *Peperomia pellucida* (Johnson, 1900). Weinstein (1926, p. 255) has described a possible case of the fusion of a tube nucleus and a male nucleus with a polar nucleus in *Phaseolus vulgaris*. In reference to the fact that sometimes in *A. Baileyana* two primary endosperm nuclei of different chromosome constitution may be formed from amongst the polars and sperms, it is to be noted that Campbell (1911, p. 783) has described two primary endosperm nuclei in *Pandanus coronatus*, and Frisendahl (1912, p. 50) suggests that in *Myricaria germanica*, though only one sperm can fuse with one polar, both polars might fuse with a sperm each.

There are a number of records of extra sperms in the embryo sac, but attention seems only to have been directed to the possibility of polyembryony or polyploidy arising therefrom. From this point of view, Schürhoff (1926, pp. 312–3) discusses the dispermy recorded in *Gagea lutea* by Němec (1912, p. 173) and in *Saxifraga granulata* by Juel (1907, p. 18), and though he records Derschau's (1918, p. 262) observation of dispermy with an antipodal in *Nigella arvensis*, he does not consider any case of it in connection with endosperm formation (pp. 338 et seq.). Ishikawa (1918, p. 295) describes extra sperms in the embryo sac of *Oenothera*, but neither he nor Gates (1928, p. 428) who discusses it considers the possibility of polyspermy with the polar nuclei. As many as six sperms have been found to enter the embryo sac of *Myricaria germanica* by Frisendahl (1912, p. 49) and of *Juglans nigra* by Nawaschin and Finn (1913, p. 19).

The formation of endosperms with more or less than 3ϕ chromosomes is not unknown. Renner (1914) and Ishikawa (1918, p. 295) record 2ϕ endosperms in *Oenothera* where there is only one polar nucleus. Sax (1918, p. 313) describes in *Fritillaria pudica* the disintegration of one of the chalazal nuclei at the 4-nucleate stage and the doubling of the chromosomes of the other at the third division, wherefore the endosperm has 4ϕ chromosomes. The suggestion that one of the extra male nuclei may have divided without fusion in *Acacia Baileyana* is not without a parallel in that Chamberlain (1916, p. 364) records the division of extra sperms in two cases in the Cycad *Stangeria paradoxa*.

By some authors the endosperm is thought to be a degenerate embryo. Sargant (1900, p. 708) suggests that the third nucleus in the triple fusion secures the degeneracy of the resulting tissue. But in *Acacia Baileyana*, the endosperms appearing polyploid do not seem any more "degenerate" than normal ones. Campbell (1902, pp. 785–6) considers that the fusion of the second male nucleus with the only available nucleus in the sac is not surprising and must be regarded as more or less accidental. The case of *Peperomia* is for Coulter

(1911, p. 383) "positive evidence that in the embryo sac there is some condition that favours nuclear fusions, quite apart from what may be called sex attraction", and he considers that "the product of such fusions . . . is simply *growth* and not *organisation*" (page 384). He concludes that triple fusion, etc., is not necessarily of phylogenetical significance, but rather a physiological problem of the conditions in the embryo sac favourable to miscellaneous nuclear fusions. Polyspermy in connection with endosperm formation, as suggested for *Acacia Baileyana*, is therefore a phenomenon reasonably to be expected.

Seed Production.

CHANGES IN THE CARPEL.

At the time of fertilization, the carpel is not more than 0·5 mm. long and, if all the ovules develop to seeds, it is about 100 mm. long at the time of dehiscence. The outward sign of post-fertilization change is that the carpel turns pink, then bright crimson, which slowly becomes duller till the full-sized pod turns green. The seeds are equally spaced in the mature pod, showing that in the young carpel they are not in pairs, as might be thought from transverse sections, but are really alternating. The breadth and length of the carpel increase for a time, and then length alone till the pod is about 25 mm. long, when the breadth continues to increase with the length. The final breadth is about 12 mm. The seeds whose funiculus has increased to 5 mm. in length stand along the middle line of the pod with their long axis parallel thereto. The significant histological changes and the dehiscence mechanism have been described in a previous paper (Newman, 1934).

CHANGES IN THE OVULE TISSUES.

The Receptacle (Nucellus).

At the time of fertilization, the embryo sac has destroyed practically all the parietal tissue above and the receptacle tissue to the side. Little more than the multiple epidermis above, and one or two layers at the side, is left. This condition persists for some time (Text-figs. 13, 14; Plate viii, figs. 9, 12, 14). In the older of these stages it is probable that some of the layers are of secondary growth replacing loss by resorption. The endosperm-filled sac is enclosed on the upper part by epidermal tissue only, which is multiple at the top (Plate viii, fig. 16), the chalazal tissue, though it becomes massive by secondary growth (Plate viii, figs. 13, 14, 16, 17), is finally overtaken by the growth of the sac (Plate viii, fig. 18). The antipodal pocket, bordered by thick-walled cells, persists into the mature seed and at some stages is overarched by the endosperm (Plate viii, figs. 9, 13). There is a column of elongated cells below the antipodal pocket connecting the vascular bundle of the ovule with the embryo sac (Plate viii, figs. 13, 16).

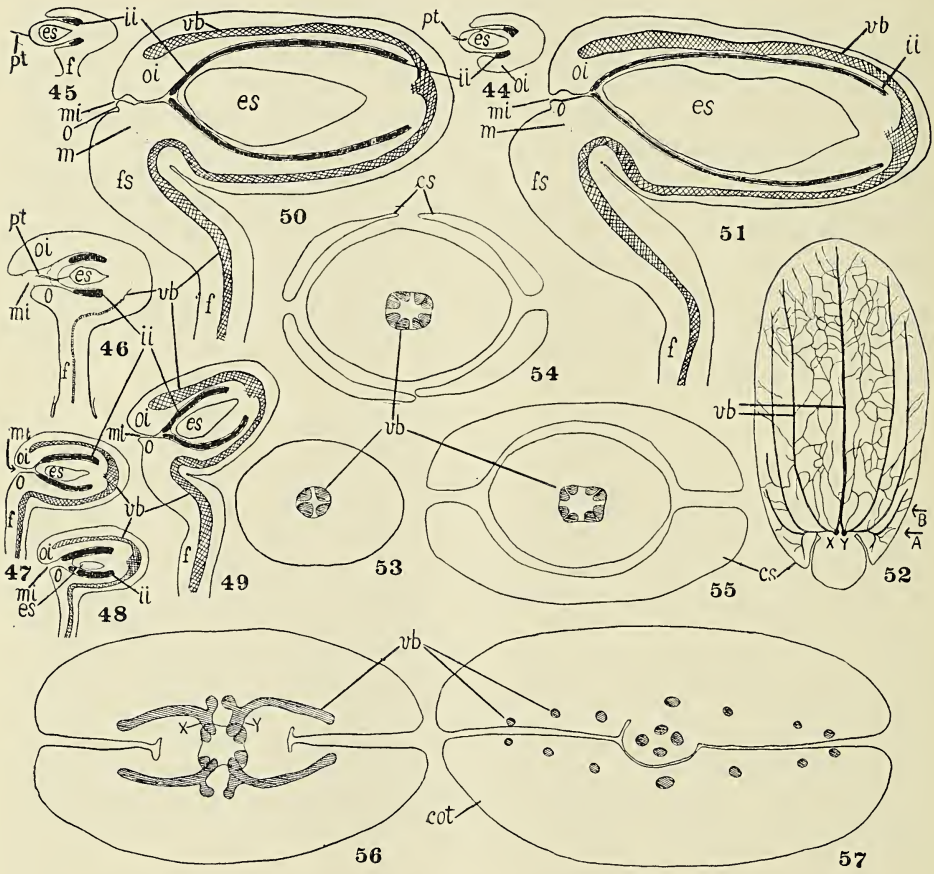
Guignard (1881, p. 29) describes the young embryo of the Acacias as in contact with the multiple epidermis of the nucellus. In two other Australian Dicotyledons with a massive integument, the embryo sac crushes all (*Aegiceras majus*, Carey and Fraser, 1932, p. 344), or almost all (*Grevillea robusta*, Brough, 1933, p. 61), of the nucellus after fertilization.

The Integuments and Funiculus.

One of the first microscopic changes after fertilization is the development of the integuments, so that the ovule, which was completely naked, acquires fully

developed integuments, forming a micropyle by the time of the first division of the zygote. The inner integument is epidermal in origin and its primordium is the first to appear (Text-fig. 22). The outer integument is subepidermal in origin. When growth finally begins, the outer integument exceeds the inner, closing over the nucellus before the inner is level with the top of the embryo sac (Text-fig. 46). The inner integument finally forms the lower part of the micropyle that is formed round the projecting remains of the pollen tube.

The inner integument is a simple urn-shaped upgrowth from a ring, two cells broad, around the chalazal epidermis. The region of the chalaza from



Text-figures 44-51.—L.Ss. showing the development of the seed after fertilization. All, except 44, are parallel to the plane of the funiculus, 44 being perpendicular to that plane. The inner integument is shown dead black, the vascular bundle is cross-hatched. The remains of the pollen tube are seen in 44-46. 44-46, × 60; 47-51, × 30.

Text-figure 52.—Cotyledon showing the vasculation on the inner face. X and Y, the two bundles leading from the embryo axis (cf. 56). The arrows A and B indicate the planes of section shown in 56 and 57; × 7.

Text-figures 53-57.—A series of transverse sections of an embryo at different levels from the radicle up to the base of the cotyledons. 53 is just below the limit of the cotyledon spurs. X and Y correspond to X and Y in 52. 56 and 57 are at the level of A and B in 52. × 25.

which the outer integument develops can be regarded as a ring containing a gap into which is fitted the funiculus. The final form of the outer integument is that of an urn with a gap down one side into which is fitted the funiculus. As this "urn" is developed by upgrowth of the broken ring primordium, whose "broken ends" are in organic meristematic connection with the funiculus, it appears to pull the funiculus parallel with the long axis of the growing seed (Text-figs. 45–47). The use of the word "pull" is doubtless inaccurate, but it describes the appearance. The real cause is probably differential growth of tissues in the funiculus, producing curvature. The general development of the integuments and funiculus is shown in Text-figures 44–51. There is a second bend in the funiculus, level with the top of the nucellus, which brings it back on itself along the surface of the seed for some distance. From there it is turned at right angles towards its insertion on the carpel (Text-figs. 49–51). From the second bend in the funiculus there is an outgrowth (*o*) to complete the micropyle (Text-figs. 46–51).

There is great difference between the integuments in size. The inner is only two cells thick, except at the micropyle of seeds well advanced (Plate viii, figs. 9, 12, 14, 16). Its inner layer is the more robust and survives being crushed by the growth of the contents of the embryo sac (*i.i.l.* in Plate viii, figs. 16, 17). The outer integument is massive and has a single vascular bundle which, with the vascular bundle of the funiculus, lies in the broad plane of the seed (Text-fig. 51; Plate viii, figs. 16, 19). The micropyle can be identified in the full-grown seed (cf. Plate viii, fig. 16, of half-grown seeds).

On the free part of the funiculus, parallel with the seed, growth in thickness occurs so that a considerable swelling takes place, mostly on the side away from the seed. This results in a cushion of pithy tissue lying against the side at the micropylar end of the seed (Text-fig. 51; Plate viii, figs. 19, 20). This tissue contains chlorophyll and does not shrivel away when the seed dries. It is usually referred to as an "aril". Ontogenetically it is a swelling of the funiculus, semi-circular in transverse section and situated some distance from the insertion of the funiculus on the chalaza.

In their order of origin and in their form and relative rate of growth, the integuments are very similar to those of most of the other Leguminosae already described; but they differ in the remarkably late time of their development, there being in the literature no suggestion that the integuments do not continue to grow immediately after their initiation. Normally, integuments are completed by the time the embryo sac reaches maturity (Martin, 1914; Weinstein, 1926, p. 252; Reeves, 1930*b*; Maheshwari, 1931; also Péchoutre, 1902, p. 148, for the Rosaceae). Guignard (1881, p. 27) describes the integuments in *Acacia* as being level with the top of the nucellus when the embryo sac is full size. It is possible that he examined carpels not long after fertilization. He also describes the micropyle as displaced towards the funiculus (p. 28), but in his figure (fig. 11) it is not so far displaced as it is in the outer (only) integument of *Cassia tomentosa* described by Saxton (1907, p. 2). At the same time Saxton describes the extraordinary phenomenon of the outer integument being developed to the full on the funicular side of the nucellus. Pammel (1899, p. 216) relates the seeds of *Acacia* to those of *Desmanthus* (Eumimoseae) and *Cassia* (Caesalpineae) on account of the inner integument having been destroyed. He is probably neglecting the micropylar region which we have seen to persist in *Acacia*

Baileyana. Allowing for this fact, it would still appear that *Acacia* and *Desmanthus* (Mimoseae) are in this more like the Papilionaceae than the Caesalpineae in which the inner integument may have more than four layers of cells (Pammel, 1899, p. 117).

Guignard (1881, p. 28) describes a vascular bundle in the outer integument of Acacias as in the species here described. Speaking of the vasculation of the ovule, Le Monnier (1872, p. 279) says: "Nous voyons donc la nervation tendre vers une forme réduite, déjà signalée et désignée sous le nom de nervation en *bouche* complète". He says that this simple vasculation is in most Caesalpineaceae and Mimosaceae (*Albizzia, Mimosa, Acacia*), and instances Papilionaceae with complex vasculation.

The funicular swelling or aril may be regarded as a third integument that arises late. Among the Dilleniaceae (Gilg, 1895, p. 107), Leguminosae (Taubert, 1894, p. 95) and Passifloraceae (Harms, 1895, p. 77) there is every gradation from less than the condition described here to complete envelopment of the seed, even of anatropous seeds. The lateness of development of the first two integuments in *Acacia Baileyana* shows that lateness of development is no bar to integumental status.

General.

Rates of enlargement of the different parts of the seed are not equal, for the endosperm may fill the sac tightly at one time and loosely at other times (Plate viii, figs. 13, 16, 17). Similarly the embryo may sometimes, after resorption of the endosperm, be loose in the cavity of the sac.

The mature seed is about 6 × 3·5 × 2 mm. There is considerable shrinkage on drying (Plate viii, fig. 20). The epidermis of the testa is composed of radially elongated, indurated cells which are continued across the insertion of the aril (Text-figs. 50, 51; Plate viii, figs. 16, 17, 19). The testa, though composed of outer integument and funiculus, has no differentiation on its surface.

The columnar cells of the epidermis of the seed are called Malpighian cells (after Malpighi, who first observed them) by Pammel (1899, p. 94), who says they are nearly universal in the Leguminosae. They have been described more recently by Elford (1930, p. 94) in *Albizzia lophantha*, and by Martin (1914, p. 156) in *Trifolium pratense*, while Cook (1924, pp. 443–4) describes the double row of them across the funicular swelling (a cleavage plane) in *Crotalaria sagittalis*. Pammel (loc. cit.) rightly objects to the term "palisade cells", as being likely to cause confusion with palisade mesophyll.

CHANGES WITHIN THE EMBRYO SAC.

General.

Though the primary zygote nucleus is formed before the primary endosperm nucleus, the latter divides first (Text-fig. 58). The sac soon begins to elongate rapidly, separating the zygote from the earlier endosperm nuclei, which appear to be formed in the lower part of the sac (Text-figs. 58, 59; Plate viii, fig. 9). The antipodals quickly degenerate after formation of the primary endosperm nucleus. The growth of the embryo and endosperm does not keep pace with the resorption of the enlarging tissues round them, so that each usually appears within a clear zone of resorption (Plate viii, figs. 13, 16–18). By the time the seed is full size, the embryo has resorbed all the endosperm (Plate viii, fig. 18). The starch disappears from the sac about the 8-nucleate stage of the endosperm.

There is a slight possibility that in the Papilionaceae the division of the zygote and primary endosperm nucleus may be tending to less separation in time, than is the case in the Mimoseae. Weinstein (1926, pp. 257–8) describes the division of the zygote as indefinite in time about the 4- or 8-nucleate endosperm stage in *Phaseolus vulgaris*. Martin (1914) says that in *Trifolium pratense* (p. 158) the endosperm usually precedes the zygote, and in *Vicia americana* (p. 162) the zygote and endosperm nucleus divide about the same time. In *Acacia Baileyana* the zygote does not divide before the 8-nucleate endosperm stage, and Maheshwari (1931, p. 250) records the same for *Albizzia lebbek*.

Pammel (1899, pp. 117–8) quotes many authors who say that there is no endosperm in the mature seed of the Leguminosae. He says that is anatomically not true, for there are usually one or a few layers left, and that *Acacia* seeds, having a much reduced endosperm, are anatomically closely related to those of *Desmanthus* and *Cassia* (p. 216). Weinstein (1926, p. 257) says that the embryo digests almost all the endosperm in the Papilionaceous *Phaseolus vulgaris*. Pammel (1899, p. 216) describes a single persistent layer of endosperm cells (aleurone layer) in *Acacia filicina*. Guignard (1881, p. 45) says that the persistence of the endosperm is variable in the Mimoseae, but it is usually all resorbed in *Acacia*. No trace of endosperm was observed here in the mature seed of *Acacia Baileyana*.

The Endosperm.

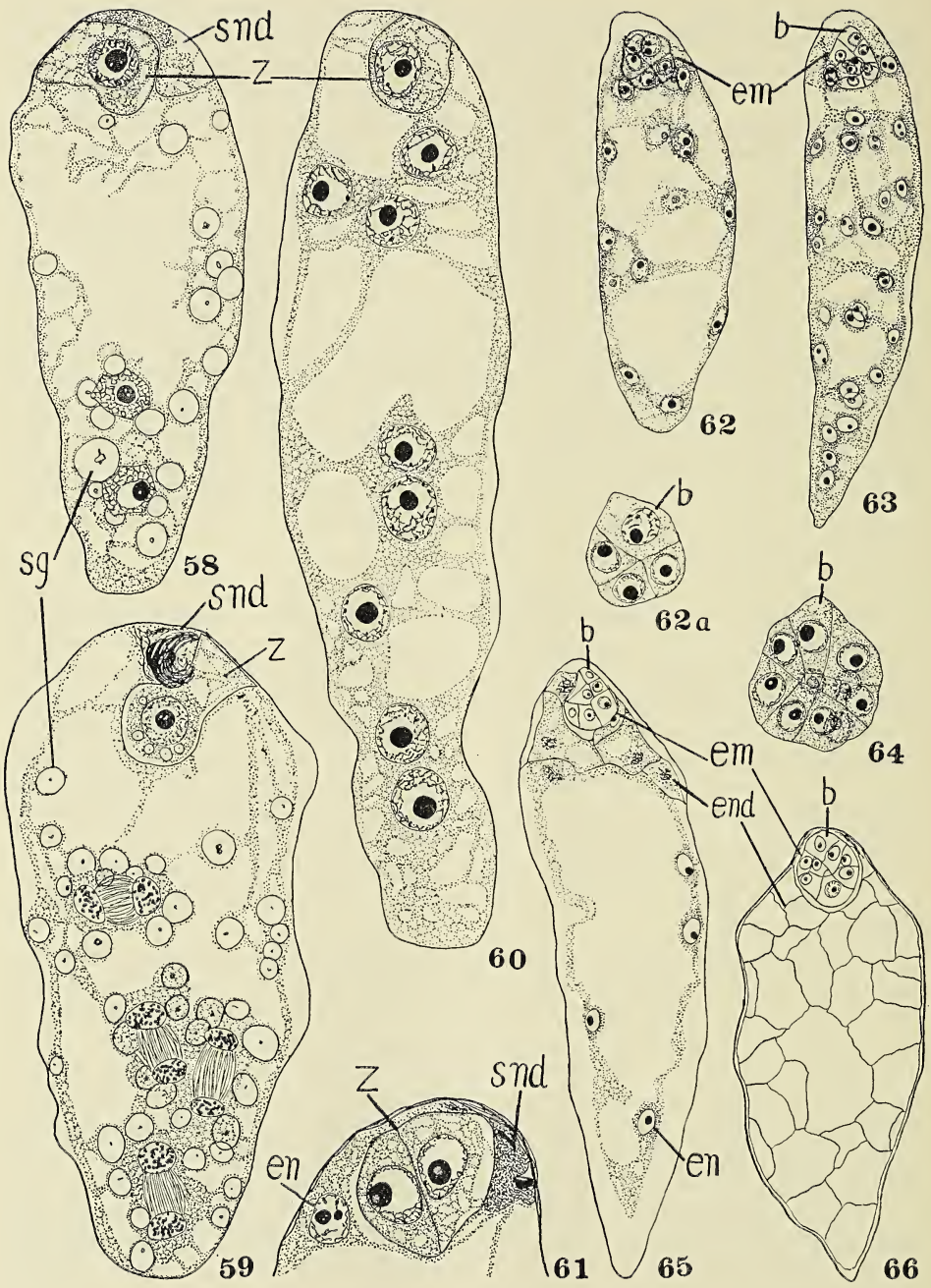
The spindles of the first two divisions of the endosperm appear to have been vertical, judging from Text-figures 58 and 59. The four resulting nuclei take a peripheral position (Plate viii, fig. 9). After the simultaneous division of these nuclei (Text-fig. 59), some of the eight formed collect round the zygote (Text-fig. 60) which is often made difficult of observation in the later stages by the collection of nuclei round it (Text-figs. 62, 63). The divisions of the endosperm nuclei after about the eight-nucleate stage are not always simultaneous. The free endosperm nuclei lie in a peripheral network of cytoplasm that is more closely meshed at the ends of the sac (Text-figs. 62, 63; Plate viii, fig. 12).

Cell formation in the endosperm begins at about the 64-nucleate stage around the embryo of about 12 cells (Text-fig. 65). Tissue formation is basipetal (Plate viii, fig. 10).

In adult or nearly adult endosperms it sometimes appears as if there is the differentiation of a slightly developed "basal apparatus" (cf. Schürhoff, 1926, p. 352 et seq.). Any differentiation that does occur is only incidental and not due to any initial organization of the endosperm nuclei. It is due to the course of cell formation which, as it reaches the base of the sac, sets up temporarily one or more "cells" that are multi-nucleate (Plate viii, fig. 11). Though wall formation finally occurs within these "cells", the common wall remains heavier than the other walls of the endosperm (Plate viii, fig. 13). There is considerable variation in the size of the cells of any one endosperm (Plate viii, figs. 16, 17).

The case shown in Text-figure 66 is unusual, for the endosperm seems to have had centripetal cell formation, and that at a very early stage in the development of the embryo (cf. Plate viii, fig. 10). The ovule itself was small for the stages of development of both the embryo and endosperm.

Schürhoff (1926, pp. 574–9) reviews researches on many species of Leguminosae, and records only "nuclear" endosperm, the type possessed by *Acacia Baileyana*. Guignard (1881, pp. 150–1) says that among the Mimoseae,



Text-figures 58-60.—L.S. embryo sac showing the nucleus of the uni-cellular zygote passing from the resting condition towards prophase, and the formation of eight endosperm nuclei. × 733.

Text-figure 61.—Two-celled zygote originally laterally attached. × 733.

Caesalpineae and the Papilionaceae without or with only a rudimentary suspensor, cell formation in the endosperm begins around the embryo of about twelve cells—as in *Acacia Baileyana*; while among the Papilionaceae with a suspensor, cell formation occurs later and later, till in the Vicieae there is no cell formation in the scanty endosperm and the suspensor serves the nutrient function. Recent researches have extended the absence of cell formation to the Genisteae (*Crotalaria sagittalis*, Cook, 1924, p. 443). In *Colutea arborescens*, Němec (1910) found that the chalazal nuclei of the peripheral layer increased greatly in size and became lenticular; cell wall formation began in the micropylar region and spread to hardly half the cavity of the sac, walls not being generally formed between the large chalazal nuclei. The temporarily multinucleate "cells" at the base of the endosperm of *Acacia Baileyana* suggest the beginning of a trend to the above condition, and through it to the condition in some of the Vicieae.

The Embryo.

The zygote, after its partial approach to division, regains the resting condition which it maintains for a long time. Its nucleus has a large nucleolus lying in a central vacuole. The threads of the peripheral chromatin reticulum are coarse and granular at first (Text-figs. 58, 59), but enter into a spireme soon after the eight-nucleate stage of the endosperm (Text-fig. 60; Plate viii, fig. 12).

The first division of the zygote is by a transverse wall, though if the egg is attached laterally, this wall may appear to be nearly vertical (Text-fig. 61 and Plate viii, fig. 14; cf. Text-figs. 58, 60 and Plate viii, figs. 9, 12). Whatever its original position, the young embryo soon appears at the apex of the sac. The second division is by a wall that is nearly vertical (Text-fig. 62*a*), its slight inclination causing the formation of a cell that has something of the appearance of a basal cell, an appearance that is retained by it or its derivative(s) till just before the formation of the primordia of the cotyledons (Text-figs. 62*a*, 64, and Plate viii, fig. 15).

The young embryo develops by irregular divisions from the quadrant stage to various forms of pear shape. It has no suspensor and is of the massive type (Text-figs. 63–6; Plate viii, figs. 15, 16). Plate viii, figure 17, shows the young cotyledons and between them the region whence the plumule will arise, the place and time of origin of the primordial meristems being indefinite.

In the mature seed the embryo occupies all the cavity within the testa except for a small residue of the chalaza and perhaps some liquid of resorption (Plate viii, fig. 18). The plane of the cotyledons is parallel with the broad and long axes of the seed, and is perpendicular to that shown for the cotyledon primordia. It is not known whether this difference of orientation is a frequent feature or not; the similar orientation of young cotyledons to that shown for the old has been seen. The cotyledons are spurred (Text-figs. 52, 54; Plate viii, fig. 18) and have the vascular bundles on the inner (adaxial) face (Text-figs. 52, 56, 57).

Text-figures 62, 63.—Sacs with 16 and 32 peripheral nuclei and 4- and 14-celled embryos (only 6 cells shown in embryo of 63). × 236.

Text-figures 62*a* and 64.—4-celled embryo from 62 and an embryo (not all cells shown) at the stage of about 60 endosperm nuclei. × 453.

Text-figure 65.—L.S. Sac showing the beginning of cell-wall formation around the embryo. × 236.

Text-figure 66.—L.S. Sac showing result of apparently centripetal wall formation in the endosperm of a diminutive seed. × 236.

The radicle is very broad and blunt, with convex sides and well differentiated meristems, but no root cap. The plumule is well advanced in organization, having the pinnae formed on the first leaf (Plate viii, fig. 19) and the primordia of three or four other leaves present (not shown in this figure).

The vasculation of one embryo was examined in detail. In the radicle the stele was tetrarch and approximately square in cross-section, with a side of the square parallel with the plane of the cotyledons (Text-figs. 53–5). In the region of the hypocotyl the bundles in each corner appeared paired. The bundles for the cotyledon arose from the adjacent members of the pairs at the corners on that side (Text-fig. 56). Soon after leaving the stele, each member of the pair of bundles for the cotyledon bifurcated. The adjacent arms of the bifurcations joined to form the midrib of the cotyledon (Text-figs. 52, 56, 57). The distant arms of the bifurcation each give rise to the three lateral and the one spur primary bundles on their respective sides of the cotyledon (Text-figs. 52, 56, 57). Secondary bundles anastomosed between the seven primary ones. The orientation of the stele in the plumule was such that a diagonal of its square outline is parallel with the plane of the cotyledons.

The transverse division of the zygote is universal in the Leguminosae (Guignard, 1881, p. 142), the second division being vertical in the Mimoseae, but, as exampled by *Acacia retinoides*, the walls in the upper and lower halves are at right angles (p. 29). The second division is in the one plane in *A. Baileyana*. The young embryo described by Guignard is very similar to that described above. In common with the other Mimoseae, *A. Baileyana* has not even a rudimentary suspensor. This is in contrast with the Rosaceae (Péchoutre, 1902, p. 155) and the greater number of the Papilionaceae (Guignard, 1881, pp. 142 et seq.).

That the radicle is without a root cap in the mature seed is in line with the observations of Kater (1927, p. 632) on *Phaseolus vulgaris*, in which plant the root cap comes with the first onset of cell division in germination. Guignard (1881, p. 33) comments on the two forms of embryo axis (radicle) in the Acacias. That of *Acacia farnesiana* is of uniform thickness, and that of *A. decurrens*, *retinoides*, *melanoxylon*, *brachybotrya*, and *exudans* bulges in the middle; also these latter species have auriculate cotyledons. *Acacia Baileyana* is of the second type. It is to be noted that among these species mentioned, *A. farnesiana* is the only one that is not endemic to Australia.

The quadrangular stele of the one embryo axis figured is in constrast with the 2/5 phyllotaxy of the leaves, the 5-rayed pedicel of the flowerhead and the 2/5 phyllotaxy of the flowers described in Part 1 (Newman, 1933*b*, pp. 148–150). Compton (1912*b*, p. 100) says the tetrarch hypocotyl is characteristic of the Leguminosae in general and the Caesalpineae and Mimoseae in particular. He gives figures of *Acacia doratoxylon* seedling, but does not show the twist in the stele found in this one of *A. Baileyana*.

Seed Germination.

Mature Seeds.

The cells of the cotyledons of the green seeds are large and contain a little starch in small grains. The cells of the dry seeds contain a large quantity of small starch grains. The difficulty of staining with iodine indicates that the starch in both conditions may not be quite normal. The drying of the seed produces a considerable contraction (Plate viii, fig. 20). The outer layer of the testa of the green seed is indurated; on drying, it becomes black. The swelling on

the funiculus (aril) does not shrivel away in the dry seed, and maintains some of its green colour for some time (the dark area on it in the dry seeds of Plate viii, fig. 20).

Acacia Baileyana is like other Acacias in the hardness and longevity of its seeds. Very drastic means are sometimes taken to produce rapid germination. Myers and Liels (1932, p. 947) made germination tests with seeds of *Acacia Baileyana*, and, by the use of boiling water before sowing, obtained 92% germination in 20 days, as against 4% germination of untreated seeds.

Dormancy and Variability.

It is well known that *Acacia Baileyana*, in common with many other species of *Acacia*, shows a high degree of variability in cultivation and in nature. This variation is usually attributed to hybridization, but in view of the following considerations some of it may arise as mutation during dormancy.

Nawaschin (1933) found that prolonged dormancy of the seeds was responsible for a tremendous increase in the rate of chromosomal mutations in *Crepis tectorum*. After rejecting selective mortality as the cause of increased rate of mutation, he say: "Secondly, the observed increase in the mutation rate cannot be attributed to accumulation of the direct effect of some external agency like radiation and the like; for the rate of mutants was shown not to be proportional to the length of the period of 'rest', but, on the contrary, must have grown with an enormous and progressive velocity until after five years it was a thousand times as great as after one year. One is forced thereby to the conclusion that the main agency that caused spontaneous chromosomal mutations should be sought not outside, but rather inside the cell. *The same would probably also hold true for factor mutations*" (italics mine). Now Kater (1927, p. 634) describes the nuclear changes in the attainment of the dormant condition in *Phaseolus vulgaris*. The stainable chromatin appears to collect in the much enlarged, central nucleolus, with very faint threads radiating from it. Earl (1927, p. 69), in a microchemical study of the nucleus in *Vicia faba*, supports the idea of the chromosome as essentially an ultramicroscopic thread of "genes" surrounded by a chromatic matrix, "the visible chromosome" that waxes and wanes from time to time and is the immediate environment of the genes (p. 71). If the observations of Kater and Earl are valid, then in the cells of dry seeds (dormant) the "gene" threads are more exposed to the influence of the intra-cellular environment than in non-dormant cells. This suggests an explanation of both the great increase in mutation rate in seedlings from long dormant seeds, and the rapidity with which that rate increases on account of the delicacy and unprotected state of the "gene" threads.

The Form of the Seedling.

The cotyledons are raised above the ground by the hypocotyl, which is from two to five centimetres long (Cambage, 1917, p. 391, records one 10·5 cm.). The first leaf is simply pinnate, all of 75 seedlings raised showing this feature. All of 49 seedlings that survived to the second leaf had this leaf bipinnate with one pair of pinnae (cf. Cambage, 1915, pp. 82–83). After the second leaf, the time and continuity of the increase in the number of pairs of pinnae vary considerably.

The first leaf was observed to be nyctitropic by closing together of the pairs of pinnae. Cambage has described such behaviour among the species of *Acacia* (1925, p. 230; 1926, p. 85).

The sequence of the seedling leaves of Acacias has been taken as indicating the origin of the bipinnate forms from pinnate forms (Cambage, 1915, p. 85). Kelly (1912, p. 117) propounds a contrary theory that the bipinnate form "is highly specialized, and is evolved from the entire form by gradation through the serrate, crenulate, and lobed forms, until the great surface aggregate of doubly-feathered leaves is attained". Zimmerman (1930) derives the bipinnate form through the pinnate form by a process of condensation from a system of alternate simple leaves (cf. Newman, 1933*a*, p. 140). Kelly (p. 122) does, however, suggest a process of condensation in the formation of the whorls of the leaves of *Acacia verticillata*. His theory of the bipinnate leaf does not account for the presence of radial steles in the rachis of the feathery leaves of many Acacias (Peters, 1927).

The condensation theory does account for both the radial steles of the adult rachis and the sequence of the seedling leaves.

Chronology and Synchronology.

This section covers the whole of the life history of *Acacia Baileyana*.

chronology.

The times stated here are for the trees at Hill Top. The young racemes appear in December, in the middle of summer. The flowers then initiated come to perfection in June and July, the depth of winter. By the end of March the young racemes are about five centimetres long, and some of the flowerheads would be nearly half size. Heads of half size have microspore germination completed and the germination of the megaspore in progress. By the end of May it is difficult to collect good stages of sporogenesis. In May there are many heads full size. Anthesis begins early in June, and continues through July, occurring during the coldest period of the year. Material collected between 1st July and 25th August showed stages from sperms present to completion of triple fusion, carpels being pink and up to 3 mm. long by the end of the process. The time taken seems long and variable. Four-nucleate endosperm was found in carpels between 6 and 12 mm. long, eight-nucleate endosperm in carpels between 3 and 6 mm. long, and sixteen-nucleate endosperm in carpels more than 25 mm. long, all collected on 22nd September. In harmony with the above, the time taken for cell formation in the endosperm seems variable. The seeds are full size early in December, but the pods have attained full size early in November. Dehiscence of the pods is in the latter half of December, one year after the initiation for flower primordia. For the Sydney district the times would be up to one month earlier.

synchronology.

The general impression gained from the course of the investigation is that both absolute and relative times are subject to variation. The following columns give the approximate synchrony of the phases of development.

Microsporogenesis and male gametogenesis.	Megasporogenesis and female gametogenesis.
Filament and anther and archesporium.	Ovule primordium.
Four sporogenous cells.	Archesporium.
Meiosis.	Primary sporogenous cell.
Germination of the spore.	Meiosis.
	Germination of the spore.

Fertilization.

Embryo.	Endosperm.	Ovule.
Fusion of nucleoli and regained resting condition.	Triple fusion.	Outer integument near top of embryo sac.
	Division of primary nucleus.	Micropyle completed.
Division of zygote.	8-nucleate.	

From here on the variation is so great that it is impossible to correlate the times of the various stages.

Conclusion.

The detailed investigation just concluded of the life history of *Acacia Baileyana*, has been carried out to provide a basis of comparison for the wider study of the genus *Acacia*. Apart from its bearing on the comparative study, this inquiry has touched on several questions of independent interest, which will receive further attention in the general course of the Studies in the Australian Acacias. These questions are:

1. The relation of the last pre-meiotic division to chromosome pairing; for, in the Acacias, it is possible to determine precisely which is the last pre-meiotic mitosis in microsporogenesis and megasporogenesis.
2. The chromatin changes during fertilization.
3. The possibility of the occurrence of polyspermy in connection with endosperm formation.
4. The effect of prolonged dormancy on mutation rate.

In the comparative aspect of the inquiry, it is not possible to draw any definite conclusions, for the evidence seems to be rather confused. A great amount of further research and of study of literature will be necessary for that purpose. It is, however, desirable to state where the confusion exists, that the way may be prepared for its resolution.

It is generally assumed that in the Rosales the Mimosa-tribe and the Rosa-tribe are closely related and primitive, and that from the Mimoseae the line of evolution in the Leguminosae was through the Caesalpineae to the Papilionaceae. We thus expect that if any characters are shared, it will be more primitive ones between the Mimoseae and Caesalpineae, and more advanced ones between the Caesalpineae and Papilionaceae. While we would not expect any sharing of characters between the Mimoseae and Papilionaceae that were not also possessed by the Caesalpineae. But it does not appear so simply as this in fact.

The Mimoseae and Papilionaceae have the following characters in common: 1. Uni-nucleate tapetal cells in the anther (primitive); 2. Delayed polar fusion (advanced); 3. Non-persistence of the inner integument in the seed (advanced); 4. The more anatropous ovule (advanced). Of these characters *Acacia Baileyana* shows the first three and is indefinite with regard to the fourth.

The Mimoseae and Caesalpineae have the following characters in common: 1. Persistent antipodals (primitive); 2. Simple vasculation of the seed; 3. Tetrarch

hypocotyl; 4. Only three and four equal megaspores (primitive); 5. Mode of cell formation in the endosperm (less advanced), shared with some Papilionaceae; 6. No suspensor, shared with some Papilionaceae; 7. Uni-cellular megarchesporium (advanced). *Acacia Baileyana* shows all these characters, but is slightly modified in 4 and 5.

Other independent features manifested by *Acacia Baileyana* are: 1. More than one pollen tube to one embryo sac (possibly primitive); 2. Delay in the growth of the integuments (advanced); 3. Secondary polyploidy (for the Acacias in general, an advanced condition over the genera having the simple basic numbers).

These considerations show that it is impossible as yet to make any pronouncement on the systematic position of *Acacia Baileyana* in the Leguminosae. They emphasize the need for more work of this kind for the elucidation of that position and for giving a fuller understanding of the systematic arrangement of the Natural Order itself.

Summary.

This paper concludes the study of the life history of *Acacia Baileyana.*

The microspores are thickened only on the face toward the outside of the pollinium. Their germination in the anther begins with vacuolation of the cytoplasm, and produces the generative cell and tube nucleus. The generative cell with chromosomes organized is spindle-shaped. The cytoplasm of the generative cell is unusual in that it is less dense than the surrounding cytoplasm.

Anthesis is proterogynous, but there is no precise method for pollination, which occurs in the depth of winter.

Germination of the pollen, whether occurring naturally or in culture, is towards the inside of the pollinium which is thereby split; and through the slits the tubes emerge, with the generative cell usually preceding the disorganized tube nucleus. Two slightly elliptical male nuclei (showing chromosomes) are discharged into the sac. Methods of pollen culture are discussed and it was found that an agar medium of 20% cane sugar and 1% agar gave best results. The pollen seems at its best about three or four days after anthesis. The path of the pollen tubes is described and it is recorded that more than one can attack one embryo sac. The empty pollen tube appears to be hardened in the ovary, and persists for a long time projecting from the tip of the ovule which is naked at fertilization. The disturbance of the contents at the top of the embryo sac is variable. There is a discussion of the entry of more than one pollen tube into one embryo sac.

Germination of the megaspore begins with vacuolation, and the usual three nuclear divisions result in the eight-nucleate sac, in which are formed later the cells of the egg apparatus and antipodal group; the egg and upper polar are regarded as probably sisters. Starch appears first in the megaspores and is present during the formation of the adult embryo sac, soon after the completion of which it fills the whole cavity of the sac, obliterating the central vacuole and obscuring the structures in the sac by its abundance. It is within the cells of the egg apparatus and antipodal group. It does not react normally with the usual reagents. The egg may be beside or below the hooked synergids, otherwise the egg apparatus is normal. The polars are unfused at fertilization. The antipodals are cells and disintegrate soon after triple fusion. The enlargement of the developing sac obliterates almost all of the parietal tissue. There is discussion of starch in the embryo sac, hooked synergids, and the time of polar fusion.

The male gametes that begin fertilization are naked nuclei containing telophase chromosomes. As fusion approaches they attain the resting condition. The egg and polar nuclei are also resting at the time of fusion, which occurs first with the egg. In the formation of the primary endosperm nucleus, fusion is first between the male and one polar and then the other polar nucleus. After fusion of the nuclei, a small extra nucleolus appears in the "egg" and "polar" nuclei, and is attributed to the male nucleus. In the zygote the nucleoli fuse, and after a partial approach to prophase the nucleus enters the resting condition. There is probably no fusion of nucleoli in the primary endosperm nucleus which divides much earlier than the zygote. There is discussion of the literature relevant to these phenomena of fertilization.

From the number of pollen tubes in excess of the ovules that enter the ovary, the fact that two tubes have been seen in several instances to attack one embryo sac, the presence in some cases of one or more small, extra nucleoli in association with the polar nuclei, and certain abnormal chromosome numbers in some endosperms, it is deduced that occasional polyspermy in connection with endosperm formation is probable. The relevant literature is discussed at length.

Post-fertilization changes in the carpel and ovule tissues are described. It is only after fertilization that the integuments develop beyond primordia, the micropyle being formed round the projecting remains of the pollen tube. There is a single vascular bundle in the outer integument. A cushion-like aril is developed on the funiculus. The epidermal layer of the testa is composed of malpighian cells.

The primary endosperm nucleus divides before the zygote. The endosperm resorbs the parietal tissue and much of the chalazal tissue and almost all of the lateral tissue of the nucellus. The embryo resorbs all the endosperm. There is free nuclear division in the endosperm till there are about 64 nuclei in the peripheral cytoplasm of the sac. At about that stage, cell formation begins round the 12-celled embryo and proceeds basipetally, forming at the base temporarily multinucleate cells, which simulate a slight "basal apparatus".

The first division of the zygote is horizontal, the second is almost vertical. There is no basal cell or suspensor. The primordial meristems are indefinite in origin. The development and vasculation of the cotyledons is described. The first leaf has the pinnae clearly shown in the adult green seed.

The mature seed, its germination and the form of the seedling are described, with discussion of recapitulation in the seedling leaves and of dormancy and variability.

The seasonal stages of the development are recorded and the relative times of the lines of development in the flower are set out in a table.

In conclusion, it is pointed out that several questions of general cytological interest arise for further investigation; and that the inquiry does not allow of any definite statement on the systematic position, but points to the need for further work of this kind for its elucidation.

I would express my thanks to Professor T. G. B. Osborn for the facilities provided in this department and for his interest in the work.

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NOTES ON THE ILLUSTRATIONS.

All the Text-figures have been prepared from camera-lucida drawings. All the figures on Plate viii are from photographs. The illustrations are the work of the writer. All magnifications have been obtained by measurement.

Annotations have been standardized throughout the Text-figures and Plate-figures. A few special letterings are given in the legends and explanations. The following are the standard letterings:

at. Antipodals; *ap.* Antipodal pocket; *b.* Cell simulating basal cell; *c.* Region of crushing or resorption; *cot.* Cotyledon; *cs.* Cotyledon spur; *e.* Egg; *ea.* Egg Apparatus; *em.* Embryo; *EN.* Primary endosperm nucleus; *en.* Endosperm nucleus; *end.* Cellular endosperm; *es.* Embryo sac; *ex.* Extine; *f.* Funiculus; *fs.* Funicular swelling (Aril); *g.* Generative cell; *gr.* Groove in extine; *in.* Intine; *ii.* Inner integument; *m.* Malpighian cells; *mi.* Micropyle; *mn.* Male nucleus; *mnl.* Male nucleolus; *o.* Outgrowth of the funiculus to complete the micropyle; *oi.* Outer integument; *pn.* Polar nucleus; *pnl.* Polar nucleolus; *pt.* Pollen tube; *sg.* Starch grain(s); *sn.* Synergid(s); *snd.* Synergid disintegrating; *SP.* Functional megaspore; *sp.* Non-functional megaspore(s); *tn.* Pollen tube nucleus; *vb.* Vascular bundle; *z.* Zygote.

EXPLANATION OF PLATE VIII.

Figures 1-5.—Germination of pollinia, showing (except 3) germination of the grains towards the inside of the pollinium. 1, 2 and 4 are from sections. 1, On a stigma, × 566; 2, In culture, showing the exit of the generative cell, and the wall of the tube continuous with the intine, × 530; 3, Two pollinia on one stigma, × 500 (approx.); 4, On a stigma, showing the wall of the tube continuous with the intine, × 530; 5, In culture showing the bursting of the pollinia and exit of the tubes, × 175 (approx.).

Figure 6.—Oblique L.S. nucellus with germinating distal megaspore, having the central vacuole plasmolysed, × 434.

Figure 7.—Side view of a three-armed metaphase plate in an abnormal endosperm, × 800.

Figure 8.—Slightly oblique section of a definitive embryo sac, showing the striated apical cytoplasm of the synergids, the nucleoli of the polar nuclei, and the abundance of starch obscuring the limits of the structures in the sac, × 530.

Figures 9-14.—Division of the zygote and development of the endosperm, from longitudinal sections of ovules. 9, Nucellus (showing multiple epidermis) and inner integument at the stage of the 4-nucleate endosperm; zygote undivided, × 240; 10, Embryo sac with bounding layer of nucellus. The upper part of the endosperm is cellular, the lower still has only peripheral nuclei, the embryo is about to form cotyledon primordia, × 250; 11, Lower part of an endosperm showing a multinucleate cell (*x*) at the base, × 132; 12, Whole ovule showing three of eight endosperm nuclei, the undivided zygote, and the micropyle in the inner integument (just missed by the section in the outer integument), × 110; 13, Part of the chalaza and lower part of the endosperm after cell formation in the temporarily multinucleate cells. Note elongated cells of the chalaza leading up to the antipodal pocket, × 120; 14, Nucellus and inner integument, showing three of sixteen endosperm nuclei, and the two-celled zygote, × 240.

Figure 15.—L.S. young embryo (from Fig. 16) showing cells simulating basal cells. Before origin of cotyledons, × 110.

Figures 16-17.—L.S. in the broad plane of young seeds before and after the origin of the cotyledons, × 27·5.

Figure 18.—L.S. in the narrow plane of a full-grown seed, showing the plumule, radicle, and cotyledons (spurred). The micropylar region and the aril were broken off, × 8.

Figure 19.—L.S. upper part of a full-grown seed, parallel with the cotyledons, showing the radicle, plumule with pinnae (*pi*) on the first leaf, and the aril, × 12.

Figure 20.—Showing the contraction of the seeds on drying. Four sizes from the largest to the smallest of both green and dry seeds were selected and arranged in the broad and narrow aspects. The two left-hand rows are the green seeds, the two right-hand rows are the dry seeds. About natural size.

THE REGIMES AND CYCLICAL VOLUME CHANGES OF THE UPPER MURRAY AND SNOWY RIVERS, NEW SOUTH WALES.

By Frank A. Craft, B.Sc., Linnean Macleay Fellow of the Society in Geography.

(Twelve Text-figures.)

[Read 26th September, 1934.]

Acknowledgements.—The writer wishes to make special mention of the assistance received during the preparation of this work. The Inspector-General of Forests, Mr. C. E. Lane Poole, supplied maps, reports, photographs and notes made by Mr. B. U. Byles during the course of an investigation of the mountainous part of the upper Murray catchment, N.S.W., and Mr. Byles supplemented these by personal discussion. Other maps were available by courtesy of the Surveyor-General and the Lands Department. The Water Conservation and Irrigation Commission supplied hydrographic records, and Messrs. Morrison and Robinson of the Hydrographic Branch afforded every facility for work, and had the stream volumes at Khancoban and Possum Point re-computed for the writer. Rainfall figures were from the Weather Bureau, Sydney. Cordial thanks are due to these various gentlemen and organizations, and also to those whose hospitality was extended in the field, particularly Mr. D. Maginnity, of Tooma, and Messrs. F. E. Anderson and R. R. Scammell of Khancoban.

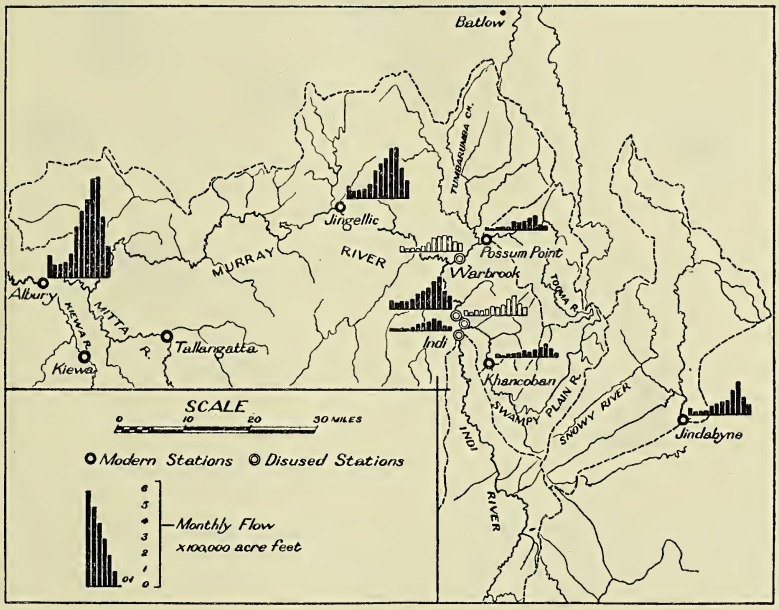
Introduction.

The study of modern erosional forms in the Hume catchment of New South Wales discloses a progressive action in the formation of gullies and terraces, and a gradual widening of the main stream channels away from curves, even in places where the banks are protected by grass, shrubs and lines of trees. These facts suggest many possibilities in the way of changing stream regime or secular alterations in volume, and it may be asked: Is the duration or intensity of the annual flood changing? Is the winter flow benefiting at the expense of the summer flow? Is there any secular change in the volume discharged, and, if so, can it be referred to such causes as deforestation or changes in the rainfall regime? The answers that can be given to these questions depend mainly on the records of stream gaugings kept by State authorities, with definite limitations imposed by short records at certain stations, and by the absence of rainfall data for the wettest part of the catchments. Thus it is impossible to consider the lag between precipitation and stream rise, but the questions suggested above can be answered with some precision, as the records available are consistent for the periods which they cover. For this reason, the secular trends disclosed below are of similar gradient when computed for partial or complete records, and when the figures for the various Murray stations are plotted against one another, they show a linear relationship (Text-figs. 8, 9). In addition, the form of the curves on which the present conclusions are based, especially in the duration and distribu-

tion of notably moist or drought periods, leaves no doubt of the general correctness of the various trends.

Regime of the Upper Murray and Snowy Rivers.

The characteristic regime shows a maximum flow in September or October and a minimum in February (Text-fig. 1). It is thus simple, and equivalent to the European regime nival de plaine.* Streams with a large proportion of catchment liable to snow in quantity (Tooma, Swampy Plain and Snowy), have a slight concavity in the graph before the wave crest, but others less influenced by snow



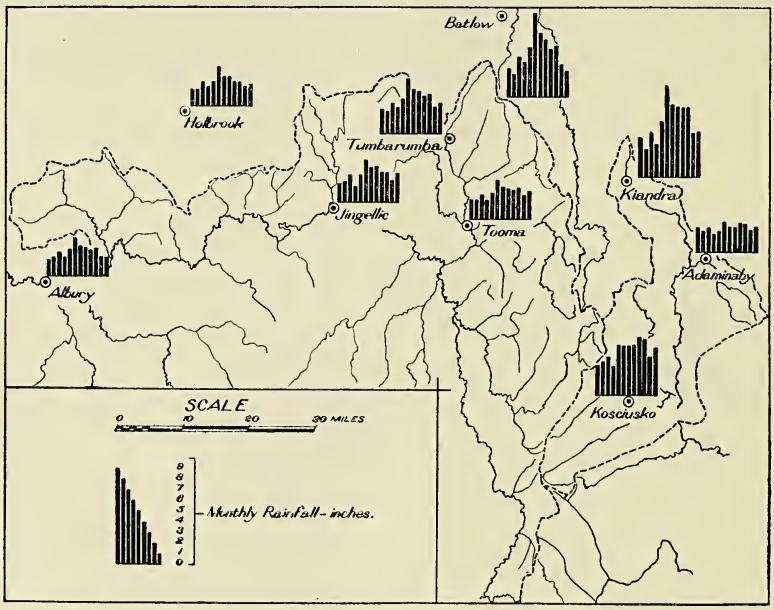
Text-fig. 1.—Stream regimes of the upper Murray and Snowy Rivers, from January on the left to December on the right. Periods of record are: Albury, 1877-1932; Jingellic, 1891-1932; Tallangatta, 1886-1932; Warbrook, 1910-1920; Indi, 1908-1920; Murray at Indi-Swampy Plain junction, 1906-1920; Swampy Plain at Indi junction, 1906-1913; Khancoban, 1927-1932; Possum Point, 1927-1932; Jindabyne, 1903-1932. Hollow columns are used to distinguish records of secondary importance in the making of the complete regime at Albury or Jingellic.

display convexity instead (Indi, Murray). The relationship between the two forms is shown in the case of Tooma River, where the modern gauge at Possum Point gives records with pre-maximum concavity, thus contrasting with the older records at Warbrook, below the junction of Tumbarumba Creek. In addition to these major features, there are minor oscillations in the late summer records of the Indi, Tooma and Swampy Plain, but they are too small to have any significance ascribed to them over so short a period.

Comparing stream and rainfall regimes (Text-fig. 2), a general similarity is seen in the minimal periods, but the rainfall maximum occurs three to four months

* See Pardé, 1933.

before the stream floods. The position is rather obscure, as the significance of the 20-year Kosciusko record is not known. If the high plateau at the head of the Tooma, Swampy Plain and Snowy Rivers has a rainfall regime like that indicated for Kosciusko, the importance now attached to conserved snow in the economy of the streams will be lessened, but it must be noted that the estimation of winter

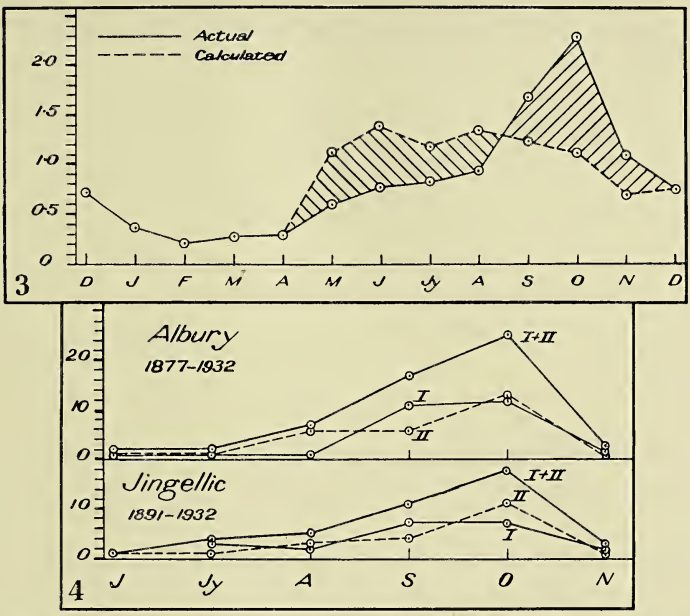


Text-fig. 2.—Rainfall regimes, from January on the left to December on the right. Periods of record are: Albury, 1877; Kiandra, 1883; Holbrook and Tooma, 1885; Tumbarumba, 1886; Adaminaby and Batlow, 1887; Jingellic, 1909; Kosciusko, 1912, extending to 1932 in each case.

precipitation at Kosciusko is likely to be inaccurate, because individual estimates of water content are not made for each sample of snow in the gauge. The best summary that can be given at present is, that a rainfall maximum is shown in June for most of the area, and that precipitation is sustained until the beginning of the warm season in October. In this way, much of the effective rain for stream flow comes in late winter or early spring both in highland and lowland areas, or the Albury river graph would show a crest before the incidence of the annual flood from the highlands in September and October. In the higher country, delay of the flood peak is caused by the accumulation of water in the form of snow (Text-fig. 3), and in the lower it is due to the necessity of making up a moisture deficiency in the ground after the warmer months. Thus highland and lowland are mutually supporting in the development of the flood wave.

The time of occurrence of the flood crest, which is a peak rather than a flat wave of any great dispersion, is controlled by such factors as flood rains on various parts of the catchment, or heavy rain falling on melting snow. Of the recorded occurrences, 43% to 45% are found in October, and the moieties of the gauging records at Jingellic and Albury give a similar time distribution (Text-fig. 4).

So far as the dry period is concerned, the most striking aspect is the close relationship between the stream and rainfall curves, even though the temperature factor cannot be taken into account because the only two recording stations



Text-fig. 3.—Effect of snow conservation on the flow of the Snowy River, Jindabyne, for the period 1912-1932. The average precipitation at the stations Adaminaby, Kiandra and Kosciusko for the months May-November was taken as the rainfall over the catchment, and the difference between run-off calculated on this basis and that actually measured at Jindabyne was reckoned as evaporation (28% of the possible). This was distributed according to a formula:

$$\text{Evap. for month} = \text{Total Evap.} \times \frac{\text{Relative Evap. for month}}{\text{Sum of Relative Evapns.}},$$

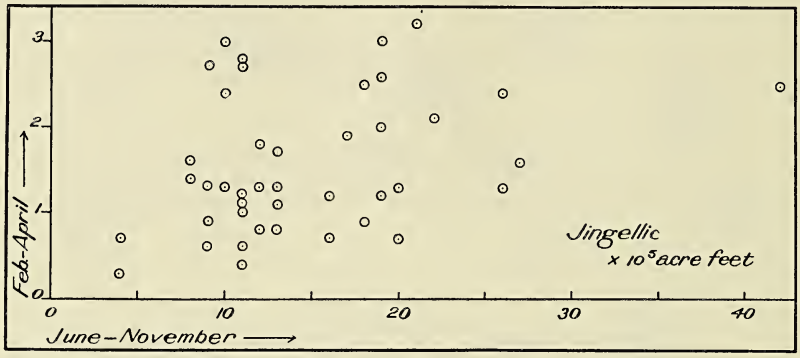
where the relative evaporation was taken as Precipitation × (T + 10), with the temperature (T° C.) as the average monthly temperatures at Kiandra and Kosciusko. This is an adaptation of de Martonne's climatological ratio for the effectiveness of precipitation (1927). The rulings show conservation (May-August) and dissipation of snow (September-November).

Text-fig. 4.—Frequencies of flood crests by months, Albury and Jingellic. The first half of each record is represented by I, and second by II, and the total by I + II.

(Kiandra and Kosciusko) are not representative. Stream flow in the dry period depends mainly on proximal rainfall, and only to a minor degree on the carry-over of water stored in the catchment as the result of winter rain and snow. This becomes clear when the rain and flow records are studied month by month, and it is demonstrated by the lack of any close correlation between the run-off in winter and that in the low-water months of the following summer (Text-fig. 5). Thus a moist winter is not necessarily an indicator of high volumes in the following summer, and a relatively large summer flow may follow a dry winter. *In other words, summer or low-water flow cannot be treated as a function of winter flow.*

Cyclical and Secular Changes in Volume.

a. Cyclical Changes.—Having described the normal seasonal fluctuations of volume, it may now be asked: have the volumes discharged annually, or during flood and low-water seasons, varied from time to time according to some general cyclical or secular law? It has long been remarked that years of exceptional drought or flood occur in Australia with a suggestion of an 11-year periodicity.



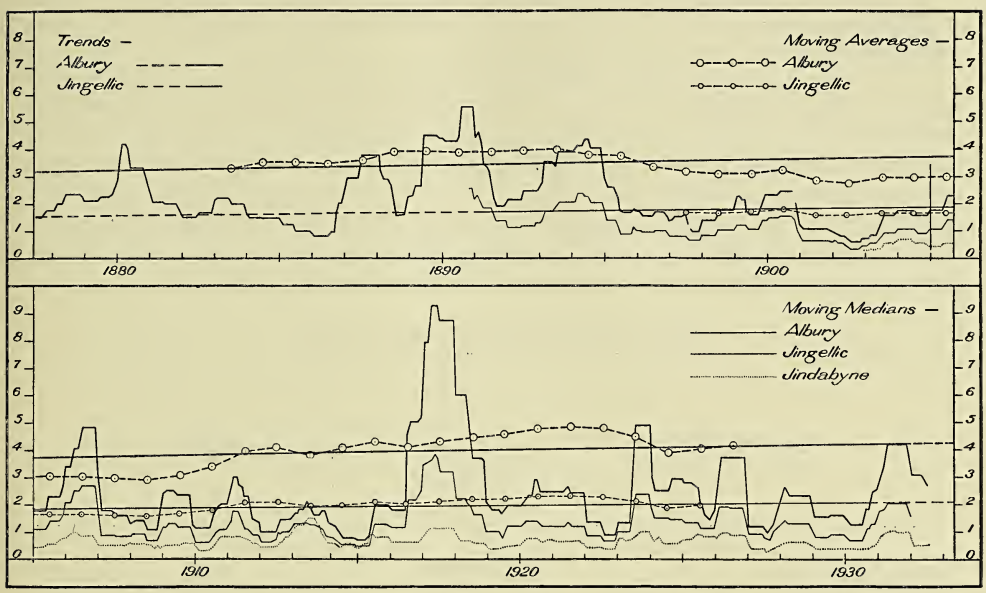
Text-fig. 5.—Low water at Jingellic plotted against the flood volume of the preceding winter for the years 1891-1932. There is no apparent relationship.

This is the case with the upper Murray, where years of outstandingly low flows were 1884, 1902, 1914 and, to a lesser extent, 1929: years of exceptional flood were 1887, 1889, 1894, 1906, 1917 and 1931. The fact has little meaning in itself, as an exceptional flood or drought may be only a local peak or trough in a series of consistently high or low values; it is necessary, for this reason, to combine the various records in series to find whether there is any true periodicity, and to see if a secular trend may be deduced.

In making such a combination, the crude annual totals are disregarded, because each represents only one out of every twelve possible combinations of twelve consecutive months, and this makes a number of anomalies possible. For instance, it is not uncommon to find a high value for one month in a consistently low series of 16 or 18 months, but the position of this high value within the normal flood limits makes an annual total possible which disguises the actual paucity of flow over a lengthy period. To overcome such difficulties, every possible combination of 12 consecutive months has been taken, the monthly gaugings arranged in order of magnitude, and the value between the sixth and seventh chosen as the median, to be attributed to the seventh month of the series. Thus with a series commencing in July, the median is credited to the following January, that of the next to February, and so on. In this way, a set of values is obtained to give a regular index of flow in the river (Text-fig. 6 shows these "moving medians").

Another method would be to use the arithmetical mean in a similar manner, but the median has several advantages in practice, of which the principal are: (1) A smoother curve is obtained in plotting, as the chance of two consecutive means being equal is small, while the median may not vary over 11 or 12 months; (2) Excessive weight is not given to one or two exceptionally large or small values in a series. In a test, it was found that the moving median gave values

to 30% below the moving mean in periods of greatest flow, and values to 20% above the moving mean in periods of excessive drought. The median curve is thus distinctively conservative; (3) For three stations—Jindabyne, Albury and



Text-fig. 6.—Fluctuations of the upper Murray and Snowy Rivers. The moving median with a 12-month period, plotted monthly, eliminates the annual wave: the 13-year moving average of annual totals eliminates the minor cycles, and the computed trend gives the secular movement of volume. For the medians, ordinate numbers are multiplied by 100,000 acre-feet: for the averages and trends, by 1,000,000 acre-feet. Scales are thus in the ratio—median : average = 12 : 10.

Jingellic, of which the first is on the upper Snowy, and the last Victorian—the curves obtained show synchronous changes of slope for all major and almost all minor variations. In this respect, the moving median is unexpectedly sensitive. The greatest anomaly is with respect to the 1931 flood on the Murray, which appeared much too low in comparison with earlier peaks, especially that of 1917. In these two cases, the Murray at Albury discharged 9 million acre-feet between June and November, 1917, and 6½ million acre-feet during a similar period in 1931: the excessive median difference was the result of high values in 1916 and 1918 compared with relatively low values during 1930 and 1932. Apart from this, however, the method appears to have given a true picture of flow conditions.

Referring to the graphs, it is found that there has been a regular cyclical variation in flow, with major crests for Albury in 1880, 1891, 1906, 1917 and 1931, and notable troughs in 1877, 1886, 1902, 1914 and 1922, giving an average interval of 13 years for the crests, and of 12 years for the troughs. In addition, the mid portion of the graph between 1894 and 1917 is consistently low, but is succeeded by greater volumes to the present day. For this reason, too much attention should not be paid to the minor cycles noted, but the record may be looked on as showing an early trough, a crest centred about 1890, a middle trough, and a later

humid period which may exist until now. This is brought out by a curve showing a 13-year moving average of annual totals, whose period was chosen to eliminate the minor cycles as far as possible.

There are minor cycles in the flow of the Murray with a 12- or 13-year period, but they are overshadowed by a major cycle which may have a period of the order of 30 years.

b. Secular Changes.—The median graphs and 13-year moving average curves show a rising tendency in the flow of the Murray, reflected in the increased volume and dispersion of major floods, but the reverse is true of the shorter record for the upper Snowy. That record includes the excessive flood of 1917, but has no equivalent of the 1931 floods on the Murray, so a calculated trend may be expected to show a slight decline. The general trends were approximated to straight lines by the calculation of least squares, both for unweighted annual flows and for 13-year moving averages, with these results (Table 1).

TABLE 1.—*Annual Trends for Various Stations.*

Station and Period.	Thousands Acre-Feet.		% Annual Increase.	% Total Increase.
	Ordinate at Beginning.	Ordinate at End.		
Albury, 1878–1932	3,190	4,210	0·5	32
Albury, 1891–1931	3,090	4,370	0·9	41 (*a*)
Jingellic, 1891–1931	1,709	2,057	0·5	20
Jingellic, 1904–1932	1,878	2,088	0·4	11
Jindabyne, 1904–1932	985	887	−0·4	−10
Moving Averages.				
Albury, 1878–1932	3,130	4,250	0·6	36
Jingellic, 1891–1931	1,400	2,320	1·3	66 (*b*)

(*a*) Probably high, as the flows immediately preceding were high. (*b*) Unduly weighted by low initial averages.

The gain on the Murray side is definite and persistent, whether determined for longer or shorter periods, and it is not yet certain that this gain has ended. However, the secular trend of the Murray has favoured increased flow over the period of record, but the Snowy appears to be losing at much the same rate as the upper Murray is gaining. The distribution of these changes within the year assigns their greater portion to the flood or winter season (Table 2), but the low water trends, although smaller in magnitude, are also positive for the Murray and negative for the Snowy (Table 3).

From this it is clear that the various fluctuations of volume of the two rivers have varied regularly over the periods recorded. The tendency for the Murray has been towards a more intense flow over the six cooler months, and the cyclical fluctuations have shown a rising trend. The reverse is true of the upper Snowy.

CAUSE OF THE CHANGES.

Having defined the nature and amount of change in the flow of the rivers, it remains to be seen whether the changes can be ascribed to any major cause

TABLE 2.—*Flood Volume Trends—(June–November).*

Station and Period.	Thousands Acre-Feet.		% Annual Increase.	% Total Increase.
	Ordinate at Beginning.	Ordinate at End.		
Albury, 1878–1932	2,440	3,400	0·6	39
Albury, 1891–1931	2,410	3,530	0·9	46
Jingellic, 1891–1931	1,326	1,614	0·5	22
Jindabyne, 1904–1932	732	698	−0·1	−4·6

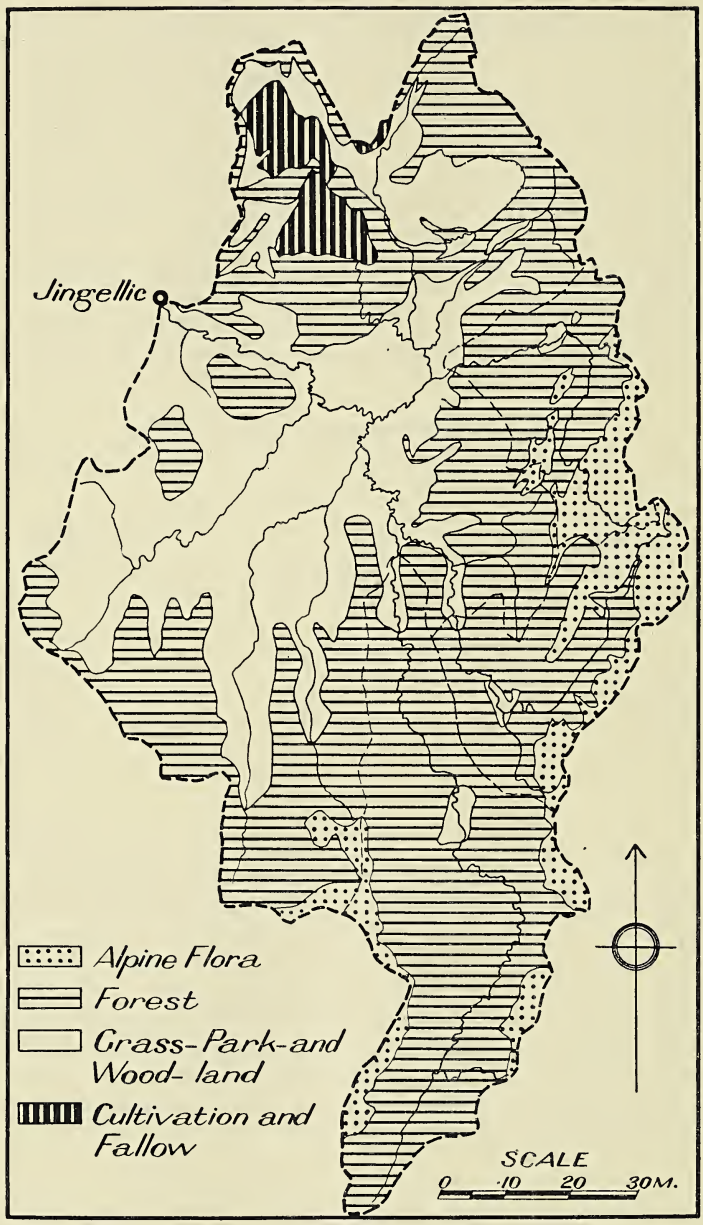
TABLE 3.—*Low Water Trends—(February–April).*

Station and Period.	Thousands Acre-Feet.		% Annual Increase.	% Total Increase.
	Ordinate at Beginning.	Ordinate at End.		
Albury, 1878–1932	291	297	0·05	2
Jingellic, 1891–1931	150	156	0·1	4
Jingellic, 1904–1932	117	189	1·6	61
Jindabyne, 1904–1932	81	76	−0·2	−6

or causes. Opposite effects in the upper Snowy and Murray suggest that the windward slopes to the west have been gaining at the expense of the leeward eastern slopes towards Jindabyne, and on a first inspection the cyclical nature of the median curves seems to point to climatic change of some kind. In the past, the possible effect of deforestation has been greatly stressed: thus Wood (1923, 1928) urged the destruction of forests as the prime cause of a supposed decrease in the summer flow of the Murray, and the increased intensity of winter floods. Despite this, deforestation would appear to be a much less potent factor than redistribution of rain within the year, and the apparent changes of rainfall are enough to give changes of river trend of the order of magnitude involved. The two aspects will be considered in turn.

a. The Factor of Deforestation (Text-fig. 7).

As the various parts of the catchment are of unequal value for the output of water, the removal of equal areas of forest from the highlands, hill country and valleys will not be expected to have the same effect on water supply. The mountain streams Indi, Swampy Plain and Tooma drain only 36% of the Jingellic catchment, but they give 69% of the annual and 76% of the summer volumes (Table 4).



Text-fig. 7.—General utilization of the Murray catchment above Jingellic. The area of partially deforested grassland, etc., to the south-west of the Murray is probably exaggerated. Boundaries of Alpine flora are largely after unpublished reports and maps by B. U. Byles (1932*b*).

TABLE 4.—*Output of Water, and Relative Efficiencies of the Various Portions of the Jingellic Catchment for the Years 1927 to 1932, inclusive.*

Relative Efficiencies of the Catchment Areas.

Stream.	Area of Catchment.	% of Total.	Volume, 1927-1932.	% of Total.	Summer Volume.	% of Total.
Tooma River	189	7·5	2,666	24	414	20·6
Swampy Plain River	228	9·0	2,651	24	578	28·8
Indi River	493	19·5	(2,320)[1]	21	(537)	26·8
Balance of Country	1,614	64·0	3,367	31	474	23·7
Murray River at Jingellic ..	2,524	100·0	11,004	100	2,003	100·0
Snowy River at Jindabyne ..	716	—	4,945	—	855	—

[1] From relationship in Text-Figure 8.

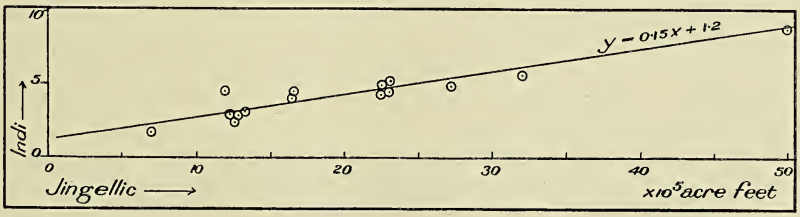
N.B.—*Summer* is taken as *December to April inclusive*, i.e., 5 months.

Efficiencies Relative to Balance of Country outside Mountain Catchments.

	Annual.	Summer.	S/A.
Tooma River	7·0	7·4	1·1
Swampy Plain River	5·8	8·6	1·5
Indi River	2·4	3·7	1·5
Balance of Country	1·0	1·0	1·0
Murray River at Jingellic	2·2	2·7	1·2
Snowy River at Jindabyne	3·4	4·0	1·2
Swampy Plain+Tooma	6·3	8·4	1·3

The Indi is interpolated on the basis of its linear relationship with Jingellic during the years 1906 to 1920 (Text-fig. 8).

On the other hand, the balance of the country, which gives 31% of the annual and 24% of the summer discharge, has suffered the greatest amount of deforestation, and, near the Murray, parts of even the steeper hills and ridges have been cleared for grazing (Table 5, Text-fig. 7).



Text-fig. 8.—Annual flows of Indi and Jingellic stations for the period 1906-1920. Records are from New South Wales and Victorian sources respectively.

TABLE 5.—*Utilization of the Murray Catchment above Jingellic.*

Utilization of the Upper Murray Catchment.

Locality.	Alpine.	Forest.	Grass and Parkland.	Grass and Cropland.	Area.
A.—By Area (Square miles).					
Tooma River	59	124	6·5	—	189·5
Swampy Plain River	73·5	148	5	—	226·5
Indi River	53·5	420	19	—	492·5
New South Wales hills	7·5	398	314	67	786·5
Victorian hills	31	333	465	—	829
Total	224·5	1,423	809·5	67	2,524
					Deforested.
B.—By Percentage.					
1.—Tooma River	31	65·5	3·5	—	3·5
2.—Swampy Plain River	32·5	65·3	2·2	—	2·2
3.—Indi River	11	85	4	—	4
4.—New South Wales hills ..	1	50·5	40	8·5	48·5
5.—Victorian hills	4	40	56	—	56
Total	9	56·5	32	2·5	34·5
% Mountains, 1, 2, 3	20·5	76	3·5	—	3·5
% Hills, 4, 5	2·5	45	48	5	53

" Grass and Parkland " includes small areas of cultivation, and is likely to include some forested areas in the Victorian hills.

In assessing the amount of forest change and actual deforestation, the first question that arises is: Has the efficiency of the mountain catchments altered as the result of vegetational changes due to bushfires, apart from complete deforestation? It appears not, because, although the flora has degenerated over considerable areas and may be greatly damaged by any future combination of years of excessive drought and fire, it still forms a mantle over the whole countryside that is effective for present water supply purposes. The vegetational changes have been studied by B. U. Byles, lately of the Commonwealth Forestry Bureau, Canberra (1932*a*), and may be summarized according to the principal divisions into Alpine and forest lands, thus:

i. *Alpine.*—Part of the original cover of low shrubs has been replaced by tufted grasses such as snow grass (*Poa caespitosa*), and the original open stands of low Eucalyptus such as snow gum (*E. coriacea*), with trees 50 feet apart or more, have been largely destroyed and replaced by coppice, part of which has been subsequently burned. On the lower slopes of the division, just above the regular forest belt, the coppice and new intergrowth of shrubs form an almost

impenetrable tangle. Parts of the highland swamp mosses have been damaged by fire, but they still conserve water.

ii. *Forest.*—On the high plateau, the forest areas south of Kosciusko and on the northerly Tooma slopes have not been greatly affected. The open forests about the heads of the Swampy Plain and Tooma Rivers have been destroyed on some ridges, and replaced by Alpine grasses or shrubs or by dense coppice: the essential change is from very open forest or park land to scrub country. In the case of the forests on the flanks of the high plateau, the old trees have been thinned out, or destroyed over small areas, of which the principal lies to the west of the upper Swampy Plain River. The former glades have been filled with bracken and low scrub, whose permanence is open to doubt, but there is no reason for supposing that the water supply has yet been affected by the changes which have decreased the vegetational cover in limited areas, and increased it in others. On the whole, the type of cover on the high plateau and its flanking slopes has not changed essentially: forest remains as forest, heath as heath, and swamp as swamp.

So far as the lower plateau and valley country in the balance of the area is concerned (N.S.W. and Victorian hills in Table 5), much of the cleared portion is lower slope or bottom land, while most of the hills and ridges do not appear to have departed greatly from their original condition. It seems that the deforested portion is that which would be expected to supply relatively little run-off in any case, so the effects of partial deforestation have probably been minimized by the location of clearings.

Summing up, it is found that changes in stream flow due to removal of tree cover must be ascribed principally to the 53% deforested or partially deforested country in the balance outside the mountains. Thus a volume which is probably less than half of the 31% contribution to the Jingellic flow comes from the deforested portion, so that changes due to deforestation involve a fraction of 15% of the Jingellic flow. It has already been shown that the total increases in annual and winter trends have amounted to 20% and 22% respectively between 1891 and 1931, or 17% and 18% respectively of the trend ordinate, so it is clear that the changes recorded are of a much greater order of magnitude than those expected from partial deforestation.

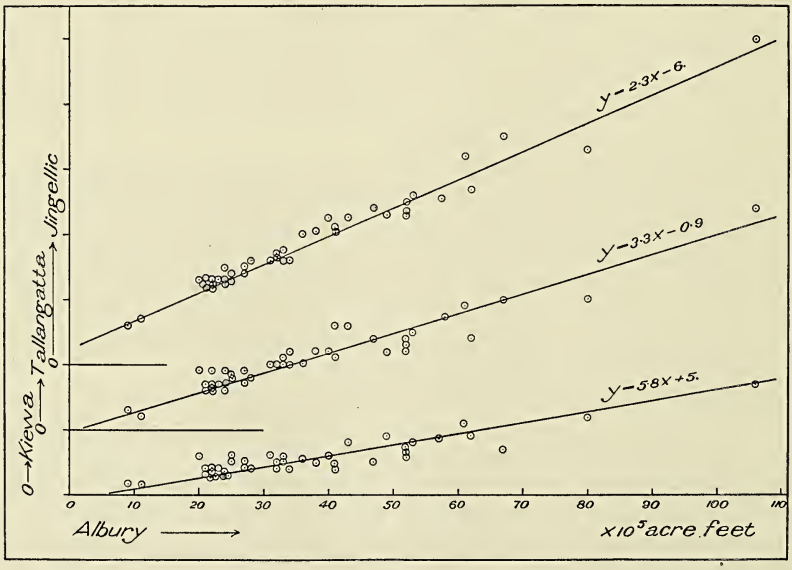
Before extending these considerations to the Albury catchment as a whole, it is necessary to consider anomalies in certain stream records. The combined figures for Jingellic, Tallangatta and Kiewa should disclose a trend like that of Albury, but actually they give only half the ordinate increase expected for the period 1891-1931—a fact reflected by trend increases of 1% and 6% for Tallangatta and Kiewa respectively. At the same time, Albury shows both positive and negative anomalies when its figures are compared with those of the contributing stations combined, with a regular distribution (Table 6).

It is difficult to see that a negative anomaly should result at all in practice, because the individual gauges are close to Albury, 80% of the annual flow is during the months June–November, and the upstream water is supplemented by perennial streams draining 1,700 square miles of additional catchment. From the distribution of the negative anomalies and their occurrence throughout the record, it appears that they are due to constant systematic errors in gauging, extending back to 1891, at any rate.

TABLE 6.—*Distribution of Anomalies between Albury Gaugings and the Combined Figures of Jingellic, Tallangatta and Kiewa.*

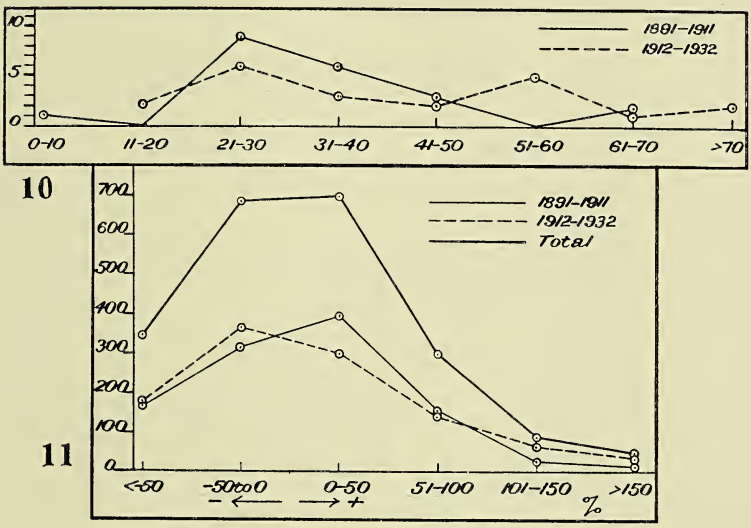
Flow at Albury— × 100,000 Acre-Feet.	Anomaly as Percentage of Albury Total.							
	Negative.				Positive.			
	<16	15–11	10–6	5–0	0–5	6–10	11–15	>16
0–10		/						
11–20	/			/	/			
21–30			////	///// ////		/		
31–40				//	//// ///			
41–50			/		/	///		
51–60						/		////
>60				/	/	/		//

What effect has this on the validity of the various trends? The contributing stations have an approximately linear relationship with Albury (Text-fig. 9),



Text-fig. 9.—Annual flows at Jingellic, Tallangatta and Kiewa plotted against Albury, with equal vertical and horizontal scales, but varying x-axes.

and are generally consistent amongst themselves, so it is possible that the lower range, especially at Albury, is too low, or that corresponding figures for the others are too high. If the former alternative is correct, the trend ascribed to Albury for the period 1891-1931 is excessive, but the others may be reasonable. If the second alternative is accepted, the Albury figures stand, and the trends for some or all of the contributing stations are increased. It is probable that some of the lower positive anomalies of Table 6 are also understated; this would affect the results in a manner similar to that in the second alternative owing to the greater frequency of high flows in the latter half of the period under discussion (Text-fig. 10), but there is no reason for doubting the general accuracy of the maxima.



Text-fig. 10.—Frequencies of volume groups recorded at Albury. Groups are in acre-feet × 100,000.

Text-fig. 11.—Frequency of occurrence of percentage departures from monthly rainfall medians at each station, for the months May-October. Omissions are noted under Table 7.

It seems reasonable to conclude that, in the extra-Jingellic catchment above Albury, no great secular volume changes are disclosed, although trends may be steeper than those actually determined for Tallangatta and Kiewa. At the most, variations due to altered conditions on the catchments are much less than those above Jingellic, although it is probable that the proportions of forest, grassland and cultivation are not dissimilar in the two areas, and the Victorian highlands at the head of Mitta River appear to have suffered more fire damage than those of New South Wales (W. J. Lakeland's unpublished report to the State Rivers and Water Supply Commission, Victoria). A legitimate conclusion appears to be that, for the whole of the Murray catchment above Albury, any effect of partial deforestation on stream flow is quite overshadowed by the operation of other factors (compare Central Board of Irrigation, 1931). The cause of stream changes must therefore be sought in other factors, such as climatic oscillations.

b. The Factor of Rainfall.

The amount of material available for climatic study is limited. There are no rainfall stations on the mountainous part of the Murray catchment, and the nearest one existing under rather similar conditions (at Charlotte's Pass, south-west of Kosciusko station) was established in 1930: up to the present, its figures are about one-third greater than corresponding readings at Kiandra and Batlow. Another disability is the lack of any temperature records for all stations except Kosciusko and Kiandra, so the consideration of rainfall variations is necessarily confined to the cool, moist winter, corresponding to the season of maximum river flow.

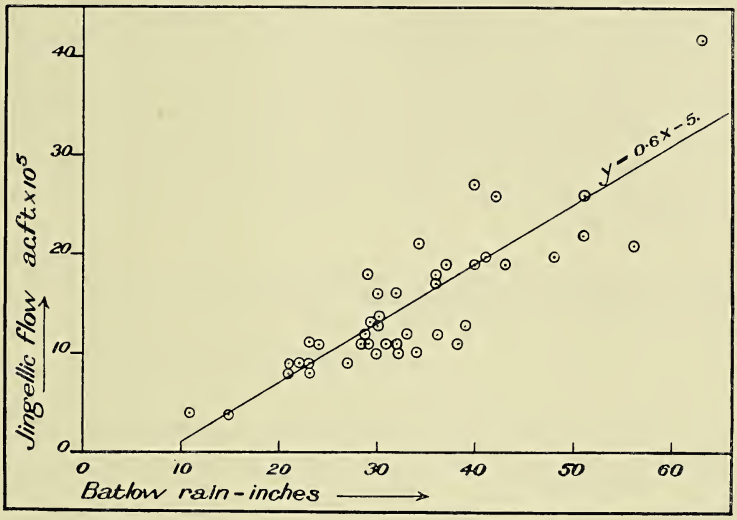
For purposes of comparison, the percentage deviation of each monthly rainfall reading from the corresponding monthly median has been taken, and the individual departures collected into groups in multiples of 50% departure for

TABLE 7.—*Exceptional Departures from Rainfall Medians.*

Departure 50–100% Below.	1887–1909.					1910–1932.					Total 1887–1909.	Total 1910–1932.
	"A."	"B."	Batlow.	Kiandra.	Adam.	"A."	"B."	Batlow.	Kiandra.	Adam.		
May	9	9	6	2	5	9	10	3	2	4	31	28
June	4	1	1	3	0	11	14	5	4	3	9	37
July	2	13	6	4	6	8	10	3	4	2	31	27
August ..	9	9	5	5	5	8	8	2	2	2	33	22
September ..	7	11	5	1	5	6	10	1	3	2	29	22
October ..	11	15	4	2	5	10	17	5	5	5	37	42
Departure >50% Above.												
May	9	9	3	2	5	13	17	6	8	9	28	53
June	7	14	4	4	9	8	14	5	4	3	38	34
July	11	13	6	9	4	8	16	5	6	7	43	42
August ..	5	9	1	5	1	9	19	5	1	2	21	38
September ..	9	7	5	3	7	7	18	6	4	6	31	41
October ..	10	10	4	2	9	9	11	3	5	4	35	32
Departure >100% Above.												
May	4	4	1	—	2	4	10	4	4	7	11	29
June	—	2	—	1	2	3	6	3	1	1	5	14
July	3	2	1	2	1	4	4	4	4	4	9	20
August ..	—	2	—	—	—	2	2	—	—	1	2	5
September ..	1	—	—	—	4	3	3	1	1	2	5	10
October ..	4	2	1	1	3	5	5	2	1	2	11	15

"A" represents the combined total of Holbrook and Albury, and "B" the combined total of Jingellic, Tumbarumba and Tooma, each station being estimated separately. The numbers of monthly totals missing are: Jingellic, 31; Tooma, 9; Adaminaby, 6. These constitute 2% of the total available, and are equally divided between the two halves. Major anomalies might be: 3 less than −50%, 4 more than 50% for the first half; 4 less than −50%, 2 more than 50% for the second.

each of the six months of the moist season. The 46-year record available has been halved, and the frequencies of each occurrence expressed by a graph for the whole period, and for the moieties (Text-fig. 11). In this, the first half shows a greater number of positive anomalies and a lesser number of negative than the second, but the position is reversed when extreme deviations are considered: these latter are of the greatest importance, as their multiple occurrences in individual winters are associated with abnormally low or high flows. Thus in the dry winter of 1902, 26 monthly totals out of 48 were less than 50% of their respective medians, while the humid winter of 1917 showed 37 monthly totals with a positive anomaly in excess of 50%. The distribution of these extremes according to various stations and groups of stations is shown by Table 7.



Text-fig. 12.—River flow at Jingellic for the months June-November plotted against Batlow rain for the months May-October in each corresponding year from 1891 to 1932.

Taking the variation groups month by month, it is seen that the second half of the period has more June records below −50% than the first, but that high positive departures have shown a consistent increase over the whole moist season. This applies particularly to the Murray side, with May, June and July benefiting most. The significance of the grouping of the extremes varies from place to place. Batlow is the key station to the highlands, because its general situation and aspect are like those of the high Murray plateau: in both cases, deep valleys radiate from the plateau mass, especially to the west and south-west, and appear to direct the prevailing winter winds blowing from low country, thus giving high rainfall on each plateau. Batlow shows a decreasing tendency in the number of very dry months, and there has been a striking increase in the number of months of excessive rainfall, mostly in the first half of winter. This gives an expectation of rising stream flows, and a similar condition may well be true of the neighbouring Murray highlands, because river flow at Jingellic plotted against rainfall at Batlow gives a series of points which lie approximately on a straight line (Text-fig. 12). Kiandra shows these rainfall changes in a lesser degree, with an increase in the number of dry months, but it is away from the highland edges.

In the lower country on the Murray side, there has been a tendency towards more extreme conditions, but it is doubtful whether an increase in the number of dry months has much effect on stream volumes, because intense or prolonged rain appears to be necessary for any considerable run-off from the deep soils of the gentler slope and plain lands. On the other hand, months of exceptional rainfall contribute much water to the streams, as a large area of catchment is involved, and precipitation is usually widespread. The increase of rainy months is greater in the low plateau and valley country represented by Jingellic, Tooma and Tumbarumba than in the plains of Holbrook and Albury, and as the former section is the more steep and rocky, the increased run-off towards more recent times may be correspondingly high.

Turning now to the upper Snowy, an increased number of months of heavy rainfall at Kiandra and Adaminaby may indicate an increased winter stream flow since the beginning of the record. The position is obscure, because stream gaugings at Jindabyne only date from 1903, and appear to have been controlled by the heavy rainfall country on the eastern side of the Main Divide between Kosciusko and the head of the Tooma River. In that period, the upper Snowy had a more regular flow than the Murray at Jingellic, thus reflecting the rainfall conditions at Kosciusko rather than the less constant precipitation elsewhere (Table 8, Text-figs. 1, 2).

TABLE 8.—*Number of Departures from Medians of June-November Flows, 1903–1932, and Correlation Coefficients for Kosciusko and Kiandra Rainfall (May–October) with Jindabyne Flow (June–December).*

	Percentage Departure from Median.					
	<−50	−50 to 0	0–50	51–100	101–150	>150
Murray at Jingellic	1	14	5	7	2	1
Snowy at Jindabyne	3	12	13	1	1	—

Correlation coefficient (r) = 0·67, probable error = 0·08 for Kosciusko rain and Jindabyne flow, 1912–1932.
r = 0·54, probable error = 0·1 for Kiandra rain and Jindabyne flow, 1903–1932.

The extremes of precipitation thus appear to favour increased flood volumes on the Murray in the latter half of the gauging period, and the question arises—are these rainfall variations enough to account for the stream fluctuations observed at Jingellic and Jindabyne? A comparison of departures from rainfall and flow medians for the various periods involved shows that there is a close relationship between the respective departure groups, which suggests that stream and rainfall variations are closely allied (Table 9).

In addition, there is a functional relationship between rainfall and stream volumes for the winter season. The flow at Jingellic is approximately related to Batlow rainfall by the equation—

Flow (acre-feet × 100,000) = 0·6 Rainfall (inches) − 5 (see also Text-fig. 12), and these two variables show a correlation coefficient of 0·86, with a probable error of 0·03. This cannot be regarded as an isolated result, because Tumbarumba, which is actually on the Murray catchment, has a correlation coefficient of 0·83 with the same flow, with a probable error of 0·03. As there is a close corres-

TABLE 9.—*Occurrence of Median Departures of Rainfall and River Flow in Percentage Groups.*

	< −50	−50 to 0	0–50	51–100	101–150	> 150
Period 1891–1932.						
River at Jingellic—						
A	1	11	7	1	1	—
B	1	8	7	3	1	1
Rainfall at Batlow—						
A	1	11	9	—	—	—
B	1	8	8	4	—	—
Period 1903–1932.						
River at Jingellic—						
C	1	7	2	3	1	1
D	—	6	4	4	1	—
Rainfall at Batlow—						
C	1	6	6	2	—	—
D	—	7	6	2	—	—
River at Jindabyne—						
C	2	4	7	1	1	—
D	1	8	6	—	—	—
Rainfall at Kiandra—						
C	1	4	9	1	—	—
D	—	10	4	1	—	—

"A"=1891–1911; "B"=1912–1932; "C"=1903–1917; "D"=1918–1932.

pondence between the median departures of Tumbarumba and those of Jingellic and Tooma rainfall stations, there is no doubt that the latter would give coefficients of a similar order if their records were not slightly imperfect. In other words, stream flow in the upper Murray bears a very close relationship to proximal rainfall, by which it is directly controlled.

Thus it has been shown that the cyclical and secular changes of the upper Murray and, by inference, the Snowy also, have been due to changes in the rainfall regime. The number of exceptionally wet months has shown a tendency to increase, and seasons of the greatest humidity correspond with maximum stream flow, with a linear relationship between precipitation and run-off for the winter season at all times. For the upper Snowy, recent years have seen a slight downward trend in exceptional rainfall and in flood volumes, but the movement towards more extreme conditions of humidity or dryness on the Murray side has given the observed fluctuations of run-off, with the factor of deforestation filling a minor role.

CONCLUSIONS.

1. Rainfall and stream regimes for the upper Murray and Snowy Rivers are similar, with a simple maximum in winter and a minimum in late summer in each case. Maximum stream flow is delayed three to four months by the accumulation of snow in the highlands, and moistening of the catchment in the lowlands.

2. The incidence of the annual flood does not show any appreciable alteration over the period of record, but the flow intensity for the six-months flood period has been increasing on the upper Murray, and decreasing on the Snowy.

3. The flow of the upper Murray shows minor cyclical variations with an average period of 12 or 13 years, and a major cycle with a period of 30 years or more.

4. The secular trend of the annual and flood volumes of the Murray is towards increases of the order of 0·5% per annum and that of low water flow is towards a slight increase. The position is reversed in detail on the upper Snowy.

5. Partial deforestation is shown to be only a slight factor in promoting volume changes.

6. Flood volumes show a high correlation with immediate rainfall, and there is an approximately linear relationship between the two. Cyclical and secular variations in flow are due to changes in the rainfall regime, which involve alterations in the amount and concentration of precipitation within the year.

7. From this, it will be seen that the upper Murray streams have become much more effective instruments of erosion during the period of the records, thus accounting mainly for lateral enlargement of channels, the gullying and removal of alluvial deposits, and the cutting of new levels in old stream terraces.

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A PRELIMINARY ACCOUNT OF THE GEOLOGY OF THE MIDDLE NORTH COAST DISTRICT OF NEW SOUTH WALES.

By A. H. Voisey, B.Sc.

(Plate xvi; one Text-figure.)

[Read 26th September, 1934.]

Introduction and Previous Records.

It is proposed in the following pages to give a general account of the geology of the Middle North Coast district of New South Wales. Subsequently special aspects will be discussed in detail, particularly the Upper Palaeozoic succession in the Macleay River district and the Lower Palaeozoic rocks of the Nambucca and Bellinger districts.

In 1845 Mr. C. Hodgkinson reported the occurrence of limestone on the Macleay River above Kempsey. Early maps of New South Wales (C. S. Wilkinson, 1880; E. F. Pittman, 1892) showed areas about Kempsey as Devonian and Silurian. De Koninck (1898) described as probably Devonian some fossils submitted to him by the Rev. W. B. Clarke. Mr. W. S. Dun (1898) stated that these fossils had been collected 40 years before, but were destroyed in the Garden Palace fire in 1882. He (1898) gave a list of Permo-Carboniferous fossils which had been submitted to the Mines Department by Mr. E. W. Rudder. These were said to come from a locality about six miles west of Kempsey.

In 1896 Mr. J. E. Carne collected a few specimens from the parish of Willi Willi, County of Dudley, and, shortly after, Mr. C. Cullen collected from this parish and also the parish of Warbro a large number of undoubted Permo-Carboniferous forms. Mr. Dun (1898) added: "These were preserved mostly in limestone of which there appears to be a considerable development, both in thickness and area, and also in associated shales. This is as far as I am aware the first recorded instance of large deposits of Permo-Carboniferous limestone in New South Wales, though limestones are well developed in the underlying Carboniferous Beds."

Dr. W. G. Woolnough (1911) gave a preliminary account of the geology of the Kempsey district, but has not continued his investigations since then. He described the limestone at Willi Willi and Moparrabah and also the underlying glacial beds, and correlated them with those at Lochinvar in the Hunter Valley.

Carne and Jones (*Min. Res. N.S.W.*, No. 25. The Limestone Deposits of N.S.W.) described the limestone from the Macleay district, giving a number of localities in which it had been recorded, and including a sketch map of the deposits.

Sundry references to the Lower Palaeozoic rocks in the region have been made, chiefly by Dr. W. H. Bryan (1928), Mr. A. K. Denmead (1928) and Mr. E. C. Andrews (1900, 1908, 1928).

Professor Sir T. W. E. David (1932), on his geological map of the Commonwealth, marked the Upper Palaeozoic rocks of the Macleay as Lower Marine of the Kamilaroi System and the Lower Palaeozoic rocks north of the Kempsey area fault as Upper Silurian. He also showed Carboniferous rocks to the south of Kempsey.

Work carried out since 1928 has revealed many interesting facts, although paucity of outcrops has been a severe handicap. West of Yessabah it is difficult to do field work because of the prevalence of scrub. It is worthy of note also that in the more settled areas the excessive growth of paspalum grass in the summer and autumn makes mapping almost impossible. Lantana is unfortunately obtaining a hold in country which has been recently cleared and is an even worse obstruction than the stinging tree brush.

In view of the obstacles which impede the geologist in this luxuriant district it is little wonder that many problems are as yet unsolved.

The following table presents a summarized statement of the stratigraphy of the area and also some suggested correlations with rocks in other areas in Eastern Australia.

Age.	Name of Series.	Rock Types.	Maximum Thickness.	Correlation.
			Ft.	
Recent		River deposits, shell beds; estuarine, marine, aeolian deposits.	100+	
Pleistocene ..	Ridge Gravel.	Gravels, conglomerates, old river silts.	50	
Jurassic-Triassic	Clarence.	Fresh-water conglomerates, sandstones and shales with coal seams and fossil wood.	4,000+	Walloon Series. Bundamba Series. Ipswich Series.
Permian (?) ..	Kempsey.	Fresh-water tuffs, sandstones, shales, and conglomerates.	5,000+	
Permian ..	Macleay.	Marine conglomerates, sandstones, shales, limestones and tuffs. *Eurydesma cordatum* Zone.	3,400+	Hunter River: Kamilaroi, Lower Marine; Drake (N.S.W.); Silverwood (Qld.).
Carboniferous ..	Kullatine.	Fresh-water tuffs, slates, mudstones, conglomerates, and varves.	5,000+	Kuttung Series (N.S.W.).
Carboniferous ..	Boonanghi.	Arkose tuffs, mudstones, conglomerates with marine fossils.	4,000+	Burindi Series (N.S.W.).
Devonian ..	Hastings.	Dacites, quartzites, jaspers, banded chert, etc.	?	Barraba. Tamworth Series. Woolomin.
	Unconformity.			
Silurian (?) ..	Coff's Harbour.	Glassy cherts, quartzites, slates, phyllite and greywacke.	?	Neranleigh Series of Brisbane Schists.
	Unconformity ?			
Ordovician (?) ..	Nambucca.	Phyllites and slates.	?	Bunya Series of Brisbane Schists; Metamorphics of South Coast of N.S.W.

Stratigraphy.

A. Lower Palaeozoic Section.

Ordovician (?).

The Nambucca Series.

This section of the metamorphic rocks which outcrop over a large area between the Hastings and Clarence Rivers consists almost entirely of phyllites and slates which have been intensely folded. There is very little variety, the fine-grained texture persisting throughout.

The fresh rock is grey to bluish-grey in colour, but weathers readily to a buff or brown, owing to the oxidation of the iron content. It is fissile, cleaving parallel to the bedding planes, and the cleavage surface possesses a sheen due to the presence of mica flakes.

Fine exposures of contorted rock are seen in the road cuttings along the Oxley Highway east of Yarrowitch, and also at Nambucca Heads. As cleavage persists parallel to the lamination, corrugated slabs of the rock, now almost a schist, are obtainable.

Microscopically, the phyllite is very fine-grained and consists largely of quartz grains less than 0·01 mm. in diameter. Mica and chloritic material are also present.

The series as a whole is characterized by an extraordinary amount of milky quartz which occurs chiefly as concordant sheets parallel to the bedding planes, even when these are puckered. Sometimes it is transgressive, as irregular veins and reefs, which, near granitic intrusions, may contain a variety of materials. Iron pyrites, stibnite, mispickel, molybdenite, galena, cassiterite, gold and silver have been found. No fossils have been recorded so far from the series in the district examined.

Silurian (?).

The Coff's Harbour Series.

North of the Bellinger River there is a change in the rock type from the phyllites and slates of the Nambucca district. This is accompanied by a marked alteration in the strike from almost north-south to east-west.

Hard bands of chert, quartzite, and indurated slate are interstratified with phyllite. The cherts are hard, glassy, and bottle-green in thin fragments. They are strongly jointed, breaking into rhombs of about 20 cubic inches each. Quartzites are very diverse in colour, being black, white and green. Flakes of iron pyrites are sometimes common along the numerous small joint planes, as, for example, in the material used in the construction of the Coff's Harbour breakwater.

Denmead (1928) records greywacke from this series.

B. Middle Palaeozoic Section.

Devonian.

The Hastings Series.

This name has been used to include all the Devonian rocks in the Hastings district. It is possible that the equivalents of all Benson's New England Devonian Series are to be found.

The jaspers, quartzites and cherts may belong to the Woolomin Series. Banded cherts and spilites are of the typical Tamworth type. The mudstones present are in part Burindi, but some may be Barraba.

The rocks are only mentioned here for the sake of completeness, as Dr. G. D. Osborne hopes shortly to publish his views upon the structures south of the Hastings River.

Correlation of the Lower Palaeozoic Rocks with the Brisbane Schist Series.

Mr. A. K. Denmead (1928, p. 103) subdivided the Brisbane Schists into four groups as follows:

4. Fernvale Series.—Serpentines, jaspers, andesitic tuffs, banded cherts, shales, claystones and limestones.
3. Neranleigh Series.—Greywackes, banded slates, grits, boulder beds and quartzites.
2. Bunya Series.—Mica phyllites and quartz-mica schists with phosphatic cherts, slates and quartzites in the upper portions of the series.
1. Greenstones, probably altered porphyrites and basalts.

He adds: "No unconformities or disconformities are known to occur in the Brisbane Schists. The beds are all folded about north-north-west and south-south-east axes."

The greenstones (1) have not been found in northern New South Wales.

The description of the Bunya phyllites (2) given by Richards (1922) would apply equally well to those of the Nambucca Series. The presence of so much milky quartz, similarly disposed, is noteworthy, while the uniformity of both series and the parallelism of the strikes provide other links.

Denmead suggests that the Coff's Harbour greywacke may prove to belong to the Neranleigh Series (3). Quartzites and slates are common to both series, but the boulder beds have not been found in the southern locality.

The Hastings Series includes serpentines, jaspers, andesitic tuffs, banded cherts, shales, and claystones. This may be in part the equivalent of the Fernvale Series (4). Denmead has correlated his series with the Woolomin Series of Benson (1913). All are definitely Devonian in age.

With regard to the ages of the other series, David writes (1932, p. 44): "In Queensland the Bunya Series, presumably of Ordovician age, is formed chiefly of mica phyllites, having a thickness of perhaps as much as 18,000 feet. The *Diplograptus* which has been found on a horizon either at the top of this series or at the base of the Neranleigh Series (Silurian ?) may indicate an age either high in the Ordovician or low in the Silurian."

The similarity between the phyllites of the South Coast of New South Wales, described by Dr. Ida A. Brown (1928), and those of the Nambucca and Bunya Series has been noted in the field.

C. UPPER PALAEOZOIC SECTION.

The Upper Palaeozoic rocks described hereunder occur in the Parrabel Anticline and outcrop to the south of the Macleay River.

Lower Carboniferous.

The Boonanghi Series.

The lowest unit so far found in the Parrabel Anticline is a remarkable agglomerate resembling the Devonian Baldwin Agglomerate of Benson (1913). It is overlain, however, by a series of arkose tuffs, sandstones, and mudstones, with a few bands of conglomerate. The tuffs contain marine fossils, chiefly crinoid ossicles, but some corals, molluscs and brachiopods. The presence of *Loxonema* and *Rhipidomella* is sufficient to prove the Lower Carboniferous age.

Plant remains have been found in thin sandstone bands and among the marine shells. The total thickness must exceed 4,000 feet.

The following section was measured along the limb of an anticline going west from the Wittitrin Post Office:

	Thickness in Feet.
Blue Sandstones and Mudstones	225
Crinoidal Arkose Tuffs	110
Fine Conglomerate with Marine Shells	30
Blue Sandstone	170
Crinoidal Arkose Tuffs	100
Blue Sandstones	185
Arkose Tuffaceous Grit	45
Slates with Worm Tracks	100
Blue Sandstone	45
Grey Sandstone	240
Crinoidal Tuffaceous Grits and Sandstones	140
Mudstones and Sandstones	155
Crinoidal Arkose Grit	150
	1,695

The topmost beds have been faulted against the Kullatine Series. Slight faulting in the series has made further measurements unreliable, owing to the similarity of the rocks.

The crinoidal arkose tuff is usually greenish-grey in colour, with pink and white specks of felspar and calcite when fresh, but it weathers to a brown colour due to the decomposition of the ferro-magnesian minerals. The grainsize varies from an average of about 4 mm. in the coarser grits to about 0·05 mm. in the fine bluish tuffaceous sandstones. The microscope reveals beautifully twinned but slightly kaolinized basic felspar up to 3 mm. in length and an abundance of chlorite which is responsible for the green colour. Calcite, representing the crinoids, corals and shell fragments, is also present, but quartz is very rare. Evidently the basic volcanic ash settled down rapidly, without suffering much transportation, in a sea teeming with crinoids, corals and brachiopods.

Lower to Upper Carboniferous.

The Kullatine Series.

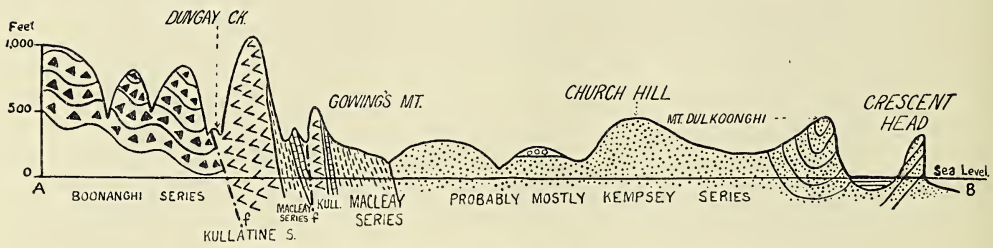
Faulted against the Boonanghi Series at Wittitrin are the lowest beds of the Kullatine freshwater series. These are sandstones, grits, fine conglomerates and interbedded acid tuffs which are overlain by thinly bedded slates and cherts containing *Rhacopteris* and large pieces of fossil wood.

The beds overlying the *Rhacopteris* horizon show abundant evidence of the presence of glaciers. About six hundred feet of heavy conglomerates and interbedded coarse grey tuffs contain dark grey varve shales showing the rhythmical banding. Boulders of igneous rock up to two feet across have been found in the conglomerates which are fluvio-glacial. Some of the boulders are angular and are definitely erratics. Typical rock types included in the conglomerate are: pink and grey granites, white quartz, quartzites, and many varieties of porphyries and sandstones. A tillite at the top of the series outcrops on the eastern side of Gowing's Mount.

The tuffs are generally more acidic than those of the Boonanghi Series. A thin section shows the presence of allotriomorphic quartz grains, but

subidiomorphic albite and orthoclase. Again there has been little transportation of the volcanic material. Quite a large proportion of chloritic volcanic ash occurs in patches throughout the rock.

The total thickness of the section is in doubt, owing to the lower portion being faulted away, and to the presence of numerous strike faults. It must, however, be in the vicinity of 5,000 feet.



Text-figure 1.—Section along line AB on map (Plate xvi).

Considering the distance from the type area for the Carboniferous in the Hunter valley and from the same series in the Werris Creek-Currabubula district, the resemblance of the Kullatine Series to the Kuttung Series is striking.

Especially is this seen in the glacial stage. A correlation of the conglomerates, varves and tillites in the three localities can hardly be disputed. This is important with reference to the views of Mr. J. H. Reid (1930) who considered rocks which he correlated with the overlying marine beds to be the marine equivalents of the Kuttung Series where it is not developed in Queensland. He was undoubtedly misled by Dr. Woolnough's (1911) statement: "The great interest and importance of the Upper Macleay Permo-Carboniferous is that the glacial beds do not appear to be the basal beds of the system, but seem to be underlain by a great but at present undetermined thickness of conformably bedded tuffs." These tuffs represent the upper beds of the Kullatine series and have associated conglomerates and varves.

It may be pointed out here that *Rhacopteris* was collected by Professor L. A. Cotton from an exposure several miles south of Kempsey. The exact locality of the occurrence is uncertain, but the writer is inclined to believe that the rocks from which the *Rhacopteris* was collected are equivalent to the Kullatine Series and must be quite distinct from the Kempsey Series (see below) which outcrops over a wide area south of Kempsey.

Lower Permian.

The Macleay Series.

Purple, red, green and blue calcareous shales overlie the Carboniferous glacial beds at Yessabah and Dondingalong. The correlation of these with the Lochinvar Glacial Beds at the base of the Kamilaroi System in the Hunter Valley, as suggested by Woolnough (1911), seems inevitable. Very good sections of these beds are to be seen in the road cuttings between Sherwood and Moparrabah. In places, granite and porphyry erratics up to two feet in diameter have been found. The more common pebbles are smaller and include granite, purple rhyolites, orthoclase-porphyries, quartz-porphyries, dacites, hornblende-andesites, glassy andesites, keratophyres, quartzites and sandstones. These are frequently faceted

and striated. Marine fossils are abundant in the shales. The thickness of the unit varies considerably, and sandstone and conglomerate bands appear.

Sandstones, mudstones and tuffs containing well preserved fossils including *Linoproductus springsurensis*, Fenestellidae, *Zaphrentis*, *Dielasma*, *Aviculopecten mitchelli*, and *Monilopora* follow.

These are overlain by the main limestone band which attains a thickness of 400 feet at Sebastopol. This is the *Eurydesma cordatum* horizon, but is made up largely of the remains of crinoids. *Trachypora wilkinsoni*, *Monilopora*, Fenestellidae and small brachiopods have been found. The rock is crystalline, fairly even in texture throughout, and is coloured pink, reddish-brown, purple and grey but is very often white.

The limestone is followed by a succession of hard silicified limestone bands which weather to brown spongy masses. Silica has replaced the *Monilopora*, *Spirifer* and a large *Pecten*, which are plentiful.

Soft sandstone and mudstone make poor outcrops in the eastern areas, but the section below was measured in the Willi Willi district in a northerly direction along Warbro Brook. The beds dip in a northerly direction at 25 degrees.

	Thickness in Feet.
Mudstones	500
Tuffaceous Mudstones and Conglomerates	400
Grits and Sandy Tuffs	100
Fossiliferous Mudstone	100
Flaky Yellow Shale	100
Limestone (Impure band)	50
Purple and Green Shales	100
Mudstone	180
Chert and Tuff	45
Soft Sandstone (*Strophalosia*)	55
Silicified Limestone (with *Monilopora*)	85
Silicified Sandstone	50
Silicified Limestone	55
Crinoidal Limestone (*Eurydesma cordatum*)	310
Sandstones and Mudstones	195
Conglomerates and Sandstones	175
Fenestellidae Cherts and Tuffs	120
Sandstones and Conglomerates	110
Fenestellidae Mudstones and Sandstones	160
Glacial Beds	500?
	3,390

Rudder's Hill, near the new entrance of the Macleay, is composed of some hundreds of feet of slate, sandstone and conglomerate. Woolnough (1911) suggested that the latter might be fluvio-glacial in origin. *Aviculopecten* cf. *mitchelli*, Fenestellidae, and other Permian fossils have since been found in the other slates below this. The whole series has been hardened by the intrusive rocks nearby. Between Clybucca and Barraganyatti a series of sandstones and shales dipping steeply to the north-west contains marine fossils, probably Permian. Crinoid stems and shells have been found by Dr. G. D. Osborne in sandstones exposed in a road cutting near Blackman's Point.

Pending a more definite identification of the fossils collected, all the occurrences of marine beds have been referred to the Macleay Series.

Permian (?).

The Kempsey Series.

Owing to the discontinuity of outcrops east of Dondingalong, it has not been possible so far to work out the geological structures. It would appear that most of the area is occupied by sandstones and tuffs with unidentified plant remains, which have been grouped under the name of "Kempsey Series".

The Kempsey Series appears to follow the trend of the Parrabel Anticline from Willawarrin to Kempsey but has not been satisfactorily separated from the soft marine beds at the top of the Macleay Series (Lower Permian)—a fact which indicates a Permian age for part at least.

Criteria used for the identification of the Kempsey Series are as follows: (1) Characteristic lithology of tuffs, sandstones and shales; (2) rhythmical deposition always marked; (3) abundant and typical shale (?) inclusions; (4) abundant but unidentifiable plant remains; (5) arrow-head markings; and (6) generally poor outcrops.

There is a great variation in the lithology of the sandstones and tuffs in colour, texture and composition, but recognition of any of them is rarely difficult. There is a certain relationship between the sediments in each locality in which they have been examined but the rhythmical deposition is universal. At Crescent Head there are alternating beds of dark sandstone and sandy tuff, usually a couple of feet in thickness. The texture varies greatly, some conglomerate bands being present. About Kempsey the tuffs are lighter in colour and there is more sandstone. Although there are some thicker bands of tuff, as at Church Hill, it is more common to find beds a foot or less thick. The rhythm is again seen at Smoky Cape, where there is some resemblance to the tuffs about Kempsey. At Racecourse Head, Delicate Nobby and the Big Hill, thin bands of mudstone, claystone and tuff occur.

Irregular and abundant inclusions of what appears to be grey shale are especially noteworthy in the Kempsey stage. They are usually in a fine-grained sandstone and suggest intraformational breccias.

Woolnough (1911) noted the plant remains at Crescent Head. These are especially abundant on some horizons in all the localities cited, and indicate the freshwater origin of the series.

A feature peculiar to the Kempsey Series is what has been called the "Arrow-head marking" which appears as a succession of Vs, one inside the other, when the rock is split parallel to the lamination. The cross section is circular. The only occurrence seen outside the series was in some mudstones low in the Boonanghi Series (Lower Carboniferous). How the marking was formed, what it represents, and its value as a criterion for stratigraphical purposes are questions not yet solved. It may be worm track, plant impression, or the result of some physical phenomenon.

A massive conglomerate, at least 500 feet thick, at Korogoro Point, overlies rhythmically-bedded tuffs and sandstones at Mt. Dulkoonghi. Woolnough (1911) believed that the conglomerate might be Trias-Jura in age, but as it resembles smaller bands in the Kempsey Series, it is retained there for the present. It occupies the centre of a syncline running north and south at Mt. Dulkoonghi, dipping north towards Korogoro Point where it attains its maximum development.

Referring to rocks which have been included under the Kempsey Series, Woolnough did not offer suggestions with regard to their age but stated: (*a*). "On the east, the Silurian rocks [Nambucca Series. A.V.] are bounded by

a series of contorted and cleaved quartzites and slates which we may refer to as the Kempsey Slates. The boundary appears to be near Hickey's Creek where a heavy conglomerate is met with. In the road sections between Hickey's Creek and Kempsey, the slaty rocks exhibit dips in all directions and there does not seem to be any well defined axis of folding." (*b*). "On the coast between Smoky Cape and South West Rocks what appear to be the equivalents of the Kempsey slates occur in broad undulations but with approximately horizontal disposition as a whole. They are black in colour and intensely hard as a result of contact metamorphism."

The conglomerate at Hickey's Creek is probably Pleistocene, similar to that at Sherwood. It unconformably underlies the older series.

It is likely that it was the highly folded Kempsey Series which influenced earlier observers in marking the area about Kempsey as Devonian and Silurian (C. S. Wilkinson, 1880; E. F. Pittman, 1892). There is even now a slight possibility that they might be Upper Devonian, but the large plant stems render this unlikely. Dr. G. D. Osborne suggested that the Crescent Head rocks might be Lower Carboniferous in age, while the conglomerate at Mt. Dulkoonghi reminded him of the Greta conglomerate of the Hunter Valley.

The position of the series in relation to the Parrabel Anticline and the fact that it is a thick unit not represented in the neighbouring sequence from Lower Carboniferous to Lower Permian suggest a Middle Permian age.

The question must be left until more detailed work is undertaken.

D. MESOZOIC.

Triassic to Jurassic.

The Clarence Series.

Some 27 miles south of Grafton the main North Coast road from Woolgoolga climbs an escarpment composed of sandstones and coarse quartz-pebble conglomerates which have the appearance of estuarine beds. They include shale bands containing well preserved plant remains. Just north of Dirty Creek a horizon of fossil wood, strongly reminiscent of the basal beds of the Walloon Series at Warwick, Queensland, occurs. Seams of carbonaceous shale and coal overlie these, then follows a thick series of sandstones.

With regard to the age of the Clarence Series Dr. A. B. Walkom (1918, p. 84) wrote: ". . . the fact that Carne (1908) indicates the presence of *Taeniopteris spatulata* (*T. Daintreei*) in the lower part of the series, is sufficient to render the correlation of any part of the Clarence Series with the Ipswich Series improbable. It is possible that the sandstones and conglomerates at the base of the Clarence Series may be the equivalents of the Bundamba, but, on the present evidence, I believe the greater part of the Clarence Series (if not all of it) is to be correlated with the Walloon Series of Queensland."

As the Grafton bore (3,070 feet) met coal seams, probably of the Ipswich Series, and did not reach the underlying Palaeozoic rock (David, 1932), it seems that the beds described above have overlapped the older series and that there is still a possibility that the three Queensland divisions are represented.

E. CAINOZOIC.

Pleistocene.

Ridge Gravels.

Extensive deposits of boulders and quartz gravel cap hills on the north and south banks of the Macleay River and are also found at Macksville on the

Nambucca River. At Sherwood, rounded jasper, quartz, chert and quartzite pebbles up to six inches in diameter form a conglomerate. This was thought by Woolnough (1911) to be Permo-Carboniferous in age—a tribute to the degree of cementation. The deposit unconformably overlies the steeply dipping Macleay Series. The age of the gravels has been determined by reference to the physiography. They have been spread out on the floor of a valley carved out of the tableland which was uplifted at the close of Tertiary times (Andrews, 1912). Since their deposition the Macleay River has become entrenched in the old valley, probably through a minor uplift towards the close of the Pleistocene. Thus it seems that the gravels were laid down during Pleistocene times.

Recent.

(i). *Estuarine Deposits.*—Below the recent sand and alluvial deposits which form the Lower Macleay flats are estuarine sands, muds and clays with some shell bands. *Spisula trigonella* and *Arca trapezia* are the chief forms and prove the estuarine origin of the sediments. The Clybucca Drainage Works revealed a bed of shells which must underlie 25 square miles of flats. A bore at Smithtown gave the following section:

	Feet.
Sub-soil	3
Silty Clay	13
Sand Drift with Shells	28
Yellow Clay	9
Mudstone and Pipeclay	9
Sand Drift with Shells	2
Mudstone and Pipeclay	11
Pipeclay	5
Total Thickness	80

The bore was started 9 feet 3 inches above the average river level, and struck shales at 80 feet below the top of the bore. The sediments have been laid down since the rise in sea-level which drowned the valleys along the coast.

(ii). *Marine Deposits.*—Some of the sediment forming the sandy flats along the coast as well as that of the sand and boulder beaches is marine in origin.

(iii). *Freshwater Deposits.*—The coastal rivers have built terraces of alluvium and gravel, and these freshwater sediments cover large areas, especially near the coast. In swampy districts, notably at Clybucca and Collombatti, there has been a slow accumulation of peat and clay.

(iv). *Aeolian Deposits.*—Sand has been blown over much of the coastal flats sometimes forming hills. It is often well mixed in with swamp muds and alluvium. On the south side of Smoky Cape it has accumulated to a height of nearly two hundred feet. A sand deposit, partly consolidated, covers the hills at Korogoro Point and the sand has been piled high on the southern and south-western sides.

IGNEOUS ROCKS.

(a). Carboniferous.

Serpentine.

The Port Macquarie serpentine is in all probability coeval with the New England occurrences of this rock, as described by Benson in 1913 (Browne, 1929). It outcrops along the coast between the Hastings River Entrance and Tacking Point, and strikes 10 degrees north of west in that locality, being nearly two

miles in width. The road cuttings along the Oxley Highway west of Wauchope reveal much of this beautiful rock. It varies greatly in colour and texture, and is sometimes silicified, giving rise to quartzites and jaspers. Kernels of the unaltered basic rock are common, while veins of magnesite and asbestos are present. The serpentine invades the cherts, slates and mudstones of the Hastings Series (Devonian).

(b). Late Permian.

The Granites and Porphyries.

"The earth-movements which affected the Permian rocks near the close of the Palaeozoic era along what is now the east coastal portion of Australia were accompanied by extensive plutonic intrusions" (David, 1932, p. 70).

The granites and porphyries which intrude Upper Palaeozoic rocks at Smoky Cape and Lower Palaeozoic rocks at Mt. Yarrahapinni are probably all of late Permian age.

Woolnough (1911) described the Laggers' Point granite. It only remains to mention that in thin section quartz, orthoclase, biotite, plagioclase, and a little iron pyrites were seen. Numerous roof pendants and inclusions of the intruded tuffs and slates are present. There appears to have been some contamination of the granite by a large inclusion of slate at Little Bay.

Woolnough mentioned sills of light and fine-grained felsitic rock connected with the granite. Point Briner at South West Rocks is composed of a porphyritic phase of this rock which proves to be a granophyre. The fresh rock is a sparkling white, but it weathers to a pale orange colour. Phenocrysts of quartz and orthoclase reach three-eighths of an inch in diameter. The granophyric structure of the groundmass is striking when seen under the microscope. The pattern, developing outwards from the phenocrysts, becomes progressively finer and ultimately gives way to a mosaic of interlocking quartz and orthoclase grains.

(c). Tertiary.

Basalts.

Great thicknesses of basalt cover the Dorrigo Plateau and Hastings Ridge to the north and south of the Macleay Valley. Woolnough (1911) records a capping of basalt some hundreds of feet in thickness resting on Lower Palaeozoic slates at Anderson's Peak, near Bellbrook.

Structural Geology.

1. Lower Palaeozoic Trends.

The metamorphic rocks outcrop from the basalt-capped Hastings Ridge in the south to the Clarence River in the north, while the New England granite bathylith which invades them forms the irregular western boundary. They are overlain by Mesozoic sediments in the north-east with a well-marked unconformity and by Upper Palaeozoic sediments in the south-east. Their relationship to the latter has not been directly ascertained, but it must surely be an unconformable one.

The trend is from north-north-east to north-north-west, south of the Bellinger River, being roughly parallel with that of the Brisbane Schists, but swings round north of Urunga to east-west. Here the beds are almost vertical and it seems that there is a series of tightly folded anticlines and synclines, but there may be several different horizons of chert and quartzite.

Bryan (1928), dealing with the Brisbane Schist Series, wrote: "This very extensive series of metamorphic rocks is almost continuous from Tweed Heads to north of Rockhampton. The Coff's Harbour schists in northern N.S.W. although out of alignment with the Queensland formation, are regarded by most geologists as being part of the same series, the lack of alignment being due to a lateral break—a drag of the rocks for about 150 miles in a direction at right angles to the strike. The series has an enormous thickness." As there is a change in the nature of the rocks coincident with the change in strike, it seems that much more work will have to be done before the reasons for this important structural break are ascertained.

The excessive alteration, puckering, and folding of the Nambucca Series is evidence of a period of intense diastrophism which took place before the Devonian rocks were laid down, since these are much less affected.

2. The Upper Palaeozoic Anticline.

The dominant structure in the southern portion of the area examined has been called the Parrabel Anticline. Into it have been folded the Upper Palaeozoic strata from Lower Carboniferous at least to Lower and probably Middle or Upper Permian. The northerly plunge of the anticline gives rise to a general semicircular outcrop of the units, and this is reflected in the topography.

Within the major structure there is considerable folding, although, towards the core, the Boonanghi Series is much more gently folded than the younger Kullatine and Macleay Series. These Lower Carboniferous rocks to the west of Wittitrin form anticlines and synclines trending north and south, and dips rarely exceed 10 degrees. There is a zone of strike faulting in the Kullatine Beds between Wittitrin and Yessabah, but the throw of the faults is not very great. A relatively large one has placed the series against the Boonanghi marine beds, giving a doubtful relationship between the two series; the strikes, however, are parallel on either side of the fault.

The Kullatine and Macleay Series in that neighbourhood are dipping steeply and are sometimes vertical or even overturned. Besides the strike faulting, two main oblique fractures have developed, and there has been some dragging of the limestone and its associates along the fault planes. At Willi Willi and Moparrabah, near the nose of the anticline, there has been less disturbance, and the rocks dip in a northerly direction at 25 degrees.

In view of the gently folded Mesozoic sediments in close proximity to Permian rocks, which have been intensely folded in the Drake District (Andrews, 1908) further to the north, it seems certain that the folding and faulting took place during late Permian times. The limits are Middle Permian and Lower Triassic, but the late Permian orogeny is recognized elsewhere (Reid, 1930; David, 1932; etc.). In view of the apparent conformity throughout the Upper Palaeozoic succession in the Parrabel Anticline, there does not appear to have been any diastrophic epoch between Lower Carboniferous and Late Permian times.

3. Faults.

David (1932) marks the junction between the Upper and Lower Palaeozoic rocks in the Macleay District as the Kempsey Area Fault. This seems to be a necessary inference in view of the difference in strikes and the fact that Permian rocks meet the Ordovician (?) without intervening Carboniferous.

Details of the fault have not been ascertained, but the junction between the series has been found near Toorooka on the Macleay River and also about three miles south of Eungai railway station. The faulting post-dated the folding of the Parrabel Anticline, as it truncates this structure. It probably occurred before the deposition of the Mesozoic sediments on the older series where Permian sediments may have been.

Denmead (1928) reports several east-west faults breaking across the strike of the Brisbane Schist Series. The Kempsey Area Fault may be contemporaneous with these. Denmead notes that some of the faulting in the Brisbane River zone is post Mesozoic, but considers the great dip-faults to be pre-Mesozoic and probably coeval with the block faults at Silverwood, Gympie and other places.

4. Igneous Intrusions.

The New England bathylith has invaded the sediments to the west. Probably contemporaneously a number of smaller intrusions occurred nearer the coast. These are chiefly in the nature of bosses and dykes.

Granite bosses are found at George's Creek (Woolnough, 1911), Smoky Cape (Woolnough, 1911), Mt. Yarrahapinni, and near Valla. Roof pendants at Smoky Cape indicate that erosion has only recently exposed this granite mass.

The age of the intrusion has been determined as post-Permian and pre-Mesozoic as the igneous rock invades Permian sediments at Rudder's Hill, Drake, Rivertree and Silverwood, and is overlain by Mesozoic sediments in the Silverwood district. It is possible, of course, that some of the granites may be older. The invasions occurred soon after the folding and faulting of the rocks at the close of Permian times.

5. The Mesozoic Basin.

Some distance to the north of Woolgoolga, near Corindi Creek, conglomerates and sandstones unconformably overlie the Lower Palaeozoic rocks and form the southern margin of the Clarence Basin. They dip in a north-westerly direction at 5 degrees. These beds are not the lowest of the sequence, but represent an overlap probably of the Bundamba Sandstones upon the Ipswich Coal-Measures (Triassic). The Jurassic Walloon Series overlaps the Bundamba Sandstones to the north and outcrops over a large region in southern Queensland. The Clarence Basin must have formed during the Triassic and was raised at the close of Jurassic times, as no Cretaceous sediments are represented.

Geological History.

The fine-grained sediments of an Ordovician sea, covering most of what is now Eastern Australia, were subjected to intensive folding and metamorphism, probably before the deposition of more variable Silurian rocks. Both series, at any rate, were folded along north-south axes prior to the development of a Devonian sea which covered most of New South Wales. It is possible that there was a land area between Coff's Harbour and the Queensland border.

Deposition continued with little interruption until well into Permian times. In common with the central districts, there was a change in the north from marine to freshwater conditions at the close of the Lower Carboniferous, but a return was made ushering in the Permian.

Violent volcanic eruptions persisted throughout the entire period during changing climatic conditions. The advent of glaciers towards the close of

Carboniferous times is demonstrated by the varve shales and tillites, while striated pebbles occur in the Lower Permian beds.

It seems that there was a freshwater lake in existence in the Macleay District during Middle Permian times.

At the close of the Permian occurred a most important diastrophic epoch which folded and faulted the Upper Palaeozoic sediments. This was closely followed by invasions of granite bringing a great variety of minerals.

Erosion during early Triassic times exposed the granites, removing the sedimentary covering. A transgression in the north of the area led to the deposition of the Clarence Series, and it was not until the close of the Jurassic that these were raised above sea-level.

Then came a long period of erosion giving rise to the formation of a Tertiary peneplain, but leaving a Main Divide at several thousand feet. The Kosciusko Uplift at the close of Tertiary times added another two thousand feet to this, leading to the rejuvenation of the streams and the development of canyons.

Earth and sea movements since have been of minor importance.

Conclusion.

Palaeontology and physiography have received scant attention in this paper because both are of sufficient importance to be treated separately. The aim of this discussion has been to present in as systematic a form as possible the broader aspects of a large area of hitherto neglected country. It will provide a basis for future work in an area which is destined to cast some light upon problems which have worried both New South Wales and Queensland geologists.

My thanks are due to all members of the geological staff of the University of Sydney for their ever-ready help and advice; to Dr. G. D. Osborne for his correction of this work; and to residents of the Macleay District for their hospitality and help during the field work. Outstanding among the latter are Mr. and Mrs. W. Newman, Mr. and Mrs. J. E. Gowing, and Mr. D. McIver.

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EXPLANATION OF PLATE XVI.

Geological Map of the Middle North Coast of New South Wales.

NOTES ON AUSTRALIAN MARINE ALGAE. VII.

THE ALGAE OF THE LOW ISLANDS.

By A. H. S. Lucas, M.A., B.Sc.

[Read 28th November, 1934.]

The Great Barrier Reef expedition led by Dr. Yonge spent a whole year, 1928–29, in an intensive and exhaustive study of the physical conditions and the animal and vegetable life of the Low Islands. These consist in a sandy cay and a mangrove swamp practically united at lowest tides, and enclosed in a rampart of coral. The lighthouse on the cay is situated in lat. 16° 37′ south. The whole lies in a favourable position, eight miles from the mainland at Port Douglas, and about three times that distance within the Great Barrier Reef, and presents biological features of its own of great interest.

In May–June, 1931, Mrs. F. Perrin and I spent a month in investigating the marine algae of the islands. By the courtesy of the Great Barrier Reef Committee, we were permitted to make use of the camp and extensive equipment so generously bequeathed by the Yonge expedition, and were aided by a grant from the Commonwealth Council for Scientific and Industrial Research. We had the good fortune to be received by Mr. F. Moorhouse, the Queensland marine biologist, who, with his assistants, Messrs. Wilse and Fison, happened to be engaged in zoological investigations at the time of our arrival. Mr. Moorhouse spared no pains in introducing us to the various flats, reefs, moats and channels, gave us a chart of the group and a table of tides for the period of our stay, and most generously assisted us by every means in his power. As the reports of Dr. Yonge's expedition were not yet available, and as Mr. Moorhouse had taken part in the expedition, his knowledge and experience so freely placed at our disposal was of inestimable value to us. We were not without an experienced guide from the start in our explorations.

We were well equipped for wading, and had the use of the boat left by the expedition. We had brought a dredge with us, but unfortunately the bottom of the accessible channels was unsuitable, and we never had sufficiently calm weather for venturing outside. Our work was then confined to the area enclosed by the rampart, and only extended to the shallower part of the slopes outside.

Dr. Geoffrey Tandy, of the British Museum, Natural History Branch, was the specialist in charge of the algae for the Yonge expedition. He very kindly later sent me the report on the structure and ecology published in 1931, to which he contributed an excellent account of the ecology of the algae, but gave no systematic account of the species.

In the present paper I have therefore drawn up a catalogue of the forms which we obtained. Most of these are mentioned by Dr. Tandy. The species which he noted, but which were not seen by us, are marked by an asterisk (*). Those which we found, but are not cited by Dr. Tandy, are marked by a dagger (†).

Catalogue of the Marine Algae of the Low Isles.

Diatomaceae.

Diatoms were plentiful, both on the Sand Flat and attached to the roots of Mangroves, but we did not pay attention to them. Tandy does not give any specific determinations.

Cyanophyceae.

Lyngbya majuscula Harv. Handsome growths.

**Hormothamnion solutum.*

**Trichodesmium scoboideum* Lucas, Proc. Linn. Soc. N.S.W., xlv, 1919.—We did not witness a descent of this alga on the island, but saw acres and acres of it floating on the sea north of Mackay and gathered buckets full. It was noted by Capt. Cook in these seas.

Chlorophyceae.

Conferva with long cells.

†*Enteromorpha compressa* (L.) Grev.—Rare.

†*E. percursa* (Ag.) J. Ag.—Abundant. Tangled around other algae.

†*Cladophora.*—A dark form. Diam. of cells 100μ. Growing on *Digenea.* Perhaps near to *C. atro-virescens* Fosl.

Boodlea paradoxa Reinb.—So determined by Tandy. Differs from *B. coacta* which has opposite branching towards the tips. Abundant, carpeting dead coral.

Anadyomene Brownii (Gray) J. Ag.

Dictyosphaeria favulosa (Mort.) Dcne.

D. Versluysii Weber & Bosse.—Almost columnar, not foliose.

**D. sericea* Harv.—I am inclined to doubt the presence of this species. It has a mesh less than half the size of the mesh of the tropical species, and grows on rocks far away from coral on the coasts of South Australia and Victoria and on the North Coast of Tasmania in cold waters.

Valonia Forbesii Harv.

**V. macrophysa* Kuetz.

V. Aegagropila (Roth.?) Ag.

Bornetella. Tandy names *B. nitida* (Harv.) Mun.-Chalm. Prof. W. A. Setchell prefers †*B. oligospora* Solms Laubach.

†*Derbesia* sp.

Caulerpa verticillata J. Ag.

†*C. Freycinetii* Ag.

†*C. sertularioides* (Gmelin) Howe.

C. sertularioides (Gmelin) Howe—tristichous form.

C. racemosa (Forsk.) J. Ag.

var. *clavifera* (Turn.) J. Ag.

var. *uvifera* (Turn.) J. Ag.

†var. *laxa* J. Ag. Small globular ramenta on short assimilators.

C. peltata Lamour.

†*C. nummularia* Harv.

Neomeris dumetosa Lamour?

Chlorodesmis comosa Bail. & Harv.

Avrainvillea erecta A. & E. S. Gepp.

†*Penicillus Arbuscula* Mont. With *Avrainvillea* on the Sand Flat.

Halimeda Tuna (Ell. & Soland.) Lamour.

H. opuntia (L.) Lamour.
H. tridentata Duchass. De Toni quotes as form of *H. incrassata.*
**H. cuneata* Hering.
Codium spongiosum Harv. Large plants.
†*C. Geppii* Schmidt.

PHAEOPHYCEAE.

Sargassum torvum J. Ag.
**S. lanceolatum* J. Ag.
**S. latifolium* (Turn.) Ag.
**S. cristaefolium* Ag.
} Eu-Sargassum

The absence of the *decurrens*-group is noteworthy. They seem to prefer the mainland coast, as at Darwin and Geraldton, or closely adjacent islands, as Stone Island, off Bowen, and Magnetic Island, off Townsville.
Turbinaria conoides Kuetz. (? *T. turbinata* recorded by Tandy).
T. ornata J. Ag.
Cystophyllum muricatum (Turn.) J. Ag.
†*Hormosira articulata* (Forsk.) Zan.
†*Gymnosorus nigrescens* (Sond.) J. Ag.
Padina australis Hauck.
**P. Commersonii* Borg.
Dictyota Bartayresiana Lamour.
**D. ciliata* J. Ag.
†*D. sandvicensis* Sond. On mangroves.
Hydroclathrus cancellatus Borg.
**Ectocarpus.*

RHODOPHYCEAE.

†*Liagora annulata* J. Ag. Rare.
L. sp. Probably undescribed. Common on Outer Reef.
†*Galaxaura rudis* Kjellm.
†*G. glaberrima* mihi. Undescribed.
†*G. elongata* J. Ag.
†*G. cohaerens* Kjellm.
†*Gelidium*? Recalling in habit *G. pusillum* (Stack.) Le Jolis.
†*Gracilaria lichenoides* (L.) Harv.
†*Rhodymenia* sp.
†*Champia affinis* (H. & H.) J. Ag.
**Laurencia botryoides* (Turn.) Gaill.
**L. papillosa* (Forsk.) Grev.
†*L. rigida* J. Ag. No palisade cells.
Acanthophora orientalis J. Ag.
Digenea simplex (Wulf.) Ag.
†*Leveillea jungermannioides* (Mart. & Hering) Harv.
Amansia glomerata Ag.
†*Rytiphloea*? 5 siphons, 5 cm. high.
Spyridia filamentosa Harv.
†*Chondrococcus Kilneri* (J. Ag.) De Toni.
Peyssonnelia sp.
†*Goniolithon laccadivicum* Fosl.
Amphiroa fragilissima (L.) Lamour.
Melobesia sp.

THE GEOLOGICAL STRUCTURE OF THE WERRIE BASIN.

By S. Warren Carey, M.Sc., Science Research Scholar and late Deas-Thomson Mineralogy Scholar, of the University of Sydney.

(Plate xvii; two Text-figures.)

[Read 31st October, 1934.]

Introduction.

Definition.—For the great trough, nearly fifty miles in length, which centres on Werris Creek, and stretches away towards the Namoi River in the north-north-west, and to within a few miles of the Liverpool Range in the south, the name Werrie Basin is proposed. The town of Werris Creek is at the centre of the basin, and the Werrie basalts cover more than a hundred square miles of the country within its boundary.

The basin lies mostly in the County of Buckland and extends eastwards into the County of Parry. The area mapped includes the parishes of Carroll, Babbinboon, Dight, Denver, Piallaway, Mooki, Clift, Currabubula, Werrie, Grenfell, Borambil, Coeypolly, Evan, Wallabadah, Quirindi and Warrah, in the county of Buckland, and the parishes of Moorowara, Somerton, Moolunmoola, Winton, Turi, and Goonoo Goonoo, in the County of Parry. This area lies within the watersheds of the Mooki and Peel Rivers, tributaries of the Namoi in the western fall of the State. Werris Creek is a town on the Great Northern Railway at the junction of the North-Western Railway and the south-west connection to Dubbo, and is distant 255 miles from Sydney.

Previous Records.—The earliest reference to the geology of this region was made by Sir T. Mitchell, who passed through it in 1831 (Mitchell, 1838). Early stratigraphical work was carried out by the Rev. W. B. Clarke (1852, 1878). Towards the end of last century, the Carboniferous marine fossils in the district attracted a good deal of attention, and extensive collections were made by the late Mr. Donald Porter of Tamworth, and by Stonier (1891), Pittman (1897), and Cullen. These were described by Etheridge (1891, 1892, 1897, 1907). The first systematic stratigraphy was carried out between 1915 and 1919 by Benson (1920), who briefly examined the Currabubula district, and made a hasty reconnaissance of the neighbouring areas, his studies being curtailed by his removal to New Zealand. At the same time palaeontological and petrological descriptions were given by his collaborators, Dun (1920) and Browne (1920). Brief references to the geology of the district have also been made by Pittman (1897), Andrews (1897, etc.), Cambage (1912), Cotton and Walkom (1912), Carne (1913), Browne (1924), David (1932) and others.

Concurrently with the present work, Messrs. Lloyd and Mulholland, of the Department of Mines, carried out a reconnaissance survey of the Gunnedah-Manilla district, and overlapped for a short distance near Somerton and Carroll. They have given freely the data which they have collected, and the author has benefited much from the discussion of border problems with them.

Scope of Paper.—It is proposed to give primarily in this work a complete account of the structural geology of the region. The Carboniferous sequence will be discussed fully in a paper at present being prepared for publication, but a general account of the stratigraphy is included here. The discussion of the petrology of all the igneous series is reserved until a later date.

A co-ordinate graticule has been incorporated in the structural map, and map references in the text have been made in accordance with this system (e.g., D9, etc.). Bearings are all referred to magnetic north.

Acknowledgments.—The writer wishes gratefully to acknowledge the constant advice and encouragement of Dr. W. R. Browne, and his very valuable criticism throughout all phases of work. It would be better to thank the residents of the district collectively rather than individually, for the writer has met kindness and hospitality on all sides, and the list of friends who have materially assisted him during the field-work is indeed a long one. One may specially mention Mr. and Mrs. Eugene McCarthy, Mr. and Mrs. C. G. Middleton, Mr. and Mrs. W. R. Bridge, Mr. P. Meizer, Mr. and Mrs. M. E. Daly, Mr. and Mrs. I. C. Thornton, Mr. L. Gilroy, Mr. M. K. Campbell and family, the Misses Dennis, Mr. Gordon, Mr. G. Bowra, Mr. Tom Creek, Mr. E. Jones, Mr. and Mrs. E. Bridge, Mr. and Mrs. Ramsay, Mrs. C. Doolan, Mr. and Mrs. Chapman, Mr. Mitchell, Mr. E. Phillips, Mr. and Mrs. Arnold Perfrement, Mrs. Henderson, Mrs. Garvin, Mr. and Mrs. H. J. Perfrement, Mr. and Mrs. Frank Swain, Mr. and Mrs. Watt, Mr. C. E. Thomas, and Mrs. C. Lobsey.

Stratigraphical Units.

The stratigraphical units which occur in the region are, in chronological order:

	Approximate thickness in feet.
Devonian:	
Barraba Series	Not determined
Carboniferous:	
Burindi Series	3,000
Kuttung Series:	
Lower Kuttung	5,000
Glacial Stage	6,000
Permian:	
Lower Coal Measures	300
Werrie Basalts	5,000
Upper Coal Measures	400
Unconformity.	
Tertiary:	
Basalts	400
Quaternary:	
Breeza Plains Alluvials	Not determined

The distribution of the above units, together with that of all the contemporaneous lavas and the subsequent intrusive rocks, is shown in the geological map (Plate xvii).

The details of the stratigraphy will be fully discussed in a later paper, but for the purpose of discussion of the structure, the following correlations may be assumed:

The Barraba, Burindi, and Kuttung series are strictly comparable with the same units as they occur in the areas where they have already been described. The Glacial Stage of the Kuttung corresponds to the Glacial Stage of Osborne (1922), and the Lower Kuttung is the equivalent of his Volcanic and Basal Stages. The base of the Glacial Stage will be referred to as the Porphyry Boulder Horizon.

In the Permian sequence, the two groups of Coal Measures are stratigraphically the same as the Greta and Newcastle Coal Measures respectively. The evidence on which this statement is based will be given in full in the stratigraphical paper. The Werrie Basalts, a thick series of altered basalts, are of Upper Marine age.

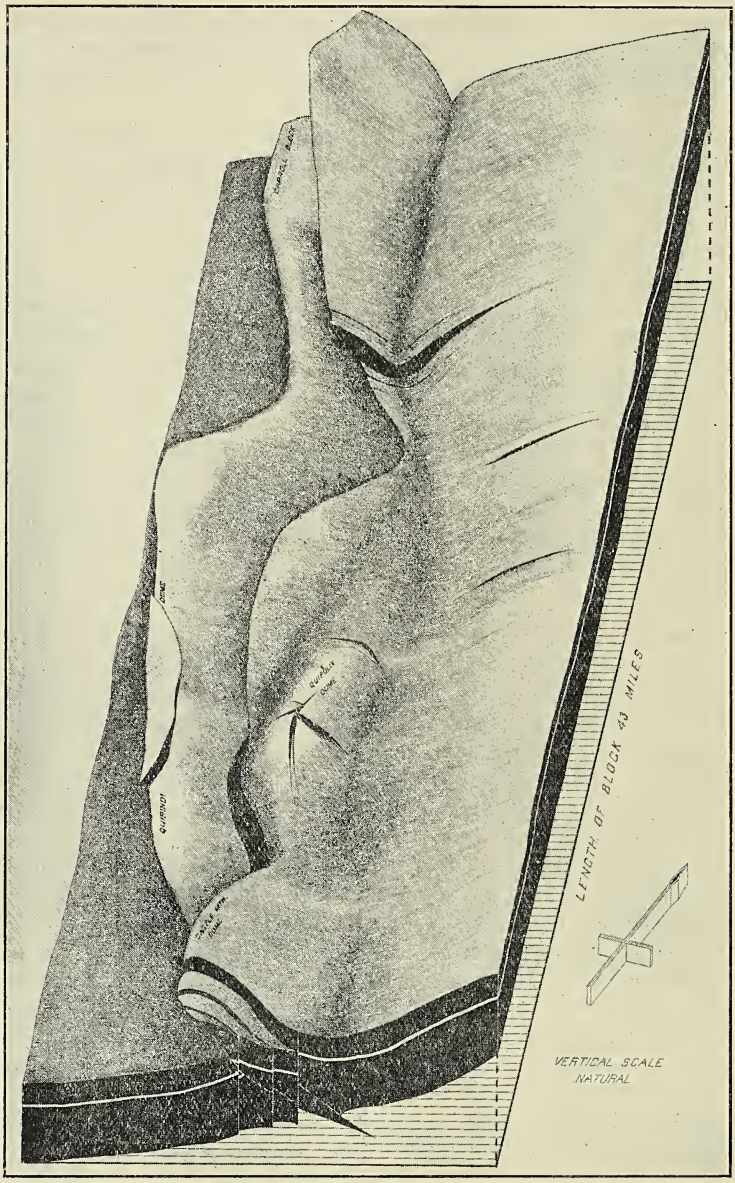
The sequence is conformable from the Barraba Series at Duri and Goonoo Goonoo to the Upper Coal Measures at Werris Creek. There are, however, some clearly recognizable time-breaks, which have not produced angular divergence. No disconformity has yet been recognized between the Upper Devonian Barraba Series and the Carboniferous Burindi Series; in fact, the zone of passage between the two series has only been arbitrarily fixed. However, several lines of evidence show that there is a distinct break at the Porphyry Boulder Horizon. Another important hiatus occurs at the top of the Kuttung, where there is a sharp change of flora and a modification in the axis of subsidence, resulting in the complete overlap of the Permian Lower Marine Series, and, in the north-west of the basin, of the Lower Coal Measures.

Folding.

The regional structure is a great basin. There are, however, a large number of major and minor units, which merge into the general concave framework. A perspective restoration of the folding and faulting is given in Text-figure 1. The basin is elongated, with an axial ratio of 5:2, along a synclinal axis, which is clearly recognizable for at least 150 miles, from the valley of Rocky Creek, west of Horton, to the Liverpool Range. A longitudinal section along this synclinal axis, together with eight transverse sections of the Werrie Basin, is included in Text-figure 2.

(i). *The Synclinal Axis.*—The synclinal axis crosses the Tamworth-Gunnedah road about a mile and a half east of Carroll Gap, trending N. 40° W. The Burindi rocks on the east of the axis dip to the west at 22°, and further east, near Somerton, the dip has declined to 12°, with a more meridional strike. A few hundred yards on the western side of the axis the dip is 18° to the east, but this rapidly steepens to 70° and 80°, with little change in strike. Southwards from here the outcropping rocks belong to the Burindi Series until the base of the Kuttung is reached near Mount Uriari. From this point to the top of the Kuttung Series in Spring Gully (D5) the average synclinal trend is N. 23½° W. The folding here is very sharp, the dip changing from as much as 70° in the eastern limb to gentle easterly dips in the western limb, in little more than a hundred yards. In spite of this angular folding there is no evidence of strike faulting in this locality, although jointing parallel to the fold axis is very pronounced and regular, a feature which has had considerable effect on the drainage.

When the Springsure Fault is crossed, the folding has lost its pinched angularity, and the floor of the basin west of Currabubula is very flat and shallow. Thus, in spite of the eight miles wide outcrop of the Werrie basalts in this region (D6, etc.), the top of the series has not been depressed sufficiently



Text-fig. 1.—Reconstruction of the folding and faulting of the Werrie Basin. The folded strata in the diagram are the Kuttung sediments, all superficial rocks having been removed and the eroded portions restored. The white band is the porphyry boulder horizon.

to allow the retention of a residual outlier of the overlying Upper Coal Measures, although this has taken place nine miles further south, where the Werrie Basalts have only half the width of outcrop.

The reason for this wide floor to the basin here is not far to seek, being due to the concurrent merging of several axes of depression with their separating arches. From the north, the main synclinal axis has been trending about N. 15° W. Another important depression, which breaches the western limb of the basin, leaving a four mile gap in the Kuttung outcrop (C5, C6), joins it from the north-west. To the south the synclinal axis branches, the main and deepest trough trending about N. 10° W. to the Werris Creek Colliery, the other branch passing to the east of Quipolly Dome. The fact that it is here, at the point of conflicting trends, that the axis of the Warrigundi injection crosses the main synclinal axis may not be without significance.

From the edge of the wide-floored basin the main synclinal axis falls sharply to the south as a narrowing trough, until the greatest depression is reached at the Colliery basin in the south of D8. Here the top of the Burindi series, which outcropped at the surface 26 miles to the north, has been depressed to a depth of the order of 19,000 feet below the surface. Thus the average angle of plunge of the fold-axis in the northern half of the basin is about 8°, but as we have seen, the rate of plunge is not uniform.

South of the Werris Creek Colliery the axis starts to rise again, but three miles to the south it is truncated by the more easterly of the two great overthrusts.

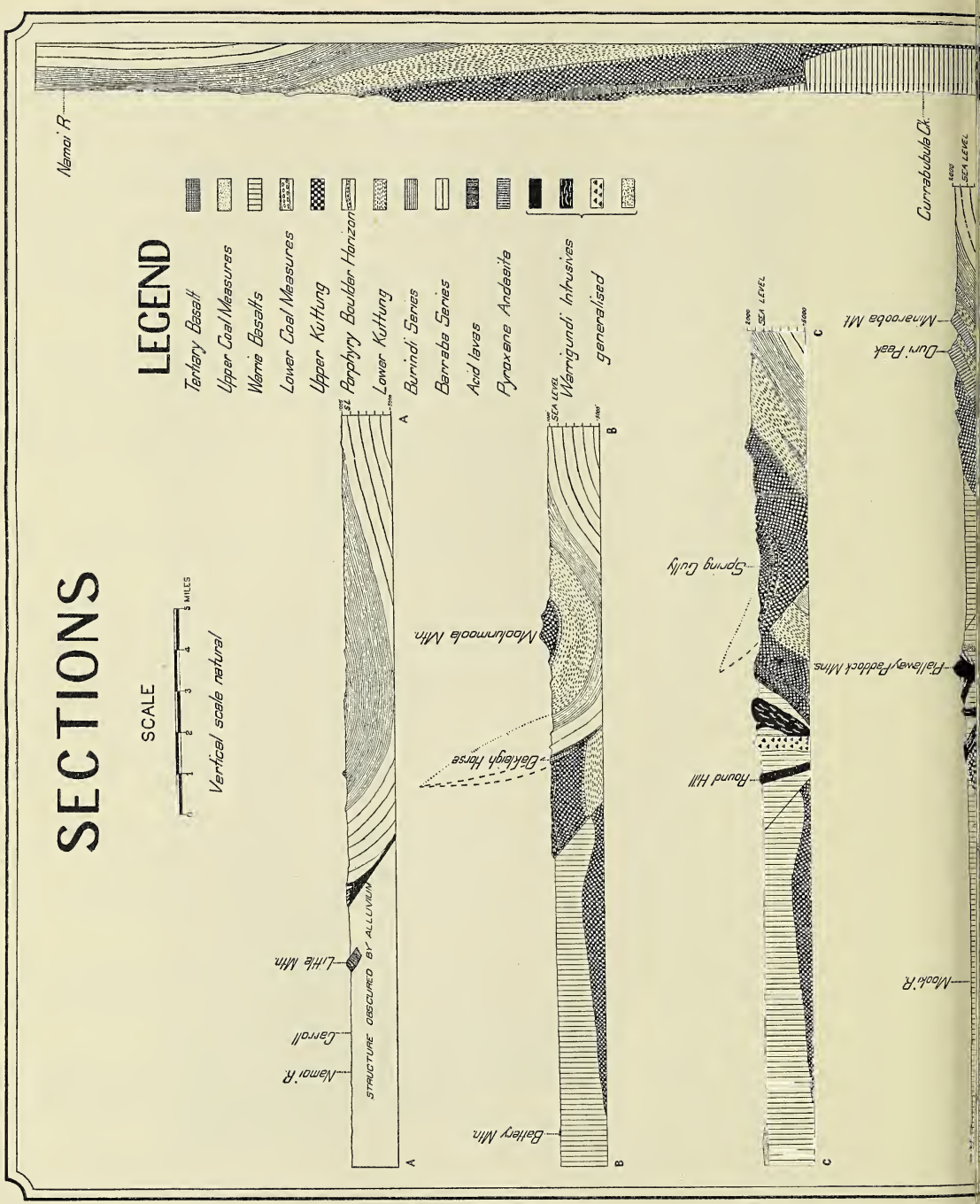
To return to the point of virgation of the synclinal axis, the eastern branch is not very marked until the arch at the northern end of Quipolly Dome is crossed, but it then falls somewhat beneath Coeypolly Creek (E9). Here an upward warp closes the Fairfield Basin, then the axis plunges steadily again to the Jacob and Joseph Basin, another open basin (E10) similar to the one west of Currabubula. Here again there are four axes of depression leading into the wide but shallow area. Two opposing plunging anticlines (the southern nose of the Quipolly Dome and the northern nose of the Castle Mountain Dome) merge into the same structure.

The synclinal axis we have been tracing rises from this depressed area, and forms a saddle in the arch which connects the Castle Mountain Dome with the eastern limb of the syncline. It then plunges uniformly to the south in the direction of Temi. South of the Great Northern Road near Mount Auburn it has not been traced by the writer.

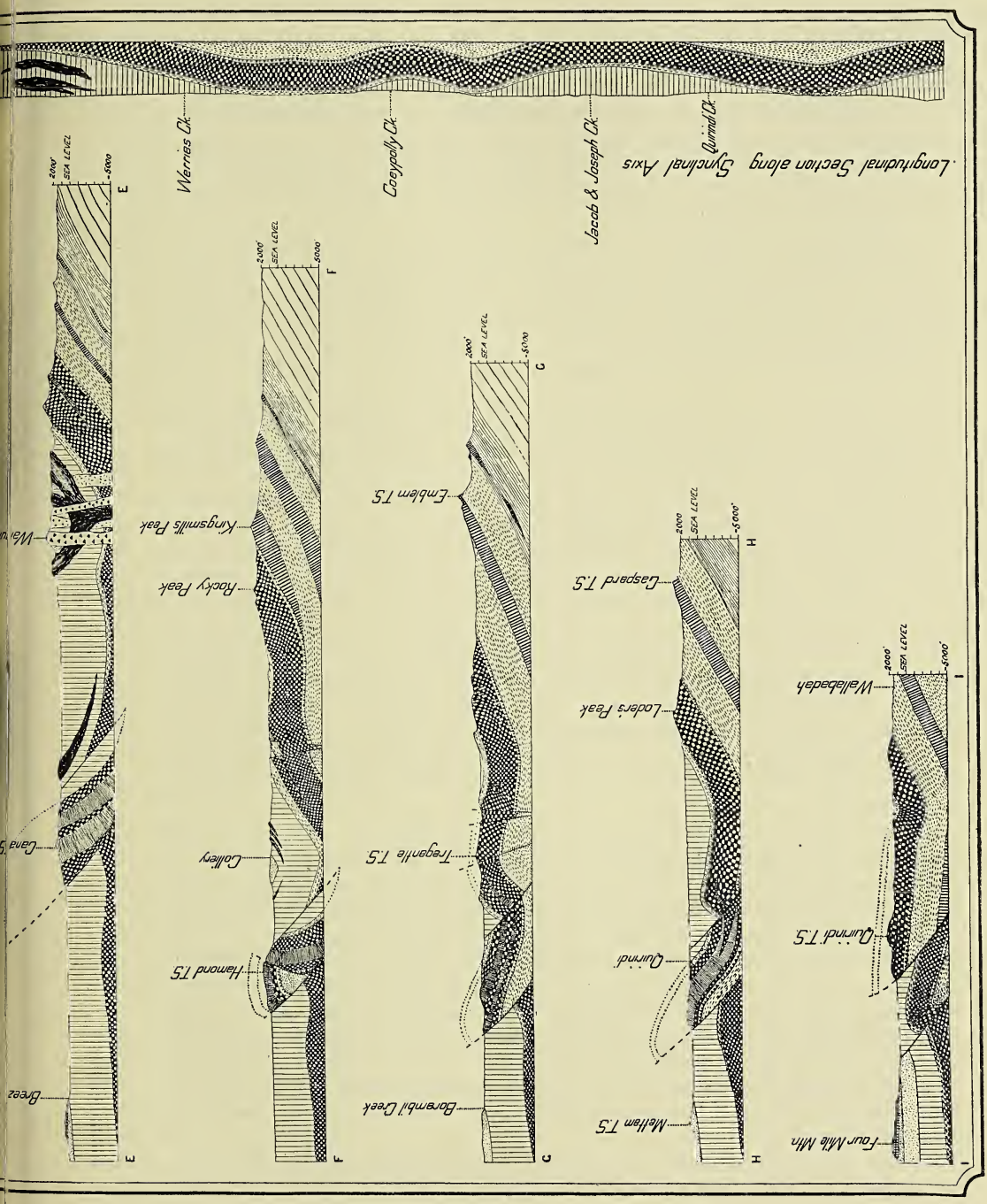
Throughout the region, the trend of the fold-axes (apart from minor warps and linking arches) usually lies between the limits N. 40° W. and N. 10° W. Values of N. 30° W. and N. 40° W. are more typical north of Currabubula Creek, while N. 20° W. is the more usual value in the southern part.

(ii). *Comparison of Eastern and Western Limbs.*—When the eastern and western limbs of the Werrie Basin on either side of the main synclinal axis are compared structurally it is found that they differ markedly throughout the region in three fundamental aspects:

(*a*). The western limb is anticlinal while the eastern is monoclinal; i.e., by going beyond the western limb one finds progressively younger beds (quite apart from the faulting), whereas beyond the eastern limb are progressively older beds. This matter is linked up with the merging of this great basin, and indeed, the



Text-figure 2.



Structural Sections of the Werrie Basin.

Text-figure 2.

Structural Sections of the Werrie Basin.

great synclinal zone itself, into the greater geanticlinal structure of the New England massif.

(*b*). Whereas the eastern limb is free from strike faulting, the western limb is followed by a system of powerful strike thrusts, which are associated in some cases with overturning of the beds. Again the difference is a major one, related to the tectonics of the whole New England region; for this thrust system has now been shown to flank the New England block continuously for one hundred and seventy miles, and shows no sign of dying out at the farthest northerly point to which it has yet been traced.

(*c*). Whereas the eastern limb is unbroken and continuous throughout the region, the western limb is broken by one minor, and two major structural breaks in the form of cross-warps, which merge into the main synclinal zone without crossing it into the eastern limb. This would tend to show that the cross-warping was produced by the same diastrophic act as the main folding, and was not due to the superimposition of one set of folds on pre-existing structures.

The first and most important of these transverse depressions is that which breaks the western range of Kuttung rocks between Currabubula and Breeza. Here the gap in the Kuttung sediments is four miles, which is mainly occupied by the overlying Werrie Basalts, but is partly filled by intrusive rocks of the Warrigundi system. The next largest is the one through which the great northern railway passes between Braefield and Quirindi. This is a mile and a quarter in width, but here the true width is indeterminate, for a powerful thrust passes through the gap. The third and smallest of these breaks is that through which Coeypolly Creek crosses the western limb. The structure here is very involved owing to the complexity of the strike-faulting. Between the most westerly thrust and the Hammond thrust the strikes are approximately east-west, dipping beneath the creek from either side at angles up to 30°, the northern dip being, if anything, the steeper. The trough of this minor syncline is extensively alluviated, apparently owing to the erosion of soft varve-shales. On the east side of the Hammond thrust, however, between this and the eastern thrust, although the strike is still locally east-west, the structure is anticlinal, and this has formed the weak feature.

(iii). *The Eastern Limb.*—The strike of the eastern limb is fairly constant throughout the area, oscillating between the limits of N. 21° W. and N. 55° W., the angle of dip varying from 20° to nearly 80°. In any transverse section the dip is usually greater at the top of the Kuttung than at the base, owing to the anticlinal arching of the strata. North of Mt. Uriari (D2) the angle of dip is usually between 15° and 35°, but this steepens rapidly as one moves southwards, until on upper Oakey Creek (D4), where the folding is very sharp, the values are between 50° and 80°. This steepening declines again as rapidly as it rose until, in the vicinity of the Springsure fault, angles as low as 28° are recorded, associated with a marked widening of the outcrop. A less noticeable steepening occurs near Currabubula, and from here southwards the dip falls slowly with a widening outcrop until the head of Coeypolly Creek is reached, whence there is little further change.

The close proximity of such irregularities as the Quipolly Dome has had little effect on the strike of the eastern limb. There is perhaps a lessening of the angle of dip, due apparently to the fact that the crustal shortening was partly taken up by the auxiliary fold.

(iv). *The Western Limb.*—The greater part of the western limb outcrops between the two great thrusts, so that the strata are not structurally continuous with the rocks of the eastern limb. The Castle Mountain Dome (E12, etc.), a large remnant of which lies to the east of the faults, may perhaps be regarded as belonging to the western limb, but its structural position is more closely analogous with that of the Quipolly Dome, which lies to the east of the synclinal axis proper (see Text-figure 1). However, about twelve miles of the western limb, containing a complete sequence from the Werrie Basalts to the Barraba Series, is still preserved in unfaulted continuity with the eastern limb in the country north of Piallaway (C3, etc.). Here the general strike is N 8½° W., and dips in general are noticeably gentler than the corresponding dips of the eastern limb, although they invariably steepen markedly as the faults are approached.

The Quirindi Dome.—The most southerly Carboniferous rocks encountered in the great wedge between the thrusts form an elongated dome twenty-one miles in length, but so narrowed by the complex strike-faulting that its greatest width is one and a quarter miles. This is the Quirindi Dome.

For the sake of simplicity we shall omit temporarily from the discussion the lens-shaped area bounded on the east by the Hammond thrust and on the west by the western overthrust, and lying between Werris Creek and Quirindi Creek. The remaining portion of the Quirindi Dome is structurally continuous, i.e., although it is more often than not bounded by faults, these do not cross the strip and so break the continuity. Hence the careful study of this strip gives a fairly complete conception of the original character of the dome before the thrusting. Fortunately the conception is completed by the remaining fragment, which lies to the west of the Hammond thrust.

The southern nose of the dome outcrops in close proximity to Borambil Creek in D11, a mile and a half south of Quirindi. Here fossils belonging to the Lower Coal Measure series have been collected. These beds can only be traced for a couple of hundred yards round the south-western side of the dome before they are truncated by the western thrust. The beds are here strongly compressed and dip to the south-west at 87°.

On the eastern side, however, the Coal Measure series can be traced under Quirindi and for seven miles along the eastern side of the dome, before being truncated by the more easterly thrust, which has been following the outcrop closely on the east all the way. Typical lithology is preserved throughout, with occasional fossiliferous outcrops. The strike at Quirindi is meridional with a dip of 40° to the west, the angle declining as one goes northwards. This is the most northerly outcrop of the Lower Coal Measures in the western limb, as they are overlapped by the Werrie Basalts further to the north-west.

Underlying the Coal Measures of the Quirindi dome are glacial beds of the Upper Kuttung, which rest on a fairly thick series of acid lavas with some interbedded sediments. These horizons all confirm the structure determined by the Coal Measures. There was originally an easterly bulge in the dome where Coeypolly Creek crosses it; this is clearly indicated by the strikes and dips of the rocks on the north side of the creek. This eastern bulge is truncated by the eastern thrust so that first the Coal-Measures, then the Kuttung sediments, and finally the lavas abut against the fault. The glacial sediments soon reappear, however, and continue to outcrop adjacent to the fault, until the strike veers away to the west of it; the Kuttung rocks are now directly overlain by Werrie

Basalts, which have meanwhile overlapped the Coal Measures. Just before the Breeza-Currabubula road is reached in C6, we come to the northern nose of the dome, and the strikes wheel to the south-west to be cut off almost immediately by the western thrust.

If we retrace our steps northwards from Coeypolly Creek, and examine the dips, we find that in the north-east corner of C9 the glacial rocks are standing vertically and are locally overturned. From here northwards the dip gradually declines to 40° at the Gap, then increases to 53° east of Cana trigonometrical station, but falls off again as the northern extremity of the dome is approached, until it is only 30° when the nose of the outcrop is rounded.

With the exception of the two small areas at the extremities, all the rocks in this remnant of the Quirindi Dome are easterly dipping. Between the Hammond thrust and eastern thrust, there is preserved a fragment of the crest and western side of the dome, which will now be described. In the vicinity of the Hammond trigonometrical station (in the north-east of C9) and on the hill to the south of it, the acid lavas are more or less horizontal adjacent to the Hammond fault. Half a chain to the east, but on the other side of the fault, the same lavas may be seen standing vertically. Tracing the horizontal lavas westwards we find that they, at first slowly, and then rapidly, increase their dip, until they pass beneath the glacial beds, dipping to the west at 80° near the western fault. As these sediments are traced northwards the dip steepens further, until they become vertical and finally inverted, dipping to the east at 70°. It is of interest to record that in the field the inversion was first detected by the anomalous position of the seasonal layers in the varves, and was subsequently confirmed by tracing the structures northwards.

Between Coeypolly Creek and Werries Creek, outcrops of the Werrie basalts can be seen on the western side of the western thrust, dipping away to the west at moderate angles.

This completes the description of the Quirindi Dome, which it will be seen is a very complex structure. It is questionable whether such an elongated and laterally-contracted structure should be called a dome (see map, Plate xvii). However, if it be classed as an anticline instead of as a dome, one is likely to overlook the longitudinal arching of the anticlinal axis, which is really very marked, as shown in Text-figure 1.

North of Quirindi Dome there is a wide structural gap through which the Breeza-Currabubula road passes. Beyond, in the north-west of C5, the Kuttung rocks emerge again in another plunging anticlinal nose, dipping to the south-west at fairly high angles in opposition to the northern nose of the Quirindi Dome. The rocks are acid lavas and glacial sediments and are conformably overlain by the Werrie Basalts.

The Kuttung outcrop here is barely a mile wide, for it disappears on the north beneath the eastern thrust. The over-riding rocks are the easterly-dipping Kuttung series of the western limb. These were originally continuous with the small structure we have been considering, but the dislocation by the thrusts has completely broken the continuity.

The Clifton-Carroll Block.—This is the most north-westerly development of Kuttung rocks in the district mapped (B, C, 2, 3). Again the structure is rendered very complex by extensive faulting. At the northern end the main thrusts diverge at a fairly large angle, forming the northern and western

boundaries of the block. The eastern thrust then turns abruptly to the south and bounds the block on the east. Here between the thrusts there is a cross-fault, the Babbinboon fault. Thus there is formed a quadrate area bounded on all sides by faults. On three sides the fault-block is the downthrown side, while on the fourth (western) side it is part of the over-riding flake. Clearly the eastern thrust has been very powerful, since it completely changes both strike and dip and throws the Barraba series over the Upper Kuttung. These faults will be further described when the regional faulting is being discussed. Still more complication is introduced by the development of a fault-horse,* three and a half miles in length and a quarter of a mile in width, owing to the anastomosing of the eastern thrust.

Prior to the faulting described above, the Clifton-Carroll block appears to have been a rather flat dome or southward-plunging anticline. The highest beds are acid lavas and glacial beds which dip to the south at angles up to 20°. Traced northwards these strata arch over and, at Thunderbolt's Lookout, become practically horizontal. Both east and west from here they dip outwards at low angles until truncated by the thrusts. To the north there is a fault scarp, falling down to Swain's Gully. There is conflict of strike along the fault, which throws down to the north. North of the fault the same flatly anticlinal structure continues. Trends are east-west and arcuate, the dip changing from 42° to the south-west to 42° to the south-east.

The Oakleigh Horse.—The elongated area which has been wedged between the eastern thrust and its auxiliary fault in C3, is composed entirely of upper Kuttung rocks. It consists of two flows of acid lava, separated by varves and conglomerate. These beds are usually standing vertically, but turn over to both east and west. The strike is meridional, parallel to the faults.

(v). *Other Structures.*—A few structures associated with the folding yet remain to be considered, viz., Quipolly Dome, Fairfield Basin, Colliery Basin and Castle Mountain Dome.

Quipolly Dome.—This is the only dome structure in the region which has escaped disruption by the strike-faulting. Even here, however, there has been considerable minor dislocation by normal fault-complexes (see Text-figure 1). The dome is eight miles in length and two miles in width, as defined by the present outcrop of the Lower Coal Measures. The axial trend is uniformly N. 13° W. At the southern end the dome arches up fairly prominently, more particularly in the south-west sector. To the north, however, it is more subdued and merges fairly flatly into the wide basin west of Currabubula, and into the flat anticlinal arch which connects the north of the dome to the eastern limb of the Werrie syncline. The Lower Coal Measures encircle the dome, enclosing four inliers of Upper Carboniferous rocks.

The Fairfield Basin.—This is the area of the Werrie Basalts lying to the east of the Quipolly Dome, and enclosed by the same warp as that which caused that structure. The basin is three miles long and a mile broad, and although the Coal Measures do not close about it, a horizon low down in the Werrie series would give a closed ring structure.

The Colliery Basin at Werris Creek (S of D8) is another small feature, which is really the lowest depression of the Werrie Basin. The junction of the Werrie

* A "horse" is a large fragment of rock broken from one (fault) block and caught between the walls of the fault (Lahee).

Basalts and the Upper Coal Measures reveals the closed structure, enclosing an area of the latter, two miles in length and a mile in width. When the small size of the basin is considered the dips are quite high.

Castle Mountain Dome.—Before being disrupted by the strike-faulting, the Castle Mountain Dome was probably quite similar to the Quipolly Dome, except that it was originally about twice the size. Its axial trend is the direct continuation of the axis of the latter, and like it, the arch connecting with the main eastern limb is in the north-east sector. The angles of dip are of similar magnitude (except in the vicinity of the great thrust), but this dome does not flatten out to the north and merge into its fronting basin as does the Quipolly Dome. This is no doubt due to the fact that the fold does not die out as in the latter case, but merely plunges beneath the basalts to re-emerge as the southern nose of the Quipolly Dome. The dome is cut off on the west by the eastern thrust, and stepped down on the south by the Colly Creek faults. On the south-east it cuts off another basin of Werrie Basalts, which continue southward beyond the area mapped.

Faulting.

Although all the proved faults of the region are referable to the one cycle of diastrophism, they fall genetically into four distinct groups:

(i) The Mooki Thrusts.

(ii) Faults confined to the Werrie Wedge: The Hammond Fault, The Oakleigh Thrust, The Babbinboon Fault.

(iii) Faults confined to the overthrust block: The Springsure Fault.

(iv) Faults due to settling at the close of the cycle: The Colly Creek Faults, The Tregantle Faults, The Purlewah Faults, The Anstey's Creek Fault, The Kingsmill Faults, The Duri Peak Faults.

(i) The Mooki Thrusts.

General Description.—The great overthrusts are by far the most interesting faults in the region from the tectonic point of view, as without doubt they form the continuation of the Hunter Overthrust, the occurrence of which in the Hunter Valley as far north as Scone has been described by Dr. G. D. Osborne (1929).

The present writer has mapped this thrust system continuously from near the junction of the Peel and Namoi Rivers to Willow Tree, a distance of more than fifty miles. However, there is still an area between Willow Tree and Scone, where the course of the faults has not been traced in the field. It is definitely known that powerful strike-faults continue through this area, but since the Wingen fault and the Brushy Hill fault, two heavy normal faults, are present as well as the thrusts, it would perhaps be wise to treat the Mooki Thrusts and the Hunter Overthrust as separate units until the intervening region is worked out. Dr. G. D. Osborne and Mr. H. G. Raggatt are engaged on the geology of this area. Meanwhile the term Mooki Thrusts will serve to designate the overthrusts throughout the belt between the Liverpool Range and the Namoi River. Within these limits the relation of the Mooki Thrusts to the Mooki River is precisely analogous to the relation of the Hunter Overthrust to the Hunter River (see Osborne, 1929, p. 446).

Throughout the Werris Creek region, the Mooki Thrusts comprise two major sub-parallel fractures, both of which are very powerful. To the south they appear to converge and continue towards Murrurundi, ultimately to join up with the

Hunter Overthrust. In the north they converge within the limits of the area mapped, the eastern fault making an abrupt sweep to the west and linking up with the western. The combined fault crosses the Namoi River, and has been traced by Messrs. Lloyd and Mulholland for a further ten miles beyond, still striking in the same direction and showing no decline in intensity.

The Western Thrust.—Throughout the Werris Creek region the western thrust marks the eastern limit of the Liverpool Plains, usually forming the boundary between the alluvials and the Carboniferous hills. This physiographic division is due to the fact that the rocks on the downthrow side are largely the soft Werrie Basalts, which have been completely base-levelled and buried under alluvium. Outcrops of the decomposing basalt with typical lithology may, however, be seen close to the fault in the north of C9.

The fault crosses the Namoi River about three miles west of its confluence with the Peel. On the other side it has been shown by Messrs. Lloyd and Mulholland to form the boundary between Upper Devonian Barraba Series (which here form the western limb of the Werrie syncline) and the Upper Kuttung. On the south of the river, the Barraba Series still outcrops on the upthrow side of the fault, but the downthrow side is buried beneath the alluvium. However, Little Mountain, at Carroll, is composed of Upper Kuttung rocks, but their strike cannot be correlated with that of the Kuttung on the other side of the fault.

Three miles east of Carroll the fault forks and encloses on three sides the rectangular Clifton-Carroll block. Here the strata are truncated almost at right angles on both sides, for they strike east and west roughly perpendicular to the two faults. The strike of the beds changes more to the north-west as the fault is approached. This is partly due to drag and partly to an original fold in the beds. The Babbinboon fault also ends abruptly against the thrust.

For six miles along the western margin of the Clifton-Carroll block the fault may be clearly traced. Where the Kuttung rocks strike away from the fault in B3, thus leaving Werrie Basalts on either side of it, it disappears under the plains alluvium for twelve miles. It reappears, however, on exactly the same strike as soon as the Kuttung rocks come to the surface in C6, whence it can be traced continuously (except for a short cover of alluvium at Lower Quipolly) for twenty-one miles.

Here it is more sinuous in its course than on the west of the Clifton block. This is probably due in part to a slight flattening of the dip of the fault-surface, and partly to the irregularity of that surface.

From the Breeza-Currabubula road in C6 to the Gap in C8, the rocks on the upthrow side are dipping in the same sense as the fault, but at a gentler angle. At the Gap the Hammond fault brings a remnant of the western flank of the Quirindi Dome against the thrust, so that from here to Quirindi Creek, the dip of the beds is in opposition to the fault. Where the changed relation is first encountered the drag is so strong that the beds in the upthrow flake are completely overturned, and dip at 70° to the east in sympathy with the fault. Two miles further south the dip is in the normal direction, but at high angles, the drag being still fairly strong, but this rapidly falls off until at Coeypolly Creek the more competent east-west strikes show no drag effects.

South of Quirindi Creek, where the Hammond fault is met again, the structure is similar to that north of the Gap. When the westerly dips at the nose of Quirindi Dome are encountered, the effect of drag again becomes apparent.

The precise course of the fault south of Quirindi Dome is not quite clear. It may swing a little to the east, crossing the railway line to the south of Braefield, and so unite with the eastern thrust; or it may, on the other hand, follow closely the course of Borambil Creek, forming the eastern boundary of the Upper Permian (?) sandstones and conglomerates. The latter is perhaps the more likely interpretation. Examination of the boundary of the conglomerates along Borambil Creek does not throw much light on the problem. They show no evidence of jointing or drag from an over-riding block.

The Eastern Thrust.—When the eastern thrust forks from the western it takes up the most easterly strike which it shows anywhere in the region, practically east-and-west. The Barraba mudstones strike right on to the fault and are truncated almost at right angles. The mass of Warrigundi rocks shown where the faults diverge is not a simple intrusion, but rather a zone of injection. Outcrops of Barraba mudstones can be found at many places in the zone, and within a chain or so of the fault. They strike N. 18° W. and dip to the east, conformably beneath the Burindi Series. Near the fault the strike changes rapidly towards the south-west under the influence of drag. Immediately across the fault are Upper Kuttung rocks, dipping at gentle angles to the south.

After striking east for three and a half miles from the junction of the faults, the eastern thrust wheels abruptly to the south and strikes in sympathy with the overlying strata for seven miles along the eastern margin of the Clifton-Carroll block. Here the fault forks again, the two branches following parallel courses, a few hundred yards apart, and re-uniting four miles further south. The narrow belt of Kuttung rocks enclosed between the two faults is strongly compressed and stands vertically.

In the next twelve miles the course of the fault makes a big sweep to the east. For the first two miles it throws the Burindi rocks over the Werrie Basalts under cover of the alluvium. It should be pointed out that the fault is here in conflict with the dominant local strike, so the Burindi beds give place to the Lower Kuttung and then to the Glacial beds, and finally the Werrie Basalts strike on to the fault. Meanwhile at Piallaway an inlier of Upper Kuttung rocks has appeared from beneath the Werrie Basalts on the downthrow side. For three miles north-west of Piallaway, elongated Warrigundi intrusions follow the fault-plane. The same feature is seen on a larger scale when the fault swings to the south-west through D6 to complete its digression before resuming its original trend.

The fault follows along the eastern margin of the Quirindi Dome for nine miles. Here it is a true strike fault and there is little truncation of the strata. However, at the Gap the cutting off of some horizons of the Glacial beds is noticeable. In the eastern end of the railway cutting at the Gap the Kuttung conglomerate which underlies the fault is distinctly sheared, and all the pebbles are polished and show well-developed pressure-striae, sometimes in three directions. At Quipolly the Kuttung strata strike into the fault for a short distance, and when they strike away again the Lower Coal Measures appear overlying them. For the next six miles the exact position of the fault cannot be definitely fixed, because the rocks on both sides are the soft Werrie Basalts which make no outcrop, but its course is picked up again where it truncates Castle Mountain Dome. Near the railway crossing in E12 the overthrust is offset a few chains to the west by the Colly Creek faults.

An interesting feature of the eastern thrust is its tendency to show abrupt changes of strike and dip, a characteristic that was also noticed in the Hunter overthrust by Dr. Osborne (1929, p. 448). These irregularities of the fault surface have important implications, and are the subject of a separate paper by the present writer.

Evidence that the Western Fault is an Overthrust.—It should be pointed out here that, although the overthrust character of the eastern thrust is absolutely proved by the field-facts, the evidence on which rests the classification of the western fault as an overthrust, is not quite so strong. The observations on which this classification is based may be summarized as under:

(i) Relation to proved eastern thrust: (*a*) The two faults have parallel trends for twenty miles along the Quirindi Dome, and every fluctuation in the course of one is matched in the course of the other. This suggests that they are also conformable underground and dip at similar angles. (*b*) Near the Namoi River the two faults converge, and thereafter but one fracture is recorded. Messrs. Lloyd and Mulholland, who traced the fault on the north of the river, found no decisive evidence to show whether it was normal or reversed, owing to the extensive alluvium along the fault zone. They are of the opinion that it is an overthrust.

(ii) Relation to the Hammond fault: The Hammond fault, which will be described presently, is a westerly-dipping underthrust. It terminates at both ends on the surface of the western fault. It is difficult or impossible to draw a satisfactory section across the Kuttung rocks and these faults in the vicinity of Hammond Trigonometrical station, if it is assumed that the western fault is normal.

(iii) Field-evidence along the fault outcrop: (*a*) The obvious explanation of the overturning of the Kuttung strata in the vicinity of the fault south of the Gap (C8) is that it is due to the fault being an overthrust. (*b*) The strong drag at both extremities of the Quirindi Dome is precisely of the nature that would be expected if the fault were an overthrust, and would be anomalous if the fault were normal. Moreover, the drag effect here is identical with that produced at the northern extremity of the Castle Mountain Dome by the proved eastern thrust.

(iv) Circumstantial evidence from tectonic principles: It will be shown later in this paper that the Hunter thrust movement is very probably a late phase of the diastrophism which wrinkled the Carboniferous and Permian strata, and not a subsequent event, as held by Dr. Osborne (1929). In regions where folding has culminated in overthrusting it is found, in general, that the outermost thrust separates rocks which are more intensely folded from rocks which are less intensely folded. This is true of the Hunter overthrust in the Hunter Valley, but if the western fault is normal it is not true in the Werrie Basin. Indeed, when one finds that on the west of the eastern thrust the rocks are more closely compressed than on the east of it, tectonic principles alone lead one to look for another contemporaneous overthust on the west of that fracture.

The evidence which might suggest that the fault is normal should also be discussed:

(i) Strong faults which have the same trend as the Hunter overthrust, yet which are normal in character, have been described from the Hunter Valley, e.g., the Brushy Hill fault, Goorangoola fault, etc. (Osborne, 1929). These, however, are all within the overthrust block.

(ii) If Dr. Osborne is correct in claiming that the Wingen fault truncates the Hunter thrust (loc. cit.), and that the fault north of Scone is normal, it might be expected that the Hunter overthrust outcrop should reappear on the east of the Wingen fault. If this is so, one might expect to find in the Werris Creek region a powerful overthrust with a strong normal fault having a similar trend, but lying to the west of it. If this interpretation is taken, difficulties immediately arise from items (ii), (iii) and (iv) above.

The balance of evidence clearly favours the interpretation of the western fault as an overthrust.

(ii) Faults confined to the Werrie Wedge.

The great wedge, fifty miles in length, varying in width between one and a half and four and a half miles, and cut off on all sides by the overthrusts, has been called the Werrie Wedge. Three faults are confined to this region, and are all genetically related to the thrusting. They are the Hammond thrust, the Oakleigh thrust and the Babbinboon fault. The Oakleigh thrust is simply a branch of the main eastern thrust, and has already been fully described.

The Babbinboon Fault.—The existence of this fault cannot yet be regarded as conclusively proven. It was first suggested by the apparent duplication of part of the Upper Kuttung, but this is not quite certain. The physiography strongly suggests a fault, but such evidence must always be treated with caution. There is a very definite conflict of strikes at the eastern end, but the dips are all rather flat in the vicinity, and the proximity of the great thrust, especially at a point where it is forking, renders this evidence inconclusive. For the rest of the course of the supposed fault the extensive alluvium obscures the outcrops. On the whole, however, the evidence points to the existence of the fault.

The fault strikes east and west between the two thrusts, and downthrows a few hundred feet to the north. It is not certain whether the fault is normal or reversed. Its course is exactly parallel to the eastern thrust immediately after its branching from the western thrust. The fault forms the southern boundary of a parallelogram-shaped area bounded on the other three sides by the thrusts. It is thought possible that the fracture developed during the thrusting and that the block lagged slightly behind the forward movement of the rest of the Werrie Wedge.

The Hammond Thrust.—The Hammond fault is a high-angle underthrust, which is beyond doubt a phase of the Hunter overthrust disturbance. In plan the fault begins and ends on the western overthrust outcrop, and there is good reason to believe that throughout its course it terminates underground on that surface. The fault is nine miles long, extending from the Gap to Quirindi Creek. The strata on the east dip to the east, and in places become vertical or slightly overturned owing to the strong drag. On the underthrow side there is usually a strong shear-zone, in places more than a chain wide. This is most marked where the acid lavas abut on either side of the fault-plane. On the upthrow side the rocks are less disturbed in the vicinity of the fault, being often sub-horizontal or dipping gently to the west. They rapidly steepen, however, and in the northern part overturn on the western thrust.

The relation of outcrop to contour indicates fairly conclusively that the fault dips to the west. The steep westerly dip of the strong shear-zones puts the question beyond doubt. As the eastern is the downthrow side it is clearly a reversed fault. Since the thrusting forces were directed to the south-south-west,

and since the upthrow side was itself moving forward at the time of the thrusting, the fault must be classified as a high angle underthrust.

The fault is possibly to be interpreted as being due to the curvature of the western thrust. The throw is of the order of 1,000 feet, but this can only be an estimate, because the beds were deformed as well as dislocated. This displacement would correspond to a flattening of the dip of the western thrust of about five and a half degrees in a distance of two and a half miles measured along the fault surface. The actual flattening may be greater than this, the residual effect being taken up by further distortion of the strata. This, however, is unlikely, because the great thickness of massive lava, which here forms the bulk of the Upper Kuttung, would not yield so readily as would the associated sediments. In fact, the presence of this competent rock, with its tendency to shear rather than to deform, is probably largely responsible for the Hammond fault.

(iii) Faults confined to the overthrust block.

The Springsure fault is the only one referable to this class. It originates on the surface of the eastern overthrust, and trends N. 68° E. almost at right angles to that surface, into the upthrow block. For some distance on either side of the fault there are parallel joints and minor shear-zones which are very regular. The evidence of these suggests that the fault dips steeply and to the north; this conclusion is supported by the rectilinear outcrop of the fault. The striations on the joint-surfaces suggest that the movement was vertically on the fault-face, and that it was not accompanied by much strike-slip displacement. This is supported by the relative displacements of horizons, on opposite sides of the synclinal axis. The downthrow is to the south, which, in view of the dip, indicates that the fault is a high angle overthrust. The throw is greatest at the eastern overthrust face, being here 3,600 feet, but it declines steadily as the fault is traced along the strike, and two and a half miles from the overthrust has fallen to 2,000 feet.

The origin of this fault is not very far to seek. The irregularity of the strike and dip of the eastern overthrust surface has already been described. It has also been pointed out that, provided the hade of the fault accommodates itself to the local strike, there will be no strains in the upthrow block.* But if the dip adjustment does not take place or is incomplete, the deficiency results in severe stresses being exerted on the over-riding block, owing to forces originating from the weight of that block. The latter must yield by distortion or shearing unless it is competent to withstand a large-scale cavity beneath it on the fault-surface.

Apparently the main overthrust surface to the north of the Springsure fault dips more steeply than it should for its particular strike. Hence the over-riding block is elevated along this section more than immediately south of the Springsure fault. (The same result would be attained if the dip of the thrust were normal on the north of the Springsure fault, but dipping too flatly on the south side.) The effect is that gravitational rotational stresses are exerted with an axis approximately parallel to the line in which the two sections of the overthrust surface would meet if produced to an edge. These result in two sets of steeply dipping shear-planes parallel to this edge, one set dipping to the north and the other set to the south, along which deformation must ensue unless the

* See succeeding paper (pp. 375-379 below).

block is competent to maintain the cavity which exists at the fault surface. In view of the direction of the external stresses exerted by the main overthrusting forces which are also acting, the northward dipping sets of shear-planes are favoured, and motion ensues along these. This tends to become localized on one plane, and the Springsure fault is the result. Since the rotational stress axes are dipping parallel to the main thrust plane, the fault will eventually tend to die out when traced eastwards along the fault outcrop, even though its actual intensity underground be unchanged.

The above interpretation is completely supported by the field-evidence.

(iv) Faults due to settling at the close of the Orogenic Cycle.

Normal faulting is not such an important feature as it is in the Carboniferous belt of the Hunter Valley. It is true that in many parts of the area minor dislocations are very numerous, and their aggregate throw must in some cases be considerable, but master normal faults are conspicuous by their absence. The part played by such faulting in the Currabubula district was overestimated by Benson (1920, pp. 307–8). Some of the faults postulated by him have been proved by detailed work to be non-existent, as, for example, the faults girdling the Upper Permian outlier at Werris Creek, the strike fault west of Kingsmill's Peak, and the numerous strike faults postulated in the Currabubula district. In many others the throw was overestimated; this applies particularly to the faults intersecting the Duri Peak andesite, and to the fault along Currabubula Creek. In some other cases, it must be admitted that there is a physiographic suggestion of faulting, but the evidence is hardly sufficient to prove or disprove dislocation.

Great caution is necessary with regard to the fault along Currabubula Creek. The mature valley crossing the upper Kuttung strata is decidedly an abnormal feature and cannot be without significance. Also there is a physiographic suggestion of truncation of the strata along the alleged line of faulting. The parallelism of numerous other features, as pointed out by Benson, must also be admitted. However, the main evidence of faulting relied upon by him, namely, the displacement of the Glacial beds, is based on an erroneous correlation of the horizons on the two sides of the creek. There is no displacement of the pyroxene-andesite, but the extensive alluvium along the creek obscures relationships higher in the series, and there is a general veering in strike in this area. However, there can be no very great displacement. Hence the existence of the fault cannot be regarded as established; nor is it completely disproved, although the magnitude of the faulting, should it exist, cannot be so great as claimed by Benson.

Some of the normal faults in the district are worthy of detailed description.

The Colly Creek Faults.—Three parallel step-faults occur in the Colly Creek valley (E12) at the south of the Castle Mountain dome. The great northern road skirts for a couple of miles the low scarp which has resulted from these dislocations. They strike the railway line near the level-crossing between Willow Tree and Braefield. An interesting feature at this point is that the overthrust appears fairly clearly to be offset by the No. 1 fault. The scarp of Kuttung rocks, the base of which marks the outcrop of the overthrust, is a few chains to the east of the railway line. Immediately the line of the Colly Creek fault is reached, the Carboniferous rocks step to the west, and outcrop at the railway line. As is to be expected, a small creek obscures the relationship at the critical point. The Colly Creek faults have an aggregate throw of 3,000 feet.

The Anstey's Creek Fault.—The Anstey's Creek fault outcrops in the N.E. corner of E7, about a mile up Anstey's Creek from Currabubula railway station. It strikes approximately east-and-west and has a throw of about 1,600 feet, measured on the displacement of the Greta Coal Measures.

The Faults of the Quipolly Dome.—The faults intersecting Quipolly Dome are clearly related to that structure (see Text-figure 1). Near the southern end of the dome is the Tregantle fault-complex, which radiates from the place where the elevation of the dome is greatest, the faults having developed through the collapse of the crest. The dislocation has taken place mainly along three fractures which are shown on the map, but there are a large number of subsidiary fractures, illustrated in Text-figure 1, which is fairly close to representation of the actual state of affairs. The meridional No. 3 fault is apparently the oldest, for it is offset by No. 1 which forms the north wall of the south-east trough. No. 3 fault strikes N. 33° W., roughly parallel to, but a little to the east of the axis of Quipolly Dome. The fault is only a little more than three miles in length, dying out in both directions. It outcrops in a cliff-section on Coeypolly Creek, in portion 271 Coeypolly, where it dips to the east at a moderate angle, the eastern being the downthrown side. The throw is greatest in the middle of its course, but it is difficult to estimate quantitatively because the fault reverses the dip. Of the two faults forming the Tregantle trough, No. 1 has the heaviest throw. Both are clearly defined in the east, where they form a marked physiographic feature, but they converge at Coeypolly Creek, and break up into a series of minor dislocations, which become lost in the Werrie Basalts. No. 1 fault forms the fissure for a decomposed dyke which belongs to the Warrigundi system. The maximum throw of this subsidence is three or four hundred feet.

In the Purlewah trough, which ruptures the dome further north, the throw is greater where it intersects the Werrie Basalts, here amounting to about 1,000 feet, but its continuation has not been traced into the hills. The locality is intensely injected by Warrigundi keratophyre, in the form of dykes, sills and small irregular masses. An interesting feature is that the dykes are not broken by the faults, the age of which can thus be assigned fairly narrow limits.

The Kingsmill Faults.—The Kingsmill faults are an interesting series of steep dip-faults which step down the Kingsmill's Peak andesite at the head of Currabubula Creek. The faults trend S. 75° E., and have an aggregate throw of more than 500 feet to the north. The fault-planes are nearly vertical and are all occupied by Warrigundi dykes.

These faults have had considerable effect on the local physiography. In conjunction with the large keratophyre boss they have determined the weak zone whereby Werries Creek crosses the resistant glacial beds; the creek follows the fault-plane for some distance. Further east, the northern flanks of Kingsmill's Peak are revealed fault-scarps which overhang the upper Currabubula Creek valley. The divide between this valley and the Back Creek valley is also determined by the faults and their associated dykes.

The Warrigundi Vulcanism.

In the course of the structural mapping of the Werrie Basin the Warrigundi intrusions have been treated as a unit, no attempt being made to unravel the intricacies and fascinating detail of the great complex. However, it is found that the intrusive rocks are intimately related to the tectonic architecture of the region and have much significance in the interpretation of the diastrophic

phenomena. Hence a brief statement concerning the nature and relations of the vulcanism is necessary. The generalizations here set forth may require some modification when the detailed examination of the great complex is undertaken.

The main axis of injection.—The greatest development of Warrigundi rocks occurs in a belt of injection about twenty miles long and four miles wide, extending from the Piallaway Paddock Mountains in C5 to the head of Currabubula Creek in E8. Within this zone the arrangement of the intrusions is strictly linear, and indeed, it would be difficult to align the principal masses more perfectly than they occur in nature. The trend of this zone is about N. 63° W., and has been called the main axis of injection.

The most important mass is that which centres round Warrigundi Mountain itself, and which has been named by Benson (1920) the Warrigundi complex. The mass bursts through the Werrie Basalts, and outcrops of the latter may be found at many places within the complex. Keratophyric rocks are probably the most abundant, and form laccolithic and irregular plug-like masses which belong to more than one outburst of activity. There is a wide variation in the facies of the igneous rocks, some appearing homogeneous and free from contamination, while others are packed with schlieren and heterogeneous streaks. Elsewhere hybridism is obvious, and partially digested fragments of Werrie basalt are recognizable. These rocks pass into injection-breccias. Intrusions of porphyrite and of quartz-dolerite are present and also a boss of granophyre. Breaking through these rocks are large masses of felsite-agglomerate, one of which rises to form Warrigundi trigonometrical station.

The Dunover Mountains and the Piallaway Paddock Mountains are also large composite masses similar to the Warrigundi complex. In these again there is an abundance of keratophyric, and brecciated and hybridized intrusions.

The remaining intrusions in the main injection-zone are non-composite, and are free from brecciation and hybridism. They include three intrusions of keratophyre in the form of a boss and two roughly stratiform but irregular sheets, and a small mass of quartz-dolerite.

Intrusions outside the main injection-zone.—Under this head fall three groups of keratophyric hybrid sheets: (1) Sheets following the western thrust; (2) Werriston and Allandale hybrid injection-zones; and (3) Laccolithic sills on the fold axes.

The first group is chiefly developed in the region where the main injection-zone crosses the eastern thrust, and extends for a few miles along the fault in either direction. The Werriston and Allandale hybrid and injection-breccia-zones penetrate the Werrie basalts for seven miles southwards from the main injection-axis, forming two parallel and inwardly dipping belts of concordant intrusions on either side of the Werrie synclinal axis. The Warrigundi rocks have interleaved themselves with their host in a very intimate manner. Of the laccolithic intrusions on the fold axes there are three examples, each of which appears to consist of hybrid rock.

The dyke systems.—There are two series of dykes, an older (basic) series and a newer (keratophyric) series. The older series have a wide distribution but they are not so numerous as the keratophyres, nearly two hundred of which have been mapped. The keratophyre dykes radiate in swarms from Warrigundi, but they are not evenly distributed about this centre. The heaviest development occurs in two swarms which leave the complex from opposite sides, and trend

in directions roughly perpendicular to the main injection-axis. The eastern swarm is more dispersed than the one on the south-south-west. In the southern sector between the two swarms there is a fairly evenly distributed display of dykes, but in the opposing sector, from the south-west to the north, dykes are rare.

This dyke activity terminates fairly abruptly on the circumference of a circular area centring on Warrigundi, with a radius of six miles. The dykes beyond this area are found to belong to the earlier series. Thus the keratophyre dykes have a clearly defined range of intrusion which may be expected to be related to the pressure with which they were injected.

Closely associated with the dykes is a series of keratophyre sills. Whereas most of the keratophyre dykes die out within a circle of six miles radius, there are quite a number of the sills which are not confined to this area; but these are almost all included if the radius is extended an extra mile. It would appear that when the injecting forces were nearly spent the keratophyres could still be injected to greater distances along incompetent bands, but as transgressive intrusions their energy was gone.

Many of the field characters of the keratophyre sills and dykes suggest that they were injected with considerable violence.

Influence of Werrie Basalts on the distribution of Warrigundi Rocks.—The complexes of the Piallaway Paddock Mountains, of the Dunover Mountains, and of Warrigundi, as well as the Werriston and Allandale injection-zones and many of the minor intrusions, are wholly confined to the Werrie basalts. Indeed, disregarding the dyke swarms and the sheets in the thrust fissure, the only intrusions in the Kuttung rocks are the keratophyre boss on Upper Werries Creek and the stratiform sheet of keratophyre south of Currabubula Creek in F7. Thus it would appear that the relative incompetency of the Werrie basalts influenced the distribution of the intrusions.

Furthermore, the same relation probably holds beneath the surface for, assuming the thrust fractures to be the channels by which the magma ascended (and this assumption seems to be justified by the field facts), it is unlikely that either the Piallaway Paddock Mountains complex or the Dunover Mountains complex invades the Kuttung to any extent, except along the fault fissures. In the Warrigundi complex some members have certainly ruptured indifferently the Kuttung series, but many of the intrusions are concordant with the Werrie basalts, and quite probably only commenced to spread out from their central conduits after that series had been reached.

Tectonic Relations of Folding, Thrusting and Vulcanism.

Significance of the main injection-axis.—The following facts bear testimony to the tectonic importance of the main injection-axis:

(1) Large discordant intrusions, such as bosses, plugs, and fissure-intrusions, as well as the quartz-dolerite masses, are confined to the main injection-zone.

(2) Apart from the dyke swarms, no intrusions are found on the northern side of the injection-axis; all satellitic intrusions are first directed to the south-south-west, but become concordant to the local structures fairly soon after leaving the main injection-zone.

(3) All intrusions within the main injection-zone which have an elongated form are oriented in sympathy with the axis.

(4) The keratophyre dyke swarms are thickest in directions at right angles to the main injection-axis. Another important bundle of dykes referable to both older and newer series extends eastwards from Warrigundi parallel to the injection axis.

(5) The trend of the injection axis is identical with the calculated true strike of the Hunter thrust movement.

Relation of thrusting to vulcanism.—It is certain that a great part of the Warrigundi activity post-dated the Hunter thrust movement, and there are strong grounds for believing that the whole of the vulcanism was post-thrust:

(1) The axis of injection, which was constant throughout the activity, shows no offsetting by the powerful eastern thrust which it must certainly do if the initiation of the vulcanism antedated the fault.

(2) The Warrigundi sheets occupy the fault fissure in the region of the injection-axis.

(3) Both older and newer series of dykes post-date the normal faulting.

There is also considerable evidence to suggest that the volcanic disturbance, although later than the thrusting, followed closely on the heels of that movement. Judging by the universal brecciation and intimate injection of the Werrie basalts, the hybrid sheets were injected with considerable violence under strong pressure and (may we presume from the extensive hybridism) at a high temperature. Furthermore, there can be no question, in view of the distribution of these intrusions, that this pressure was not hydrostatic, but directed. For the only intrusion on the north side of the injection axis (the Church Hill sheet) is close to the axis and oriented parallel to it, whereas on the south side of the axis long zones of injection penetrate the sediments for seven miles, and maintain that brecciated aspect and intimacy of injection throughout that distance. In both these principal injection zones the direction of intrusion is first to the south-south-west, at right angles to the main axis of injection and transgressive to the strike of the country rock. Then in both cases, at a distance of about two and a half miles from the axis, the intrusions wheel to the south and thereafter become concordant and follow the trend of the sediments.

Furthermore, there is a close relationship between the trend of the vulcanism and the direction of thrusting. For the calculated true strike of the thrust movement, inferred from the nature of the thrust surface, is N. 64° W.; the satellitic intrusions moved at right angles to this direction before becoming concordant.

This precise correspondence of the vector properties of the forces involved in the thrusting and the vulcanism, and the close field association of these phenomena, are surely not without significance. The obvious inference is that the Warrigundi vulcanism followed closely on the heels of the Hunter thrust movement, and was a concluding phase of the same diastrophic disturbance.

Relation of thrusting to folding.—Dr. Osborne (1929, p. 489) regards the Hunter overthrust disturbance as distinct from and later than the folding of the strata, basing his conclusion on the following evidence: (1) The thrust has modified the structures which were fully developed by the completion of that diastrophism; (2) It shows a trend quite different from the main trends in the lower Hunter valley; (3) It truncates many of the normal faults in the Kuttung terrain.

The additional evidence offered by the Werrie Basin, which was not available to Dr. Osborne, sheds quite a different light on these statements. Thus, with regard to (2), there can be no question now that the trend of the thrust is essentially identical with that of the folding. For the dominant trend of the folding between Glennies Creek and Wingen ranges between N. 15° W. and N. 30° W. (Osborne, loc. cit., p. 456), and this trend persists northwards to the Namoi River and, according to Benson (1920, p. 278), to the Gwydir valley, a total distance of 180 miles. Thus for four-fifths of the distance that the thrust system has so far been traced, it is parallel to the fold axes. The lower Hunter is abnormal from this point of view, forming as it does a zone of conflict between the two main trends, from the north-north-west and from the north (Osborne, 1929, p. 460). It is a zone of domes and basins—a transitional zone from the folded country in the north and the relatively undisturbed country in the south. It is in this region that the trends fray out and lose their identity. The overthrust itself frays out in the same zone and loses itself in a multiplicity of fractures of which the Webber's Creek fault, the Lachnagar fault, the Rosebrook fault, and perhaps the Kilfoyle's Creek fault, are the most important. It is not surprising that it is difficult to reconcile the trend of the thrust in this zone with that of the local structures. Rather, I would suggest, the relationship is precisely what one would expect.

With regard to (1), it is hard to see that the fact that the thrust has modified the folded structures implies in any way that it belongs to a later diastrophism. For in the normal sequence of such a disturbance the first act is the relief of the stress by folding; and as the stress becomes intensified, or is applied too suddenly to be relieved by plastic deformation, thrust-fractures must follow. But even during the thrusting the beds may be yielding by distortion, and to find an impress of the thrust on the folded structures is not abnormal.

On the other hand the evidence for believing the thrust to belong to the same movement as the diastrophism is strong. Indeed, the fact that in the Werris Creek region the thrusts are parallel to the main fold axes, and the outermost thrust separates more highly folded rocks from less highly folded rocks, all of which were laid down prior to the folding, is in itself almost conclusive evidence that the faulting is cognate with the folding (see Sections, Text-fig. 2).

Another line of evidence is afforded by the Warrigundi vulcanism. This complex, which was formerly regarded as of Carboniferous or early Permian age, is now shown to be post-Permian and later than the overthrust. Moreover, the forces of the folding, the forces of the thrusting, and the injecting forces of the Warrigundi vulcanism, all acted in the same direction. Their strong field-association suggests that they all belong to the same diastrophism. There is need for caution here, however, for the trends of the tectonic axes were fairly constant in this part of the continent throughout the upper Palaeozoic and Mesozoic eras.

Although the writer has little hesitation in suggesting that the folding, the Hunter thrust movement, and the Warrigundi vulcanism, all belong to the same general disturbance, he is not prepared to state whether the age of the diastrophism is pre- or post-Triassic. However, the consideration of this question opens up so many kindred problems, that its investigation immediately entangles one in a general discussion of the age and sequence of the earth-movements which have disturbed the New England region, matters which are beyond the scope of the present paper.

Summary.

The Werrie Basin is a structural trough, some forty miles in length, lying in the Werris Creek district, New South Wales. The basin is elongated along the Werrie synclinal axis which is a persistent structure in the region. The folded strata present a conformable sequence from the Upper Devonian Barraba series to the Permian Upper Coal Measures.

Complexity is introduced by a system of powerful overthrusts, which trend N. 30° W. and flank the basin on the west. Associated with the thrusts are some interesting subsidiary faults. The overthrusts are probably an extension of the Hunter Thrust System, and it is contended that they were part of the same orogeny as the folding of the strata, and were not a later feature as hitherto claimed.

The region is injected by a complex series of intrusions, an interim classification of which is made. An extensive series of hybrids are developed by digestion of the Werrie Basalts by the intrusive rocks. The vulcanism is intimately related to the tectonics, and probably followed closely the folding and overthrusting.

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EXPLANATION OF PLATE XVII.

Geological Map of the Werrie Basin. The dotted boundaries north of the Carroll-Somerton Road are taken from the reconnaissance survey carried out by Messrs. Lloyd and Mulholland, of the New South Wales Geological Survey.

NOTE ON THE IMPLICATIONS OF THE IRREGULAR STRIKE-LINES OF THE MOOKI THRUST SYSTEM.

By S. Warren Carey, M.Sc., Science Research Scholar and late Deas-Thomson Mineralogy Scholar of the University of Sydney.

(One Text-figure.)

[Read 31st October, 1934.]

During the examination of the geological structure of the Werrie Basin, it was found that the fault-surfaces of the Mooki thrusts displayed large-scale irregularities. Similar features have also been observed by Dr. G. D. Osborne (These Proceedings, 1929, p. 446, etc.), who described the Hunter overthrust, which has now been shown probably to belong to the same fracture system as the Mooki thrusts. In the Werrie Basin area it has been possible to obtain some idea of the nature and genesis of the irregularities. In view of the rarity of such phenomena, it is thought desirable to place on record a preliminary note on some observations on this matter.

Evidence of the irregularity of the fault-surfaces.—It is quite clear from the map (see Plate xvii) that the Mooki thrusts, particularly the eastern one, are characterized by a swinging strike, although the general trend is constant. Strike changes are apt to be quite abrupt. This is particularly noticeable in the eastern thrust in the northern half of the area examined by the author. There is little change in elevation along the line of outcrop of the fault-surface, and since the strike changes are of too great a magnitude to be accounted for by the relation of outcrop to contour, there can be no doubt that the swinging strike indicates that the fault-surface is not a plane.

Further, there is definite evidence of equally marked variations in the hade of the fault-surface. It is usually very difficult to determine the angle of dip. Outcrop-contour methods are generally unsatisfactory because the relief along the outcrop is never great, and piedmont alluvium and subdued outcrops frequently do not allow a sufficiently precise delineation of the position of the outcrop to give a quantitative result. Furthermore, where the fault can be defined exactly, one can never be sure that the observed oscillation in position of the fault is due solely to the change in elevation and not to the inherent irregularity of the fault-surface.

The average angle of dip for the region is probably between forty and fifty degrees. A greater steepness of dip along the Oakleigh horse is shown by the relation of outcrop to contour, and by the attitude of the fault block. That the angle is shallower between Piallaway and the southern end of the Oakleigh horse is indicated by the Warrigundi sheets which occupy the fault-plane. These

dip to the north-east at 45°. In contrast to this the Warrigundi rocks which occupy the fault-plane after the fault has veered to the south-west in D6* and C6, dip at 70° and 80°, so it is clear that the attitude of the fault has steepened again.

Cause of the Irregularity.—The irregularities occur in the locality where the fault is most in conflict with the structures it transgresses. For the greater part of its course the trend of the fault is more or less conformable to the trend of the local structures, a characteristic which has also been observed by Dr. Osborne in the Hunter Valley (l.c., 1929, p. 446).

It would appear that the fault-surface tends to compromise between the direction of its trend, and the planes of least resistance of the structures.

The course of the fault will now be followed with this in mind. The fault has been traced by Messrs. Lloyd and Mulholland from the north-north-west down to the Namoi River, striking in harmony with the Barraba beds on the western limb of the Werrie syncline. But from the Horton River to the Namoi, the synclinal axis has been rising steadily, flattening out in the Peel-Namoi region. South of the Peel, however, the synclinal axis plunges rather rapidly for the next thirty miles, the average angle of plunge being about 8°. This alteration considerably changes the strike of the western limb, which is now in oblique opposition to the fault. Thus we have the great thrust striking at a glancing angle against the major tectonic structure of the whole region—the Werrie Syncline.

The fault accomplishes the trangression by a series of side-steps, its course becoming very erratic. At the Namoi the strike swings 20° to the south-east, and the fault begins to truncate the Barraba series. East of Carroll, the fault forks, the eastern branch shearing perpendicularly across the strike of the Barraba series, almost to the base of the Burindi. It then makes almost a right-angled turn to the south, and its course is parallel to the strike for six miles, with the dip becoming progressively steeper and with further branching of the fault-surface. As soon as the surface unites again, it turns abruptly and shelves at a comparatively shallow dip for ten miles right across the major strikes, before wheeling to the west with a steep dip to link up with the strike of the sediments again. This it follows closely for some miles until, at Quipolly, it swings to the east once more and truncates the axis of the syncline. Thus between this point and the Namoi River the fault has completed the transgression of the western limb of the syncline, ascending stratigraphically from the Barraba Series to a horizon well up in the Permian.

Mechanism of Thrust Movement on an Irregular Surface.—In the preceding paragraphs it has been shown that large-scale irregularities are found both in the strike and the dip of the fault-surface. Next it has been demonstrated that this is due to the influence of the structures in the country rock on the course of the fault. It yet remains to be shown how it is possible for the thrust-block to override such an irregular surface without large cavities being formed along the fault and without rupturing the overthrust block. For it must be borne in mind that the departure from a simple plane surface is as much as two miles, and that the fault changes very rapidly from a high-angle to a comparatively low-angle thrust.

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* These map-references refer to the co-ordinate graticule on the geological map of the Werrie Basin which accompanies the author's paper on the structure of that region (see Plate xvii).

Let us consider more closely the details of the thrusting along the 20-mile front of the fault centring on Piallaway. The direction of movement of the thrust-block will be discussed later, but at present it may be assumed that it moved approximately in a south-west or south-south-west direction. The precise direction is immaterial to the validity of the present argument.

In view of the strike of the fault along the Oakleigh horse, thrusting to the south-south-west must be accompanied by considerable lateral shift. In the next section, between Oakleigh and Piallaway, where the trend of the fault is more transverse to the direction of motion of the thrust flake, the thrust movement of the south-south-west would have to be taken up largely by overthrusting, which would dominate over lateral shift. Now the condition which must be satisfied if the over-riding block is to remain intact is that the apparent dips measured in the direction of thrusting for the two sections of the fault-surface, must be equal. Hence the true dip of the fault-surface between Oakleigh and Piallaway must be considerably lower than along the Oakleigh horse, for otherwise the vertical displacement in the former position would be considerably greater than in the latter for the same horizontal displacement. This is precisely what is found to take place in the field, for the dip along the Oakleigh horse is considerably steeper than in the Piallaway section.

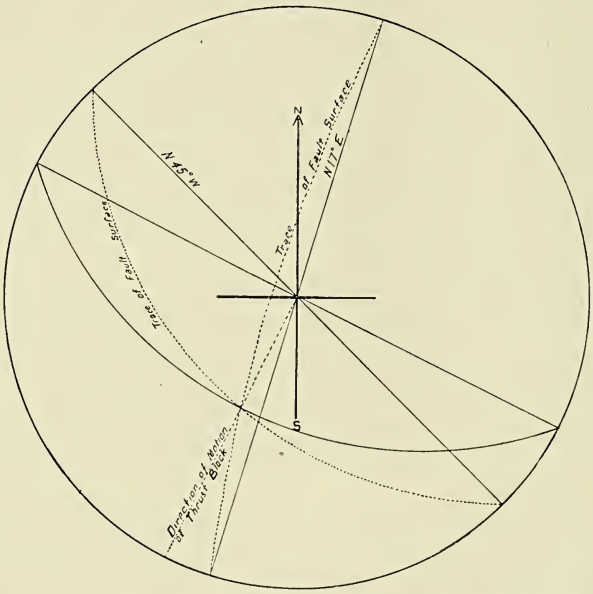
Furthermore, when the strike swings westward in C6, the dip of the fault must theoretically steepen again, if the equilibrium of the thrust-flake is to be maintained. Again it is found that this is what happens in the field.

Thus the important principle can be enunciated, that it is possible for a *thrust-flake to over-ride along an irregular strike line, accompanied by considerable lateral shifting, yet without producing any strains in the over-riding flake, or any openings along the fault-surface, provided that the hade of the fault accommodates itself to the local trend.*

Implications of thrust movement on irregular strike line.—Thus far the discussion has been qualitative. But the concluding statement of the last paragraph has an important corollary with a quantitative application: namely, that in the case of such a fault-fracture, where there is considerable lateral slipping, it is possible to calculate in three dimensions the true direction of movement of the thrust-flake, with no other data than the strike and dip of the fault along two important trends.

The underlying principle here is that if a body is moving over two intersecting planes, the only direction in which it can move and remain in contact with both surfaces, is parallel to the edge in which the two planes intersect. Hence, the strike and dip of the fault at two localities being known, the direction of the line of intersection of these two planes is readily obtained, either by geometrical construction or by making use of the stereographic projection. The latter method consists merely of plotting the traces of the two fault-surfaces on a stereogram over a stereographic net. The point of intersection of the traces gives immediately the pole of the edge along which these surfaces meet. Hence the required direction of movement can be obtained immediately, and the elevation to the horizon of the movement along this direction can be read off from the stereographic net. Furthermore, without any additional construction we can read off the hade of the fault-surface and calculate the ratio of overthrusting to lateral slipping for any locality where we know the strike (see stereogram, Text-figure 1).

The only assumptions which must be made for the application of these methods are that the fault-surfaces remain in contact and that the upthrow block is not distorted. The fact that the dip of the fault-surface probably flattens considerably at greater depths does not seriously affect the argument. The extent to which the above assumptions are departed from can be detected in the field. For example, the Springsure fault is almost certainly a rupture in the over-thrust flake due to the fact that the hade of the thrust did not adjust itself completely to the changing direction of strike. The fluctuation in the strike of the Kuttung strata in C4 is possibly attributable to the same cause.



Text-fig. 1.—Stereographic Projection of the fault surface of the eastern thrust at successive localities, for determination of direction of movement of the thrust flake.

Application to the fault-surface at Piallaway.—The principles above outlined were applied to the case at Piallaway. It must, however, be borne in mind that the results may have to be modified, since the conditions are not fully satisfied. The strikes used were N. 45° W. dipping at 45° to the north-east, which is the main trend in C4, and N. 17° E. at 80° to the south-east, which is the dominant trend in D6. The construction is given in Text-figure 1. The following results were obtained:

	Geometrical Method.	Stereographic Method.
Direction of thrust movement	S. 26½° W.	S. 26° W.
Elevation to the horizon of the thrust movement	43¼°	43½°

That is, the combined effect of the overthrusting and lateral slipping is equivalent to a simple dip-slip overthrust striking N. 64° W. and dipping to the north-east at 43°. The average strike in the region is N. 30° W., from which an average dip of 48½° is calculated. Comparing these values with those above

we find that on an average for every chain that the thrust block has moved, there have been 18½ yards horizontal dip-slip, 12½ yards horizontal strike-slip to the south, and 15½ yards elevation; the last value is the only one which would have to be modified if an underground flattening of the dip be assumed.

The fact that the fault brings into opposition structures which do not match indicates that there is considerable lateral shift. This is so marked at Quirindi that a dip-section suggests that the western and not the eastern is the upthrow side, the apparent anomaly being due to the fact that the trough of a deep syncline is brought against the flank of an anticline.

An important inference from this result is that in any attempt to obtain the throw and heave of the thrust-movement the section must be drawn in the true direction of the movement of the thrust-sheet, and not in the direction of true dip of the fault-surface at the locality of section.

It is significant that the true strike of the overthrust movement above calculated is identical with the observed trend of the axis of Warrigundi injection.

THE CORPUS LUTEUM IN CERTAIN OVIPAROUS AND VIVIPAROUS REPTILES.

By H. Claire Weekes, D.Sc.
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(Plates ix–xiv.)

[Read 31st October, 1934.]

Introduction.

The need for a comparative study of the corpus luteum in oviparous and viviparous reptiles becomes apparent when the facts concerned in the present transitional state of the reptilian reproductive cycle from oviparity to viviparity are considered. Among certain reptiles (lizards and snakes) there are oviparous species which lay their eggs after a short retention of only a few weeks within the oviducts; ovo-viviparous species which hold eggs within the oviducts for a longer and variable period, perhaps, as in *Anguis fragilis*, for almost as long as the life of the embryo in the egg in the nest; and, finally, truly viviparous species from which the young are born without egg-membranes, after a gestation period of approximately three months. The viviparous species vary further among themselves, some having no apparent reduction in the yolk-content of the ovum at the time of ovulation and a simple allantoplacenta, presumably for respiration (Weekes, 1927), and others with an obvious reduction in yolk-content and a comparatively complex small allantoplacenta for the nutrition of the embryo (Harrison and Weekes, 1925).* Here is excellent material for an investigation of the rôle played by the corpus luteum in these reptiles during the variable periods of retention, and it is with such an investigation that this paper is concerned.

In 1892 Strahl described "Die Rückbildung reifer Eierstockseier im Ovarium von *Lacerta agilis*", in 1893 Mingazzini published a paper on "Corpi lutei veri et falsi dei Rettili", and in 1903 Lucien wrote a "Note préliminaire sur les premières Phases de la Formation des Corps Jaunes chez certains Reptiles". More recently Hett (1924) described in detail the development and structure of the corpus luteum in *Lacerta agilis*, but as far as the author can ascertain no attempt has been made to make a systematic or comparative study of the corpus luteum of oviparous and viviparous reptiles.

Lizards were examined in Europe and Australia. In the Australian oviparous lizard *Amphibolurus muricatus*, and the Australian viviparous lizard *Lygosoma* (*Hinulia*) *quoyi*, a complete study was made of the development and structure of the corpus luteum from the stage immediately following ovulation to the time

* Much of the work referred to in these introductory remarks is embodied in a paper by the author which will probably be published shortly in an English journal.

of the complete disappearance of the corpus luteum from the ovary. Corpora lutea in six other species of viviparous lizards were examined at various stages during pregnancy and after the birth of the young. These were (*a*) the Australian *Egernia whitei*, *E. cunninghami* and *Lygosoma* (*Hemiergis*) *quadridigitatum*, three lizards with no apparent reduction in the yolk-content of the ovum at the time of ovulation and with a simple allantoplacenta presumably for respiration (Weekes, 1930); (*b*) the Australian lizards *Lygosoma* (*Liolepisma*) *weekesae* and *L.* (*L.*) *entrecasteauxi*, the latter with an obvious reduction in yolk-content and both with a specialized allantoplacenta presumably for the nutrition of the embryo (Weekes, 1929), and (*c*) the European viviparous lizard *Lacerta vivipara* which has a simple allantoplacenta. There were no stages available early enough for an investigation of the yolk-content of the ova of *L.* (*L*) *weekesae* or *L. vivipara* at the time of ovulation.

The material was collected in Australia regularly twice a week from the beginning of September until the end of February during 1932–1933 and 1933–1934, and in Europe, in the Auvergnes, the Pyrenees and the French Alps, during July, August and September of 1931.

For advice on the use of fixatives I am indebted to Miss R. Deanesly, University of London (University College), who advised Ciaccio's fluid for general cytological detail. Bouin's and Zenker's fluids were also used, but Ciaccio's fixative gave the best results (Deanesly, 1930*b*). The ovaries were sectioned at 7μ or 8μ. Iron haematoxylin was used after all fixatives and as counterstains, eosin and Van Gieson were used.

The corpus luteum in the oviparous lizard Amphibolurus muricatus.

A. muricatus is common around Sydney, New South Wales, measures from six to ten inches in length and lays from three to seven eggs at each breeding season. No viviparous Amphibolurid has so far been recorded. In the summer of 1932-1933, when investigations were first begun, the facts observed indicated two breeding seasons during that summer. The lizards first examined, on the 26th September, were non-pregnant and the ova in the ovaries were comparatively small. During the ensuing four weeks the ova were obviously developing toward maturation and ovulation and the first pregnant female was collected on the 28th October. Between the 28th October and the end of November all the females, as well as having eggs within their oviducts, had several enlarged ova within the ovaries. During the first week in December the eggs were laid, and of the sixteen females examined in the second week of December, fifteen were non-pregnant, with ova almost ready for ovulation and a second breeding season. Between the middle of December and the end of January all the females collected were pregnant. The ova in the ovaries of these lizards were quite small and there were no preparations for a further breeding season. Apparently all the eggs were laid by the end of January, for during February none of the lizards collected were pregnant.

During the summer of 1933-34 there was no such regularity of breeding habit. Pregnant females were first collected on the 20th September, five weeks earlier than the first pregnancy of 1932, and from the 20th September until the 30th December both pregnant and non-pregnant lizards could be collected at any time, the pregnant lizards carrying eggs at different stages of development. After the 30th December no pregnant lizards were collected.

During the earlier months, September, October and November, the pregnant lizards examined also carried enlarged ova within the ovaries, but the lizards examined in December had no enlarged ova and apparently were not preparing for a further breeding season in spite of the favourable climatic conditions of January. Therefore it does seem probable that each lizard has no more than two breeding seasons each summer.

From the facts observed then, *A. muricatus* has more than one breeding season each summer, probably two, prepares for the second breeding season while still pregnant, and the several breeding seasons may or may not occur regularly among lizards of the same locality.

The structure of the ovum and its follicle is essentially the same as that described by Hett (1924) for *L. agilis*, in which the follicle cells in early stages of development are of two kinds, both small and considerably enlarged (Figure 3 on Plate xiii is an illustration of a young follicle of *L.* (*L.*) *weekesae*). Immediately prior to ovulation the largest ova measure approximately 10 mm. in diameter and are surrounded by a thin covering of sheath tissue of two or three layers of greatly stretched fibrous connective tissue cells. At this stage there is no distinction between theca externa and interna.

The structure of the follicle immediately after ovulation.—Many lizards were collected having eggs within the oviducts without shell or even shell membrane, and with no visible signs of the beginnings of segmentation. Only one lizard was opened while the ova were actually ovulating. In this lizard there were three ova in one oviduct and three were closely packed together in the body cavity at the entrance of the other oviduct in which there were already two ova. All the large ova had been expelled from the ovaries.

With the collapse of the follicle, after the expulsion of the ovum, the relaxed sheath tissue is much thicker than in the stretched condition and there is now a definite distinction between theca externa and interna. The theca externa is more fibrous than the theca interna and contains the large blood vessels. The theca interna consists of layers of irregularly arranged cells of indefinite cell limits with oval, lightly staining nuclei of various sizes. The theca interna cells are associated with connective tissue fibres, capillaries and spindle-shaped cells of the fibroblastic type. These theca interna cells are probably a less differentiated form of the fibroblasts. As a result of the collapse of the follicle the follicular epithelium is much folded (Plate ix, fig. 5), and torn fibrous connective tissue, capillaries and loose corpuscles may be caught up between the folds. The epithelial cells are cuboid with characteristic spherical, lightly-staining nuclei and relatively deeply staining cytoplasm. At this stage these cells all show the same reaction to staining reagents. The burst follicle measures approximately 2·5 mm. × 1·5 mm.

The corpus luteum in early stages of development.—Copulation among the lizards was not observed, so that it cannot be used as a gauge in estimating the age of the corpus luteum in its various stages of development. Even if copulation had been observed, the time relationship between copulation and ovulation is not known. The only guide in estimating the age of the corpus luteum is the age of the embryo within the oviducts.

When the egg is still without shell membranes and segmentation has only just begun, the follicle has already begun to recover from its collapse (Plate ix, fig. 1). The torn fibrous connective tissue beneath the follicular epithelium is repaired; the capillaries are now numerous and are interspersed among irregular

nests of theca interna cells, which are in a state of active growth. The cells of the follicular epithelium have begun to divide, filling the interstices between the folds. They divide mitotically and amitotically, but mitotic figures are rare.

The corpus luteum at the stage when the medullary folds have begun to develop.—At this stage the eggs are still without shell. There is no change in the size of the follicle. The follicular epithelial cells have filled the clefts between the folds and there is only a suggestion of the original form of the folds. The walls of the follicle may converge (Plate ix, fig. 2); the cicatrix is still evident and there may be blood clots and cell débris within the cavity of the follicle. The epithelial cells have the same structure as at earlier stages, although in some specimens the cells nearest the theca interna may have particularly deeply staining nuclei (Plate x, fig. 1). Connective tissue fibres and a few spindle-shaped fibroblastic cells have grown up from the theca interna into the folds of the follicular epithelium, capillaries are developing.

The corpus luteum when the unflexed embryo lies on its side on the yolk-sac and the allantois is a small swelling at the posterior end of the embryo.—The corpus luteum is now kidney-shaped and is filled with follicular epithelial cells which will henceforth be termed "luteal cells" (Plate ix, fig. 3; Pl. x, fig. 2). The form of the original folds may still be recognized at the periphery of the luteal tissue. The luteal cells have irregular shapes and in some specimens the cell walls are more distinct than in others. Also in some specimens all the nuclei take a deep stain, while in others some may stain deeply and some lightly. The spindle-shaped fibroblastic cells have penetrated throughout the luteal tissue and there may be a thick core of such fibrous tissue at the centre of the corpus luteum carrying comparatively large blood vessels. These fibroblastic cells are definitely associated with the blood vessels and do not ramify among the individual luteal cells. The connective tissue fibres alone penetrate between the luteal cells. There is less sheath tissue than at earlier stages (Plate x, fig. 2).

The corpus luteum immediately before egg laying.—At this stage the embryo is flexed, the heart visible as a swelling at the anterior end, and the allantois enlarged to about 3 mm. in diameter. This is the oldest stage found in the eggs within the oviducts and is apparently the most advanced stage reached by the embryo at the time of the laying of the eggs. From a comparison with the embryos of the viviparous *L.* (*Hinulia*) *quoyi*, it is possible to estimate approximately that the embryo of *A. muricatus* is about ten days old at this stage (see description of *L.* (*Hinulia*) *quoyi* below).

The corpus luteum is shrunken and measures approximately 1·2 mm. × 0·5 mm. (Plate ix, fig. 4), and the luteal cells have all the appearances of degeneration (Plate x, fig. 3). The cell cytoplasm is more vacuolated than at earlier stages and easily splits during fixation and embedding. The nuclei are shrunken and collapsed and even pycnotic. The degenerating tissue is deeply impregnated by septa of fibroblastic cells of the theca interna. Few of the sheath tissue cells are degenerating.

The fate of the corpus luteum after the laying of the eggs.—At the time of the first ovulation the ovary contains, as well as the large ova ready for ovulation, a number of small ova with a diameter of approximately 1 or 2 mm. After ovulation, and while the lizard carries eggs within the oviducts and corpora lutea within the ovaries, these small ova begin to enlarge, obviously, as described above, in preparation for a further breeding season, and by the time of the

laying of the eggs these developing ova may measure as much as 6 mm. in diameter (Plate ix, fig. 4). When the ova have attained a diameter of about 10 mm. the eggs have been laid and all the corpora lutea have disappeared from the ovaries. In one lizard, which laid its eggs on 29th November, the corpora lutea had all disappeared by the 11th December. If the period of non-pregnancy between the breeding seasons is approximately two weeks, as supposed, the "post-partum" existence of the corpus luteum within the ovary must be something less than two weeks.

The corpora lutea of the different breeding seasons are naturally identical in structure, but those of the first pregnancy are associated with developing ova and those of the last pregnancy with atretic follicles. During the last pregnancy even medium-sized ova are atretic, and after the laying of the eggs the corpora lutea degenerate among degenerating follicles.

The corpus luteum in the viviparous lizard Lygosoma (Hinulia) quoyi.

In *L.* (*Hinulia*) *quoyi* there is no apparent reduction in the yolk-content of the ovum at the time of ovulation and there is only a simple allantoplacenta, presumably for respiration.

Specimens of *L.* (*Hinulia*) *quoyi* were collected from the heights of Elanora, in the environs of Sydney, during October, 1932. Until the 20th October no pregnant lizards were found, although, judging from their size, the ova in the ovaries were almost ready for ovulation. On the 24th October eight of the ten females collected were pregnant, so that it was possible to determine within a few days the time of ovulation and the age of the developing embryos. Such regularity among viviparous lizards is by no means the rule, as is shown by a comparison of the dates of various stages in the development of the embryos of specimens of *L.* (*Hinulia*) *quoyi* collected from other localities.

The ovary at the time of ovulation is essentially similar in structure to that of the oviparous *A. muricatus* described above, so that further description is unnecessary here. The mature ova are also approximately the same size as those in *A. muricatus*, measuring about 10 mm. in diameter.

The corpus luteum in early stages of development.—The youngest corpus luteum examined was taken from a lizard collected on the 25th September, 1933. There were no signs of egg segmentation or of shell membrane. The burst follicles were flaccid and bloody and had collapsed down to about 2·5 mm. × 1 mm. The follicular epithelium is a deeply folded single layer of cuboid cells with deeply-staining cytoplasm and round, lightly-staining, vesicular nuclei. The sheath tissue resembles that described above for *A. muricatus* at a similar stage.

The next earliest stage in the development of the corpus luteum was collected on the 25th September, 1933. The embryonic shield was visible in the eggs and the burst follicles were tauter and less bloody, although well vascularized by vessels in the sheath tissue visible to the naked eye. In section the original folds of the follicular epithelium are still evident as a columnar arrangement of the epithelial cells upon the underlying theca interna. The interstices of the folds have been filled with epithelial cells. At this stage there is often the same variation in staining as occurs among the nuclei of the follicular epithelial cells of *A. muricatus*, some of the nuclei taking a light stain in iron haematoxylin and others a deep stain.

The corpus luteum when the embryo lies on its side on the yolk-sac and the allantois is a small diverticulum.—Lizards with embryos at this stage in develop-

ment were collected on the 9th and 15th October, 1933. The corpus luteum is now solid, but is still a flat sac and measures approximately 2 mm. × 1 mm. (Plate x, fig. 4). As in *A. muricatus*, the corpus luteum has been mostly filled by the amitotic division of the follicular epithelial cells. The luteal cells at this stage are comparatively long and narrow, often with indefinite cell limits, and the nuclei may take either a light or dark stain from iron haematoxylin (Plate xii, fig. 2). The sheath tissue is unchanged. The theca interna fibroblasts do not grow among the luteal cells. The corpuscles are concentrated in the theca interna immediately beneath the luteal cells (Plate x, fig. 4).

The corpus luteum at about the middle of the second week of pregnancy, when the limbs are developing and the allantois has united with the chorion.—The females with embryos at this stage in development were collected on 15th and 22nd October and on 9th November, 1933. The corpus luteum is now kidney-shaped with dimensions about 1·5 mm. × 1 mm. (Plate xi, fig. 1), and is densely packed with luteal cells of irregular shape, with or without distinct cell limits. The luteal cells are only approximately half the size of those at earlier stages, although the nuclei are apparently unchanged (compare the luteal cells in Plate xi, figure 3, with those in Plate xii, figure 2). The cicatrix is healed by fibrous tissue from the sheath and is plugged with luteal cells. The sheath is thinner than at earlier stages, due to a superficial penetration between the luteal cells by the spindle-shaped fibroblastic cells of the theca interna (Plate x, fig. 1). However, the penetration does not extend far and there are never any blood vessels within the corpus luteum among the luteal cells.

The corpus luteum at the stage when the digits of the embryo are differentiating and the chorio-allantoic vesicle fills about one-third of the incubatory chamber.—Lizards with young at this stage of development were collected on 10th, 15th, and 22nd November, 1933. The corpus luteum may be spherical or kidney-shaped, and still measures approximately 1·5 mm. × 1 mm. The luteal cells have the same appearance as at the stage described above. The sheath tissue is now reduced to about one-half its original width, and at the periphery the luteal cells are cut into numerous "nests" by the theca interna.

From this stage on, until the embryo is well advanced in development, has acquired pigmented scales and is approximately at the end of the second month of the gestation period, there is no obvious change in the structure of the corpus luteum, but at about the end of the second month the first signs of degeneration of the luteal cells appear. The luteal cells at the centre of the corpus luteum become enlarged and vacuolated and their nuclei are collapsed and shrunken (Plate xi, fig. 2). Also a peculiar, dense, pink-staining coagulum often appears amongst the luteal cells and at the periphery of the corpus luteum between the luteal cells and the theca interna. There are only a few isolated degenerating cells in the sheath tissue. The degeneration of the luteal cells once begun continues until, by the time the embryo has reached a stage in development where the yolk-sac is withdrawn into the alimentary canal and the time of birth is obviously near, the degeneration has spread throughout the luteal cells (Plate xi, fig. 4). Degeneration is assumed from the vacuolated appearance of the cell cytoplasm, the breaking down of the nuclear membrane and the general collapse and shrinkage of all the nuclei. The progress in degeneration is accompanied by an increase in the amount of coagulum between the luteal cells. Since the coagulum increases as the degeneration progresses, it is thought to be probably a product of that degeneration.

The corpus luteum at the time of birth.—Pregnant females of *L.* (*Hinulia*) *quoyi* were kept in captivity during the last few weeks of their pregnancy so that the birth of the young could be observed and corpora lutea obtained from the females while giving birth to young. The ovaries were taken from five lizards in this condition (Plate xii, fig. 3). The luteal cells show widespread degeneration (Plate xii, figs. 4, 5), and in one specimen of *L.* (*L.*) *weekesae* examined at a similar stage, the corpus luteum was so filled with coagulum, that it was at first mistaken for a gland in the process of active secretion (Plate xiii, fig. 5). However, the great decrease in the number of luteal cells, and the dead or dying state of those present, strongly suggest that the coagulum is no more than a product of the degeneration of the luteal cells.

Those lizards observed gave birth to young at intervals ranging from ten minutes to two hours between each birth, and the members of each litter, with the exception of those from one particular female, were all born within twenty-four hours of the first birth. From this particular female two young were born on 13th February, 1933, and a third nine days later, on 22nd February.* It would be interesting to observe other lizards to see if this irregularity is a common habit, for if the habit is a common one these lizards would be the only amniota known to give birth to young of the same litter at such widely separated intervals. And it would be interesting to investigate the fate of the corpora lutea under such conditions. Is the birth of each foetus accompanied by the disappearance of one corpus luteum, do the corpora lutea all disappear after the first birth, or do they all persist until the last birth? The ovaries of the female mentioned above were examined twenty-four hours after the birth of the last foetus and all three corpora lutea were in the last stages of degeneration.

The degeneration of the corpus luteum after the birth of the young.—The type of luteal degeneration after the birth of the young is typical for all the lizards examined, and at first sight the degenerating corpus luteum may be mistaken for a degenerating follicle. The luteal cells enlarge enormously, and are greatly vacuolated (Plate xii, fig. 6). The coagulum between the luteal cells and the theca interna is thrown into folds as the corpus luteum shrinks. In their degeneration the sheath tissue cells are also enlarged and vacuolated. The corpus luteum is last visible as a small orange speck among the ova. There were no corpora lutea in the ovaries of females examined two weeks after the birth of the young.

The corpus luteum in the Australian viviparous lizards Egernia whitei, Lygosoma (Hemiergis) quadridigitatum, E. cunninghami, Lygosoma (Liolepisma) weekesae, L. (L.) entrecasteauxi *and the European lizard* Lacerta vivipara.

E. whitei and *L.* (*Hemiergis*) *quadridigitatum* are both lizards with no apparent reduction in the yolk-content of the ovum at the time of ovulation and with a simple allantoplacenta presumably for respiration. The corpus luteum has fundamentally the same structure in both lizards, and is essentially similar to that described above for *L.* (*Hinulia*) *quoyi*. There are the same small, round luteal cells with round, or sometimes oval, lightly-staining nuclei; there are only

* These dates are much later than those given for the birth of the young among specimens of *L.* (*Hinulia*) *quoyi* collected around Sydney. The lizard referred to was caught at Jenolan, which has a much later spring than Sydney.

superficial ingrowths of fibroblasts among the luteal cells and consequently there are no blood vessels among the luteal cells (Plate xiii, fig. 1).

E. cunninghami is the largest lizard examined, and the sac-like corpus luteum measures as much as 5 mm. × 3 mm. The sheath tissue is correspondingly thick and has the same structure as that described for *A. muricatus* and *L.* (*Hinulia*) *quoyi*. The luteal cells are also essentially similar to those described for the other lizards, except that they also include scattered giant cells (Plate xiii, fig. 2). There are large blood vessels and blood clots among the luteal cells, but since these have very little supporting tissue from the theca interna and often no distinct vessel walls, they are thought to be in traumatic cavities formed by the tearing of the follicle wall on the expulsion of the large egg. There are none of the ingrowing septa of fibroblasts from the theca interna so characteristic of *A. muricatus*.

L. (*L.*) *weekesae* and *L.* (*L.*) *entrecasteauxi* are two closely related skinks and are both restricted to high altitudes. With *Chalcides tridactylus* in Italy, these lizards have the most highly specialized allantoplacenta so far found among reptiles. As in all other viviparous lizards examined, the corpus luteum is present within the ovary until a few weeks after the birth of the young, that is, for approximately three and a half months. The mature corpus luteum in each species is spherical, measures about 0·5 mm. in diameter, and is the smallest corpus luteum yet found among lizards (Plate xiii, fig. 3). The sheath tissue is correspondingly thin, but the theca externa and interna are well differentiated. The theca interna contains spindle-shaped fibroblastic cells whose nuclei may be twice the size of those of the luteal cells (Plate xii, fig. 4). The fibroblastic cells penetrate the luteal tissue providing blood vessels and dividing the luteal tissue into nests of cells. As in *A. muricatus*, the fibroblastic cells are definitely associated with the blood vessels and do not ramify between the individual luteal cells. Only the connective tissue fibres penetrate between the cells.

As in *L.* (*Hinulia*) *quoyi* the luteal cells begin to degenerate within a month of the birth of the young, and by the time of birth all the luteal cells are dead or dying. As mentioned above, in one of the specimens of *L.* (*L.*) *weekesae*, examined while the young were being born, many of the luteal cells had disappeared and the "nests" were filled with coagulum, the whole corpus luteum having something of the appearance of a mammary gland (Plate xiii, fig. 5). The corpora lutea in both ovaries had the same structure, and when they were first examined it was thought that the tissue may be glandular and in the act of secreting the coagulum. And, curiously enough, a coagulum of similar appearance occurred in globules at the surface of the uterine wall surrounding the embryos (Plate xiv, fig. 1). But a closer examination showed that the luteal cells were either dead or dying and the coagulum was thought to be merely a product of the cell degeneration.

Lacerta vivipara is a small viviparous skink. Specimens were collected from the Auvergnes mountains during July, 1931, and from the Pyrenees and the French Alps in August, 1931. The available material consists of two females with young corpora lutea, eleven with old degenerating corpora lutea, twenty with corpora lutea of "post-partum", and the ovaries of five females were examined while the young were being born.

Like *L.* (*L.*) *weekesae* and *L.* (*L.*) *entrecasteauxi*, *Lacerta vivipara* has a corpus luteum that measures only 0·5 mm. in diameter. The sheath tissue has

the same structure as that described above for the Australian lizards, and is well illustrated by figure 2 on Plate xiv. At the youngest stage examined, the corpus luteum is a flat sac, filled with luteal cells, which have not yet been invaded by the sheath tissue (Plate xiv, fig. 2). The luteal cells are bigger than those in the corpus luteum of any Australian lizard so far examined, and most closely resemble the mammalian luteal cells.

Unfortunately the only other stages available are old, within a few weeks, and even days, of birth. At this stage the luteal tissue is degenerating. The luteal cells are slightly larger than at earlier stages, and the cell cytoplasm is vacuolated and many of the cell nuclei are shrunken. The degeneration first begins at the centre of the corpus luteum. In figure 3 on Plate xiv, some of the luteal cells at the periphery still have the appearances of healthy cells. A coagulum, similar to that described above for other lizards, occurs among the luteal cells at the time of the birth of the young. The luteal tissue now contains the spindle-shaped fibroblastic cells of the theca interna, which are not only associated with the blood vessels, but penetrate between the luteal cells (Plate xiv, fig. 3). The sheath tissue is greatly depleted (Plate xiv, fig. 4), and may consist of no more than one or two layers of connective-tissue cells.

Discussion.

After much discussion about the types of luteal cells in the mammalian corpus luteum, the function of the cells of the theca interna within the corpus luteum and the nature and function of the ovarian interstitial tissue, the general consensus of opinion at the moment seems to be that the luteal cells are formed by the hypertrophy of the follicular epithelium (Hill and Gatenby, 1926), that the fate of the theca interna is still a matter of dispute, the problem being complicated by histological species differences (Deanesly, 1930*b*), and that the whole problem of determining the part played by the interstitial tissue "is complicated by the lack of any agreed definition of interstitial tissue and by the uncertain behaviour of atretic follicles" (Parkes, 1929). In reptiles the luteal cells are without doubt derived from the follicular epithelial cells, and there are also differences in the behaviour of the theca interna cells in different genera of lizards, but these differences do more to illuminate than to complicate an understanding of the significance of the theca interna. Among the one reptilian family Scincidae there are at least three different types of behaviour of the theca interna, and yet the type of reproductive cycle in each species is fundamentally similar: (1) In the viviparous skinks *L.* (*Hinulia*) *quoyi*, *L.* (*Hemiergis*) *quadridigitatum* and *E. whitei*, there are no ingrowths of theca interna fibroblasts among the luteal cells; (2) In the viviparous skinks *L.* (*L.*) *weekesae* and *L.* (*L.*) *entrecasteauxi* the fibroblasts grow amongst the luteal cells in definite strands, providing the luteal cells with blood vessels. These fibroblasts are only associated with the blood vessels and do not penetrate between the individual luteal cells; (3) In the viviparous skink *L. vivipara* there are the same septa of theca interna cells providing the blood vessels and in addition the fibroblastic cells do penetrate between the luteal cells. There are no variations in the particular reproductive cycle of any of these lizards to account for these differences. Certainly *L.* (*L.*) *weekesae* and *L.* (*L.*) *entrecasteauxi* have a comparatively highly specialized allantoplacenta, but ingrowths of fibroblasts among luteal cells cannot be particularly associated with placentation as it occurs in the oviparous lizards *A. muricatus* (as described

above) and *L. agilis* (Hett, 1924). Nor can the differences in corpus luteum vascularization and theca interna invasion be associated with a variation in the size of the ripe follicles, as is suggested for the mammals (Deanesly, 1930*b*).

Marshall (1922), after mentioning Mingazzini's belief that the corpus luteum in reptiles "is identical with the mammalian corpus luteum", wrote "it is noteworthy that the above mentioned animals (reptiles) which show luteal hypertrophy are all viviparous". But further investigations (Hett, 1924, and the present investigation) have shown that luteal formation is to be also associated with oviparity.

The corpus luteum in the oviparous lizard *A. muricatus* disappears soon after the laying of the eggs, having had an intra-ovarian existence of approximately three weeks. The corpus luteum in the viviparous lizards remains in the ovary throughout the gestation period of three months and disappears within two weeks after the birth of the young. There is, then, perhaps some relationship between the presence of the corpus luteum within the ovary and the retention of the eggs within the oviduct.

In the viviparous lizards atresia of ova begins early in the gestation period and continues until the birth of the young. It seems more likely that such atresia is controlled by some factor other than the presence of corpora lutea within the ovary, as had been suggested for mammals, since in the oviparous *A. muricatus* ova develop to within a short time of ovulation in the presence of healthy corpora lutea.

Summary.

A description is given of the development and structure of the corpus luteum in oviparous and viviparous lizards. In all the lizards examined the luteal cells are formed by the division, mitotic and amitotic, of the cells of the follicular epithelium. Mitotic figures are rare. The behaviour of the theca interna varies with the subgenus of the lizard. In the oviparous lizard *Amphibolurus muricatus* the spindle-shaped fibroblastic cells of the theca interna grow among the luteal cells, providing blood vessels. These fibroblasts are definitely associated with the blood vessels, and only connective tissue fibres extend between the individual luteal cells. In the viviparous lizards *Lygosoma* (*Hinulia*) *quoyi*, *L.* (*Hemiergis*) *quadridigitatum*, *Egernia whitei* and probably *E. cunninghami*, there are no ingrowths of thecal fibroblasts among the luteal cells. In the viviparous lizards *L.* (*Liolepisma*) *weekesae* and *L.* (*L.*) *entrecasteauxi*, two lizards with a comparatively highly specialized allantoplacenta, there are definite ingrowths of theca interna fibroblasts, but, as in *A. muricatus*, only connective tissue fibres actually penetrate between the individual luteal cells. In the viviparous *Lacerta vivipara* and, according to Hett, the oviparous *Lacerta agilis*, not only are the fibroblastic cells of the theca interna associated with blood vessels among the luteal cells, but they also penetrate between the individual luteal cells.

In the oviparous *A. muricatus* the corpus luteum has an intra-ovarian existence of approximately three weeks, degeneration of the luteal tissue beginning while the lizard is still carrying the eggs and continuing until the time of egg laying, when all the luteal cells are either dead or dying.

In the viviparous lizards the corpus luteum has an intra-ovarian existence of approximately three and a half months, degeneration beginning at about the end of the second month of pregnancy and continuing during the last month of

pregnancy until, by the time of the birth of the young, the degeneration has spread throughout the luteal tissue.

The oviparous *A. muricatus* has at least two breeding seasons each summer. The viviparous lizards have but one annual breeding season. In the viviparous species atresia begins during the early stages of pregnancy while the ova are quite small. In the oviparous lizard atresia rarely occurs during the first pregnancy; ova enlarge in preparation for a second breeding season in the presence of healthy corpora lutea in the ovary and also in the presence of eggs within the oviducts.

DESCRIPTION OF PLATES IX-XIV.

Abbreviations.—*b.v.*, blood vessel; *c.*, coagulum; *d.l.*, degenerating luteal cells; *f.b.*, fibroblastic cell of theca interna; *f.c.t.*, connective tissue fibres; *f.e.*, follicular epithelial cells; *t.e.*, theca externa; *t.i.*, theca interna; *s.t.*, degenerating sheath tissue.

Plate ix.

Fig. 1.—Follicle of *A. muricatus* after expulsion of the ovum, showing the sheath tissue and folded follicular epithelium. × 20.

Fig. 2.—Follicle of *A. muricatus* at the stage when the medullary folds have begun to develop in the eggs within the oviducts. × 20.

Fig. 3.—Mature corpus luteum of *A. muricatus* showing ingrowths of fibroblasts among the luteal cells. × 60.

Fig. 4.—Corpus luteum of *A. muricatus* at the time of laying of the eggs in the company of several enlarged ova which are preparing for a further breeding season. × 20.

Fig. 5.—Section through the folded follicular epithelium of *A. muricatus* at the stage illustrated by figure 1, showing the tear between the theca interna and the epithelial tissue and a few loose cells and capillaries. × 375.

Plate x.

Fig. 1.—Section through the edge of the corpus luteum of *A. muricatus* at the stage illustrated by figure 2 on Plate ix, showing ingrowths of spindle-shaped fibroblastic cells from the theca interna. × 375.

Fig. 2.—Section through the mature corpus luteum of *A. muricatus*. × 375.

Fig. 3.—Section through the degenerating corpus luteum of *A. muricatus* at the stage immediately prior to egg laying. × 375.

Fig 4.—Young corpus luteum of *L.* (*Hinulia*) *quoyi* showing cicatrix, luteal cells, theca externa and interna. × 40.

Fig. 5.—Ovary of *L.* (*Hinulia*) *quoyi* showing relationship in size between a young corpus luteum and the remainder of the ovary. × 20.

Plate xi.

Fig. 1.—Corpus luteum of *L.* (*Hinulia*) *quoyi* at the middle of the second week of pregnancy showing superficial ingrowths of theca interna among the luteal cells. × 60.

Fig. 2.—Corpus luteum of *L.* (*Hinulia*) *quoyi* at the end of the second month of pregnancy showing the first signs of the degeneration of the luteal cells. × 50.

Fig. 3.—Section through the edge of a corpus luteum of *L.* (*Hinulia*) *quoyi* at the stage illustrated by figure 1 on Plate xi, showing the reduction in size of the luteal cells since the stage illustrated by figure 2 on Plate xii, and the darkly and lightly staining follicular epithelial cells. × 375.

Fig. 4.—Section through the edge of a degenerating corpus luteum of *L.* (*Hinulia*) *quoyi* immediately before the birth of the young. × 375.

Plate xii.

Fig. 1.—Section showing superficial ingrowth of the theca interna of *L.* (*Hinulia*) *quoyi* among the luteal cells and the "nests" of cells so formed. × 375.

Fig. 2.—Section through the edge of a young corpus luteum of *L.* (*Hinulia*) *quoyi* showing lightly and darkly staining follicular epithelial cells. × 375.

Fig. 3.—Ovary of *L.* (*Hinulia*) *quoyi* showing the relationship between the corpus luteum and the rest of the ovary at the time of the birth of the young. × 19.

Fig. 4.—Section through the edge of a degenerating corpus luteum removed from a lizard giving birth to young, showing the coagulum and degenerating luteal cells. × 375.

Fig. 5.—Section through the entire corpus luteum removed from a lizard giving birth to young. × 47.

Fig. 6.—Section through the degenerating corpus luteum of *L.* (*Hinulia*) *quoyi* after the birth of the young. × 60.

Plate xiii.

Fig. 1.—Section through the edge of a corpus luteum of *E. whitei* at the end of the second week of pregnancy when the corpus luteum is considered mature. × 375.

Fig. 2.—Section through edge of a mature corpus luteum of *E. cunninghami* showing a few scattered giant cells. × 375.

Fig. 3.—Corpus luteum of *L.* (*L.*) *weekesae* at the end of the first month of pregnancy. × 120.

Fig. 4.—Section of the interior of the corpus luteum of *L.* (*L.*) *weekesae* at the stage when there is little yolk left within the yolk-sac of the developing embryos and the embryos are in an advanced stage of development, showing the degeneration of the luteal cells and the large healthy nuclei of the spindle-shaped cells of the theca interna. × 375.

Fig. 5.—Section through the edge of the corpus luteum of *L.* (*L.*) *weekesae* taken from a lizard while giving birth to young, showing the degeneration of the luteal tissue and the presence of coagulum within the corpus luteum. × 375.

Plate xiv.

Fig. 1.—Section through one of the folds in the uterine wall in the placental area of *L.* (*L.*) *weekesae* showing the globules of coagulum. × 375.

Fig. 2.—Part of a young corpus luteum of *L. vivipara* showing the theca externa, theca interna and the large luteal cells. × 80.

Fig. 3.—Section through the edge of a corpus luteum of *L. vivipara* immediately before the birth of the young, showing the blood vessels among the luteal cells and the spindle-shaped cells of the theca interna between the luteal cells. × 375.

Fig. 4.—The corpus luteum of *L. vivipara* immediately before the birth of the young, showing the much depleted sheath tissue and its ramification among the luteal cells. × 80.

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FURTHER INVESTIGATIONS ON THE EMBRYOLOGY OF VIVIPAROUS SEEDS.

By Gladys Carey, M.Sc.

(Plate xv; thirty-eight Text-figures.)

[Read 28th November, 1934.]

The embryology of *Avicennia officinalis* was investigated by Treub in 1883. Some years later, Karsten (1891) published an extensive work embracing all known species of mangroves.* Haberlandt (1895) examined the embryos of several genera from the point of view of nutrition. Cooke (1917) amplified Karsten's brief mention of the embryology of *Rhizophora Mangle*. Recently, Carey and Fraser (1932) described the embryology of *Aegiceras majus*.

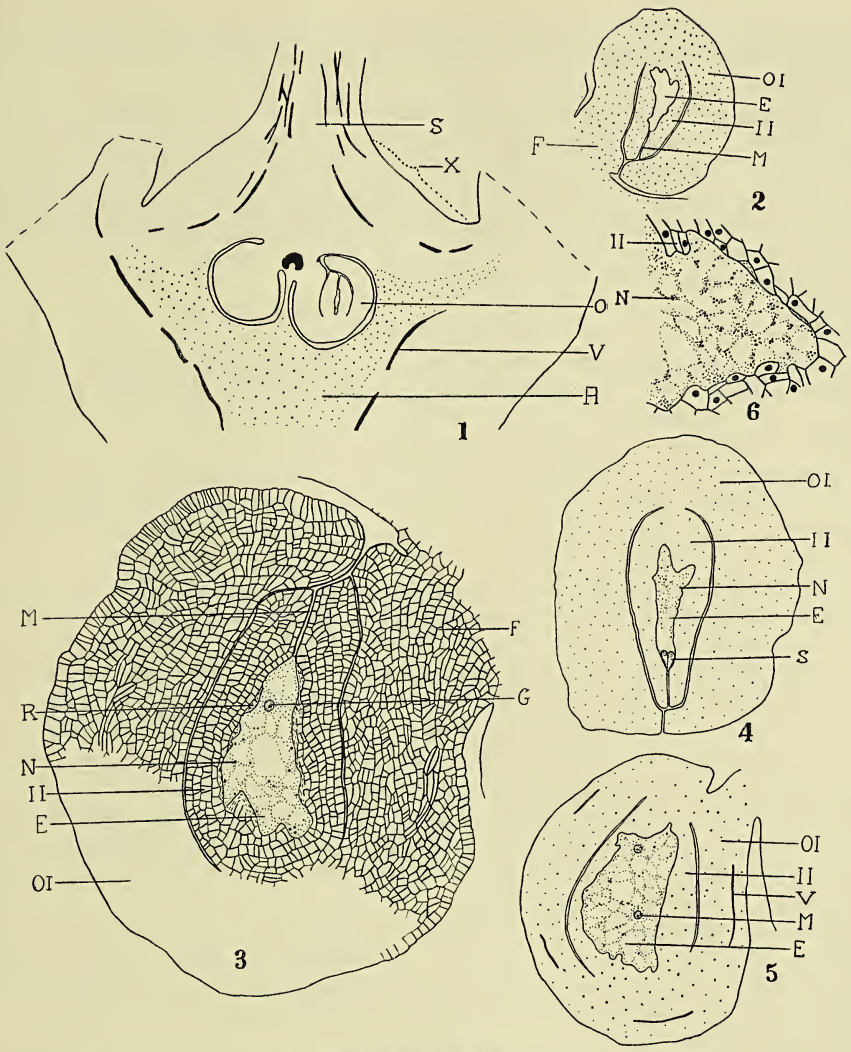
Embryological material of *Rhizophora mucronata* and *Ceriops Candolleana* obtained in the Southern Tropics from the coastal town of Yeppoon, about twenty-five miles from Rockhampton, Queensland, was available to the writer. This material showed that a re-examination of the embryology of these types would prove interesting.

Rhizophora mucronata Lam.

As the general structure of the flower of *Rhizophora mucronata* has been described by systematists (Bentham, Manson Bailey), it will not be included here, but the ovary and receptacle deserve further mention.

The gynoecium.—An examination of the wall of the half inferior ovary shows an interesting arrangement of tissues, where it is fused to the receptacle. The outer walls of the epidermal layer are thickened and covered with a wide cuticle. Beneath this peripheral layer lies a small-celled tissue in which groups of 'stone' cells are freely scattered. Passing inward, there next occurs a wide band of large parenchymatous cells among which branched sclereids are scattered freely. Sclereids of this type are characteristically found in many parts of the plant body among species of this family, as has been noted by Solereder (1908). The parenchymatous cells of this area are filled with a densely granular cytoplasm and those lying on the inner side in close proximity to the vascular strand contain druses of calcium oxalate. Inside this tissue lies an aerenchyma (A in Text-figure 1) which, extending round the loculus and passing up under the other floral parts, eventually merges into the more compact tissue of the ovary wall at the base of the style. Here the cells which are also parenchymatous are arranged in compact vertical rows. The cells are cubical, but gradually become vertically elongated toward the middle and apex of the style. The presence

* Karsten's "Ueber die Mangrove-Vegetation im Malayischen Archipel" is unavailable in Australia. However, through the courtesy of Sir Arthur Hill, Director of Kew Gardens, England, a typewritten copy of pages 11-17 and 31-41 was made available to the writer, who wishes to express her sincerest thanks to Sir Arthur Hill.



Text-figures 1-6.

1.—A diagram of a longitudinal section of the ovary of a flower of *Rhizophora mucronata*. S, style; X, zone which later increases most in size; V, vascular tissue; O, ovules; A, aerenchyma (× 11·5).

2.—An ovule of *Rhizophora mucronata* showing the intrusion of the embryo sac into the inner integument. OI, outer integument; II, inner integument; M, micropyle; F, funicle; E, embryo sac (× 41).

3.—A detailed study of the ovule as shown in Text-figure 2. OI, outer integument; II, inner integument; E, embryo sac; N, deeply staining granules; R, resorbed tissue of the inner integument; F, funicle; M, micropyle; G, egg nucleus (× 112).

4.—A tangential section of an enlarging ovule showing the haustorial action of the embryo sac. OI, outer integument; II, inner integument; E, embryo sac; N, deeply staining granules; S, synergids (× 41).

5.—An enlarging ovule of *Rhizophora mucronata* before fertilization. OI, outer integument; II, inner integument; E, embryo sac; V, vascular tissue; M, endosperm nucleus (× 41).

6.—A detailed study of a portion of the embryo sac shown in Text-figure 5. II, inner integument; N, deeply staining granules (× 208).

of aerenchyma in close association with the ovules not only of this genus but of other truly viviparous plants such as *Bruguiera* and *Ceriops* seems to be significant.

Dividing the cavity of the ovary into two loculi is the placenta. To it are attached four anatropous ovules, each by its own massive funicle. These ovules are joined to the placenta at the stylar end, just above the latter's horseshoe-shaped vascular strand (Text-figure 1). This strand passes through the placenta in a horizontal direction till it joins the conducting tissue running vertically up the ovary wall. The lower part of the narrow placenta is composed of parenchymatous cells, staining deeply with dyes.

Development of Ovule.

In the youngest ovule examined by the writer the embryo sac was clearly differentiated. However, the stages prior to this are fully described by Karsten (1891). The embryo sac lies in a nucellus, which is surrounded by two rather massive integuments. The outer integument is the more massive and towards its periphery a vascular strand is soon initiated, passing three-quarters of the way round the ovule. The narrow micropyle which is directed toward the placenta is not coincident through the two investments (Text-figures 2, 3, M), but takes a sharp turn between the inner and outer integuments.

Before the bud opens the enlargement of the embryo sac results in the complete disappearance of the nucellus. Then, as the flower expands, the ovule increases in size by divisions within the integuments, accompanied by the continued enlargement of the embryo sac, which at this stage attacks the tissue of the inner integument, throwing out haustorial folds (Text-figures 2, 3). The resorption of the inner integument covers a considerable period of time, as the tissue being invaded is constantly dividing. In fact, the ovule increases to approximately four times its size at anthesis before resorption is complete (compare Text-figures 2, 7). This resorption is greatest at the chalazal end of the embryo sac, where the larger haustorial folds enter the integumental tissue (Text-figures 2, 4, 5). The resorption of the cells by one of these folds of the embryo sac is shown in Text-figure 6.

Towards the micropyle the resorption is slower and it is there that the most actively meristematic cells of the inner integument are found. Thus by their division they maintain, for a period, a considerable width of this integument in the micropylar region, and are last to disappear under the haustorial action of the embryo sac (Text-figure 7).

During this development the different staining properties of the inner and outer integuments become very marked. The inner integument stains more lightly than previously with basic dyes such as aniline blue, while the outer integument which has become densely packed with tannin and food material, strongly holds any dye into which it is placed.

In Karsten's account, no description is given of the appearance of the two integuments or of their development as the embryo sac enlarges, although these features might be shown in his text-figures, which were not available to the writer. He simply states that the inner integument undergoes resorption while eventually only a few cells remain at the micropylar end.

Meanwhile, within the embryo sac, the female gametophyte has been differentiated. Karsten records that the first division of the embryo sac nucleus occurs after the resorption of the nucellus. Two pear-shaped synergids lie at the

micropylar end of the embryo sac (Text-figure 4, S) close to the egg (Text-figure 3, G). Towards the middle of the embryo sac is the endosperm nucleus (Text-figure 5, M). The antipodal cells, Karsten states, are not visible in the growing embryo sac, and this has been confirmed by the present investigation.

In the embryo sac of the young flower a few granules are scattered evenly throughout the cytoplasm (Text-figures 3, 4, N). These granules, which may be of a nutritive nature, gradually decrease in size as they increase in number with the enlargement of the embryo sac (Text-figure 6, N).

Fertilization.

Actual fertilization has not been observed by the writer, but Text-figure 7 shows what are apparently the remains of pollen tubes passing through the inner integument. This fact was also recorded by Karsten, so fertilization must occur at a stage between those shown in Text-figures 5 and 7.

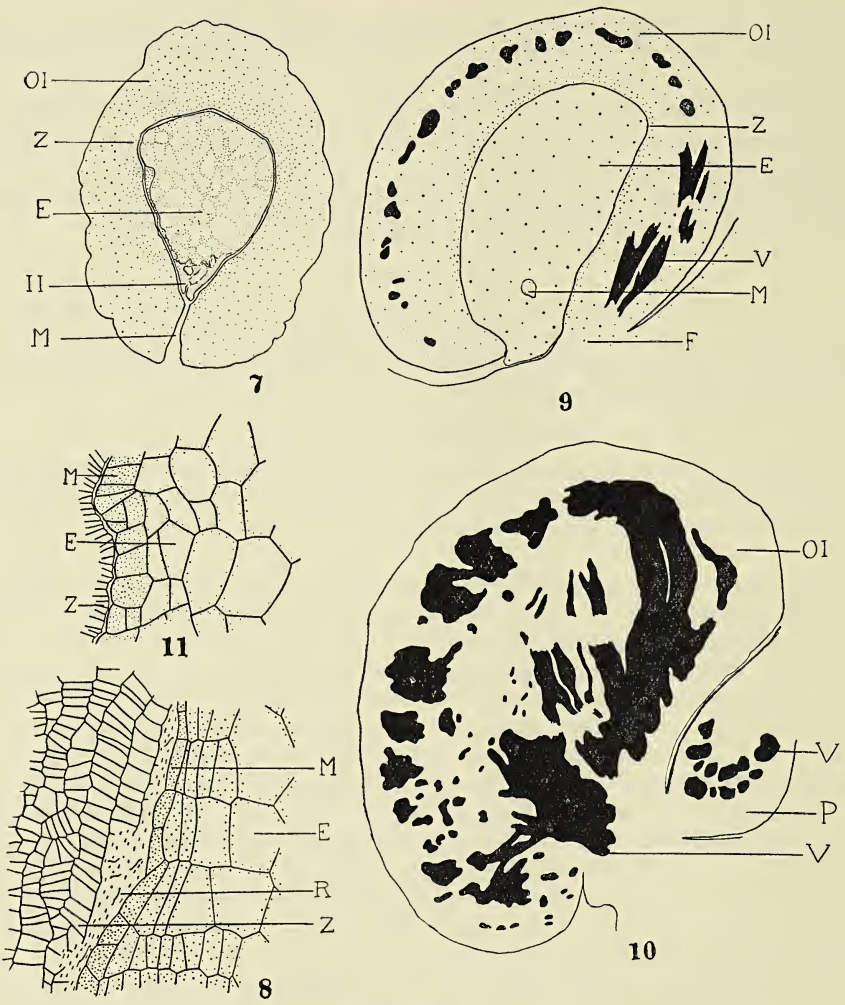
Post-fertilization Development.

All four ovules may develop to fertilization, but after that, one gradually becomes dominant, causing the abortion of the other three. The petals and stamens fall away, leaving the enlarging ovary surrounded by the persistent calyx.

After fertilization the remnants of the inner integument are resorbed and cell wall formation occurs in the embryo sac (Text-figure 8, E). The cells so formed evidently arise first at the periphery and then in radiating series towards the centre, forming an endosperm of large thin-walled cells. The peripheral layer of this endosperm lying next the integument is clearly differentiated from the rest of the endospermic tissue by the densely protoplasmic nature of its cells, as well as by their smaller size (Text-figure 8, M). This layer, which was noted by Haberlandt in the older stages of the seed and compared by him with the 'epithelial' layer of grass embryos, is a meristematic one. It extends right round the endosperm and for a time its cells divide equally, but later the divisions in the micropylar region become the more rapid, resulting in the passage of the endosperm into the loculus. The cells throughout the endosperm are densely packed with food material similar to that which is found in great quantities in the integumental cells.

The endosperm is surrounded by the integument in which differentiation has occurred. Just previous to the formation of the endosperm, indications of two distinct zones become evident (Text-figure 7, Z and OI). These gradually become more distinct as the fertilized ovule enlarges (Text-figure 9, Z and OI). In the larger and outer zone (OI) is an extensive development of vascular tissue, shown in Text-figures 9, 10 (V). These conducting strands lie in a ground tissue of small parenchymatous cells, forming a zone which expands slowly and gives rigidity to the developing seed. Throughout its development it remains free from the invasion by the endosperm.

Inside this zone lies a narrower one (Text-figure 9, Z), extending right round the inner limit of the integument, except in the region of the micropyle. This zone is formed of cells arranged in several rows parallel to the circumference of the endosperm against which they abut. The junction between these two tissues is marked by slight irregularities due to the absorption of the integumental cells. This zone divides radially at a rate rather quicker than that at which the endosperm is resorbing it, so, for a time, it increases in width radially.



Text-figs. 7-11.

7.—A tangential section of an ovule showing the last remnants of the inner integument. OI, outer integument; Z, inner zone of the integument; II, inner integument; E, embryo sac; M, micropyle (× 23).

8.—A portion of a developing seed showing the endosperm. R, resorbed tissue of the outer integument; E, endosperm; Z, inner zone of the outer integument; M, meristematic zone of the endosperm (× 208).

9.—Diagram of a longitudinal section of a developing seed of *Rhizophora mucronata* in which the endosperm has developed for some time. This section passes through the outer edge of the micropyle, but not through the slit in the integument. Z, inner zone of the integument; OI, outer integument; V, vascular supply; E, endosperm; F, edge of the funicle; M, embryo (× 11·5).

10.—A tangential section through the integument of an enlarging seed of *Rhizophora mucronata,* showing the extensive development of vascular tissue. OI, outer integument; P, placenta; V, vascular tissue (× 11·5).

11.—A detailed study of a portion of a seed such as that shown in Text-figure 9. Z, inner zone of the outer integument; M, meristematic layer of the endosperm; E, endosperm (× 208).

Judging by the staining properties of these cells, enzymes do not penetrate more than two or three cell layers of the outer integument. However, the most rapid divisions occur parallel to the long axes of the cells. These take place with such rapidity that the rows of cells, instead of being quite vertical, become slightly folded so that the endosperm which lies in intimate contact seems to penetrate this food-packed area in gentle undulations (Text-figure 11).

One of the striking characteristics of the whole integument is the smallness of its cells, which are only a little larger than those in the ovule of the open flower. The size of the cells, combined with the very abundant food supplies which they hold, may account for the greater resistance of this outer integument to the endosperm.

The enlargement of the integument carries that part of the developing seed opposite the funicle well beyond the micropyle, which then appears to be eccentrically placed (Text-figure 12). However, all the cells in this part of the integument do not divide at an even rate and, by their differential growth, the integument is divided in the micropylar region into two equal lobes. These lobes are separated by a slit (D) running from the outer edge of the integument into the micropyle (M). The base of this slit is oblique, as it is much deeper at the micropylar than at the outer edge.

The micropyle itself, which was originally tubular, is now but a circular aperture at which the edge of the endosperm can be seen (Text-figures 9, 12, M). As the developing ovule enlarges, the micropyle gapes widely (M) and the slit in the integument (D) gradually opens (Text-figures 13, 14), till an almost circular aperture of considerable size is formed, through which the broad face of the endosperm advances. This expansion is purely mechanical, occurring as a result of the force exerted on the outer zone of the integument by the rapid divisions in the inner zone. This view with regard to the opening of the micropyle is contrary to the view expressed by Karsten, who definitely states that it is not due to the growth of the integument but is governed by the pressure of the embryo. "Das wirkliche Auseinanderdrängen der Mikropyle glaube ich in allen Fällen dem Keimlinge selbst zuschreiben zu müssen, soweit es sich nicht um actives Wachsthum des Integumentes handelt."

The embryo, which till now has been ignored in this discussion, is well differentiated before the endosperm emerges from the seed. The youngest embryo in the material at the writer's disposal was found in the endosperm at the micropylar end of a seed 0·4 cm. in length (Text-figure 9, M). It consists of an undifferentiated mass of embryonal tissue (Text-figure 15, E), attached by a massive suspensor (S) to the surrounding nutritive endosperm. This suspensor differs from that of *Rhizophora Mangle*, which Cooke (1907) describes as a linear series of cells. The embryo grows as the endosperm enlarges so that, by the time the seed is one centimetre in length, it can be clearly discerned with the naked eye (Text-figure 16, E). There are two cotyledons, which are fused throughout the greater part of their length, while the free tips are closely appressed to one another.

The endosperm, by the division of the outermost layer of its cells, now emerges through the micropylar opening into the loculus of the ovary. It endeavours to penetrate the ovary wall. However, this action is slow compared with the rate of increase of the endosperm, so as a result this tissue spreads out in the chamber of the loculus and falls back over the integument of the

seed. In extreme cases the endosperm seems to cover the integument almost entirely.

Development of the Ovary.

By enzyme action the advancing face of the endosperm invades the ovary wall which has been undergoing change to accommodate the enlarging fertilized ovule. In order to understand the structure of the ovary wall at this stage, it will be necessary to return to the ovary as it is in the flower and trace the changes which occur in its tissues till the time now under discussion.

In the flower, as the ovules enlarge the young ovary expands differentially, the greatest development being in that region of the ovary wall lying between the base of the style and the loculus (X in Text-figure 1). The remainder of the ovary wall just keeps pace with the growth of the contained ovules and, after fertilization, with that of the dominant fertilized ovule, which crushes to one side the second loculus of the ovary in which the other ovules have aborted. During this growth the divisions of the placenta lag behind those of the growing seed (Text-figure 16, P). Thus the placenta, as the seed enlarges, becomes tightly drawn against it, causing a deeper and deeper depression in the integument (Text-figures 13, 14, C, 25, D).

The most remarkable expansion, as mentioned above, is in that part of the ovary wall at the base of the style. In this region of the flower the parenchymatous cells are arranged in more or less vertical rows, among which extend the vascular strands connecting with the apex of the style. As the flower ages and the petals fall, these parenchymatous cells divide with increasing rapidity till this zone becomes an extensive conical mass of tissue (Text-figure 16, X), at whose apex can be seen the two fused styles (Text-figure 16, S) surmounted by the bifid stigma. An examination of the tissues of this cone shows that there is a central area (Text-figure 16, A) cut off from the rest of the wall by vascular strands (V), as in the young flower (Text-figure 1). The cells of this central area do not divide with the same rapidity as those towards the periphery of the cone, and so early lose their regular arrangement and show indications of maturation. This is indicated by the more rapid enlargement of the cells and the increase in thickness of their walls.

When the endosperm emerges into the loculus of the ovary a further change occurs in this median region of the cone. The intercellular spaces between those cells bordering the loculus enlarge and, as they continue to expand, those spaces lying more deeply in the tissue also become larger. Thus is formed an aerenchyma, into which the endosperm advances (Text-figure 16, A). As the ovary as a whole continues to expand, the aerenchyma penetrates further and further into this median region of the cone in the direction of the style.

Outside this median region, the parenchymatous cells, rich in tannin, retain their regular arrangement as they divide actively. Branched sclereids and 'stone' cells are differentiated, especially in the hypodermal region, while the vascular

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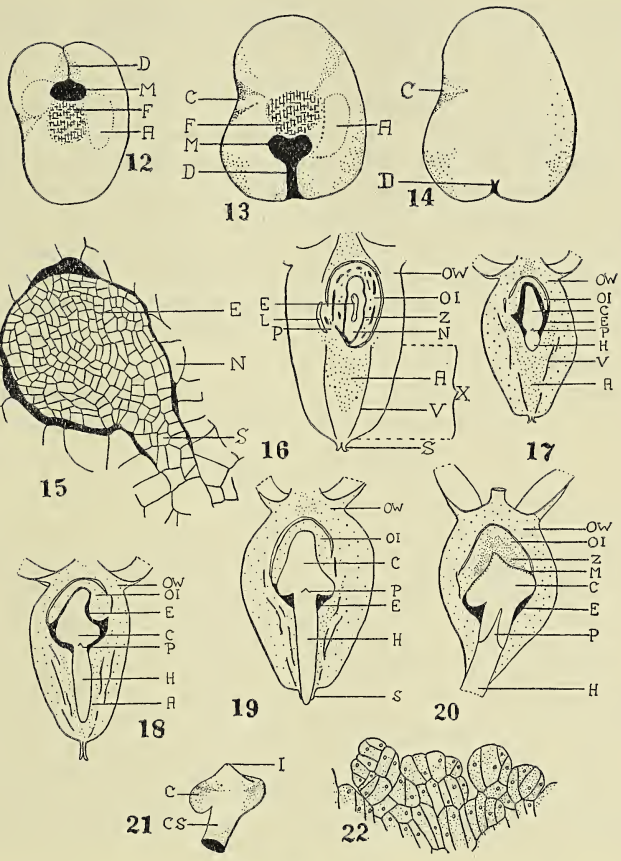
20.—A longitudinal section of a fruit of *Rhizophora mucronata* in which there has been an abnormal development of the inner zone of the integument. OW, ovary wall; OI, outer integument; Z, inner zone of the outer integument; M, meristematic zone of the cotyledons; E, endosperm; P, plumule; H, hypocotyl; C, cotyledons (× 0·8).

21.—The cotyledons removed from the fruit shown in Text-figure 20. C, head of the cotyledons; CS, cotyledonary sheath; I, indentation between the two cotyledons (× 0·8).

22.—A portion of the surface of a cotyledonary head showing the papillae (× 208).



Text-figs. 12-22.

12.—A developing seed prior to the emergence of the endosperm from the micropyle. F, funicle; A, position of contact of the aborted ovules; M, micropyle at which the face of the endosperm can be seen; D, slit in the integument (× 5).

13.—A developing seed of *Rhizophora mucronata* in which the endosperm is beginning to emerge. F, funicle; A, position of contact of aborted ovules; M, micropyle; D, widening slit in the integument; C, constriction caused by the placenta (× 4·5).

14.—The other side of the seed represented in Text-figure 13. D, the limit of the depression in the integument; C, constriction caused by the placenta (× 4·5).

15.—An embryo of a seed of *Rhizophora mucronata* such as is seen in Text-figure 9. N, endosperm; S, suspensor; E, meristematic cells of the embryo (× 112).

16.—A fruit of *Rhizophora mucronata* in which the endosperm is passing through the enlarged micropylar opening of the seed. OW, ovary wall; OI, outer integument; E, embryo; L, aborted loculus; P, placenta; N, endosperm; Z, inner zone of the outer integument; A, median region of the ovary wall; V, vascular strands; S, fused styles (× 5·5).

17.—An older fruit of *Rhizophora mucronata* showing the development of the embryo. OW, ovary wall; OI, outer integument; E, endosperm; C, cotyledons; P, plumule; H, hypocotyl; A, aerenchyma; V, vascular strands (× 0·8).

18.—An older fruit than that shown in Text-figure 17. OW, ovary wall; OI, outer integument; E, endosperm; C, cotyledons; P, plumule; H, hypocotyl; A, aerenchyma (× 0·8).

19.—A fruit from which the hypocotyl is emerging. OW, ovary wall; OI, outer integument; E, endosperm; C, cotyledons; P, plumule; H, hypocotyl; S, style (× 0·8).

strands increase in size and number. Thus this outer region is gradually modified so that later it is able to support the weight of the large embryo.

Development of the Embryo.

The invasion of the aerenchyma of the ovary wall by the endosperm causes a lysis of the invaded tissue, so that a fluid may actually lie between the advancing endosperm and the unaltered cells. Meanwhile the embryo retained within the developing seed shows an extensive growth of the cotyledons (C) which, by their enlargement, eventually push the hypocotyl (H) through the micropyle into the ovary wall (Text-figure 17). Then the hypocotyl, by its own elongation, passes through the enveloping endosperm into the aerenchyma of the ovary wall, which now occupies all the median region of the cone. The endosperm thus remains as a collar around the cotyledonary part of the embryo as noted by Haberlandt (1895).

The hypocotyl elongates into the aerenchyma by the resorption of the cells in advance of it (Text-figure 18). These cells are more or less uniform in size, but there is an increasing tendency for their elongation in a vertical direction. This is due to pressure exerted by the continued divisions of the cells outside this zone and by the enlargement of the seed.

This growth of the hypocotyl is accompanied by a slower but continued enlargement of the cotyledonary head at the expense of the endosperm (Text-figure 18, C). It will be noted that the growth of the cotyledonary head is differential, being governed by the nature of the surrounding cells. Where the advance is made into large thin-walled endospermic cells outside the micropyle, the greatest expansion of the head occurs. Inside the integument, the cells of the inner zone of that tissue, by the rate of their division, govern the degree of expansion of the head. In Text-figure 20 there has been an abnormal development of this inner zone (Z), so that the apex of the cotyledonary head is conical (Text-figure 21) instead of its usual shape. In such a cotyledonary head a minute depression at the apex marks the division between the two fused cotyledons.

The cotyledonary head when fully formed resembles a "Phrygian cap" (Karsten, 1891), and occupies the whole of the integument except for a single layer of endosperm. It conceals the plumule (P) at its base (Text-figure 19). By the time the cotyledonary head has so developed, the hypocotyl has pierced the ovary wall, by forcing its way between the two fused styles where the vascular strands converge (Text-figure 19, S). The pressure and resultant injury caused by this action are felt by a cap of loose spongy tissue which covers the meristem at the end of the hypocotyl. The elongation of the hypocotyl is accompanied by an increase in girth of that organ, which continues to maturity (Plate xv, fig. 1, A). Thus the aperture through which it emerged from the fruit is gradually widened by growth pressure.

The final stage in the development of the embryo is the elongation of the cotyledonary sheath (CS, Text-figure 24), in response to the plumule within it. The base of this sheath eventually passes through the aperture of the fruit (Plate xv, fig. 1, B) so that later the concealed plumule and hypocotyl can drop freely to the mud.

These phases in the growth of the embryo were outlined by Karsten, but no account is given by him of the cell structure of the ovary wall and the endosperm.

Structure of Mature Ovary Wall.

The now massive embryo is held in position by the extremely rigid wall of the fruit. At the periphery there is a zone of compact tannin-filled cells among which 'stone' cells and sclereids occur (especially the former). This grades into a spongy tissue, in which the spaces between the elongated parenchymatous cells are large. In spite of this, however, the area is rigid owing to the presence of many branched sclereids which project into these air spaces. The nearer the centre of the ovary wall the larger the spaces become and the greater the signs of pressure shown by the cells. Those few cells which yet remain of the original aerenchymatous zone of the wall show a pronounced elongation in a vertical direction, the air spaces between them being long and narrow. During this elongation some of the cells lose their rectangular form and taper almost to a point at one end while retaining their original width at the other. They contain an abundance of tannin and greater quantities of calcium oxalate than previously. It seems significant that the extension of the air space system of the ovary wall should continue as the embryo grows.

Nutrition of the Embryo.

The embryo, when it is initiated, receives its nutriment from the endosperm, which at that time is rapidly extending under the action of its peripheral meristematic layer. There is an intimate junction along an irregularly undulating line between this layer (M) and the integument (Z) (Text-figure 11). During and after the passage of the endosperm through the micropyle the embryo grows at its expense. As the cotyledons become larger and larger the endosperm within the integument seems gradually to lose its meristematic properties. The line of junction between the endosperm and the integument gradually straightens out and eventually the peripheral layer, which has ceased to divide, alone remains unresorbed. Its cells enlarge and form a sharply defined layer between the cotyledons and the integument (Text-figure 23, E). This is the layer which was noted by Haberlandt and compared by him, with regard to its appearance, with the epithelium of the embryos of grasses. This layer, the last remnant of the endosperm, has by now also lost its power to secrete enzymes for the digestion of the foods in the integument, so we find Haberlandt recording his failure to detect any secretion by this layer at all. But, failing to realize its endospermic nature, he wrote as follows: "Das Endosperm umhüllt nicht nur den in der Samenschale steckenden, kegelförmigen Theil des Cotyledonarkörpers sondern legt sich in Gestalt eines breiten Kragens auch an den Wulst und an den obersten Theil der Cotyledonarscheide an. Gegen die Samen-resp. Fruchtschale grenzt sich das Endosperm ringsum *ganz glatt* mit einer Zellschicht ab welche durch die Form ihrer Zellen, den reichen plasmatischen Inhalt und die Beschaffenheit ihrer verdickten Zellwände lebhaft an die 'Kleberschicht' des Gramineen-Endosperms zur Zeit der Keimung erinnert." This layer is, however, endospermic, but in the later stages of the development of the embryo its haustorial function is passed over to the cotyledons themselves.

The expansion of the cotyledons within the integument takes place by the division of a comparatively wide peripheral zone of densely protoplasmic cells. It becomes increasingly obvious that the divisions in these cells do not occur at an even rate. As a result the surface becomes uneven and appears to be 'warted' and papillate (Text-figure 22), as noted by Haberlandt. He found that these cells actively secrete enzymes, and there is no doubt that in the older

embryos the function of obtaining food is passed from the endosperm, which is almost digested, to the cells of the cotyledons. But Haberlandt, with access to old embryos only, implies that the cotyledons alone are responsible throughout the life of the embryo. ("Die oberste Lage ist mit äusserst zahlreichen, ein-bis mehrzelligen Papillen und Wärzchen versehen, welche die absorbirende Oberfläche bedeutend vergrössern und die eigentlichen Saugorgane, die Haustorien des Keimlings verstellen.")

A section of an old seed (Text-figure 23) shows that the papillae of the cotyledons (C) do not lie in intimate contact with the single layer of the endosperm (E), but are separated from it by a nutritive fluid in which indistinguishable remnants of digested endospermic cells (R) may be seen. The endospermic layer lies close to what remains of the inner zone (Z) of the integument. The divisions of the cells of this zone have not kept pace with their resorption by the cotyledons, and therefore the width of the zone has been reduced to two or, in places, three cell layers. Behind this zone lie the mature cells of the rest of the integument, through which pass the conducting strands. Thus the embryo is nearer the source of food supply at maturity than at any other time.

The growth of the large cotyledonary head exerts a definite pressure on the integument. This is shown by the cells of the inner zone, whose long axes become obliquely directed towards the embryo, instead of remaining at right angles to it, as they originally were.

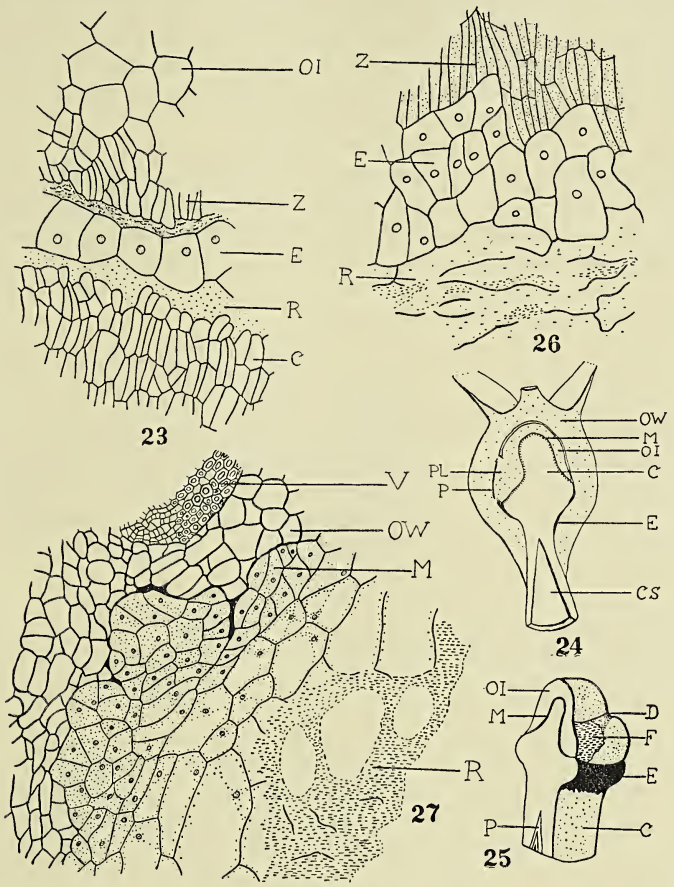
Outside the seed, food is obtained from the ovary wall. This is passed to the embryo by the cells of the endospermic collar (E), which surround first the hypocotyl (H) and later the cotyledonary sheath (CS) (Text-figures 19, 24, 25). Haberlandt (1895) records that the endosperm merely lies in intimate contact with the ovary wall, but the present investigations show that shallow haustorial folds are formed. They are certainly not deep, not to be compared with those which occur, for example, in *Aegiceras majus*, but nevertheless seem to be quite definite. The divisions of the endosperm outside the seed are so rapid that several layers of equally dense cells are found at the periphery; thus the identity of the single meristematic layer is lost. These divisions result in the formation of haustorial folds at intervals right round the endospermic collar. Some longitudinal sections fail to show their presence, while in others they are quite distinct. The first indication of their formation is seen in a fruit in which the hypocotyl is elongating rapidly through the ovary wall (Text-figure 18). Their development continues as the embryo ages till by resorption they (M) come into close proximity to the vascular strands (V) of the ovary wall (Text-figure 27).

These folds are very shallow, due possibly to the degree of compactness of the cells invaded and the degree of concentration of food within them. Rather deeper folds were found in a fruit in which there had been an abnormal development of the inner zone of the integument (Text-figure 20). In that case, owing to the abnormality, folds were found penetrating the integument in the region of the micropyle as well as the ovary wall. An examination of Text-figure 26 shows that in the micropylar region (Z) the folds were deeper and narrower.

In the endospermic collar there is a gradual transition, as one would expect, from the actively dividing cells to those which are being resorbed in the vicinity of the embryo. The latter are large, with little cytoplasm, and stain but faintly

with dyes (Text-figure 27). These are the 'bladdery' cells whose function Haberlandt suggests may be that of a water reservoir.

Thus in the nutrition of the large embryo, both the endosperm and the papillae of its cotyledons play a part.



Text-figs. 23-27.

23.—A detailed examination of a portion of an almost mature fruit. OI, outer integument; Z, inner zone of the integument; E, endosperm; R, resorbed endosperm; C, meristematic zone of the cotyledons (× 208).

24.—A fully mature fruit of *Rhizophora mucronata*. OW, ovary; OI, outer integument; C, cotyledons; M, meristematic zone of the cotyledons; PL, placenta and funicle; P, aborted loculus; CS, cotyledonary sheath to the plumule; E, endosperm (× 0·8).

25.—The seed and upper part of the embryo removed from a fruit such as that of Text-figure 24. OI, outer integument; M, meristematic zone of the cotyledons; F, funicle; D, depression in the seed left by the tightly drawn placenta which has been removed; E, last remnants of the endosperm; C, cotyledons; P, plumule (× 1·2).

26.—A detailed study of those tissues which surround the cotyledonary head at the micropylar end of the mature seed of Text-figure 20. Z, inner zone of the outer integument; E, last remnants of the endosperm; R, resorbed endosperm (× 208).

27.—A detailed study of the tissues outside the integument in a mature fruit. OW, ovary wall; V, vascular tissue of the ovary wall; M, meristematic zone of the endosperm; R, resorbed endosperm lying next to the cotyledonary sheath (× 112).

Mature Embryo.

The extraordinary size of the mature embryos of this genus is so well known as not to require any further mention (Plate xv, fig. 2, A). The vascular strands of the cotyledonary sheath snap and the plumule and hypocotyl fall to the ground (Plate xv, fig. 2, B). The hypocotyl is rigid enough to penetrate the mud (Kerner, 1894), in spite of the presence of aerenchyma, because of the development of a multitude of branched sclereids. The structures concerned in the aeration of this massive hypocotyl are discussed by Madeline Carson (1907).

Stored Foods.

In this discussion no mention has been made of the nature of the food concerned in the nutrition of the embryo. Throughout the development from the ovule in the flower to the shedding of the embryo from the fruit, the content of all parenchymatous cells of the integument stain very deeply with dyes. This is true to a less extent of many of the cells of the ovary wall and also of the embryo as it builds up its own food supply.

Microchemical tests (Haas and Hill, 1928) show the presence of great quantities of starch in the hypocotyl of the mature embryo. The abundant general occurrence of tannin is evident especially in the integument, placenta and cotyledons. The rôle played by tannin in the physiology of the mangroves is still a matter of dispute. Various hypotheses have been advanced (Bowman, 1917), but none of them are entirely satisfactory. It is thought that proteinaceous foods may be present also, their reaction masked by the presence of tannin. Bowman (1917) records dextrose in the seedlings of *Rhizophora Mangle.*

Ceriops Candolleana Arn.

The developmental stages of *Ceriops Candolleana*, from the opening of the flower bud to the shedding of the embryo, are essentially the same as those seen in *Rhizophora mucronata.* However, there are minor differences which make a comparison interesting.

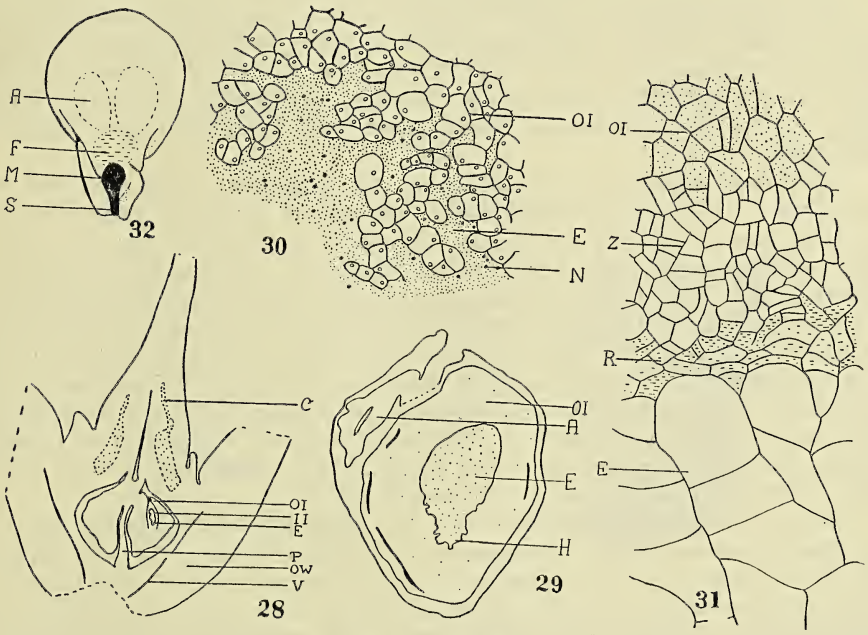
The general features of the flower are as well known as those of *Rhizophora*, and therefore require no further comment. However, it must be remembered throughout the discussion that the flower, and consequently the embryo arising from it, is much smaller than that of the genus already described. Karsten takes *Ceriops Candolleana* as his type genus with which he contrasts *Rhizophora.* His description of *Ceriops*, however, is no fuller than his account of *Rhizophora* already discussed.

The Gynoecium.

The wall of the ovary is composed of parenchymatous cells, among which 'stone' cells and sclereids are not developed. Another result of the smaller size of the flower is the absence of aerenchyma. This type of tissue does appear later, however, in association with the developing embryo. The parenchymatous tannin-filled cells of the ovary gradually merge into those of the style. These cells contrast sharply with a zone of clear cells lying beneath the hypodermis. This zone extends in the direction of the style, from an area in the ovary wall just above the loculus. At its upper end it is only one cell wide (Text-figure 28, C). On the inside of this zone lie the vascular strands. These enclose parenchymatous cells, also vertically arranged, but smaller in size than those nearer the periphery.

Development of the Ovule.

The ovary is trilocular or bilocular, each chamber holding two anatropous ovules. The structure and early development of each ovule is similar to that of *Rhizophora mucronata.* However, the inner integument does not appear to have retained its meristematic properties to the same extent and its rectangular cells stain but lightly with dyes such as aniline blue. The outline of the ovule is sinuous through the irregular growth of the cells of the outer integument, the greatest development taking place in the chalazal region, so that the embryo sac (E) seems to be placed well forward at the micropylar end of the ovule (Text-figure 28). The cellulose walls of the outer integumental cells are comparatively thicker than those in *Rhizophora.* The whole of this tissue, particularly the peripheral layers, stains deeply with dyes owing to the accumulation of tannin and foods in the cells. Thus the outer integument stands out sharply from the inner. Definite spiral thickenings are initiated in the vascular



Text-figs. 28-32.

28.—A longitudinal section of the ovary of an open flower of *Ceriops Candolleana.* OW, ovary wall; P, placenta; V, vascular tissue; OI, outer integument of the ovule; II, inner integument; E, embryo sac (× 11·5).

29.—A longitudinal section of an ovule of *Ceriops Candolleana* in which the embryo sac is enlarging. E, embryo sac; H, haustorial region of the embryo sac; OI, outer integument; A, aborted ovule (× 23).

30.—A detailed study of the haustorial region of the embryo sac shown in Text-figure 29. OI, outer integument; E, embryo sac; N, deeply staining granules (× 208).

31.—A detailed study of part of a seed in which the endosperm has been formed. OI. outer integument; Z, inner zone of the outer integument; R, resorbed tissue of the integument; E, endosperm (× 208).

32.—A seed of *Ceriops Candolleana* in which the endosperm is emerging through the micropylar opening. F, funicle; M, micropyle; S, slit in the integument; A, position of contact of aborted ovules (× 7).

zone, which extends right round the integument as in the ovule of *Rhizophora mucronata.*

After the resorption of the inner integument at the chalazal end of the ovule, the embryo sac (E), as it enlarges, develops haustorial projections (H) into the outer integument (Text-figure 29). Thus the embryo sac makes the greatest advance into that region of the integument which has shown the most extensive development. In Text-figure 30 the intrusion of the embryo sac (E) into the integument (OI) is shown in detail, also the deeply staining granules (N) which lie throughout the sac tending, at the periphery, to aggregate in groups.

By this time some of the ovules are aborted and eventually all are pushed to one side by the most vigorous, which occupies then all the space of the loculus. It is evident that the tissue of the ovary does not expand quickly enough to allow the development of more than one ovule from this stage onwards.

Post-fertilization Development.

When the ovule has enlarged to approximately three times its original size, it is fertilized and an endospermic tissue of large thin-walled cells is formed radiating out from the centre of the embryo sac. There is a gradual transition from those cells at the centre to the peripheral ones which are dividing. Thus there is no sharp definition of meristematic tissue as there is in *Rhizophora mucronata.*

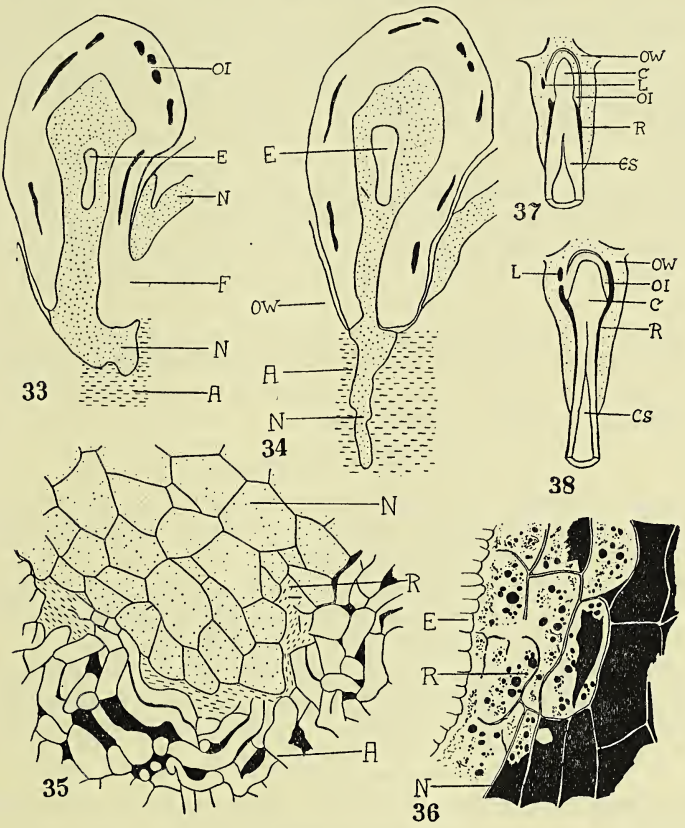
With the formation of the endosperm the integument is differentiated into two zones. The outer and larger zone, although not nearly as massive as that in *Rhizophora mucronata,* develops a comparatively extensive vascular system. The parenchymatous cells among these strands are rich in tannin and food material. The inner zone is comparatively narrow and composed of cells rather irregularly arranged (Text-figure 31, Z; cf. *Rhizophora mucronata*), but dividing at a rate equal to that of the intrusion of the endosperm (E) into them, so that this zone maintains a fairly constant diameter. The rate of resorption of the integument at first seems to be greatest at the chalazal end of the developing seed, where there may be quite a wide band filled with disintegration products between the endosperm and the tissue being invaded. Elsewhere the two tissues (Z and E) lie in direct contact (Text-figure 31).

As the integument increases in size the micropyle becomes longer but does not lose its tubular form. This passage is widened, however, by the divisions in the inner zone of the integument. This widening must be mechanical, as there is no evidence of haustorial action on the part of the endosperm as it passes down it. By the differential growth of the integument at the lower end of the micropyle a slit is formed as in *Rhizophora mucronata.* This slit (S) expands with the tubular micropyle (M) (Text-figure 32), till an aperture of considerable size is formed, through which the endosperm emerges. As it passes out into the loculus it increases in extent so rapidly that it folds back over the seed, sometimes completely enveloping the latter. At the same time its folds (N) enter the median region of the ovary wall (A) (Text-figures 33, 34) and to some extent the placenta in the funicular region (F).

Development of the Ovary Wall.

During this development changes have taken place in the ovary wall resulting in the formation of a cone of tissue between the loculus and the base of the style as in *Rhizophora mucronata.* This cone shows the same features as that of

Rhizophora, except for the lack of an extensive development of strengthening tissue. Thus in the median region an aerenchyma is formed, whose cells have lost their uniformity through strains put upon them as they matured, by the continued growth of the peripheral tissues. The advance of the face of the endosperm (N) into this tissue is shown in Text-figure 35.



Text-figs. 33-38.

33.—A longitudinal section through a seed of *Ceriops Candolleana* from which the endosperm is penetrating the ovary wall. OI, outer integument; E, embryo; N, endosperm; F, funicle; A, median region of the ovary wall which is aerenchymatous (× 11·5).

34.—A tangential section of a seed such as that shown in Text-figure 33. N, endosperm; E, embryo; OW, ovary wall; A, aerenchyma (× 11·5).

35.—A detailed study of the advancing face of the endosperm shown in Text-figure 33. N, endosperm; R, resorbed tissue of the ovary wall; A, aerenchyma (× 112).

36.—Endosperm in contact with the growing embryo as shown in Text-figure 33. E, embryo; R, endosperm being resorbed; N, endosperm (× 112).

37.—A mature fruit of *Ceriops Candolleana*. OW, ovary wall; OI, outer integument; C, cotyledonary head; L, aborted loculus filled with endosperm; R, remnants of endosperm and resorbed tissue of the ovary wall; CS, cotyledonary sheath (× 1·2).

38.—A very large mature fruit of *Ceriops Candolleana* showing a tendency towards lateral expansion of the cotyledonary head. OW, ovary wall; OI, outer integument; C, cotyledonary head; CS, cotyledonary sheath; L, aborted loculus filled with endosperm; R, resorbed tissue of the ovary wall and remnants of endosperm (× 1·2).

Development of the Embryo.

While the advance is made by the endosperm, growth of the embryo progresses as in *Rhizophora mucronata*. Around the embryo (E) is a resorption zone (R) in which food supplies are gradually exhausted (Text-figure 36). The food material in the endosperm (N) is undoubtedly the same as that in the integument, for the cells of both tissues give the same reaction to dyes. In fact, the only distinction between the two lies in the extreme difference in size of their cells.

This embryo differs from that of *Rhizophora mucronata* in one feature only, namely the shape of the cotyledonary head. In *Ceriops Candolleana* this head is in most cases cylindrical at maturity (Text-figure 37, C). In a few of the larger fruits a slight lateral expansion corresponding to the extensive lateral growth of the cotyledonary head in *Rhizophora* is shown (Text-figure 38, C). In *Rhizophora mucronata* the lateral expansion of the head resting against the ovary wall holds the heavy embryo firmly (Text-figure 24). In *Ceriops Candolleana*, however, there is generally no such support, and although irregularities developed on the surface of the hypocotyl may be of some aid, the embryo is readily dislodged.

The hypocotyl, which attained a length of approximately 11 cm. in the material available, is strengthened by an extensive development of collenchyma beneath the epidermis. The lumina of the epidermal cells are very much reduced and the whole is covered by a thick cuticle.

Nutrition of the Embryo.

Inside the integument the embryo is nourished by the aid of, first, the endosperm and, later, the papillae which are formed over the surface of the cotyledonary head as in *Rhizophora mucronata*.

Outside the seed, the endosperm undoubtedly obtains food from the wall of the ovary and placenta, although it does not produce haustorial processes into any region. It merely lies in contact with the food-bearing areas.

The writer wishes to express her sincerest thanks to Professor Osborn, University of Sydney, for suggestions and kindly criticism throughout the course of the work, and to Mr. R. E. Vallis for the collection of material.

Summary.

1. The young ovule of *Rhizophora mucronata* consists of two massive integuments surrounding a nucellus and an embryo sac.

2. Before the bud opens the embryo sac resorbs the nucellus. It then, by intrusive folds, invades the inner integument, which increases in size in spite of this invasion.

3. Within the embryo sac lie the synergids, the egg nucleus and the endosperm nucleus. No antipodal cells are seen. Numerous deeply staining granules are found in the cytoplasm.

4. By the time the ovule has increased to approximately four times its original size the inner integument has been completely resorbed and fertilization has occurred. An endospermic tissue is then laid down in the embryo sac.

5. The outer integument is differentiated into two zones, an outer which contains the extensive vascular supply, and an inner in which the cells are regularly arranged and meristematic.

6. The endosperm expands by the division of a peripheral layer of comparatively small densely protoplasmic cells. The identity of this single meristematic

layer is lost, at the micropylar end of the endosperm, owing to the rapidity of its divisions as it advances into the loculus of the ovary.

7. The micropyle is at this period an aperture of considerable size owing to the pressure exerted on it and the adjoining slit in the integument by the dividing cells of the inner zone of the integument.

8. The advance of the endosperm is more rapid than its penetration into the ovary wall, so it falls back over the integument of the developing seed.

9. The embryo is well differentiated even before the endosperm leaves the micropyle. It was seen first as an undifferentiated mass of tissue attached by a suspensor to the endosperm. Later, two almost wholly fused cotyledons and a hypocotyl are differentiated.

10. During this development changes have occurred in the ovary wall, giving rise to an extensive cone of tissue between the loculus and the base of the style. Into the aerenchymatous median region of this cone the endosperm advances.

11. It is soon overtaken by the hypocotyl which is being forced downward by the growth of the cotyledons, which can no longer be wholly retained within the integument. The further advance of the hypocotyl is made by its own elongation, through the aerenchymatous zone, till it forces its way between the two fused styles.

12. During the elongation of the hypocotyl the cotyledonary head continues its expansion till at maturity it is shaped like a "Phrygian cap". The rate of this expansion is governed by the nature of the surrounding cells.

13. The final stage in the development of the embryo is the elongation of the cotyledonary sheath, which conceals the plumule. This extension continues till the base of the sheath emerges from the fruit.

14. During the development of the embryo, food is obtained inside the developing seed from the integument by the endosperm in the early stages, and later by the papillae and 'warts' of the cotyledons. Outside the seed the endosperm is reduced to a collar, first round the hypocotyl and later around the cotyledonary sheath. This endosperm penetrates the ovary wall by extremely shallow folds, and thus obtains food from it. At maturity the embryo is in close contact with the vascular tissue of both the ovary wall and integument.

15. The tissues of the ovary wall are differentiated so as to support the weight of the extremely large embryo and at the same time supply the oxygen required. When ready for dispersal the vascular strands of the cotyledonary sheath snap and the embryo falls into the mud, leaving the cotyledonary head behind.

16. In general, the development of *Ceriops Candolleana* is similar to that of *Rhizophora mucronata*.

17. The trilocular or bilocular ovary contains two ovules in each loculus. Each has an outer massive integument and a smaller inner integument surrounding a nucellus and an embryo sac.

18. The nucellus and inner integument are soon resorbed and the embryo sac encroaches on the massive outer integument. At the chalazal end, where the integument is widest, haustorial processes are developed.

19. After fertilization an endospermic tissue is formed in the embryo sac. This increases by the division of its cells, but there is no one meristematic layer as there is in *Rhizophora mucronata*.

20. The outer integument is differentiated into two zones, the inner one of which is not as sharply defined as it is in *Rhizophora*, nor are the cells as regularly arranged.

21. The divisions in the inner zone of the integument widen the micropyle but do not alter its tubular form. At the lower end an aperture of considerable size is formed, as the slit in the integument is gradually widened and thus increases the size of the opening. The endosperm without resorption advances down this enlarged passage and enters the loculus of the ovary.

22. The endosperm invades the median region of the enlarged ovary wall as in *Rhizophora mucronata* and also may enter the placenta at the upper end of the funicle.

23. The development of the smaller embryo is similar to that of *Rhizophora mucronata*. Its cotyledonary head is, however, cylindrical in shape.

24. In the nutrition of this smaller embryo endospermic folds are not formed, and for its support less strengthening tissue is differentiated in the ovary wall.

EXPLANATION OF PLATE XV.

Fig. 1.—Developing embryos of *Rhizophora mucronata*. A, a fruit in which the hypocotyl is elongating downward outside the ovary wall; B, a fruit from which the base of the cotyledonary sheath at the top of the hypocotyl has emerged; C, a fruit in which two embryos are maturing (× 0·43).

Fig. 2.—Developing embryos of *Rhizophora mucronata*. A, a mature embryo; B, the embryo released from the fruit; C, the growing embryo (× 0·3).

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AUSTRALIAN HESPERIIDAE. V.

NOTES, AND DESCRIPTION OF A NEW FORM.

By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.

[Read 28th November, 1934.]

This part contains many extensions of the range of species sent me by several collectors since my paper in These Proceedings last year. Brigadier W. H. Evans has also forwarded me notes from England.

Euschemon rafflesia rafflesia Macleay, 1827.

Dr. T. Guthrie has caught this butterfly at Wallis Lake (February) and Smith Lake, near Bungwahl (March), thus extending its southern limit about 70 miles.

Netrocoryne repanda Felder, 1867.

The statement by A. W. Scott (Australian Lepidoptera and their Transformations, ii, 1891, p. 13) that "When but a few days old the infant larva cuts a small and perfectly circular piece, about the size of a pea, from the leaf, and attaches it with silken threads to the upper surface of the same or another leaf, thus forming a secure habitation under which it dwells, and from whence it issues in search of food, by a small aperture at the upper end. As the increasing size of the larva demands more roomy accommodation, larger pieces of the leaf are cut out and similarly attached, the old dwellings being then deserted, and as they soon become brown and shrivelled they impart to the tree in time a somewhat diseased appearance. When almost mature the larva selects a larger leaf, and cutting out a sufficient portion to comfortably cover its body, secures this to a fresh leaf." has always seemed to me far from accurate. The circular piece cut out must weigh about five times the weight of the baby larva, and this piece was never found by me away from the circular hole in the leaf, but always beside it.

Thanks to my young friend, Mr. M. F. Day, who kept careful watch over some eggs at Killara, we were able to watch the whole process, and we found that the newly hatched larva was an expert builder.

Mr. Day had previously found that the larvae emerged from the eggs in the early afternoon. On 11th December, 1932, he telephoned me that a larva had just emerged, and by the time I reached his home another had emerged. The following notes are taken from the actions of these two larvae.

The young larva, without eating the empty eggshell, first sought a suitable position on the leaf about an inch away from the egg. It then spun some silk; around this it began to eat out of the leaf, working on the upper surface, a circle nearly one-third of an inch in diameter. The larva was within the circle and did not swallow the portions of the leaf, but deposited them outside the circle. The leaf was not cut through, the veins not being cut at this stage. After cutting for a few minutes the larva would place some more silk within the circle. Although the order in which the parts of the circle were cut was different in the

two cases observed, at the end of about an hour the result was the same. The cut disc was almost a perfect circle except a small portion of the arc about one-tenth of an inch, which was left uncut. On either side of this uncut portion at the ends of the cut circle a further cut was made at right angles to the circumference, extending both inside and outside. Silk strands were then laid from about the centre of the disc across the uncut part to well outside the disc.

The larva then, carefully working from inside the disc, began to cut away the veins, and when the last vein was cut through the disc suddenly sprang to a position of 30 degrees with the leaf. More silk was then stretched from the disc over the uncut portion to the leaf outside. As the silk dried, the disc gradually rose to the vertical and then downwards on to the leaf, the uncut portion being the hinge. As silk had been placed over the disc, it had become dome-shaped by the silk drying. About two hours were occupied in reaching this stage.

The outside of the dome was the underside of the leaf now lying on the upperside of the leaf. This dome was now sealed down with silk, the larva working inside and cutting the upperside of the leaf to give a firm attachment. About four hours were taken for the larva to construct its home. Later a hole was eaten from the side of the house to allow the larva to come out to feed.

Our experience has been that usually only one disc is cut, within which the larva lives until its house becomes too small for it. In two or three cases, apparently only when its home became damaged, another house was made simply by cutting an irregular piece from the edge of the leaf and turning it over.

On July 21, 1934, we went to Narrabeen and Mr. Day fortunately found a larva just beginning its second and final house. From near the middle of the right hand edge of the leaf a long narrow pad of silk is placed extending in a slanting direction nearly to the midrib. Starting slightly nearer the tip of the leaf than the top of this silk pad, the larva ate a long slanting irregular cut out of the leaf, ending it midway between the bottom of the silk pad and the midrib. This cut was eaten quite through, the portions of the leaf were not all swallowed but placed on one side, nor was the cut made in one operation as the larva moved away to strengthen the silk pad. A little more than an hour was spent in reaching this stage. Then the larva went to the edge of the leaf about opposite the end of the first cut and made another irregular cut towards the midrib, ending below the silk pad. It then put long strands of silk between the ends of the two cuts and the cut portion of the leaf began to rise as the silk dried. The larva then extended the two cuts in the direction of the midrib, but kept them a slight distance apart and placed further silk between them. The portion of the leaf between the cuts acts as the hinge on which the cut part is brought over. After a little more than two hours the cut portion was nearly touching the remainder of the leaf. A stout strand of silk was placed from ceiling to floor to anchor the roof. Later on a further short straight cut was made on the portion of the leaf to the left of the midrib, for the purpose of turning it up for the door of the home, the door always being placed looking towards the stem of the leaf. Many stout strands of silk were placed to anchor the roof to the floor and these were strengthened from day to day. Before eating other leaves that portion of the leaf between the entrance of its house and the attachment of the leaf is eaten first, excepting the midrib, then the larva firmly attaches the stem of the leaf with silk to the branch. Larvae have been watched both on *Callicoma serratifolia* and *Endiandra Sieberi*. Although larvae may begin their cutting on

either side of the midrib, I have found more starting on the right than on the left side.

NOTOCRYPTA WAIGENSIS LEUCOGASTER Staudinger, 1889.

Mr. M. J. Manski found at Cairns a full grown larva in a curled-up leaf of *Alpinia caerulea*. He tells me it was green. The pupa was also green with a long hair-like spike extending from the thorax to the posterior end. The food-plant is called "Wild Ginger".

TRAPEZITES ELIENA ELIENA Hewitson, 1868.

Mr. E. O. Edwards has caught this species at Mitchell, Qld., from November to February. This is much further from the coast than any other record.

TRAPEZITES PHIGALIOIDES Waterhouse, 1903.

For the first time I have taken this species and *Trap. iacchoides* at the same locality. Three males of the former and one of the latter species were caught by me within half an hour at Berowra, N.S.W., on 28th October, 1933. It has also been taken at Lawson by Mr. J. C. Macdonald, this being a lower elevation in the Blue Mts. than any yet recorded. It has also been recorded from Stanthorpe, Qld., in October by Mr. W. B. Barnard.

TRAPEZITES PETALIA Hewitson, 1868.

Mr. E. O. Edwards has caught this at Mitchell, Qld., in December. This is much further from the coast than any other record. At Milmerran, Qld., Mr. J. Macqueen, from an egg laid on *Xerotes* in September, bred a male at the end of January. I have carefully searched for it on the Blue Mts. without success.

TRAPEZITES LUTEUS LUTEUS Tepper, 1882.

Mr. J. Macqueen saw an egg in September laid on a species of *Xerotes* near Milmerran, Qld. This was watched and a female emerged on 7th February. Nearby on the same plant was the egg of *Trap. petalia* mentioned previously. Another larva gave a male on 11th March. Mr. Macqueen lent me the cast larval heads and the pupal shells of the three specimens. The heads were rough but not hairy, that of *petalia* mottled with dark and pale brown, that of *luteus* pale brown, sides nearly black and a black vertical median band in front. I could not find any marked differences in the three pupal shells. This butterfly has been caught near Binnaway, N.S.W., in March by Mr. C. F. Garnsey. I find that the apiculus to the antenna is much shorter in *luteus* than in *petalia*.

NEOHESPERILLA XANTHOMERA Meyrick and Lower, 1902.

Mr. T. G. Campbell has taken this at Melville Is., N. Terr., in October.

HESPERILLA MASTERSI Waterhouse, 1900.

The northern range of this rare species has been extended to Mt. Warning, Tweed River, where a male was taken in November by Mr. A. J. Marshall. It has also been caught at Narara, near Gosford, by Mr. L. H. Moss-Robinson in

November. By the efforts of Dr. T. Guthrie and his son, a small area on the cliff edge near Bulli Pass has been found where males are to be seen flying. The butterflies were settled on trees which had grown up from a ledge some twenty feet below the cliff edge. Mr. T. Guthrie found that by shattering a small piece of sandstone on the rocky edge of the cliff, thus spreading the fragments of stone, some butterflies were induced to fly up over the cliff and settle on trees. Here they could be caught with ease. They settled with wings partly depressed and with heads outwards. Many specimens did not settle but flew past too swiftly to be caught. During February and March of this year, with seven collectors we were able to secure twenty males, many of which were in poor condition.

HESPERILLA DONNYSA DILUTA Waterhouse, 1932.

Mr. M. W. Mules has succeeded in finding the larvae of this race at several places in South Australia and has sent me bred specimens from Mt. Lofty, Mylor and Second Valley. Most of these emerged in November. The race is variable in size and the number and size of the spots on the forewings.

HESPERILLA IDOTHEA IDOTHEA Miskin, 1889.

New records are Mt. Warning, N.S.W., a male taken in November by Mr. A. J. Marshall; Bulli Pass, a female in March by Mr. D. F. Waterhouse; Mt. Evelyn, Vict., both sexes in November by Mr. A. L. Brown; and Frankston, Vict., a female in February by Mr. C. Ives.

HESPERILLA IDOTHEA CLARA Waterhouse, 1932.

Mr. M. W. Mules has found a few pupae of this rare race, so I am able to give a description of the hitherto unknown female. In the bred males the elongate pale orange patch on the upperside of the hindwing is very well marked and the hyaline spots of the forewing have a silky sheen in most specimens. On the underside of the hindwing most specimens are without dots, but some have them in areas 2, 3 and 6.

The female has all the spots on the upper side larger than those of the typical race and the hyaline spots are silky. In addition there is an opaque orange spot in 1*a* one-third from base of forewing, the two outer spots in this area are joined. In the allotype there is an indistinct dot below the subapicals and nearer the termen. On the underside of the hindwing, two specimens have no dots and two a small one in area 2. Mr. Mules bred four females, two of which are before me and photographs of the others. The allotype is from Aldgate, S. Aust., bred 28th November, 1933, and the others from Mt. Lofty, bred from 26th November to 1st December, 1933.

HESPERILLA ANDERSONI Kirby, 1893.

Several males have been taken this year near the top of Bulli Pass in February and early March.

TARACTROCERA DOLON Plotz.

Taract. dolon, Waterhouse, These PROCEEDINGS, 1933, p. 463.

I caught this species sparingly at Urunga, N. S. Wales, in the first week of September, 1934. This is a new record for N. S. Wales and extends the range of the species about 200 miles southwards.

TARACTROCERA ANISOMORPHA Lower, 1911.

New records are Milmerran, Qld., in October and November (J. Macqueen) and Mitchell, Qld., in January (E. O. Edwards).

TARACTROCERA INA IOLA Waterhouse, 1933.

Mr. V. Lindsay has sent me a series of this butterfly from Mackay caught from 14th March to 15th April, 1934. As a number of the specimens were worn I believe that the best month to search for this race would be February. It has a second brood in September and October. Mr. F. A. McNeill, who caught this race at Hayman Is. in January, 1933, did not find it there in May, 1933, nor in January and June of 1934, although he captured many specimens of *Ocybadistes tanus* on these other trips.

BAORIS BADA SIDA, n. subsp.

Parnara guttatus bada, Waterhouse and Lyell, *Butt. Aust.*, p. 212, figs. 714, 715, 1914; *Baoris guttatus bada*, Waterhouse, *What Butterfly is That?*, p. 263, pl. xxxiv, fig. 12, 1932.

Brigadier W. H. Evans, who is now at work on the Indo-Australian Hesperiidae at the British Museum, writes that from an examination of the genitalia *bada* and *guttatus* are distinct species. In certain parts of India they fly together in the same way as do *Ocybadistes flavovittata* and *O. walkeri* at Sydney and elsewhere in Australia. He considers that Australian specimens constitute a distinct race of *bada*.

The Australian race differs from Indian specimens in having only two spots in areas 2 and 3 of both wings, whereas in typical *bada* the forewing usually has another spot in area 4, and the hindwing discal spots in areas 2 to 6.

The figures quoted depict this race very well. The holotype male, now in the Australian Museum, Sydney, is the specimen used for fig. 714 from Kuranda, Qld., in January. I have it from Kuranda in January, March, June and December; Herberton in January; Mackay in March, and Brisbane in January, April and May.

NOTES ON AUSTRALIAN LYCAENIDAE. VII.

DESCRIPTIONS OF NEW RACES.

By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.

[Read 28th November, 1934.]

Since the last part in These Proceedings for 1928, more material has come to hand, and also Brigadier W. H. Evans has compared specimens I forwarded with the types in the British Museum and sent me notes thereon.

Genus Hypochrysops Felder, 1860.

Wiener Ent. Monat., iv, 1860, p. 243; Reise Novara, Lepidoptera, 1865, p. 251; *Miletus*, Waterhouse (not Hübner), Proc. Linn. Soc. N.S.W., 1903, p. 158; *Miletus*, Waterhouse and Lyell (not Hübner), *Butt. Aust.*, 1914, p. 84.

When in 1903 I used the generic name *Miletus* for these brilliant Lycaenids, I did so on the authority of Scudder (Historical Sketch, p. 219, 1875), who fixed as genotype *Papilio polycletus* Linn., the first species mentioned by Hübner. Mr. N. D. Riley informs me that Scudder's action was invalid, as Westwood (*Gen. Diurn. Lep.*, 1852, p. 502) definitely fixed *symethus* Cram., another species mentioned by Hübner, as the genotype. The appropriate name *Hypochrysops* Felder is available for these species. If the genotype has not already been fixed, I select *P. polycletus* Linn., the first species mentioned by Felder in 1860.

Hypochrysops elgneri barnardi, n. subsp.

Male.—Upperside differs from the typical race in its brighter purple colour and having the veins (excepting near apex of forewing) outlined with bluish-purple when viewed obliquely. Underside, the ground colour is yellowish-brown and the markings are brighter than in the typical race.

Female.—Upperside differs from the typical race in having the orange areas much brighter and larger; in the allotype the orange extends to the termen of hindwing. Underside ground colour much paler, so that the markings, which are darker, stand out more prominently, orange central area of forewing brighter and larger.

Both sexes are considerably larger than those of the typical race from Prince of Wales Island.

Described from two pairs in the Australian Museum caught by Mr. W. B. Barnard at Cape York in June. The holotype male, in addition, has a dull orange central patch on the underside of forewing.

Nacaduba ancyra halys, n. subsp.

Nac. ancyra (in part), Waterhouse, Proc. Linn. Soc. N.S.W., 1903, p. 225; *Nac. ancyra florinda*, Waterhouse & Lyell, *Butt. Aust.*, 1914, p. 97, figs. 318–321; *Nac. ancyra florinda*, Waterhouse, *What Butterfly is That?*, 1932, p. 155, pl. xxii, fig. 3.

Brigadier Evans has examined the holotype male of *florinda* from Lifu, Loyalty Is., in the British Museum. He says it is quite distinct from what is known in Australia as *florinda*. It is much bluer on the upperside and the markings on the underside are very much narrower, on the hindwing the bar at the end of cell is separated by its own width from the discal band, whereas in Australian specimens they are conjoined or nearly so.

As the race has been described and figured twice, there is no need to repeat the description here. I have assigned the type locality as Ballina, Richmond River, N.S.W., and the type series two males and a female caught in September, 1902. The race is found along the coast from the Manning River to Mackay, with Townsville specimens not quite typical. One specimen has been caught near Sydney, where its food plant grows in a few suitable localities. Specimens of the female from Brisbane in the winter have the blue areas above much more extended.

Ogyris amaryllis Hewitson.

Cat. Lycaenidae Brit. Museum, 1862, p. 3, No. 11, Pl. 1, figs. 5, 6.

Hewitson described this species from a female in the British Museum, from Moreton Bay, using the MS. name Newman had attached to the type. The species has a very wide range in Australia, both on the coast and inland. The typical race with broad margins to the wings on the upperside (especially in the female) is known only from Brisbane, Richmond River and Tuggerah. I have searched for it near Sydney, at Newport, where the *Loranthus* grows on which its larvae feed, but without success. I have specimens from all the States, excepting Tasmania, but the material is as yet insufficient to determine if there are more races than *hewitsoni* Waterhouse, 1902, from Townsville (Types in Australian Museum), *meridionalis* Bethune-Baker, 1905, from Victoria (Holotype male in British Museum from Birchip, 1st March, 1902) and the marked race from Canberra described below.

Ogyris amaryllis amata, n. subsp.

Male.—Upperside bright shining dark blue with a markedly broad black margin to the termen of both wings. Underside mottled browns and blacks with white bands lined with silky-blue across cell of forewing.

Female.—Upperside, shining dark blue with broader black margins than in male. Underside, similar to the male, but with a bright scarlet spot in cell of forewing.

This race is nearest to typical *amaryllis*, but in both sexes is smaller and the blue of the upperside is considerably darker and richer. The black termen of the hindwing in the male is as broad as that of the forewing, which is not the case in typical male *amaryllis*. The first specimen was caught near the Cotter River Dam, Canberra, F.C.T., by Mr. G. M. Goldfinch. The next year I found larvae and pupae in September; these were not attended by ants, which is unusual in this species. In November the race was not uncommon near the junction of the Murrumbidgee and Cotter Rivers. I have caught it there from October to March, the later specimens being worn. Males that emerged in October had a pupal duration of 43–45 days, both sexes that emerged in November had a pupal duration of 27–33 days.

The holotype male emerged on 16th November, 1929, the allotype female on 24th November, 1929, and, with paratypes of both sexes, are in the Australian Museum.

Ogyris olane Hewitson.

Cat. Lycaenidae Brit. Museum, 1862, p. 2, No. 10, Pl. 1, figs. 10, 11.

Hewitson described and figured this species from a single female in his collection with no more definite locality than Australia. When, on his death, his collection went to the British Museum, the catalogue of it by Kirby shows that it contained only one specimen. This specimen, the holotype, has a label in Hewitson's writing "*olane*", with another label added later "Australia". Both Hewitson's description and figure, a copy of which is before me, have always occasioned comment, as the colour on the upperside is more extensive and bluer than any hitherto known specimen, and the size also is much smaller.

Miskin (These Proceedings, 1890, p. 27) remarks: "Hewitson's figure and description evidently represent the female, although the blue is shown as extending rather too much into the wing, but the colour agrees well."

Bethune-Baker, in his monograph on the genus *Ogyris* (*Trans. Ent. Soc. Lond.*, 1905, p. 283–4) says: "The description is of the form now found flying in Australia; it does not agree with the colour on the upperside of Hewitson's type, which is paler and brighter blue, the underside agrees, however, fairly closely. I have no doubt that the two insects are the same species, but that Hewitson's type may have undergone some change (possibly chemical) which has effected the difference in colour."

In July, 1933, Brigadier Evans examined the type and reported "The only difference in figure and type from three females in the British Museum is that the blue area above is lighter and may be due to age, chemicals, etc.".

However, in the spring of 1933, Mr. E. O. Edwards sent me some specimens he had bred at Mitchell, Qld., about 300 miles west of Brisbane. I at once saw that both in colour and size the females agreed with Hewitson's figure. I then sent a Mitchell specimen to London with a female from the Blue Mts., N.S.W. Brigadier Evans replied in February, 1934: "Your Mitchell specimen looks just like a fresh specimen of the type marked Australia. The other three females in the British Museum are from Victoria and resemble the second specimen—purple instead of blue above."

The colour of the type female therefore has not changed, but represents the true colour of inland specimens. It is not easy to understand how a specimen from an inland locality reached London earlier than 1862. At that time it is very doubtful if it could have come from anywhere near Mitchell. It may have come from western New South Wales, as I have a similar, though worn, female from Brewarrina caught by Mr. G. H. Wylde.

I cannot understand why Bethune-Baker places *Ogyris catharina* Felder, 1865, as a synonym of *O. olane*. Felder begins his description "♂. Alae supra dilute cyaneae", and begins his description of *Hypochrysops theon* with the same words. This shows that it cannot have anything to do with *olane*, but must be one of the races of *O. amaryllis* or *O. oroetes*. Until the type is found the question cannot be settled.

Ogyris olane olane Hewitson, 1862.

The male is much smaller than coastal specimens and the purple of the upperside is slightly brighter and, in the three males before me, extends into the cell of the forewing and on the hindwing extends much nearer the termen. The females can readily be distinguished by the blue colour of the upperside.

The material before me consists of two males bred from Mitchell in October; six females from Mitchell bred in May, September and October; a worn pair from Brewarrina caught in September. Mr. Edwards found that at Mitchell the larvae varied in colour and the pupal duration was 26–36 days. Mr. M. W. Mules has sent me a bred pair from Woodside, S. Aust. These are small, but not quite typical. The other three South Australian specimens before me are old and worn. From Clermont, Qld., Mr. E. J. Dumigan sent me a pair which also are not quite typical, but much nearer the next race. More material is required from both these localities. All the above specimens are in the Australian Museum, excepting one male from Mitchell, belonging to Mr. Edwards.

At Brewarrina and Clermont, both *O. olane* and the allied *O. barnardi* were caught, the latter being much commoner. At Mitchell, *O. barnardi* has not been found, whilst at Milmerran, about 200 miles away, Mr. J. Macqueen has so far only taken *O. barnardi*.

Ogyris olane ocela, n. subsp.

O. olane, Anderson and Spry, *Vict. Butt.*, 1893, p. 105, fig.; Bethune-Baker, *Trans. Ent. Soc. Lond.*, 1905, p. 283; Waterhouse and Lyell, *Butt. Aust.*, 1914, p. 119, figs. 391-2, 421, 423.

This is the *Ogyris olane* of all previous writers, excepting the original description and figure of Hewitson, and is well known to collectors. In both sexes it is considerably larger than the typical race.

Female.—Upperside brown, apical area of forewing paler brown, centrobasal areas of both wings purple, not always, as in holotype, entering cell of forewing.

Male.—Upperside brown with centrobasal areas very dull purple.

As the type of the typical race is a female, I have assigned a female from Woodford, N.S.W., bred on 9th October, 1933, as the holotype of this race, with allotype male and paratypes in the Australian Museum from the same locality, bred from September to November. It is found in the Blue Mts. from Glenbrook to Mt. Victoria (500 to 3,500 ft.). I have taken it about 80 feet above sea-level 30 miles west of Sydney. Victorian specimens from near sea-level to about 2,000 feet are this race, and also the few Mr. L. Franzen has sent me from Brisbane.

Deudoryx epijarbas dido, n. subsp.

D. epijarbas diovis (in part) Waterhouse and Lyell, *Butt. Aust.*, 1914, p. 132, figs. 199, 200 (not fig. 198).

Male.—Upperside, forewing black, central patch below cell extending to base dull red; cilia faintly brown. Hindwing dull red with veins black, costa and base black; cilia brown. Underside, similar to *D. epijarbas diovis*, but with a purplish suffusion over wings and fewer metallic scales near tornus of hindwing.

Female.—Upperside, brown with costa and termen of forewing broadly dark brown; cilia brown. Underside as in male, but purplish suffusion not so marked.

The holotype male is from Kuranda, Qld., in March, and the allotype female from Kuranda in February, with paratypes from Kuranda in February to April in the Australian Museum.

The description of the race *diovis* given in 1914 was taken chiefly from Kuranda specimens, as we had a longer and better series from there at that time. A fine series from Brisbane shows that the colour of the males is much brighter, the cilia are orange-red and the veins of the hindwing are only marked with black just near the termen. The female is grey-brown and has orange-red

cilia like the male. In both sexes the metallic scales are more numerous near the tornus of hindwing below. That portion of the face between the eyes and below the base of the antennae has an orange-red patch in *diovis*, whereas in *dido* it is smaller and brown.

Brigadier Evans has examined the specimens of *D. epijarbas* from Australia in the British Museum, and finds that the above distinctions hold as to locality. Both Hewitson's description and figures of *diovis* show that his types must have come from near Brisbane. They agree with other specimens from Brisbane in the British and Australian Museums. The type male is labelled "Austral. Strang. *diovis*." in Hewitson's handwriting. Strang. doubtless means Frederick Strange, who did not collect very far north of Brisbane. As far as the specimens before me show, the race *diovis* is found from the Manning River to Mackay.

NOTES ON THE GENUS *OPHIODESMA* (DIPT., STRATIOMYIIDAE).

By Mary E. Fuller, B.Sc., Assistant Research Officer, Council for Scientific and Industrial Research, Canberra, F.C.T.

(Eleven Text-figures.)

[Read 28th November, 1934.]

Introduction.

In January, 1933, the larvae and puparia of a species of Stratiomyiid were collected in great abundance feeding on the moist, rotting tissue between the central core and outer wall of dead *Xanthorrhoea* stumps on the slopes of Mt. McDonald near Canberra. The following month a small species of *Ophiodesma*, which is described below as *O. minor*, emerged from the puparia.

Some adults and preserved larvae of another species of *Ophiodesma* were recently received from Mr. J. H. Bowen of the Forests Commission of Victoria. Later, in March, 1934, he sent a piece of grass-tree containing live larvae and puparia. Early in April a fly, which was identical with the dark-winged *Ophiodesma* bred by him, emerged from this material. This species was also new and is described below as *O. brunnipennis*.

Historical and Synonymy.

In 1896 Froggatt described the larva and adult of a Stratiomyiid, which he bred, along with a number of other insects, from *Xanthorrhoea*. Froggatt believed this species to be identical with Bigot's *Ephippium albitarsis*. His brief description of the larva might apply to a number of Stratiomyiids, whilst his description and drawing of the adult are of little assistance in determining the species. However, the fact that he describes the wings as dusky and the antennae as spindle-shaped inclines one to believe that his species is the same as *O. brunnipennis*, n.sp., bred from *Xanthorrhoea australis* in Victoria.

In 1916 A. White published a revision of the Australian Stratiomyiidae. In this he erected the genus *Negritomyia* for *Ephippium albitarsis* Bigot. Specimens of *N. albitarsis* from North Queensland show it to be a very distinct fly from any of those bred from *Xanthorrhoea*. White also erected the genus *Ophiodesma* for *Odontomyia flavipalpis* Macquart. He considered *Ophiodesma* to be fairly typical of the subfamily Clitellarinae. The two new species bred from grass-tree agree with White's definition of *Ophiodesma*.

In 1920, Hardy recorded *Ophiodesma flavipalpis* as the only species of the genus. In 1932, he described a new species, *O. innoda*, from Queensland. This is closely related to the type species, differing chiefly in the frons of the female.

In Malloch's key to Dipterous larvae, the larvae described below run close to the Clitellarinae and to an unknown genus represented by a larva taken from a rat's nest. Most of the genera in this sub-family are aquatic, but *Hermetia*

is terrestrial. The larvae of this and of *Ophiodesma* have some points of resemblance, although on arrangement of body bristles and shape of head *Ophiodesma* is closer to Malloch's *genus incertus* 2. The arrangement of the mouth parts is very similar to that of *Nemotelus*, also a member of the Clitellarinae, as described and figured by Bischoff. This species, however, is aquatic. On the whole the relationships of the larvae of *Ophiodesma* seem to be with the aquatic Clitellarinae, rather than with any of the described terrestrial Stratiomyiidae.

Key to Species.

1. Frons of female with smooth central area and no interruption of median line ..... *O. innodus* Hardy.
   Frons of female with central area corrugated and a ridge issuing from the median line 2
2. Antennae long and narrow, twice the head length, pubescence yellow ..... *O. flavipalpis* Macq.
   Antennae shorter and spindle-shaped, from 1·3 head length to same length as head, pubescence silvery white 3
3. Wings smoky-brown, frons of female with few hairs, length 7·5 to 8 mm. ..... *O. brunnipennis*, n. sp.
   Wings hyaline, frons of female more hairy, length 3 to 5 mm. .... *O. minor*, n. sp.

Ophiodesma flavipalpis Macq.

White redescribed this species in 1916, when proposing the genus *Ophiodesma*. In 1932, Hardy gave a description of the frons of the female. I have examined specimens collected at National Park, Sydney. The species is readily distinguishable from those I have bred from *Xanthorrhoea* on the shape and length of the antennae and the yellow pubescence. *Distribution.*—New South Wales and Victoria.

Ophiodesma innoda Hardy.

This species has not been examined, but is apparently easy to distinguish by the smooth frons of the female. *Distribution.*—Queensland.

Ophiodesma brunnipennis, n. sp.

♀. The length is 8 mm. The whole body is black, with the exception of the tarsi, which are a dirty white. The thorax and undersurface of the abdomen are covered with short, flat, silvery-white hairs. The dorsal surface of the abdomen has some patches of these hairs along the lateral edges, the rest being black and shining. The scutellar spines are black and well separated. The whole surface of the body is minutely punctate.

The frons is a little more than one-quarter the head width, corrugated and rugose, without hairs except for two small patches behind the antennae and a few on the ocellar area. The margin behind the eyes is comparatively wide, with sparse silvery hairs. There is a fringe of silver hairs above the mouth. The antennae are one and one-third times the length of the head and are spindle-shaped. The first segment is twice as long as the second, the third is wider than these two, and the segments become narrower from the fourth to the tenth. The third segment is as long as the first and the rest are shorter. The apical segment is narrowest and is papilla-like. The wings are dark smoky brown. The abdomen is considerably broader than in *O. flavipalpis*.

♂. Similar to, but slightly smaller and narrower than, the female. The antennae are shorter and more slender, only slightly longer than the length of the

head. It differs chiefly from the female in having the dorsum of the thorax covered with a dense pile of upstanding black hairs and in having no silver pubescence on the thorax.

Distribution.—Anglesea, Victoria (January, 1933; April, 1934). Bred from *Xanthorrhoea australis.* The holotype male, allotype female and a paratype male are in the collection of the Division of Economic Entomology, Canberra.

Ophiodesma minor, n. sp.

♀. The smallest fly just exceeded 3 mm. and the largest was 5 mm. in length. It is black with whitish tarsi, as in other species of the genus. The hairs on the thorax show a tendency to form lines. The body is covered with short, whitish hairs, sometimes tending to pale yellow. The dorsum of the abdomen is bare except for some patches of hairs on the sides. The scutellar spines are slightly longer than in the previous species and brownish in colour. The wings are hyaline. The frons is nearly one-third the head width and is covered with hairs except for the corrugated part near the middle. The antennae are about the same length as the head and have the same structure as in *O. brunnipennis*, but are slightly thicker.

♂. Similar to the female but rather more slender. The thorax is covered with a dense pile of whitish hairs.

This species differs from *O. flavipalpis* in the shape and length of the antennae, and from *O. brunnipennis* by its smaller size and hyaline wings.

Distribution.—Mt. McDonald, F.C.T., near Mullion Creek, N.S.W. (January, 1933). Bred from *Xanthorrhoea* species. The holotype male and allotype female are in the collection of the Division of Economic Entomology, Canberra. A number of paratypes are in the same collection.

Description of the larva of O. minor. (Text-fig. 1.)

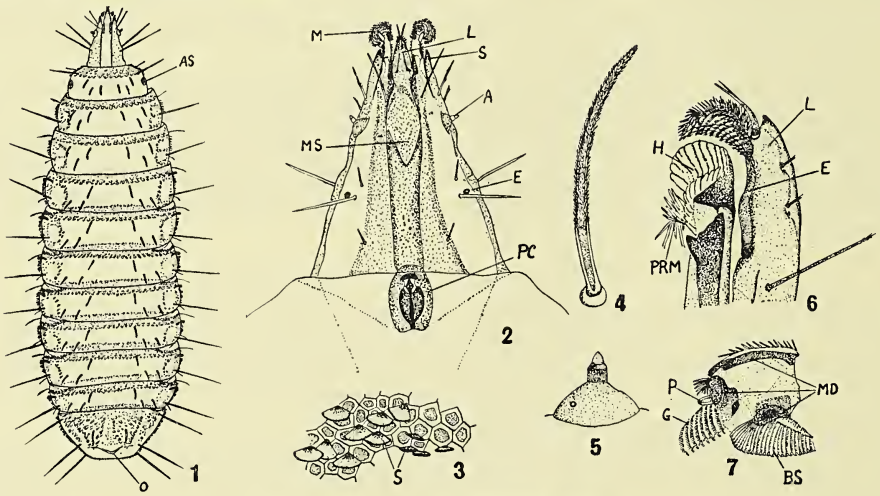
The length of the full-grown larva is from 8 to 9 mm. The skin is of a creamy colour, but the larva appears to be light brown on account of the dense covering of scales and hairs. It is somewhat cylindrical when young, but becomes flattened in the later stages, both dorsal and ventral surfaces remaining slightly convex with the lateral edges produced to a ridge.

The larva has eleven body segments and an elongate, conical head. All the body segments are much broader than long, with the exception of the eighth, which is almost as long as wide, with the lateral edges sloping towards each other posteriorly and the dorsal surface also sloping down posteriorly. The constrictions between the body segments are not very sharply pronounced. The body bristles are long and conspicuous, giving the larva a shaggy appearance. The integument is divided into hexagonal areas, but the markings are very faint and further obscured by the dense covering of scales, each arising in the angles between the hexagonal areas (Text-fig. 3). The integumental markings become more distinct on pupation.

On the dorsal surface of each segment, except the last, are six large bristles, three on each side of the centre. These project straight up from the back and then bend slightly towards the centre. On the thoracic segments these are arranged in triangular formation, there being a pair near the anterior border each side of the centre and one below and between them. On the abdominal segments the arrangement is a bristle near the anterior border and a more lateral pair near the posterior border on each side. There is only one pair of

corresponding bristles on the last segment near the centre. Laterally on the dorsal surface of each segment a large bristle projects outwards near the lower edge. In addition to these, on abdominal segments one to seven there is a shorter, thick, inwardly curved bristle laterally near the upper edge. The eighth segment has a pair of long bristles at the lower corners and a pair near the upper corners. All these bristles are compound, having a series of tiny spines up the sides (Text-fig. 4).

On the ventral surface of the thoracic segments there is a pair of bristles each side of the centre about the middle of the segment. These project straight down and are thin and bifid. Near the upper corner is a fine bristle projecting sideways and visible from above. The abdominal segments each have four fine bristles near the middle arranged in a straight line, two on each side of the centre. There is also a bristle at the upper corner and one at the lower, both visible from above, the upper one being larger and stronger. All the ventral bristles are finer than the dorsal. The last segment has four near the middle on each side of the anus, a large strong pair on the lower corners and a fine pair on the posterior edge.



Text-figs. 1-7. *Ophiodesma minor.*

1.—Larva, × 7·6. *a*, anterior spiracle; *o*, opening of air chamber.

2.—Head of larva, × 37. *a*, antenna; *e*, eye rudiment; *l*, labrum; *m*, maxilla; *ms*, median sclerite; *pc*, pharyngeal chamber; *s*, side lobe.

3.—Larval integument, × 133. *s*, scales.

4.—Dorsal bristle of larva, × 120.

5.—Antenna, × 120.

6.—Labrum and hypopharynx, × 67. *e*, epipharynx; *h*, hypopharynx; *l*, labrum; *prm*, prementum.

7.—Maxilla, × 67. *bs*, banded segment; *g*, galea; *md*, mandible; *p*, palp.

The anterior border of each thoracic segment both dorsally and ventrally is thickly covered with an armour of several rows of tiny scales set closely together. The rest of the segment dorsally is clothed with larger, less heavily chitinized scales, many of which are fan-shaped and project from the surface, either standing straight up on end or sloping backwards (Text-fig. 3). They are more abundant along the sides, where they overlap like shingles. On the abdominal segments

the scales are also smaller, more closely set along the anterior and posterior borders, and larger and more loosely arranged on the rest of the segment. Some are divided at the ends, and there are all gradations from simple bristles to broad scales.

The ventral surface of the thoracic segments is not so scaly, the integument being simply divided into more or less hexagonal areas and devoid of upstanding scales, except near the lateral edges, where they occupy an area in the vicinity of the forked hairs. The abdominal segments are also smoother on the ventral surface, the scales being confined to the sides. On the ventral surface of the eighth segment, near the anterior border, is a semi-circular fold in the skin. The edges of this are sharply defined by strong bristles. At right angles to the fold and running from its centre longitudinally down the middle of the segment about half-way to the posterior border is the anal slit. The lips are armed on the inner edge with a series of strong inwardly and backwardly directed teeth. Running from the end of the slit to the posterior border is a deep narrow groove. The eighth segment is extremely bristly on the dorsal surface, except below the opening of the air chamber, which is situated in the centre of a transverse postero-dorsal groove. There is a pair of branched hairs just anterior to the pair of posterior bristles on the dorsal surface.

The spiracles.—The posterior spiracles are internal, opening into an air chamber situated beneath the dorsal surface on the last segment. The opening of the air chamber is protected by a pair of elliptically curved lips which are strongly chitinized and ornamented with a series of rounded bosses. The chamber which opens through these lips runs back to the posterior end of the anus. The spiracles open one each side of the anterior end of the air chamber. Each is ring-shaped, with a strong chitinous rim bearing a pattern of bars and scallops similar to the slits in a Calliphorid spiracle. The centre is occupied by a perforated membrane. Just behind the spiracle the tracheal trunk ends in a sieve chamber in which long hairs project inwards from the wall.

The anterior spiracles occur on the first thoracic segment laterally. Each consists of a mound of strong chitin, the surface of which slopes towards the posterior and contains a pair of slits converging at their posterior ends. They are oval in shape, with a strong chitinous rim and one diagonal bar crossing the lumen towards the bottom end. Behind the slits is a "button", an irregular chitinous scar, and below them is the felt or sieve chamber which is the end of the tracheal trunk. There are no body spiracles visible. If present, they are completely obscured by the scales and bristles.

The head (Text-fig. 2) is of the typical elongate, conical shape, with the central sclerite constricted slightly towards the end and then narrowed to a point forming the labrum. The lateral plates lying each side of the base of the labrum and sheathing the maxillae are more pronounced than those in *Actina incisuralis* (Fuller, 1934). The maxillae extend forwards each side of the labrum, the plumose galeas being normally curved under, occupying a ventral position. A little behind the bases of the maxillae are the antennae (Text-fig. 5), which are lateral and composed of three segments, the basal one being large and mound-like, the second more strongly chitinized, narrow, and much shorter than in *Actina*, and the apical segment small and dome-shaped. The lateral swellings, said to represent rudimentary eyes, are not very well developed in this species, but there is a pigmented spot and a large bristle in a corresponding position in mature larvae. The scales covering the head integument are not conspicuous

and upstanding, being more in the nature of small bosses. The central sclerite is devoid of scales or plates. There are five pairs of small bristles on the under-surface of the head, the posterior pair being nearest the centre. On the dorsal surface are four pairs of large bristles, a pair being associated with the eye spot on each side, a pair at the base of the labrum, and a pair at the base of the lateral plates. There is also a small bristle on each side anterior to the large eye bristles and one each side of the central sclerite near the posterior border of the head.

Mouth parts.—The labrum is the apical termination of the dorsal head plate and lies between the two maxillae, which extend a little in front of it. The labium is situated behind and below the hypopharynx, which is closely appressed to the ventral face of the labrum. The lateralia or side lobes of the head are produced to a point and lie on the outside of the posterior half of the maxillae.

The labrum (Text-fig. 6) is curved ventrally and is wide at the base and narrowed anteriorly. At its apex is a short chitinous point. Below and behind this is a pair of large strong bristles, which project forward and are noticeable from the dorsal surface. Slightly behind these and so curved that it occupies a ventral position is a large plumose structure. It is composed of delicate chitin shaped like a shallow trough and is covered with striations and rows of fine hairs. A narrow, slightly curved chitinous plate lies attached to the ventral surface of the labrum and represents the epipharynx. The hypopharynx (Text-fig. 6) lies close, but not attached, to the epipharynx. It is almost as large as the labrum and consists of an elongated sclerite with a chitinous strut up the centre and a triangular support behind the apex, which is curved, striated and finely toothed.

The labium consists of the mentum, two membranous lobes running from the lateralia beneath the maxillae and meeting at the median prementum. The lobes are of thin chitin, small, narrow and ornamented with some fine hairs. The prementum is a small tufted sclerite attached to the ventral surface of the hypopharynx. In a position representing the submentum is a smooth narrow sclerite running back towards the centre of the head and readily detached from the integument.

The maxilla (Text-fig. 7) has the mandible fused with its inner face as in *Actina incisuralis*. It is a comparatively short, broad structure, slightly convex on the outer surface. The dorsal edge is fringed with a row of forwardly-directed bristles. Anterior to these is a small chitinous knob bearing a fan-shaped tuft of bristles. The apex of the maxilla is strongly curved so that the galea is antero-ventral in position. It is a broad piece of delicate chitin bearing combs of fine hooked hairs. Above and behind this is the palp which is short and broad. Most of the ventral edge is occupied by the "banded segment" of Bischoff, a curved piece of chitin with radiating striations and a dissected ventral edge.

The mandible consists of several strong masses of chitin connected by thinner portions. There is a dense rounded mass above the banded segment, a strong bar along the dorsal edge of the maxilla, and another mass near the apex of the maxilla at the base of the palp. The "kaumagen" of Bischoff is a large globular chamber at the posterior end of the pharynx. It contains a large chitinous mass through which runs a rod connecting with a smaller piece of chitin near the anterior end of the chamber. Viewed from the side, however, it is seen to be an

adaptation of the wall of the pharynx, both dorsal and ventral walls being greatly thickened. The dorsal mass of chitin is sharply curved and pressed against the ventral one, the whole appearing to be a valve structure (Text-fig. 10).

Description of the larva of O. brunnipennis.

The larvae examined varied in length from 6 to 14 mm. They are similar in appearance to *O. minor*, but are slightly broader and darker brown in colour, and in general considerably more robust. The body bristles are longer, stouter and darker in colour and the head narrower and more elongate than in *O. minor*.

The larva of *O. brunnipennis* may be distinguished from that of *O. minor* by the following characteristics: The anterior dorso-lateral abdominal bristle is slender and almost as long as the posterior one, whereas in *O. minor* it is short, stout and club-shaped. There are three pairs of dorsal bristles as in the smaller species, but the two innermost pairs are arranged in two straight lines running down the back, whereas in *O. minor* the posterior is slightly lateral to the anterior. In some larvae the dorsal bristles are so long and curved inwards that they meet in an arch over the back.

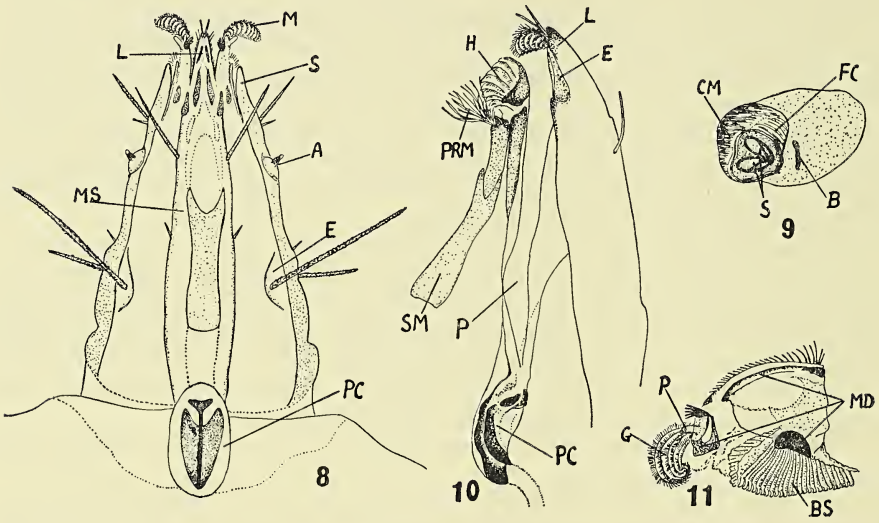
The small body scales are much denser in this species and are just as abundant and close on the ventral as on the dorsal surface. Also, laterally on each segment, both dorsally and ventrally, there is a patch of enlarged integumental plates. They are rounded and light brown in colour and form a roughly circular patch. They occur in the same position and resemble the lateral ring of spots in *Actina incisuralis*. The hexagonal areas of the skin are more pronounced than in *O. minor*, especially on the eighth segment.

There are no visible body spiracles such as occur in other larvae of the same subfamily (Malloch, 1917).

The head (Text-fig. 8) is more elongated than in *O. minor*. The central dorsal sclerite is not more chitinous than the rest of the head but has a smooth surface, whereas the rest is rugose. Near the base of the head are a pair of lateral swellings which are not present in *O. minor*. Anterior to these are the eye rudiments, associated with each of which are two bristles. One arises dorsally and is very large and strong; the other is lateral and smaller. Arising from the median sclerite in a position just anterior to the antennae is another pair of large bristles. Anterior to these is a pair of similar bristles arising from the side lobes of the head. There is one other pair of dorsal bristles situated on the edge of the central sclerite about the middle of the head. They are very small and inconspicuous. The side lobes are prominent at the anterior end of the head, sheathing the maxillae. On the ventral surface is a large oval-shaped sclerite extending from near the posterior edge of the head to the prementum. There is a pair of bristles arising from the lateral edges of the head just anterior to the eye swellings and another pair on the innermost edges of the side lobes. These are much smaller than the dorsal bristles. There is one very small pair near the submentum corresponding to those at the middle of the dorsal sclerite. The anterior part of the ventral surface of the head is occupied by many plumose and membranous structures, namely, the lobes of the mentum, the prementum, the hypopharynx and the plume of the labrum.

The mouth parts.—In arrangement the mouth parts are the same as those of *O. minor*, the labrum and hypopharynx (Text-fig. 10) having the same structure, but naturally being much larger. The plume of the labrum is, however, relatively smaller. The two lobes of the mentum, which are roughly triangular in shape

and stretch from the side lobes to the prementum, are rather more delicate and membranous than in *O. minor*. The apical tuft of hairs on the prementum is rather more profuse in this species. The submentum is conspicuous, being large, more chitinized than the surrounding integument and forked at the anterior end, where it connects with the rest of the labrum. The "kaumagen" is essentially the same in both, the central chitinous mass being more elongated in *O. brunnipennis*.



Text-figs. 8-11. *Ophiodesma brunnipennis*.

8.—Head of larva, × 30. *a*, antenna; *e*, eye rudiment; *l*, labrum; *m*, maxilla; *ms*, median sclerite; *pc*, pharyngeal chamber; *s*, side lobe.

9.—Anterior spiracle, × 56. *b*, button; *cm*, chitinous mound; *fc*, felt chamber; *s*, slits.

10.—Labrum and hypopharynx, × 30. *e*, epipharynx; *h*, hypopharynx; *l*, labrum; *p*, pharynx; *pc*, pharyngeal chamber; *prm*, prementum; *sm*, submentum.

11.—Maxilla, × 56. *bs*, banded segment; *g*, galea; *md*, mandible; *p*, palp.

The puparium.

In both species the method of pupation and dehiscence of the puparium is the same. Pupation takes place inside the old larval skin, which becomes hard and inflexible. There is no external change in appearance except that the hexagonal plates of the integument become more noticeable. Dehiscence takes place by the splitting off of the first segment and head in the form of a cap and by the median, longitudinal cleavage of the second, third and fourth segments, the last also splitting transversely.

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NOTES ON SOME CARBONIFEROUS PLANTS FROM NEW SOUTH WALES.

By A. B. Walkom, D.Sc.

(Plate xviii.)

[Read 28th November, 1934.]

Some four years ago the late Sir Edgeworth David asked me to examine a small collection of Carboniferous plants. This collection had been gathered together in connection with the works of Sir Edgeworth David and Mr. C. A. Süssmilch on the Upper Palaeozoic formations of New South Wales, at a time when there was much discussion as to the correlation of the Australian Carboniferous-Permian succession with that of other continents. It was hoped that a detailed examination of the plants would contribute towards the solution of this problem. The opinions prompted by the examination were communicated verbally to Sir Edgeworth, but various circumstances have caused undue delay in the completion of the work for publication. My thanks are due to Dr. G. D. Osborne for much information regarding the localities and the horizons on which the species occur.

The reference of more or less fragmentary Carboniferous plants to their correct genera is not an easy task without opportunity of comparison with type specimens. The descriptions published below represent some small additions to our knowledge of the Carboniferous flora of New South Wales.

The species described are: *Rhacopteris ovata* (McCoy), *Cardiopteris* cf. *frondosa* Göppert, ?*Sphenopteridium cuneatum*, n. sp., ?*Noeggerathia* sp., *Adiantites*(?) *robustus*, n. sp.

The specimens were all obtained from rocks belonging to the Upper Stage of the Kuttung Series. This Series has been divided into three Stages by G. D. Osborne, viz., Basal, Volcanic and Glacial Stages. In nearly all the localities from which the fossils under examination were obtained the horizon represented is somewhere about the middle of the upper (Glacial) Stage. The number of species present is small, but the distribution and association of these species supports the suggestion that in the various localities the plant-bearing strata represent approximately the same horizon. The distribution of the species is as follows:

Paterson: *Rhacopteris ovata*, ?*Noeggerathia* sp.
Felspar Creek: *Rhacopteris ovata*, *Adiantites*(?) *robustus*.
Hawes Farm: *Adiantites*(?) *robustus*, *Cardiopteris* cf. *frondosa*.
Hillsborough: *Adiantites*(?) *robustus*.
Brandy Hill: *Rhacopteris ovata*.
Westbrook: *Rhacopteris ovata*.
Moonabung: *Adiantites*(?) *robustus*.
Currabubula: *Sphenopteridium cuneatum*, ?*Noeggerathia* sp., *Cardiopteris* cf. *frondosa*, *Adiantites*(?) *robustus*.

This collection of species indicates a flora essentially of Lower Carboniferous age when compared with floras in the Northern Hemisphere. *Rhacopteris* occurs in both Lower and Upper Carboniferous, but is comparatively rare in Upper Carboniferous; *Noeggerathia*, *Sphenopteridium* and *Cardiopteris* are Lower Carboniferous genera, though forms of similar habit to *Cardiopteris* occur in the Upper Carboniferous and it is possible that *Neuropteridium* of Triassic age may not be generically distinct from the *Cardiopteris* of the Carboniferous; *Adiantites* occurs in both Lower and Upper Carboniferous.

RHACOPTERIS OVATA (McCoy).

Otopteris ovata McCoy, *Ann. Mag. Nat. Hist.*, xx, 1847, p. 148, Pl. ix, fig. 2.—*Rhacopteris inaequilatera* Feistmantel, *Mem. Geol. Surv. N.S.W.*, Pal. No. 3, 1890, 97.—*Aneimites ovata* Arber, *Q.J.G.S.*, *lviii*, 1902, 21; Dun, *Rec. Geol. Surv. N.S.W.*, viii (2), 1905, p. 159, Plates xxii-xxiii.

That the plant referred to *Rhacopteris inaequilatera* Göppert by Feistmantel (1890, p. 97) is identical with that named *Otopteris ovata* by McCoy (1847, p. 148) has been shown sufficiently clearly by W. S. Dun (1905), and the specific name *ovata* must be retained for the plant. *Otopteris ovata* McCoy was transferred to Dawson's genus *Aneimites* by Arber (1902, p. 21) chiefly on the grounds on which Etheridge had assigned a Queensland plant to that genus under the name *Aneimites austrina*. Etheridge's species, however, differs from the specimens described by McCoy and Feistmantel in the important particular that it is a bipinnate form, whereas the latter are simply pinnate, and there is considerable difference in the pinnules, both in shape and venation. Dun expressed the opinion that there is a strong generic resemblance between the two, but he retained *austrina* as a species distinct from *ovata*.

The reference of the species *ovata* to the genus *Aneimites* has little, if any, evidence to support it. Arber, as noted above, referred it to *Aneimites* because Etheridge included the species *austrina* in that genus. In view of the fact that the species *austrina* is apparently very distinct from *ovata*, this reference is not convincing. Dun (1905, p. 159) excluded *ovata* from the genus *Rhacopteris* on the ground that it could not be included under Schimper's original definition of that genus in which "the pinnules are more or less deeply incised in the direction of the nervures, so that each segment contains one or two branches of the nervation" (1869, pp. 481–2). This, however, overlooks the fact that Schimper extended his conception of the genus in 1879 and included species such as Göppert's *R. inaequilatera* in which the pinnules are not so incised. Kidston, before his death, had commenced a Monograph of the Fossil Plants from the Carboniferous Rocks of Great Britain, of which he completed six Parts. His description of the genus *Rhacopteris* may be quoted here, in view of the abundance of the species *ovata* on certain horizons in the Carboniferous of New South Wales. He defines it as follows (1923*b*, p. 203): "Frond pinnate, linear, narrowing towards the base and contracted into a point at the apex. Rachis straight or rarely slightly flexuous. Pinnules alternate, close, overlapping or touching, sometimes more or less distant, flabelliform, semiflabelliform, or rhomboidal, entire, crenate, lobed or divided into narrow linear segments, placed at right angles or slightly obliquely to the axis. Fructification (in the only known case) consists of a terminal dichotomous panicle, which bears exannulate sporangia."

Since this description was published, Walton (1926) has added to our knowledge of the genus by his description of a specimen with fronds attached to a stem, and of a specimen showing the fructification.

The species *ovata* appears to differ quite distinctly from figures of typical *R. inaequilatera* Göppert, especially in the general shape of the pinnules and in the absence of the marked unilateral character of the venation of Göppert's species.

Walton (1926, p. 208) has suggested that *R. inaequilatera* Feistmantel (*non* Göppert) should be assigned to the new species described by him as *R. circularis*. If this were so, it would seem that *R. circularis* Walton would have to be regarded as a synonym of *R. ovata* (McCoy), with which *R. inaequilatera* Feistmantel is considered to be synonymous. However, the Australian species appears to differ just as much from *R. circularis* in its venation and in the shape of the pinnules as it does from the European *R. inaequilatera*, and there is no adequate reason for considering it synonymous with either of the European species mentioned.

Localities: Paterson, Sugarloaf Creek, near Stroud, 5 miles N.E. of Stroud, Westbrook, Brandy Hill, Felspar Creek, and Sawyer's Point, Karuah R.

CARDIOPTERIS cf. FRONDOSA Göppert. Plate xviii, fig. 1.

Specimens from Currabubula and Gosforth are considered to belong to *Cardiopteris*. They have large, more or less semicircular pinnules attached to the rachis at the central part of the straight side where the lamina narrows to form a very short petiole. The pinnules are from 15 to 26 mm. long and 23–32 mm. wide. The venation consists of a series of fine veins radiating from the point of attachment and curving gently outwards. The outer margin appears to be broadly lobed.

It is impossible to say from the few fragmentary specimens available whether they are different from described species such as *C. frondosa* Göpp., *C. polymorpha* Göpp., and *C. Hochstetteri* (Ett.). They differ, for example, from some figured examples of *C. frondosa* in having the pinnules longer than broad and in being narrowed to a somewhat more definite petiole. The degree of difference between previously described species is not great, as evidenced by the fact that Oberste-Brink (1914) joins *C. polymorpha*, *C. Hochstetteri* and other species as synonyms with *C. frondosa*.

Localities: Hawes Farm (Gosforth), and Currabubula.

? SPHENOPTERIDIUM CUNEATUM, n. sp. Plate xviii, fig. 2.

Two specimens from Currabubula are with some hesitation referred to the genus *Sphenopteridium* Schimper, and described as a new species. They are both rather fragmentary, but show portions of a frond which is at least bipinnate and has a comparatively stout rachis, whose surface bears numerous fine longitudinal striations. The pinnae are alternate or almost opposite and, where complete, have a general rhomboidal outline. The pinnules are elongate wedge-shaped, narrowed to a short footstalk at their base, and have the outer margins dissected more or less deeply. The venation is not well preserved, but it appears to consist of divergent fine veins which branch occasionally.

It is not always easy to decide the generic position of such specimens, especially without access to types of the various form-genera known from the Carboniferous. I have placed these specimens in *Sphenopteridium* rather than *Rhacopteris* in view of the apparent bipinnate nature of the frond. The pinnae

in these specimens indeed show a considerable degree of similarity to the deeply-dissected pinnules of *Rhacopteris transitionis* (cf. Kidston, 1923*b*, Pl. li–liii). It seems apparent, however, in our specimens that what I regard as pinnules do definitely narrow into a short footstalk, and are not segments of a larger pinnule as in *R. transitionis*.

The specimens from Currabubula may belong to the same species as those figured by Dun (1905, Pl. xxii, figs. 1, 2) as *Rhacopteris intermedia* Feistmantel from Paterson, N.S.W. (they are inadvertently named *R. meridionalis* in the explanation of the Plate). One would be justified in regarding his figure 1 as portion of a bipinnate frond, and it might quite easily be that the much-dissected "pinnules" in his figure 2 are actually pinnae. Both the Currabubula and Paterson specimens would appear to be distinct from Feistmantel's figure and short description of *Rhacopteris intermedia* though, as Dun points out, Feistmantel's figure (1890, Pl. vi, fig. 3) does not altogether give an accurate impression of the character of the specimen. Our specimens show a somewhat close resemblance to *Sphenopteridium pachyrrhachis* Göppert, as seen by comparison with Kidston's figures of that species (1923*a*, Plate xxxvii, esp. figs. 6–7, and Pl. xxxviii, esp. fig. 1). The genus *Sphenopteridium* occurs in Great Britain only in rocks of Lower Carboniferous age.

Locality: Currabubula.

? Noeggerathia sp. Plate xviii, fig. 3.

A few specimens are doubtfully referred to *Noeggerathia*. They consist of axes bearing ovate pinnae which have numerous fine radiating veins which divide frequently. The pinnae merge gradually into a short petiole and they do not appear to be attached laterally as they are in *Rhacopteris*. The general shape of the pinnae resembles that in *N. foliosa* (cf. Seward, 1910, fig. 302, p. 429); *N. saxonica* Gothan has larger and more elongate pinnae.

Generic determination of these fragmentary specimens is not easy, and they are placed with *Noeggerathia* for the present, in the hope that discovery of better specimens may at some future date enable more precise determination to be made.

Numerous fragmentary specimens from Paterson may belong to this genus. Gothan (1931) states that *Noeggerathia* has the leaves attached to the stem spirally. The Paterson specimens have the leaves not attached in regular vertical series, and one specimen (No. 24) appears to indicate definitely a spiral arrangement. This may account for the irregular appearance of those specimens in which several pinnules are preserved.

Localities: Paterson and Currabubula.

Adiantites(?) robustus, n. sp. Plate xviii, fig. 4.

Frond bi- (? tri-) pinnate. Pinnules large (1·5 × 1 cm.), inaequilaterally cuneate, with well rounded apices and gradually contracted to short petiole at base. Apical pinnule larger (2 × 1·5 cm.), usually with broadly lobed margin. A single vein enters each pinnule and divides repeatedly, thus producing numerous fine radiating veins.

These specimens are referred to the genus *Adiantites* with some hesitation. The pinnules may be compared with those of *A. tenuifolius* (cf. Kidston, 1923*a*, Pl. xlv, fig. 5), and also with some examples of *A. adiantoides* (cf. Kidston, ibid., Pl. xlv, figs. 4 and 4*a*). In these latter the terminal pinnules closely resemble the specimens described here.

Localities: Felspar Creek, Seaham; Hillsborough, Moonabung, Hawes Farm, and Currabubula.

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EXPLANATION OF PLATE XVIII.

Fig. 1.—*Cardiopteris* cf. *frondosa*. Nat. size.

Fig. 2.—?*Sphenopteridium cuncatum*, n. sp. ×4/3.

Fig. 3*a*, 3*b*.—?*Noeggerathia* sp. Fig. 3*a*, nat. size; 3*b*, ×2.

Fig. 4.—*Adianites* (?) *robustus*, n. sp. ×4/3.

The photographs were taken by Mr. H. Gooch, of the Geology Department of the University of Sydney, to whom my thanks are due for his excellent results obtained from somewhat unsatisfactory material.

RICHARD HIND CAMBAGE.
1859–1928.

(*Memorial Series No. 4.*)
(With Portrait.)

Cambage designed and erected a life structure which rested on sure and strong foundations, one which was at once dignified, imposing, and eminently serviceable. He sought the truth always in his work; he was a wise and loved counsellor; a renowned peacemaker, although steadfastly setting his face against exhibitionism and chicanery in science; a man with true domestic instincts; an excellent citizen, passionately devoted to the cause of philanthropy, as well as to that of natural science.

Cambage's scientific career was determined at a somewhat early period of life, and there were no breaks, or sharp cusps, to interrupt the even sweep of the curve marking the path of his continuous progress. Once having determined on a course of action he never looked back.

Possessed of an ambitious and progressive nature, he, even as a mere youth, saw very little hope of solid accomplishment in the joint working of a farm. He thereupon entered upon the profession of land surveying, which kept him in touch with Nature in all its moods. From this surveying apprenticeship, he passed on to high executive positions, not only in survey, but in scientific councils, which, however, were all of an honorary nature. As President and Secretary of many important scientific societies, his work brought him into intimate contact with all the leaders of scientific thought in Australasia. His relations with his colleagues were unusually harmonious, being singularly free from jealousies, or aversions of personal or professional nature. His marked tact and love of peace smoothed over many difficulties of the kind which naturally arise in discussions involving not only expenditure of important trust funds, but principles also of professional and scientific procedure.

He had no enemies, and all esteemed it a privilege to be his friend, even when he strongly opposed measures which, in his opinion, were not in accordance with true scientific spirit. His services were sought also in matters of public speaking at scientific functions, his voice for such being excellent—strong and pleasing, his method of address simple, clear, frank, convincing, and full of kindliness.

Cambage's whole scientific life might be summarized, on the one hand, as a gradual but uninterrupted progress from the position of a mere ardent lover of Nature, to that of a keen student becoming more impelled, by his own self-perfecting nature, to concentrate first on the general study of plants, then to confine attention to phanerogams, thence through a few families to two large genera; and, on the other hand, as the history of one who, step by step, passed from the status of simple membership in societies and institutions to positions of the highest administration in same. Rarely, indeed, does one see these two

admirable qualities developed in the same individual. But Cambage could always be depended upon; once a scientific position had been accepted he saw it through thoroughly and cheerfully.

This gradual growth of an aptitude for specialization from an early, simple, and broad general love of Nature was merely an expression of his intense desire to understand the organic cosmos, which appealed so powerfully to his religious and aesthetic temperament. With this was coupled also the growing appreciation of the insufficiency of the ordinary individual span of life to compass the study of the cosmos as a whole. It was a natural sequence that he should undertake a disinterested and intensive study of a typical detail in Nature, such as the genus *Eucalyptus* or *Acacia*, as the best method of approach to the probable principle underlying all.

These progressive steps are plainly discernible. His boyhood and early adolescence on a farm facing the open sea, backed by high hills and rugged plateau slopes, the latter covered with magnificent forest and jungle growths, beheld the ordinary Nature student change into the ardent naturalist. Guiding the plough through the cultivation areas; learning to ride "buckjumpers"; or rough-riding after cattle "across country" in the wild fastnesses of the Milton hinterland, he was accustomed to the ways of all the native birds and animals. He knew, almost instinctively, what class of country he wandered into, from the general appearance of the vegetation, or from the familiar sounds of the birds around; whether near the sea, within the coastal ranges, on the high plateaus, the inland slopes, or the western plains. He could reproduce the calls of almost every bird and "animal" in the South Coast district, while his mimicry of the chatter of aborigines was indescribably faithful and humorous. Only, however, on rare occasions could he be persuaded to exercise these gifts of mimicry to his friends, as he had an abhorrence of public display of knowledge or skill.

Such was the grand early mental equipment which, later, was to express itself in an original contribution to our knowledge of plant associations in Eastern Australia.

When the necessity arose to leave the home, with all its cherished associations, and to face the outside world, with its keen competition, his strong domestic instincts produced an actual feeling of keen dislike towards certain natural objects encountered in the new sphere, and to the presence of which he had been accustomed daily during his previous home life. Thus for years he could scarcely endure the pungent scent, and blaze of purple bloom, of the mint-bush (*Prostanthera incisa*) in spring-time. "As I scrambled up the precipitous sides of the National Park gorges", he said, "clinging to the 'mint' bushes for support, and thinking of home at the same time, the scent of this beautiful shrub produced a strong sense of aversion in me." This was merely the natural outcome of the presence of an external stimulus, whereby he had been forced from a cherished spot containing certain plant associations which he loved, to another, with similar natural associations, but with a totally different residential environment.

His work as a surveyor led him into many strange and unsettled areas, preventing him, for very many years, from having much settled "home" life. Nevertheless, to one possessed of his strong domestic leanings, the ordinary routine life of a field surveyor was insufficient to satisfy the ever-present ideals of progress, and to keep the mind occupied satisfactorily between times. To this end he commenced seriously the study of botany, not with the view of becoming

a taxonomist, but rather with the object of understanding plant assemblages and their environment, especially in connection with temperature, rainfall, atmospheric humidity, soil, "aspect", and physiography, generally.

It was his custom, on long "outback" surveying undertakings, to note and collect all the main plant types occurring along the road (or railway line), the mile pegs being favourite data for locality reference. The specimens secured thus he studied later with the aid of detailed "lands" maps, and in this way gradually ascertained the general range of various endemic genera and species of phanerogams. The cryptogams, outside the vasculares, he did not study in detail, as, with few exceptions, they were not among the larger or conspicuous plants seen along his routes. From constant observation, aided by an intelligent use of a surveyor's tomahawk, his knowledge soon eclipsed that of Jem, the Splitter, and of whom Cambage himself continually said:

"His knowledge was this—he could tell in the dark
What timbers would split by the feel of the bark."

He would wax enthusiastic, and begin to quote from his favourite authors, Shakespeare and Scott, as soon as he saw the first outposts of a plant, hitherto unfamiliar, or unknown, to him, coming into view. He would examine the stranger, name it provisionally; note its peculiarities, whether xerophilous or otherwise, frequenter of forest, jungle, or open land, lover of sandy soil, acid swamp, drained hillside, bleak plateau, eastern or western fall, and so on. Upon the recurrence of similar geographical and soil conditions, in another area, he would commence the search for the expected "strangers", and his excitement and enthusiasm would run high as he found his expected plants and animals, one after the other. He would clap his companion's shoulder suddenly, and pointing repeatedly, but with increasing emphasis, rapidity, and precision, in a certain direction, he would exclaim:

"And still from copse and heather deep
Fancy saw spears and broadswords peep."*

"And there, my friend, peeps also the new eculapyt (or other rare plant) I have been expecting."

At the outset of each trip he would enter the name *Wahlenbergia gracilis* (blue-bell) on his list of plants seen, because he knew the ubiquitous nature of the little flower. So soon as he had seen it actually en route, he would stop at the nearest post-office and send a telegram to his old friend, J. H. Maiden: "Great news, have just seen *Wahlenbergia gracilis*." This little joke would cheer the hearts of Cambage and Maiden for days, and was merely an excuse to let off some superfluous exuberance of spirits. It helped Maiden wonderfully also, as in mind he saw himself with Cambage in the open gathering in the rich harvest of the Australian flora.

Like the late J. E. Carne, a former Government geologist of the State, Cambage appeared to have an intuitive knowledge of "direction", finding his way, as it were, instinctively, in the wildest areas of the eastern States. His knowledge of the individual species to be expected in various plant assemblages caused him, from geographical considerations, to criticize the accepted classification of certain species which he had noted, so to speak, out of their proper associations. In this connection it is not out of place to state the pre-eminence of Cambage in naming a species, at a glance, from a distance. From a horse-drawn vehicle, motor-car, or fast-moving train, he could detect the plants with

* Scott, "Lady of the Lake", Canto v, Stan. xi.

an accuracy which only those botanical colleagues who were accustomed to travel with him could appreciate or even believe. It was not that he was blind to the motto, "Wherefore by their fruits ye shall know them", but he knew also that the plants carried tell-tale vegetal characteristics on a larger scale, and that the sum total of these and other traces were as sure as the great test of the fruits. His keen eye detected at a glance their "habit" of growth, their place in the plant association, their seedling forms, their "sapling stage" characteristics, their adventitious growths, adult appearance, inflorescence, the soils they favoured, and so on.

In this way he was enabled to direct the attention of the official authorities on plant classification to the fact that plants included hitherto under certain well-known species should themselves be raised to specific rank, as being distinct from any type species hitherto described. Thus, when for the first time he found that "gidgea" was confined, in New South Wales, to the Trans-Darling area north of Broken Hill; that it was a gregarious type, with a peculiar habit; and with a penetrating odour all its own; he at once knew it to be distinct from the species of Acacia occurring farther east, and within which previously it had been included. It was only natural to name the important new species *Acacia Cambagei*. Similarly, he indicated the necessary raising of the "belah" (a "she-oak") to specific rank. His geographical and ecological notes were so convincing that the new species was named *Causuarina Cambagei*. So also for *Eucalyptus Cambagei*. Only trained field botanists would be able to recognize the skill and intuition needed in an amateur botanist, pressed hard by the exigencies of technical work and of travel, without herbarium facilities en route, to enable him to recognize the specific rank of types which had been described and included under other species by excellent herbaria botanists.

The peculiar method of clearing up the difficulty surrounding *Eucalyptus pulverulenta* (Simms) and *Eucalyptus pulvigera* (Allan Cunningham) is an example of Cambage's keen "bush" insight. *Eucalyptus pulverulenta* (Simms) was named from seedlings grown in England in 1819. Allan Cunningham found and named *Eucalyptus pulvigera* in 1822. Cambage wondered whether some confusion had not arisen in this connection, when he read the descriptions. Thereupon, in October, 1904, in company with J. H. Maiden, he visited the Cox's River in order to find Cunningham's locality. His knowledge of bushcraft led him easily to the tree answering Cunningham's description. (He had already found these trees at Cow Flat, near Bathurst, in 1900—hence his criticism.) He experimented with seeds collected from Cox's River, and obtained seedlings which produced flowers within three years and six months, so that it was possible for seeds collected at Cox's River in 1813 to have been sent to England, then grown and described by Simms in 1819. The description of *Eucalyptus pulverulenta* fitted the young plants of Cunningham's *Eucalyptus pulvigera*, and thus an important point was settled satisfactorily in *Eucalyptus* taxonomy.

Gradually he was led from the simple Linnean classification of his plants into genera and species, to the recognition of their proper places in their families. This later step assisted him materially during the visit of the botanists attending the British Association Meeting in 1914.

Three great departures were made from his earlier "naturalist" collecting as time progressed, one being the recognition of the important edaphic, geographical station, and climatic "aspect", factors in the Australian vegetation; the second being the special attention directed to the genus *Eucalyptus*; and the

third being the special attention devoted to the seedling stages of the genus *Acacia*.

It is well known to students of soils that, with a rainfall exceeding a certain figure (proportioned to the temperature variations of a locality), the vegetation tends to become less and less dependent on the soil factor, as seen so well in the "tapestry" and swamp vegetation of western New Zealand, of New Guinea (rain forest), Java, and Ceylon. In Australia, however, owing to the long continued and generally low rainfall of the continent, the edaphic factor is one of the most important in the study of the endemic Australian flora. This point Cambage had studied closely, having selected the main types of Australian rocks, and obtained the quantitative chemical analyses of each. Thus, from the mere inspection of a typical rock specimen from an extensive geological formation or occurrence in Australia, and having the additional knowledge dealing with its position in latitude and longitude, the general height of the area concerned above sea level, he was able to forecast all the larger plant forms to be expected from such area.

The study of soil and climate led him, gradually, to specialize in the study of the Eucalypts. In this subject he attained eminence. The study of the genus *Eucalyptus* he commenced with the Rev. Dr. W. Woolls, for whom he made plant collections between 1880 and 1890, and from whom he received his first botanical lessons. Later he worked carefully over the various *Eucalyptus* species with his colleagues and friends, J. H. Maiden, Henry Deane, J. J. Fletcher, R. T. Baker, H. G. Smith, E. Cheel, and others.

His intimate acquaintance with the more generalized, or primitive, forms of the genus, coupled with the knowledge that the "Eucalyptus" fossils recorded from the various Tertiary deposits of the northern hemisphere did not at all suggest the forms of *Eucalyptus* as known to Australian botanists, led him to follow Bentham, Engler, Deane, and others, in rejecting as absurd the idea that the genus "*Eucalyptus*" had been cosmopolitan in its range, with later contraction of habitat to the Australasian region. His work, as also that of his colleagues, indicated, definitely, that this great genus, exceeding four hundred species, and exhibiting a most marked vitality and plasticity, had originated in Australia and had never moved far from the land of its birth.

The contemplation of the eucalypt monarchs of Eastern Australia, exceeding three hundred feet in height, in very many instances, stirred the aspiring side of Cambage's nature. The writer has seen Cambage and Maiden lost in wonder and admiration at the sight of these forest giants. During such reverent contemplation, one or the other of the two would never fail to make the remark to the effect that the close study of such magnificent organisms definitely tended to free the mind from any meanness or pettiness of character.

During his visit to Japan in 1926 as a Commonwealth delegate to the Third Pacific Science Congress, via the Malay Archipelago and the Philippine Islands, Cambage became much impressed with the idea that, not only had the Wallace and the Weber Lines been obstacles to any general spread of Eucalyptus beyond Australia, but that another and extremely important barrier had been opposed to their dispersion by the enormous "rain-forest" belt of New Guinea and the associated regions. This vast compound island arc, one of almost perpetual precipitation, was a sufficient barrier to eucalypt movement towards Asia, especially where associated with seaways instead of areas of relatively low rainfall.

Noteworthy, however, as were the contributions of Cambage to our knowledge of the geographical distribution of *Eucalyptus*, they are eclipsed by his detailed observations on the youthful stages of *Acacia*.

The published work of his colleagues suggested that the ancestral form of *Acacia* was a tree or woody shrub, with leaves simply pinnate, a regular corolla, and with stamens definite and free, as suggested by a careful study of the genera *Mimosa*, *Parkia*, *Acacia*, and *Inga*, and of the closely-related family (Caesalpiniaceae) of the Cassias. Cambage, with his great love for the weight, as well as the nature, of the evidence, determined to throw as much light as possible on this important problem, by the examination of the young stages of growth in the various species of the genus. He recognized the magnitude of the task which lay before one who should experiment conscientiously with the whole 700–1,000 species recorded (more than 500 endemic Australian species). In the first place there would be the difficulty experienced in securing seeds for planting; in the second, the extreme difficulties to be met in ascertaining whether the plants grown from seeds would be true to type; in the third place, the necessity for extensive garden facilities for the growing of numerous individuals in each species, and for making careful observations, measurements, notes, and photographs, of the several critical stages of seedling development. He decided thus to select typical plants as a beginning, and to confine his attention to the careful observation and description (for publication) of ten good species each year. Naturally his attention was specially turned towards the phyllodineous forms so characteristic of Australia.

The seeds chosen by him were examined carefully, the size, shape, and colour being noted. Six to eight seeds were planted in a pot. Notes were made of the dates of planting, and of the first appearance of the seedlings; the size, shape, and colour of the stem, cotyledons, first leaf, second leaf, and so on; also the distance apart of the leaves as measured along the stem.

One plant of each species, in the cotyledon stage, was secured, pressed, and described. Each leaf was pressed separately. It was found preferable to adopt this procedure, inasmuch as the earlier leaves became damaged, or fell off, if left to themselves on the plant, until the seedling had reached the final stage for observation purposes. These leaves were noted carefully and numbered, and were placed in position later on the plant for photographic records. The seedlings were allowed to grow until the adult foliage had developed definitely; pods and seeds were photographed with the seedling. *Acacia* species, to the number of 133, have been described in the *Journal of the Royal Society of New South Wales*. A number of other species were described fully and a number also in part, but not published because of Cambage's sudden illness and death. "This work", according to Walkom, "is to be carried to completion at the Botany School of the University (Sydney) under the care of Professor T. G. B. Osborn."

In the work of tending, observing, and photographing the seedlings, his daughter, Miss M. Cambage, assisted very materially, and to her also is due the preparation of the accompanying list of Cambage's scientific publications.

Richard Hind Cambage was born at Milton, New South Wales, on the 7th November, 1859. He received his early education at State and private schools. He was employed as a teacher, for a short time, in the Milton State School, under Mr. H. Skillman.

At the age of eighteen years he was attached, as assistant, to Mr. Surveyor M. J. Callaghan, with a view to entering the surveying profession. While with Mr. Callaghan he was engaged, firstly, in the districts surrounding Milton, passing thence to Yalwal, and later to National Park, in 1879 and 1880, at which time it was surveyed by Callaghan. At the time of that survey, the Park was practically inaccessible and almost unknown. It could be reached by the mail coach, which left the General Post Office, in Sydney, every morning for Kogarah; thence one had to make private arrangements to reach the Park itself. The Illawarra Line was not opened as far as Hurstville until 1884. "Exciting moments were experienced while crossing Port Hacking in a boat, behind which the saddle horses, firmly held, were accustomed to swim. The dingo was exceedingly common about National Park in those days, and the howling of numbers of these wild dogs of an evening, as they emerged from the Woronora Gorge", caused the youthful student Cambage to experience horripilation and a feeling of intense "creepiness", especially in the loneliness of a bush camp.

Part of his training was with Surveyor F. L. Burdett, in the Manly area. He studied mathematics under the late H. S. Hawkins, and obtained the designation of Licensed Surveyor in June, 1882, having previously passed the examination for Draftsman in the Lands Department.

After being engaged for three years as a draftsman in that Department, he was appointed, in 1885, to the Department of Mines as a mining surveyor.

From 1903 until 1918 he was a member of the Licensed Surveyors' Examination Board, and, from 1909 until 1915, Lecturer in Surveying at the Sydney Technical College.

Three times (1907-1909) he accepted the office of President of the Institute of Surveyors.

His duties as Mining Surveyor caused him to visit every mining field of importance in New South Wales, with the exception of Broken Hill, which he only visited as late as 1921, in another connection.

Many instances of the caprices of mining fortune came under his notice as years passed. During the silver boom in 1885, he was camped at Wiseman's Creek, near Bathurst, for a period exceeding two months, surveying leases for silver, and, with the exception of several blocks, the whole of the leases were abandoned within a few months.

He had a similar experience near The Peaks, at Burragorang, whereas, a mere couple of miles away, lay the rich silver lodes of Yerranderie, which, however, were not discovered until years after.

Again, during the great silver boom at Rivertree, Boorook, Boonoo Boonoo and Drake, he measured leases for silver month after month about 1887, only to see most of them abandoned shortly after measurement.

While surveying leases at Barmedman in December, 1893, he heard of the discovery of gold at a farming centre called Wyalong, a few miles away. The announcement caused no marked excitement, and few there were who could have foreseen the meteoric rise of this field, which produced, within a few years, gold to the value of £1,500,000.

Again, when Cambage was engaged measuring a gold lease, on the 26th December, 1896, over an old "prospecting" shaft at Mount Boppy, about twenty-eight miles easterly from Cobar, very few could have foreseen that this lease

covered the famous "inverted saddle" reef of Canbelego, which produced gold to the value of £2,000,000, approximately, between 1903 and 1918.

Cambage, in his humorous way, summarized one aspect of the history of gold and silver mining in the State by reference to an instance of faith in mining which came under his personal notice in New England about 1889.

"A promising-looking gold reef had been discovered in an uninhabited locality, and the land pegged around in all directions, over one hundred gold leases being applied for, though no additional discovery of any significance was made. A battery was being erected, on the original field, and, in the meantime, the whole energy of the new arrivals was devoted to the purpose of building a town. Allotments were 'pegged out', sold, 'jumped' by the original holders, and resold; buildings of sawn boards and galvanized iron were erected; shops opened; a progress committee formed; and a very large stump was planed carefully to do duty as a billiard table. Finally, the battery was completed, but the first 'crushing' put through proved the reef to be unpayable; the houses began to fall like houses of cards, and were carted whence they came. Old 'diggers', speaking of the incident later, would remark that there were two 'rushes' in connection with that field, one to it, and the other from it."

Severe variations in climatic conditions were encountered in the various country centres visited in succession. In the Cobar-Canbelego district the thermometer had been seen at 120° F. in the shade; in the west or trans-Darling area, 125° F. in the shade had been experienced, whereas in the Kiandra district severe storms had interrupted surveying operations, necessitating a struggle once by him of fifteen miles through snow averaging twelve to twenty-four inches in depth.

Cambage, through his duties as a mining surveyor, had an excellent knowledge of the main coal occurrences and resources of the State. In the year 1900 he was commissioned to ascertain exactly the position of certain colliery workings situated under the Newcastle Harbour and the neighbouring ocean, and to determine also the amount of cover between such workings and the bed of the harbour or ocean above. This official decision was made as an independent check on the colliery surveys, inasmuch as hundreds of lives were affected by the condition of these underground workings. Cambage was accustomed, in this new work, to quote Shakespeare's line, "How use doth breed habit in a man", as he himself became accustomed to the litter, difficulties, and dangers, of a coal mine, with no more than 150 feet of coal between him and the ocean, and with the sound of ocean waves and of passing steamers distinctly audible at times.

Other experiences of Cambage may serve to illustrate the many-sidedness of his scientific and technical experience, and the high opinion in which he was held as a capable and honourable official.

Immediately after the disastrous explosion at the Mount Kembla Colliery in 1902, when more than ninety lives were lost, he was commissioned to make an official and detailed underground survey in the vicinity of the actual explosion about a mile from the colliery entrance, in order that a plan might be prepared indicating the position of objects, such as fragments of skips, rails, and other colliery material, as they were found after the explosion, from which the direction of the explosive activity might be deduced. His "careful and exhaustive examination" provided some of the principal evidence upon which the findings of the Royal Commission, appointed to deal with such matters, were based. This

finding by the Commission reversed the verdict which had been delivered previously by the coroner's jury, the members of which had deliberated without the invaluable aid of his survey.

In his survey of the Balmain Colliery workings, he found it necessary, as a preliminary, to transfer his azimuth, in one operation, from the surface to a depth of 2,920 ft. To overcome the unsteadiness of the plummet, which was continually and markedly inclined to the vertical (owing to descending water, strong air currents, and so on), he had recourse to various devices to obtain a satisfactory datum point below for his survey. He finally obtained satisfactory results by establishing a base line of 16 feet in length, swinging the plummets (31 lb.) freely in the air, and taking the mean of a series of oscillations as being the point vertically beneath the point of suspension of the plummet wire at the surface.

He was appointed Chief Mining Surveyor in 1902, a position which he held until his appointment in January, 1916, as Under Secretary of Mines.

He was a member of the Royal Australian Historical Society, and he was enabled to elucidate many difficult points in the interpretation of the records of certain explorers, by reason of his intimate knowledge of field survey methods, and of woodcraft in the State, together with his general knowledge of geography, geology and botany. Thus, although the journals left by the explorers did not always indicate definitely the paths followed by them, nevertheless Cambage was enabled to trace their paths by the land-marks mentioned by them. The bibliography attached indicates the more important of these retraced exploring paths.

His youthful experience at National Park caused him to question the completeness of the geological map of the area at that period, because of the peculiar vegetation which favoured a certain rock formation. Subsequent examination proved him to be right in relying upon the botanical indications. In 1828, Surveyor Florance had surveyed the coastal district of Ulladulla. In 1915, Cambage carefully examined Florance's field-book, and he noted there an entry "Two Flints". On visiting the spot, he noticed the rocks mentioned by Florance, and secured specimens for examination by the Department of Mines. As a result, this flinty material was ascertained to make an excellent firebrick, and an important industry was thereupon commenced.

Cambage retired from the Public Service on the 7th November, 1924. In addition to the positions held by him successively of Mining Surveyor, Chief Mining Surveyor and Draftsman, Under Secretary and Superintendent of Explosives, he occupied many other positions of trust in the State Civil Service, such as Chairman of the Prospecting Board, Mine Managers' Examination Board, and Licensed Surveyors' Examination Board.

Very little opportunity was afforded him for recreation, or even for the home life he so much valued, by reason of the increasing demands made on his time in non-official hours. More and more, as time progressed, was he besieged with requests to assist in the organization and administration of scientific, and related, societies and institutions, and in many other ways he assisted most definitely in the removal of the disabilities under which Science labours generally.

Positions of increasing responsibility and honour came during the period 1909-1928 inclusive. He was Secretary to the Royal Society of New South Wales for the period 1914-1928, with the exception of the years 1923 and 1924;

he was President of that Society in 1912 and 1923. To our Society, of which he had been a member since 1899, and a member of the Council since 1906, he contributed eighteen papers dealing with local plant assemblages in Australia. He was elected President in 1924.

He was an Elective Trustee of the Australian Museum from 1925 until his death.

He accepted the position of Honorary Secretary to the Australian National Research Council at its inception in 1919, and continued in that important position until 1926. As Secretary, he had the onerous task of organizing the Second Pan-Pacific Science Congress, held in Melbourne and Sydney in 1923. He was elected President of the Council for the period 1926-1928, and he was elected President of the Australasian Association for the Advancement of Science in 1928. Cambage, Sir T. W. Edgeworth David and Sir David Masson are the only scientists who have held both these important positions.

He was created C.B.E. in 1925. He, however, looked not so much to such a minor and belated recognition of his services as his true reward, as to the joy which comes from creative work undertaken in the quest of Truth.

It must not be forgotten that Cambage took an intense interest in ordinary human activities amid his scientific work. He was a member of the Masonic Order and held high office in local lodges. He retained his boyish enthusiasm to the last. This was shown in various ways. He had a great love of children, and had a wonderful way of explaining things simply to them. Sickness among his friends aroused his deepest sympathy and affection. Music affected him deeply, especially that composed in the major key. To the very last, the mere contact with Nature would set him whistling and singing tunes like a schoolboy on a holiday. Sports such as cricket appealed strongly to him. He attended all Test and Sheffield Shield matches, as well as many grade matches. He knew from memory all the major batting and bowling records since 1881. He was no indifferent player himself at the game. At Milton, one of his instructors in bowling was "Twopenny", a member of the team of aborigines which visited England in 1868.

Perhaps one of the most interesting sidelights shed on Cambage's nature is furnished by his association with the work of the "Australian Wattle League", founded in 1909 in Sydney, to inculcate the spread of a definite "wattle" sentiment in Australia. He attended the first meeting, and remained an enthusiastic member of Council from its inception. He occupied positions of Vice-President and Acting President. Members of our Linnean Council with whom he co-operated in this work will remember his keen desire to effect beautification of city and country landscapes by means of well selected Australian plants. His favourite method was to enlist the active and practical sympathy of children and adolescents, as he felt that, by this means, the work would be simplified and rendered more popular and permanent. The success of the efforts of himself and of his colleagues is reflected in the spread of "wattle" planting both in public and private gardens.

He married Fanny Skillman (died 1897), daughter of the late Henry Skillman. Their family consisted of two sons, Arthur and Geoffrey, and two daughters, Mabel and Muriel (Mrs. Holt). Both sons served in the European War.

Cambage, like J. H. Maiden, was deeply religious, but it was the ethical side of religion which appealed most to him.

Death came most unexpectedly, from an attack of heart disease, on the 28th November, 1928, at a time when, to all appearances, he was enjoying the best

of health. He became ill and died suddenly at his home, "Wyaglan", 49 Park Road, Burwood. A host shares the sorrow of his going. Tributes to his character have come in from all quarters. This feeling of general loss has been summarized by Walkom in the obituary note in our PROCEEDINGS for 1929:

"He will be sadly missed by all his colleagues and friends, for he possessed, to a rare degree, the qualities of tact, moderation, charitable judgment, and geniality, which made him beloved by all who knew him."

The loss which we all feel does not dim, rather does it reveal clearly, the advance and enrichment of science generally by workers such as Cambage, with the added joy, as exemplified in his life, of harmonious co-operation in scientific research.

E.C.A.

LIST OF PAPERS BY R. H. CAMBAGE.

(Prepared by Mabel F. Cambage.)

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1907.

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Botanical, Topographical and Geological Notes on some Routes of Allan Cunningham. *Journ. Roy. Soc. N.S.W.*, Vol. xliii, p. 123. (*With J. H. Maiden.*)

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1913.

On a New Species of *Eucalyptus* from Northern Queensland. *Journ. Roy. Soc. N.S.W.*, Vol. xlvii, p. 215. (*With J. H. Maiden.*)

"Development and Distribution of the Genus *Eucalyptus*." Presidential Address to the Royal Society of N.S.W. *Journ. Roy. Soc. N.S.W.*, Vol. xlvii, p. 1.

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The Birth of a South Coast Village. *Daily Telegraph*, 14th March, 1914, and *Ulladulla and Milton Times*, 21st March, 1914.

Dimorphic Foliage of *Acacia rubida*, and Fructification during Bipinnate Stage. *Journ. Roy. Soc. N.S.W.*, Vol. xlviii, p. 136.

Botany of New South Wales—The Western Plains. *Brit. Assocn. Adv. Sci.,* N.S.W. Handbook, 1914, p. 417. (*With J. H. Maiden.*)

Botany of New South Wales—Tableland and Sub-alpine Areas. *Brit. Assocn. Adv. Sci.,* N.S.W. Handbook, 1914, p. 407. (*With J. H. Maiden.*)

Eastern Australian Topography and its Effect on the Native Flora. *Rept. Brit. Assocn. Adv. Sci.,* 1914 (1915), p. 448.

Notes on the Evolution of the Genus *Eucalyptus.* *Rept. Brit. Assocn. Adv. Sci.,* 1914 (1915), p. 582.

The Mountains of Eastern Australia and their Effect on the Native Vegetation. *Journ. Roy. Soc. N.S.W.,* Vol. xlviii, p. 267.

Observations in North Queensland. *The Surveyor,* Vol. xxvii, p. 208.

Observations on some Reputed Natural *Eucalyptus* Hybrids, together with Descriptions of Two New Species. *Journ. Roy. Soc. N.S.W.,* Vol. xlviii, p. 415. (*With J. H. Maiden.*)

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Botanical Notes, Boggabri to Moree and towards New England. Guide Book to the Excursion to the Moree District and the Northern Rivers, p. 9. *N.S.W. Guide Books to the Pan-Pacific Sci. Congress, Australia.*

Exploration and Crossing of the Blue Mountains. Guide Book to the Excursion to the Blue Mountains, Jenolan Caves and Lithgow, p. 1. *N.S.W. Guide Books to the Pan-Pacific Sci. Congress, Australia.*

Botanical Notes on the Trip to the Jenolan Caves. Guide Book to the Excursion to the Blue Mountains, Jenolan Caves and Lithgow, p. 7. *N.S.W. Guide Books to the Pan-Pacific Sci. Congress, Australia.*

The Native Flora of the Federal Capital Territory. Guide Book to the Excursion to Yass-Canberra and the Murrumbidgee Irrigation Area, p. 9. *N.S.W. Guide Books to the Pan-Pacific Sci. Congress, Australia.*

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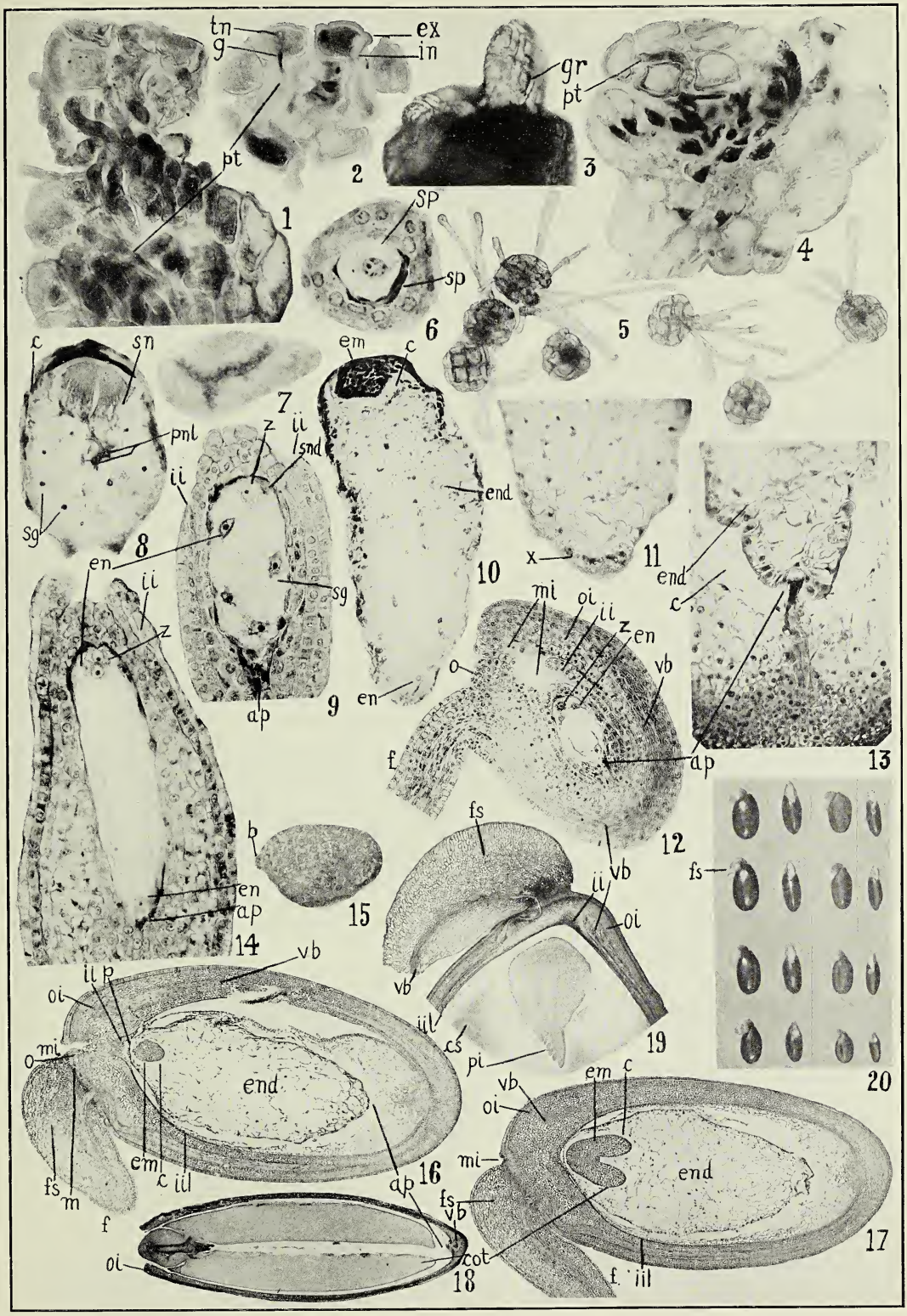
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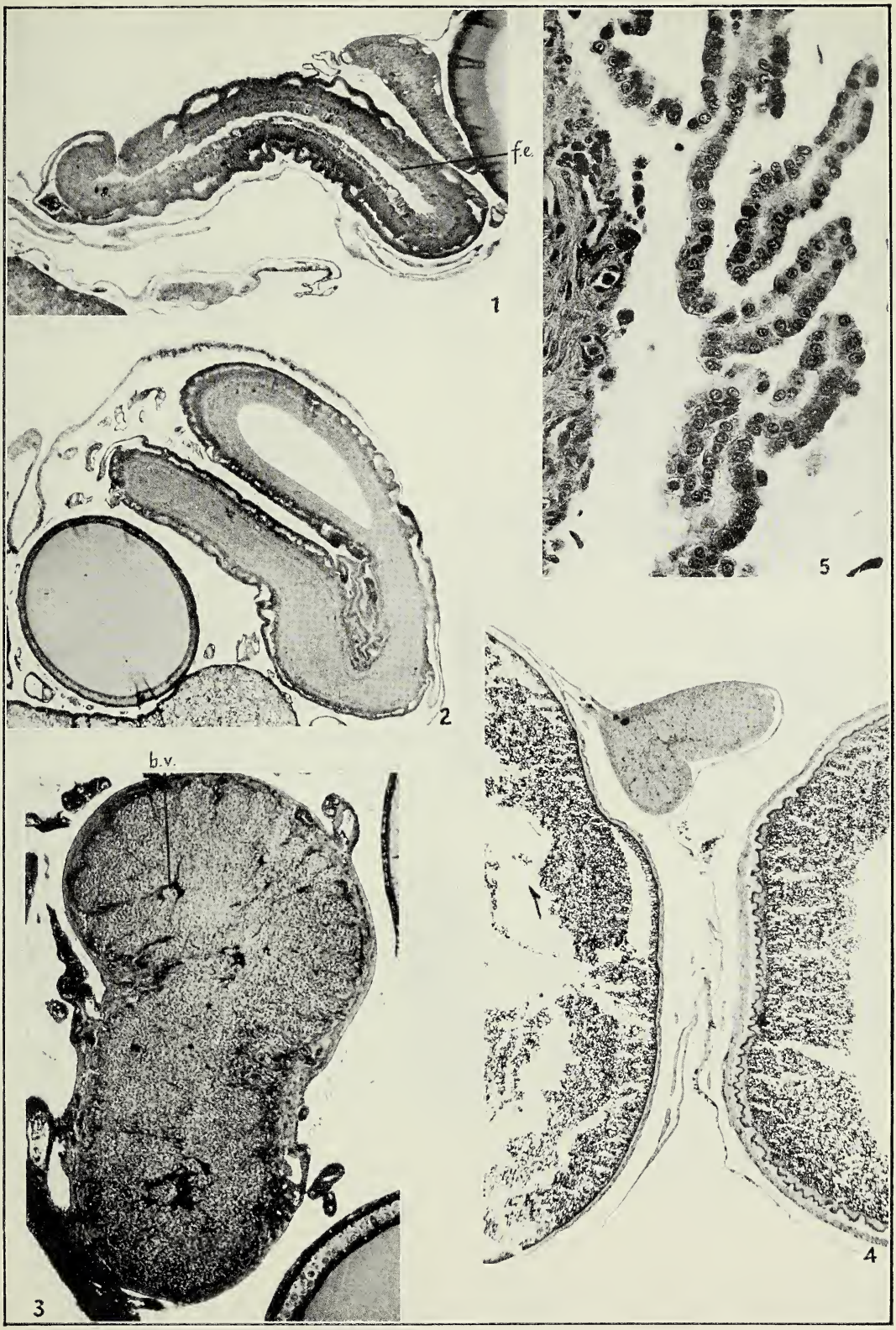
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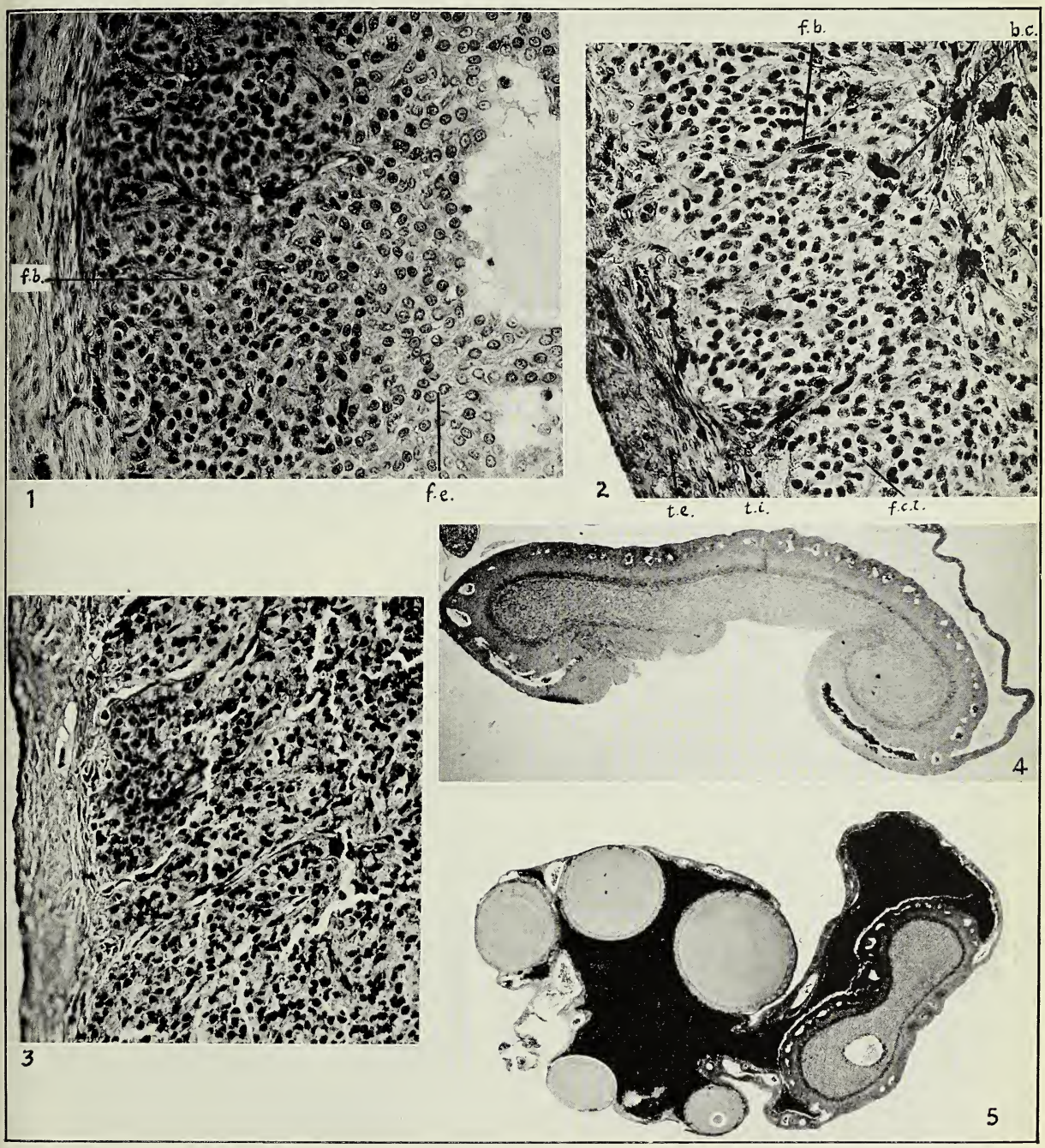
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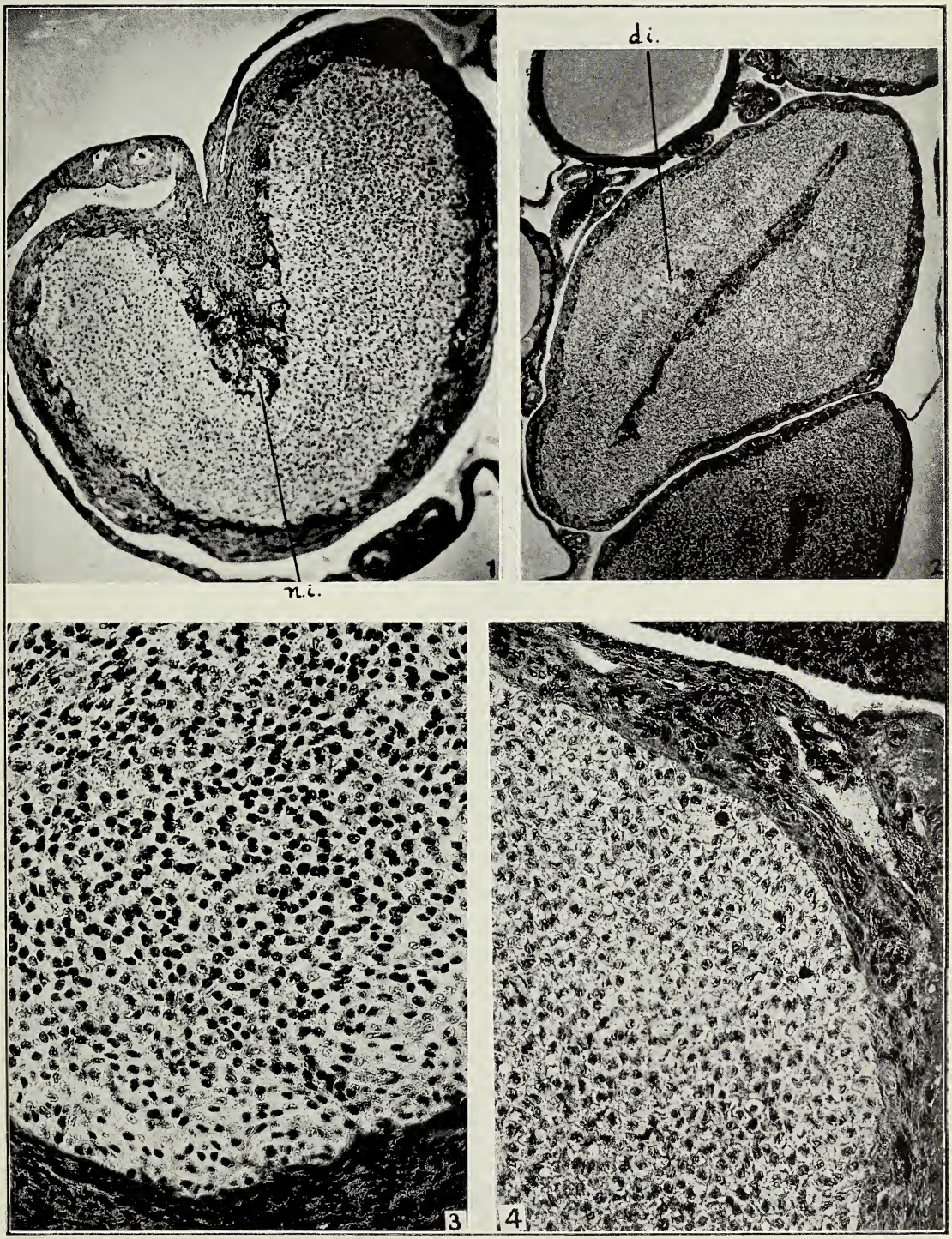
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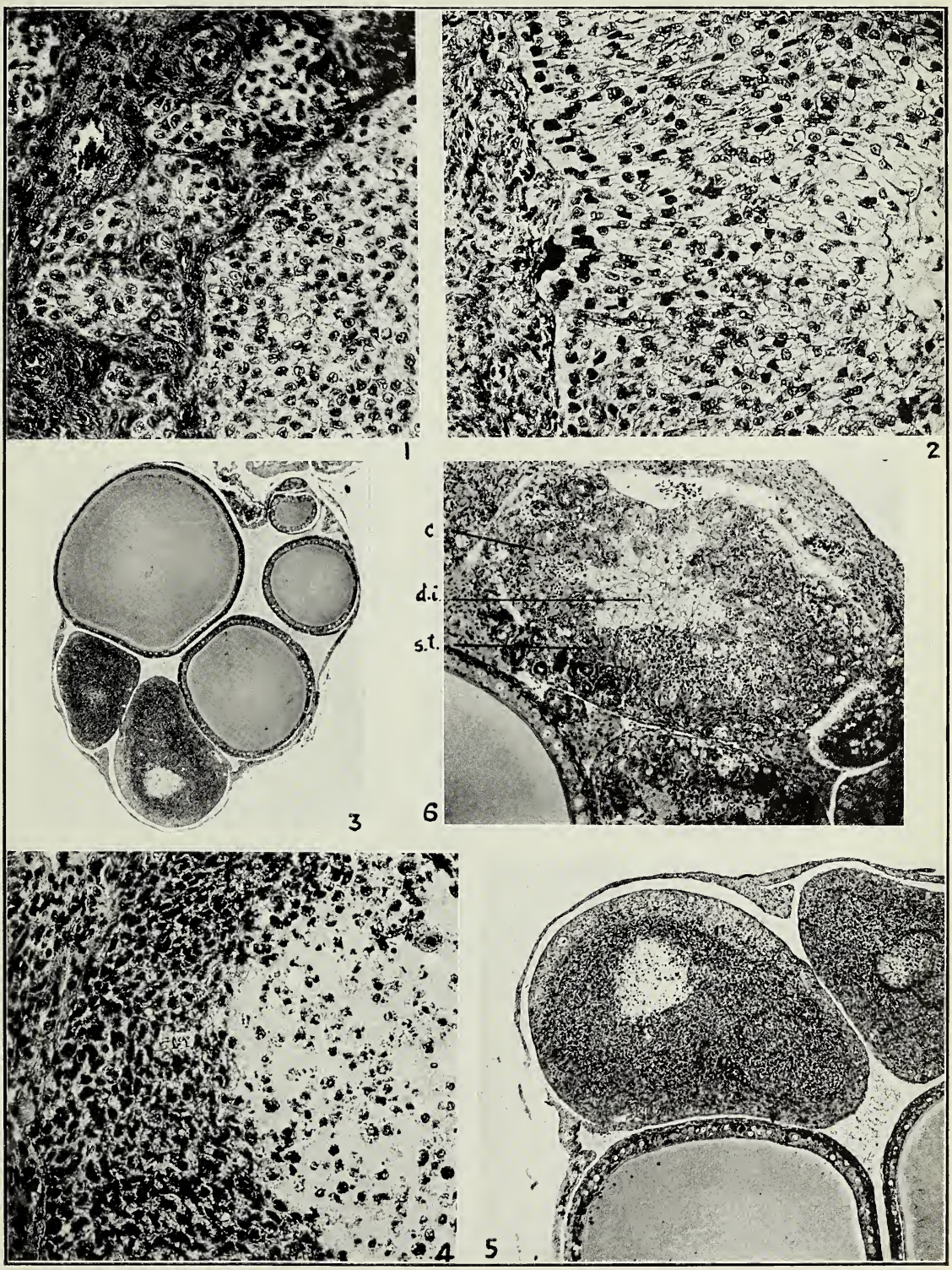
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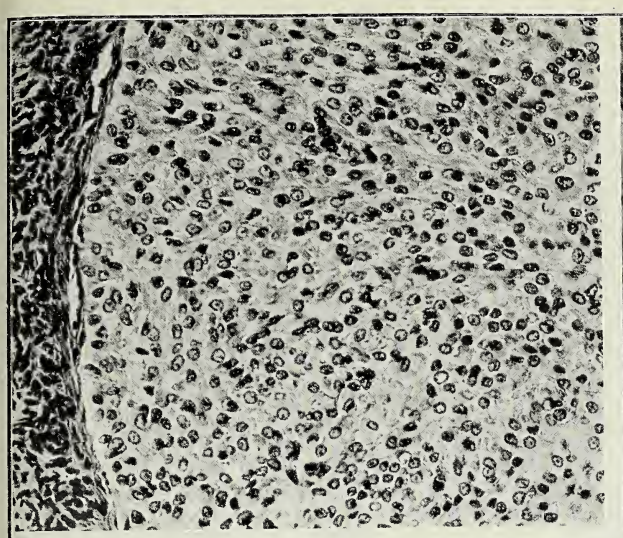

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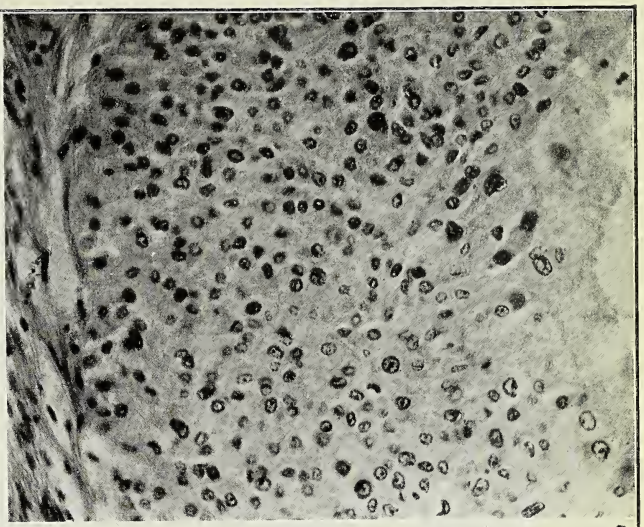

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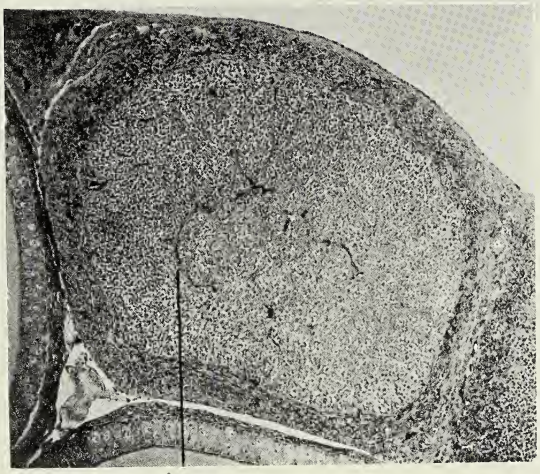

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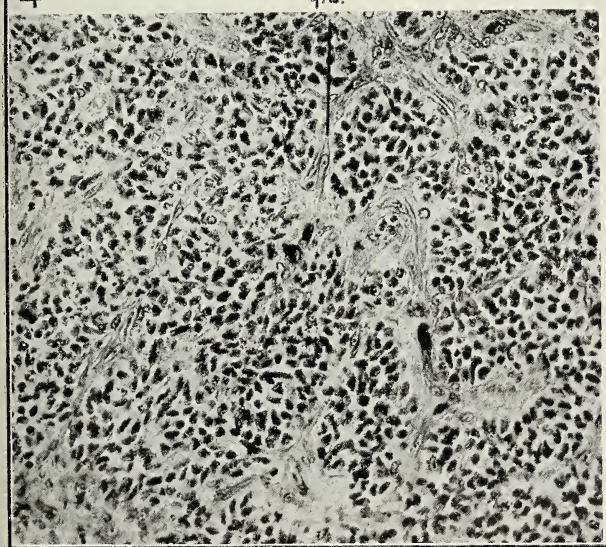

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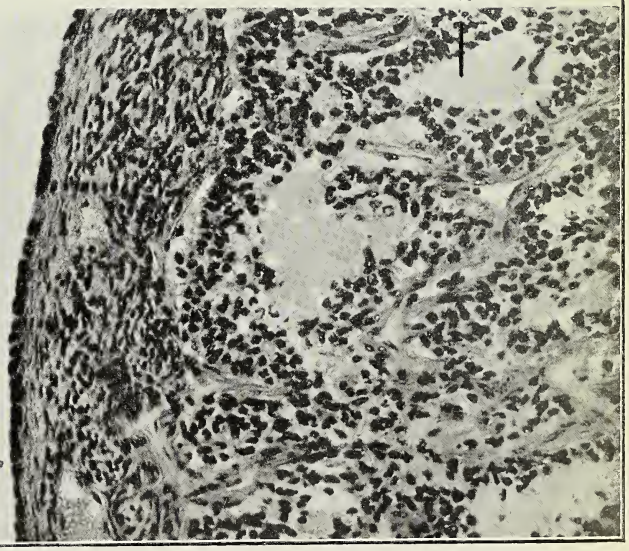

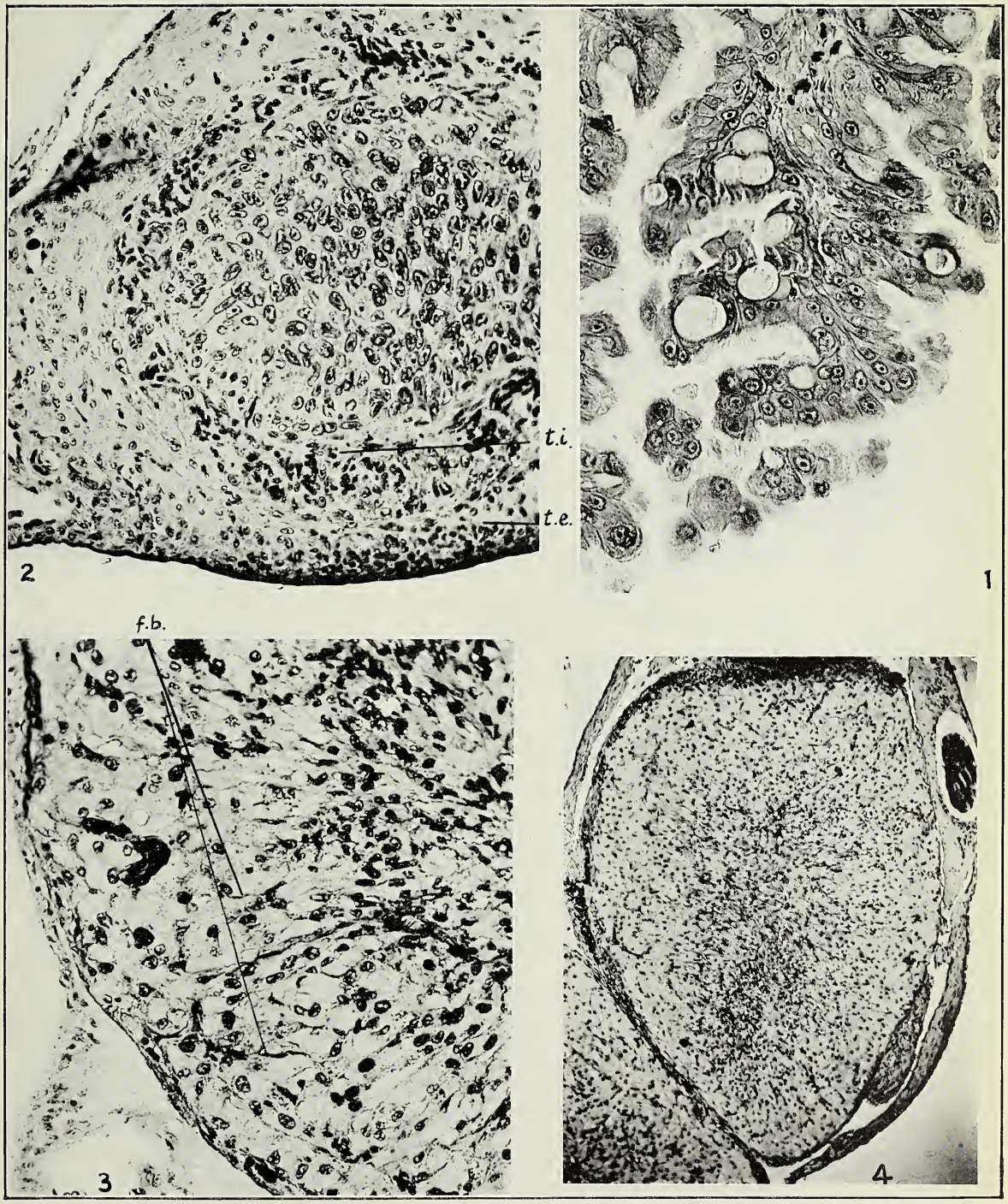
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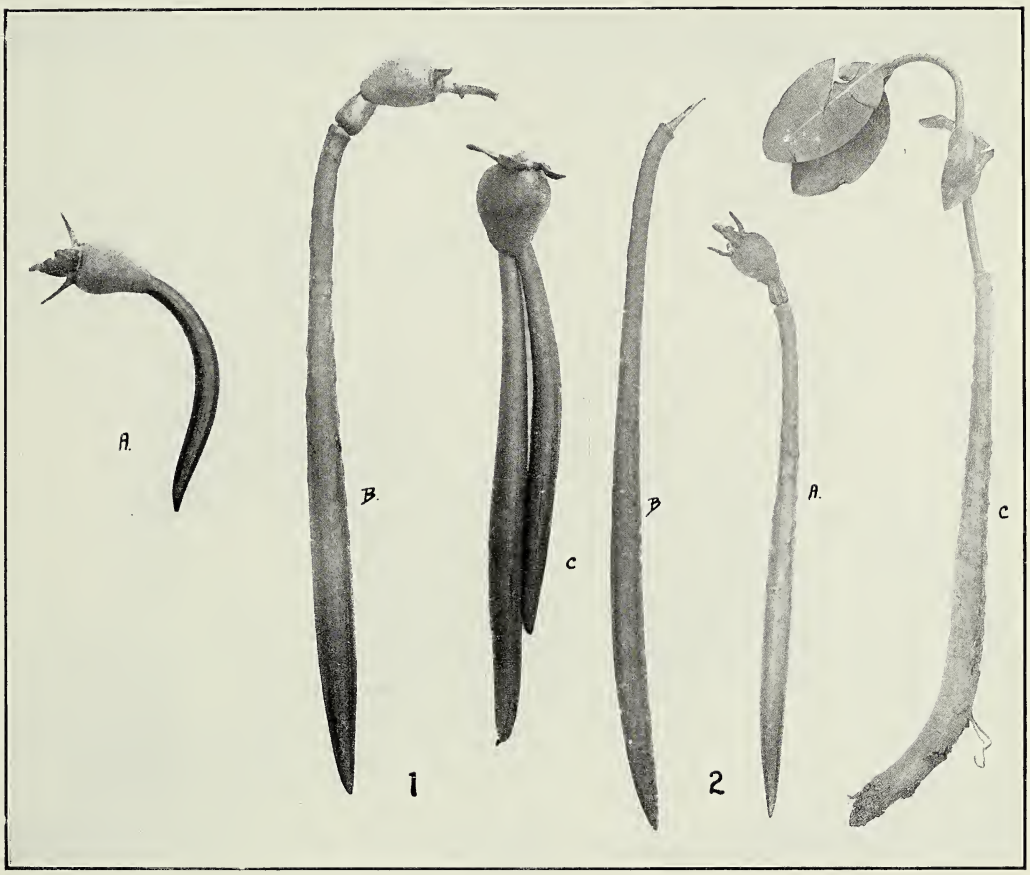
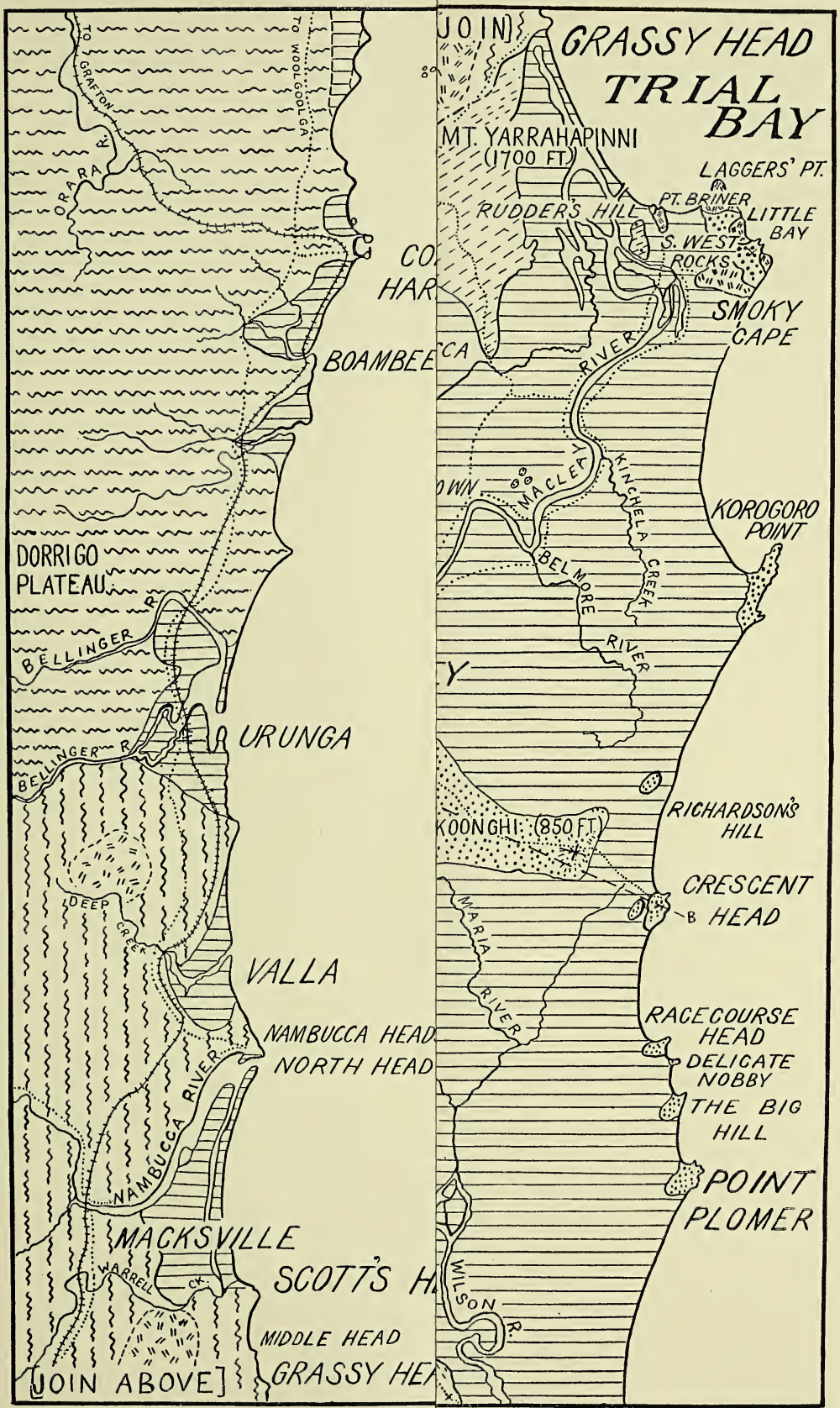


Developing embryos of *Rhizophora mucronata.*


TO GRAFTON
TO WOOLGOOLGA
ORARA R.
JOIN
GRASSY HEAD
TRIAL BAY
MT. YARRAHAPINNI (1700 FT.)
LAGGERS' PT.
PT. BRINER
LITTLE BAY
RUDDER'S HILL
S. WEST ROCKS
SMOKY CAPE
BOAMBEE
RIVER
MACLEAY
KINCHELA CREEK
KOROGORO POINT
DORRIGO PLATEAU
BELLINGER R.
BELMORE RIVER
URUNGA
RICHARDSON'S HILL
KOONGHI (850 FT.)
CRESCENT HEAD
DEEP CREEK
MARIA RIVER
VALLA
NAMBUCCA HEAD
NORTH HEAD
RACECOURSE HEAD
DELICATE NOBBY
THE BIG HILL
NAMBUCCA RIVER
POINT PLOMER
MACKSVILLE
WARRELL CK.
WILSON R.
MIDDLE HEAD
[JOIN ABOVE]

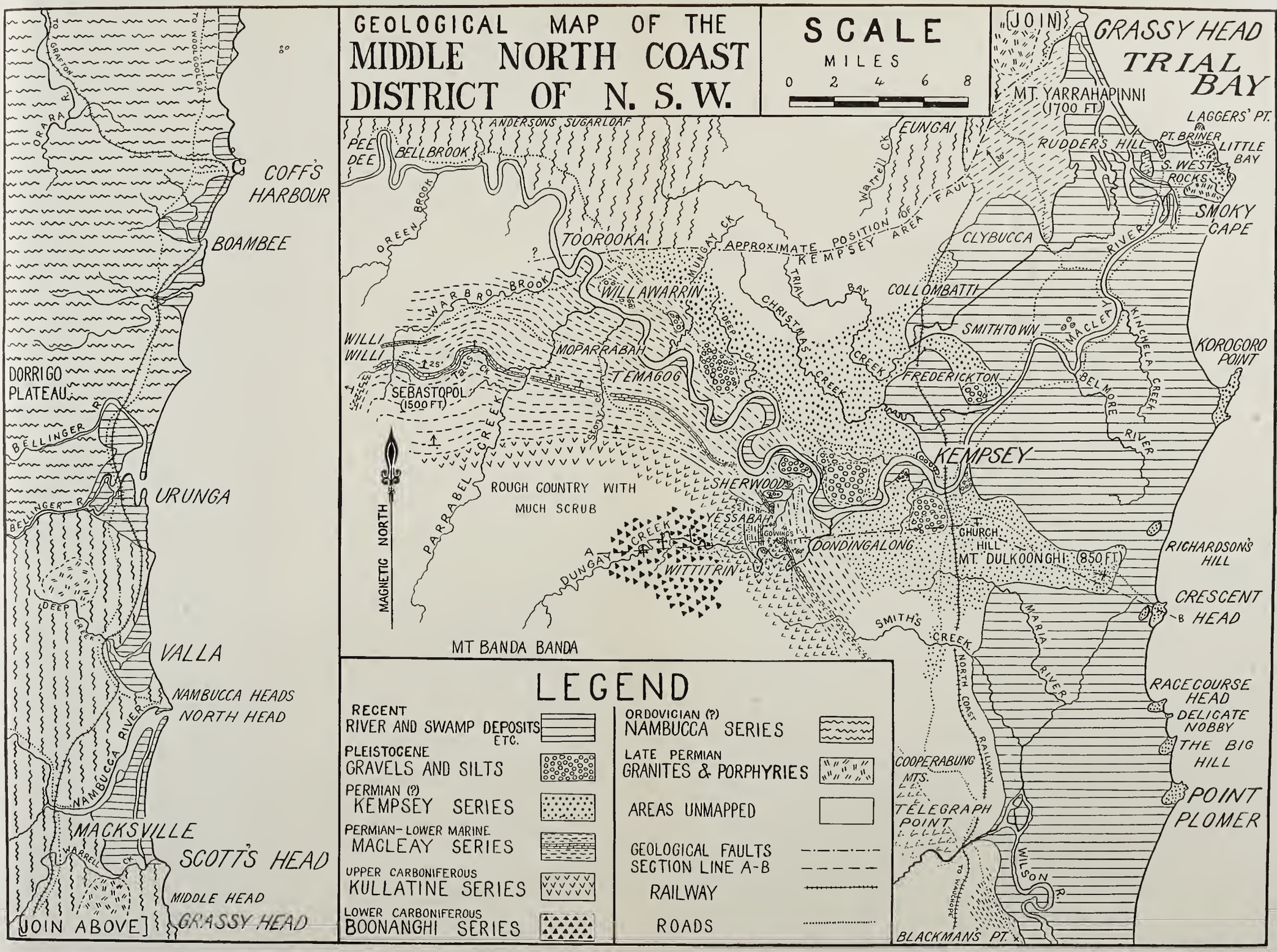

GEOLOGICAL MAP OF THE
MIDDLE NORTH COAST
DISTRICT OF N. S. W.
SCALE
MILES
0 2 4 6 8
TO GRAFTON
TO WOOLGOOLGA
ORARA R.
COFF'S HARBOUR
BOAMBEE
DORRIGO PLATEAU
BELLINGER R.
URUNGA
VALLA
NAMBUCCA HEADS
NORTH HEAD
NAMBUCCA RIVER
DEEP CREEK
MACKSVILLE
SCOTT'S HEAD
MIDDLE HEAD
[JOIN ABOVE]
GRASSY HEAD
ANDERSONS
SUGARLOAF
PEE DEE
BELLBROOK
OREEN BROOK
TOOROOKA
MUNGAY CK
APPROXIMATE POSITION OF KEMPSEY AREA FAULT
Wattell Ck
EUNGAI
WARBRO BROOK
WILLAWARRIN
CHRISTMAS CREEK
TRIAL BAY
WILLI WILLI
MOPARRABAH
TEMAGOG
SEBASTOPOL (1500 FT)
TALLIS CK
PARRABEL CREEK
ROUGH COUNTRY WITH MUCH SCRUB
SHERWOOD
YESSABAH
DONDINGALONG
WITTITRIN
MAGNETIC NORTH
MT BANDA BANDA
CLYBUCCA
COLLOMBATTI
SMITHTOWN
FREDERICKTON
KEMPSEY
KINCHELA CREEK
BELMORE RIVER
MACLEAY RIVER
KOROGORO POINT
CHURCH HILL
MT. DULKOONGHI (850 FT)
RICHARDSONS HILL
CRESCENT HEAD
SMITH'S CREEK
NORTH COAST RAILWAY
MARIA RIVER
RACECOURSE HEAD
DELICATE NOBBY
THE BIG HILL
POINT PLOMER
COOPERABUNG MTS.
TELEGRAPH POINT
WILSON R.
TO WAUCHOPE
BLACKMANS PT.
[JOIN]
GRASSY HEAD
TRIAL BAY
MT. YARRAHAPINNI (1700 FT)
LAGGERS' PT.
PT. BRINER
LITTLE BAY
RUDDERS HILL
S. WEST ROCKS
SMOKY CAPE
LEGEND
RECENT
RIVER AND SWAMP DEPOSITS ETC.
PLEISTOCENE
GRAVELS AND SILTS
PERMIAN (?)
KEMPSEY SERIES
PERMIAN-LOWER MARINE
MACLEAY SERIES
UPPER CARBONIFEROUS
KULLATINE SERIES
LOWER CARBONIFEROUS
BOONANGHI SERIES
ORDOVICIAN (?)
NAMBUCCA SERIES
LATE PERMIAN
GRANITES & PORPHYRIES
AREAS UNMAPPED
GEOLOGICAL FAULTS
SECTION LINE A-B
RAILWAY
ROADS

PLATE XVII.

GEOLOGICAL MAP OF THE WERRIE BASIN

SCALE

MILES 0 1 2 3 4 5 MILES

CHAINS 0 20 40 60 80 160 240 320 400 CHAINS

Magnetic

LEGEND

- Alluvials
- Upper Coal Measures
- Werrie Traps
- Lower Coal Measures
- Glacial Stage
- Lower Kuttung
- Burindi Series
- Barraba Series
- Porphyry Boulder Horizon
- Acid lavas
- Hornblende Andesite
- Pyroxene Andesite
- Warrigundi Intrusives
- Tertiary Basalt
- " "

Namoi River

Mooki River

Carroll

Breeza

Piallaway

Currabubula Creek

Currabubula

Quirindi

Werris Creek

Borambil Creek

Jacob & Joseph Creek

Wallabadah

Braefield

Gunnedah

Tamworth

Narrabri

Coonabarabran

Coonamble

Walgett

Moree

Inverell

Glen Innes

Armidale

Gloucester

Stroud

Maitland

Muswellbrook

Singleton

Merriwa

Wingen

Murrurundi

Scone

Nundle

Nowendoc

Barraba

Manilla

Bingara

Ashford

Warialda

Wee Waa

Narrabri

Coonabarabran

Coonamble

Walgett

Moree

Inverell

Glen Innes

Armidale

Tamworth

Breeza

Werris Creek

Nundle

Nowendoc

Gloucester

Murrurundi

Scone

Wingen

Merriwa

Muswellbrook

Singleton

Stroud

Maitland

NEWCASTLE

Barraba

Burindi

Manilla

Bingara

Ashford

Warialda

Inverell

LOCALITY SKETCH MAP

LEGEND

Alluvials	Faults
Basalt	1. Hunter Thrust System
Mesozoic	2. Brushy Hill Fault
Permian	3. Clarangola "
Kuttung	4. Webbers Creek "
Burindi	5. Serpentine "
Devonian	Warrigundi Axis
Silurian	Werrie Synclinal Axis
Cretaceous	Anticlinorium Axis

PIALLAWAY PADDOCK MTNS.

DUNOVER MTNS.

WARRIGUNDI

SPRINGSURE FAULT

ALLANDALE INJECTION

QUIRINDI INJECTION ZONE

WERRISTON INJECTION ZONE

WERRIS CREEK

QUIRINDI BASIN

QUIPOLLY DOME

PURLEWAH FAULTS

Quipolly Creek

FAIRFIELD BASIN

TRECANTLE FAULTS No 1 No 2 No 3

JACOB & JOSEPH BASIN

OXLEY DOME

ANSTEYS CK FAULT

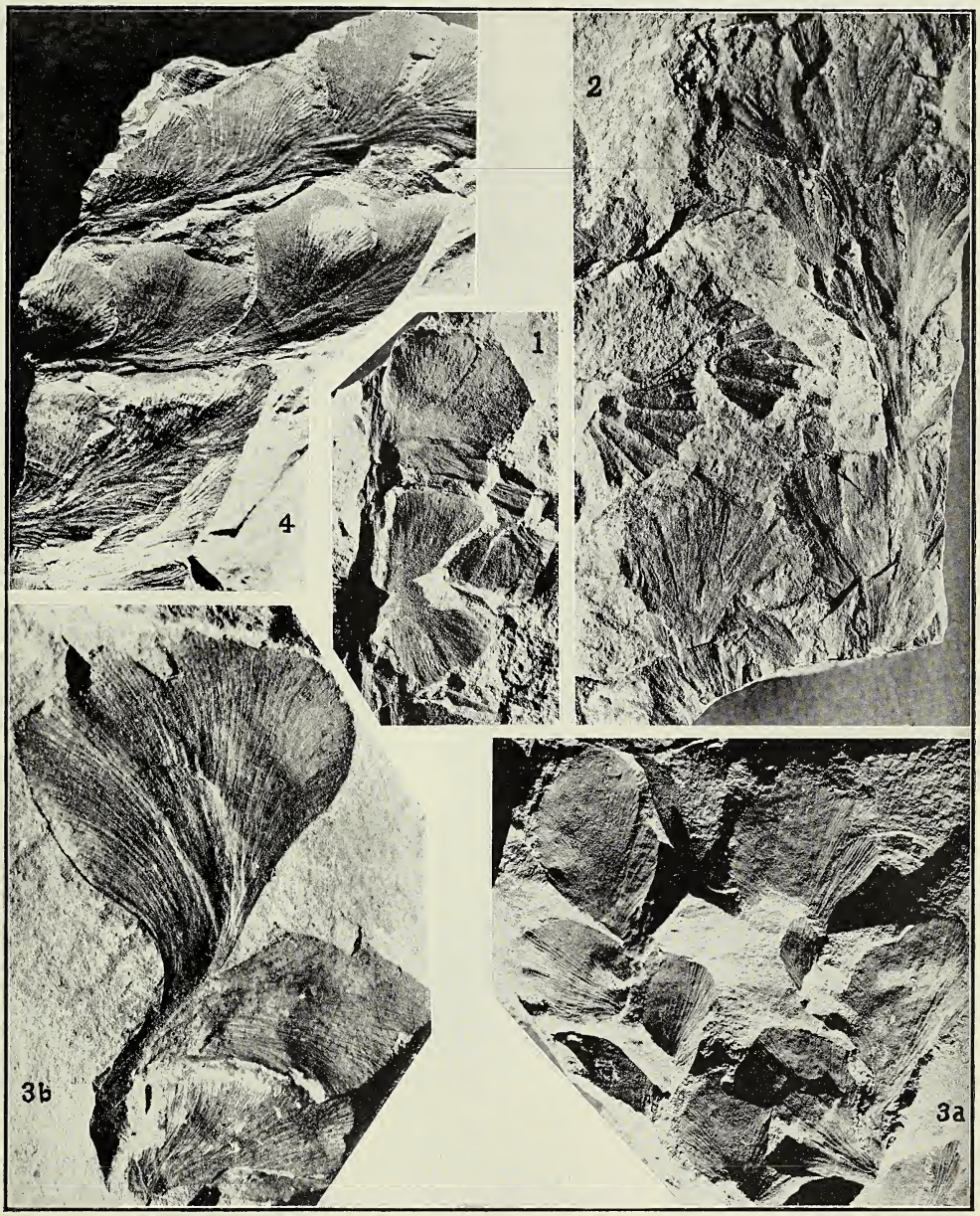
FORAN CREEK FAULTS No 1 No 2

MARBLE BASIN
IN THE
GEOLOGICAL MAP

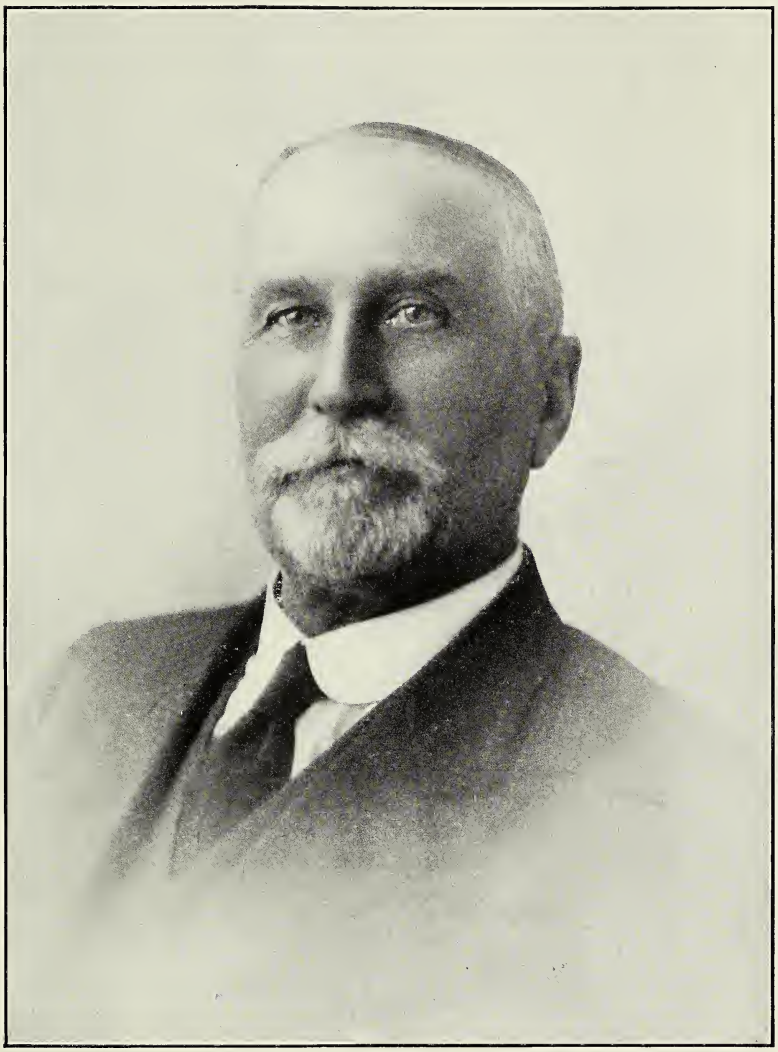
SCALE

LEGEND

Gneiss, Stripes
Tower Dol. Hornblende
Marble, Tales
Ribbon Dol. Hornblende
Syenite



Carboniferous Fossil Plants.



R. H. Cambage

ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.

28th March, 1934.

Professor W. J. Dakin, D.Sc., President, in the Chair.

The Donations and Exchanges received since the previous Monthly Meeting (29th November, 1933) amounting to 53 Volumes, 429 Parts or Numbers, 24 Bulletins, 13 Reports and 47 Pamphlets, received from 177 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. Notes on Australian Diptera. xxxiv. By J. R. Malloch. (*Communicated by F. H. Taylor.*)

2. Studies on Saprophytic Mycobacteria and Corynebacteria. By H. L. Jensen, Macleay Bacteriologist to the Society.

3. The early Stages of *Sciadocera rufomaculata* (Diptera: Phoridae). By Mary E. Fuller, B.Sc.

4. Australian Rust Studies. iv. Natural Infection of Barberries by Black Stem Rust in Australia. By W. L. Waterhouse, D.Sc.Agr.

ORDINARY MONTHLY MEETING.

18th April, 1934.

Professor W. J. Dakin, D.Sc., President, in the Chair.

Mr. S. Warren Carey, B.Sc., Hurlstone Park, and Mr. Robert L. S. Kaleski, Moorebank, via Liverpool, N.S.W., were elected Ordinary Members of the Society.

The President announced that the Council had elected Mr. E. Cheel, Professor T. G. B. Osborn, Dr. C. Anderson and Professor A. N. Burkitt to be Vice-Presidents for the Session 1934-35.

The President also announced that the Council had elected Dr. G. A. Waterhouse to be Honorary Treasurer for the Session 1934-35.

An invitation was extended to members to a meeting of the Sydney University Biological Society, to be held in the Botany School, Sydney University, on Tuesday, 8th May, at 7.30 p.m., when a discussion will take place on Protoplasm.

The President offered congratulations to Mr. N. A. Burges, M.Sc., Linnean Macleay Fellow of the Society in Botany, on the award of the James King of Irrawang Travelling Scholarship.

Attention was drawn to the efforts being made by the Dalrymple-Hay Forest Preservation Committee to obtain by purchase an area of eleven acres of the Pymble Forest for a Nature Reserve. Subscriptions are being invited by the Committee towards the cost of the project.

The Donations and Exchanges received since the previous Monthly Meeting (28th March, 1934) amounting to 8 Volumes, 53 Parts or Numbers, 2 Bulletins and 1 Report, received from 48 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Notes on Australian Orchids: A Review of the Genus *Cymbidium* in Australia. By Rev. H. M. R. Rupp, B.A.

2. Remarks on some Australian Cestodaria. By Professor T. Harvey Johnston.

3. Notes on some Monocotylid Trematodes. By Professor T. Harvey Johnston.

4. A Preliminary Investigation of the Natural History of the Tiger Flathead (*Neoplatycephalus macrodon*) on the South-eastern Australian Coast. By A. N. Colefax, B.Sc.

NOTES AND EXHIBITS.

Rev. H. M. R. Rupp exhibited a flowering specimen of *Dendrobium Bowmanii* (Proserpine district), a North Queensland orchid which has been lost sight of for many years.

Mr. G. P. Whitley exhibited a small Angler Fish (*Tetrabrachium ocellatum* Günther) from Hayman Island, Queensland, where Mr. F. A. McNeill had recently dredged it. This is the second example of the species which was only known hitherto from the type, obtained by the *Challenger* Expedition from south of New Guinea.

Miss L. Fraser and Miss J. Vickery exhibited specimens of *Conospermum* spp. from Glenbrook. Two species could be recognized as *C. taxifolium* Sm. and *C. longifolium* var. *angustifolium*. Several intermediate forms were also exhibited which showed leaf and inflorescence characters intermediate between these two. It had been found that very few seeds were set by these intermediate forms. The plants were markedly larger and more robust than either *C. taxifolium* or *C. longifolium* var. *angustifolium*. A microscopical examination of the pollen of the intermediate forms showed that there was a high degree of sterility. It is suggested that these intermediate plants originated as hybrids between *C. taxifolium* and *C. longifolium* var. *angustifolium*. All these specimens were found growing in the same area of about an acre.

ORDINARY MONTHLY MEETING.

30th May, 1934.

Mr. E. Cheel, Vice-President, in the Chair.

Mr. A. H. Voisey, B.Sc., Sydney University, was elected an Ordinary Member of the Society.

The Chairman offered congratulations to Mr. E. C. Andrews on his election to Honorary Fellowship of the Royal Society of New Zealand.

The Chairman called the attention of members to the Supplement to the Catalogue of Scientific and Technical Periodicals now available from the Council for Scientific and Industrial Research.

The Donations and Exchanges received since the previous Monthly Meeting (18th April, 1934) amounting to 23 Volumes, 165 Parts or Numbers, 11 Bulletins, 2 Reports, 16 Pamphlets and 6 Maps, received from 91 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. An Investigation of the Sooty Moulds of New South Wales: ii. An Examination of the Cultural Behaviour of certain Sooty Mould Fungi. By Lilian Fraser, M.Sc., Linnean Macleay Fellow of the Society in Botany.

2. Contributions to the Microbiology of Australian Soils. i. Numbers of Micro-organisms in Soil, and their Relation to certain External Factors. By H. L. Jensen, Macleay Bacteriologist to the Society.

3. The Habitat, Character, and Floral Structure of *Cryptanthemis Slateri* (Orchidaceae). By Rev. H. M. R. Rupp, B.A.

NOTES AND EXHIBITS.

Mr. J. G. Churchward exhibited photographs and living specimens of wheat seedlings showing white infection spots on the coleoptile and leaf, caused by the flag-smut of wheat, *Urocystis tritici*. This is the first record of such infection spots.

Rev. H. M. R. Rupp exhibited specimens of (1) young growth of *Dipodium punctatum* R.B., showing leaf development, (2) *Pterostylis reflexa* R.Br., and (3) *Cryptanthemis Slateri* Rupp.

Dr. G. A. Waterhouse sent for exhibition the life-history of *Cynthia arsinoe ada* received from Mr. M. J. Manski of Cairns, Qld. This consisted of an enlarged drawing of the egg, photographs of larva and pupa, preserved larva and empty pupal shell. Mr. Manski has found the larvae of this butterfly feeding on *Modecca populifolia* and has given a description of the life-history (*North Queensland Naturalist*, Vol. 1, 1933, and Vol. 2, 1934). He has found the larvae of *Cethosia cydippe chrysippe* feeding on the same plant.

Mr. David G. Stead exhibited portions of an example of a Salmon-Catfish, *Neoarius australis*, taken by hook and line by R. Palmer of Watson's Bay, from the ocean bottom at about 120 feet depth, off North Head, Port Jackson, on 11th May. The specimen was a mature female, measuring 594 mm. in total length. Mr. Stead stated that although during some years past he had known of two instances of alleged capture of this fish in the waters of Port Jackson, the present was the first authentic case, and constituted an extension of the known range of the species southwards. Catfishes of this group are very abundant in tropical waters of Australia, especially so in the waters of the Malayan region. *Neoarius australis* is further of considerable interest because of its habit of oral gestation. The eggs, which are very large for a teleostean fish—up to 19 mm. in longest diameter—are incubated in the mouth of the male parent. Not only this, but the young are carried in the mouth also for some time after they hatch and when they are able to swim quite well. Mr. Stead stated that he had taken young of as much as 50 mm. in length from the parent's mouth. In New South Wales waters, *Neoarius australis*, which is a good edible fish, is most abundant in the estuaries of the Clarence and Richmond Rivers; but is still more abundant farther north in Queensland waters. The habit of carrying eggs and young in the mouth has given rise to the idea prevalent among some northern fishermen that this species eats its own eggs and young. The specimen under discussion contained in its stomach one Gurnard, *Chelidonichthys*, the remains of another, the beaks of a species of cephalopod, and a small sand mollusc, unidentified.

Mr. E. Cheel, Curator of the National Herbarium, exhibited samples of fifteen distinct kinds of seeds of weeds which he had collected in his clothes whilst

travelling by bus from Calgary, in Canada, to California, U.S.A. In crossing the border of the Oregon State into California, a rigorous inspection is made by the Californian State Inspectors of all parcels and luggage, for any fruit, flowers, or plants, with a view of preventing spores of parasitic fungi or other plant diseases being introduced into the State. Mr. Cheel contends that the spores of fungi causing plant diseases are carried in passengers' clothes when travelling from place to place, or in different countries, and that the only way to prevent spores of fungi or weed seeds from being conveyed to different parts of the world is to use a vacuum cleaning machine to gather up dust, weed seeds or other materials which cling to the clothes of human beings, or the furs of animals, and feathers of birds, when travelling from place to place. Spores of fungi also cling to the coverings of seeds of crop plants, as well as those of weed seeds, and during severe wind storms weed seeds, in addition to the multitude of microscopic spores, are carried very long distances. Even the vehicles, such as trains, trams, buses, and other automobiles, as well as vehicles drawn by horses, carry weed seeds and spores of fungi in the dust or mud particles which cling to the wheels or other parts. Certain forms of insects travel long distances, either by their own means of locomotion, or by the aid of other means of locomotion, and carry with them microscopic organisms of many kinds. In view of this, many of our present-day methods of trying to prevent the importation of certain plant diseases should be reviewed.

Mr. E. Cheel, Curator of the National Herbarium, exhibited some air-dried flower-pots made from a composition of peat, cow manure, and clay, which not only acted as containers for seedling wattles and gum trees, but serve as food for the seedlings, and are specially serviceable in transplanting seedling trees from the seed pans to dry districts. This system of handling seedling trees is adopted at the Summerland Experiment Station, Winslow, British Columbia, which Mr. Cheel observed when visiting Canada as one of the delegates to the Fifth Pacific Science Congress. One of the great difficulties in establishing plantations of young trees in dry districts is the question of water. Plants established in the composition flower-pots are able to resist the dry conditions much better than those freshly transferred from the nurseries, or even from the ordinary burnt clay flower-pots.

Rev. H. M. R. Rupp brought to the notice of members the need for adding many of the orchids to the list of protected plants. He was supported by a number of members, and it was decided to refer the matter to the Council of the Society.

ORDINARY MONTHLY MEETING.

27th June, 1934.

Professor W. J. Dakin, D.Sc., President, in the Chair.

Messrs. W. E. Day, Strathfield, and H. Womersley, F.R.E.S., Adelaide, South Australia, were elected Ordinary Members of the Society.

The Chairman offered congratulations to Mr. John Andrews, B.A., on the award to him of a Rockefeller Scholarship, enabling him to continue his studies at Cambridge.

The Donations and Exchanges received since the previous Monthly Meeting (30th May, 1934) amounting to 4 Volumes, 64 Parts or Numbers, 3 Bulletins and 3 Reports, received from 51 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. The Gasteromycetes of Australasia. xvi. Hymenogastraceae. Part i. The Genera *Rhizopogon*, *Melanogaster* and *Hymenogaster*. By G. H. Cunningham, D.Sc., Ph.D., F.R.S.N.Z.

2. Further Additions to the Flora of the Comboyne Plateau. By E. C. Chisholm, M.B., Ch.M.

3. Miscellaneous Notes on Australian Diptera. ii. By G. H. Hardy.

4. Notes on the Australian Species of *Molophilus* (Tipulidae, Diptera). ii. By C. P. Alexander. (*Communicated by I. M. Mackerras, M.B., Ch.M., B.Sc.*)

5. A Note on the Occurrence of Seedling Lesions caused by Cereal Smuts. By J. G. Churchward, B.Sc.Agr.

NOTES AND EXHIBITS.

Professor W. J. Dakin exhibited large specimens (8½ inches long) of the prawn—*Peneus plebejus* Hess., with ripening gonads taken from the ocean off the New South Wales coast, also large specimens from Port Jackson, and microscopic specimens of the prawn larvae from the ocean off Sydney and the entrance to Port Jackson. After several years' observations it could be said quite definitely that the King Prawn (*P. plebejus*) of the New South Wales estuaries and coastal lakes such as Lake Illawarra and the Tuggerah Lake, never matured its ovaries or testes in the lakes or estuaries. After a period of fairly rapid growth in spring time the growing prawns migrated towards the sea. The outgoing "mobs" could be well observed at the entrance to Lake Illawarra on moonless or dark nights in the summer months. The largest prawns caught at Sydney were usually obtained in late summer from the seaward part of Port Jackson, viz., Watson's Bay, off Parsley Bay and Clifton Gardens, and only some of these showed the beginnings of ovarian development. The eggs of the Peneid prawns were never carried in the abdomen but shed freely into the sea. Fertilized eggs and also larval stages had been captured at certain seasons during three years' work at sea. It was the larval stages (invisible to the fishermen) which invaded the lakes and rivers and developed into the commercial sized prawns on the rich inshore feeding grounds. The breeding of the School Prawn was similar but there was some evidence that a less common prawn species, *Penaeopsis monoceros* De Man., bred in Lake Illawarra and also in Cook's River during late summer. Recent evidence tends to show that the large King Prawns leaving the lakes and harbours for the sea are only twelve months to fifteen months old. Possibly these prawns only breed once—in any case no one knows what becomes of them in the sea after the first breeding season.

Professor W. J. Dakin exhibited a specimen of the so-called Milkfish, *Chanos chanos* Forskål (Bañgos of Philippine Islands, Bandeng of Malaya, and Ibya of Nauru). The specimen was obtained by him at Nauru, Pacific Ocean.

The natives of Nauru at certain seasons of the year collect the Ibya larvae from pools on the fringing coral reef. The tiny larvae are taken in large shells or other receptacles and after having been kept for two or three weeks in containers in the native huts are gradually introduced into the almost fresh water of the inland lake. Here in crowded, shallow ponds, they flourish until a couple of feet in length.

The story of the cultivation of this fish in Java and the Philippines is little known outside those regions. It is itself very unusual because *Chanos chanos* is one of the few typical marine fish (i.e., a fish shedding its eggs only in the sea)

to be cultivated. The action of the natives of Nauru in transferring the larvae to brackish water with a salinity of less than 0·9% is, however, far more remarkable and the ability of the young fish to withstand these changes and flourish in the primitive ponds of the Nauruans is extraordinary.

The custom is an ancient one and Professor Dakin suggests that it was probably carried to Nauru in remote times, possibly by the first natives to reach these islets, from Western Pacific countries. Use was made of the inland "lagoon" without understanding the difficulties which might have been involved with most other fish species in transferring young stages to such water. An examination of the physiological phenomena involved is to be made on another visit to the island.

Miss Lilian Fraser, for Dr. E. C. Chisholm, exhibited specimens of *Athyrium umbrosum* Ait., and of the new variety of that species described by Dr. Chisholm from the Comboyne Plateau.

ORDINARY MONTHLY MEETING.

25th JULY, 1934.

Professor W. J. Dakin, D.Sc., President, in the Chair.

Mr. H. J. Davidson, Croydon Park, was elected an Ordinary Member of the Society.

The Chairman referred to the deaths of Mr. Walter H. Bone and Mr. T. McDonnough, who had been members of the Society since 1923 and 1907 respectively.

The Donations and Exchanges received since the previous Monthly Meeting (27th June, 1934) amounting to 21 Volumes, 101 Parts or Numbers, 15 Bulletins, 8 Reports and 1 Pamphlet, received from 63 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Studies in Australian Acacias. iii. Supplementary Observations on the Habit, Carpel, Spore-production and Chromosomes of *Acacia Baileyana* F.v.M. By I. V. Newman, M.Sc., Ph.D., F.L.S., Linnean Macleay Fellow of the Society in Botany.

2. The Early Stages of *Actina incisuralis* Macq. (Diptera, Stratiomyiidae). By Mary E. Fuller, B.Sc.

3. Contributions to the Microbiology of Australian Soils. ii. A Comparison of the Rossi-Cholodny Method and Plate Method for Studying the Soil Microflora. By H. L. Jensen, Macleay Bacteriologist to the Society.

4. Studies in the Genus *Uromycladium* (Uredineae). i. By Alan Burges, M.Sc., Linnean Macleay Fellow of the Society in Botany.

NOTES AND EXHIBITS.

Professor W. J. Dakin exhibited a tube containing several hundred eggs of the Australian pilchard, *Sardinia neopilchardus*. The eggs were a portion only of one plankton catch taken off Sydney on 15th July, 1934. This plankton catch consisted of almost nothing else but pilchard eggs. A special point of interest lay in the fact that the largest previously obtained catch of pilchard eggs was made on 18th July, 1932. It is remarkable how constant the appearance of the pilchard eggs has been during the last four years.

Dr. G. A. Waterhouse contributed the following note: Butterflies are appearing on the wing near Sydney much earlier this season than usual. New records are: *Candalides acasta* at Hornsby by Dr. T. Guthrie on 15th July; *C. acasta* at Killara by myself on 16th July; *Hypocysta euphemia*, *Candalides hyacinthina* and *Paralucia aurifer* at Narrabeen by Messrs. M. Day and D. F. Waterhouse on 21st July. All were freshly emerged specimens.

Mr. D. G. Stead referred to the long-proposed memorial to Sir Joseph Banks and the need for legislative action to enable the fund to be used for the purpose for which it was collected.

ORDINARY MONTHLY MEETING.

29th August, 1934.

C. Anderson, M.A., D.Sc., Vice-President, in the Chair.

The Chairman referred to the death of Professor Sir T. W. Edgeworth David, and the following resolution was carried, the members standing in silence:

> The members of the Linnean Society of New South Wales place on record their deep sorrow at the death of Sir Edgeworth David, who had been a member of the Society for almost fifty years, twice President (1893/4 and 1894/5), and member of Council since 1891, and who had, during that time, endeared himself to all. His great achievements in geology and exploration, his services to his country in time of war, and his wonderful influence for good on all with whom he came in contact, marked him as one of the greatest Australians of his time, and his death leaves a gap which it seems impossible to fill. The members express their most sincere and heartfelt sympathy with Lady David in her bereavement.

The Donations and Exchanges received since the previous Monthly Meeting (25th July, 1934) amounting to 25 Volumes, 235 Parts or Numbers, 4 Bulletins, 2 Reports and 21 Pamphlets, received from 93 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. Australian and New Guinea Coleoptera. Notes and New Species. No. 3. By H. J. Carter, B.A., F.R.E.S.

2. Notes on Australian Chenopodiaceae. By R. H. Anderson, B.Sc.Agr.

3. Note on *Campanularia integra* and *Orthopyxis caliculata*. By W. M. Baîe, F.R.M.S.

4. The Diptera of the Territory of New Guinea. i. Family Culicidae. By F. H. Taylor.

NOTES AND EXHIBITS.

Dr. W. L. Waterhouse exhibited specimens of F3 oat plants derived from a cross between "Algerian" and "Victoria" showing segregation for the albino characteristic. Such plants occur in varying ratios in different families. Genetical and cytological studies are in progress designed to explain this happening.

Dr. I. V. Newman exhibited herbarium specimens of *Acacia discolor*, illustrating the variations in floral colour. It is known that in the neighbourhood of Sydney the colour is very pale, while on the sandstone highlands around, the colour of some plants is a very deep yellow. This distinction between the colours was found to be not clearly defined on Burragorang tableland, at about 1,800 feet

altitude; but in the Mount Tomah and Mount Wilson region at about 3,000 feet the colour seemed to be only deep yellow. This problem is typical of many that confront the systematist in the Acacias, concerning not only flower colour, but also foliage and epidermal characters.

An analysis of the components of the floral colour showed that there were three grades of coloration in each of petals, filaments and anthers. The "floral colour" is the combined effect of the three, which appear to be possessed independently. The analysis was of twenty plants and is therefore only suggestive. A genetical examination would probably show a mechanism of a type similar to the following: Two colour factors which are multiple allelomorphs of which one or both must be present for colour to be manifested; a set of three factors which determine whether the colour shall be applied to the petals, filaments or anthers; these three factors would be on different chromosomes, with that for the petals linked with one of the colour factors, and that for the filaments with the other colour factor; finally, another factor, linked possibly with the filament factor, either causing climatic conditions of the sandstone highlands to have a lethal effect increasing with altitude; or causing the climatic conditions of the Sydney district to inhibit the filament colour.

Dr. G. A. Waterhouse drew attention to two recent changes in the generic names of Australian butterflies. As the result of a report on the generic names of the British Rhopalocera, published by the Royal Entomological Society of London, 23rd February, 1934, it has been shown that the generic names *Cynthia* Fabricius and *Issoria* Hübner have not been correctly used. Capt. A. F. Hemming, in *Entomologist*, 1934, lxvii, p. 77, has supplied new generic names, viz., *Vindula*, genotype *Papilio arsinoë* Cram. and *Vagrans*, genotype *Papilio egista* Cram. The Australian butterflies will then be known as *Vindula arsinoë ada* and *Vagrans egista propinqua.*

Mr. T. C. Roughley exhibited two sealed jars containing specimens of goldfish (*Carassius auratus*) and the heads of snakes (*Elaphe* sp.). These were preserved in a transparent liquid and showed both fish and snakes in their natural colours, and also treated to render them transparent. As far as could be judged, the preservation of colour was perfect. The specimens were on loan from Messrs. Gollin and Co., Merchants, of Sydney, and had been received from a firm in Japan who stated that patent rights were being taken out for the processes. Details are being sought with the object of applying the methods to the preservation of specimens in Australia.

ORDINARY MONTHLY MEETING.

26th September, 1934.

Professor W. J. Dakin, D.Sc., President, in the Chair.

Miss Alma T. Melvaine, Centennial Park, Mr. N. J. B. Plomley, Potts Point, Mr. N. H. White, Beecroft, and Miss Janet M. Wilson, Hunter's Hill, were elected Ordinary Members of the Society.

A letter was read from Lady David and family, returning thanks for sympathy of Members of the Society.

The Chairman announced that the Council is prepared to receive applications for four Linnean Macleay Fellowships tenable for one year from 1st March, 1935, from qualified candidates. Applications should be lodged with the Secretary,

who will afford all necessary information to intending candidates, not later than Wednesday, 7th November, 1934.

The Donations and Exchanges received since the previous Monthly Meeting (29th August, 1934) amounting to 16 Volumes, 68 Parts or Numbers, 3 Bulletins, 2 Reports and 2 Pamphlets, received from 49 Societies and Institutions and 2 private donors, were laid upon the table.

PAPERS READ.

1. Studies in the Australian Acacias. iv. The Life-history of *A. Baileyana* F.v.M. Part 2. By I. V. Newman, M.Sc., Ph.D., F.L.S., Linnean Macleay Fellow of the Society in Botany.

2. The Regimes and Cyclical Volume Changes of the Upper Murray and Snowy Rivers, N.S.W. By F. A. Craft, B.Sc., Linnean Macleay Fellow of the Society in Geography.

3. A Preliminary Account of the Geology of the Middle North Coast District of New South Wales. By A. H. Voisey, B.Sc.

NOTES AND EXHIBITS.

Mr. David G. Stead referred to the whale which had appeared in Port Jackson on 29th August, 1934, and which had been struck and killed by the Manly ferry "Baragoola", when opposite Sydney Heads. Next day the body rose to the surface and was then towed about four miles east-south-east and set adrift. There was a very heavy SE. swell running and the whale reappeared at Sydney Heads next day. It was then towed about fourteen miles out and a very strong SE. gale brought it back ashore near Botany Heads. It was then towed about twenty miles out and has not been seen since. The specimen was seen and identified by Professor Dakin as a male Right Whale. Right Whales are now relatively rare on the Australian coast compared with the early whaling days of 1800 to 1840.

Mr. E. Cheel exhibited a copy of a work entitled "Toadstools and Mushrooms and other Larger Fungi of South Australia", by Professor J. B. Cleland. The work is one of a series published by the Government of South Australia under the auspices of the South Australian Branch of the British Science Guild.

Mr. Cheel also exhibited an albino seedling plant of *Crinum Moorei* Hook. f. From a batch of fifty-two (52) seedlings there are four albino forms. A normal seedling was exhibited for comparison.

Mr. R. N. Robertson gave a preliminary account of the work of the University Scientific Expedition to Myall Lakes.

ORDINARY MONTHLY MEETING.

31st October, 1934.

Professor W. J. Dakin, D.Sc., President, in the Chair.

The Chairman referred to the death of Mr. W. S. Dun, a past President of the Society, who had been a Corresponding Member since 1932.

Candidates for Linnean Macleay Fellowships, 1935–36, were reminded that Wednesday, 7th November, is the last day for receiving applications.

The Chairman announced that Dr. W. R. Browne had been elected a Member of Council in place of the late Sir Edgeworth David.

The Donations and Exchanges received since the previous Monthly Meeting (26th September, 1934) amounting to 9 Volumes, 117 Parts or Numbers, 28 Bulletins, 6 Reports and 3 Pamphlets, received from 67 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. The Geological Structure of the Werrie Basin. By S. Warren Carey, M.Sc.

2. Note on the Implications of the Irregular Strike-lines of the Mooki Thrust System. By S. Warren Carey, M.Sc.

3. The Corpus Luteum in certain Oviparous and Viviparous Reptiles. By H. Claire Weekes, D.Sc.

NOTES AND EXHIBITS.

Miss Lilian Fraser exhibited specimens of *Corynelia uberata* Fries (Coryneliaceae, Sphaeriales). This fungus is known from Africa, Japan, New Zealand and the Philippine Islands on various species of *Podocarpus*. It has once been recorded from the Barron River district, Queensland, on *Podocarpus pedunculatus*. The material exhibited is from Ulladulla, N.S.W., where it was collected on 27th September, 1934, on *Podocarpus spinulosa* R.Br., and is the first to be recorded from this State.

Dr. I. V. Newman exhibited photographs illustrating the methods that produced successful intra-specific crossing (as far as production of half-grown pods) in *Acacia discolor*. The photographs showed flowerheads before and after emasculation, young pods resulting about six and ten weeks after the cross was made, and the wire frames, dress net and cellophane ("bags") used in the protracted protection of the work from foreign pollen and the weather. The "bags" were in good condition after twelve weeks, including two periods of very heavy wind and rain.

Dr. I. V. Newman reported on a search for the natural habitat of the Cootamundra Wattle (*Acacia Baileyana*). In a fairly extensive tour through the district concerned, it was located growing naturally in only one small area about six miles north of Cootamundra on stony ridges. The soil is a reddish slate (probably Silurian), and has on its surface numerous white to pink granitic pebbles. The apparently very restricted natural distribution of the species, in spite of its widespread viability in cultivation, presents an ecological problem of considerable interest. Dr. Newman would be glad to receive any information about the localities where *Acacia Baileyana* is thought to occur naturally.

ORDINARY MONTHLY MEETING.

28th November, 1934.

Professor W. J. Dakin, D.Sc., President, in the Chair.

The Chairman announced that the Council had reappointed Miss Lilian Fraser, M.Sc., and Dr. I. V. Newman, M.Sc., to Linnean Macleay Fellowships in Botany for one year from 1st March, 1935; and had appointed Mr. R. N. Robertson, B.Sc., to a Linnean Macleay Fellowship in Botany for a period of one year from 1st March, 1935.

The Donations and Exchanges received since the previous Monthly Meeting (31st October, 1934) amounting to 5 Volumes, 161 Parts or Numbers, 1 Bulletin, 6 Reports and 8 Pamphlets, received from 78 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Further Investigations on the Embryology of Viviparous Seeds. By Gladys Carey, M.Sc.

2. Australian Hesperiidae. v. Notes, and Description of a new Form. By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.

3. Notes on the Genus *Ophiodesma* (Diptera, Stratiomyiidae). By Mary E. Fuller, B.Sc.

4. Notes on Australian Lycaenidae. vii. Descriptions of new Races. By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.

5. Notes on Australian Marine Algae. vii. The Algae of the Low Islands. By A. H. S. Lucas, M.A., B.Sc.

6. Notes on some Carboniferous Plants from New South Wales. By A. B. Walkom, D.Sc.

NOTES AND EXHIBITS.

Dr. G. A. Waterhouse exhibited a remarkable aberrant specimen of *Vanessa cardui kershawi* McCoy caught by him at Blackheath in November of this year. A somewhat similar aberration from Fernshawe, Victoria, was described by W. H. Miskin in These Proceedings, 1888, p. 1515. Miskin considered his specimen a distinct species and named it *Pyrameis lucasi*. In These Proceedings, 1888, p. 1250, another aberration was described by A. S. Olliff as ab. *suffusa*. It was caught by the late George Masters at Bombala, and was also exhibited together with the normal form of the "Painted Lady". The ab. *lucasi* is in the South Australian Museum, the other specimens are at the Australian Museum, Sydney.

Dr. G. A. Waterhouse also exhibited a specimen of *Toxidia peroni* Latr., taken by him this month at Blackheath, 3,500 feet. This is the first record of the genus above 2,000 feet in the Blue Mountains.

Rev. H. M. R. Rupp exhibited (1) herbarium specimens of rare North Queensland orchids, *Liparis Nugentae* Bail., *Dendrobium Tofftii* Bail., *D. Johannis* Reichb. f., *D. fusiforme* Bail., *D. Adae* Bail., *D. agrostophyllum* F.v.M., *Bulbophyllum Baileyi* F.v.M.(?), *B. Macphersonii* Rupp, *Eulophia venosa* Reichb. f., *Cymbidium Hillii* F.v.M., *Dipodium ensifolium* F.v.M., *Taeniophyllum* sp., *Cheirostylis ovata* (Bail.) Schlecht.; (2) herbarium specimens of a form of *Thelymitra aristata* Lindl., which is found associated with *Dendrobium Kingianum* in Northern New South Wales and South Queensland; (3) *Taeniophyllum Muelleri* from Brunswick Heads; and (4) living specimens of *Prasophyllum odoratum* Rogers, from Round Mountain, New England, at 5,000 feet.

Mr. E. Cheel exhibited seedling Eucalyptus, raised from seed collected at Batlow, which in no way differ in their characters from seedlings raised from seed of *Eucalyptus radiata* Sieber in the Blue Mountains and Southern Tableland districts. This species is included as a synonym under *E. amygdalina* Labill., by Bentham, Mueller, and others, but was upheld as a distinct species by Maiden. Several supposed new species have been proposed, as, for example, *E. australiana*, *E. phellandra* and *E. Robertsoni*, for very slight variations in colour and chemical constituents, which it is suggested by the exhibitor are caused by climatic and soil conditions. Seedlings of *Acacia podalyriaefolia* (Queensland Silver Wattle) were also exhibited, grown in ordinary burnt flower-pots to compare them with those grown in air-dried containers made from a composition of clay, peat and cow-dung. Plants of Acacias and Eucalyptus grown in the latter are much stronger in growth than those in ordinary flower-pots.

DONATIONS AND EXCHANGES.

Received during the period 30th November, 1933, to 28th November, 1934.

(*From the respective Societies, etc., unless otherwise mentioned.*)

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