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TITLE AND INDEX.

The Blood of Magelona.

By

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With Plate 1.

The small Annelid first discovered and briefly described by Fr. Müller[1] in 1858 has more recently received more elaborate treatment at the hands of Professor W. M'Intosh.[2] It presents several peculiarities deserving of still more detailed research; and, at Professor Lankester's request, Dr. M'Intosh has kindly sent to me from time to time living specimens, obtained at St. Andrews, which have served as the starting-point of my own observations.

Amongst these peculiarities, the most striking and astonishing is afforded by the contents of the blood-vessels; and I propose at present to limit my remarks to an enumeration and description of the observations and experiments which I have made on this fluid.

In order to obtain a greater quantity of quite fresh material I spent a week at the Marine Laboratory at St. Andrews during the summer of 1894. Professor M'Intosh was good enough to send me a list of low tides—at which time only can Magelona be obtained in any considerable number. My very hearty thanks are due to Dr. M'Intosh for his permission to make use of the laboratory and appliances for the purpose

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[1] Fr. Müller, "Einiges über d. Annelidenfauna d. Insel S. Catharina," &c., 'Arch. f. Naturgesch.,' 1858, p. 211.

[2] W. C. M'Intosh, "Beiträge zur Anat. von Magelona," 'Zeit. f. wiss. Zool.,' 31, 1878.

of my study, and for his advice and kindness in aid of my work there.

Magelona lives in the sand at and below ordinary low-water mark, and the lower the tide the more abundant are the worms. My sojourn at St. Andrews was timed so as to cover particularly low tides occurring between August 30th and September 4th. I found the worms limited to a comparatively small area on the sands near the harbour, close to the Laboratory, though they occur more sparingly over a larger area. The work involved in their capture is rather heavy, as they occur at a depth from eight to sixteen inches below the surface of the sand. I was fortunately able to obtain the help of the laboratory attendant, A. W. Brown, who accompanied me in my search. The process was as follows:—Having selected a spot which he believed from experience to be likely, Brown dug as deeply into the sand as possible. As he raised the spade-load the sand naturally broke across, and if Magelona was present the worms would be seen stretching across the gaps thus formed in the spadeful of sand. The worms are rather brittle, and considerable care had to be exercised in raising the mass of sand, and further separating it, so as to liberate the worms. Sometimes such a spadeful would produce only one or two worms, at other times considerable numbers might be obtained; but the work of sorting through such masses of wet sand was no light task. We usually spent a couple of hours in this manner till the tide drove us back from the Magelona area.

The body of Magelona papillicornis presents two regions,—a short "thorax," with thick, muscular wall; and an "abdomen," through whose thin walls the gut and its sandy contents can be seen. The general appearance then of the worm is sand-colour, for there is no pigment in the skin or body wall, but the very short thorax is of a faint madder-pink tint, or in some cases dull white, according, as later observations of captive specimens showed, to the condition of oxidation of the blood. When the worms, separated more or less from the sand, are placed in clean aërated sea water the colour of the thorax soon becomes a deeper madder-rose colour; as the water becomes foul the tint of the worm becomes fainter and fainter, till the thorax is white. I first observed this change while working upon worms sent from St. Andrews to me at Oxford. The worms had been put into clean sea water on their arrival, and had been put aside overnight. Next morning they were no longer madder-rose, but white. On pointing this out to Professor Lankester, he at once suggested aërating the water by squirting air into it; this I did, and soon the madder-rose tint reappeared. It was this small but extremely interesting change in colour which called our attention to the blood, for it was evident that we had to deal with a respiratory pigment of a kind unusual in the Chætopoda.

The fact that the tint of the worm is due to contained blood, and not to any pigment in the skin, is readily recognised by the unaided eye when the alternating processes of eversion and retraction of the "proboscis" or "introvert" is watched. So long as the introvert is at rest within the body the thorax is coloured; when eversion takes place the tint becomes quite faint (Pl. 1, fig. 2),—in fact, frequently the thorax becomes white. The blood in the thorax is contained in greatly dilated vessels, which block up and obliterate nearly the whole of the cœlom (fig. 3); the introvert is a hollow sac traversed by thin bundles of retractor muscles, the cavity of the sac being continuous with the dilated vessels, so that on eversion nearly the whole of the blood in the thorax is driven into the introvert—this flow of blood is, of course, the cause of the eversion,—and the thorax is more or less completely deprived of its colour. The fact that the abdomen is not tinted by the blood to any great degree is due to the small size of the blood-vessels in this region.

The arrangement of these blood-vessels has been minutely described by M'Intosh, and need not detain us at present. But the remarks of this author, so far as they relate to the blood itself, may here be quoted:—"The blood is a coagulable pale rose-red fluid, containing numerous corpuscles. On being shed these group themselves in different clumps. The size of the spherules is nearly constant, although variations may occur. They exhibit molecular movement, and their contour is changed by pressure. Many are ovoid, others circular or irregular. If studied within the blood-vessels the corpuscles exhibit a refringent body or nucleus-like central structure. In addition to these spherules various other elements exist, which may perhaps be explained as a development of spherules inside cells. Here and there a coagulum may be seen between the corpuscles. Treated with strong acetic acid, very noticeable changes occur. The whole field is now covered with a granular débris (Pl. 38, fig. 9), and in place of the corpuscles we see masses of granular cells of larger size. The acid probably dissolves the envelope of the corpuscles or alters their walls, so that the (probably fatty) contents run together to form larger masses."

It will be seen later that this description, though true to a certain extent, does not exhaust the subject. I may mention that nearly the whole of my own observations had been made before I had acquainted myself with the above account of the blood given by M'Intosh,—that is, in reading his paper some time back I had not paid special attention to his statements as to the blood itself.

1. Spectroscopic Examination.—After observing the remarkable change of colour on oxidation I wished to examine the blood spectroscopically, and to this end I sought for some reagent which would extract the pigment; but though I was unsuccessful in my attempts, yet these experiments are, I believe, worthy of record, as the action upon the blood of some of the reagents is sufficiently peculiar. These will be described below.

Having been unsuccessful in extracting the colouring matter, I examined the blood itself by means of Zeiss's spectroscope. For this purpose I compressed a worm with its introvert everted, so as to give a thin film of pink fluid, and examined it through the micro-spectroscope; but no absorption bands were visible. I then had short pieces of glass tubing cut and fixed to glass slips, so that I could fill them to a greater or less extent, and get a column of fluid of different depths. The process of obtaining sufficient blood to fill even a tube one eighth of an inch deep was tedious. The method I adopted was as follows:—A number of living worms were taken, one by one, laid on blotting-paper, so as to dry them as much as possible; then, while holding them just above the stout piece of tube, I snipped the everted introvert or the thorax itself; the worms were then left head downwards over the tubing, and the blood gradually flowed out of the cut end down the side of the tube and collected at the bottom. A considerable number of worms had to be thus treated, and as the blood tends to coagulate the process occupied considerable time; nevertheless I was able to collect what appeared to be a sufficient quantity of blood for spectroscopic examination. The result, however, was nil. I could obtain no absorption bands, though I used both bright sunlight and gaslight, and took all precautions to keep the light out of the apparatus except that which passed through the blood. I also employed solutions of blood in salt solutions and in water. These solutions were colourless, but I thought it possible that even then the colouring matter might give some result; but I was equally unsuccessful.

I believe, then, that we must conclude that the colouring matter of the blood of Magelona causes no absorption bands when a beam of light passes through it, and is spectroscopically analysed.

2. The Histology of the Blood.—The fact that all the reagents which I employed had greater or less action on the blood rendered difficult the ascertainment of the real structural condition of the fluid. The only way in which the true conditions could be studied was by compressing the worm and examining the fluid as it flows along the vessels; for even the mere shedding of the blood, without the addition of reagents, might be supposed to produce certain alterations in its condition, though from what follows I do not think this to be the case. The blood thus examined in situ is seen to consist of very small madder-rose coloured globules, varying in size within certain small limits. These globules choke the vessels, and there appears to be very little plasma. The appearance presented in sections of worms fixed in Hermann's solution is

very similar to that exhibited by the living subject. Further, these corpuscles or globules do not flow freely in the vessels as the walls contract, but adhere together in clumps, and sometimes a mass or clump will be separated by some considerable space from neighbouring masses, appearing to indicate a colourless plasma. This massing of the globules also occurs in the freshly shed blood, as will be seen hereafter, but its occurrence in the blood-vessels is extremely peculiar, and M'Intosh expresses the phenomenon by speaking of the blood as "coagulable"—a term which perhaps is scarcely true in its original sense, for there is no evidence of the separation of "fibrin" or anything of that nature; the globules or corpuscles rather adhere together.

The general shape of the corpuscles is spherical; in size they average 0·002 mm. in diameter in the living condition; they are not amœboid; they are homogeneous, and rather oily in appearance. They are not nucleated, as the addition of reagents will show; and I did not observe the refringent body within them mentioned by M'Intosh. Nuclei, however, do exist in the blood, though usually in an isolated condition, and are not recognisable with certainty in the living worm; but in stained sections, as well as in preparations treated with osmic acid, followed by picro-carmine, such nuclei are more or less abundant (fig. 4), and though usually quite deprived of any protoplasmic envelope, yet in some cases I noted a granular mass surrounding the nucleus, without any boundary or recognisable limit, and I believe this to be the fluid plasma of the blood, coagulated by the reagents. In a preparation of the blood mounted in glycerine, in which the globules have undergone a considerable amount of fusion, so that the globules are of very varied sizes, I note several instances of what appear to be nucleated corpuscles. In these cases the nucleus, of the usual size, is deeply stained, and lies at one side of an unstained "globule" (figs. 8, 9); sometimes, in fact, the outline of the nucleus seems to project slightly beyond the general outline of the globule, but this may be due to the greater refractive index of the former. These globules, of which I give some figures (fig. 6), vary in size, but are much larger than the unaltered corpuscle as seen in absolutely fresh blood, and I suggest that two or more normal globules have fused together and involved the nucleus. The isolated nuclei may occur singly or in groups of three or four (fig. 7).

The size of the nucleus, as seen in sections, is rather greater than that of the globules themselves (Pl. 1, fig. 4). The chromatin granules vary considerably in number and arrangement; sometimes there is but one such granule, at other times several. In the glycerine preparation the former condition is more frequent, and the chromosome is then rod-like (fig. 7, *a*, *b*, *c*).

A. The readiest way to obtain the blood as free as possible from other matters is to dry a worm by placing it on blotting-paper, place it on a dry slide, and pierce with a sharp needle the proboscis, which is pretty sure to be everted. The blood now oozes out slowly, but does not flow freely, the globules adhere together in masses, and the masses are connected by narrower bridges of corpuscles, giving rise to a coarse network. This mass changes its shape and arrangement, as neighbouring nodes or clumps run together by the shortening of the bridges; further, very delicate threads (really due to strings of globules) are seen (*t.*) traversing the meshes, and owing to the continued stretching of the narrowing bridges isolated clumps of corpuscles may come to occupy the meshes as these threads snap asunder. This change of arrangement may be due to evaporation of the plasm and to surface tension. The appearance presented by such a drop of blood shed in this way, and examined without a cover-slip, is shown in fig. 10. The whole mass is pink in colour, highly refringent and oily-looking; no outlines of the separate corpuscles are visible in the larger masses, though in the smaller groups they may be recognised.

When such a drop of blood is covered (fig. 11) the outlines of the corpuscles become evident; and though the majority are similar in size, here and there larger ones are met with, and it is quite possible that the latter are nuclei. The change in arrangement of the bridges and meshes is seen to continue. The appearance presented by this mass of corpuscles is strikingly similar to the "soapy foams" manufactured by Butschli's method; the "alveolar layer" is formed by regular arrangement of the corpuscles along the margin of the mass, and the slow movement recalls that described by him.

B. The blood when freshly drawn by rupture of the "introvert" in sea water (after removal of as much of the sea water as possible from the slide), and at once covered, presented the following appearance. Instead of a mass of similar small globules, these were seen to be of various sizes,—most of them much larger than the corpuscles seen within the vessels, being as much as 0·04 mm. in diameter (fig. 15).

From later experiments, carried out with greater care so that no water should be present, I am led to believe that the result here obtained was due to the presence of a certain amount of sea water on the slide; this causes the globules to fuse with one another, hence the varied sizes of the globules.

3. Appearances presented by the Blood on the Addition of Various Reagents.

1. Normal salt solution, passed under the cover-slip of such a preparation as described above (A.), causes the globules to separate from the masses if there has been no great amount of pressure. If the latter has occurred, only the corpuscles lying at the edge of the mass separate. At first the colour is unchanged, but soon it disappears.

This disappearance of the colour was much more evident when the tubes used for spectroscopic analysis containing a little salt solution, the worms cut as above described, and the blood allowed to flow into the salt solution. I hoped to get a pink solution, but the colour very soon changed and became colourless. This may be due to deoxidation rather than to any destructive power of the salt; but whatever the cause, the result was a disappearance of colour.

2. Distilled Water.—When water is added to blood already treated with salt solution, the following extraordinary series of phenomena ensues:—As the water displaces the salt solution the outlines of the globules disappear: this

takes place naturally at the edge of the masses first, and then the mass presents the appearance of a colourless, oily-looking drop, in which more or less numerous rounded granules are embedded (fig. 12). These granules are the globules, and the longer the water acts the fewer distinct globules remain, till finally the mass of globules is replaced by a homogeneous, oily-looking drop (fig. 13). Meanwhile the movement already described in the fresh blood is going on, and is aided by the current of water as it is drawn under the cover-slip ; the narrow bridges uniting the masses become drawn out into longer and thinner threads—the globules of which they were composed have fused, and the threads, like the masses at the nodes of the network, become homogeneous. These threads may thin out till they break, the two ends are drawn into the masses at the nodes, and the latter become rounded off. In such a way the network may be resolved into a number of larger and smaller droplets, clear, colourless, and without any indication of the globules of which they were originally composed.

If a group of globules or corpuscles not forming part of a network be examined, it can be readily seen that the neighbouring globules do fuse with one another, forming larger globules: these larger ones fuse with others, and thus, as a greater and greater number of globules become involved, a great oily-looking droplet is formed, in which all trace of the original globules has disappeared. In this reaction there is no swelling up of the original globule—neighbouring globules fuse with one another (fig. 14).

The addition of normal salt solution to such a mass, so as to replace the water, did not lead to the reconstitution of separate globules, so that there can be no mistake about the actual fusion.

Such a droplet is shown in fig. 16; after salt solution has been added, it lost its circular shape, and became irregular there being a marked movement—almost amœboid in general appearance; and small irregular outgrowths comparable to pseudopodia became formed, and some of these separated from the mass as pear-shaped, and later circular droplets (*x*.). It may be suggested that these are the original globules, but such is not the case; they are very much smaller, and vary more in size. Further, only a few such separations occurred, even after prolonged action of the salt solution.

When water is added to freshly drawn blood the same series of reactions occur (fig. 14). The colour of the corpuscles is quickly changed by the water, the masses becoming colourless. I also "bled" worms into a few drops of water in a tube, in the hope of obtaining a solution of colouring matter.

The reaction of the corpuscles or globules to water indicates that these coloured globules are not provided with any membrane or envelope. They appear to be droplets of coloured material, and their general appearance suggested some oily substance.

Chloroform.—Employing freshly shed blood on a dry slide, and running in chloroform as soon as possible, I observed the gradual disappearance of the corpuscles. Each corpuscle as the chloroform reached it first lost its colour, then rapidly became smaller and smaller, till nothing was left but a few very minute granules. Amongst these a number of small ovoid, highly refringent bodies, being a faint olive-green in tint, make their appearance.

Here, too, I have no doubt as to the fact that the corpuscles are dissolved: there is no mere "diminution in size," such as is observable in the case of mammalian corpuscles treated with chloroform; there is an absolute disappearance of the globules of Magelona, the only trace of them that remains being a few granules.

Ether produced effects similar to those produced by chloroform. Both these reactions seem to point to fat or oil of some kind.

Absolute alcohol gave the same reaction. I added nitric acid (10 per cent.) to the small olive-green refringent bodies, and found that they are insoluble in the acid. But both these and the smaller granules were dissolved in strong nitric acid.

Alcohol (70 per cent.) had similar action.

In all the above cases the colour of the corpuscle disappeared.

Osmic acid coagulates the substance of the corpuscles, but does not otherwise change them. They only become distinctly brown after some minutes, and do not give the dark brown or black colour characteristic of fat.

Nitric acid (25 per cent.) and Hydrochloric acid (20 per cent.) cause the corpuscles to become granular, though they do not actually disappear. The colour is changed.

Potash (30 per cent.) has a similar action.

Glacial acetic acid dissolves the globules, leaving minute granules, though the action is very slow.

Further, picro-carmine stains the globules, as also does eosin : they retain their homogeneous appearance, however.

These tests are unfortunately inadequate for the identification of the substance of which these globules are composed ; but from the ether, chloroform, and alcohol reactions, I think we may conclude that it is one of the " fats " which are soluble in these reagents, and moreover, give rise to crystalline bodies on evaporation. And amongst these fatty bodies, lecithin appears to give a similar reaction with water, in that it swells up in a peculiar way, forming droplets and threads, as I have described above.

4. General Remarks.

From these observations it will be seen that the blood of Magelona is totally different in structure from that of any other Chætopod, in that it consists mainly of very small madder-rose coloured, non-nucleated globules, embedded (rather than floating) in a very small amount of colourless plasma : amongst the corpuscles occur isolated nuclei. It was originally demonstrated by Professor Lankester that nuclei occur in the red fluid of the common earthworm, and this observation has been extended to sundry other Annelids by various observers. In these cases, as in Magelona, the nucleus is surrounded by very little, if any, protoplasm, and floats freely in the perfectly liquid plasma, which is coloured red by hæmoglobin, or in a few cases green by chlorocruorin or chlorochromin ; while in some Oligochætes the plasma is colourless. No other structural element has been described in the fluid contained in the blood-vessels of any Annelid. But a few worms are known in which the blood-vessels are absent, whilst the fluid in the cœlom is coloured; and in these cases (Glycera, Capitellidæ, Polycirrus) the hæmoglobin exists within the corpuscles, the plasma of the cœlomic fluid being colourless. The coloured corpuscles of this fluid in Glycera and Capitellidæ are, however, entirely unlike the coloured globules in the blood of Magelona.

In the case of Capitella I took the opportunity of examining the corpuscles during my stay at St. Andrews, as I was able to get abundant material. My observations are not new; Claparède and Eisig have already sufficiently demonstrated the character and constitution of these corpuscles. Lankester[1] was the first to show by spectroscopic examination that they contain hæmoglobin. The corpuscles when drawn fresh from the worm are circular, somewhat flattened discs, yellowish red in colour. A distinct membrane is visible, and granules of various small sizes are present. Stained with picro-carmine, a small round nucleus is seen in each corpuscle. When fresh corpuscles are treated with salt solution no effect is noticeable. On the addition of distilled water the hæmoglobin is dissolved out and the nucleus is rendered distinct, and the corpuscle itself becomes slightly smaller. This is no doubt due to osmosis, the water passing into the corpuscle and causing it to become spherical: it thus loses in diameter in one direction as it gains in the other,—a process exactly like that occurring when Vertebrate corpuscles are similarly treated.

Prolonged action of water causes the outline of the corpuscles to become less and less distinct, till it is almost impossible to recognise it, the nucleus and refringent bodies alone remaining. This reaction is quite different from what we have seen to occur in the case of Magelona, but resembles the corresponding reaction with human blood.

Chloroform dissolves the hæmoglobin, the corpuscles become granular, and the outline becomes gradually less distinct, but the membrane remains for a long time. But there is no

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[1] 'Proc. Roy. Soc.,' xxi, 1873, p. 70.

marked change in size; there is nothing approaching the gradual though rapid disappearance of the globules seen in the case of Magelona.

Ultimately, though after a considerable time, the corpuscles appear to become dissolved, breaking up into granules.

In Glycera, too, the corpuscles, as Claparède, Lankester, and others have shown, are nucleated—the nucleus being oval and the corpuscle larger than that of Capitella. I was unable to obtain Glycera in any quantity,—in fact, I only came across two small specimens while collecting Magelona, and was unable to make many observations on them. But previous authors have compared these corpuscles with those of Vertebrates.

The so-called "corpuscles" or coloured globules of Magelona thus differ from the coloured corpuscles observed in other Annelids, not only in position, viz. within blood-vessels instead of in the cœlom, but also in structure and in their behaviour to chemicals, and I believe that they are different in constitution.

These coloured globules in Magelona are to be compared with the coloured plasma of the ordinary Chætopod blood, rather than with the coloured corpuscles of Capitella, Glycera, and Polycirrus. These globules, in fact, though recognisable as separate elements, do adhere together in the blood-vessels to form a fluid of the consistency of thick oil. If we suppose that a little more water were present in their composition we may imagine the globules to fuse with one another, and so form a more freely flowing plasma—such as is obtainable by experiment. This plasma would then be quite comparable with that of the blood of ordinary Annelids. But if we imagine the individual globules to have a firmer envelope—more resistent to reagents than it is in fact—we should have more perfectly defined corpuscles, comparable to the hæmatids in the blood of mammals. These adhere together, just as those of Magelona do, on being shed from the vessels.

The globules of Magelona stand, as it were, midway between the coloured liquid plasma of Annelids generally and the coloured corpuscles of mammalian blood. The latter are known not to be cells, but to be parts of cells, produced in many cases within cells by the modification of the protoplasm, its coloration and subsequent separation into globules, which are then set free by the breaking up of the parent cell.

With regard to the development of the globules in Magelona I have not yet come to any definite conclusion, though I expect to find that a similar origin of the corpuscles obtains.[1] The formation of the plasma in ordinary Annelids is practically on the same lines, but the fluid, in place of separating as globules or corpuscles, is discharged en masse (see Lankester's observations "On the Connective and Vasifactive Tissues of the Medicinal Leech," 'Q. J. Micr. Sci.,' vol. xx, 1880, p. 307).

5. The Colouring Matter of the Blood.—We have already seen that no absorption bands were obtainable by means of the spectroscope, nor have I been able to separate any pigment by the use of various reagents. But from mere tint alone, and its change of colour on deoxidation, it is evident that the pigment is quite different from any hitherto recorded amongst the Chætopods; it is most evidently not hæmoglobin. The other colouring matters known in the Chætopods are the greens of the Sabellids and Chlorhæmids, known as chlorocruorin.

In no other Chætopod do we find the madder-rose colour characteristic of Magelona; but in Sipunculids a similar blood-pigment exists, presenting a similar loss of colour on deoxidation. This colouring matter, as seen in Sipunculus nudus, closely resembles that of Magelona. Its peculiarities were first described by Lankester,[2] and subsequently by Krukenberg,[3] who gave to it the name "Hæmerythrin."

The blood-pigment in the Sipunculids occurs in the nucleated circular disc-shaped corpuscles of the fluid contained in the

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[1] Miss Buchanan describes some of the early phenomena of the formation of the blood of Magelona ('Rept. Brit. Assoc.,' 1895, p. 469), in which she suggests that the "corpuscles" arise from subdivision of multinucleate corpuscles derived, apparently, from a special blood-forming organ in the dorsal vessel.

[2] Lankester, 'Proc. Roy. Soc.,' xxi, p. 80.

[3] Krukenberg, 'Vergl. Physiol. Stud.,' 1st reihe, 3te Abth, p. 82.

body-cavity. In Phoronis the pigment is hæmoglobin, as Lankester showed by its spectrum, and is not hæmerythrin, as Krukenberg assumes. In Phascolosoma elongatum Schwalbe describes the tint as light rose or faint greyish red (matt grauröthlich), which on oxidation grows darker, and finally becomes "burgunderrothe." This description of the colour scarcely agrees with that of Magelona, nor does that given by Ehlers and Keferstein for other members of the group—Sipunculus and Priapulus,—for they term the colour of the body-fluid "wine-red;" but in Sipunculus nudus at any rate, as I can testify from my own observations, the tint is very close to that seen in Magelona.

6. Relation of Vessels to Cœlom.—The fact that in the thorax the ventral vessel dilates to such an enormous extent as to nearly obliterate the cœlom is a very interesting and important piece of evidence in favour of Professor Lankester's suggestions ('Quart. Journ. Mic. Sci.,' xxxiv, 1893) as to the manner in which the heart of Arthropods, with its series of ostia for the entrance of blood, has been derived from a Chætopod vascular system, owing to the enlargement of the afferent vessels or veins, till the latter fuse with one another to form a great "pericardial blood sinus," to the exclusion of the cœlom. Here, in Magelona, we have a great dilatation of the ventral vessel and lower part of the "afferent" vessel leading upwards to the dorsal vessel. This great lateral dilatation (*l. ext.*) communicates with the ventral vessel just behind the septum, between consecutive segments, by a comparatively narrow opening, as shown in the figure. If this dilatation extended further upwards to the dorsal vessel we should have a condition closely approaching that of the Arthropod vascular system. This ventral vessel of Annelids no doubt corresponds to the great ventral blood sinus of Astacus, &c., whence the blood makes its way up to the heart, either directly or by way of the gills.

I hope, in a later contribution, to give a further account of the vascular system of this interesting worm, Magelona.

EXPLANATION OF PLATE 1,

Illustrating Dr. W. Blaxland Benham's Paper on "The Blood of Magelona."

Explanation of Figures.

Fig. 1.—Side view of the anterior region of Magelona, with the "proboscis" withdrawn. The thorax is coloured by the blood contained in its vessels.

Fig. 2.—Side view of the anterior region of Magelona, with "proboscis" (*a*) everted. The thorax is now almost colourless, the blood being driven into the proboscis.

Fig. 3.—A transverse section through the thorax of Magelona, showing the great dilatation of the ventral blood-trunk and its extension into the "lateral chamber" of the body. On the right side one of the dorso-ventral muscles is represented separating the lateral extension of the vessel from the median portion. This dilated vessel comes to occupy almost the entire cœlom. The epidermis (*ep.*) is somewhat diagrammatically represented; the remainder is drawn with the camera. *D. v.* Dorsal blood-vessel, with thick muscular coat. *V. v.* The dilated ventral vessel, with thin nucleated wall. *lat. ext.* and *L. ext.* Lateral extension of the ventral vessel. *l. v.* Vessel from ventral to dorsal vessel. *Cœ.* Cœlom. N. Nerve-cord. G. The gut. *circ.* Circular coat of muscles of the body-wall. *l. m.* Longitudinal muscles. *dor. v. m.* Dorso-ventral muscle. *obl.* Oblique transverse muscle. (Camera Zeiss B 2.)

Fig. 4.—A group of blood-globules. (× 550.) Camera drawing of contents of a blood-vessel from a section stained in borax carmine. The size of the corpuscles is practically unaltered by the preservatives. *n.* Nucleus.

Fig. 5.—Two globules from same section, greatly magnified. The contents have been coagulated by reagents.

Fig. 6.—A group of globules (× 550) from a preparation of blood killed with Fleming's solution, stained in picro-carmine, and mounted in glycerine. The globules have "fused" with one another, so that the field is filled by larger globules of various sizes. A coagulated plasma (*pl.*) is represented. A nucleus (*n.*) shows the relative size of the globules. (Camera drawing.)

Fig. 7.—Some isolated nuclei, showing varying numbers of chromatic masses. From same preparation.

Fig. 8.—An example of nuclei apparently contained within large globules (from picro-carmine, glycerine preparation). *n.* Nucleus. *pl.* Plasma. Camera. × 550.

Fig. 9.—Other examples of the same more highly magnified. In *a* the nucleus, overlying the globule, projects beyond its margin.

Fig. 10.—Freshly drawn blood, without reagent, uncovered (Zeiss, F 2). The globules do not freely separate from one another, but adhere together, forming an irregular mass or network. *c*. A few isolated globules. *t*. Delicate thread-like bridges of corpuscles. *t'*. The same broken across by the movement of the mass, resulting in the isolation of some globules.

Fig. 11.—A portion of the same preparation covered; the same magnification (Zeiss, F. 2). The irregular mass is now seen to consist of masses of corpuscles or globules, forming a network with irregular meshes.

Fig. 12.—A portion of a similar drop of blood in salt solution, to which water has been added. The threads of the network have become greatly elongated and more delicate. The margins (*a*) of the masses have become homogeneous, owing to the fusion of neighbouring globules; these still exist unaltered in the centre of the nodes (*b*).

Fig. 13.—Further action of water (lower magnification).

Fig. 14.—A small drop of blood after addition of water, showing the fusion of a large number of globules to form larger and larger clear masses.

Fig. 15.—Another drop of blood, with a trace of sea water. (Camera drawing. × 550.) Various sized drops have been formed by fusion of globules.

Fig. 16.—Action of salt solution after water. (*a*) Mass in water, action commencing. (*b*) A mass of globules in water have fused to form a round mass. (*c*) Salt solution added; change of shape and movement of the mass; protrusion of processes. (*d*) The changes are more marked, and small droplets (*x*) are separating from the ends of processes. (This figure is drawn on a slightly larger scale than the other two.) In the mass there is a hole (*y*) which in *d* has made its way to margin.

Fission in Nemertines.

By

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With Plates 2 and 3.

It is a well-known fact that many Nemertines break up into pieces when irritated; but although this statement is current in text-books as well as in special memoirs the matter has received very little attention, and I find no account of any internal changes which may take place in the tissues of the body previous to the process of fragmentation. Indeed, it appears that the statement is made rather vaguely, and its application is scarcely so general as might be inferred. There is no doubt but that Carinella, Lineus, and other elongated and comparatively slender forms do fragment, and that these fragments can remain alive for a considerable time, as Dalyell, and later M'Intosh have recorded; and further, it appears that the anterior end of such a fragmented Lineus may produce a new posterior end, and M'Intosh figures various stages in the formation of a head to a more posterior piece. As the specimen which he kept under observation lived in very unfavorable conditions of food, &c., he did not observe the completion of the head even after some months, but remarks that in a state of nature such a regeneration most probably takes place frequently.[1] Further, we are left somewhat in doubt as to whether a Nemertine does of its own accord, and independently of irritation, normally break up into pieces.

[1] M'Intosh, 'Mar. Brit. Annelids: Nemertea,' p. 125.

My attention was called to this matter in 1894 on examining a small Carinella from St. Andrews that happened to be amongst a number of specimens of Magelona, which Professor M'Intosh had most kindly sent to me for the purpose of certain work on the latter worm on which I was engaged.

This Carinella presented, in the hinder region of its body, two conspicuous constrictions at nearly equal distances from one another, *A B*, and each piece thus marked out was further constricted, though much less deeply, *C D*, into two nearly equal portions (Pl. 2, fig. 1). So striking was this apparent "segmentation" of the body, that I preserved the worm for sectionising. It was killed in corrosive sublimate to which 1 per cent. acetic acid was added.

Later on in the year, while working in the Marine Laboratory at St. Andrews, with a view to collect and observe living Magelona, I came across two more specimens of this same Nemertine, which I found living in the sand with the Polychæte below the ordinary low-water mark. Both these worms were about the same size as the one I had obtained previously, and both presented similar phenomena of "segmentation." One of these was unfortunately mislaid; the other I killed, stained, and mounted entire.

The Carinella to which these observations refer is a small worm about two inches (55 mm.) in length when in moderate extension. It is pure white, without eye-spots, and without pigment except for a girdle of a faint yellowish-brown colour, about a quarter of the worm's length from the anterior end (fig. 1, *b*). This is very faint even in life, and is due to pigment in the epidermis. Further, the proboscis is coloured faint blood red for a short region just in front of this pigmented band (*p*).

The body is nearly cylindrical in section; the head is pointed, and slightly marked off from the body by a lateral vertical furrow on each side at the level of the mouth; the head is not noticeably wider than the body (fig. 2).

The posterior end of the worm, as longitudinal sections showed, is not complete—a portion has already been separated, so that I cannot state the true length; but at first sight this end does appear entire and rounded off (Pl. 2, fig. 1).

In transverse sections (fig. 10) probably the most noticeable feature is the thinness of the circular muscles; so thin is this layer that it cannot be distinguished in transverse section through the middle of the body until longitudinal sections are called in to help:[1] the basement membrane is also thin.

The two nerve-cords lie between the basement membrane and the circular muscles, and this position at once shows that the worm belongs to the genus Carinella; but as to its specific identity I cannot be so sure. I hesitate to confer a new name on the worm, as it bears a certain likeness to C. linearis, Montagu, which is described by M'Intosh; and one of his two woodcuts illustrating this species (p. 206) also shows constrictions of the hinder end, recalling at once the phenomenon presented by the present worm, although the "segments" are not so nearly equal in size. But this point would not be of any moment, for in the stained entire worm (Specimen II) there is less equality in the size of these "segments" than in the one I first noted and drew when alive. There is, however, a statement in M'Intosh's description which renders an identification doubtful, for he states that C. linearis is "flattened," and this is certainly not the case with my worm at any rate—transverse sections do not exhibit any flattening. M'Intosh states that "the inner muscle of the body-wall shows a marked tendency to separate in the dorsum." If this means that the longitudinal coat is traversed by a band of tissue in middle line my specimen agrees with his. Nevertheless no great weight can be placed on this fact, for Bürger has shown that this occurs in probably all species of Carinella. But from the general description, and from quotations from Montagu's MS., it appears at any rate probable that the present worm is C. linearis, for it agrees in habitat, and in the fact that it "secretes a tenacious slime from its body, which, collecting sand, readily forms a covering

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[1] The thickness of the circular muscle-coat has been intentionally exaggerated in the figure.

like that of Sabella." It agrees more closely with this species than with any more recently described, such as C. albida, Bürger, so that I must leave the matter of species open.

The hardened specimen was sectionised as follows:—(1) The anterior end was cut sagittally (vertical longitudinal); (2) the hinder end was cut horizontally, though rather obliquely to the horizontal plane; (3) the middle region of this body was transversely sectionised. The stain used was carmalum, though some sections were stained with picro-carmine.

With regard to the posterior "segmented" region of the body, one is struck at once by the fact that at the level of each of the four constrictions there is a transversely arranged row of small nuclei traversing the longitudinal muscles. They are readily seen even with a low power (fig. 3), and are more evident at the deeper constrictions A, B, than at the shallower ones C, D.

What appears to be the commencement of the phenomenon is illustrated by the sections across the constriction C (fig. 4). At this point the tissues are as yet perfect—there is no rupture. The section figured passes through the lateral line of the body, on one side cutting along the nerve (*N*); at the opposite side the nerve is not involved. The nuclei constituting the transverse row are not as yet as definitely arranged as they will be; nevertheless they are more numerous along the level of the constrictions than elsewhere, and take a deeper tint in the stain. It may here be mentioned that the accompanying figures are drawn with the camera, and so far as was possible every nucleus is put in its true position, except in the case of the epidermis and intestinal epithelium where these are involved. The nuclei which are thus conspicuous appear to belong to the connective tissue in which the longitudinal muscles are wrapped; they are smaller and more deeply stained than those of the muscles. Although the impression given by the section fig. 4, through the region C, appears to indicate an irregular transverse line, yet at a further stage this line becomes very much more distinctly transverse, and, moreover, it is in reality double; the nuclei are arranged into two rows close to one another, as is shown in fig. 5, through the region D. Here, however, we have a further phenomenon: the double row of connective-tissue nuclei having been established, the longitudinal muscles break across between the two rows of nuclei. This rupture appears to start just below the epidermis, and then travels inwards. But already the epidermis exhibits a furrow even at an earlier stage, as at C (fig. 4), so that it is not merely the result of a contraction of the muscles.

The muscles, once ruptured, naturally contract, and leave a space which appears in sections to be partially occupied by a coagulum (x), though it may be a pre-formed material—part of the connective tissue. This appears to be the more likely, as is seen at a later stage in the process, as in fig. 6, which passes through the middle of the region A. Here the rupture of the muscle has gone a step further, and is extending towards the opposite side; this figure also illustrates another point—viz. that the rupture may commence at one point of a plane and extend in all directions in a radial direction, so that while it is complete at one side of the body it may not have yet commenced on the opposite side.

In this figure, for instance, the muscles have shrunk considerably at the left side; yet, though the rupture is extending towards the right, the muscles are still entire below the epidermis of the right side. By the rupture of the muscles the linear arrangement of the connective-tissue nuclei is to some extent destroyed.

Finally, the epidermis, which during this process has become thinner, as well as furrowed at the plane of constriction, gives way; but the basement membrane still appears to resist the rupture, for in fig. 7 there is a distinct membrane (*bm.*) left after shrinkage of the epidermis. We must consider this basement membrane, as Hubrecht and others have suggested, as a firm skeletal tissue, and its resistance to the process here described is only what would be expected.

When the rupture is complete, or even before it has travelled all the way round the worm, the circular muscles come into play (right side of fig. 8), and drawing together the margins of the wound formed by the rupture, form a boundary to the portion separated as well as to the anterior region. The gonads are thus held in place, and do not project through the wound, and hence the rounded end of the body looks like the true anal end. During the above process the intestine has, of course, become nipped.

After the epidermis has been ruptured one notices the surfaces of the wound to be covered with a flat epithelium (fig. 8, *ep′*). Whence comes this? Is it derived from the connective tissue? It looks as if the row of nuclei before mentioned had flattened out, and so given rise to the flat nuclei of this membrane.

This appears to be the general history of the process of fission. But we are no nearer to the answer—how do the muscles become ruptured? why do they all give way at this particular plane? Further, is it merely a rupture of the fibrillæ, or is there a degeneration of these fibrillæ over a certain small area, viz. between the two rows of nuclei? Have these nuclei, or rather the cells belonging to these nuclei, any part to play in this rupture or degeneration, or are they merely a preparation for the new membrane which forms the ends of the fragments of the body?

At present I am unable to answer these questions with certainty. It appears to me, after a careful study of my preparations, that the muscle-fibrils do rupture; at any rate, if there is a degeneration of tissue, it occurs over only a very minute distance: the ends of the ruptured fibrils appear clean-cut (fig. 6), and I see no sign of any modification in their substance which would point to a degeneration.

With regard to the second part of the query, viz. the action of the row of nuclei, I would suggest that they do play an active part in the process. The muscle-fibrils are wrapped together by connective tissue, which has the form of a network, through the meshes of which the fibrillæ pass (fig. 9). At the point of future rupture this network is denser and the meshes smaller, and it may be that the cell-substance becomes actively contractile, and really nips the muscle-fibrils in two. On the other hand, we must not overlook the possibility of the occurrence of some kind of solvent action—the fibrils may be "eaten through," as it were; but I know of no means of deciding the matter.

The process, whatever its details, seems to be different from that which occurs in Planarians, such as Microstoma, which reproduce asexually by fission.

In his account of the process, van Wagner ('Zool. Jahrbuch,' iv, 1891) expressly states that there are no nuclei in the "septa," which make their appearance along the lines of the future separation of the individual into zooids. Each septum is represented in v. Wagner's illustrations as being of some homogeneous tissue, passing from the subepidermic muscles to the muscularis of the intestine. He gives no details as to how the "parenchyma" separates, which bear any resemblance to those detailed in the process of rupture of the muscles seen in this Nemertine. Further, there is a great deal of "regeneration"—i. e. formation of new brain, new pharynx, &c.—in Microstoma before separation takes place. Of this there is no trace in Carinella. I need not enter here upon the vexed question as to the distinction between "division" and "gemmation." In Carinella there seems no doubt that the process is "division."

A second part of the problem relates to the meaning of the whole process in regard to the life of the animal. It is generally assumed, and apparently rightly assumed, that the process of rupture will be of advantage to the Nemertine, in that each of the pieces thus formed will be able to give rise to gonads, as M'Intosh observed; in most cases, however, there does not seem to be any direct relation between rupture and genital maturity. But in the present instance there is such a relation, for in both the specimens the genital elements are only present in the hinder part of the worm, which is being separated off from the rest.

In the specimen I (fig. 1), which is a female, the gonads are present in each of the four "segments," and no trace of ova exists in front of the line B, while behind the line A the ova are larger and more numerous than in front of it.

The specimen II, which was mounted entire, is a male, and the spermatozoa exist only in the hindermost part of the body.

It would appear, therefore, that the gonads make their appearance simultaneously over a certain stretch of the body, commencing at the hindermost region; that as they ripen this region begins to be constricted off from the rest of the body. A second tract now commences to ripen, and in its turn becomes marked off from the non-sexual anterior region of the body; and so the process goes on up to the point of origin of the proboscis.

Further, each such region may become restricted into two (or more?) pieces; and it will be very interesting to ascertain whether this segmentation goes any further than in the specimens to hand. It is possible that the segmentation of this sexual region of the body, which is already beginning in our specimens, may ultimately become so far repeated that each "segment" will contain only a single pair of ovaries. In that case we should have a strong case in support of Hubrecht's theory of segmentation, as elaborated in his 'Report on the Nemertines of the Challenger Expedition.'

However that may be, we have in this Carinella what appears to be an undoubted preparation for the spontaneous subdivision of the sexual region of the body into a number of isolated portions, and this subdivision is due to the development of the gonads, and is thus directly related to the propagation of the species.

We have yet to learn whether each of the pieces so isolated will produce a new head; but it appears to me a needless assumption that this would happen. As each "segment" drops off, the tissues after decomposition might set free the generative products; but since genital ducts (fig. 3, *g.d.*) are already forming, and are in the hindmost segments nearly completed, it appears that the segments live an independent life for some time after separation. This fact, therefore, militates against the idea of any greatly extended "segmentation."

Anatomical.—The Nemertine which forms the subject of the present contribution exhibits one or two points of interest in its histology, which differs from that described by Bürger[1] for Carinella and its immediate allies.

The lateral nerve-stems do not exhibit the characters described and figured by that author, who finds an inner and an outer neurilemma separated by a considerable space. In this lie numerous ganglion-cells, chiefly collected above and below the "punktsubstanz," which is surrounded by the inner neurilemma, and to which the processes of the ganglion-cells pass. In the present worm the ganglion-cells are very few, at any rate towards the middle of the worm, though they are more numerous anteriorly. But these cells lie not only above and below, but at the side of the nerve (fig. 11). Further, I do not find distinct inner and outer neurilemma. The nerve-cord is surrounded by a distinct but delicate membrane, with flattened nuclei (*m′ m″*); this appears to correspond to Bürger's outer neurilemma. The ganglion-cells are situated in a network of tissue, resembling, in general, the substance of an ordinary Invertebrate nerve-cord, and the meshes of this network are occupied by fine dots—the "punktsubstanz" (*p.*).

Lying near the centre of the nerve-cord is a distinct tube, with well-marked wall, against which lie here and there nuclei resembling those of the ganglion-cells. This tube (*ch.*) usually appears empty, but in some sections a faint coagulum with very minute scarcely visible granules in it. There is no network, such as occurs in a nerve-cord, and I take this tube to be a "giant fibre" or "neurochord," such as Bürger finds in Nemertine nerve-trunks generally.

In Carinella, according to that author, there are none, whereas in the Schizonemerti he finds several of them. It might be suggested that what I regard as the wall of a tube or neurochord is, in reality, Bürger's "inner neurilemma;" but the contents of this tube are certainly not like the structure seen in an ordinary Invertebrate nerve-cord. My sections were stained in picro-carmine, and others in alum carmine. I did not employ hæmatoxylin, and it is possible that a

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[1] "Unters. ub. d. Anat. u. Histol. d. Nemertinen," 'Zeit. für wiss. Zool.,' 50.

renewed investigation with other preservatives and stains may lead to a different interpretation of this "tube;" but, so far as my preparations go, I cannot think that this is an "inner neurilemma," or that the contents form the "punktsubstanz."

The muscles of the body-wall are chiefly interesting for the great thickness of the longitudinal coat, and the very feeble development of the circular coat in the greater part of the body, though anteriorly this coat becomes rather thicker.

The "inner coat of circular muscles," which has so often been described for the Palæonemertini, has been identified by Bürger as the muscle of the rhynchocœle (proboscis sac) and gut, which, owing to the slight development of the parenchyma, comes to lie immediately within the longitudinal coat. This explanation brings the muscular system of the Palæonemertini into agreement with the general scheme of Nemertine musculature.

This inner coat (*rh.c.*) is in the present worm very thin indeed, but can easily be recognised in longitudinal sections. I have exaggerated its thickness in the figure of a transverse section. This inner coat can be traced as a sheath round the rhynchocœle and intestine (*int. c.*), and a second coat surrounding the rhynchocœle alone.

Bürger describes a decussation of this inner coat in the median dorsal line. I am unable to satisfy myself whether this exists in the present worm; but traversing the longitudinal muscles is a vertical strand of tissue (fig. 10, *x.*) staining like the basement tissue and continuous with it dorsally, and with a similar tissue surrounding the rhynchocœle; whether the circular muscles accompany this strand—as I believe they do—I was unable to determine. The intestine, as I have just stated, is partially—i. e. on the ventral side—surrounded by a layer of circular muscles; in addition, its dorsal wall is formed by a fairly thick layer of longitudinal fibres (*int. lg.*), lying between the intestinal epithelium and the wall of the rhynchocœle.

The proboscis presents throughout the greater part of its extent a glandular epithelium, surrounded by circular muscles, and then by a thick coat of longitudinal muscles. But the epithelium changes its character for a short space near its anterior end; the gland-cells, so conspicuous elsewhere, no longer catch the eye in section, if indeed they are present; but the cells are long, narrow, with flat nuclei at the sides, and close to the free end there is a series of round nuclei arranged in a well-defined row.

In longitudinal section this region occurs between 2 and 3 mm. from the anterior end; whether it corresponds to the blood-red tract on the proboscis, noticeable in the living worm, I am not certain.

In all the Palæonemertini the parenchyma is but very feebly developed, but in the present worm, at any rate behind the middle of the body, it is practically absent. I can detect no space between the wall of the gut-muscle, and body-wall, i. e. between the inner circular muscles and the longitudinal muscles, except the longitudinal blood-vessel on each side and a nearly homogeneous tissue (*y.*) passing up from it to the inner wall of the intestine; this tissue resembles the ordinary connective tissue, which occurs in some sections in sheets quite like this little piece. This is all that represents the "parenchyma" posteriorly.

There is one point in which this Carinella does not agree with Bürger's statement as to the arrangement of the gonads. He states that in the Palæonemertini there is usually more than a single pair of gonads in a transverse plane, so that a transverse section through this region would exhibit more than two gonads and ducts. This is not the case with the present Carinella. The gonads are strictly paired; there is one, and only one, on each side,—each with its duct formed in the usual way. Each ovary when nearly ripe consists of three or four large ova, surrounded by a common membrane of flat cells, which is continuous with a heap of indifferent rounded cells on the outer side of the ripe cells (fig. 12). Amongst this mass of rounded cells one can distinguish one or more cells, still small, but distinctly larger than the rest, with a distinct germinal vesicle (*ov.*); these are evidently young ova.

EXPLANATION OF PLATES 2 and 3,

Illustrating Dr. W. Blaxland Benham's Paper on "Fission in Nemertines."

Fig. 1.—View of Carinella (No. 1) immediately after death, showing the "segmentation" of the hinder part of the body. (× 6.) *A*, *B*, *C*, *D*, indicate the constrictions in order of depth, *A* being deepest. The drawing also shows the general appearance of the worm. *p* is the red region of the proboscis. The body is coloured orange in the region just in front of *b*.

Fig. 2.—Ventral view of the anterior end, to show the shape of the head. *M.* Mouth. *R.* Aperture of the rhynchodœum. *L.* Ciliated furrows.

Fig. 3.—Camera drawing of the hinder end of the worm. *A*, *B*, *C*, *D*. The constricted regions, each marked out internally by a double row of nuclei. The section is nearly horizontal. *ov.* Ovaries, fully developed in the hinder "segments." *ov'.* Less developed ovarian sacs in anterior regions. *g.d.* Genital duct. *int.* Intestine. *ep.* Epidermis. *lg.* Longitudinal muscle. Mag. Zeiss Aa 2.

Fig. 4.—The region *C* enlarged. The section is at a different level from that of the preceding figure, as it cuts the nerve-cord on the left, and does not involve the intestine. *ep.* Epidermis. *b.m.* Basement tissue. *circ.* Circular muscles. *lg.* Longitudinal muscles. *n.* The transverse row of nuclei. *N.* Lateral nerve-stem. Mag. Zeiss B 4.

Fig. 5.—Horizontal section through the region D, to show the next stage in the process of fission. The longitudinal muscles have ruptured, contracted, and left a cavity just below the nerve-cord. *x.* A coagulum.

Fig. 6.—The next stage in the process, illustrated by section through the region *A*. The ruptured muscles are more numerous, and the cavity (*sp.*) therefore more extensive, and is traversed by connective tissue (*c.t.*). Mag. Zeiss B 4.

Fig. 7.—Another portion of the same region, to show the coagulum (*x.*), the broken ends of the longitudinal muscle-fibres, and the unruptured basement membrane (*b.m.*). *bv.* is the lateral blood-vessel.

Fig. 8.—Portion of A (fig. 3) at a different level, enlarged. The rupture has extended nearly right across, and the ends of the two pieces are bending inwards owing to the contraction of the circular coat of muscles. This figure also shows the flattened epithelium (*ep'.*) which covers the broken ends of the muscles.

Fig. 9.—A somewhat diagrammatised view of the muscle-fibres and connective tissue in the region of one of the "septa." *m.* Muscle-fibres. *c.t.* Connective-tissue network, through the meshes of which the fibrils pass: the network is denser in the region of the "septum" than elsewhere. *n'* Nucleus of "septum."

Fig. 10.—Transverse section of the worm (mag. B 2, cam.). *ep.* Epidermis. *b.t.* Basement tissue. *bv.* Blood-vessel. *circ.* Circular muscles of body-wall. *lg.* Longitudinal muscles. *int.* Intestine. *int.c.* Circular muscle of intestine. *int. lg.* Longitudinal muscle of intestine. *Pr.* Proboscis. *P. ep.* Outer epithelium of proboscis. *Rh.* Rhynchocœl. *R.ep.* Epithelium of rhynchocœl. *rh.c.* Its coat of circular muscles. *N.* Lateral nerve-stem. *x.* Streak of tissue resembling connective tissue interrupting the longitudinal muscles dorsal (? decussation of *rh.c.*). *y.* "Connective tissue" near blood-vessel.

Fig. 11.—View of section across lateral nerve-stem. *b.t.* Subepidermic basement tissue. *circ.* Circular coat of muscles. *ch.* Neurochord, with distinct membrane and (?) coagulum within. *m'.* Outer membrane (? neurilemma). *m''.* Inner membrane, separated at one point by a space (*sp.*), probably due to shrinkage. *n.g.* Nuclei of nerve-cells. *n.s.* Nuclei of sheath. *p.* Punktsubstanz in the meshes of nerve-cord. *D.V.* indicate the dorsal and ventral surfaces of the nerve-cord.

Fig. 12.—A portion of a section across the region A to show the ripe ovary. *ov.* Ovary. *O.* A ripe ovum. *w.* Wall of ovary. *s.* "Septum." *b.m.* Basement tissue exposed after the rupture of the epidermis.

Studies on the Nervous System of Crustacea.

By

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With Plate 4.

IV. Further Observations on the Nerve Elements of the Embryonic Lobster.

In the first part of these studies[1] an account was given of certain nerve elements which had been demonstrated by the action of dilute solutions of methylene blue upon the ganglia of the embryonic lobster (Homarus vulgaris). The elements then described arose, in most cases, from cells which lay in the anterior ganglia of the thorax. In the present paper a number of additional elements occurring in these ganglia will be noticed, together with those found in the posterior thoracic and in the abdominal ganglia.

The method of investigation has been the same as that described in my former communication, the results in this case, however, having been obtained principally from embryos which were near the point of hatching. Several of the new elements differ in essential points from any of those previously described, and are of interest in throwing additional light upon the manner in which different portions of the central nervous system, or different movements of the body, are co-ordinated one with another.

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[1] This Journal, vol. 36, pt. 4, 1894; a preliminary notice occurs in 'Proceed. Roy. Soc.,' vol. lv.

The observations will be dealt with in the following order:

I. Elements arising from cells situated in the THORACIC GANGLIA.

(*a*) Elements of types the same as or similar to those previously described.

(*b*) Elements belonging to types not previously described.

II. Elements arising from cells situated in the ABDOMINAL GANGLIA.

III. Elements arising from cells outside the central nervous system.

I. THORACIC GANGLIA.

(*a*) ELEMENTS SIMILAR TO THOSE PREVIOUSLY DESCRIBED.

B, THORAX XI[1] (fig. 1).—The cell lies in the anterior portion of the lateral mass of ganglion-cells of Thorax XI, and gives off a fine fibre, which passes into the neuropile ("punkt-substance"), and there breaks up into three main branches. Of these branches one passes forwards into the next ganglion in front, another backwards to the ganglion behind, whilst the third curves round the central ganglion-cells, and, keeping close to these, runs forward towards the brain on the opposite side of the cord to that on which its cell lies.

By actual observation this fibre has been traced as far forwards as Th. VIII, but there can be no doubt that it behaves in the same way as B, Th. V, and B, Th. VIII (Pt. I, pl. 35, fig. 3),[2] and runs forward to the brain. A comparison of the three elements makes it evident that they belong to one and the same system, B, Th. VIII, and B, Th. XI, especially resem-

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[1] The denomination of the elements to be adopted here will be a continuation of the system used in the first paper. On comparing fig. 1 of this paper with fig. 1 on Pl. 35 of Part I (this Journal, vol. 36), it will be seen that in the present case the lateral mass of ganglion-cells in each ganglion (shaded blue) is more completely divided into an anterior and a posterior portion by the neuropile (left white in the figure) and the fibres of the anterior nerve-root. The present diagram represents more nearly the appearance presented by very late embryos, whilst the former figure represents that found in earlier ones.

[2] This Journal, vol. 36.

bling one another in details of arrangement. Also, in a preparation of an earlier embryo, in which the fibres B, Th. v, and B, Th. viii, were completely stained, a third fibre was observed ending with them in the brain, running close to them along the cord, but proceeding backwards beyond Th. viii. Its destination at that time remained undetermined, but there can be little doubt that it was the fibre of this element, B, Th. xi.

It will be observed, too, that Th. xi is exactly the ganglion in which we should expect to find another element of this class. Such elements have already been described (see Pt. I, pl. 36, fig. 3) in Th. ii (with branches to Th. i and Th. iii), in Th. v (with branches to Th. iv and Th. vi), in Th. viii (with branches to Th. vii and Th. ix), and now we find a similar one in Th. xi (with branches to Th. x and Abd. i). In this way each ganglion of the thorax must be influenced by these elements, which end in a particular region of the brain.

The series of elements of which the element B, Th. xi, is a type resembles in many respects the series of elements described by Retzius,[1] in Amphioxus lanceolatus, the cells of which give rise to the giant fibres in the nerve-cord of that animal. These fibres, after leaving the cell and crossing to the opposite side of the cord, are described as running forwards for some distance, but their ultimate fate was not determined. A knowledge of the nature and position of their endings would be of great interest.

PROBABLE MOTOR ELEMENTS OF ANTERIOR ROOTS.—The elements E, G, and H (fig. 1. Compare also Pt. I, pl. 35, fig. 1), the fibres of which leave the ganglia by the anterior nerve-roots, and which have already been described for the anterior ganglia, occur also in Th. ix, x, and xi.

The elements E (*b*) and E (*c*) (fig. 1) resemble in general features the element E, but differ from it in the number and mode of branching of the fibres which they give off to the neuropile. Their characteristic appearance and the situation of the cells may be seen from the figure. They occur upon both sides in the ganglia from Th. viii to Th. xi.

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[1] Retzius, 'Biol. Untersuch. Neue Folge,' ii, 1891.

The element F (*b*) (fig. 1), which occurs in Th. x and xi, resembles the element F (Pt. I, pl. 35, fig. 1), and may be the representative of that element in these two ganglia.

The element P, Th. vi (fig. 1), presents a striking appearance when stained, and differs in important respects from the elements previously described. The cell lies in the anterior portion of the lateral mass of ganglion-cells. The fibre curves backwards to the neuropile, and after giving off what, from its relatively small diameter, may be regarded as a subsidiary branch, divides into two main branches, one of which passes immediately out of the ganglion through the anterior nerve-root, whilst the other runs across as a stout transverse fibre to the opposite side, where it turns back again forming a loop with itself, and was traced as far as the centre of the ganglion. When the element has stained upon both sides the two transverse branches lie close together and appear as one stout fibre. The subsidiary branch, which leaves the fibre before it bifurcates, takes the somewhat complicated curved course represented in the figure, and was traced to the neuropile of the opposite side. As, however, neither this nor the main branch was observed to break up into finer branches, it seems probable that the staining was in all cases somewhat incomplete. Similar elements have not been found in any other ganglion.

PROBABLE MOTOR ELEMENTS OF POSTERIOR ROOTS.—The cells of the elements just described all send out fibres through the anterior nerve-root of the ganglion in which the cell is situated. In the two following cases, however, the fibre leaves by the posterior root.

In Th. viii, an element (fig. 1, K, Th. viii) similar to K, Th. iii (Pt. I, pl. 35, fig. 1), has stained. The cell is situated in the central mass of ganglion cells, the fibre decussates with its fellow of the opposite side and passes out at the posterior root of the ganglion. This element has been found only in Th. iii and Th. viii.

In Th. xi is an element which most nearly resembles the element J of the anterior ganglia. This is denominated J (*b*) (fig. 1). The cell is situated at the posterior end of the central mass of ganglion cells of the ganglion, and is relatively large. From the cell the fibre passes forwards and slightly outwards to the centre of the neuropile, where after turning downwards it bifurcates, sending one branch out of the ganglion through the posterior root, whilst the other runs as a transverse fibre to the neuropile of the opposite side. The element has not stained in any other ganglion of the thorax, but as will be seen later, what is probably the same element occurs in the abdominal ganglia.

The element *O* in Th. vii (fig. 1) also sends its fibre through the posterior nerve-root. The cell lies in the anterior portion of the central mass of ganglion cells and pursues the course indicated in the figure, giving off branches to the neuropile on the side only on which the cell lies. The element occurs on both sides of the ganglion Th. vii, but corresponding elements have never stained in any other ganglion.

Elements belonging to new types.—The motor elements referred to in Part I, and those already noticed in the present paper, are all characterised by the fact that the fibre leaves the central nervous system through one of the roots of that ganglion in which the cell attached to it is situated. The portion of the element which lies within the central nervous system is therefore entirely confined to one ganglion. In the cases now to be described, whilst the cell lies in one ganglion the fibre passes out of the cord by the nerve-root of some other ganglion.

The element Q, Th. vii, is an instance of this class. The cell lies in the anterior portion of the central mass of ganglion cells of Th. vii, gives off a fibre which runs outwards and then upwards to Th. vi, where it passes out by the posterior root of the ganglion. The fibre gives off a stout arborescent branch in Th. vii, and a straight transverse branch in Th. vi, which passes across to the opposite side of that ganglion. This pair of elements has only stained in Th. vii.

Three pairs of elements having many of the characteristics of the above, but differing in detail, are found in Th. iv, v, and VI. The element R, Th. VI, shows their principal characters. The cell in this case lies in the posterior portion of the central mass of ganglion cells of Th. VI.[1] It is somewhat smaller than the cell of the element Q, and its fibre runs forwards for some distance before turning outwards. After proceeding in the outward direction, the fibre again turns forwards and runs into Th. V, leaving the central nervous system by the posterior root of that ganglion. Two principal branches are given off during its course, one arborescing in the neuropile of Th. VI, the other in that of Th. V.

Another pair of elements, whose cells lie in one ganglion whilst the fibres pass out through the posterior roots of the ganglion in front, is that lettered S in Th. XI (fig. 1). In this case, however, the elements of the opposite sides decussate, giving rise to the characteristic figure shown (fig. 1). The cell of this element is small, and lies on the central surface of the ganglion. The element occurs also in the abdominal ganglia, and will be subsequently described in more detail. It has not stained in any other ganglion of the thorax, except Th. XI.

ELEMENTS HAVING TWO OR MORE BRANCHES WHICH PASS OUT OF THE CENTRAL NERVOUS SYSTEM BY THE NERVE-ROOTS OF DIFFERENT GANGLIA.—Two pairs of elements of this kind have stained in the thorax, the cells of one pair being found in Th. VII, those of the other in Th. VIII. In the latter case (Fig. 1, T, Th VIII) the cell lies in the anterior portion of the lateral mass of ganglion cells, near the point at which the anterior nerve-root leaves the ganglion. The cell gives off a moderately fine fibre, which very soon bifurcates, one branch passing immediately out of the ganglion through the anterior nerve-root, whilst the other runs forwards along the ganglionic cord. The forward branch, keeping close to the lateral masses

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[1] As was mentioned in Part I (see this Journal, vol. 36, p. 465) the central masses of ganglion-cells of the embryo, shaded blue in fig. 1, divide at a later stage into an anterior and a posterior portion, the two portions belonging to two adjacent ganglia. The line of demarcation is seen in Th. IX (fig. 1).

of ganglion cells, pursues a perfectly straight course until it reaches Th. III, where it gives off a branch, which passes out through the posterior root of that ganglion. After giving off this branch the fibre continues to Th. II, where it turns and leaves the ganglion through the posterior root. In one or two preparations, another branch appeared to be given off from the fibre in Th. IV, and to pass through the posterior root of that ganglion, but I was never able to make myself quite sure of this point.

From the preceding description and the figure (fig. 1), it will be seen therefore that the element T, Th. VIII supplies fibres to three (possibly four) nerve-roots of different ganglia, namely, the anterior nerve-root of Th. VIII, the posterior root of Th. IV (probable), the posterior root of Th. III, and the posterior root of Th. II, and that all these fibres have their origin in a single cell.

A corresponding element occurs also in Th. VII (fig. 1, T, Th. VII). The cell is similarly situated to that of Th. VIII, and a fibre passes almost immediately to the anterior root of Th. VII. A second fibre pursues a straight course forwards, keeping close to the corresponding fibre of Th. VIII, until it reaches Th. III, where it gives off a branch to the posterior nerve-root of that ganglion. The fibre then continues to run forwards, but its ultimate destination has not been satisfactorily determined. It appears to turn inwards in Th. II.

Mention may here be made of a fibre which stains in almost every preparation from the earliest stages onwards. It is inserted in fig. 1, T (*a*). The fibre appears to run longitudinally through the ganglionic cord from the level of Th. II to the posterior region of the brain, and to give off branches to two nerve-roots. One branch passes out through the posterior root of Th. II, whilst the second leaves the brain by a small nerve which arises immediately anterior to the nerve which supplies Antenna II. A few small fibres are given off to the neuropile of the brain at the angle which the latter branch makes with the longitudinal fibre.

No cell has ever been seen to stain in connection with the fibre just described, and whether the originating cell lies inside or outside the central nervous system remains unknown. It is possible that we are here dealing with an element similar to the elements T in Th. VII and VIII, the cell of which however has never taken up the methylene blue.

Elements in which one ganglion cell gives rise to two or more fibres passing out of the ganglion by different nerve-roots have been described by Retzius in Aulastomum gulo.[1] In that case the two fibres traced passed out by the two roots of the ganglion in which the cell lay, whilst a third, whose ultimate fate was not determined, passed into the general mass of longitudinal fibres of the ganglionic chain.

MISCELLANEOUS ELEMENTS.—In Th. IV a system of elements occurs, which offers certain difficulties in resolving it into its component parts. It is found to stain either completely or incompletely in embryos at almost all stages of development. Its position and relations to the neighbouring ganglia are shown in fig. 1 (U, Th. iv), whilst the details will be best seen in fig. 4. As may be gathered from the latter figure only two cells, belonging to corresponding elements of the opposite sides, have stained, but it appears to me to be most probable that the system contains several sets of elements, the cells of some of which have never taken up the methylene blue. The only clue which it has been possible to obtain as to the course pursued by the individual elements is the fact that in a number of preparations of late embryos (near hatching) the portion of the system represented in fig. 5 has been alone stained, and may therefore represent a single element. If this be the case, the course of the element may be described as follows (cf. fig. 1, U., figs. 4 and 5): Starting from a cell in the anterior portion of the lateral mass of ganglion cells of Th. iv, the fibre runs near the dorsal surface of the ganglion with an almost straight course inwards towards its centre, where it gives off a pair of branches (figs. 4 and 5, *c*.) which run down-

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[1] Retzius, 'Biol. Untersuch. Neue Folge,' ii. 'Zur Kenntniss des centralen nervensystems der Würmer.'

wards and break up into tufts of fibres near the ventral surface. The original fibre continues its course to a point a little beyond the centre of the dorsal surface of the ganglion, where it bifurcates, one branch turning upwards and curving outwards to the posterior root of Th. III (figs. 4 and 5, *a*), whilst the second branch continues in a transverse direction for some distance, and then turns suddenly forwards and runs into the neuropile of Th. III (figs. 4 and 5, *b*). Its fate here is a little uncertain, but it often presents an appearance which suggests that it ends in a tuft of fine branches, as in fig. 4, *b*. (on the right hand side of the figure). It should be mentioned that there is one difficulty in regarding the portion represented in fig. 5 as a single element, namely, that two central branches (*c*) are stained, whereas there appear to be only two when the complete system (fig. 4) is stained.

Returning to fig. 4, it will be seen that the whole system there represented contains, in the first place, two elements similar to that in fig. 5, and lying upon opposite sides of the ganglion. In addition to this pair of elements, there is a fibre upon each side (fig. 4, *d*.), which appears to start from the point where the transverse fibre turns forwards to form the branch *b*. This fibre (*d*) runs backwards for a short distance and then turns outwards to the posterior root of Th. IV. It is, however, probably not simply a branch of the element already described, but has a transverse portion of its own running parallel and close to the transverse portion of that element. In some preparations it is clear that the main transverse fibre of the whole system is of a composite nature. This is indicated on the right-hand side of fig. 4.

A third fibre belonging to the system (fig. 4, *e*) appears to spring from near the centre of the transverse fibre, to curve forwards, and finally to pass out at the posterior nerve-root of Th. III. It seems to be impossible to determine from embryos whether the fibres *d* and *e* are independent elements whose cells have never stained, or merely branches of the other elements of the system. It is to be hoped that the study of young adults may throw light upon this point.

Two other fibres in the same region often stain, and are shown in fig. 4, *f* and *g*. The fibre *f* appears to enter by the posterior nerve-root of Th. III, to pass transversely across the ganglion, and leave by the posterior root of the opposite side, the straight course being broken by a slight indentation at the middle line. It is not unlikely that there are in reality two elements which decussate in the middle line, and are there connected with cells which have remained unstained. The fibre *g* has a similar relation to the posterior roots of Th. IV.

Traces of a system of elements similar to that just described occur in Th. III.

A pair of elements exists in each ganglion from Th. VI to Th. X, which unfortunately seldom stains, but when stained presents several points of interest. The appearance is generally that shown in fig. 1, Th. IX, W., but in one preparation the element stained on one side only of the ganglion, and fortunately showed the position of the cell. This element, which actually occurred in Th. VI is inserted in fig. 1 for the sake of clearness in Th. X. (W.). Since in another preparation in which the element was stained, a cell just commenced to take up a similar position, I feel little doubt that this figure (fig. 1, Th. X., W.) represents the true condition of the element. Its course may then be described as follows:—Starting from a cell, which lies in the anterior portion of the central mass of ganglion cells, the fibre passes first backwards, decussates with its fellow of the opposite side, and then turns outwards to the neuropile, upon entering which it gives off a small tuft of fine branches. After giving off this tuft, the fibre continues to run transversely through the neuropile to about the level of the lateral mass of ganglion cells, where it bends suddenly forwards, giving off a short richly arborescent branch at the angle, and then runs to the next ganglion in front, in the neuropile of which it ends in another tuft of fine branches. No branch has stained which passes out through either of the nerve-roots. If the above description represents in reality the entire course of the element, it must serve to put different parts of two adjacent ganglia into communication with each other.

II. Abdominal Ganglia.

Method of Preparation.—Staining of elements in the abdominal ganglia can be observed in two ways. In the case of embryos at an early or medium stage of development which have been prepared, as described in Part I, for the staining of elements in the thorax and in which the abdomen is allowed to remain undisturbed, fibres which have taken up the methylene blue in the thorax often continue to absorb the colouring matter in the abdomen, and the cells with which they are connected are thus brought to light. The best results for the abdominal ganglia can, however, be obtained by special preparation of embryos which are very near the hatching point. In such embryos the abdominal ganglia may be dissected out from the surrounding tissue by careful manipulation with needles. Special care must be taken not to injure or stretch the ganglia and their continuity with the ganglia of the thorax should be maintained. If the embryos, thus prepared, be placed with the dorsal surface uppermost in very dilute methylene blue (1 : 100,000 may be used to commence with, and the strength gradually increased), satisfactory staining of many of the elements of the abdomen will soon take place.

A variation of this method, which often gives good results, consists in removing, or even simply tearing, with needles the cuticle on the ventral surface of the abdomen (after having first turned the abdomen backwards, and caused it to lie in a line with the thorax), and allowing the embryo to lie in the methylene blue with the ventral surface uppermost. In this case, as soon as the staining is thought to be satisfactory, the ganglia must be dissected out before they are examined. A cover-glass may be placed upon them, and the elements rapidly drawn, or the preparation may be fixed with ammonium picrate, and mounted in glycerine diluted with an equal volume of saturated solution of the picrate. Such preparations, however, only retain their full colour for a comparatively short time. For practical purposes a large number of fresh preparations, examined with a cover-glass, have been found more instructive and satisfactory. The same elements are seen again and again with such frequency, that little doubt can remain as to the accuracy of an observation.

The elements of the abdomen are similar in kind to those described for the thorax, and will be considered under the same general headings.

ELEMENTS OF WHICH BOTH CELL AND FIBRE LIE ENTIRELY IN THE GANGLIONIC CHAIN.—In each of the abdominal ganglia, from Abd. II to Abd. VI, a pair of elements similar to that represented in fig. 6, B (*b*) has been found to exist. Each element has its origin in a large cell situated in the anterior lateral portion of the ganglion near its ventral surface. From this cell a fibre arises which runs inwards and backwards, decussating with its fellow of the opposite side at the middle line and subsequently giving rise to two fibres, one of which runs backwards, whilst the other runs forwards towards the brain. The backward branch breaks up into fine fibres in the neuropile of the ganglion in which the cell lies. The forward branch runs as a longitudinal fibre along the ganglionic cord and in all probability enters the brain. Unfortunately, owing to difficulties of technique, it has never been possible to trace a single longitudinal fibre of one of these elements through its entire course, but a consideration of the whole evidence leaves little doubt as to their entrance into the brain. One of the most satisfactory direct observations was made upon an embryo near the point of hatching, in which the abdominal ganglia had been dissected out, as described above. In such preparations the pair of elements under consideration most frequently stains in Ab. II, and the fibres can generally be traced forwards through Th. X and IX. In one preparation, however, where there was a wound at the level of Th. III, the fibres of the elements upon both sides were distinctly visible as far forwards as this point.

But it is in embryos at an earlier stage, in which the abdomen has been left uninjured, that these elements most frequently appear. In order to make the evidence clear it is necessary to again draw attention to the method of preparation adopted for such embryos, when it is desired to obtain staining of the longitudinal fibres. The yolk is removed with needles, and the embryo placed with the exposed thoracic ganglia uppermost in the dilute methylene blue, the abdomen being allowed to remain turned in underneath the thorax. The ganglionic cord is then cut across, generally at the level of the œsophagus, and the methylene blue enters the fibres at the wound. In preparations so made the elements under consideration (B (*b*), figs. 6 and 7) have frequently taken up the blue, and can be well seen on turning the embryo over and lifting back the abdomen. The longitudinal fibres of the posterior ganglia can be traced through the anterior ones and show no sign of terminating. They are clearly continued forward into the thorax, although they cannot be individually followed on account of the flexure of the abdomen. On turning the embryo back again so that the thoracic ganglia can be examined, all the longitudinal fibres coming from the abdomen are seen to commence at the wound which has been made, and when this wound lies at the level of the œsophagus it is obvious that they must be fibres which enter the brain. No endings of longitudinal fibres coming from the abdomen have ever been observed in the thorax, and preparations of the kind just described have been so frequently made that there can be practically no doubt that the fibres in question enter the brain.

These elements (B (*b*), figs. 6 and 7) are evidently the same as those seen by Retzius in the abdominal ganglia of the adult Astacus. (See 'Biol. Untersuch.' Neue Folge I, pl. xi, fig. 1; pl. ix, fig. 4.)

A pair of elements of this kind, as has been already stated, occurs in Abd. VI, and is represented in fig. 7. In this ganglion a second pair of elements, whose cells are situated in the posterior portion of the ganglion, also frequently stains. The fibres from these cells (fig. 7, B (*c*)) have been traced as far forwards as the abdominal flexure, in preparations in which the only wound in the thorax has been at the level of the œsophagus, and they probably therefore enter the brain. The fact that two pairs of elements in Abd. VI send fibres to the brain, whilst only one pair has been found in the other abdominal ganglia is in accordance with the known composite nature of this ganglion.

Probable Motor Elements.—Of elements consisting of a cell in a ganglion and a fibre passing out of the cord by one of the nerve-roots, two principal kinds have been found in the abdomen, as in the thorax, namely (1) those in which the fibre passes out through one of the roots of the ganglion in which the cell lies, the whole of the element within the central nervous system being confined to one ganglion; and (2) those in which the fibre passes out through a nerve-root of some ganglion other than that in which the cell lies.

These elements are represented in figs. 2 and 3; fig. 2 giving the appearance presented when the elements upon both sides of a ganglion are stained; fig. 3, that when they are stained upon one side only, and indicating therefore the course of the individual elements. Each of the elements to be described has been found in all the ganglia from Abd. I to Abd. V.

Elements confined to one Ganglion.—The element *a*, shown in figs. 2 and 3, takes its origin in a cell, which lies near the centre of the ganglion and at its ventral surface. The fibre passes first upwards and outwards, turns inwards, and after a short course divides into two branches, one of which passes out of the ganglion by the posterior nerve-roots, whilst the other runs across to the opposite side, keeping close to the corresponding branch from the element of that side (fig. 2) and subsequently breaks up on the opposite side of the ganglion. The fibre gives off numerous fine branches during its course through the ganglion, which have not been represented in the somewhat diagrammatic figs. 2 and 3, but which may be seen in fig. 8, drawn from a preparation fixed with ammonium picrate (fig. 8, *a*; Abd. II and III).

Element *b* (figs. 2, 3 and 8) is similar in most respects to the element just described. It differs chiefly in the position of the cell, which lies in the posterior lateral portion of the ganglion. The fibre curves first upwards and forwards, and then downwards, when it divides into two branches similar to those of element *a*.

The element J (*b*), which has already been described as occurring in the last ganglion of the thorax (fig. 1, Th. XI) is found also in the ganglion of the abdomen (Abd. I–V), and is shown in figs. 2 and 3. The cell lies near the middle of the posterior end of the ganglion. The fibre runs at first forwards and outwards, and then turns inwards and backwards, giving off a small branch to the neuropile at the angle. Subsequently it divides into two branches, one of which passes out at the posterior root, whilst the other runs over to the opposite side of the ganglion, where it breaks up in the neuropile.

The element D (figs. 2 and 3) arises from a comparatively small cell, which lies in the anterior half of the ganglion near the middle line. The fibre runs backwards and slightly outwards, decussates with its fellow of the opposite side forming the characteristic figure represented in fig. 2, gives off a small arborescent branch to the neuropile, and then runs backwards to the posterior root of the ganglion through which it passes.

ELEMENTS NOT CONFINED TO ONE GANGLION.—Two pairs of elements have taken up the stain in each of the abdominal ganglia, whose fibres pass out through one of the roots of the ganglion immediately anterior to that in which the cell lies.

The element *e* (figs. 2 and 3) has the cell situated near the middle line at the anterior end of the ganglion. From the cell, which is small, the fibre runs outwards and backwards, and then, turning sharply inwards, runs as a transverse fibre close to its fellow of the opposite side. On reaching the other side it turns forwards, giving off an arborescent branch at the angle, runs into the next ganglion in front, and there passes out at the posterior root. When the elements upon opposite sides are stained it is generally impossible to distinguish the two transverse fibres, which lie so close together in this and in the other similar cases in the abdominal ganglia, that they appear as one.

The element S (figs. 2 and 3) is similar to the element S already described in the thorax (Th. xi, fig. 1). The cell, which is very small, lies near the centre of the ganglion and at the ventral surface. The fibre runs first upwards, backwards, and outwards, and then curves forwards and inwards. After running for some distance in this direction it decussates with its fellow of the opposite side, the two fibres lying for a short distance close together. The fibre then turns forwards and outwards, gives off an arborescent branch to the neuropile, and then proceeds forwards in a straight line to the ganglion in front, where it passes out by the middle root of the three which spring from that ganglion.

From the foregoing description of the motor elements found in the abdomen, it will be noticed that they, in nearly every case, supply fibres to the posterior nerve-roots of the ganglia, whilst the greater number of those described for the thorax in this and the previous paper send their fibres to the anterior nerve-roots, a few only supplying the posterior roots. The probable reason for this difference is not difficult to find. The anterior roots chiefly supply the appendages, which are well developed in the thorax of the embryo, whilst in the abdomen they are wanting. The posterior roots, on the other hand, supply the muscles of the body itself, which are well developed in the abdomen, but less so in the thorax owing to the considerable space occupied by the still unabsorbed yolk.

III. Elements Arising from Cells Outside the Central Nervous System.

In Part I a number of elements were described, arising from cells which lay in the ectoderm of the dorsal surface of the abdomen. These cells give off fibres which enter the abdominal ganglia and there bifurcate in the Y-shaped figure, which is characteristic of sensory nerve-fibres in all divisions of the animal kingdom, sending one branch forwards and the other backwards along the ganglionic cord. Numerous elements of this kind have stained in embryos near the point of hatching, and it has been possible to trace the fibres inside the central nervous system for considerably greater distances than was done before.

In the thorax, elements having the characteristic Y-shaped bifurcation enter the various ganglia by the posterior roots. One such fibre is represented in fig. 1 at M, Th. x. From this ganglion (Th. x) it has been traced forwards by direct observations as far as Th. i, but there was no indication of a definite ending there, the blue colour becoming gradually less distinct and suggesting that the true termination had not been reached.[1] From Th. xi the element has also been traced as far as Th. i.

In the abdomen, elements of this kind enter by the middle root of the three which belong to each ganglion. From Abd. i the forward branch has been actually traced as far as Th. ii, but gave no indication of a definite ending there.

From the three ganglia already mentioned the forward fibre has been directly observed to pass through at least nine or ten ganglia. Cases in which the fibre could be traced from these and neighbouring ganglia through five, six, and seven ganglia occurred in a large proportion of the numerous preparations of late embryos that were made. The fibres from spindle-shaped cells lying in the telson can, in embryos of moderate age, be seen to enter the last abdominal ganglion and then to run forward through the anterior ganglia. Such fibres have been traced as far as Abd. i, but could not be followed further on account of the flexure of the abdomen.

The fact mentioned in Part I, that elements of the kind

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[1] If an element stains at all frequently it is generally possible to form an opinion as to whether the actual termination has been reached, or whether the staining is incomplete. In the former case the terminal portion is, generally, at least as deeply stained as any other part of the element, and it may continue to take on a stronger colour after there has been a considerable fading of the other parts. In the case of incomplete staining, on the other hand, the colour becomes more and more faint towards the end of the fibre until it finally disappears.

under consideration frequently stain in the abdomen, when the longitudinal fibres commence to take up the methylene blue at a wound made at the level of the œsophagus, from considerations of a similar nature to those already adduced in the case of the abdominal elements B (*b*), leaves little doubt that the fibres actually go to the brain. The observations now recorded, although they do not directly demonstrate the point, render it still more probable.

With regard to the second branch given off by these elements after entering a ganglion, which is directed backwards along the ganglionic cord, no definite termination has been found. It has never been seen to pass through more than three ganglia, and can generally only be followed through two. This, however, is probably due to incomplete staining, and the entire course of this branch remains yet to be determined.

EXPLANATION OF PLATE 4.

Illustrating Mr. Edgar J. Allen's "Studies on the Nervous System of Crustacea."

Fig. 1.—Brain and thoracic ganglia of Homarus embryo. *œs.* Œsophagus. *tr. br.* Transverse bridge behind œsophagus. *com.* Œsophageal commissure. *ant.* II. Ganglion of Antenna II. Th. I—IX. Thoracic ganglia. For individual elements see text. Somewhat diagrammatic.

Fig. 2.—Three abdominal ganglia of Homarus embryo. Motor elements inserted upon both sides. For individual elements see text. Somewhat diagrammatic.

Fig. 3.—Ditto. Motor elements inserted upon one side only.

Figs. 4 and 5.—System of nerve elements in Th. III and Th. IV of Homarus embryo.

Fig. 6.—Abdominal ganglion of Homarus embryo. B (*b*). Element sending fibre to brain.

Fig. 7.—Sixth abdominal ganglion of Homarus embryo. B (*b*) and B (*c*). Two elements sending fibres to brain.

Fig. 8.—Second and third abdominal ganglia of Homarus embryo. Camera drawing from preparation preserved in ammonium picrate. *a. b.* motor elements.

Notes on Oligochætes, with the Description of a New Species.

By

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With Plates 5 and 6.

The following observations were chiefly made on some worms sent to me by Mr. Damon from a garden at Weymouth. I have to thank Professor Ray Lankester for much help during my researches.

On the Structure of Enchytræus hortensis, n. sp.

At first sight this little Enchytræid presents no very distinctive characters. It is, when full grown, about 15 mm. in length, and milky white in colour, the anterior end being sometimes yellowish. The chætæ (fig. 18) have a straight shaft and a hooked inner end, but this hook is not always so pronounced or so sharp as in the chæta figured. The bundles contain from three to four chætæ, generally three in the dorsal and four in the ventral bundle. There are no dorsal pores. A small dorsal head-pore is situated between the prostomium and first segment. The brain (fig. 1, *br.*) is larger behind than in front; its posterior margin is slightly indented or rounded. The dorsal blood-vessel arises from the wall of the intestine about the 17th segment. Three pairs of septal glands (fig. 1, *sept. gl.*) are present; two sets of bulky glands in front, and a third pair of smaller glands behind, each of which is subdivided into two lobes. The well-developed salivary glands (fig. 1, *sal. gl.*) are unbranched and of considerable length. The nephridium (fig. 2) is compact, with a portion of the canal slightly coiled in the pre-septal region. The funnel of the sperm-duct is of moderate length and very thick-walled. The spermatheca has a distinct duct beset with glandular cells near its external aperture, and possesses a posterior blind sac (fig. 23, *post. sac*). Three chief varieties of corpuscles are found in the cœlom; one of these bears a peculiar product in the shape of a coiled thread, to be described in detail further on. In a favourable light the cuticle can be seen in most specimens to be covered throughout with fine hair-like processes (fig. 8, *h.p.*), similar to those described in Vermiculus (8). This species is probably distributed all over England, as I have found it near Oxford, London, and Weymouth.

On the Nephridium of Enchytræus hortensis.

I have thought it worth while to give in detail the results of observations carried on for some years on the nephridia, since not only does a great deal remain to be described in these interesting organs, notwithstanding the large number of authors who have written on the subject, but also on account of the recent publication by M. Bolsius of descriptions totally at variance with the observations of other naturalists and my own (4).

As M. Bolsius gives an account of the literature, I need only say that former writers (Claparède, Eisen, Vejdovsky, Michaelsen, Ude, &c.) all agree in describing the nephridium of Enchytræids as consisting of a more or less compact mass of cells pierced by a continuous ciliated convoluted canal leading from the nephrostome to the exterior. Bolsius, on the contrary, declares that the lumen of the canal forms a complex network "des canalicules anastomosés dans toutes les directions;" and, moreover, that it is totally devoid of cilia: "Les canalicules et le canal collecteur ont été dessinés par nous sans cils vibratiles: c'est que nous n'en avons pas trouvés, ou plutôt c'est que nous en avons constaté l'absence complète dans nos nombreuses préparations." Since the first of these statements has been included in the excellent monograph Mr. Beddard has just published (2), it seems all the more important that it should be criticised before it becomes generally accepted.

Let us now examine the structure of the nephridium in Enchytræus hortensis as seen in the living animal. The organ (fig. 2) consists of an oval main body, flattened from side to side, and narrowing in front to a neck, which piercing the septum ends in an open funnel (fig. 2, *neph. st.*). Behind the nephridium passes into a lobe leading to the body-wall. The protoplasm of the nephridial cells, whose boundaries I have been unable to distinguish, is very granular, especially in the anterior region, which is frequently of a brownish tinge. The funnel (figs. 3—5) has a protruding upper lip (*up. l.*) and a truncated lower lip (*l. l.*). At the extremity and along the edges of the upper lip are set numerous very long extremely fine waving cilia (*ext. cil.*, figs. 4 and 5), while from the inner surface springs a large bunch of powerful undulating cilia (*fl.*). As far as I have been able to determine, cilia are not present on the lower lip; but rising from its middle region is a peculiar sharp protoplasmic process (*m. p.*, figs. 4 and 5), sometimes branched and ragged.

Already in Nereis (7) and Vermiculus (8) I have drawn attention to the two kinds of cilia attached to the lip of the nephrostome, which indeed have not escaped the notice of previous authors, but the exact disposition and differences of which have not been sufficiently insisted upon. Whilst the inner beat rapidly, simultaneously, and rhythmically, forming an undulating bunch[1] or "flame," which, no doubt, propels liquid down the lumen of the canal; the long external cilia, on the other hand, do not beat in unison: each cilium seems to move independently with trembling motion, sweeping down towards the protruding process of the lower lip. These cilia seem rather to guard the mouth of the funnel and select

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[1] The seat of the motion seems to be at the base of the cilia, the wave passing along them as an undulation passes along a cord shaken at one extremity.

particles from the cœlomic fluid than to propel it down the canal.

Passing backwards from the nephrostome is the nephridial canal (*neph. c.*, figs. 2, 3, and 5). I may say at once that, although I have not been able to follow it throughout its whole extent with certainty, owing to the opaque and granular nature of the post-septal region and the small dimensions of the tortuous lumen, I believe the main duct to be continuous and single (i. e. without anastomosing branches), except in that region which leads directly to the exterior, where the lumen occasionally undergoes secondary subdivision (figs. 2 and 7). Although, therefore, I cannot claim to be able to prove the unbranched character of the canal, yet amongst the number of Enchytræid nephridia I have had under observation during the last three or four years I have never come across a single undoubted case of such anastomosing. The course of the canal drawn in fig. 2 does not profess to be accurately represented in all its details, nevertheless I have been able to observe that at least the main features of the canal's course, if not the less important of its convolutions, are constant, not only in the different nephridia of the same worm, but also in the nephridia of different individuals of the same species. For the first part of its course it has a very narrow lumen, and is not ciliated. It then widens slightly, and undergoes several complicated twists in the more posterior and dorsal region of the main body of the nephridium. It is along this second region of the canal that here and there we find a slight oval enlargement of the lumen, in which is situated a bunch or "flame" of cilia (*c. a.*, fig. 2), similar to the "flame" in the nephrostome, and constantly driving the liquid in one direction, namely, to the exterior.[1] As far as I can make out, there are no more than

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[1] Anyone examining the living worm could hardly miss seeing these cilia. It is, of course, just possible that the worms observed by M. Bolsius were of exceptional structure, but I am more inclined to think that he was misled, both with regard to the absence of cilia and the anastomosing of the canal by employing the method of sections alone.

five such ciliated regions in each nephridium.[1] Their essential similarity to the "ciliated ampullæ" found in the nephridium of Vermiculus (**8**) scarcely needs pointing out. From the second region the canal passes to a third, where the lumen is often wider still, and is entirely devoid of cilia. The course of this, the terminal region of the canal, lies along the postero-dorsal edge of the main body, and from thence passes through the posterior limb to the external pore. It will be noticed that the blind sacculations of the canal (mentioned by Michaelsen, **9***a*) are here very large (fig. 2, *bl. br.*), and frequently a subdivision of the lumen takes place, forming a more or less complicated network (figs. 2 and 7), which must not, however, be confused with the supposed anastomosing branches between the different regions of the canal. Finally the lumen expands to form a vesicle (*e. v.*), which opens to the exterior by a small transversely elongated pore in front of the ventral chætæ.

Sections only confirm these observations. No limits are distinguishable between the cells. The funnel has two nuclei in its upper lip near the point of insertion of the cilia (fig. 3), and one at the base. Small deeply staining nuclei are seen in the main body (*n.*, fig. 3), and larger nuclei are distributed apparently in more intimate connection with the second and third region of the nephridial canal (*n.*, fig. 6).

On the Cœlomic Corpuscles of Enchytræus hortensis.

Most characteristic of this worm are the cœlomic corpuscles; these are of three kinds. Floating in the cœlomic fluid, or creeping on the surfaces exposed to it, may be seen a small number of amœboid corpuscles of very variable character. Some (fig. 28, *a.*) are more or less spherical with short-pointed processes; their protoplasm is pretty clear, and contains, as a rule, a few highly refringent round granules, apparently of a

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[1] M. Bolsius (**4**) justly criticises previous authors for describing the canal as ciliated, and yet not figuring any cilia. M. Roule (**10**) alone does so, and represents them erroneously along the entire length of the canal.

fatty nature. Others are formed of more opaque and finely granular protoplasm, prolonged into fine branching processes of great length (fig. 28, *b*.): corpuscles intermediate in character between these two forms also occur.

The second variety is very characteristic of the Enchytræidæ in general, and has been described by almost every writer on this group of the Oligochæta. Much larger than the amœboid form (nearly twice the size), these corpuscles are of regular and constant oval shape, somewhat flattened, thicker in the middle than at the periphery, and frequently bluntly pointed at one or both ends. The body of the cell is made up of large spherical, clear, and refringent granules, embedded in a delicate meshwork of protoplasm (fig. 15, *a*). The nucleus is round or slightly oval, in which case its long axis is invariably situated at right angles to that of the corpuscle; staining reveals a dark nucleolus lying in the less deeply staining nucleus, *n* (fig. 12, *a*). These corpuscles are found either freely floating in the cœlom, or attached to the body-wall or septa by means of a short stalk, apparently of cuticular nature. In the latter case the corpuscle is always fixed by its more pointed extremity. The remains of the stalk of attachment may generally be detected on those corpuscles which float freely (*st.*, fig. 15, *a*). Although my observations as to the origin of these corpuscles are unfortunately neither complete nor conclusive, yet I am strongly inclined to believe that they arise from the cœlomic epithelium lining the body-wall and septa. Certain it is that smaller, flatter, and younger-looking corpuscles of similar structure may sometimes be seen attached to the epithelium. The fact that similar apparently young corpuscles may occasionally be seen floating freely in the fluid does not seem to me fatal to the view that normally they remain attached to their place of origin until they have reached their complete development. Never have I found intermediate stages between these oval corpuscles and the amœboid variety, or the granular cells of the modified epithelium covering the gut, from which they differ markedly, as already noticed by Vejdovsky (**13**). In the youngest worms I have been able to examine, the oval corpuscles are relatively about as abundant as in the adult; but the free ones appear to be more rounded and flattened, and with fewer granules, thus resembling what I have taken for the younger stages in the adult. As no definite signs of extensive disintegration of the corpuscles are apparent, and as I have never observed any case of their multiplication by division, it would seem that the life of each individual corpuscle must be of considerable length, and that they are but rarely renewed.

The third and most interesting kind of cœlomic corpuscle should probably be reckoned as a variety of that just described. The body of the cell, though smaller, is formed of a similar meshwork, enclosing granules of identical appearance and properties; the nucleus also resembles that of the ordinary oval corpuscle (*n.*, fig. 12), but lying on one side is a colourless refringent body of peculiar structure. This body, in the fully developed form, is of the shape of a thick disc or of a truncated cone, thicker at the edge than in the centre (*thr.*, figs. 12—15), the flat surface being next to the nucleus. When the cœlomic corpuscles are squeezed out of the worm under a cover-glass, and they come into contact with some strange fluid, such as distilled water, or even salt solution, it becomes apparent that the refringent body is formed of a long thread of transparent homogeneous substance, closely coiled like a rope (fig. 13). Surrounded by a thin layer of protoplasm the thread-coil is obviously an endoplastic product of the cœlomic corpuscle. At first I took these strange bodies for parasites, but subsequent observations have proved this view to be false.

As already mentioned, immediately the corpuscle comes into contact with some foreign liquid, such as distilled water, weak acids, or alkalies, the body of the cell begins to disintegrate, the coil of thread swells and gradually unwinds, forming a tangle of loops, amongst which I have never detected free ends (fig. 13). The thread appears to be thicker in some places than in others, or perhaps it would be more correct to say that the coils stick together in certain regions.

Like the ordinary oval cells, the thread-corpuscles are found both floating and attached by a stalk to the body-wall or septa. In the latter case the thread-coil is invariably situated on that side of the nucleus which is far from the point of attachment. Looking in the adult worm for possible stages in the development of thread-corpuscles, smaller cells can be found in which the coil is smaller relatively to the granular cell body (figs. 10, 11, *d*, *e*, *f*, and 12, *b*). Such small and apparently young cells are scarce, and generally attached. Turning now to very young worms, we find in them the thread-corpuscles scarcely less abundant than in the adult relatively to the whole number of cœlomic corpuscles. They are, however, as a rule, flatter and more oval in shape (fig. 9), with more loosely packed granules and smaller thread-coils. Indeed, these refringent bodies differ from those of the adult, not so much in the circumference of the disc as in its thickness (*cp.* figs. 9, *d*, and 13, *a*, both side views). Similar shallow discs occasionally occur in the adult (fig. 10, *a*). It will be seen, moreover, that in what I have taken to be the younger stage of development the disc presents its edge to the nucleus (figs. 9 and 10); whilst in the later stages the nucleus is lodged on its flat surface (figs. 12, *c*, and 13). Whether the disc has during growth turned round or merely changed shape is a doubtful point. These facts lead to the conclusion that the thread-corpuscles originate from the cœlomic epithelium lining the body-wall or septa, passing through stages essentially similar to those of the young corpuscles of the ordinary oval type, and are not formed by the development of a thread within full-grown oval corpuscles. The thread itself would appear to be formed at the expense of the granules, *cp.* (figs. 9, 10, and 13); but this appearance may be deceptive, and merely due to the increase in size of the thread alone. The chemical nature of the substance composing the thread is discussed in detail below; it differs widely in its chemical properties from that of which the granules are formed, and from chitin.

On the function or fate of the thread in the cœlomic corpuscle of this Enchytræid I am sorry to say that my observations throw no light. It occurs in immature and mature worms at all seasons of the year. It has been searched for in vain, either discharged into the cœlomic fluid or amongst the tissues of the body. Nor have empty cells been found which could have discharged the thread. It might be suggested that this thread is an excretory product; however, as far as I have been able to make out, it is never got rid of,—indeed, it would seem to be most ill adapted for passing through the complicated coils of the nephridial canal. Possibly it may be a waste product of harmless nature, which is allowed to remain and accumulate throughout life, but here also facts are wanting to enable us to come to any definite conclusion.

Amongst the other Enchytræids or the Oligochætes in general no products in the cœlomic corpuscles which could be compared to these threads seem to have been hitherto observed. Amongst the Polychætes, on the other hand, there have been described in Ophelia radiata amœboid cœlomic corpuscles containing a chitinous rod[1] of unknown function, first noticed by Claparède (**5**), and recently studied in great detail by Dr. Shaepi (**11**). The latter adopts the view urged by Dr. Eisig (**6**), that these rods of chitin are of the nature of an excretory product.[2]

In the epidermis of many fish and amphibia cells have been described which secrete a thread-like substance.

Perhaps the thread-cells of Myxine, described by Johannes Müller, Blomfield (**3**), and others, resemble more closely the thread-corpuscles of Enchytræus hortensis than any other cell hitherto known, especially in the earlier stages of their development. But here, again, the product appears to be of different chemical nature, and the cells in their origin and situation are so different that they scarcely help us to solve the problem.

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[1] I have found similar but longer chitinous rods in Ophelia limacina.

[2] As the thread in Enchytræus hortensis is certainly not of chitin, a comparison with Ophelia (even supposing the excretory nature of the rod had been proved) would not warrant our coming to a similar conclusion.

On the Spermatheca of Enchytræids.

In 1885 (9) Dr. Michaelsen first made known the remarkable discovery that the spermatheca in the Enchytræidæ, which lies in the 5th segment, communicates directly with the alimentary canal. More recently Mr. Beddard (1) has shown that the same thing occurs in Sutroa, and he discusses the subject in the monograph already mentioned (2, pp. 127–8). As such a case of the direct communication of the cavity of the œsophagus with the exterior by means of a sac invaginated from or derived from the epidermis is unknown in any other group of Invertebrates, and is of great morphological interest, I give a series of longitudinal and transverse sections through these organs. Fig. 27 represents a longitudinal horizontal section through the 5th segment of Marionia enchytræoides St. Loup.[1]

As the section is slightly oblique it shows on one side the opening of the spermatheca to the exterior (*sp. op.*), and on the other the opening into the alimentary canal (*int. op.*). In Pachydrilus, and forms closely allied to it, such as Marionia, the spermatheca is simple, and opens into the œsophagus at its hinder extremity. The spermatheca figured contains no spermatozoa, showing that the internal opening is formed before the spermatozoa are received, and the point at which the fusion has taken place between the two organs can be detected, since the lining of the œsophagus is ciliated (*œs.*), while that of the spermatheca is not (*sp.*).

In Enchytræus hortensis the spermatheca fuses with and opens into the œsophagus at a point more nearly opposite its external opening, sending backwards a large blind sac in which are lodged the bulk of the spermatozoa.

It will be seen that the communication between the spermatheca and the alimentary canal is very wide (figs. 21 and 25, and the diagram, fig. 23); the external spermathecal pore remains of normal size (*sp. op.*). The spermatozoa (*sptz.*, figs.

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[1] Professor Marion kindly sent me a number of these worms from Marseilles.

20—25) arrange themselves round the walls of the spermatheca, with their long heads deeply sunk in or between the lining cells, and their tails hanging into the cavity. Many bundles of spermatozoa also lie loose in the cavity, and may get carried into the alimentary canal (Michaelsen, 9).

On the Cœlomic Corpuscles of Pachydrilus, sp. (?).

It is not without hesitation that I put on record the following very incomplete observations on a small species of Pachydrilus, of which I unfortunately only found two specimens amongst the Enchytræids sent to me by Mr. Damon from Weymouth.

On examining the worm under the microscope, the cœlom was seen to contain a number of remarkably long and slender cells, attached to the body wall by one extremity (fig. 16). The longest of these cells reached nearly across a segment, being abont ten times as long as an ordinary cœlomic corpuscle (*cp.*, *a.*, and *c.*, fig. 17). Near the middle was an oval clear region, indicating the position of the nucleus (*n.*, fig. 17), whilst the body of the cell is formed of granular protoplasm, in which the granules could be observed circulating. No thick or definite wall was apparent covering the somewhat irregular surface, and the whole cell appeared to be very flexible, being twisted about backwards and forwards with the motion of the cœlomic fluid. An expanded sucker-like foot or base (*ft.*) served to fix it to the body-wall. In stained sections the nucleus appears small and rounded as in the ordinary oval corpuscles.

Although it may seem extremely probable that these strangely shaped cells were parasitic Protozoa, yet the fact that there were present cells representing in appearance every stage between the elongated form and the ordinary cœlomic corpuscle (fig. 16) suggests that the former are derived from the latter.

Notes on the Action of Chemical Reagents on the Cœlomic Corpuscles of Enchytræus hortensis and Vermiculus pilosus.[1]

In a former paper I described the characteristic cœlomic corpuscles of Vermiculus pilosus (8, fig. 28, pl. 28); they are spherical cells, filled with large oval refringent granules.

If these be watched under the high power of the microscope in distilled water, or even in normal salt solution, the large white granules will be seen to dissolve, whilst minute and yellower-looking granules come into view.[2] Under the influence of weak alcohol, a solution of iodine, very weak acids, or alkalies the same thing occurs. With osmic acid (1 per cent.) the dissolution of the large granules takes place with almost explosive rapidity, the small granules in this, as in the other cases, remaining sharply defined. Whether the smaller granules are hidden by the larger, and only become visible when these have been dissolved, or whether they remain as an actual residue from the large granules, is a point difficult to settle. I feel convinced from appearances observed that the large granules really include the smaller.

It is difficult, if not impossible, to permanently fix the large granules. Sometimes they could be fixed for a time by a sudden drenching with absolute alcohol, and they would then be unaffected by ether.

The small highly refringent granules, which remain when the large have disappeared, are insoluble in water, iodine solution, alcohol, and ether. They are soluble in a solution of caustic potash, the mineral acids, in oxalic acid, and with difficulty in acetic acid.

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[1] I am indebted to Professor Gotch for many useful hints while conducting these experiments.

[2] The difficulty of conducting chemical experiments on small bodies which have to be watched under the high power is very great, and often renders the result uncertain. I have, therefore, always repeated the experiments many times over, and used strong solutions of the reagents (unless otherwise stated).

Turning now to the oval corpuscles of Enchytræus hortensis, we find here also white granules soluble in distilled water, in potash, lime water, acetic and tannic acid, with difficulty (perhaps not entirely) in oxalic acid, and also with difficulty in weak mineral acids, but easily in strong. When treated with osmic acid (2 per cent.) these granules are generally reduced to smaller and more refringent bodies. This also takes place under the influence of alcohol, strongly recalling the much more pronounced action in the large granules in Vermiculus. The white granules are insoluble in ether, and weak mineral acids are unaffected by silver nitrate and by iodine. They do not answer to the xanthoproteic test, and are not doubly refractile.

It would seem possible that we have in these granules, more firmly combined, the same two substances which are so easily separable in the corpuscles of Vermiculus.

The Thread.—The coiled thread in the cœlomic corpuscles of Enchytræus hortensis is insoluble in distilled water (hot or cold) and salt solution. Iodine solution shrivels it slightly, and stains it yellowish brown. In strong alcohol the thread contracts to an irregular mass, which is not farther acted upon by ether. In strong potash (30 per cent. sol. of KOH) the thread is not dissolved in the cold; but as soon as the cell has been destroyed it uncoils, forming very characteristic U-shaped loops, the two limbs of the U being closely applied (fig. 14). When heated in strong potash portions of the thread are dissolved or broken up into minute globules, a highly refringent thick U-shaped loop remaining. On boiling this portion appears to be dissolved.[1] A solution of silver nitrate, oxalic and picric acids produces no effect. Glacial acetic acid, on the contrary, has a most marked influence. Under its action the thread swells up and becomes transparent, then melts down to an irregular coagulated mass. On further action this refringent mass swells up again, and begins vio-

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[1] It is almost impossible to make quite certain as to whether the thread is really dissolved in boiling (in this and other cases), as the operation cannot be conducted under the microscope.

lently to "boil up," and becomes dissolved, leaving only one (or two) minute yellowish and very refringent coagulated granules, which undergo no further change. Strong HCl and H_2SO_4 have at first somewhat the same action as acetic acid, swelling up the thread to a transparent viscid mass, which, however, is not dissolved in the cold. Strong HNO_3 acts in the same way, the swollen thread being further reduced to a small granular mass, which, on heating, is broken up into globules, and finally dissolved on boiling (?). Osmic acid shrivels the thread a little, and stains it a pale greyish tint. With tannic acid it becomes reduced to an irregular shrivelled mass. The thread is insoluble in lime water,—in fact, the addition of lime water to the cœlomic fluid is one of the best methods of showing up the threads in a mass of cells[1] (figs. 15, 16).

The xanthoproteic test gives no result as with the white granules. The thread does not stain readily with eosin; but, on the other hand, it stains readily with methyl blue, and especially with methyl green. In an acidified solution of Victoria blue it stains dark purple, and again dark blue in an alcoholic solution of cyanin.

The chief results are shown below in tabular form. The sign + means that the substance is soluble in the reagent, the sign – that it is not obviously soluble without heating.

Products in the cœlomic corpuscles.	Distilled water.	Alcohol.	Ether.	Caustic potash.	Lime water.	Tannic acid.	Oxalic acid.	Acetic acid.	HCl.	HNO_3.	H_2SO_4.	Osmic acid.	Iodine.
Of Vermiculus—													
1. Large white granules . .	+	+ –	–	+	...	...	+	+	+	+	+	+	+
2. Small residual granules . .	–	–	–	+	...	...	+	+	+	+	+	–	–
Of Enchytræus—													
3. White granules	+	–	–	+	+	+	+ partially.	+	+	+	+	+ –	–
4. Thread . . .	–	–	–	–	–	–	–	+	–	–	–	–	–

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[1] The thread does not give rise to double refraction.

From this table it will be seen that we have at least four distinct endoplastic products and perhaps three distinct chemical substances in the cœlomic corpuscles of Vermiculus and Enchytræus, which are probably of an albuminoid nature.[1] That none of the products are mucin is proved by their solubility in acetic acid; that none of them are chitin is proved by the first three being soluble in caustic potash and the fourth in acetic acid. That they are neither of a fatty nor of an amyloid nature is shown by the action of ether, osmic acid, and iodine (which does not stain them dark).

Notes on the Cuticle and Chætæ of Oligochætes.

It has long been known that the cuticle of the Oligochæta is not made of chitin (Timm, 12; Eisig, 6), since it is readily soluble in caustic potash; but few, if any, observations seem to have been made with a view to acquiring a more definite knowledge of the character of the substance of which it is formed. Below are given the results of some experiments performed on the cuticle of the common earthworm, Lumbricus herculæus. The worms were killed in 30 per cent. alcohol, and placed for a time in water until the cuticle could be easily peeled off. The cuticle, having been thoroughly washed in salt solution and distilled water, was then experimented upon in test-tubes. It is insoluble in alcohol and ether; soluble in hot distilled water (before boiling-point is reached), in solutions of ammonia or weak potash, in lime water, in weak mineral acids, in oxalic acid, and with some difficulty in acetic acid.[2] Cuticle dissolved in distilled water, boiled and filtered, gives a slightly viscid solution of whitish opalescent colour, which does not thicken on cooling. On

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[1] In a recent paper on "The Process of Secretion in the Skin of the Common Eel," Professor E. Waymouth Reid comes to the conclusion that the thread-like secretions from the epidermis are formed of an albuminoid possibly allied to keratin ('Phil. Trans.,' v., 185, B. 1894). The substance presents no great resemblance to that found in Enchytræus.

[2] The same results were obtained with the cuticle of Vermiculus and Enchytræus.

evaporation the solution leaves a film of transparent substance without crystallisation. Boiled with caustic potash and cupric sulphate we get no reduction. The solution answers to a certain extent to the proteid tests, turning straw-coloured with the xanthoproteic test, and pale lilac with the biuret test. Boiling with Millon's reagent produces no more than a pinkish hue. Tannic acid in the solution acidified with acetic acid gives a white precipitate.[1] Sodium sulphate and potassium ferrocyanide give no precipitate. If we treat the solution with absolute alcohol we get a white precipitate, and the filtered liquid answers no more to the above tests.

The Chætæ.—It is generally assumed that the chætæ are chitinous, but this seems to be by no means always the case. The chætæ of Vermiculus and Enchytræus are insoluble in distilled water (hot or cold), alcohol, ether, caustic potash (even boiling), acetic and oxalic acids, hydrochloric acid (even after prolonged boiling for some minutes). In strong sulphuric acid they become swollen and soft, finally dissolving on heating.

The chætæ of the earthworm are insoluble in distilled water, alcohol, ether, caustic potash, lime water, acetic and oxalic acids; soluble in strong hot sulphuric acid. Boiled in strong caustic potash the chætæ become somewhat swollen and broken up, but do not dissolve. If they be now washed and placed in concentrated hydrochloric acid the proximal region (that part which lies in the body-wall) is rapidly dissolved, partially in the largest chætæ, and almost entirely in the smaller. If the acid be now boiled the resisting distal region is soon dissolved, leaving only a thin colourless layer which formed a sort of cap over the chæta. This shell appears to be insoluble in hydrochloric acid like the entire chæta in Vermiculus. The chætæ of Vermiculus, Enchytræus, and Lumbricus become orange with xanthoproteic test, and crimson with Millon's test.

Below are set forth in tabular form the chief of these results:

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[1] It behaves, in fact, somewhat like a peptone.

	Distilled water boiling.	Alcohol.	Ether.	Caustic potash.	Lime water.	Acetic acid.	H_2SO_4.	HCl.	Xanthoproteic test.	Millon's test.
1. Cuticle of Lumbricus, &c . .	+	–	–	+	+	+	+	+	Pale yellow.	Pale pink.
2. Chætæ of Vermiculus and Enchytræus . . .	–	–	–	–	–	–	–	–	Orange.	Red.
3. Chætæ of Lumbricus	–	–	–	–	–	–	–	+ with insol. residue.	Orange.	Red.

From this table it would again appear that we have three albuminoid substances distinct from each other, and from those found in the cœlomic corpuscles. The chætæ of the small worms (Vermiculus and Enchytræus) are formed of a substance which is not chitin, since it is insoluble in HCl. The chætæ of Lumbricus, on the contrary, are probably chiefly composed of chitin, or some substance closely allied to it, since they are insoluble in caustic potash, and partially soluble in HCl. On the other hand, so far as the solubilities show, the cuticle appears to be formed of a substance closely allied neither to chitin nor to mucin.

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EXPLANATION OF PLATES 5 and 6,

Illustrating Mr. Edwin S. Goodrich's "Notes on Oligochætes, with the Description of a New Species."

List of Reference Letters.

bl. br. Blind branch of the nephridial canal. *br.* Brain. *b.w.* Body-wall. *c. a.* Ciliated enlargement of nephridial canal. *circ. m.* Circular muscles. *cœl.* Cœlom. *cœl. corp.* Cœlomic corpuscle. *cœl. epith.* Cœlomic epithelium. *d. bl. v.* Dorsal blood-vessel. *epid.* Epidermis. *e. v.* End vesicle. *ext. cil.* External cilia. *f.* Point at which the spermatheca has fused with the œsophagus. *fl.* Flame-like bunch of cilia. *ft.* Expanded foot whereby the cell is fixed to the body-wall. *gl.* Spermathecal gland. *h. p.* Hair-like processes. *i. e.* Internal hooked end. *int. op.* Internal opening of the spermatheca into the œsophagus. *l. l.* Lower lip. *long. m.* Longitudinal muscles. *m. p.* Median process. *n.* Nucleus. *n. c.* Ventral nerve-cord. *neph. c.* Nephridial canal. *neph.p.* Nephridiopore. *neph.st.* Nephridiostome. *œs.* Œsophagus. *op. sp. d.* Opening of spermathecal duct into the main chamber of the spermatheca. *post. sac.* Posterior sac of the spermatheca. *s.* Septum. *sal. gl.* Salivary gland. *sept. gl.* Septal gland. *sp.* Spermatheca. *sp. d.* Spermathecal duct. *sp. op.* Spermathecal opening. *sptz.* Spermatozoa. *st.* Stalk of attachment. *thr.* Thread in the cœlomic corpuscle. *u.pl.* Upper lip. *v. bl.v.* Ventral blood-vessel.

All the figures, except figs. 16, 17, and 28, refer to Enchytræus hortensis, n. sp.

FIG. 1.—Enlarged view of the anterior region, showing the shape of the brain, salivary glands, and septal glands.

FIG. 2.—Enlarged view of the nephridium, drawn from the living.

FIG. 3.—Section through part of the nephridium and nephrostome. Z. apoch. 4 mm., oc. 4 c. cam.

FIG. 4.—Enlarged ventral view of the nephrostome, from the living.

FIG. 5.—Enlarged side view of the same.

FIG. 6.—Transverse section through the posterior region of the nephridium. Z., D, oc. 4, cam.

FIG. 7.—Enlarged view of a portion of the last region of the nephridial canal, from the living.

FIG. 8.—Optical section through the body-wall. Z., D, oc. 3.

FIG. 9.—Thread-corpuscles from a young worm (fresh). *a*, *b*, *c*. Front views. *d*. Side view. Z., D, oc. 4.

FIG. 10.—Young (?) thread-corpuscles from an adult worm. *a*. Side view. *b*. Front view. Much enlarged (fresh).

FIG. 11.—Oval (*a*, *b*, *c*) and thread-corpuscles (*d*, *e*, *f*). Flemming and carm.-alum. Z., D, oc. 4, cam.

FIG. 12.—Oval (*a*) and thread-corpuscles (*b*, *c*). Corrosive and bor. carmine. (The thread has been acted upon by the reagents leaving the cavity it formerly filled.) Z., F, oc. 2, cam.

FIG. 13.—Series of figures indicating the action of water on the thread-corpuscle (*a*). Much enlarged.

FIG. 14.—The thread after the action of caustic potash. Enlarged.

FIGS. 15 and 16.—An oval corpuscle before (*a*) and after (*a'*), and a thread-corpuscle before (*b*) and after (*b'*), the action of lime water.

FIG. 17.—Enlarged view of a portion of Pachydrilus, sp. (?), showing the long cells in the cœlom; from the living.

FIG. 17A.—Section through an elongated cell from the cœlom of Pachydrilus, sp. (?). Corrosive, bor. carmine. Z., D, oc. 4, cam.

FIG. 18.—Chæta. Z., D, oc. 4, cam.

FIGS. 19, 20, 21, and 22.—Series of transverse sections through the spermatheca, taken from before backwards. Z., B, oc. 3, cam.

FIG. 23.—Diagram showing the communication of the spermathecæ with the exterior and the œsophagus; in longitudinal section.

FIGS. 24, 25, and 26.—Series of longitudinal horizontal sections taken from above downwards, showing the relations of the spermatheca. Z., B, oc. 4 comp., cam.

FIG. 27.—Longitudinal horizontal section through the fifth segment of Marionia enchytræoides. Z., B, oc. 4, cam.

FIG. 28.—Amœboid corpuscles (fresh). Much enlarged.

On the Development of Lichenopora verrucaria, Fabr.

By

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With Plates 7—10, and two figures in text.

I HAVE formerly had occasion to describe certain very remarkable phenomena in the development of Crisia (6), and I then ventured to suggest that embryonic fission would be found to be characteristic of the whole group of Cyclostomatous Polyzoa. The development of Crisia being, to the best of my belief, without an exact parallel in the entire animal kingdom, it was important to test my former results by the study of some other Cyclostome. A chance discovery of large numbers of the colonies of Lichenopora verrucaria, Fabr., in all stages of development, enabled me not only to confirm the main fact of the occurrence of embryonic fission, but to discover certain previously unsuspected phenomena in the life-history of that species. An abstract of my results has been communicated to the Royal Society (8).

It would not be easy to find two genera of Cyclostomata which are more unlike than Crisia and Lichenopora; and the occurrence of a fundamentally similar mode of development in the two forms may be taken as giving good reason to believe that we are really dealing with a normal characteristic of the group. Crisia is an erect, branching form, whose calcareous branches are interrupted at intervals by chitinous joints. Development here takes place in the interior of a pear-shaped ovicell, which replaces a zoœcium at a greater or smaller distance from a joint, according to the species. Lichenopora, on the contrary, is a plano-convex disc, usually closely attached by its flat surface to some foreign object; its zoœcia project from its upper side, and between them is a calcareous lamina or "crust," which forms the roof of a large compound ovicell. The development of this ovicell commences with the early stages in the growth of the colony. Whilst a Crisia-colony may produce a profusion of ovicells at the breeding season, or may be entirely devoid of these structures, the ovicell of Lichenopora is a single, complicated structure, whose growth is intimately connected with the development of the external features of the colony. In dealing with this question I am obliged to limit myself to L. verrucaria, the only species of which I have obtained an ample supply of material. It may, however, be pointed out that, if this species does not materially differ from other species of the same genus, it is the character of the ovicell which has been taken as the distinguishing feature of the genus or even of the family to which it belongs.

According to Hincks (9, p. 471) the zoœcia of the Lichenoporidæ are "disposed in more or less distinct series, which radiate from a free central area." The area here referred to is, in L. verrucaria, the roof of the ovicell, and the definition applies only to moderately advanced colonies (Pl. 7, fig. 7), in which the ovicell possesses a calcareous roof. But when development has reached a certain stage, every colony possesses an ovicell, and this is in marked contrast to most of the Cyclostomata, in which ovicells are not present in a very large proportion of the colonies which may be examined.

A still more noteworthy feature remains to be pointed out. The internal processes which precede the external appearance of the ovicell commence almost with the beginning of colonial life. The individual formed by the metamorphosis of the free larva gives rise, almost at the same time, to two new zoœcia. One of these two commonly becomes fertile, and forms the starting-point of the series of stages by which the ovicell becomes stocked with numerous larvæ. The other zoœcia of the colony remain, for the most part, unfertile, although many of them produce spermatozoa. It is clear that they have the function, not only of feeding themselves, but also of providing nutritive material at the expense of which the ovicell and its brood of larvæ may develop. The restriction of the female reproductive function to a single individual, or at least to a very small number of individuals of the colony, is by no means in accordance with what is known of other colonial animals. The remarkable nature of the phenomenon will be most clearly realised when it is understood that the fertile zoœcium is usually one of the two "blastozoites," which are first formed by budding from the "oozoite." [1]

My material was collected in Norway at Lervik, in Stordö, and at Godösund, off the north coast of Tysnaesö, during the end of June and the beginning of July. At that time of the year there is no difficulty in collecting an indefinite number of colonies from the earliest stages immediately after metamorphosis to the fully developed condition. The entire colonies were preserved for the most part in corrosive sublimate, to which, in some cases, a few drops of nitric acid and of acetic acid were added. The internal details were studied principally from sections, which were prepared for me by my wife, but to some extent in entire colonies stained without decalcification. The external features were investigated in dry mounts and in Canada-balsam preparations, whether stained or unstained.

Owing to its discoidal or flattened form, the colony will obviously tend to rest on one of its flattened surfaces when it is mounted. In order to examine certain features which can only be made out when the colony is looked at edgeways, it is necessary to make some special arrangement. This has been successfully accomplished by folding a piece of black paper into

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[1] These terms, first introduced by Lacaze-Duthiers, have been appropriately employed by Prouho (18) in describing the colonies of Polyzoa. The oozoite is the individual developed from an egg, i. e. the metamorphosed larva or primary zoœcium of the colony. The blastozoite is an individual which has been formed as a bud.

a series of ridges whose cross section has the form of ⋀⋀⋀. The Lichenopora is then mounted (dry) on the slopes of the ridges; and this allows of the examination of one edge of the colony. An improvement on this method, whereby each colony could be examined in a series of positions, was effected by taking a short length (about 18 mm.) of brass tubing, through the axis of which a long needle was passed, the interval between the needle and the tubing being then filled up with sealing-wax. The outer surface of the brass was covered with black paper, on which numerous colonies were mounted. The needle, to which a suitable head is attached, serves as an axis permitting the revolution of the brass cylinder under the microscope.

The largest colony, among my preparations, has a maximum diameter of 5·47 mm. The older colonies are invariably altered in appearance by the occurrence of secondary thickenings of the surface.

Literature.—A large number of descriptions and figures of the ovicells of Cyclostomata are scattered through the literature of the Polyzoa, and some of these are alluded to below. The only paper which needs special notice here is the second of Smitt's admirable series of memoirs dealing with the Scandinavian Polyzoa (20). Smitt has thoroughly understood the general growth of the colony, and to a large extent that of the ovicell of L. verrucaria, the particular species we are considering. But as Smitt was not concerned with the embryonic development, he paid no attention to the earliest processes in the formation of the ovicell. As, moreover, I cannot agree with all the statements of this observer, a complete account of the development of the entire colony must be given. In further justification of this course, I may mention that although it is perfectly obvious to any one who has made an independent study of L. verrucaria that Smitt had grasped many of the important facts, the figures which he has given are insufficient to explain his meaning to anyone who is not well acquainted with the species.

Smitt has described correctly the general growth of the colony, and he has clearly appreciated the arrangement of the alveoli (see below) or interstitial spaces. He has the merit of having pointed out that these structures give rise to the ovicell, and he calls attention to the important fact that they do not reach the basal lamina of the colony. He has further stated quite correctly that the central area of the colony, which is at the same time an important part of the ovicell, owes its character as a space devoid of zoœcia to the fact that the area originates by the divergence from one another of the most centrally placed zoœcia. Smitt has also given some account of the secondary thickening of the colony.

The size of the largest colonies (exceeding 8 mm.) recorded by Smitt is somewhat greater than that of the largest colonies I have found. I have not been able to discover any colony in which the ovicell had as many trumpet-shaped openings (one to eight) as are described by Smitt. I do not think that so large a number would ever occur in a young colony, in which the number seems to be invariably one or two, and in this respect I find myself in agreement with Levinsen (**12**, p. 28); but I think that it is perfectly possible that a larger number of openings are developed in colonies in which a considerable number of primary embryos (cf. p. 133) are formed as a second generation. I have obtained no actual evidence that this is the case, and I have some reason for believing that the larvæ of the second generation make use of the old apertures of the ovicells. Ridley has suggested (**19**, p. 452) that Smitt has mistaken zoœcia in which incomplete transverse septa have been developed for the apertures of ovicells.

I do not think that Smitt is right when he describes (p. 478) the secondary thickening by the formation of the so-called "cancelli" (cf. my figs. 8 and 9) as giving rise to two or three ovicells, arranged in superposed layers. I do not believe that there is ever more than a single space which is occupied by embryos, although that space can fuse with other spaces by the absorption of the calcareous septa which are at first present.

Smitt describes (p. 476) the first septum formed in the young colony at the outset of its growth as bending to the left. He appears to have missed the curious fact that the growth is to the left in some colonies, and to the right in others. He has, I think, not quite appreciated the way in which the proximal part of the colony becomes covered by the growing edge. His fig. 7 (pl. x) omits an essential part of the arrangement,—that is to say, the actual growing edge shown in my own figs. 3—5.

Smitt describes the colour of the ovicell as inclining to blue (" till färgen dragande åt blått "). I suspect that this was due to the use of a glass which was not quite achromatic. The ovicell is, according to my observations, perfectly white. Finally, I must call attention to the small, scattered tubes with an even, round mouth which Smitt describes as sometimes occurring in the colony. These he compares with the small tubes of Diastopora hyalina (= D. obelia, Johnst.), and suggests that they may have something to do with the production of the male generative organs. This suggestion is clearly wrong, since the testes are developed inside ordinary zoœcia. I have not observed these small tubes as a part of the Lichenopora, but I think it possible that Smitt may be referring to the Infusorian Folliculina, whose tubes are commonly found growing on the Lichenopora.

External Features of the Colony.—Fig. 7 represents a mature specimen, with a diameter of 1·92 mm., in which secondary thickenings have hardly commenced. The colony is nearly circular, and it is surrounded by the delicate calcareous " basal lamina," which in this particular case is upturned, although more usually it is closely adnate to the seaweed. The arrangement of the zoœcia may be understood by imagining a number of the quills of quill pens to be arranged in an obliquely vertical position, radiating from a common centre. Those near the centre will approach the vertical position, while those nearer the margin are more nearly horizontal. It must further be supposed that the nib of each pen is uppermost, or nearer the centre, so that the orifice of the tube is completely concealed when the colony is looked at from above, except in those individuals which stand nearly vertically. The cylindrical zoœcium is, in fact, obliquely cut off in the way which has been indicated by the above comparison, and this will be better understood by referring to fig. 6. The "nib" of the zoœcium is commonly in the form of a single spike, but it may be split, so that two, three, or even more spikes occur. These are very delicate structures in young zoœcia, but they are readily broken off, or lost in other ways, in old zoœcia. In young colonies the zoœcia usually possess more than one spike each. At the growing margins of old specimens the occurrence of a single spike is much more common—if, indeed, it is not the rule.

Between the more centrally placed zoœcia stretches a calcareous lamina (fig. 7)—the roof of the ovicell. This lamina is not even, but is obviously composed of a number of convex portions, separated from one another by shallow grooves. The ovicell opens to the exterior by means of a trumpet-shaped aperture, within whose expanded mouth is a straight edge, turned towards the centre of the colony. The section of the trumpet is at this level semicircular. The straight edge corresponds to the level at which the trumpet springs from the roof of the ovicell. On the opposite side, however, the wall of the trumpet is longer, so that it becomes continuous with the roof of the ovicell at a somewhat lower level. Its passage into the roof is at the same time more gradual and less angular than on the side which faces the centre of the colony.

This arrangement of the aperture of the ovicell may be regarded as characteristic of L. verrucaria. The straight edge may correspond with the valve which I have described (5) in the ovicell of Crisia, and its function may be to restrain the too rapid birth of the larvæ.

The early stages in the growth of a Cyclostome colony have been well described by Barrois (2 and 3), and my results agree with his so far as the general character of the growth is concerned. It has not, however, been previously noticed that the study of the earliest stages of the colony is essential for the proper understanding of the ovicell of Lichenopora.

Fig. 1 (Pl. 7) gives two views of an extremely young colony of L. verrucaria. The colony is attached by means of a circular disc, whose diameter is ·16 mm. The disc is formed, as Barrois has shown, by the calcification of the body-wall of the fixed larva. It gives off a calcareous tube which lies nearly horizontally, and ends in an open[1] mouth, whose diameter is ·18 mm. On looking down into this mouth (Fig. 1, B), it is seen that the cavity is divided by a septum which appears triradiate in end view. The septum does not in any part reach the margin of the aperture of the tube, while proximally it passes into the lower wall of the tube in such a way that the cavity of the disc is continuous with the part marked 1, and is entirely cut off from 2 and 3.

A curious point may now be noticed. About half the colonies of L. verrucaria may be described as "right-handed," and about half as "left-handed," and this will become intelligible from a consideration of the woodcut (Fig. 1).

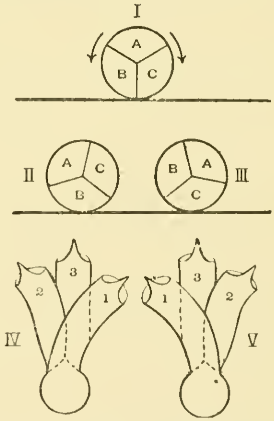

Fig. 1.—Lichenopora verrucaria; diagram to explain the difference between "right-handed" and "left-handed" colonies. The growing margin of the colonies is omitted. I, II, and III are supposed to be seen from above, as in Pl. 7, fig. 2. (For explanation, see text.)

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[1] The mouth appears open (as in later stages) because it is uncalcified. The delicate layer of cells which stretches across it, and can readily be demonstrated in sections, disappears in the dried colony.

I shows the end view of a young colony, similar to fig. 1, Plate 7. The space or zoœcium A is uppermost, while B and C are nearer to the seaweed. Assuming it to be possible for the whole tube shown in I to roll over, it is obvious that it can do so in the direction shown by either of the two arrows. Should it roll to the left, we shall have the condition shown in II, where A and C have come to the upper surface, while B alone is left in contact with the seaweed. III shows the result of the rotation of I to the right.

Returning to Pl. 7, fig. 1, it will be understood that the young colony is attached by the flat surface of its plano-convex disc, as well as by the flattened wall of the zoœcia 2 and 3. This precludes any actual rotation of the parts already developed, but it does not preclude an alteration in the relative position of 1, 2, and 3, as the colony increases in length. This it does in such a way as to assume the position which would be arrived at if it at first grew quite symmetrically, but subsequently experienced a rotation of the common mouth of the tube, while leaving its proximal end unaltered. In other words, the zoœcium 1 may either grow to the right or to the left, as shown in IV and V of the woodcut, the other two zoœcia experiencing a corresponding change of position. A colony in which 1, as seen under the compound microscope, has grown to the right, will be described as "right-handed" (IV), while a "left-handed" colony has the appearance of V in the woodcut.

It is obvious that a cross-section of either IV or V, immediately above the constriction which marks the passage of 1 into the disc, will have the appearance of I; while a section taken more distally will show the first zoœcium (1) in the position of A in II or III, according as we are dealing with a "right-handed" or a "left-handed" colony. It is clear that the zoœcium 3 in IV corresponds with B in II; while 3 in V corresponds with C in III; and the object of giving different symbols to these zoœcia in IV and V is to call attention to the fact that the individual properties of the zoœcia in the older colony depend on the direction in which the primary zoœcium grows at the commencement of the formation of the colony. The whole colony acquires a certain symmetry with regard to 3, the axial zoœcium, and in studying the characteristics of 2 and 3 it matters not which of these corresponds with B and which with C in I of the diagram. The necessity for a close attention to these zoœcia will become apparent later.

The distinction between right- and left-handed colonies persists throughout life, although it ceases to be obvious in colonies of more than a certain age, when looked at in the usual position, from above. The difference can readily be appreciated in young colonies, in which the early stages of the embryonic development are taking place. This will be seen by comparing fig. 3 (left-handed) with fig. 4 (right-handed).

The two kinds of colonies seem to occur in about equal numbers. Of sixteen chosen at random as a test case, eight were right-handed and eight were left-handed; and this result agrees with the other observations I have made on this point.

The actual position of the three zoœcia can be seen from fig. 2, which is an end view of a young colony which was proved to be left-handed by examining it in another position. 1 is the primary zoœcium, which in future will be designated by the symbol z^1, the symbols z^2 and z^3 being employed for the zoœcia 2 and 3 respectively in either IV or V of the woodcut (p. 78). The tubular end of z^2 has in fig. 2 reached a higher stage of development than that of z^1. z^3 is in contact with the surface of attachment, while z^1 and z^2 are on the free surface of the colony. The position of these three zoœcia is also shown in fig. 3, a somewhat later stage seen from above. The colony may be described as having the form of a flattened funnel, whose narrow end originates in the disc. The funnel is attached by one of its flattened sides; and its lip, which is closely attached to the seaweed on this side, here projects considerably further than on the opposite side. The wide end of the funnel is, in fact, obliquely truncated.

z^3 has acquired an axial position, which it retains throughout the later development. z^1 and z^2 are, at their upper ends, arranged symmetrically with regard to z^3, although the woodcut on p. 78 (IV and V) shows that z^2 and z^3 are at their bases symmetrical with regard to z^1, and are clearly a pair of sister zooecia produced by the primary zooecium of the colony.

Figs. 2 and 14 illustrate further the manner in which the number of zooecia becomes increased. This happens by the forking of a pre-existing septum; and the zooecia are at first bounded externally by the common growing rim of the colony. The way in which the zooecium is completed externally is shown in fig. 14, which represents a part of the growing margin of an old Lichenopora. No sooner is the outer wall completed than the zooecium commences to grow upwards as a free tube, although its inner side has before then commenced its upward growth. The obliquely truncated character of the adult orifice is thus a marked feature even at the first formation of a zooecium.

Fig. 14 shows that the septa do not reach the actual rim of the colony, and that the outer wall of the zooecium always grows up from within the edge. Since this happens in the entire circuit of the mouth of the funnel-shaped colony, part of the rim capable of forming new zooecia is left all round, and this is the proximate cause of the assumption of the completely discoidal shape which is so characteristic of the genus Lichenopora. The growing edge is well seen in figs. 3 and 4, from which it is evident that that part of the rim which is situated on the proximal side of the first three zooecia grows at first much less energetically than the opposite part.

We may here notice an important generic difference between Lichenopora and such a genus as Tubulipora. In the latter, z^1 and z^2 are formed in such a way that the proximal part of the rim of the young funnel-shaped colony is used up in forming their outer walls. There is thus no edge capable of giving rise to new zooecia between z^1 and z^2 on the one hand and the disc of fixation on the other hand. The colony thus assumes a fan-like shape instead of the discoidal form which is assumed by Lichenopora. This distinction has already been pointed out by Smitt (**20**, p. 476).

Fig. 4 represents a right-handed colony of Lichenopora which has a maximum diameter of ·59 mm. The number of zoœcia has increased, and it will be noticed that the zoœcium which we have called z^3 still maintains its axial position in the colony. The zoœcium between z^3 and z^1 may be termed z^4, while that between z^3 and z^2 will be called z^5. It will be unnecessary to give special symbols to the other zoœcia.

Growth has, so far, proceeded almost exclusively on the distal side of the first three zoœcia; but the characteristic features of the adult Lichenopora are soon acquired by the growth of that part of the margin of the colony which intervenes between them and the disc. In fig. 2 the diverging zoœcia z^1 and z^2 are separated by a quadrangular area which is the outer wall of a pyramidal space situated between z^1, z^3, z^2, and the outer wall of the funnel-shaped colony. In fig. 4 this space has become divided into two, and at a later stage two or three zoœcia will be found between the distal ends of z^1 and z^2, and directed in such a way that they radiate from z^3 towards the disc of attachment. The position of these zoœcia is shown in figs. 5 and 12. Their development has taken place simultaneously with the extension of the proximal part of the rim of the funnel, which grows in such a way as to cover that part of the funnel which intervenes between the disc and the open mouth. The rim or basal lamina here grows horizontally, keeping in close contact with the wall of the funnel, and finally covering it and the disc completely. Having done this, it comes in contact with the seaweed on the proximal side of the disc of attachment; and the latter is thus completely covered. Growth has not, however, been confined to this region. The colony has been increasing horizontally in every direction, z^3 forming a centre approximately equidistant from all parts of the margin.

The general nature of these processes will be understood by comparing figs. 5 and 7. In the fully formed discoidal Lichenopora no trace can be seen from the upper side of the proximal part of the funnel; but it is merely necessary to turn the colony over to find that that part persists throughout life, without any increase of size. A back view of the adult colony, showing the disc and the proximal part of the funnel, has been well figured by Smitt (20, pl. xi, fig. 6). It is obvious that the increase of the diameter of the colony is accompanied by an increase in the number of zoœcia which are present.

The divergence of the zoœcia from the centre of the discoidal colony results in the occurrence of a central space, round which the zoœcia are arranged; and this space is the commencement of the ovicell. Two points must be here expressly noticed: firstly, that the ovicell is not restricted to certain colonies, but is developed in all colonies which reach the proper stage of growth; and secondly, that the description of the young ovicell must be given with a word of warning. The account of the growth of the colony has been taken from entire specimens, and largely from dried specimens. In the latter at least, we should not expect to find much trace of any structures which are not calcareous; and even in dealing with Canada-balsam preparations of entire colonies, it is extremely difficult to see much of the delicate, uncalcified membranes which really exist. But it must here be noticed that the study of sections shows emphatically that the various spaces of the colony are roofed in by living membranes. Thus the spaces at the growing edge shown in fig. 14 are really closed, and the same is true of the interzoœcial spaces which give rise to the ovicell. Even the orifices of the zoœcia are not widely-open tubes, but are closed during life by a membranous diaphragm, which can be widened to allow of the protrusion of the tentacles. Of all this, nothing appears in the dried colony; but it must be clearly understood that the cavity of a young ovicell is morphologically a body-cavity, and is not an external space converted into an ovicell by the formation of a calcareous roof.

The development of the ovicell can be most easily described after the structure of the complete ovicell is understood. Fig. 6 represents a thick free-hand section showing the whole length of a single radius of a colony which has not been decalcified. The zoœcia diverge from the centre of the colony. Each zoœcium reaches the attached basal lamina, a short part of which it forms. The older zoœcia are very much longer than the younger ones. The roof of the ovicell connects the diverging zoœcia, and the cavity of the ovicell is clearly, in the central part of the colony, a space which completely surrounds a part of the zoœcia. The roof of the ovicell is not perfectly even, but is formed of convex portions, shown in surface view in fig. 7.

The ovicell increases in size during the growth of the colony; and the nature of this increase may be understood from fig. 14. The marginal spaces, marked out by the vertical septa which start from the basal lamina, are all destined to give rise to zoœcia, which are the only spaces which extend down to the base. The zoœcium is first clearly indicated by the appearance of one or more of the spikes which occur on the upper margin of the orifice of all the zoœcia. At about this stage (fig. 14, A), one of the septa forming the side walls of the zoœcium gives off a branch which runs more or less transversely. The cavity of the young zoœcium is in this way cut off from the cavity on the distal side of it. Up to this time the zoœcium has been a short horizontally-placed tube, whose lower wall is part of the basal lamina, and whose free upper wall is parallel to the base. No sooner is the cavity of the zoœcium completed on its distal side than it begins to alter its direction of growth. The woodcut Fig. 2 is a diagrammatic representation of the margin of a colony. The thick lines represent two young zoœcia and part of the basal lamina as they would be seen in a radial section, and the dotted lines represent the condition of the corresponding parts after a certain amount of growth has taken

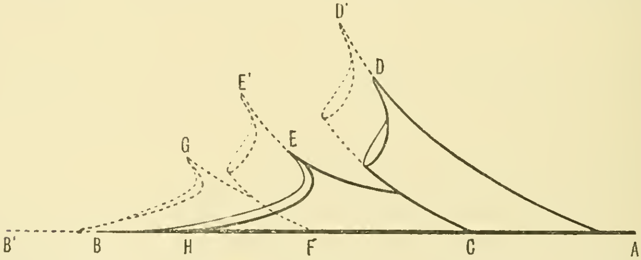

Fig. 2.—Diagram of the growth of the margin of the colony of Lichenopora verrucaria. (For explanation, see text.)

place; A C H B is the basal lamina. The zoœcium whose point is marked D has its upper end free, even in the earlier condition, while that marked E is still incomplete on its distal side (cf. fig. 14). It is soon completed on that side by an obliquely vertical septum, which starts at F; and the prolongation of this septum forms the lower wall of the zoœcium. By the time that the margin of the colony has extended to B^1, the two radial septa, which at first formed the lateral parts of the zoœcium E, have grown in length and in height; and they are supposed to have meanwhile given rise to the beginning of a new zoœcium, G, which has reached the condition of E in the earlier phase.

In examining the woodcut in the condition indicated by the dotted lines, it is clear that a space occurs between the two older zoœcia, and a much younger one between the two younger zoœcia. Smitt (20) alludes to a space of this nature as an "interstitialrum;" but it will be convenient to substitute the term "alveolus."

The zoœcia may be arranged in radial series, as shown in the woodcut; or their position may be for the most part alternate, as in fig. 14. The upper sides of the zoœcia are marked with longitudinal ridges, which have been omitted from most of the figures for the sake of simplicity, but are shown in figs. 8 and 9. The projecting spikes of the zoœcia are commonly continuous with these ridges, some of which become exaggerated at their lower ends to form lateral walls for the alveoli. These are thus pyramidal spaces, pointed at their lower ends, and at first only closed by membrane above. They increase in length by the growth of the zoœcia, and by the extension of the vertical septa on sides where they are not bounded by zoœcia. The septa do not, however, grow so high as the zoœcia; but after they have reached a certain height, each alveolus commences to become roofed by the calcification of the membrane which is already present in that situation. The calcification of the roof of each alveolus begins at the margin and gradually advances to the centre, in the same way that an opening is gradually closed by the contraction of a sphincter muscle. An alveolus which is incompletely roofed in is shown in fig. 6.

The original extent of the alveoli is indicated by the grooves, which correspond with the original septa, on the surface of the ovicell (*cf.* figs. 7 and 14). It is obvious that the ovicell is gradually increased in size by the addition of fresh alveoli all round its margin. The vertical septa are absorbed after the alveolus has become part of the ovicell, and a continuous space thus results, through which the more centrally placed zoœcia pass as free pillars. Fig. 6 illustrates this point, and the conformation of that part of the roof of the ovicell which lies to the left of the right-hand zoœcium indicates the loss of the vertical septa which were at first present.

We have still to consider the earliest development of the ovicell, which, to the best of my belief, has not been studied in detail by any previous observer. Fig. 12, though by no means an early stage, will serve to introduce us to a phenomenon which is of the highest importance for the understanding of the history of the colony. This phenomenon may be spoken of as the occlusion of the fertile zoœcium.

In fig. 12, all parts of the ovicell which have received a complete roof are shaded. The preparation is a transparent one, made in Canada balsam, so that the walls of the zoœcia can be seen through the roof of the ovicell. Parts which are seen through some other part of the colony are indicated in dotted lines. The colony is left-handed—z^1 and z^3 project in the ordinary way beyond the roof of the ovicell, while z^2, the occluded zoœcium, is completely closed by the roof, and would probably not have been visible at all in a dried, opaque preparation. In the immediate neighbourhood of the occluded zoœcium arises the trumpet-shaped aperture of the ovicell. The study of decalcified sections is necessary in order to understand the significance of these facts, but it must for the present be assumed that we are justified in alluding to z^2 in this colony as the "fertile" zoœcium—i. e. as the zoœcium in which the embryo is first developed.

The roofing in of the ovicell commences with the occlusion of the fertile zoœcium. This process is not easy to see in a colony which is resting in its position of most stable equilibrium on its flat surface; but it can be seen without difficulty in a colony of suitable age which has been mounted on a rotating cylinder in the manner described on p. 74. No general rule can be laid down with regard to the size of the entire colony in its relation to the closure of the ovicell. The smallest colony in which I have found this process actually beginning measured ·77 mm. in diameter, while the largest colony in the same condition as regards its ovicell was 1·13 mm. across. In nearly all the cases I have actually observed at this stage, z^2 was the fertile zoœcium, although this rule is by no means invariable. A reference to the woodcut on p. 78 will show that the orifice of z^2 may be described as having an axial and an abaxial side. The occlusion of the zoœcium commences with the formation of a calcareous film, starting from the abaxial edge of the zoœcium. This film grows inwards as a cap to the zoœcium (fig. 13); but while it is closely fitted on to, and indeed arises from the abaxial edge of the orifice, it grows over the axial side of the edge as an arch which does not fuse with the edge. The film is the beginning of the roof of the ovicell; and it is clear from fig. 13 that a passage leading from z^2 into the cavity of the ovicell is left between the calcareous film and the axial side of the edge of the orifice of z^2. Through this passage the embryo passes from the fertile zoœcium into the ovicell. It should perhaps be pointed out that this statement is to some extent a matter of inference. I cannot claim to have first found this passage in a particular colony, and then to have observed the embryo on its way through the passage. But I have been able to show that the embryo actually passes from the fertile zoœcium into the ovicell through an aperture close below the roof of the latter; and it may fairly be concluded that the passage whose formation we have just considered is really formed for this purpose.

No sooner has the fertile zoœcium been occluded than the formation of the orifice of the ovicell is commenced. This is seen in an early stage in fig. 5, where the trumpet-shaped mouth is not yet formed. Transparent preparations (fig. 12) show that the trumpet is developed in the immediate neighbourhood of the occluded zoœcium. The appearance of the fully formed trumpet is shown in fig. 7.

The occlusion of a fertile zoœcium may or may not result in the obliteration of all signs of its presence. In fig. 13 the principal spike of z^2 is still visible externally, in spite of the occlusion of that part of the orifice. In other cases, a careful examination of a colony may result in the detection of the ends of two or three spikes in the immediate neighbourhood of the aperture of the ovicell, which clearly belong to a zoœcium, and from their relation to the trumpet must have belonged to the occluded fertile zoœcium. What is probably part of the orifice of z^2 is seen as a zigzag line below the aperture of the ovicell in fig. 7.

The study of sections shows certainly that z^2 is not necessarily the fertile zoœcium, although the cases in which either this or z^3 is fertile very largely preponderate over all other cases put together. The study of entire colonies amply confirms this, if we may for the present assume that the conjunction of an occluded zoœcium with a trumpet-shaped aperture belonging to the ovicell is a strong reason for believing the zoœcium to have been fertile. In many cases where the opening of the ovicell is formed in connection with z^3, it occupies a very characteristic position with regard to that zoœcium, being placed immediately on the distal side of the original orifice of z^3, and with its trumpet-like mouth directed towards the disc from which the colony started its growth. The opening of the ovicell less commonly has a similar relation to z^2.

It will be remembered that some few of the oldest zoœcia of each colony form a group which diverge from the centre of the discoidal colony. These zoœcia are connected with one another by vertical septa which do not necessarily reach the roof of the ovicell. In other words, a part of the roof which starts at one vertical septum does not always become connected with the adjacent septum, but may form an arch extending completely above that septum to one beyond it. In this way is formed what may be called a compound alveolus; i.e. an alveolus which at its formation is partially subdivided by one or more vertical septa which do not reach the roof of the ovicell. The closure of the central part of the ovicell commonly and probably usually takes place by the formation of one or more compound alveoli, whereas the extension of the ovicell in a mature colony appears to take place for the most part by the formation of simple alveoli.

The extent of the central area of the colony, devoid of zoœcia, depends in the first instance on the extent to which the older zoœcia diverge from one another; but it may be increased by the occlusion of zoœcia. This process, which can be best made out in transparent preparations, has nothing to do with the occlusion of the fertile zoœcium. It is highly probable that the occlusion follows the loss of the polypide.[1] The process does not appear to take place to any great extent in young and healthy colonies of L. verrucaria, but in old colonies a considerable number of the more centrally placed zoœcia may be occluded. A calcareous lid may in these cases be added in the position of the original orifice (Pl. 7, fig. 9), and it may or may not be formed in an oblique position corresponding with the original condition of the orifice. This is very different from the state of an occluded fertile zoœcium, in which the closure takes place at the level of the roof of the ovicell.

All the older colonies of Lichenopora differ from those which have so far been described by the occurrence of a very striking process of secondary thickening of the surface. Since old colonies are further remarkable for producing new broods of embryos (cf. p. 132), which are developed in a different way from the first brood, the idea suggests itself that the secondarily thickened colonies are the result of a second year's growth. I have no actual evidence in favour of this suggestion, but the fact that secondary broods of larvæ are produced

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[1] Cf. my former paper on Crisia (5, p. 142).

in old colonies at the same time of year as primary broods from young colonies is in favour of that view.

In fig. 14 places will be noticed, as at B, where the neighbouring alveoli do not meet accurately. These places are the "cancelli" which are so commonly met with in accounts of the genus Lichenopora. The cancelli do not at first develop to any great extent; but this condition is altered in the old colonies (figs. 8, 9).

Fig. 9 shows three zoœcia of an old colony. One of these zoœcia has been occluded by a calcareous cap at a considerable height above the level of the ovicell. This is quite similar to the structures which are well known to occur in profusion over the more centrally placed zoœcia of certain species of Diastopora.

The alveoli which are shown in fig. 9 are separated from one another by shallow grooves. At these regions, and at the junction of a zoœcium with the roof of the ovicell, vertical septa are rising up. Fig. 8 shows the appearance of a colony after this secondary thickening has been proceeding for a longer period. The system of vertical septa, which in the earlier stage started only at the intersection of the alveoli with one another or with the zoœcia, has now extended so as to cover the entire surface of the ovicell. The porous roof of the latter can be seen at the bottom of the open cancelli, which have for the most part no calcareous roof. The base of the right-hand zoœcium is surrounded by very large cancelli, the walls of which (as in fig. 9) are continuous with the longitudinal ridges of the outside of the zoœcium. These cancelli are obviously encroaching on the base of the zoœcium, which can be seen at the bottom of the spaces. Those marked "cancelli" are beginning to acquire a calcareous roof. The process of roofing in is much further advanced at the base of the left-hand zoœcium, where one of the cancelli is completely closed. In this way the bases of the zoœcia of old colonies commonly become surrounded by a set of blister-like swellings, which have been formed above the original roof of the ovicell. These are presumably the structures which Smitt regards as forming a new ovicell superposed on the old one (cf. p. 75). Judging by the analogy of the walls of the alveoli, I think it possible that the floor of these blister-like spaces may ultimately be absorbed, and the ovicell thereby enlarged.

It is hardly possible to examine figs. 8 and 9 without feeling convinced that there must be a layer of living tissue outside the roof of the ovicell. Although I have not obtained complete evidence with regard to the morphological character of this layer, its presence can be demonstrated in vertical sections of stained colonies which have not been decalcified. In preparations of this nature a film of stained nucleated tissue can be seen, passing over the outer side of the calcareous parts of the upper surface of the colony, and thus covering the upper side of the roof of the ovicell, and extending up the outside of the zoœcial tubes to the orifices of the latter, where the tissue passes round to join the part of the body-wall which is invaginated into the orifice of each zoœcium. The ridges on the outer side of the zoœcia are as a matter of fact undeveloped septa, which can continue their growth under certain circumstances. It is thus natural to find that the outer wall as well as the inner wall of the young and active zoœcia should be covered with living tissue.

Where the protoplasmic layer passes over the convex surface of an alveolus, or up the uniform surface of a zoœcium, it is usually tightly stretched over the adjacent calcareous matter. But in places where it crosses a groove between two alveoli, the layer usually appears as a tangent of the two curved surfaces. Hence one sees in sections a more or less triangular space, roofed only by a delicate membrane, at the junction of two alveoli. It is obvious that this is in accord with the arrangements shown in fig. 9.

The calcareous part of the upper surface of a Lichenopora is thus not the outermost layer; and it becomes a question how far it corresponds with the "ectocyst" of some other Polyzoa. In the Entoprocta, the Phylactolæmata, and the Ctenostomata, in which calcification does not usually occur, the outermost layer is a mere cuticle; and it is to this layer that Allman (1, pp. 8, 13) gave the name of "ectocyst." There is, however, a good deal of reason for believing that the arrangements are not quite so simple in calcareous Polyzoa. Ostroumoff (14) announced in 1885 that the use of silver nitrate demonstrated the evidence of an epithelial layer external to the calcareous skeleton in several genera of calcareous Polyzoa; and later (15, p. 12) expressed himself to the effect that in calcareous forms, such as Lepralia, the calcareous matter separated the ectoderm into two layers, one of which is outside the skeleton. Vigelius (22, sep., pp. 3, 4, pl. vi, fig. 24) describes and figures an extra-skeletal layer in an encrusting Cheilostome, and in a later paper (23) states that the skeleton is probably usually formed inside the ectoderm-cells. Pergens (17) finds that the skeleton of the calcareous forms examined by him is overlaid by a cuticle merely.

The relation of the calcareous skeleton to the parts of the living body-wall appears to need further elucidation; but the condition found in Lichenopora makes it probable that, in that genus at least, there is more than mere ectoderm outside the calcareous layers of the upper surface of the colony. The cavities of the cancelli are probably morphologically parts of the body-cavity; and as such are no doubt surrounded by more than ectoderm.

It appears to me extremely likely that the relations of the calcareous septa in Lichenopora may not be very different from those of the septa of a Zoantharian Coral, as shown by Koch's well-known researches. The outer wall of the young funnel-shaped colony (fig. 3) is immediately derived from the body-wall of the metamorphosed larva; and it is of course a young condition of the basal lamina. All the septa which divide the zoœcia, the alveoli, and the cancelli from one another are ultimately derived from the basal lamina; the first formation of a young septum at the growing edge always appearing as an outgrowth from that layer (fig. 14), and other septa being always formed from pre-existing septa.

I have obtained no evidence of the existence of soft tissues on the lower side of the basal lamina, and I do not think it likely that any such exist. The view which seems to me to be suggested by my observations and by those of previous workers is that the basal lamina is the outermost layer of the body-wall; that the body-cavity it encloses has been repeatedly subdivided by the ingrowth of a series of branching and anastomosing ridges or septa from the body-wall. The whole upper surface of a Lichenopora colony thus corresponds with what would be seen in an end view of a growing point of Crisia. But whilst in the latter the growing edge is subdivided by a very simple set of septa, which result in the formation of only two series of zoœcia, that of Lichenopora is divided by an immensely complicated series of septa. The parallel is not, however, quite accurate; since in Crisia, as in Tubulipora (cf. p. 81), the septa reach the growing edge of the colony, and the mature zoœcia are thus completely outside the "growing-point," because part of the growing edge is used up in toto in the formation of each zoœcium. The morphology of the Lichenopora colony can be most easily understood by considering a young colony like fig. 3. It will then be seen that while the lateral body-wall is complete from the beginning, the mouth of the expanded funnel is closed by a living body-wall. While this is constantly encroached on and altered by the formation of septa, whether those giving rise to new zoœcia or those which form alveoli or cancelli, the body-wall is never completely calcified in this region. For this uncalcified body-wall, which closes the mouth of the funnel-shaped colony of Lichenopora, of the growing points of Crisia, &c., the name "terminal membrane" may be suggested. It is this layer which gives rise to the polypide-buds, and is invaginated into the orifice of every zoœcium.

If the septa are really, as there seems every reason to believe, derivatives of the basal lamina, there is no reason for not regarding them as ingrowths of a true calcified ectocyst; and they may accordingly be compared, in a general way, with the septa of a Coral (as already pointed out), or with the chitinous ingrowths which form the endoskeleton of a crayfish.

Internal Structure.—The general appearance of a section through a colony in which the production of the first brood of embryos is at its height will be understood from fig. 11, representing a section, parallel to the flat surface, of a colony in about the same stage as that shown in fig. 12.[1] The section has a maximum diameter of ·80 mm. The ovicell may be explained by comparing its contents with an Amœba with a series of blunt pseudopodia extending in the intervals between the zoœcia. The "pseudopodia" contain a considerable number of secondary embryos, and the nucleus may be represented by the "fertile brown body."

This structure, although an inert body which plays no direct part in the development, is in fact the centre about which all the most important phenomena in the development of the ovicell take place. The "pseudopodia" form a complex structure for which the name "embryophore" may be suggested, and they lie in a cavity which may be regarded as the body-cavity of the ovicell.

The zoœcia can be identified, in a good and well orientated series of sections, by an examination of the proximal end of the colony, which, it will be remembered, retains throughout life the form assumed by the young Lichenopora. Hence it may be confidently stated that z^1 is a section of the primary individual of the colony, and that z^2 and z^3 represent respectively the second and third zoœcia, as defined in the earlier part of this paper.

z^1 possesses a polypide, whose tentacles, enclosed in their tentacle-sheath, are seen in the figure; z^2 is quite empty basally, but contains some embryos distally, as shown by the figure; z^3 contains a brown body basally, but it has no polypide, and it opens at the level of the section into the ovicell. Two of the zoœcia contain brown bodies, that of A not being visible in the section figured.

The fertile brown body is in the neighbourhood of z^2, near whose upper end is developed the trumpet-shaped aperture of

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[1] The secondary embryos are more developed in fig. 11 than they would have been in fig. 12.

the ovicell (not seen in the section figured). There is no aperture in connection with z^3, or indeed with any of the other zoœcia. The colony has every appearance of being perfectly healthy. The sections of its basal part show that nearly every zoœcium has a functional polypide. Only one of these polypides has any trace of a testis, which consists of a small mass of degenerating spermatozoa.

The occurrence of an ordinary brown body in z^3 makes it improbable, as will be shown later, that this was the fertile zoœcium; and it is in the highest degree probable that the primary embryo of this colony was produced by z^2. This is indicated by the position of the aperture of the ovicell and by that of the fertile brown body, as well as by the occurrence of embryos within the cavity of z^2. The connexion between z^3 and the ovicell probably implies that z^3 had been occluded (cf. p. 89).

My preparations include a practically continuous set of stages between fig. 11 and the commencement of the development; and my results are based on the examination of complete series of sections through some three hundred colonies, in eighty-nine of which no embryos can be detected, while in seven more, degeneration had set in after the commencement of the development. The large number of fertile colonies examined enables me, to a large extent, to eliminate abnormalities in the development.

An examination of the cases in which normal embryonic development was not found will give some useful information. The negative result in at least twenty cases was probably due to the fact that the colonies were too young. A careful comparison of my measurements of entire colonies and of sections shows that the commencement of the embryonic development is to be looked for in colonies which measure about ·40—·43 mm. in total length, and about ·25 mm. in transverse diameter, i.e. in colonies which are at about the stage of fig. 2.

In the next place I am able to confirm the suggestion I formerly made (6, p. 212) to the effect that the normal development of the ovicell is dependent on the activity of the polypides. On decalcifying a number of colonies of Lichenopora, a considerable number of all ages and sizes will be found to be practically empty. In studying the embryonic development, time is simply wasted if preparations are made of colonies in which the polypides are not for the most part fully active and functional, or at least in which the polypides have not recently been functional. A recently degenerated polypide may be difficult to distinguish, in a preparation of an entire colony, from a functional polypide; whereas it is quite easy to recognise the small, compact, brown body which indicates that the histolysis of the polypide took place at some more distant period.

The conditions under which the embryos are nourished appear to be very different in different Cyclostomes. In Crisia ramosa I have shown that the embryos are contained in a highly protoplasmic reticulum, which, it can hardly be doubted, serves for the transference of nutriment to the developing larvæ. In C. eburnea the reticulum is reduced to a minimum, and the path of the nutrient substances is probably somewhat different from that in C. ramosa. Analogous phenomena probably occur in the genus Lichenopora; and L. verrucaria may be compared with C. eburnea, in which the reticulum is but slightly developed. Although I have not yet been able to obtain a supply of material for the proper examination of other species of Lichenopora, I have obtained a series of sections through a single fertile colony of L. hispida, Flem. The ovicell contains a comparatively small number of young secondary embryos, which are embedded in a large solid nucleated mass which probably corresponds, in function at least, with the "follicle" of C. ramosa (cf. 6, Pl. xxii, fig. 6).

My examination of this single series of sections of L. hispida enables me to state that the embryonic development of that species probably differs to a very considerable extent from that of L. verrucaria. Another curious difference between the two species may here be pointed out. While in

L. verrucaria the brown bodies formed by the degeneration of the polypides are absorbed from time to time, so that a zoœcium hardly ever contains more than one or at most two brown bodies, those of L. hispida (again judging from my single series of sections) accumulate at the basal end of the zoœcium, a considerable part of which is tightly packed by a mass of brown bodies.

It seems clear that considerable differences in detail occur in the embryonic development of different Cyclostomes; but I believe that it will be found that the phenomena are fundamentally the same throughout the group.

Whatever may be the character of the arrangement by which the embryos are directly nourished, there can be no doubt that it is the polypides which ultimately supply the material at the expense of which they grow. In a very large proportion of the cases in which no embryo could be discovered, the polypides were not functional in all or some of the zoœcia. A similar result is obtained by the examination of the degeneration of the embryo in fertile colonies. Leaving out of account doubtful cases, I have fifteen colonies in which degeneration of the embryo has clearly occurred. In eleven of these cases all the polypides of the colony had degenerated, this being probably the proximate cause of the degeneration of the embryo. In some cases new polypide buds were being developed, and the colony would obviously have survived, and would probably have developed a new embryo from one of the younger polypides. One of the other four cases probably points in the same direction. The fertile zoœcium contains two brown bodies, a polypide, and an embryo which commenced to degenerate in the "suspensor stage" (cf. fig. 24, a normal embryo at this stage). The remains of the embryo are between the two brown bodies, and it is highly probable that the distal brown body represents the polypide which originally supported the suspensor. The abnormal degeneration of this polypide, at an earlier period, probably resulted in the degeneration of the embryo, which is still just recognisable, although a new polypide has grown up in the fertile zoœcium.

A much larger number of degenerating embryos might have been obtained, if the colonies of which sections were to be cut had been taken at random, instead of having been chosen with some regard to the condition of their polypides.

I am unable to suggest any definite cause for the degeneration in most cases. A Protozoon, a species of Folliculina, is commonly found with the basal end of its tube embedded in the Lichenopora, its free end projecting from the surface of the colony. These organisms can often be recognised in the sections of the colonies, and in many cases they are found in degenerating specimens. It is quite possible that the Folliculina may in these cases be the cause of degeneration; but it is equally possible that it is the effect, and that the Protozoa settle down in parts of the colony which have lost their zoœcia. They are found, not uncommonly, in parts of the colony in which their presence does not seem to have had any effect on the adjacent zoœcia.

Degeneration may start at any stage of the embryonic development. I have observed it most commonly in colonies in which the embryo had developed up to the "suspensor stage;" but I have also found it commencing at later stages, as, for instance, at the beginning of embryonic fission, or even later.

In describing the development of the structures found within the ovicell of Lichenopora verrucaria, it is desirable to keep the account of the first brood of larvæ entirely separate from that of later broods. The appearance of an ovicell containing larvæ belonging to the first brood has already been considered (fig. 11); and this is the condition which is usually found in colonies which have a diameter of 1 mm. or thereabouts. The origin of all these complicated structures is to be looked for in colonies which consist of only three or four zoœcia.

For descriptive purposes it will be convenient to classify the embryos in a certain number of stages; and it will be seen that the form of the entire colony has a distinct relation to these stages, although wide variations occur in the period at which any particular stage of development is passed through.

The following stages are naturally marked out by the phenomena of the development.

Stage A.—Formation of the definitive egg (figs. 15—18). The entire colony in which this stage occurs measures about ·45 mm. in length, and about ·25 in transverse diameter (between figs. 2 and 3).

Stage B.—Formation of the follicle and suspensor (figs. 19—22). The colony does not differ materially in size from those in which Stage A occurs.

Stage C.—"Suspensor stage" (figs. 10, 23, 24), the embryo being supported by a functional polypide. Colony in the condition of figs. 3 and 4; usually about ·50—·60 mm. long, and about ·35—·55 mm. broad.

Stage D.—The polypide has degenerated, and the embryo is supported by a brown body found near the distal end of the fertile zoœcium (figs. 27, 28). Colony as in Stage C.

Stage E.—Disappearance of the "suspensor" and enlargement of the embryo (figs. 29, 30).

Stage F.—Commencement of embryonic fission (figs. 31—35). Diameter of colony about ·60—·80 mm.

Stage G.—Fully formed ovicell (figs. 7, 11, 12).

The measurements given here and elsewhere, so far as they refer to sections, must be taken as approximate. The plane of the sections may not be such as to permit of a satisfactory measurement being taken at all, while in the case of an oblique series the whole length or breadth of a colony may not be seen in any one section; and the necessity of estimating the length obviously introduces a source of error. The delicate calcareous lamina which forms the edge of the entire colony is usually not distinct in sections. Lastly, there is considerable variation in the size of the colony and in the time at which development commences.

In spite of these drawbacks, I believe that it will be useful to record the measurements of the colony, wherever possible, as a guide to future investigators. The measurements given in the sequel refer in all cases, unless the contrary is stated, to the sections, and not to the colony before decalcification.

During my study of the development of L. verrucaria, I have been much struck with the frequency with which the zoœcia z^2 and z^3 form the starting point of the ovicell. This result was first obtained by a study of sections; but, as has already been pointed out, it was afterwards amply verified by an investigation of the entire colonies. Some statistics will bring out the striking nature of this phenomenon. In 108 colonies belonging to Stages B to G, or being fertile colonies in which degeneration of the embryo was taking place, I have been able to determine the fertile zoœcium. In the cases of the older colonies (Stages E to G), it is easier to recognise the fertile zoœcium when it happens to be z^2 or z^3 than when it is a younger zoœcium; and the older stages have consequently been omitted in the second column of the table.

Table showing the Frequency of the Occurrence of z^2 or z^3 as the Fertile Zoœcium.

	Stages B—G and degenerating fertile colonies.	Stages B—D.
No. of cases in which z^2 is fertile	44	29
,, ,, z^3 ,,	21	15
,, ,, z^2 or z^3 ,,	8	5
,, ,, ? z^2 ,,	15	12
,, ,, ? z^3 ,,	8	6
,, ,, a younger zoœcium is fertile	6	5
,, ,, two zoœcia are fertile	6	3
,, ,, the fertile zoœcium could be determined	108	75
Total number of colonies investigated	175	95

As it is by no means easy to determine the fertile zoœcium in unfavorably orientated sections, there is obviously room for error in the above results; but as I have only entered cases in which I have felt confident that I could really determine which zoœcium was fertile, I believe that the table is substantially accurate. In estimating the bearing of these numbers it must be noticed that in a considerable proportion of the cases in which the fertile zoœcium is entered as ? z^2 or

?z^3, the doubt usually arises in consequence of the difficulty of distinguishing between z^2 and z^3 in the sections. Thus in most cases where a fertile zoœcium was marked ?z^2, it was certainly z^3 if it was not z^2.

Another line in the table refers to cases in which the fertile zoœcium was either z^2 or z^3, but it was not certain which of these two was fertile.

We thus obtain the result that in the colonies of all ages up to Stage G the fertile zoœcium was either z^2 or z^3 in 96 cases, while a younger zoœcium was fertile in only 6 cases in which a single embryo was present. The corresponding numbers for Stages B to D only are 67 and 5.

Even if a liberal deduction is made from the 96 of the first column or the 67 of the second, on the ground of uncertainty or possible errors of observation, we are still entitled to consider that the fertile zoœcium which produces the first brood of embryos in L. verrucaria is normally one of the two zoœcia which are first formed by budding after the larva has metamorphosed itself into the primary zoœcium of the colony. Two of the six cases alluded to in the table as colonies in which two zoœcia are fertile, have embryos in both z^2 and z^3. In two more cases the fertile zoœcia were probably z^2 and z^3. In the fifth case z^2, and in the sixth case z^3 was fertile in addition to a younger zoœcium than either of these two.

The table further brings out the fact that z^2 is more often fertile than z^3. An examination of young colonies which have been stained and mounted whole, without decalcification, shows that z^2 is really older than z^3, although there is no evidence of this in the later stages. Thus a colony ·32 mm. long by ·15 mm. broad had a mature polypide in z^1, and a small polypide-bud in z^2. Another, ·35 mm. by ·24 mm., had polypides in z^1 and z^2; while a third, ·43 mm. by ·27 mm., was developing for the first time a polypide-bud in z^3, in addition to having functional polypides in the older zoœcia.

z^2 is thus clearly older than z^3, and we accordingly have the following striking result. There is a strong tendency in the development of Lichenopora verrucaria for the ovicell to owe its origin to the oldest zoœcium which is formed as a bud and does not result from the metamorphosis of the larva; or, in other words, the ovicell tends to be formed from the first blastozoite of the colony. I have found no case in which the ovicell owes its origin to z^1; but it must not therefore be concluded that the primary individual differs from the others in being devoid of generative organs. z^1 commonly has a well-developed testis, while I have on several occasions observed structures in z^1 which I consider to be egg-cells.

It will be seen from the figures of the entire colonies that the determination of z^2 and z^3 is easy enough in sections in many cases in which the orientation is good. It is more difficult when, as commonly happens, the disc from which the colony originates is injured or lost when the Lichenopora is removed from the seaweed. The determination of the fertile zoœcium is greatly facilitated by noticing the position of the tentacles of the polypides.

The woodcut on p. 78 shows that z^1 may be considered to have an inner (axial) and an outer side. During the retracted condition of the polypide the tentacles lie close to the inner side of the zoœcium, while the cæcum of the stomach is situated more externally. The orientation of the polypide of z^3 is like that of the polypide of z^1; but the polypide of z^2 faces in the opposite direction, its tentacles lying, like those of z^1, close to the inner border of the zoœcium. This appears to be true of all the polypides developed in any zoœcium. After a given polypide has degenerated into the condition of a brown body, the newly formed polypide is found to have the same orientation of its tentacles as its predecessor had. The younger zoœcia have a corresponding arrangement. In any colony the polypides are normally orientated during retraction in such a way that the tentacles of a polypide are nearer to the centre of the circle enclosed by the growing margin of the colony than is the stomach. This point is, however, not brought out by any of the figures which illustrate this paper. It may be noted that the number of the tentacles is constantly eight.

A further point which deserves special notice is the character of the "brown bodies." Barrois (2 and 3) has shown that the brown body formed by the degenerating parts of the larva during metamorphosis has disappeared completely by the time that the first polypide is mature. He has not, however, described the way in which this disappearance takes place. Ostroumoff (16, p. 185) states that the cæcum of the primary polypide is formed "at the cost of the brown body;" but he does not enter into further details.

I can confirm Barrois' statements with regard to the disappearance of the degenerated remains of the larva, since I have found that the primary zoœcium, when very young, possesses a mature polypide, but has no trace of a brown body. I have found this condition lasting till the stage is reached when z^2 has a mature polypide, and z^3 possesses either a bud or a more or less mature polypide. At a later stage the primary zoœcium contains a brown body as well as a polypide. The smallest colonies in which I have found this condition measured ·33 × ·16 mm. and ·35 × ·21 mm. respectively. This implies that the functional polypide is in these cases not the original tenant of the zoœcium, although in some colonies of the same or even a larger size I have found no brown body. The degeneration of a polypide, in fact, results in the formation of a "brown body," which in the younger stages of the colony nearly always remains as a distinct structure in the zoœcium. In the older stages, as we shall have occasion to see, the brown bodies commonly disappear from the zoœcia. When present they are easy to recognise, as they appear as bright yellow bodies even in sections which have been stained with Grenacher's hæmatoxylin. A part of the cæcum of the stomach has the same colour in sections.

I do not think that the primary polypide of z^1 develops a testis, although that organ is commonly present as an appendage of the polypide of z^1 in cases where the corresponding zoœcium possesses a brown body.

Stage A.—Formation of the Definitive Egg.

Figs. 17 and 18 have already been described in my preliminary note (8). Fig. 17 represents a colony consisting of three fully formed zoœcia only. The section is parallel to the surface of attachment, in what may be called a horizontal plane. The examination of the complete series of sections showed that both z^1 and z^2 have a brown body, a polypide, and a testis. The level of the section figured is not such as to show the characteristic orientation of z^2 (see p. 102); z^3 has a brown body, a polypide, and a conspicuous cell (seen more highly magnified in fig. 18), which obviously resembles an egg. A few nuclei to the right of the egg probably represent the commencement of the investments of the embryo. Spermatozoa were found floating freely in the body-cavity of z^1 and z^2, but none were found in the fertile zoœcium in this particular case.

I have not observed the process of fertilisation with any degree of certainty, but I believe that it must occur at about this stage. The fertile zoœcium may or may not have a testis, while testes are commonly present in other zoœcia, particularly during the early stages of embryonic development. In some cases, and particularly in old colonies in which new broods of embryos are developing, the testes are enormous, being sometimes as much as ·30 mm. long. It can hardly be doubted from these facts that fertilisation does occur at some period. Considerable masses of ripe spermatozoa are found in the body-cavity of many of the zoœcia; and it is probable that they pass thence, in some way, to the fertile zoœcium. The young spermatozoa are always in groups of four, as in Crisia (6).

The correct identification of the large cell shown in fig. 18 is clearly of the first importance, and I have thought it desirable to figure two other cases of the same kind (figs. 15 and 16).

Fig. 15 shows an egg attached to a polypide-bud. z^1, z^2, and z^3 contained polypides, but none of the other zoœcia were old enough to possess more than buds. The egg seems to belong to the primary polypide-bud of a zoœcium which is younger than z^2 and z^3, since no brown body could be detected in it. A precisely similar egg occurred in another polypide bud of the same age in the same colony.

Fig. 16 shows part of the polypide of z^3 of a rather long and narrow colony, measuring ·48 mm. in length. The first three zoœcia are fully formed; and each has a brown body, a polypide, and a testis. z^1 has either one or two eggs, and z^3 has the two eggs shown in the figure. I have observed in all six cases in which eggs were developed in z^1, and in one of these the egg was found in the recently formed brown body. It appears to me that z^1 may occasionally give rise to true eggs; but I have observed no single case in which an embryo is formed in that zoœcium. It is probable that the eggs shown in fig. 16 would (one or both) have developed, and that the zoœcium (z^3) which contains them would have become fertile.

In another case the zoœcia of a comparatively old colony had formerly contained brown bodies and polypides. All the latter had, however, degenerated (probably simultaneously), forming a series of recent brown bodies, in which the remains of testes can be detected. Each zoœcium thus contains an old brown body, and a younger, half-formed brown body; and, as is commonly noticed in such cases, new polypide-buds have been developed to take the place of the old polypides. One of these, already recognisable as a young polypide, was found to possess an egg similar to that shown in fig. 15. The colony having undergone a complete process of degeneration, it is not surprising to find that this egg is developed in a zoœcium which is younger than either z^2 or z^3.

It is obvious from the foregoing statements that the first appearance of the eggs differs in different cases. Either one or two eggs may be present, and they may occur with or without a testis. In one case I have found them in all the first three zoœcia. More commonly I have detected an egg in only one zoœcium in a colony. The diameter of the egg is about 14 μ (average of four measurements). This is not very different from the measurement (17·6 μ) which I have recorded (6) for the egg of Crisia, and the correspondence is even closer if we take the largest Lichenopora egg (16 μ) of which I have a record.

In a single case I have found an egg-like cell, 9·6 μ in diameter, at the growing margin of a colony. This cell corresponds closely in appearance and position with the eggs which I have described in the growing-points of Crisia. I do not, however, feel by any means sure that this condition really represents a normal phase of the development. Some of my other preparations suggest that the egg is more probably differentiated in situ from the outer layer of a young polypide bud. Moreover the brown body with which the developing embryo is associated implies the loss of a polypide in the fertile zoœcium. One might therefore expect, a priori, that the egg would make its appearance in a bud formed to replace a pre-existing polypide, and not in a part of the growing edge where no polypides have yet become mature.

I have found cells which I regard as eggs in thirty-eight colonies. In most cases I have been unable to detect more than a single egg in a colony, although in some cases two or even three eggs may occur in a single zoœcium. The egg-bearing zoœcium is commonly z^2 or z^3, but in several colonies the egg occurred in a younger zoœcium. In one or two of the latter cases either z^2 or z^3 was already preoccupied with an embryo of its own. The observations I have noted down with regard to the occurrence of these cells point strongly in the direction of their being eggs. They do not occur promiscuously in all the zoœcia. Should a colony have been successful in developing an embryo no further trace is ordinarily seen of eggs. In young colonies which have no embryo these cells are of common occurrence, and in very young colonies they are found in just those zoœcia which might be expected to produce them. At the same time the results are not perfectly consistent, and I can best interpret them by assuming that there is considerable variation with regard to the first origin of the eggs. This appears to me to be particularly the case with young colonies in which the development has not been quite normal, whether in consequence of the degeneration of the polypides or from other causes.

Stage B.—Formation of the Follicle, &c.

Although the embryo and its investments can be recognised with certainty at this stage, it is by no means easy to make out all the details.

Fig. 19 shows a part of the polypide, with the embryo, of a colony which possessed functional polypides in z^1, z^2, and z^3, and had two other zoœcia which had reached the stage at which the polypide-bud becomes obvious. The fertile zoœcium is either z^2 or z^3; it possesses a brown body and a small testis, neither of which is shown in the section figured. The body-cavity contains some ripe spermatozoa, some of which are seen in the immediate neighbourhood of the embryo. The latter consists of several nuclei embedded in a mass of protoplasm which lies in a definite cavity. This is bounded by a layer of cells which may be termed the follicle.

Fig. 22 is from z^2 in an older colony which had four old and one half-grown polypide, and two buds. No brown bodies could be distinguished in this case—a very unusual phenomenon in colonies of this age, although quite common in older colonies. The four mature polypides are, however, conspicuously old, and their alimentary canals have solid contents which are probably the missing brown bodies. This question will be considered later. The investments of the embryo are rather more definite than in fig. 19, and it is more difficult to make out with certainty the limit between the follicle and the embryo. At least five of the central group of nuclei clearly belong to the latter.

Fig. 21 shows a transverse section of the follicle and embryo at a stage between the last two figures. The colony measured ·40 by ·21 mm., and possessed three polypides only, of which either z^2 or z^3 was fertile. The follicle is somewhat thicker than in the cases previously considered, and possesses more than one layer of nuclei. A brown body is present, as usual, in the fertile zoœcium.

Fig. 20 is from a colony which possessed three polypides only, each of them being accompanied by a brown body. The fertile zoœcium is almost certainly z^2, but if not it is z^3. The structures connected with the embryo show a distinct advance in development. The follicle is more fully formed, and there is also present an elongated group of nuclei which is easily recognised as the "suspensor" of the next stage.

My notes show a perfectly consistent result with regard to the age of the colony at which this stage is passed through. This is brought out by the following table:

Embryos in Stage B.

	No. of colonies
Colonies possessing three polypides only . . .	16
,, ,, four or five polypides . . .	3
Colony larger, the fertile zoœcium being younger than z^2 or z^3	1
Sections not good and result uncertain . . .	5
Total number of colonies examined . . .	25

It is clear that Stage B is most commonly passed through in colonies which contain three fully developed polypides, with perhaps one or two young buds in younger zoœcia. The measurements of the colonies are remarkably uniform at this stage, the total length of the colony (in section) ranging from ·40 to ·48 mm.

It may be noted that although most of the above colonies were in the three-polypide stage, it does not follow that any colony containing that number of polypides will also contain an embryo in Stage B. We have already seen that a considerable number of these colonies contain eggs. In some cases, moreover, it appears that the polypides may be well formed in z^1—z^3 before any of these zoœcia undergo a histolysis of their polypide, or at least before the polypides of z^2 and z^3 experience that fate. Now since the occurrence of a brown body is all but universal in all fertile zoœcia, of whatever age, and probably occurs in all fertile zoœcia which are developing normally, we can hardly expect to find an embryo in any z^2 or z^3 in which the first polypide of the zoœcium has not had time to degenerate and to be replaced by a new one. The brown body which is found in connection with the developing embryo is alluded to in this paper as the fertile brown body.

The exact origin of the cells forming the embryonic investments could not be made out, but I feel confident that they are not formed as a modification of an ordinary polypide-bud. They appear to me to be differentiated in situ from the cells of the funicular tissue which surround the egg, aided probably by the cells which form the capsule of the fertile brown body. On two occasions I have, however, found young colonies in which the appearances could be interpreted by supposing that a polypide-bud was concerned in the production of the structures connected with the embryo. I have come to the conclusion that such a view would be erroneous; and I regard the colonies in question as really belonging to Stage D, although they have reached that stage rather precociously.

Stage C.—"Suspensor Stage," with Brown Body and Polypide.

I have ventured to call this stage by a name taken from the development of the embryo in a flowering plant, in consequence of the resemblance of a cord of cells supporting the embryo to the structure known to botanists as the suspensor. By this term I refer to the inner cord of cords (figs. 23, 24) which is contained in an investment continuous with the cells which immediately surround the embryo. These cells, which enclose the embryo, may be termed the "follicle" (fig. 24).

The whole set of structures which are developed in immediate relation with the embryo form the "embryophore," a structure which has been seen at a later stage of development in fig. 11 (cf. p. 94).

The general appearance of the embryo, with its embryonic membranes, at this stage, may be gathered from fig. 10, representing part of the fertile polypide in a colony which is about ·67 mm. long. The colony possesses in all about nine brown bodies, one of which is accompanied by a polypide-bud, and the rest are in zoœcia which have a functional polypide: that is, about nine zoœcia are fully formed, and of these the third (probably) is fertile. The fertile polypide, like some of the others, has a testis, from which the embryophore hangs down freely into the body-cavity. The fertile brown body occurs in the immediate neighbourhood of the embryo. This stage is clearly not very different from fig. 20, which has already been described.

Fig. 23 is from a somewhat younger colony (measuring ·53 by ·32 mm.). Five zoœcia are here fully formed, with brown bodies and polypides, and of these z^2 is fertile. The outline of the fertile brown body is projected from other sections on to the figure. In this case the fertile zoœcium has no testis, although that organ is present in some of the other zoœcia. The suspensor is, as is frequently the case, curved in such a way as to keep the follicle in close contact with the brown body; but this curved condition may be merely the position assumed during the retraction of the polypide. The suspensor obviously consists of more than a single row of cells. Its investing cells are intimately connected with a layer which forms a kind of capsule round the fertile brown body. The follicle consists of a protoplasmic mass containing two more or less distinct layers of nuclei, covered externally by a few more flattened nuclei, which probably belong to an external flat epithelial layer.

Fig. 24 (from a colony ·48 by ·45 mm.) shows the embryo and its accessories with unusual clearness. The fertile zoœcium is z^3. The section suggests that the suspensor is really a tube, and that the two rows of nuclei are on opposite walls of its lumen. This is borne out by other sections, and particularly by transverse sections. The lumen can sometimes be made out; but it probably does not always exist as anything more than the finest passage.

Fig. 25 represents an unusual condition, in which two embryos are developing in the same follicle. The colony was about ·56 mm. long, and z^2 was fertile. I have found two perfectly similar cases belonging to the next stage (Stage D), and it is quite possible that the phenomenon is not very uncommon. After the commencement of embryonic fission, at any rate, it would be quite impossible to say whether one embryo or two were originally present. It will be remembered that two eggs are sometimes borne by a single polypide (fig. 16). It may fairly be inferred that under certain circumstances both eggs may develop.

Some idea of the general appearance of the embryo at Stage C may be obtained by the inspection of figs. 23, 24, but it is often by no means easy to make out the structure of the embryo, or indeed to be sure how many nuclei belong to it, and how many may have been derived from intrusive follicle-cells. I have previously pointed out (6, p. 215) that the follicle-cells in Crisia do push their way in among the blastomeres; and I have obtained a good many preparations of Lichenopora in which this process appears to be taking place. I can say no more with regard to the structure of the embryo than that it is a mass of protoplasm containing nuclei; and I am unable to say whether, at this stage or even later, these nuclei are arranged with any relation to embryonic layers.

Whatever doubt may exist with regard to the exact details in Stages A and B, there cannot be the slightest doubt that the "suspensor stage" is a perfectly normal phase of the development. I have examined some thirty-eight colonies in which the suspensor was present in the condition described above. With hardly any exception, I have found this stage in colonies which measure ·40—·68 mm. in length (in sections) and ·30—·55 mm. in breadth. The fertile zoœcium may or may not have a testis, and I cannot lay down any general rule on the subject.

In two or three observed cases more than one zoœcium was fertile. The only other variation which need be recorded, although it might equally well have been considered under the next stage, is the occasional occurrence of a young polypide bud in a zoœcium which has reached the normal suspensor stage, and has recently lost its polypide by degeneration.

In some cases this bud appears simultaneously with the development, in other zoœcia, of buds which are clearly formed in consequence of the degeneration of the polypides. This is a case of a phenomenon repeatedly noticed, in which an epidemic of degeneration attacks all the polypides of a colony simultaneously. In a large number of cases this probably has no permanently injurious effect on the colony, as new polypide buds are developed in all the zoœcia, even while many of the parts of the degenerating polypides are still distinctly recognisable. I am convinced that the simultaneous degeneration of the polypides is often responsible for the degeneration of the embryo; and in some of the above-mentioned cases in which a young bud occurs in the fertile zoœcium, the embryo would probably have ultimately become involved in the brown body This is borne out by examination of a colony, ·51 mm. long by ·37 mm. broad, in which all the polypides had moderately recently degenerated. Polypide-buds are being developed to replace them, and an advanced bud is present in the fertile zoœcium. This bud possesses an egg, although eggs could not be found in any of the other zoœcia. The inference is that the egg was destined to replace the (degenerating) embryo present in the same zoœcium.

Should the buds become functional polypides with sufficient rapidity, I see no reason why the embryo should not survive. It is possible, on the contrary, that the occurrence of a young polypide-bud together with a degenerating polypide in the fertile zoœcium (Stage C) always implies that the embryo has already commenced to degenerate. I am induced by the study of one series of sections to think that this is not necessarily the case. The fertile zoœcium contains a polypide which is clearly young. The brown body is large; near the suspensor it is distinctly old, while at the opposite end it is as distinctly newly formed. The embryo and its accessories are normal in character. This case suggests a fusion of the original fertile brown body with a new one formed by the degeneration of the fertile polypide. A new polypide has, however, been developed in the same zoœcium, and the health of the embryo does not seem to have been in any way affected by these changes.

It is impossible to avoid being struck with the very remarkable similarity between the stage which has just been described in Lichenopora and a phase in the development of Plumatella, as described by Kraepelin (11; see especially pl. ii, figs. 65—68). The figures given by that observer might almost do duty for Lichenopora, except that the "suspensor" is rather longer and the "follicle" less complicated than in that genus. The "suspensor" of the fresh-water form is, moreover, attached to the body-wall instead of being borne by a polypide or by a brown body.

Kraepelin and Braem (4) have investigated the origin of this structure in Plumatella, and they both arrive at the conclusion that the structure which supports and contains the egg is a polypide-bud. Braem, indeed, dissents from the statement of Metschnikoff (13), by whom the structure was first described, to the effect that it is an ordinary bud; and points out certain differences between it and a bud which is destined to grow into a polypide. But the embryophore in Phylactolæmata would appear to be a two-layered bud, and the part which corresponds to my "suspensor" is simply the inner or ectodermic layer of that bud.

Braem further calls attention to the occurrence, in the morula stage, of certain nuclei which are smaller than those of the segmentation spheres. These may possibly have some relation with the smaller nuclei which I have myself noticed in Lichenopora during Stage C.

The earliest changes undergone by the fertilised ovum of Plumatella, according to Kraepelin's account, appear to be extremely similar to those which occur in Cyclostomes. In Plumatella, as in Lichenopora, a time arrives when the embryo is a sharply marked spheroidal mass supported by the end of the "suspensor."

From this stage the development of the Phylactolæmata is very different from that of the Cyclostomata. In the former group the embryo enlarges, becomes two-layered and acquires a central cavity which is completely closed on all sides. One or more polypide-buds are invaginated from the two-layered body-wall into the central body-cavity, and the embryo finally escapes as a larva provided with a larger or smaller number of polypides. In Lichenopora, on the contrary, the morula enlarges while retaining an embryonic, undifferentiated character in its cells. It then undergoes repeated fission, and the definitive secondary embryos produced in this way then acquire a two-layered character which is strikingly suggestive of the Phylactolæmatous embryo.

In spite of the extraordinary resemblance between the "suspensor stage" of Lichenopora and that of Plumatella, I have not been able to convince myself that the result is arrived at, in the former, in the way described by Kraepelin for the latter. The structure of the embryophore in Lichenopora would indeed be most easily explained by supposing the "suspensor" to represent the ectodermic part of a bud, but I have not been able to obtain any evidence that this is the case. There are, however, instances among marine Polyzoa where a new polypide-bud is formed in the immediate neighbourhood of the brown body (cf. 7, p. 140), instead of in close connection with the body-wall. It is possible that the Lichenopora suspensor may belong to this little-understood class of polypide buds, but I must emphasise the fact that I have no internal evidence tending to prove that it is a bud.

Were it not for the very marked similarity of the early stages of the two groups there would be little reason for anticipating an agreement in detail between Cyclostomata and Phylactolæmata, particularly as the details of Lichenopora are so different from those of Crisia, another Cyclostome.

Kraepelin (10) has, moreover, urged a series of reasons for believing that the Ctenostomata, among the marine Polyzoa, are the nearest allies of the Phylactolæmata. As I have made no special study of the latter group, I have arrived at no conclusions of my own with regard to their affinities, but the details of their early developmental phenomena appear to me to be sufficiently similar to those of Cyclostomes to make it worth while to call special attention to the fact.

One other suggestion may be made with regard to the

Phylactolæmata. In spite of the admirable researches of Braem (4) and of Kraepelin (11), the mode of the first origin of the statoblasts cannot be said to be beyond doubt. Although in the absence of any observations of my own on this point I do not wish to commit myself to this view, it appears to me not impossible that some connexion exists between the formation of the statoblasts and the process of embryonic fission. The natural view of older writers that the statoblasts are winter eggs may hereafter prove to have had more truth in it than has recently been supposed. Verworn (21), indeed, has attempted to resuscitate the older view, although his results have not commended themselves to later inquirers. Braem's description and figures in particular lend some colour to the suggestion that the formation of the statoblasts may be a modified form of embryonic fission. For fear of being misunderstood I must, however, repeat my statement that I do not consider that I have sufficient grounds either for accepting or for rejecting this suggestion.

We may now return to the consideration of Lichenopora, and we pass to—

Stage D.—Suspensor Stage, with Definitive Fertile Brown Body.

The normal occurrence of this stage is supported in the clearest possible manner by my sections.

Fig. 28 represents a typical case. The colony measures ·43 by ·37 mm., and it contains six brown bodies, one of which is fertile, while each of the others is accompanied by a polypide. No other zoœcium is sufficiently old to have a polypide, and the colony is one in which this stage of development has been reached comparatively early. z^2 is fertile ; it contains a brown body, from which the embryophore hangs down into the zoœcium. The brown body is not directly connected with the orifice of the zoœcium, although it is now situated near the upper end of the body-cavity.

Fig. 27 (Pl. 9) is probably a somewhat later stage, in which the brown body has come close up to the layer of body-wall which is invaginated at the orifice of the zoœcium. The colony is larger than the preceding specimen, measuring ·69 mm. by ·51 mm., and possessing at least twelve brown bodies. The fertile zoœcium is here neither z^2 nor z^3, but a younger individual of the colony. The figure shows that the suspensor and the follicle are still easily recognised. The brown body has, however, acquired a much more definite capsule of cells than it had in the previous stage. This capsule is not so fully formed in the somewhat earlier condition shown in fig. 28; but in fig. 27 it has become extremely definite. Its protoplasm and its numerous nuclei take up hæmatoxylin with an avidity that shows that the tissue is actively growing, and it is indeed this tissue which appears to be, somewhat later, closely concerned with the development of the trumpet-shaped aperture of the ovicell. The embryo is distinctly larger than it was in Stage C.

Fig. 26 represents the embryo of another colony (in Stage D), which was slightly younger than that from which fig. 28 was taken, as it had only five brown bodies and four polypides; z^2 was fertile. The embryo in this case possesses a peripheral layer of nuclei, which surround a central group of three nuclei. I am unable to say whether there is any morphological difference between the central group and the others.

It might be supposed, a priori, that Stage D originates by the degeneration of the fertile polypide in Stage C. I have distinct evidence that this is the case. The polypide is seen to begin to degenerate, and the brown body already present begins to become confluent with it. The old brown body and the degenerating polypide become surrounded by a common capsule of cells. The fertile brown body of Stage D hence differs from that of Stage C, inasmuch as it contains the remains of what was the fertile polypide in the earlier stage, in addition to the original brown body. Should development proceed normally, no further polypide is developed in the fertile zoœcium, and the brown body moves to its upper end, and eventually comes into close relation with what was formerly its orifice.

The size of the colony during Stage D is in most cases from

·50 to ·70 mm. in length, and from ·35 to ·55 mm. in breadth, although these limits may be passed in either direction. The average of eight cases in which I was able to estimate the length of the colony (in sections) was ·53 mm., and the average breadth (twenty-two cases) was ·44 mm. The entire colony (fig. 4) might well have been in this stage, although still older colonies are commonly in Stage D, as may be shown by counting in the sections the number of their fully formed zoœcia.

The distinction between Stages C and D is obvious enough as regards the embryo and its connected structures. But the change from one stage to the other implies no more than the degeneration of a polypide and its alteration into the condition of a brown body. We should not, therefore, expect to be able to distinguish by external features alone between colonies in the two stages. This is all the more difficult, since the period in the growth of a colony which corresponds with a particular stage in the embryonic development varies within wide limits.

Stage E.—**Disappearance of the Suspensor and Enlargement of the Embryo.**

This stage immediately precedes the beginning of embryonic fission. Fig. 29 represents an embryo found in a colony measuring ·56 mm. in breadth. The fertile zoœcium was almost certainly z^3. The embryo has unmistakably increased in size compared with the embryos in the previous stage. While that of fig. 27 measures 28 μ in greatest length, that of fig. 29 measures 70 μ, which is exactly two and a half times as much. Other changes have also taken place. The suspensor has ceased to be a definite structure, and the embryo has moved towards the brown body, so as to take the place originally occupied by the suspensor. The follicle is still distinct in this series of sections, but the section figured only cuts its edge. The first indication of the commencement of this stage is given by the longitudinal elongation of the embryo, which then begins to extend beyond the original limits of the follicle into the stalk connecting the latter with the brown body. We have seen that the suspensor is potentially a tube, and it appears to me that the cells of the suspensor lose the regularity of their arrangement, and that the embryo probably passes into the midst of the altered cells of the suspensor, perhaps by widening out the original lumen. There are, however, some reasons for thinking that the suspensor may be pushed to one side during the elongation of the embryo, and I cannot pronounce definitely on this point. In any case the suspensor ceases to be recognisable shortly after the close of Stage D, and the embryo invariably elongates so as to approach the fertile brown body with its distal or upper end. Towards the end of Stage E the embryo may have completely left its original follicle, and may lie entirely in the place of the original suspensor.

I have found but few colonies (not more than seven or eight) in this stage; but those few formed a series completely bridging over the interval between Stages D and F. The length of four of these embryos was 30, 53, 70 (fig. 29), 72 μ respectively. The average transverse diameter of the colonies measured in Stage E (seven cases) was ·562 mm., the extremes being ·48 (·77 long) and ·62 mm.

The embryophore shown in fig. 29 occupies a position in the zoœcium exactly like that of the corresponding structure in fig. 27; that is to say, the cells surrounding the brown body are in contact with an invagination of the body-wall at the orifice of the fertile zoœcium. The invagination is, however, considerably deeper in the zoœcium from which fig. 29 is taken than in that shown in fig. 27. A thin layer of cells, not present in the earlier stage, now stretches across the mouth of the invagination from one edge of the rim of the zoœcium to the opposite edge.

I regard this layer as the remains of the calcareous film which occludes the mouth of the fertile zoœcium (cf. pp. 86, 87). The smallest entire colony in which occlusion was just commencing measures ·77 mm. in transverse diameter, whereas the largest colony in Stage E (measured from sections) was ·62 mm. broad. This difference is quite unimportant, partly because of the variation in the size of colonies at the same stage of embryonic development, and partly because, in comparing the measurements of entire colonies with those of sections, something must be deducted from the former series of measurements. The calcareous lamina which borders the entire colony is usually not very apparent in sections, or may become somewhat crumpled. In correlating the entire colonies with the sections it will be well to notice that sections of colonies in Stage E give no evidence of an aperture belonging to the ovicell.

Special attention may here be directed to the fact that a brown body may often be seen in the occluded zoœcium of an entire colony. That brown body is of course the fertile brown body; and the fact that it may be visible in a dry colony when other zoœcia are not seen to possess a similar structure is of course due to the constant occurrence of the fertile brown body near the original orifice. If brown bodies are present in the other zoœcia, they are usually placed at the end of the cæcum of the stomach, and are consequently deeply placed in the colony, in a position where they cannot be seen.

The fertile zoœcium to which fig. 29 refers has yet one further point of interest. At a short distance below the embryo its cavity is completely divided by a septum which passes transversely to the long axis of the zoœcium. This septum, which is commonly noticed in, and is indeed probably a normal feature of, later stages as well, is probably calcareous during life. It cuts off the proximal, empty end of the zoœcium from the distal end which contains the embryo.

Stage F.—Commencement of Embryonic Fission.

This stage is by far the most important of all, as demonstrating the fundamental identity of the developmental processes in Crisia and Lichenopora. Fortunately there is no stage in the latter in which my evidence is clearer than in this one. I have obtained some twenty-seven series, any one of which by itself would have been almost sufficient to prove the occurrence of embryonic fission.

The youngest figured (fig. 31) shows an embryo at the very beginning of this stage. The figure is taken from a colony which measures ·83 mm. in transverse diameter. The diameter of the embryo is $45\,\mu$, but it must be remembered, in comparing it with fig. 29, that it is cut transversely to its long axis. The embryo is now provided with a clear outer layer of nuclei. The preparation for fission is indicated by the tendency of the centrally placed nuclei to arrange themselves in groups or in regular series, and by the appearance of the small slits or vacuoles marked **S** in the figure.

Fig. 35 is a longitudinal section through an older embryo, in which fission has definitely begun. The brown body (not cut in this section) is unaltered, and the embryophore still hangs down freely into the fertile zoœcium. The embryo is no longer a rounded mass, but it consists of an irregular series of pieces, which show clear evidence of being engaged in fission. The embryonic protoplasm and nuclei take up hæmatoxylin or borax carmine with great readiness; and there can be no doubt from their appearance that they are engaged in active growth. The pieces into which the embryo divides at this stage have no very regular arrangement; but, as will be seen from figs. 33—35, the embryonic fragments are at first arranged irregularly round a more or less definite central space. The appearance of figs. 31 and 33 suggests that a kind of vacuolation of the central part of the primary embryo takes place, and that the embryonic cells thereby become dissociated into a series of peripherally situated groups. In tracing an embryo, such as that shown in fig. 34, through a series of sections, the parts of the primary embryo, where not completely separated from one another, are seen to be connected in the most irregular manner. Sometimes they are united with one another laterally; sometimes an embryo is united with its vis-à-vis by a diagonal connection passing across the centre of the whole mass; sometimes a piece of embryonic tissue is prolonged into several finger-like processes, not unlike those of the primary embryo of Crisia (6, pl. xxiii, fig. 11). There is, in fact, no regularity or definite method in the breaking up of the primary embryo of Lichenopora; and every primary embryo examined at this stage differs in these respects from every other primary embryo.

The main fact is, however, the same. The embryo at this stage has ceased to be a coherent structure, and has resolved itself into a number of complicated lobes of embryonic tissue, some of which have actually become separate from their neighbours, and some are ready to become separate at a moment's notice.

Even now a differentiation of two kinds of embryonic cells is not necessarily apparent. In fig. 34 there is some indication of the occurrence of inner cells, which are probably destined to give rise to the inner layer of the secondary embryo. Other preparations do not show any such clear differentiation.

The general features of this stage are very characteristic. The fertile brown body is invariably present, and it is situated near the upper end of the fertile zoœcium. The embryophore is shaped something like the lower (closed) end of a test-tube, and it still hangs down freely into the body-cavity of the zoœcium. The embryo or its parts usually lie in spaces which probably appear in the surrounding cells of the embryophore, by a process of vacuolation of the protoplasm. The aperture of the ovicell is beginning to develop.

The present is a convenient place to raise the question of the function of the suspensor. It might have been supposed that it was a tube carrying spermatozoa to the egg, if it had not been for the fact that the suspensor is formed after the development of the embryo has commenced. The time at which one would expect fertilisation to take place is the stage before the embryonic investments are completed, when the egg is hardly separated from the fluid of the body-cavity. At this time spermatozoa are commonly found in the neighbourhood of the egg or of the embryo in its early stages (cf. fig. 19).

The function of the suspensor appears to me to be probably connected with the nutrition of the embryo. During Stages C and D the suspensor remains quiescent; but it probably contributes to the formation of the mass of protoplasm in which the secondary embryos are supported from Stage F onwards.

It may be noted that the embryophore may now contain egg-like cells (fig. 34, *a*), which are similar to the giant-cells that I have described in Crisia. I have never found these cells showing the slightest evidence of being really eggs; whereas the dividing primary embryo is quite unmistakable at this stage. I therefore attribute a purely subsidiary part to these cells, and I do not believe that they have any direct share in the development of embryos. I have not found giant-cells during the earlier stages of the development.

The aperture of the ovicell commences to develop at this stage, as is distinctly shown by the sections. We have seen that the fertile brown body of earlier stages is surrounded by a deeply staining mass of cells which may be in immediate contact with an invagination of the body-wall (fig. 27). In this stage the condition closely resembles a stage which I have described in Crisia (6, pl. xxiii, fig. 12), except that the latter has no brown body. The tubular aperture of the ovicell of both Crisia and Lichenopora is closely connected at its base with the deeply staining mass of cells or its derivatives. In the latter genus these cells grow towards the distal surface of the zoœcium which contains them, just as in Crisia they grow towards the distal surface of the ovicell. A cavity next appears in the mass of cells, immediately above (distal to) the brown body. This cavity, which is at first merely a series of vacuoles, is usually perfectly definite near the brown body, and may extend as a space, which appears crescentic in a longitudinal section, halfway round the brown body. Tracing this space upwards, it becomes less definite, and it extends into the base of the tubular aperture of the ovicell. A transverse section of the "aperture" at this stage usually shows an external thin, body-wall which surrounds the part of the body-cavity which extends into the tube. The centre of the transverse section is occupied by a solid mass of cells, whose diameter is about half of that of the entire tube. Lower down the solid mass becomes excavated by a lumen which becomes continuous with the cavity which occurs near the brown body. Below the latter the cavity passes into an irregular space, traversed by strands of nucleated protoplasm, which thus divides the space into smaller cavities in which the derivatives of the primary embryo lie.

I believe that the processes which take place at this stage are practically like those which occur in Crisia. The whole mass of the embryophore becomes highly vacuolated, and is thereby transformed into a series of more or less definite spaces in which the secondary embryos will lie. These spaces become more definite near the aperture of the ovicell. In the next stage I have often observed mature embryos in the tubular aperture, obviously on their way out to the exterior.

Very few of the colonies which I have observed in this stage have a smaller transverse diameter (in sections) than ·60 mm. The extreme measurements I have noted are ·45 mm. and 1·04 mm. The average of the measurements of the transverse diameter of twenty-four colonies in this stage is ·747 mm. There is great probability that Stage F corresponds with a condition of the entire colony in which the fertile zoœcium is occluded, and the very beginning of the formation of the roof of the ovicell is taking place.

Stage G.—**Ovicell well developed.**

The Production of the First Brood of Secondary Embryos is at its Height.

Fig. 11, which shows a characteristic horizontal section of a colony in this stage, has already been described (p. 94). The fertile brown body still remains compact and conspicuous; and it occurs in the immediate neighbourhood of the trumpet-shaped aperture of the ovicell. During this stage it is, however, no longer found in the fertile zoœcium, which in the section drawn (fig. 11, z^2) is seen to contain some secondary embryos at its upper end. The cavity of this zoœcium has become continuous with that of the ovicell in the manner previously described (p. 87), and the brown body has passed out into the cavity of the ovicell proper. The brown body still forms a kind of centre from which the lobes of the embryophore start; and its position at the base of the aperture of the ovicell materially aids in the discovery of that structure in the series of sections.

The secondary embryos do not lie freely in the cavity of the ovicell, but are still contained in a protoplasmic reticulum, which is the modified embryophore. The latter has largely increased in size with the commencement of embryonic fission, and has become branched, its lobes extending round the zoœcia, which pass through the cavity of the ovicell (cf. fig. 6). The general appearance of a young embryophore in this stage in an entire colony is shown in fig. 12.

The most striking difference between the development at this stage and that of Crisia consists in the absence of the primary embryo of the latter, and it often requires close examination to prove that fission is still proceeding in Stage G. Such, however, is undoubtedly the case, although there is no coherent primary embryo left at this period.

Fig. 37 illustrates the manner in which the number of secondary embryos is increased during Stage G. An embryo similar to the smallest ones seen in fig. 11 is dividing transversely. The external and internal layers, which are so characteristic a feature of the Cyclostome embryo, are now well marked, and the inner layers of the two halves of the dividing embryo are completely separated from one another. The longest diameter of the embryo figured is 56 μ.

In some colonies it is easy to demonstrate the occurrence of this process, and there are many cases where its recent occurrence may be inferred from the fact of two small embryos lying close together in a position which suggests that they have recently separated from one another. It is obvious that if the embryo shown in fig. 37 had been cut transversely to its longest diameter it would have been by no means easy to be sure that fission was taking place. Another difficulty in proving the occurrence of this process is due to the fact that the normal development of a secondary embryo which is not going to divide further may, in section, appear very similar to the dividing embryos. The young definitive secondary embryo, which is destined to form a single larva, is a small ovoid mass of cells consisting of a well-defined external layer and an equally clearly defined inner layer. One wall of the embryo becomes invaginated to form the larval "sucker" (cf. 6, pl. xxiv, figs. 22, 23). This process is seen to be taking place in some of the embryos shown in fig. 11.

It is not always easy to distinguish between cases in which the sucker is being invaginated and cases of embryonic fission. One difference may, however, be pointed out between the two processes. The invagination of the sucker never results in the division of the inner layer of cells into two separate portions, nor does this layer even appear divided in a section of the embryo. Fission, on the contrary, results in the complete separation of the inner layer into two halves, one of which belongs to each of the products of division. In some cases the ovicell contains larger and more irregular masses of embryonic tissue. These probably give rise to more than two secondary embryos.

I have satisfied myself of the normal occurrence of the process of fission, as described above, in a number of colonies; and I believe that the process continues, in healthy colonies, for a considerable time. I have not made preparations of colonies of all the larger sizes; and I am not able to say what is the upper limit of size reached during this stage. The largest colony among my sections, in which the embryonic structures are in Stage G, measures 1·60 mm. in diameter, and the smallest measures ·80 mm. I have, however, found mature larvæ in somewhat abnormal colonies which measure only ·56 mm. in diameter. The average diameter of fifteen colonies measured is ·93 mm.

Although the fertile brown body passes into the cavity of the ovicell during this stage, it is still possible to obtain satisfactory evidence of the identity of the fertile zoœcium in well-orientated horizontal sections. If an ordinary zoœcium loses its polypide without developing a new bud to take its place, the previous existence of the polypide is shown by the occurrence of a brown body in the zoœcium. There is no way by which the brown body can be got rid of except through the agency of a new polypide. In the fertile zoœcium, on the contrary, the brown body passes upwards to the neighbourhood of the orifice (beginning of Stage D), and the basal end of the zoœcium is left completely empty. In examining the base of colonies in the later stages of embryonic development, one of the oldest zoœcia is usually found to be empty; and it may safely be inferred, in most cases, that this was the fertile zoœcium. z^1 commonly possesses a functional polypide even during Stage G; and either z^2 or z^3, as the case may be, is usually in the same condition. The other one of these two is, however, usually empty. In some cases the lower half of the fertile zoœcium is seen to be cut off from the upper by a transverse septum, as described in Stage E (see p. 108). It is probable that this is the normal arrangement, and that the function of the septum is to restrict the embryos to that part of the fertile zoœcium which is on a level with the rest of the ovicell.

The active production of secondary embryos during this stage seems to have a well-marked effect on two sets of structures in the rest of the colony; namely, on the testes and on the brown bodies.

Colonies which are in the earlier stages (A—C) have testes in some of their zoœcia in the great majority of cases. There can be no doubt that the colony of L. verrucaria is ordinarily hermaphrodite; and, as we have seen, a testis may or may not be present, with the embryo, in the fertile zoœcium. Prouho (18) has recorded some extremely interesting observations on the succession of the polypides in Alcyonidium duplex; in which a polypide which produces spermatozoa degenerates into the condition of a brown body, and is succeeded, as a normal part of the life-history, by a polypide which produces an ovary. It is quite possible that phenomena of an analogous nature may occur in Lichenopora, although the details are obviously different. If continuous observations of the zoœcia of a young living colony could be made from day to day, it might be possible to show that the apparent irregularity in the production of testes did really follow some definite law. The only general statements that I can make are to the effect that testes may be present during any of Stages A—G; but that while they are normally present in the younger stages they are much less common in the older ones. Thus of nineteen colonies in Stage F, in which I have noted this particular point, seven had well-developed testes, while twelve had none at all, or only slight remains. In some cases in which no functional testes occur in the colony, the former presence of these bodies can be proved by the presence of their degenerating remains in the recently formed brown bodies. Of ten colonies in Stage G, in which I have noted the presence or absence of testes, only one had well-developed male organs; while in nine none were present, or at most the last remains of testes which had previously been active.

This seems to indicate that the energies of the colony are given as much as possible to the production of embryos during Stage G, and the development of spermatozoa is meanwhile suppressed.

It has already been pointed out that the healthy development of the embryos is dependent on the functional activity of the polypides. Were these to degenerate to any great extent during Stage G, it is probable that the development of the embryos would be interfered with. This is borne out by the examination of various colonies in which degeneration is actually taking place, and even more strikingly by the character of certain colonies in which the embryonic development has clearly been modified by conditions of insufficient nutrition. These are colonies in which all or most of the polypides have degenerated. The ovicell should be in Stage G, and it has actually succeeded in producing perhaps three to six mature embryos. But instead of finding the ovicell crammed with embryos of all ages intermediate between these and the youngest secondary embryos, the ovicell contains nothing in addition to the mature embryos except a very few small fragments of embryonic tissue. It may be concluded that these are not colonies in which the production of secondary embryos is approaching an end, from the fact that the ovicell is small and the embryophore is compact and unbranched.

Some colonies in Stage G which have no polypides, or only one or two polypides, appear quite healthy. It is probable that in these cases the production of embryos would have soon been injuriously affected, as a single polypide is probably insufficient for the nutrition of a whole ovicell full of embryos. This probability is increased when it is noticed, as is commonly the case, that many of the remaining polypides have quite recently degenerated; showing that the colony has had a full complement of polypides up to a very recent period.

The interdependence of the development of the embryos and the nutritive conditions of the whole colony is, however, nowhere more clearly shown than in the very remarkable fact that a large proportion of the older colonies have no brown bodies at all. A brown body is of course present in a zoœcium which has lost its polypide altogether, without developing a bud to replace it. But most of the zoœcia in a healthy colony —during Stage G, for instance—contain a polypide without any brown body. In the earlier stages, where the mass of embryonic tissue present in the colony is very small, polypides can degenerate, and new buds can develop to take their place without materially affecting the health of the colony. And as a matter of fact we do find that most young colonies contain polypides, degenerating polypides, fully formed brown bodies, and young polypide-buds, which are developing to take the place of the old polypides.

Were any extensive degeneration of the polypides to take place in any colony containing numerous embryos, it is probable that the colony could no longer bear the strain of producing its embryos. In a large proportion of the colonies in Stage G, there is no trace of the complete degeneration of polypides, there are no brown bodies, and there are no polypide buds, either in new zoœcia or in old ones. Even the increase of the size of the colony, by the formation of new zoœcia, thus appears to be retarded during the height of the formation of secondary embryos.

I have formerly brought forward certain evidence (7) tending to show that the formation of brown bodies is, to a large extent, a kind of excretory process, and it would be surprising if Lichenopora were altogether exempt from the necessity of forming brown bodies, whatever their function may be. The explanation of the apparent anomaly of the absence of these structures appears to me to be that parts of the alimentary canal degenerate during the functional activity of the polypide. A newly formed polypide has the inner border of the epithelial cells of its alimentary canal clear and sharply defined. Parts of the alimentary canal of old polypides are in the same condition, but certain parts of the cæcum of the stomach are in a very different state. The cæcum is coloured during life with the pigment which is so characteristic of parts of the alimentary canal in Polyzoa. In sections these parts contain a very small quantity of protoplasm, and consist principally of yellowish granules which are very similar to the granules which largely compose the brown bodies—that is to say, there is no very great difference between the latter and those parts of the alimentary canal which are pigmented during life. I believe that this implies that excretory substaces accumulate in the epithelium of the alimentary canal as the polypide grows older. In the case of the younger colonies the entire polypide usually atrophies in course of time ; but in the case of older colonies, in which it is of the utmost importance that every zoœcium should be contributing its share towards the nutrition of the ovicell, the excretory granules are discharged into the stomach continuously during the life of the polypide.

The facts are that the alimentary canal of these polypides usually contains solid substances which resemble fragments of brown bodies—that certain parts of the epithelium have no definite inner limit, but pass off into a cloud of granules which extend into the alimentary canal, and that the polypides are usually distinctly larger than those of young colonies. It is not always easy to get polypides (in sections) which are well orientated for the purpose of measurement ; but the measurements I have been able to obtain support the impression one receives from the inspection of colonies of different ages, that polypides in old zoœcia, which have no brown bodies, are distinctly larger than those commonly met with in younger colonies in which brown bodies are present in the same zoœcia. The significance of the larger size of these older polypides is, as I take it, that they have gone on growing after the time when degeneration would have taken place in a younger colony. The difference in the size of the polypides, at different ages of the colony, becomes very apparent in comparing the size of the brown bodies formed from their degeneration. The diameter of the fertile brown body in young colonies is about ·05 mm.; that of a fertile brown body belonging to a later generation (fig. 36), and formed in colonies in which large polypides are present, may be as much as ·09 or ·10 mm.

It is not always easy to decide, in a given case, whether the appearance of the alimentary canal implies the passage of a regular brown body into the canal or the partial degeneration of part of the epithelium. I have no doubt that the old brown bodies may be removed by passing into the alimentary canal of the newly formed polypide, as in Flustra and some other Polyzoa. Although one or even two brown bodies may occur in a single zoœcium of Lichenopora verrucaria, I do not think I have ever found more than two; and in most cases where a polypide has recently degenerated, one does not find an older brown body as well, even though the age of the colony makes it certain that there has been an older brown body. In some of these cases it is probable that the old brown body fuses with the degenerating polypide; but in others it may be that the old brown body has passed into the alimentary canal before the degeneration of the polypide again takes place. Some of my sections indicate the occurrence of this process, and the brown body seems to become attached to the wall of the stomach, and finally to pass into it. Nuclear structures and other parts of the brown body may in these cases occur freely in the lumen of the alimentary canal. Even without actual evidence of this kind it would almost be necessary to assume that this takes place; for in no other way do I see any explanation of the total absence of brown bodies in old zoœcia. In L. hispida the alimentary canal probably does not absorb the brown body, since a considerable number of old brown bodies occur in the proximal parts of the zoœcia (cf. p. 97).

The old polypides are not merely different in size from the young ones, but their several parts may be very differently arranged, during the retracted condition at least. The polypide of young colonies is like that of many other Polyzoa,—e. g. that of Alcyonidium as figured by Prouho (18, pl. xxiii, fig. 3). The short pharynx lies in the same line as the tentacles, and from its lower end a long œsophagus passes upwards (parallel with the tentacles) to open into the stomach (cf. fig. 19). The intestine and rectum continue the direction of the œsophagus, while the cæcum hangs down into the body-cavity parallel with the œsophagus. The apex of the cæcum is formed of more protoplasmic cells, but its sides contain the yellow granules which have already been mentioned. In the polypides of old colonies the whole of the cæcum is much swollen. Its apex has not altered its place, as is shown by the position of the group of protoplasmic cells. The upper end of the stomach or the region of the intestine is, however, commonly bent, so that the intestine and rectum may be directed downwards (away from the orifice of the zoœcium). The walls of the cæcum are at the same time greatly swollen and very granular. The lumen may be in places quite obliterated; and in any case, parts of the wall have no sharp inner boundary. The epithelium here shades off quite gradually into the granular contents of the stomach. This might be ascribed to defective preservation, were it not for the fact that other parts of the same sections are well preserved. But since, in many cases, no polypide-buds are being formed, and since none of the zoœcia are losing their polypides, I believe that this is an arrangement by which none of the zoœcia are rendered inefficient for nutritive purposes during the time at which there is the greatest strain on the energies of the colony.

The phenomenon which has just been described appears to be characteristic of old colonies (Stage G and later stages), but it is by no means restricted to these. Brown bodies are absent in a considerable number of colonies in Stage F, and rarely in earlier stages, sometimes occurring even in quite young colonies.

Whatever the fate of other brown bodies, the fertile brown body always occurs in a normal colony. I have not examined many colonies larger than 1·5 mm. in diameter, and I cannot say how long this structure remains compact. In one colony I found a fertile brown body which had almost divided into two, and I have also noticed a brown body of the second generation of embryos divided into a considerable number of fragments which are contained in the embryophore. In all the colonies I have examined in Stage G the fertile brown body is still compact.

The Occurrence of Second Broods of Embryos.

My observations on this part of the development are very incomplete, but I have noticed one or two facts of interest. There is no doubt that new broods do make their appearance in old colonies, and this may possibly indicate a second year's growth (cf. p. 89). That we are not here dealing with the first brood is shown by the large size of the colony, and by the fact that it possesses a large ovicell, which, however, contains no embryos.

I have not traced the first origin of the new brood of embryos. Fig. 36 is from a colony 2·2 mm. in diameter. No other primary embryo was found. Most of the polypides had enormous testes, and a few had egg-cells in a corresponding position near the apex of the cæcum. The embryo is carried by an embryophore supported by a fertile brown body, and corresponds in general with Stage D or E of the first brood. I have not been able to obtain a stage intermediate between the occurrence of eggs at the lower end of a polypide and the section figured. It does not appear to me probable that a normal suspensor is formed. The cells which surround the embryo are exceedingly loose and scanty, and the part of the embryophore between the brown body and the embryo is short and has but few nuclei. It seems to be growing down from the brown body to enclose the embryo. The very large size of the brown body is at once apparent, and judging by the condition of the other polypides of the colony it may be inferred that it has been formed by the degeneration of a large polypide (cf. p. 130). The investment of the brown body is well developed, highly protoplasmic, and full of nuclei.

Another old colony in which I have found the same processes taking place measured 3·4 mm. Its ovicell was well developed, and the polypides and testes were large. The ordinary zoœcia were not accompanied by brown bodies, and no eggs were found. In this case I discovered no less than eleven primary embryos, each of which was contained in an embryophore supported by a large fertile brown body. The evidence given by these cases is quite concordant. The brown body is as characteristic a feature of the second generation as it was of the first, and its presence indicates that the primary embryo is developed in relation with a polypide. Moreover the space in which the embryophore of fig. 36 lies is clearly a zoœcium. One of the eleven embryos of the larger colony has already given rise to a good many secondary embryos, and its brown body is broken up into fragments. The other ten have a compact brown body, and are in a condition which exactly corresponds with Stage F of the first brood. In all these primary embryos, fission has commenced and is going on vigorously. In one case the embryophore is beginning to grow out of the space in which it was produced into the general cavity of the ovicell.

The later development of the primary embryos of the second brood is thus identical with that of the first brood, but it is probable that the details of the early development are somewhat different. One of the noteworthy features of the case is the large number of zoœcia which may become fertile in a single colony.

I have unfortunately no other observations on this interesting part of the life-history of L. verrucaria. From the great clearness of the embryo in all the cases observed, it is quite possible that the earlier processes of the development would be more easily made out in the second brood than in the first brood.

General Conclusions.

The only genus with which Lichenopora can be compared, as regards the embryonic development, is Crisia. In no other case have the early processes been described at all.

In Crisia certain zoœcia take on the character of ovicells. A polypide-bud makes its appearance in the young ovicell while the latter is at the growing-point of the branch, and is not externally marked out in any way as an ovicell. The bud becomes connected with an egg, and develops a tentacle-sheath which shows it to be a modified polypide. The greater part of the bud, however, forms what may now, on the analogy of Lichenopora, be termed an embryophore; and in this structure the embryo develops and undergoes its fission. There is no fertile brown body; and the ovicell is recognisable externally as a structure which looks like a zoœcium that has been inflated.

While the ovicell of Crisia is thus clearly a modified zoœcium, which develops a polypide-bud in the ordinary way at the growing-point, the morphology of the ovicell of Lichenopora is more obscure. There is no doubt that the embryo is formed in a zoœcium; but it is formed in a fully developed zoœcium which probably is normally tenanted by two successive polypides. Each of these becomes a brown body in turn, the second brown body fusing with the first to form the characteristic fertile brown body. The exact origin of the embryophore is not as clear as it was in Crisia; but there is nothing to show that it is morphologically a bud. The later history is, however, not dissimilar. The embryophore becomes vacuolated, and in the vacuoles so formed the secondary embryos are later found. Certain differences in the details of the embryonic fission have already been pointed out. The fertile zoœcium becomes occluded, and its cavity then becomes continuous with a series of alveoli or interzoœcial spaces, which occur between the upper ends of the zoœcia. The ovicell is increased in size by the addition of fresh alveoli.

What, then, is the morphology of the ovicell? Are we to regard it as formed by the fusion of a number of zoœcia, represented by the constituent alveoli? Or, is the ovicell a highly modified zoœcium, or two zoœcia in cases where two zoœcia are originally fertile? Or, lastly, is no direct comparison possible between Crisia and Lichenopora in respect of their ovicells? The last question may probably be dismissed with the reply that the fundamental process of embryonic fission, and the character of the embryophore, are so similar in the two cases that the ovicells must be regarded in general as homologous structures. An objection to considering the alveoli to be suppressed zoœcia is to be found in the fact that the zoœcia reach the basal lamina of the colony, and the alveoli do not. This has previously been correctly pointed out by Smitt (20). The alveoli do not, moreover, develop a polypide bud at any period.

We must not lose sight of the fact that Crisia and Lichenopora are two very widely separated genera. It would not, indeed, be easy to choose any other pair of recent Cyclostomes which would be less nearly related to one another. More light will probably be thrown on the morphology of the ovicell of Lichenopora by the examination of genera which are less different from Crisia.

I have obviously been fortunate in being able to study the ovicells of L. verrucaria. Waters has more than once (24, 26) alluded to the importance of examining the ovicells of this genus, and has stated that in some species "large numbers of specimens may be examined without any ovicell being found." Whether this is due to the absence of the ovicells in these cases, or merely to the difficulty of recognising them, I have no means of deciding. But it must be expressly noted that Waters states (24, p. 261), in describing L. novæzelandiæ, Busk, that "where there is no ovicell the zoœcial tubes run into the centre, the central depression forming an inverted cone without cancelli;" and a similar statement is made on the next page for L. grignonensis, Busk. Waters unfortunately does not figure any of these specimens with a depressed centre and without cancelli; but these features certainly point to the conclusion that no ovicell is present. Waters' statements are in strong contrast with my own results on L. verrucaria, in which the ovicell is potentially present, as shown by the alterations in the fertile zoœcium in most colonies which consist of no more than four or five, or even three zoœcia; and it is actually present and recognisable from the outside in all colonies which have reached a slightly later stage.

It would no doubt be going too far to assume that what is true for L. verrucaria necessarily holds for other species of Lichenopora. I am not at present able to make an independent examination of other species; and although the ovicells of some of them have been described by Waters (24, 26) and others, the descriptions refer almost entirely to the external form, and I can find practically no points of comparison which assist in forming a conclusion as to the morphology of the ovicell. Waters in one place (25, p. 277) alludes to a feature which may have some relation with some of the phenomena described above in L. verrucaria. Speaking of Hornera ("Idmonea") fissurata, Busk, Waters states that he could not discover any opening to the ovicell, but that one of the lateral zoœcia was much larger than the others, and it appeared that this change was "connected with the functions of the ovicell." In each of the ovicells subsequently examined by Mr. Kirkpatrick one or two zoœcia in proximity to the ovicell were enlarged and altered in direction. It would be interesting to know whether the enlarged zoœcium in this case had any resemblance to the fertile zoœcium in L. verrucaria.

The ovicell seems to be practically identical in all species of Lichenopora in which it has been described. It always forms an inflated area between the upstanding zoœcia, and it is usually known to occupy the centre of the colony. In some species it is extremely difficult to recognise the ovicell at all. I cannot help suspecting that the ovicell normally develops at an early stage in most, if not all, of the species of Lichenopora, and that the presence of cancelli between the rows of zooecia is an indication that the ovicell is developing, even though no other evidence is obtained of its presence.

There are, however, other genera of Cyclostomata in which the ovicell is of a simpler character than in Lichenopora. Thus in Discotubigera lineata, MacG., as figured by Waters (26, pl. xv, fig. 5), the ovicell is a lobed structure which extends over a comparatively small area of the discoidal colony near its margin. It opens by a single aperture to the exterior. A similar form of ovicell occurs in the genus Diastopora. It appears to me that these ovicells resemble those of Lichenopora reduced to simpler terms, and they are, perhaps, to some extent intermediate between the two genera which I have specially studied. Taking into account the origin of the ovicell in Lichenopora from an ordinary zooecium, the fact that the ovicell of Crisia is demonstrably a modified zooecium, and the existence of intermediates between these two extremes, I venture to suggest that that of Lichenopora is also to be regarded as formed by the modification of a zooecium. The fertile zooecium is prevented by the position which it occupies near the centre of the full-grown colony from expanding at its basal end. Expansion of some kind is necessary, in order to provide room for the swarm of secondary embryos; and if there is anything in this suggestion, it may be supposed that the significance of the process is that the fertile zooecium has become swollen at its upper end. Instead of growing out as a free appendage of the colony, the swollen part has applied itself to the upper surfaces of the zooecia, and has filled up all the spaces intervening between the zooecia. The result is the same as if the ovicell had become amœboid, its pseudopodia extending between the zooecia, embracing them, and anastomosing on the further side of each. In the cases where two or more zooecia become fertile, the ovicell may be regarded as being composed of as many original zooecia.

The actual formation of the ovicell, by the formation of the alveoli and their subsequent fusion with one another, is of course somewhat different from this hypothetical process; but I claim to have established the facts (1) that the processes which precede the formation of the ovicell take place in a fertile zoœcium, and (2) that the development of the calcareous roof of the ovicell starts from the region of the orifice of the fertile zoœcium.

It remains to be seen whether the ovicells of such genera as Hornera, Diastopora, Tubulipora, and Idmonea fit in with this idea; and I hope to have an opportunity of making a more extended study of this question.

Next to the demonstration of the occurrence of embryonic fission, a process which had been previously proved for Crisia, the most striking fact which I have succeeded in establishing is the restriction of the production of an embryo to one or two of the oldest zoœcia in the normal development.

Even the second brood of embryos is really dependent on this function of the fertile zoœcium, or zoœcia, of the first generation; for they are nourished in the ovicell which was developed in connection with the primary fertile zoœcia. In the great majority of colonial animals a large number or all of the individuals of the colony become fertile. The phenomena which occur in Lichenopora are perhaps due to the fact that the colony in this genus is to be regarded as an individual of a higher order. The discoidal form and the close association of the zoœcia have produced the result that the colony behaves in this respect as if it were a single individual. The production of fertile eggs is thus limited to one or two individuals, and in fact to one or two of the zoœcia which are first formed as buds from the primary individual of the colony. In the case of Crisia, where the association of the different zoœcia is much less intimate, a considerable number of the individuals of a colony may become fertile. Here, however, there is something analogous in the behaviour of the internodes, each of which in the great majority of species normally produces no more than a single ovicell.

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DESCRIPTION OF PLATES 7—10,

Illustrating Mr. Sidney F. Harmer's paper "On the Development of Lichenopora verrucaria, Fabr."

All the figures refer to Lichenopora verrucaria, Fabr. Slight variations in the position of the camera lucida are responsible for the fact that they are not absolutely drawn to scale. All the figures on Plate 7, and figs. 12, 13, on Plate 8, were drawn with Zeiss A. Figs. 11, 14, and 17 were drawn with Zeiss C, and the others with Zeiss F.

PLATE 7.

Fig. 1.—Two views of a very young left-handed colony (diameter ·18 mm.). 1, 2, and 3 are the first three zoœcia.

Fig. 2.—Somewhat older left-handed colony (diameter ·30 mm.) seen from above.

Fig. 3.—Left-handed colony with four zoœcia (1, 2, 3, 4). (Diameter ·48 mm.; extreme length, ·64 mm.)

Fig. 4.—Right-handed colony with seven complete zoœcia. The proximal lip of the colony is beginning to grow towards the disc (broken), and the commencement of two new zoœcia can be seen in the space between the first three zoœcia (1, 2, and 3). (Diameter ·59 mm.)

Fig. 5.—Colony in which the roof of the ovicell is developing. The colony is probably left-handed, with occluded z^2. The aperture of the ovicell is not

yet completely formed. The proximal edge of the basal lamina has nearly reached the disc. (Diameter, 1·18 mm.)

Fig. 6.—Thick radial section of part of an old colony, showing the relations of the ovicell to the zoœcia. (Diameter of the right-hand zoœcium, outside the ovicell, = ·192 mm.)

Fig. 7.—A fully developed discoidal colony (diameter 1·92 mm.). The ovicell is obviously composed of a number of alveoli. The colony is probably left-handed, with occluded z^2, some indication of which can probably be seen just beneath the single aperture of the ovicell. The zoœcium to the left of the latter and above it is probably z^3.

Fig. 8.—Two zoœcia from a very old colony, with secondary thickening. The porous roof of the ovicell is seen at the bottom of a set of honeycomb-like spaces, the so-called "cancelli;" some of these are covering the bases of the zoœcia, and in the left-hand zoœcium these are entirely or partially roofed. Two of the blister-like swellings thus formed have part of their roof still uncalcified. (Diameter of zoœcia ·14 mm.)

Fig. 9.—From another old colony. The alveoli are still distinctly visible, and the cancelli are commencing in the interalveolar grooves, or at the base of the zoœcia. The left-hand zoœcium is closed by a porous calcareous cap. (Diameter of zoœcia ·13 mm.)

PLATE 8.

(N.B.—The measurements given below [except for figs. 12, 13] were made from the sections.)

Fig. 10.—Part of a longitudinal section through the fertile zoœcium (? z^3) of a colony, ·67 mm. in length, with about nine fully-formed zoœcia. The elongated structure to the right of the fertile brown body is the embryophore.

Fig. 11.—Section (diameter ·80 mm.) of a colony with fully formed ovicell. The section is parallel to the flat surface of the plano-convex colony, and cuts the convex side near its upper surface (cf. fig. 6). The only zoœcia seen in the section are thus the more centrally placed ones. z^2 was presumably the fertile zoœcium, as it is empty basally, and contains secondary embryos, at its upper end. The fertile brown body has passed into the ovicell. z^3 also contains secondary embryos, but has a brown body basally, and was probably occluded without being fertile. The secondary embryos are contained in the "embryophore," whose lobes extend, in the cavity of the ovicell, between the zoœcia. The zoœcium A contained a brown body lower down.

Fig. 12.—Entire colony (diameter 1·41 mm.), stained and mounted in Canada balsam. The shaded part shows how much of the ovicell is completely roofed. The alveoli which are still unroofed are not specially indicated. The ovicell has an aperture, at the base of which is the fertile brown body.

The embryophore is younger than in fig. 11. Parts of the zoœcia which are seen either through other zoœcia or through the roof of the ovicell are indicated by dotted lines. The colony is left-handed. z^2 is occluded (and was obviously fertile), and would hardly have been visible at all in a dry preparation.

Fig. 13.—Occlusion of the fertile zoœcium in a left-handed colony (diameter ·88 mm.). The roofing of the ovicell has only just commenced, as a calcareous film starting from the outer border of z^2, and sweeping inwards in such a way as to leave z^2 open to the cavity of the ovicell. Although the figure is from a dry mount, the remains of the fertile brown body (not shown in the figure) are visible through the opening into z^2.

Fig. 14.—Part of the growing edge of an adult colony, more highly magnified, showing the way in which new zoœcia are formed, and representing various stages in the development of the alveoli. See also pp. 81, 84.

(Figs. 15—35, and Fig. 37, refer to the development of the first brood of secondary embryos.

PLATE 9.

Fig. 15.—A polypide-bud with an egg. One other bud in the same colony had an egg in a similar position.

Fig. 16.—From a colony, ·48 mm. long, consisting of three zoœcia. One or two egg-cells were discovered in z^1, as well as in the zoœcium (z^3) drawn.

Fig. 17.—Horizontal section of a colony, ·43 mm. long and ·25 mm. broad, consisting of three complete zoœcia only.

Fig. 18.—Part of the left-hand zoœcium (? z^3) of the last figure, more highly magnified. The egg measures $12{\cdot}8\ \mu$ (= ·0128 mm.).

Fig. 19.—From a colony consisting of three mature zoœcia. Development of the egg has commenced, and the follicle is becoming definite. The heads of mature spermatozoa are seen in the body-cavity.

Fig. 20.—From a colony consisting of three mature zoœcia. The follicle is more developed, and the suspensor has become a definite structure. (Diameter of the embryo, $11{\cdot}2\ \mu$.)

Fig. 21.—From a colony, ·40 mm. long and ·21 mm. broad, consisting of three mature zoœcia. The follicle is cut transversely, and the embryo is in about the same stage as that of Fig. 19.

Fig. 22.—From a colony consisting of four mature and one half-grown zoœcium. The suspensor is not yet clearly formed.

Fig. 23.—From a colony, ·53 mm. long and ·32 mm. broad, consisting of five mature zoœcia. The figure is combined from three sections of the oœcium, the fertile brown body being projected on to the rest of the drawing.

The suspensor and the cells which surround it are closely connected with a mass of cells, A, which form part of the investment of the brown body.

Fig. 24.—Embryophore from a colony ·48 mm. long and ·45 mm. broad. (Length of suspensor, 41·6 μ ; transverse diameter of embryo, 20·8 μ.)

Fig. 25.—Showing the abnormal development of two embryos within the same embryophore. From a colony ·56 mm. long, consisting of five mature zoœcia.

Fig. 26.—Embryo (Stage D) from a colony ·56 mm. long and ·37 mm. broad, consisting of five zoœcia. The outer layer of nuclei is unusually distinct.

Fig. 27.—From a colony ·69 mm. long and ·51 mm. broad, consisting of about twelve mature zoœcia. The fertile polypide has degenerated, and the brown body has approached the orifice of the zoœcium. The embryo is 28 μ long, and the length of the entire embryophore with the brown body is ·93 μ.

PLATE 10.

Fig. 28.—From a younger colony, ·43 mm. long and ·37 mm. broad, consisting of six mature zoœcia. The brown body has not yet reached the orifice of the zoœcium, and development is consequently not quite so advanced as in Fig. 27.

Fig. 29.—From a considerably older colony, ·56 mm. broad. The upper end of the embryophore had met the orifice, as in Fig. 27, and evidence was obtained that the zoœcium was occluded by a membrane stretching across the orifice. Length of the embryo 70 μ.

Fig. 30.—(Stage E.) Obliquely longitudinal section through the embryophore of a colony ·62 mm. broad. The upper end of the figure was turned towards the brown body. Diameter of the embryo 30·4 μ.

Fig. 31.—Embryo from a colony ·83 mm. broad. The occurrence of the split-like spaces s, and the arrangement of the inner mass of nuclei indicate that embryonic fission is about to commence. Longest diameter of embryo 45·6 μ.

Figs. 32 and 33 are consecutive transverse sections of the larger portion of an embryo at the beginning of its fission. From a colony ·93 mm. broad, containing two fertile zoœcia. The longest diameter of the embryo is ·68 μ. A smaller piece of the embryonic tissue, not shown in the figures, is already completely separated from the portion drawn.

Fig. 34.—Transverse section of the older embryophore from a colony (·86 mm. broad) containing two fertile zoœcia. Embryonic fission is actively proceeding. The diameter of the giant-cell A is 17·6 μ, and that of its nucleus is 9·6 μ.

FIG. 35.—Longitudinal section of the embryophore, with actively dividing primary embryo. The brown body is not seen in this section, but would have come at the upper end of the figure. From a colony ·53 mm. long.

FIG. 36.—Longitudinal section of a young embryophore belonging to a second or later generation. The brown body is conspicuously larger than that of the corresponding stage (Fig. 28) of the first generation. The embryophore lies in a space which is clearly a zoœcium. (Diameter of the colony 2·20 mm. Length of the embryo plus the embryophore 167·2 μ. Longest diameter of the brown body 83·6 μ; of the embryo, 36 μ.)

FIG. 37.—Showing the fission of a young secondary embryo, belonging to the first brood. From a colony ·93 mm. long and ·88 mm. broad, similar to that shown in Fig. 11. The longest measurement of the dividing embryo is 56 μ.

Letters from New Guinea on Nautilus and some other Organisms.

By

Arthur Willey, D.Sc.

Ralum (New Britain), German New Guinea,
viâ Singapore;
April 5th, 1895.

Dear Professor Lankester,—Although I have not seen any mature ova of the pearly Nautilus since my last letter to you, yet I have made some further observations on the adult, which may be of interest.

1. Ectoparasites.—In my previous note[1] I accidentally omitted to mention the occurrence of numerous Copepod parasites in the mantle chamber of the Nautilus. They are present in nearly every individual that I have examined, and are found attached to the branchiæ, the internal surface of the funnel, and in other regions of the pallial chamber.

The parasites are a species of the genus Caligus,[2] and possess the characteristic semilunar suckers on the first pair of antennæ.

When Nautili are placed in jars the Caligids emerge in large numbers from the mantle chamber, and swim about actively in the water, usually in close proximity to the sides of the vessels, from which they can be removed only with some difficulty, owing to the great adhering power of the above-mentioned suckers.

2. Movements.—I send you a photograph of a Nautilus in its ordinary swimming attitude,—such a figure, I believe,

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[1] 'Natural Science,' May, 1894.

[2] C. nautili, pending a more detailed description.

not having been previously published.[1] From the photograph it will be seen that in swimming the animal elevates itself to such an extent that the eyes are raised above the free margin of the mouth of the shell. As to its movements on the surface of the water, there is very little to add to the excellent account given by the late Professor Moseley in his 'Notes by a Naturalist on H.M.S. Challenger.'

I can emphatically confirm Moseley when he says that "it is probably a mistake to suppose that it ever comes to the surface voluntarily to swim about." Nevertheless a Nautilus is not necessarily ruined by being brought up from the bottom in a fish basket. If liberated within a reasonable time it is capable of returning to its natural habitat. I have proved this experimentally.

When freshly captured Nautili are placed in aquaria they rise to the surface and sink to the bottom with the greatest facility. The rising to the surface, according to my observations, is effected solely by the muscular activity of the animal, and is in no way dependent on any physical modification of the gas in the air-chambers. The presence of the latter renders the shell extremely light and buoyant, so that it is, under normal circumstances, completely under the control of the muscles of the animal. I say "under normal circumstances" advisedly, because there is one thing which the Nautilus cannot do, namely, turn upside down. It is necessary to insist on this, because Moseley gives a translation of the account given by Rumphius at the beginning of last century, which, I regret to say, so far as my experience has gone, is very wide of the mark. Always remembering that Rumphius was the first to demonstrate the cephalopodous character of the pearly Nautilus, the suspicion is forced upon me that he derived his account of its habits from the narrative of an ill-informed and imaginative Malay fisherman. Natives are so often remarkably well informed about the habits of animals, that the above supposition can by no means be taken as conveying a reproach to the old master.

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[1] This photograph is reproduced as Fig. 24 at the end of this article.

"On the bottom," says Rumphius, according to Moseley's translation, "the animal creeps with the other side[1] uppermost, with the head and tentacles on the bottom, and makes tolerably fast progress." The only comment I can make on this statement is that it is inconceivable. I wish I had the work of Rumphius to refer to, in order to find out how he succeeded in seeing the Nautilus at all on the bottom. He goes on to say, "The animals remain mostly at the bottom, creeping sometimes into hoop-nets set for fish and lobster-pots; but after a storm, when the weather becomes calm, they are to be seen floating in troops on the surface of the water. . . . The floating, however, does not last long, for, drawing in all their tentacles, the animals turn their boats over and go down again to the bottom."

The Nautilus can no more turn its boat over than a successful balloon ascent can end by the cage coming down uppermost. Anyone can convince himself of this by placing an empty Nautilus shell in water. A remarkably small weight is sufficient to sink such an empty shell; and when the living animal retracts itself and ceases all muscular action, thereby converting itself, as it were, into a dead weight, it is heavy enough to sink several shells in addition to its own.

There is a slight error in Moseley's account of the movements of the Nautilus, which may as well be corrected. He says, "On either side of the base of the membranous operculum-like headfold . . . the fold of the mantle closing the gill-cavity was to be seen rising and falling, with a regular pulsating motion, as the animal in breathing took in the water, to be expelled by the siphon." It is not a fold of the mantle which is thus seen to pulsate, but the posterior free membrane-like expansion of the funnel on either side.

Besides observing the movements of the Nautilus in the narrow limits of jars and buckets, I have also placed them in the sea in shallow water, and will briefly describe one such experiment.

On March 16th a Kanaka brought me six Nautili. All of them sank to the bottom of the buckets except one, which

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[1] That is, the ventral side.

swam about on the top all the time. About an hour afterwards I took the latter out in a canoe to observe its movements in one to three fathoms of water. On placing it in the sea it remained at first on the surface, swimming actively backwards, i. e. with the shell directed forwards. It frequently swam to the bottom and back again to the surface—often also swimming in the middle stratum of water. I have never found any necessity for framing an elaborate theory as to the rising and sinking of the shell.

3. The Position of the Spadix or Hectocotylus.—I was surprised to find that the spadix in the male developed variably on the right and left sides of the cephalic system. Out of thirty-seven males which were examined ad hoc, twenty-three had the spadix on the left side, and fourteen had it on the right side.

4. Pallial Arteries.—I will say a few words about the pallial arteries, in order to refer to the arterial blood-supply of the siphuncular pedicle. Anatomical evidence seems to point to the conclusion that the latter structure has more of a vestigial than of an actively functional physiological importance. Embryology will show whether or not it has any original relation to the primitive shell-gland.

The so-called lesser aorta of Owen, arising from the anterior slightly incurved margin of the heart, divides immediately, as is known, into two branches. These are respectively the anterior and posterior pallial arteries.

The anterior pallial artery bends inwards and somewhat downwards to the middle line, and then runs forwards below the skin on the surface of the renal sacs. At the point where it turns forwards a small intestinal branch is given off. Arrived at the anterior limit of the renal sacs, the anterior pallial artery passes into the substance of the mantle, and runs towards the free margin of the mantle, shortly before reaching which it bifurcates into two main marginal arteries, from which numerous radial arteries are given off (see Fig. 1).

Exactly at the point where the anterior pallial artery passes into the substance of the mantle a pair of branches, right and left, arise from it almost at right angles to it. These may be called the branchio-osphradial branches of the anterior pallial

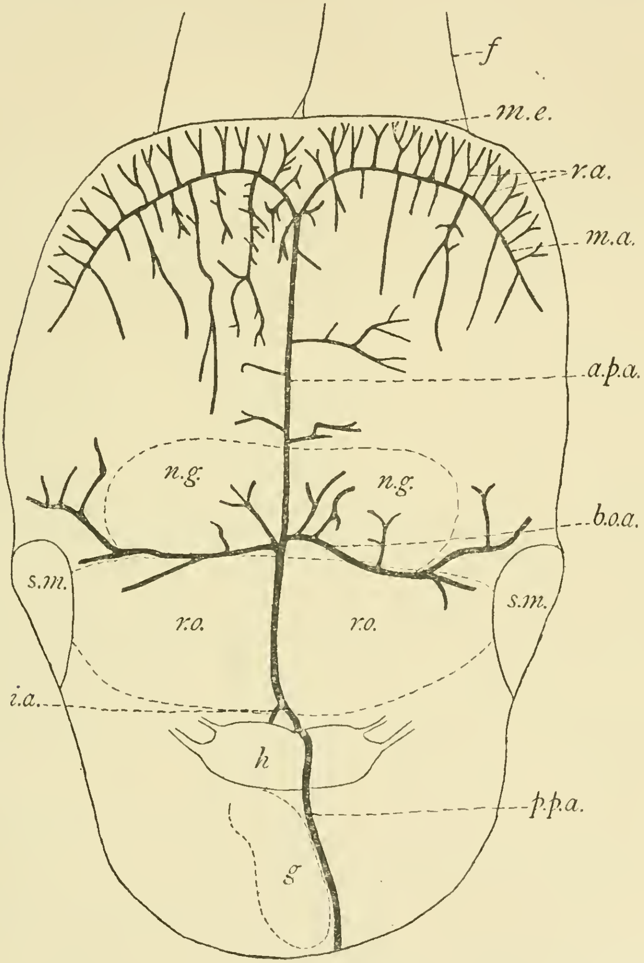


Fig. 1.—N. pompilius, ♀. View of ventral surface of pallial and visceral regions, to show the course of the pallial arteries. *f.* Funnel. *m. e.* Free edge of mantle. *r. a.* Radial pallial arteries. *m. a.* Marginal pallial artery. *a. p. a.* Anterior pallial artery. *n. g.* Region of nidamental gland. *b. o. a.* Branchio-osphradial artery. *s. m.* Shell-muscle. *r. o.* Region of renal organs. *h.* Heart. *p. p. a.* Posterior pallial artery. *g.* Gonad. *i. a.* Intestinal branch of anterior pallial artery.

artery, since among their minor ramifications they send up branches to the tips of the branchiæ supplying the integument of the latter, and also a small branch into each of the osphradia (i. e. into the osphradia of Lankester and Bourne, and into those which I described in my last letter). In the female they also supply the nidamental gland.

The posterior pallial artery runs backwards over the ventral surface of the heart, leaves the pericardium through the orifice described by Owen, and then passes onwards below the skin to the left of the genital gland, between the latter and the gizzard. Upon reaching approximately the middle point of the posterior rounded surface of the body it, too, passes into the integument, and immediately divides into two main branches, right and left, which supply the dorsal and posterior regions of the mantle, including the siphuncular pedicle. A variable number of small secondary or tertiary branches go up into the siphuncular pedicle, but there is one branch which is essentially the siphuncular artery (see Figs. 2 and 3). But even the definite siphuncular artery is not constant in its origin, but arises now from the right and now from the left of the two main branches of the posterior pallial artery. The siphuncular artery is therefore a minor ramification of the posterior pallial artery.

Owen, followed by Vrolik, described the latter as passing in toto into the siphuncle. Keferstein, whose figure is more accurate in this respect, says that it passes " nach hinten zur Körperhaut und besonders zum Sipho."

Injection indicates that the arteries which supply the siphuncle are homodynamous with the other ramifications of the posterior pallial artery.

5. Pallial Veins.—It is not now necessary to go into details with regard to the pallial veins, but I will point out how they may be seen to great advantage.

When a Nautilus becomes moribund it usually rises to the surface, owing to an abundant production of gas in the interior of the body. If it is allowed to die, and is then removed from the shell, the veins are found to be injected with gas of some sort, and the finest ramifications of the veins, in the mantle at least, are displayed with a clearness which could be hardly attained by artificial injection.

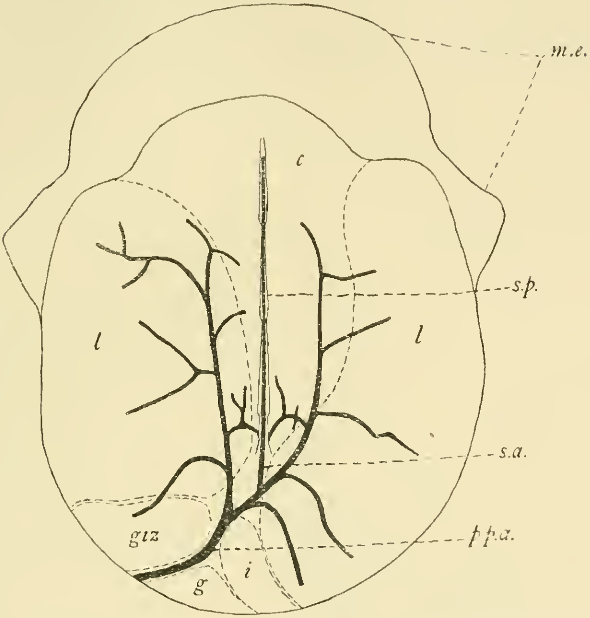


Fig. 2.—N. pompilius, ♂. View of dorsal surface of pallio-visceral region, to show the principal ramifications of the posterior pallial artery. *m. e.* Free mantle edge. *c.* Region of crop. *s. p.* Siphuncular pedicle. *l.* Region of liver. *s. a.* Siphuncular artery arising from the right of the two main branches of posterior pallial artery. *p. p. a.* Posterior pallial artery. *giz.* Region of gizzard. *g.* Region of gonad. *i.* Region of intestine.

N.B.—In front of siphuncular artery are seen two small branches which bend backwards and enter the siphuncular pedicle on its dorsal aspect. The pedicle is here represented turned forwards to expose its ventral surface.

The mantle is simply riddled by these veins in a manner which defies one's powers of draughtsmanship. The veins are collected into two main trunks, which lie on either side of the anterior pallial artery, and proceed backwards to open into the afferent branchial vessels. At the sides of the mantle there are also a number of lateral pallial veins, which open into a large sinus situated over the shell muscle.

6. Miscellaneous.—In New Hanover and New Ireland the Nautilus shell is called "Togol," and is used as a decoration on the outriggers of the canoes and on the houses, and also as a drinking vessel and for baling out canoes. Occasionally the shell of Nautilus umbilicatus is obtained, and the new-comer then acquires the useful information that that is the male of the Nautilus! This seems to be the idea of the Kanakas as well as of the outlying white men.

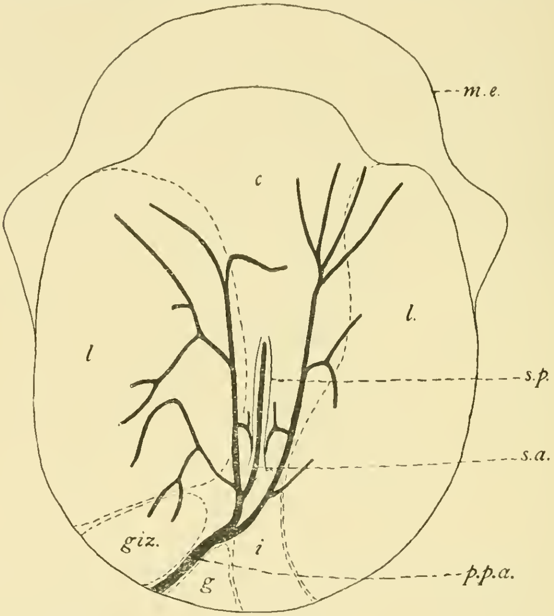


Fig. 3.—N. pompilius, ♂. Similar view as in Fig. B, to show the siphuncular artery arising from the left of the two main branches of the posterior pallial artery. Letters as in Fig. B.

In New Hanover, where primitive institutions still largely flourish undisturbed (including cannibalism), a curious custom prevails, of which I became aware while engaged in collecting finger-prints. The natives employ the cheiromantic creases for the purpose of creating factitious social groups or families, within the limits of which marriage is tabooed. They trace a fancied resemblance between the creases of the hand and the form of the wings of a given bird, and name accordingly. All those whose hand-creases are referable to the same bird constitute one family or "tā-uk," apart from any question of blood relationship. Thus a man of the "kanai ta-uk," or family of the sea-gull, cannot marry a woman of that "ta-uk."

It is also tabu to eat bird-flesh, but they all eat pork—exactly the reverse of what occurs in New Britain, at least as far as the men are concerned.

Probably most of the fighting in New Hanover is due to the complicated relations of the sexes. "Plenty fight belong Mary."

Finally, I may conclude these brief notes by adding that if a Kanaka kills another Kanaka of his own ta-uk he does not eat him, according to my information.—Yours very truly,

Arthur Willey.

Ralum, New Britain,
viâ Singapore;
June 4th, 1895.

Dear Professor Lankester,—The following are a few zoological observations, relating chiefly to the fauna of Blanche Bay, which I have incidentally made during the last few months.

1. Polyclades.—The Polyclade fauna is rich both in species and individuals. Most of those that I have hitherto had any opportunity of observing have been taken close to the shore of the island of Rakaiya (or Raluan), in Blanche Bay, from the lower surfaces or in the crevices of volcanic stones.

I have, however, on several occasions also obtained them from the reef opposite Ralum. Although a fact of no absolute value proceeding from so limited an experience, it is nevertheless worth mentioning that the Polyclades from the reef off Ralum have all belonged to the subdivision Cotylea, and included a very fine Thysanozoon, attaining a length of 66 mm.; whereas those from the stones off Rakaiya, which I have collected in much larger numbers, have all been representatives of the subdivision Acotylea.

Several of the latter have laid their egg-plates in my jars. There are, among others, two well-marked species of Stylochus, both characterised by their uniformly pitted or granular appearance, but in one case of an opaque dark ashy colour, and in the other of a light brown sandy complexion. As I cannot match these with any descriptions in the literature at my command, it will do no great harm to refer to the former as S. cinereus and to the latter as S. arenosus.

Stylochus cinereus has a length of 24 to 27 mm., and a width of 10 mm.; tentacles brownish yellow, covered with eyes, and 3·5 mm. from anterior margin of body; cerebral eyes extending over proximal portion of outgoing nerves; anterior marginal eyes extending backwards to level of tentacles; margin of body cloudy, but light and unpigmented.

S. arenosus has a length of 41 to 45 mm., and a width of 16 mm.; tentacles covered with eyes except the tip, which is orange-coloured; tentacles 5·5 mm. from anterior margin; cerebral and marginal eyes as in S. cinereus; margin of body nearly colourless and translucent; about twelve pairs of intestinal diverticula.

It is difficult to obtain uninjured examples of S. cinereus, as it tears with the greatest readiness while being detached from the stones on which it lives. Lacerated examples presenting a ragged appearance thrive well in aquaria. The tendency to laceration seems to be a characteristic of the species as much as any anatomical feature. There is a species of Cryptocelis (marginal eyes all round body) common here, which practises deliberate autotomy, this being one of its most characteristic peculiarities.

S. cinereus laid several irregular patches of eggs on April 27th. The eggs were disposed in no particular order in a somewhat granular gelatinous matrix, each ovum being surrounded by its own membrane, and measuring 12 to 13 μ in diameter. Before the commencement of segmentation the ova of this species pass through a pronounced amœboid stage (Figs. 4 and 5), subsequently becoming round again. It is also a favorable species for observing amœboid movements of the polar bodies. The movements are sluggish but unmistakable, and sometimes the polar bodies become widely separated from one another (Fig. 6).

Fig. 4.

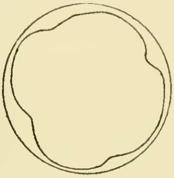
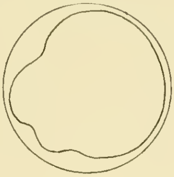


Fig. 5.



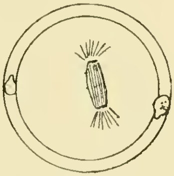


Fig. 6.

Figs. 4 and 5.—Ova of Stylochus cinereus before commencement of segmentation, to show the amœboid phase. Zeiss, 3 c, cam. luc.

Fig. 6.—Ovum of S. cinereus preparing for the first division, to show the amœboid character of the polar bodies. Zeiss, 3 c, cam. luc.

Stylochus arenosus laid one irregularly contoured plate of eggs on May 6th. The ova were arranged in distinct rows, each ovum surrounded by its own proper membrane, and measuring 9 to 10 μ.

The egg-discs of two species of Planocera, occurring like the above species in shallow water off Rakaiya, offer a strong contrast to the egg-plates of Stylochus. I am under the necessity of naming these, at least provisionally, on the same principle as the above-described species of Stylochus.

Planocera discus (mihi) attains a length of 45·5 mm., with a width of 28 mm. The dorsal surface is coloured with delicate yellowish-brown (umber) reticulated markings, on which are scattered black nodal spots; interspaces whitish;

margin of body of the delicate brown ground colour interrupted by narrow white streaks; mid-dorsal region pitted with numerous minute black spots; tentacles brown with rose-yellow tip, 13 mm. from anterior margin; large tentacular eyes at base of tentacles, more numerous than the smaller cerebral eyes; latter numbering about twenty-two to twenty-five on each side; female genital aperture about same distance from posterior end as the tentacles are from the anterior end; pharyngeal bursæ, seen from below, dense white; intestinal diverticula six or seven pairs.

The margin of the body is always sinuous or skirt-like, and when at rest the animal is capable of assuming a nearly circular form. Both this and the following species can be handled with impunity, neither of them evincing the slightest disposition to laceration.

Planocera discoides (mihi) is, for a Polyclade, an object of great beauty. I obtained two specimens of it from the bottom of a volcanic stone, on the top of which corals and sponges were growing off the south-west shore of Rakaiya, in some two or three feet of water at low tide.

It reaches the length of 75 mm., with a width of 36 mm., always with a sinuous margin. Like the preceding species, it can assume an almost circular form. The body is remarkably transparent; intestinal rami, seen from above, light brown, moniliform, anastomosing; interspaces beset with numerous minute rubiginous spots; larger dark brown nodal spots scattered about dorsal surface; margin of body light, pellucid; tentacles pellucid, 22 mm. from anterior margin; female aperture same distance from posterior margin; large dense white shell-gland between the two genital orifices; eyes about twice as numerous as in P. discus; cerebrum in a clear pellucid area, which is deeply indented or excavated ventrally; seven or eight pairs of intestinal diverticula, which present a dull greyish-white colour from below.

P. discus laid a circular disc of egg-capsules on April 30th. The disc had the appearance of consisting of a series of concentric circles, but closer examination showed that the rows were arranged spirally, the spirals being here and there interrupted (Fig. 7). The egg-disc measured 15 mm. in diameter.

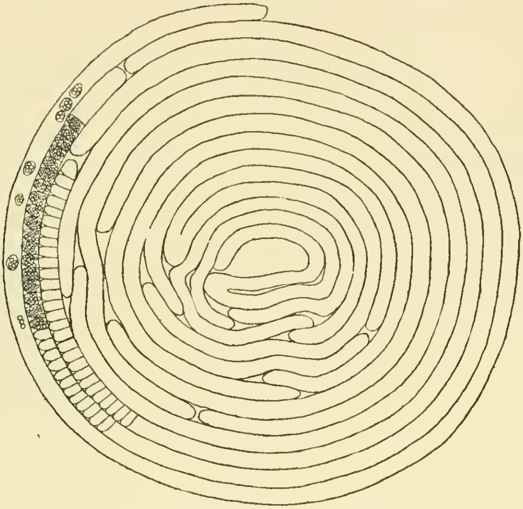


FIG. 7.—Enlarged view of the egg-disc of Planocera discus. Only a few of the egg-capsules have been inserted in the drawing.

Each row consists of numerous capsules packed closely together in what amounts to a common gelatinous tube. The spirals can be unwound. In the outermost spiral were a few irregularly dispersed capsules. The normal capsules contained each from eight to eleven ova, and the latter had no other membrane round them individually.

On May 4th the same individual, which had been kept isolated all the time, laid another much smaller disc of egg-capsules. I left these undisturbed, and in the course of time many of the ova developed into ciliated embryos with a pair of large primary eyes. The embryos swim about actively in the capsules, three or four to seven or eight in each capsule, surrounded by the fragments of those eggs which had not developed. Many of the embryos had developed abnormally, owing probably to the fact that the water in which they were kept had not been changed frequently enough. Before segmentation commences, some of the ova in each capsule present an appearance of approaching fragmentation, and it is probable that this is a regular occurrence. Here also the polar bodies execute amœboid movements.

In the case of P. discoides I found two egg-discs on May 27th on the same stone on which the adults were living. To the unaided eye they were not to be distinguished from those of P. discus, but microscopic examination showed that the gelatinous matrix[1] in which the egg-capsules were arranged in concentric rows was more continuous, and not divisible into concentrically disposed tubes; and, above all, that in each egg-capsule there were only four ova (Fig. 8).

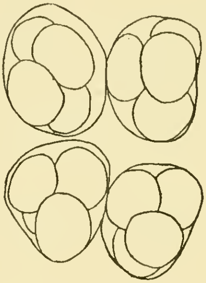


Fig. 8.—Four egg-capsules from an egg-disc of Planocera discoides each capsule contains four ova. Zeiss, 3 A, cam. luc.

Of the four ova in each capsule, as a rule, only two develop into ciliated embryos; frequently, however, three, and rarely only one. I have in no instance found four ciliated embryos in a capsule. Those ova which do not develop undergo fragmentation. I think the particles of the fragmented ova must be dissolved in the fluid contained in the capsules, and not absorbed by the remaining ova in the solid form. When two or three embryos are revolving in a capsule, there is usually no trace whatever of the previous existence of other ova in the same capsule; and when there is only one embryo in a capsule it is no larger than other embryos.

It is chiefly before the embryos begin to revolve that the

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[1] A large number of amœboid bodies may be observed in the matrix in which the egg-capsules are embedded in this species.

actual evidence of fragmentation is to be obtained (Figs. 9—11). Only rarely are the rounded particles derived from the fragmentation of the original ova, to be seen floating about in those capsules in which the embryos are revolving.

Fig. 9.

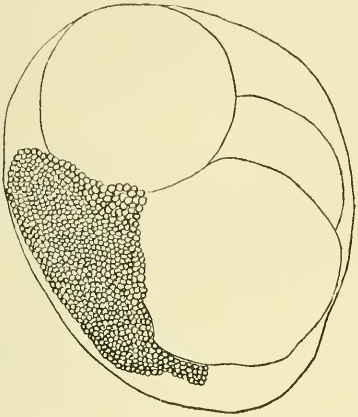


Fig. 10.

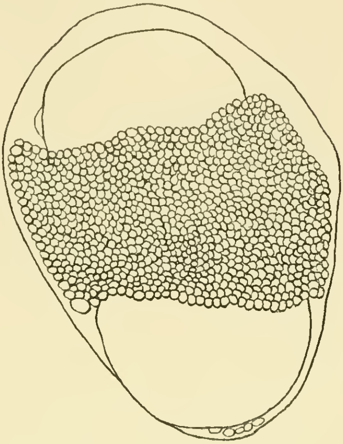
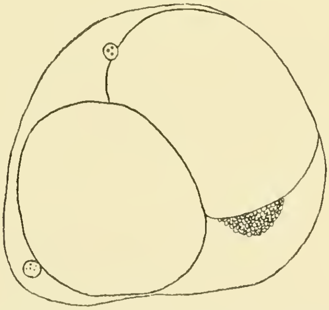


Fig. 11.



Figs. 9, 10, and 11.—Planocera discoides. Egg-capsules. In Fig. 9 one ovum has undergone fragmentation; in Fig. 10 two ova have undergone fragmentation; in Fig. 11 the remains of the fragmented particles are seen lying against an embryo which had already acquired cilia, but had not commenced to rotate. Zeiss, 3 c, cam. luc.

2. Cirripathes anguina.—From the reef off Ralum I obtained a fine specimen of this unbranched Antipatharian, upwards of 9 feet in length. It reached up close to the surface

at low water. The natives here call it "a pada ur-a-ta," or simply "a ur-a-ta," which means "the bones of the sea."

3. Nudibranchiata.—The Nudibranch molluscs, particularly the Dorididæ, are represented here by a great wealth of species of all sizes up to 60 mm. by 45 mm., many of them being brilliantly coloured. Their spiral egg-bands may be obtained without difficulty. Several species, including two Æolids, have laid their eggs in my dishes.

On the reef off Ralum, and in Blanche Bay too, there are to be found large numbers of very long spirally coiled ribbons, so thickly encrusted with sand that they appear to consist of nothing but sand. The natives call these "a pipia," which means "earth" or "ground." Some are tough and elastic, others brittle. They are the egg-bands either of species of Dorididæ, or of other Opisthobranchiate Mollusca, but I have not yet been able to identify them.

4. Onchidium.—One of the commonest Mollusca in the shallow water off the south-west shore of Rakaiya is a species of Onchidium. It is often found in the very heart of large friable stones, approximately at low-water mark, but sometimes further out. It occurs in other parts of Blanche Bay as well. What service the dorsal eyes can be to it is not easy to imagine. Semper supposed it was to enable the Onchidium to perceive and escape from what he says is its chief enemy, Periophthalmus. But although I have seen a small species of Periophthalmus at Rakaiya, on the muddy shore of the so-called lagoon, it is difficult to accept Semper's view.

The papillæ which carry the eyes are obviously homologous with the retractile branched respiratory papillæ in the posterior dorsal region, and every transition can be observed between them.

When kept in confinement in jars, Onchidium asserts its pulmonate qualities by often creeping out of the jars for long distances.

5. Larvæ of Polygordius and Squilla.—It is worth recording the presence of larvæ of Polygordius in the "Auftrieb" in Blanche Bay. In the narrow strait which separates

Rakaiya from the mainland I have taken one larva of Polygordius in an advanced stage of metamorphosis, when the long body has grown out behind the trochophore. On the same occasion the "Auftrieb" contained also larvæ of Squilla.

6. Phosphorescence.—The astonishing phosphorescence which is to be observed when fishing with the tow-net at night in Blanche Bay is in large measure due to Copepods and Ostracods.

7. Ascidians.—The Ascidian fauna here is richer than I expected to find it, since, as Herdman has pointed out, the tropics are not the metropolis of the Ascidians.

The Didemnidæ, which form one of the most difficult groups of compound Ascidians from a systematic point of view, are strongly represented by red, white, yellow, and green varieties.

Botryllus also occurs, though not common. I only know at present of two species—one very thin and white, attached to the lower surface of corals; the other thicker and purple, found growing on a Tridacna shell.

In regard to the compound Ascidians, I have been struck by the apparent absence of any member of the Polyclinidæ.

The simple Ascidians are represented by numerous species, one of which especially has peculiarities of such a nature that I will describe it at some length, reserving an account of the other Ascidians for a future occasion.

8. Styeloides eviscerans, n. sp.—In 1885, Sluiter described, in the 'Natuurkundig Tijdschrift voor Ned-Indie,' Bd. xlv, a simple Ascidian, under the name of Styeloides abranchiata, n. gen. et sp., in which the branchial sac and intestine were absent. Such was the condition of the animal in other respects that Sluiter was led to suppose that this must be the normal state of things, and founded the new genus accordingly.

In his extremely useful "Revised Classification of the Tunicata" ('Journ. Linn. Soc. Zool.,' vol. xxiii), Herdman, commenting on this species of Sluiter's, says, "This is such an exceptional and remarkable case that I cannot help suspecting that the single specimen examined by Sluiter was merely an individual abnormality."

I venture to hope that I have found the solution to this enigma in the species about to be described.

Fig. 12.—Group of seven individuals of Styeloides eviscerans, n. sp. represented as lying attached to the surface of a fragment of stone. In the large individual to the right the digestive tract is indicated in process of extrusion through the atrial aperture. *a.* Anus with frilled margin. *i.* Intestine. *br. s.* Branchial sac. *e.* Endostyle. *h.* Foreign organisms attached to test.

The species is not common, but I have obtained three or four examples of it from the lower surface of stones off the south-west shore of Rakaiya, in one half to one fathom of water.

The accompanying sketch (Fig. 12) represents a fine and typical group of individuals of this species. The members of the group are so intimately connected together by the mutual fusion of their tests that one would at once suppose that they had arisen from a parent stock by budding. Such, however, is not the case, since by making incisions it is found that it is only a fusion of test-substance, and not a true organic union. Moreover sometimes isolated individuals are to be found, as in Fig. 13.

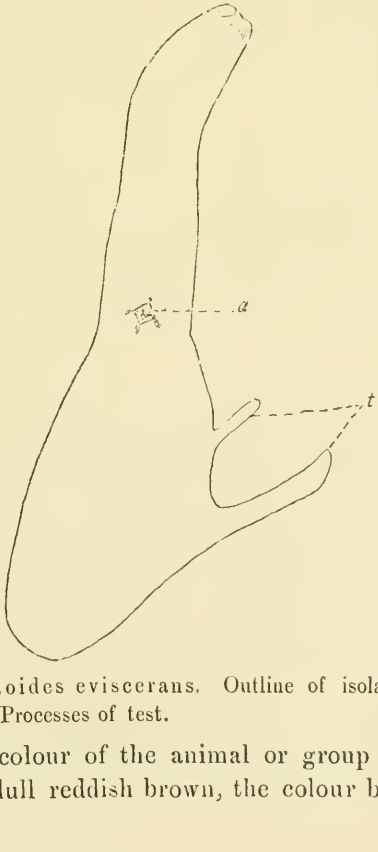


FIG. 13.—Styeloides eviscerans. Outline of isolated specimen. *a.* Atrial siphon. *t.* Processes of test.

The general colour of the animal or group of animals is a characteristic dull reddish brown, the colour being more pronounced in the neighbourhood of the apertures, while the lips of the latter are a pure dark red, interrupted by four light streaks which indicate the quadripartite character both of the buccal and atrial orifices.

As seen in the figures, the individuals are not always attached to the rock by the same side, but sometimes by the ventral side, sometimes by the right, and sometimes again by the left side (Fig. 12).

The total length of the group represented in Fig. 12 was 91·5 mm., and the greatest breadth of the group 31 mm. The animal of which an outline is given in Fig. 13 measured 51·5 mm. in length, and the atrial opening was 20·5 mm. removed from the buccal aperture. By its external appearance alone it is an extremely well-marked species. The surface of the coriaceous test is in some places wrinkled and in other places smooth.

The most remarkable peculiarity of the new species, however, is the faculty which it possesses of evisceration.

After I had had them for a short time in a vessel where everything was fresh and in good condition, I suddenly discovered a number of digestive tracts lying at the bottom. On then inspecting the Ascidians, of which there were several species present at the time, I found that they were all living and in a healthy condition.

Eventually I actually observed the process of evisceration taking place (cf. large individual to the right in Fig. 12). It takes a rather long time before the process is completed. It is effected by violent periodic contractions of the atrial siphon. After it is over the animal presents a perfectly normal and healthy appearance, opens and closes its siphons, and is susceptible to irritation and to the influence of cocaine. So constant is this ejection of the digestive tract that if it is desired to preserve specimens intact, they must be placed in alcohol immediately after capture.

The dissection of an individual which has ejected its branchial sac and intestine discovers no laceration whatever; and undoubtedly, in ignorance of the habit of evisceration, one would be tempted to suppose, as Sluiter did, that the absence of an alimentary canal was the normal condition.

In adopting Sluiter's generic name the diagnosis must of course be amended.

Before evisceration takes place the branchial sac is found to have the usual vascular connections with the mantle, but the endostylar area seems to have a very loose attachment to the mantle, and can be readily detached. When the branchial sac is ejected the dorsal tubercle (Figs. 14 and 15) and peripharyngeal groove are left behind, and there is a corresponding triangular excision in the wall of the ejected branchial sac.

FIG. 14.

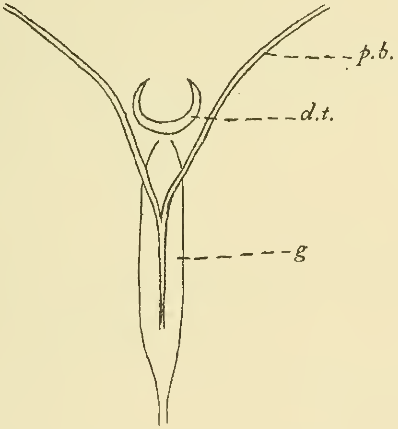


FIG. 15.

FIG. 14.—Styeloides eviscerans. Dorsal tubercle. *p. b.* Peripharyngeal band. *d. t.* Dorsal tubercle. *g.* Ganglion.

FIG. 15.—Dorsal tubercle of another individual of S. eviscerans.

The dorsal lamina is a simple undulating or crumpled membrane, and there are four folds of the wall of the branchial sac on each side.

The genital saccules have the characteristic subcylindrical form, and occur on both sides attached to the mantle. Curious bodies called endocarps, whose nature I do not understand, also occur on the inner surface of the mantle as in Sluiter's species.

The latter is probably a distinct species from the one I have described, although there are many features common to them both, particularly the external form and mode of attachment.

I am a little puzzled to understand what Sluiter says about the endostyle, and am inclined to think there must be some mistake about it, as there is no trace of a typical endostylar epithelium in the section figured by him. I have even observed a line or ridge in the ventral surface of the mantle corresponding very closely to his Taf. viii, fig. 2, but this possibly represents the former line of contact between the endostyle and the mantle.

There are naturally a great many more questions to be answered in connection with this remarkable Ascidian, but I have probably said enough to show that its property of evisceration is its most distinguishing peculiarity, and thus to afford an explanation for an otherwise inexplicable anomaly.

Yours very truly,
ARTHUR WILLEY.

RALUM, GERMAN NEW GUINEA,
viâ SINGAPORE;
September 24th, 1895.

DEAR PROFESSOR LANKESTER,

1. Significance of the Siphuncle in Nautilus pompilius.

Being desirous of obtaining, if possible, experimental evidence as to the physiological significance of the siphuncle in the pearly Nautilus, I have made several successful attempts to cut the siphuncle without otherwise injuring the animal. The evidence supplied by the experiment cannot be regarded as conclusive, on account of the altered conditions of depth and temperature to which the Nautilus is exposed by being brought up to the surface, but it may be well to consider what the results indicate.

At first I sawed through the shell into one of the chambers, and then cut the siphuncle. This method has the disadvantages of injuriously affecting the efficiency of the chambers, and of causing a more or less considerable loss of blood to the animal. The latter will, however, live in confinement about as long as untouched individuals.

A young Nautilus operated upon in this way on June 26th was placed in the sea in shallow water, for its movements to be watched. It sank slowly to the bottom, and then for a long time made active revolving motions about the vertical axis, but scarcely made any progressive movements.

On another occasion (July 10th), after several trials, I found that the best way of performing the operation is to saw through the shell in the neighbourhood of the posterior portion of the body of the animal, over the cardiac region, and not to tamper with the chambers. If the shell be held mouth downwards, this point lies approximately in the same vertical and transverse plane with the points where the free margin of the mouth of the shell merges into the umbilicus. When a large enough hole has been made in the shell to admit the scissors, the shell being still held upside down, the ventral visceral portion of the body usually detaches itself from the shell, or can be readily caused to do so, and, sinking inwards, exposes the root of the siphuncle, which can then be severed. On returning the shell to its normal position the body immediately resumes its normal intimate contact with the wall of the cavity in which it lives, and the pressure so exerted prevents any extensive loss of blood. Under these conditions the operation does not, as a rule, appear to affect the vitality of the animal in any degree.

A Nautilus[1] which was treated in this way on July 10th, on being placed in the sea swam about very vigorously for some time in the middle stratum of water, but most of the time at a little distance from the bottom. On September 13th I operated on four more individuals taken in Talli Bay, on

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[1] It should perhaps be mentioned that in this particular individual I accidentally cut into the last chamber, and plugged the opening with wax.

the north coast of the Gazelle peninsula. One of them showed a tendency to sink to the bottom, which it always performed very gradually. In this one I had accidentally punctured the mantle over the heart. The others remained floating and swimming about on the surface during the whole time of observation. They did not go far in one steady direction, but tended to go in circles, as in fact did another one whose siphuncle was uncut. If one of the individuals floating at the surface was forced down to the bottom with a hand-net, it would slowly rise to the surface again. This also often happens with a Nautilus that has not been operated on.

The results indicated by the above experiments, which, it may be added, are worth repeating, may be summarised as follows:

The cutting of the siphuncle (α) does not temporarily affect the vitality of the animal; (β) does not prevent it from making movements of translation;[1] (γ) does not prevent it from floating at the surface; (δ) does not prevent it from sinking to the bottom.

It still remains to be ascertained whether a Nautilus whose siphuncle has been cut, having sunk to the bottom of the sea in shallow water, will undertake a journey to the surface. My experiment of July 10th would seem to indicate that this might be expected to occur.

The above experiments do not appear to oppose the view which I expressed in a former communication—that the siphuncle of Nautilus pompilius is, in some measure, of the nature of a vestigial structure.

It might indeed be legitimate to suppose, on the principle of the correlation of organs, that in the Nautiloidea the course of evolution has led to a reduction of the siphuncle pari passu with an increase in the efficiency of the chambers as hydrostatic organs.

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[1] In speaking above of progressive movements I mean, of course, in the usual backward direction.

2. Some Features in the Arterial System of N. pompilius, as determined by Injection.

(1) Circulus Pallialis.—After successful injections a singular feature in the circulatory system is to be observed. The marginal pallial artery, which I described and figured in a former note, is found to pass on each side, dorso-laterally, into a branch of the dorsal aorta, so that a complete arterial circuit is produced.

I have even partially injected the marginal pallial arteries from the dorsal aorta itself, but the injection fluid did not proceed very far in this centripetal direction, owing no doubt to the resistance it met with from the action of the heart.

For this remarkable arterial circuit, produced by the confluence of the marginal pallial arteries, which arise ultimately as branches from the so-called "lesser aorta," with a pair of branches[1] from the great aorta, I propose the above name of "circulus pallialis." It is illustrated in the accompanying sketches (Figs. 16 and 17).

In Fig. 16 the posterior convex extremity of the body is supposed to be somewhat tilted up, in order to show the whole outline of the septum-producing area of the mantle. This outline is very distinct in fresh specimens, and the region of the mantle enclosed by it is distinguished from the surrounding portions of the mantle by its greater thickness and opacity. As already stated, this is the portion of the mantle which manufactures the septa, and it has an abundant arterial supply through the ramifications of the two main branches of the posterior pallial artery. These ramifications may be grouped together as the pallio-septal arteries; and it is surprising to see how rigidly they are confined within the septal contour.

It will be noticed that the latter makes on each side a

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[1] For reasons which will presently appear, these may be called the pallio-nuchal arteries.

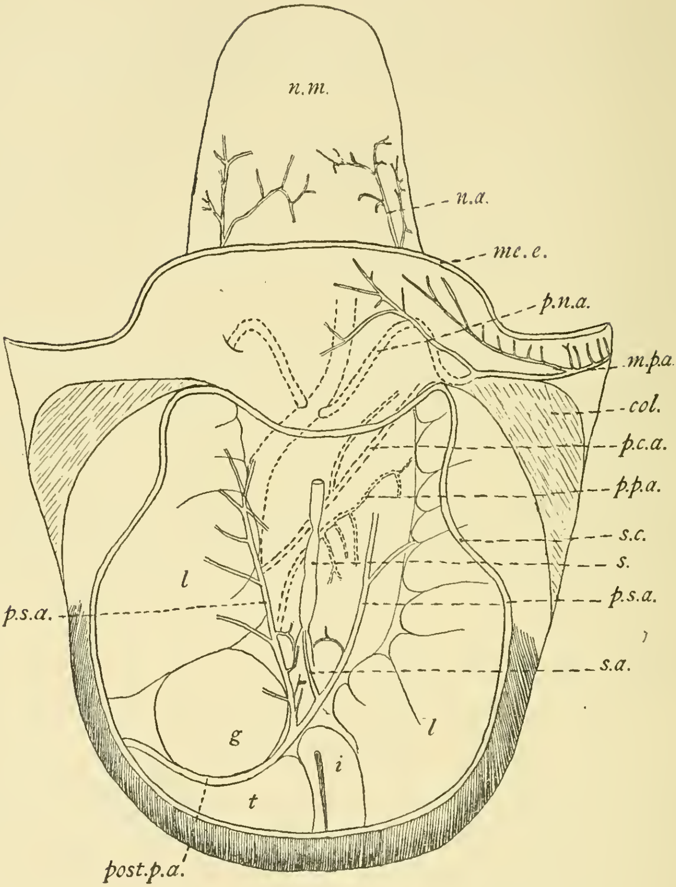

FIG. 16.—N. pompilius, ♂. Dorso-posterior aspect of visceral region, to illustrate the circulus pallialis and the septal contour. *n. m.* Nuchal membrane. *n. a.* Nuchal artery. *m. e.* Free mantle-edge. *p. n. a.* Pallio-nuchal artery. *m. p. a.* Marginal pallial artery. *col.* Columellar or shell muscle. *p. c. a.* Posterior columellar artery. *p. p. a.* Posterior proventricular artery. *s. c.* Septal contour. *s.* Siphuncle. *p. s. a.* Pallio-septal arteries. *s. a.* Siphuncular artery. *l.* Liver. *i.* Intestine. *t.* Testis. *post. p. a.* Posterior pallial artery. *g.* Gizzard.

N.B.—The dorsal aorta and its branches are indicated by dotted lines. They show dimly through the skin when injected.

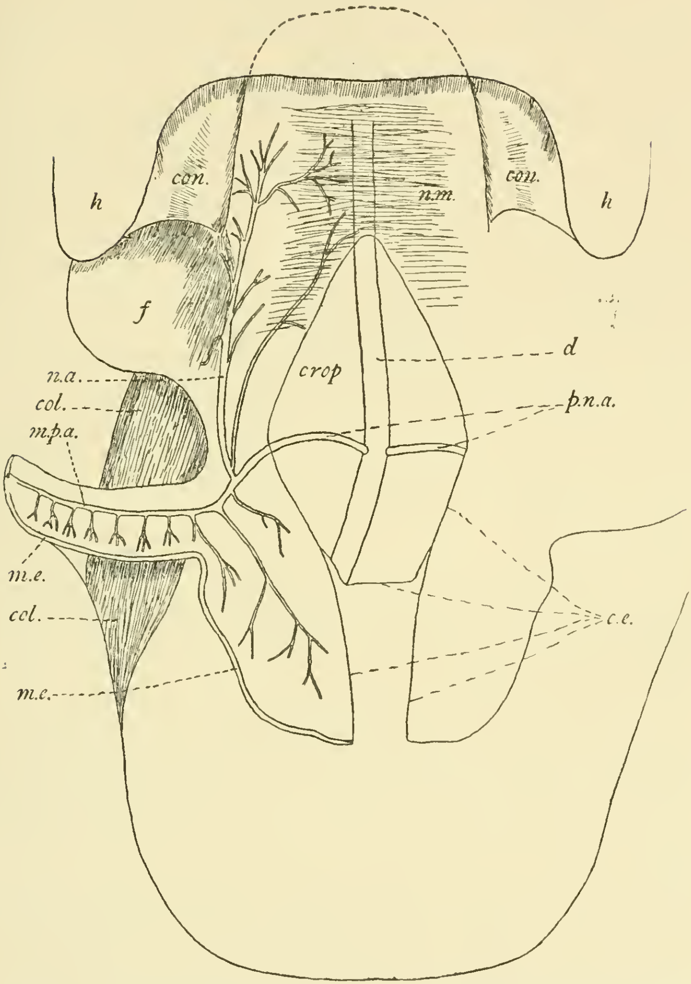

Fig. 17.—N. pompilius, ♂. View of nuchal region, to further illustrate the circulus pallialis. The dorsal free mantle-edge is reflected and a median incision made. *h.* Hood. *con.* Concavity at base of hood, in which the nuchal membrane (*n. m.*) lies. *f.* Dorso-posterior portion of funnel. *n. a.* Nuchal artery. *col.* Columellar muscle. *m. p. a.* Marginal pallial artery. *p. n. a.* Pallio-nuchal arteries. *d. a.* Dorsal aorta. *m. e.* Free mantle-edge. *c. e.* Cut edges of mantle and body-wall.

N.B.—The dorsal aorta shapes its course in this region in accordance with the state of repletion of the crop.

symmetrical figure with the outline of the great shell-muscles[1] where the latter abut on the shell.

In Fig. 17 the union of the marginal pallial artery with the left pallio-nuchal artery is represented from the inner surface of the mantle. Here it is seen that the two arteries unite in the dorso-lateral angle where the mantle and the funnel-flap fuse with the body-wall; and furthermore, that from the same point an artery is given off which passes forwards and gives off branches to the nuchal membrane. The latter structure was accurately described by Owen as a "semilunar ridge" lying in the concavity at the base of the hood, and applied to the involute convexity of the shell.

Owen thought it might serve to prevent the shell from encroaching too much upon the hood "in the act of creeping." We now know that the animal does not creep on its hood with reversed shell.

The nuchal membrane would seem to be responsible for the dense black colour of the involute portion of the shell, and possibly also exerts a lubricating influence. Keferstein calls it the "Nackenlappen."

(2) Genital Arteries (Fig. 18).—No less than three arteries arise directly from the heart which, to my knowledge, have hitherto escaped attention. They are (*a*) the artery of the genital duct or gonaducal artery; (*b*) the artery of the genital gland or genital artery; (*c*) the artery of the pear-shaped gland.

The accompanying sketch (Fig. 18) obviates the necessity of a detailed description. The genital artery is submedian, and the main trunk lies on the dorsal side of the genital gland.

Both the gonaducal artery and the artery of the pear-shaped gland give off a branch which passes into the perigonadial membrane, and this apparently trifling fact, combined with the subsymmetrical relations of the gonaduct and the pear-shaped gland, may indicate that the latter is the metamorphosed genital duct of the left side, and not, as I believe has been

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[1] For purposes of nomenclature it will be found convenient to speak of the great shell-muscles as the columellar muscles.

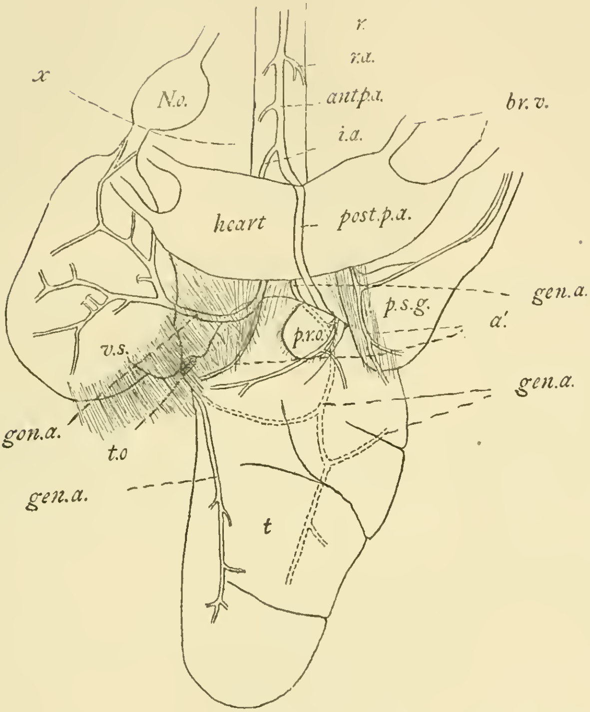

Fig. 18.—N. pompilius, ♂. Genital arteries from below. *r.* Rectum. *r. a.* Rectal artery. (N.B.—The rectal arteries are very variable.) *ant. p. a.* Anterior pallial artery. *i. a.* Intestinal artery. (N.B.—This artery usually passes to the right of the rectum, as shown in this figure; but in one instance I have observed it to pass down to the left of the rectum.) *br. v.* Branchial veins. *post. p. a.* Posterior pallial artery. *p. s. g.* Pear-shaped gland with its artery. *a'.* Branches of the preceding artery and of the gonaducal artery, which supply the superjacent perigonoidal membrane. *gen. a.* Genital artery and its branches. *t.* Testis. *t. o.* Aperture of testis. *p. v. o.* Orifice of communication between the pericardial and visceral portions of body-cavity, through which the posterior pallial artery passes. *gon. a.* Gonaducal artery. *v. s.* Vesicula seminalis. (N.B.—This structure, the testis and pear-shaped gland are closely united to the heart by a membrane.) *N. v.* Needhamian vesicle or spermatophore sac. *x.* Dotted line to indicate where the pallial duplicature merges into the body-wall ventrally.

suggested, the morphological equivalent of an entire left genital apparatus.

In the female the ramifications of the genital artery pass up on to the surface of the individual ova, and form a kind of capillary system, the finer branches following, but not always confined to, the reticular markings formed by the ridges of the follicular membrane which project into the yolk (Figs. 4 and 5).

The meshes formed on the surface of the ova by the intersection of the follicular ridges or plications are much wider in submature ova than in the less mature, and the ridges would presumably be found to flatten out in completely ripe eggs, although it has not been my good fortune hitherto to have found any such. At the animal pole of the egg the ridges are absent, and those which lie at the margin of this area form incomplete meshes as described by Kölliker in the ovarian ova of other Cephalopods (Fig. 19).

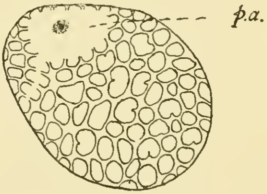

Fig. 19.—Fresh ovarian ovum of N. pompilius, to show the reticular markings produced by the plications of the follicle. *p. a.* Clear polar area, in the centre of which lies the germinal tract.

The clear polar area of the ovum has usually a subtriangular shape, and from each of the corners of the triangle what may be called a line of weakness occurs in the follicular wall, bound on either side by incomplete meshes (Fig. 19).

The arteries which traverse the surface of the ova give off minute branches which pass inwards, as it were, into the depths of the follicular ridges; and these deep-lying vessels anastomose with one another, while the superficial branches appear, as a rule, not to form anastomoses. It may be added that the impression of anastomoses is much more readily conveyed by examination with a hand-lens than it is by the use of the compound microscope.

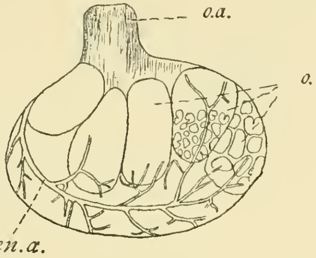

Fig. 20.—Ovary removed from body, and seen from dorsal aspect. On the right of the figure the follicular meshes of a submature and a half-mature ovum are partially inserted to show difference in size. *o. a.* Neck of ovarian sac, which bears the aperture. *o.* Ova. *gen. a.* Genital artery. Only the more superficial branches are indicated.

The germinal tract appears in the centre of the clear polar area as a faint whitish spot, and is turned towards the ventral aspect of the ovary (Fig. 20). The older ovarian ova are rendered shapeless by mutual pressure, with, however, a roughly oval outline. In this condition an ovum may measure 15·5 mm. in length, with a breadth of 11·5 mm. When the pressure is released by slitting open the ovary the ova round up, and those which are submature have an average diameter of some 10 mm. The yolk is viscous and glutinous, and possesses a translucent brownish tinge. The nearly ripe ova rupture with the utmost facility.

From a consideration of the size and relative states of maturity of the ova, it might be expected that they are laid singly. Every month, from December to September inclusive, I have been able to obtain over-ripe males (with spermatophores in the dorsal buccal recess and in the Needhamian vesicle) and submature females. Once in July I obtained a male with a discharged spermatophore capsule in the buccal recess; in fact, I have found this more than once.

From these facts, and from the fact which I have previously mentioned of the relative scarcity of the females in comparison with the males, I draw three provisional conclusions: firstly, that during the process of reproduction (fecundation and spawning) the females live in retirement; secondly, that the females practise what the Germans call "Brutpflege;" and lastly (what I regard as almost certain), that reproduction takes place all the year round.

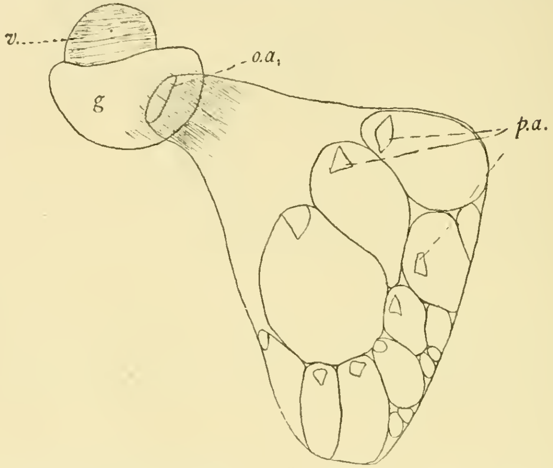

FIG. 21.—Female genital organs of N. pompilius, seen from below, to show the direction in which the polar areas of the ova lie. *p. a.* Polar areas of ovarian ova. *o. a.* Aperture of ovarian sac. *g.* Uterine portion of oviduct. *v.* Vaginal portion of oviduct.

(3) Cephalic Arteries (Figs. 22 and 23).—For a description of these arteries it will suffice to refer to the explanation of the figures. I will, however, call attention to the variability of the right and left anterior proventricular arteries; the latter was absent from the individual represented in fig. 7. The two main trunks into which the dorsal aorta divides behind the brain may be called the right and left innominate arteries.

It is a singular fact that the great median buccal artery always springs from the right innominate artery. The constancy of this origin would seem to indicate that it is potentially a paired structure.

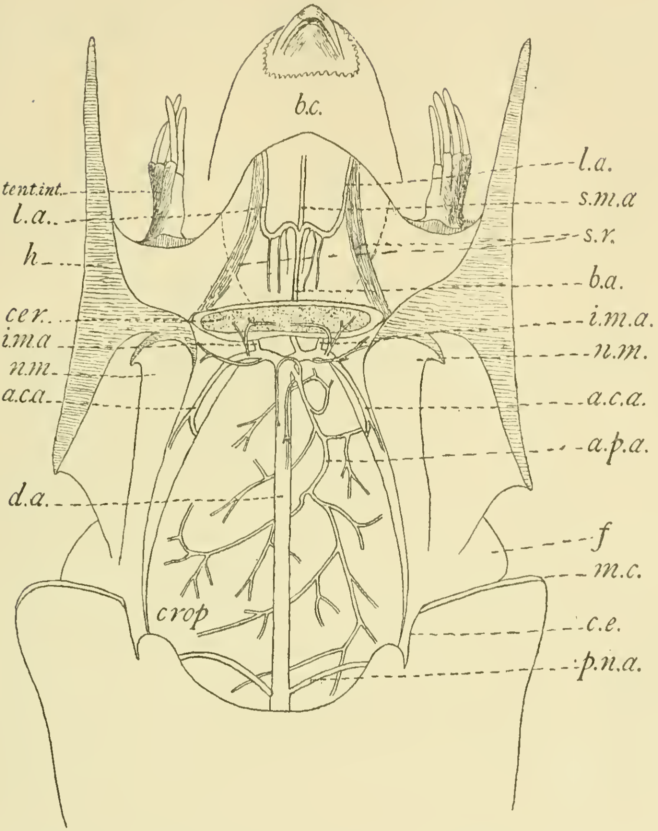

FIG. 22.—N. pompilius, ♂. Dissection, from above, of the cephalic region to show the cephalic arteries. An incision has been made through the nuchal membrane, the hood, and the buccal membrane. The brain-capsule has been opened, and the median portion of the mantle behind the nuchal region has been removed. *b. c.* Buccal cone. *tent. int.* Dorso-lateral inner row of tentacles (the superior labial processes of Owen). *l. a.* Labial arteries supplying the buccal membrane and fringe. *s. m. a.* Superior mandibular artery. *s. r.* Superior retractor muscles of the jaws (Owen). *b. a.* Buccal artery. *i. m. a.* Paired inferior mandibular arteries. *n. m.* Nuchal membrane. *a. c. a.* Anterior columellar artery. *a. p. a.* Anterior proventricular artery. *f.* Dorso-posterior portion of funnel. *m. e.* Free mantle-edges *c. e.* Cut edge of mantle. *p. n. a.* Pallio-nuchal artery. *d. a.* Dorsal aorta. *cer.* Brain with cerebral arteries. *h.* Cut edge of hood.

N.B.—Apart from the cerebral arteries, all the anteriorly directed branches of the innominate arteries pass below the cerebral capsule.

Attention may also be drawn to the two arterioles which arise from the base of the right proventricular artery and supply the wall of the dorsal aorta.

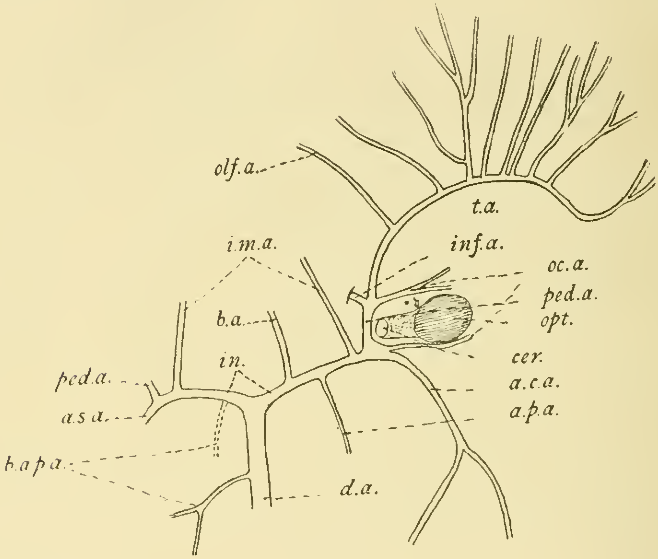

Fig. 23.—N. pompilius, ♂. Sketch to show the arteries which arise from the innominate arteries after the brain has been cut through. *t. a.* Right tentacular artery, which gives off branches to all the tentacles of its side. The innermost or mesiad branch (*olf. a.*) supplies the bipartite laminated organ of van der Hœven, which possibly represents a pair of inferior labial processes, and may have an olfactory function. *inf. a.* Infundibular artery, which passes through the cartilage into the funnel. The latter also receives minor branches from the columellar arteries. *oc. a.* Arteries to the eye. *ped. a.* Pedal artery, a convenient name for the common trunk from which the infundibular and tentacular arteries arise. *opt.* Optic ganglion. *cer.* Brain cut across and drawn aside. *a. c. a.* Anterior columellar artery. *a. p. a.* Right anterior proventricular artery. Compare its origin in Fig. 7, where it arises from the aorta. *d. a.* Dorsal aorta. *l. a. p. a.* Left anterior proventricular artery, usually but not invariably present; it sometimes arises from the left innominate artery, as indicated by the dotted lines; and sometimes, as in this example, from the dorsal aorta. *in.* Innominate arteries. *b. a.* Buccal artery. *i. m. a.* Inferior mandibular arteries.

3. Further Remarks.

(1) Capillaries.—As far as I have been able to observe, there seems to be a true capillary system in the free portion of the mantle, that is to say, in the pallial duplicature. I have previously described the pallial arteries and veins. There may be another system of capillaries in the funnel, which has an astonishingly rich vascular supply, and at whose base two large veins, the infundibular veins, may be observed to pass into the vena cava. But I have observed no veins in connection with the genital organs, and I gathered from micro-

Fig. 24.—Photograph of a living specimen of Nautilus pompilius, taken by A. Willey at Ralum in 1895.

scopic examination that the follicular arteries on the surface of the ova possessed free openings.

(2) Blood.—I will here only mention that the blood is a syrupy fluid with a pronounced blue tint, which becomes very dark on exposure to the air. The corpuscles comprise amœboid and fusiform cells, the latter being somewhat Gregarina-like in appearance.

Yours very truly,
Arthur Willey.

The Brain of a Fœtal Ornithorhynchus.[1]

Part I.—The Fore-brain.

By

G. Elliot Smith, M.D., Ch.M.,
Demonstrator of Anatomy, University of Sydney, N.S.W.

With Plate 11.

The fœtus, with whose brain this paper is concerned, was received already preserved in alcohol from the Australian Museum of Sydney by Professor J. T. Wilson, who has described in full the external appearances and measurements.[2] It is sufficient here to mention that its extreme length, measured along the dorsal contour, is 80 mm.

The head was split sagittally some distance from the middle line, and the larger piece, after being embedded in celloidin, was cut in a complete series of coronal sections, each 50 μ thick. These were stained with hæmatoxylin and decolourised with alcohol acidulated with picric acid, which afforded a very useful counter-stain. By means of the picric stain the nerve-fibres were clearly demonstrated, so that it was easy to make out their general distribution sufficiently accurately to compare

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[1] This paper forms part of a thesis dealing with the "Anatomy and Histology of the Cerebrum of the Non-placental Mammal," which was awarded the University Medal when presented to the examiners for the M.D. degree at the University of Sydney, March, 1895. The account of the gross anatomy is now being published elsewhere. The account of the histology of the adult brain will be published shortly.

[2] "Description (with figures) of a Young Specimen of Ornithorhynchus anatinus," 'Proceedings of Linnean Society N.S.W.,' vol. ix, part 4, 2nd series) p. 682.

with Weigert- and Golgi-stained specimens of the adult brain. For the opportunity of examining this valuable series I am deeply indebted to the generosity of Professor Wilson, whose kindly interest and valuable advice I gratefully acknowledge.

In recording the disposition of parts in a single stage of a developing brain, the account, in the absence of other stages to show the origin and destiny of the various regions, must be almost purely descriptive. This paper, therefore, will indicate the apparent differences in the specimen under discussion from the ordinarily accepted account, rather than attempt to express an opinion upon any of the morphological questions raised. Many interesting and important facts are elucidated, however, by a comparison with the adult brain, a description of whose histology forms the bulk of the thesis of which this paper constitutes a part.

A comparison with some valuable serial sections of fœtal Perameles and Macropus in various stages of development has thrown a considerable amount of light upon many otherwise obscure points. These specimens were placed at my disposal by Professor Wilson and Mr. J. P. Hill. I have also examined some imperfect series of brains of fœtal Phalangista. Several fœtal Echidnæ, which were lately received, are unfortunately not ready for examination, but will be described subsequently.

The literature of this subject is very scanty and incomplete. Before the Linnean Society of New South Wales, Dr. C. J. Martin and Mr. J. P. Hill recently described the condition of the neural plate in the early embryo of Platypus,[1] and Selenka has described early stages of the Opossum brain.[2] C. L. Herrick has published brief notes on, and figured sections of, the fœtal brain of Didelphys.[3] Osborn,[4] in his well-known paper upon the corpus callosum, described the hippocampal

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[1] "On a Platypus Embryo from the Intra-uterine Egg," 'Proceedings Linnean Society of New South Wales,' vol. ix, part 4, 2nd series, p. 736.

[2] 'Das Opossum,' Wiesbaden, 1887.

[3] 'Journal of Comparative Neurology,' 1894.

[4] 'Morphologisches Jahrbuch,' Bd. xii.

region of the cerebrum of pouch specimens of Macropus of various ages. These brief notes are all that I know referring to the development of the brain of the non-placental mammal.

In connection with Osborn's work, one cannot refrain from expressing regret that he was so biassed by his previous work upon the Amphibian and Sauropsidan cerebrum (Part I of his paper) as to misrepresent the condition which obtains in the young kangaroo. I am well acquainted with the deceptive appearance which is presented by the brain of the fœtal Macropus, especially when coloured with ordinary nuclear stains—an appearance which lent itself so unfortunately to Osborn's purpose; but the important position occupied by the marsupial in his series should have demanded a more critical examination than his paper indicates. For, as the connecting link between the whole sub-mammalia—to which his argument mainly applied—and the mammalia—to which alone can the distinguishing names be applied a priori—Macropus formed the link upon which the cohesion of the whole chain of his argument depended. By his erroneous interpretation of the condition in Macropus his argument lost all its cogency; for in showing, as he clearly did, the homology of that commissural band, which in the non-placental mammal is undoubtedly fornix commissure, with the dorsal commissure of Sauropsida and Amphibia, he prepared the way for the statement that the corpus callosum—as distinct from the fornix commissure—exists only in Placentalia.

In describing the fœtal brain there is, unfortunately, no satisfactory account of the adult brain to which one can refer. The accounts of Meckel and Zuckerkandl are quite valueless, from the fact that their descriptions were based upon very badly preserved material. Owen's description and Garner's notes are reliable as far as they go, but they are very brief and general, and deal only with the macroscopic anatomy, as also does Turner's paper. The only attempt at a systematic account of the histology—that of Hill—is so clearly biassed by its writer's previous work, that it gives a very erroneous and altogether misleading idea of the structures it is supposed to describe. In this account, therefore, such brief references will be made to the histology of the adult brain as are necessary to a proper understanding of the fœtal structures.

Forming as it does the link between the Mammalia and the lower Vertebrates, Ornithorhynchus occupies a position of supreme importance and interest to the morphologist. This importance is enhanced in the case of the brain, because this organ presents a number of very significant transitional features, several of which shed an important light upon the morphology of the cerebrum in the whole Vertebrate series. In addition there are a number of purely "individual" features—notably the enormous development of the trigeminal nerve and sensory tract—which give added interest to the study. Although in the histological differentiation of its parts, and in their general arrangement, the cerebrum of Platypus clearly conforms to the mammalian type, yet numerous features—such as the arrangement of the hippocampus, the disposition of the structures in the lamina terminalis, and the "precommissural area"—indicate its close Sauropsidan affinities. It is of interest to note that the resemblances to the lower brain are even more marked in the fœtus under consideration than in the adult.

General Account of the Fore-brain.

At the outset one is immediately confronted with the difficulties of the vexed question of nomenclature. With the increasing knowledge of brain anatomy it is perhaps only natural that more exact divisions and distinguishing terms, more in accordance with the advanced ideas, should be introduced. But when familiar terms are used in an altogether unfamiliar sense, or applied to entirely different parts of the brain in order to give place to new terms no more appropriate than those they supersede, the enormous intrinsic difficulty of this subject becomes seriously increased, and an undesirable element of confusion is introduced. The accurate system of nomenclature introduced by His loses much of its value by a confusing application of Huxley's terms "prosencephalon" and "thalamencephalon" in quite a different sense from that in which they are universally used, which must prevent the general acceptance of his suggestions. Although His' system of nomenclature is otherwise very convenient for descriptive purposes, the morphological value of his divisions is seriously open to question, especially the somewhat arbitrary limits to his "Endhirn." The nomenclature of v. Kupffer seriously adds to the confusion. One cannot but admire the exactness of Burt Wilder's definitive terms, but they are so uncouth and bizarre that the English student has to learn a new language before he can master the simplest description. In this paper the most unambiguous terms will be selected from the different systems, the alternative names being indicated in brackets; but as far as possible Huxley's well-known nomenclature will be employed.

Each cerebral hemisphere consists of an ovate mass, attached to the lateral aspect of the front end of the neural tube. The maximum length of each hemisphere, including the bulbus olfactorii, is 5·15 mm., and at its mid-point its height and depth are about half that measurement. The diencephalon (with the median part of the "Endhirn"), whose extent is schematically represented by the shaded area in fig. 1, is of the same depth as the posterior part of the hemisphere, but is much shorter. Posteriorly the hemisphere overlaps the mesencephalon (*mes.*) to a slight extent.

In a median sagittal section through the fore-brain, which is represented somewhat diagrammatically in fig. 2, the optic nerve is seen as a prominent object (*opt. n.*) in the floor, so that it forms a convenient starting-point. Immediately behind the optic nerve the floor sinks to form the recessus infundibuli (*r. i.*) of His (recessus postopticus of Burckhardt), from the posterior extremity of which the tubular hypophysis (*hyp.*) extends at first downwards, and then bends forwards at its extremity. The anterior wall of this extremity contains a number of neuroblasts and a distinct layer of nerve-fibres, which extends upwards on to the floor of the third ventricle. The bent extremity of the tubular hypophysis is closely surrounded by the large glandular (buccal) part of the hypophysis (*pit.*), which extends forwards for a considerable distance. It consists of a dense mass of highly convoluted tubules (fig. 11, *pit.*), lined with cubical epithelium. Immediately in front of the optic chiasma the floor again becomes depressed (fig. 2, *r. o.*), and on either side of the middle line forms a distinct recess (fig. 11, *r. o.*). A comparison with the early stage of the Perameles brain shows that this recess is the remains of the optic diverticulum, and therefore corresponds to His's recessus opticus (præopticus—Burckhardt). According to His, the recessus opticus corresponds to the anterior extremity of the limiting furrow (Grenzfurche) between his alar (Flügelplatte) and basal (Grundplatte) laminæ, to which Reichert has given the name "sulcus Monroi," without, however, recognising its important morphological significance.

Immediately in front of the recessus opticus the median wall takes a sudden bend into the vertical direction, and at the same time becomes enormously thickened to form a large mass rhomboidal in section (fig. 2, *l. inf.*), which His calls the "lamina terminalis" and Burckhardt the "lamina infra-neuroporica." According to His it is formed by the meeting and fusion in the middle line of his Flügelplatten, but according to v. Kupffer and Burckhardt it forms part of the floor (Bodenplatte). The researches of His seem to indicate clearly enough that it corresponds to part of the frontal suture (Schlussnaht), but more convincing evidence is required before it can be granted that it is formed purely from the Flügel-, and not also from the Grund-, platte. This question will be again referred to later on. In the dorsal part of the lamina infra-neuroporica a large rounded mass of fibres will be seen (*a. c.*) near the posterior surface. This is the anterior commissure. In all Vertebrates this phylogenetically very ancient and primitive connecting link between the two hemispheres crosses the middle line in the same position in the lamina infra-neuroporica, so that it forms an easily recognisable basis for comparing the perplexing regions which surround it. Immediately in front and above it there is a small scattered bundle, consisting as yet of very few fibres, which also cross the middle line in the same lamina. This is the first rudiment of the fornix-commissure (fig. 3, *f. c.*). It will be noticed that it lies below the foramen of Monro and in the floor of a diverticulum of the third ventricle (figs. 2 and 3), which is often known as the ventriculus communis (Osborn). In the adult Ornithorhynchus brain the fornix commissure occupies a very different position, i. e. in front and above the foramen of Monro, and entirely dorsal to the third ventricle. This altered position of the commissure in adult Mammalia and many Sauropsida probably depends mainly upon the growth of the lamina terminalis, especially that part lying between the anterior and fornix commissures; but partly also on the backward growth of the hemisphere, which is accompanied by a corresponding growth of its dorsal commissure. In many Amphibia, where the lamina terminalis does not grow to the same extent as it does in the higher animals, the fornix commissure maintains into adult life a position exactly corresponding to that met with in the fœtal Platypus. In the arrangement of their commissures the Sauropsida are intermediate between the Amphibia and Prototheria.[1]

Above the lamina terminalis the median wall suddenly becomes thin again and forms a thin plate, which appears to spring from the anterior edge of the lamina terminalis. This thin wall (fig. 3, *r. n.*), which is distinguished by von Kupffer as the lobus olfactorius impar, bounds a little diverticulum (fig. 3*), which Burckhardt calls the recessus neuroporicus. The same region is distinguished by His as the angulus terminalis, and is regarded as the dorsal limit of the frontal suture line, and the last point to lose its connection with the ectoderm. Immediately dorsal to it there is a

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[1] Further and more detailed examinations of the cerebrum of the adult Ornithorhynchus and a number of reptiles since this paper was written have demonstrated a much closer resemblance between adult and fœtus than this paper indicates, as well as the marked similarity of both to the higher Reptilian condition. A more detailed account of the region of the commissures will be published in a short time.

small transverse layer (*l. sup.*), which Burckhardt calls the lamina supra-neuroporica, and describes as "ein kurzer ependymatöser Abschnitt, . . . der erste Abschnitt der Scheitelplatte." All authorities now seem to agree in regarding this as the anterior extremity of the roof (Deckplatte). This must be admitted if the angulus terminalis is really the dorsal extremity of the "vordere Schlussnaht." The lamina supraneuroporica takes a sudden bend backwards (fig. 3) to form a horizontal band, which gives origin in many lowly Vertebrates to the plexus inferiores, and in higher animals to the plexus laterales as well, or exclusively. In the specimen under consideration, however, although the plexus laterales do not actually spring from this lamina, they are formed from the caudal prolongations of its lateral parts (vide fig. 15) on either side of the paraphysis (*par.*). Immediately dorsal to this lamina the anterior wall of the third ventricle is bulged out to form a large sac (fig. 2, *par.*), which constitutes the paraphysis of Selenka, of which a fuller description will be given below.

The whole extent of the roof (actual) of the third ventricle as far back as the superior commissure (fig. 2, *s. c.*) is deeply invaginated to form a complex choroidal fold (fig. 2, *ch.* 3; also figs. 9—15), which later on forms the "diaplexus" of Wilder. It is evident, therefore, that no Zirbelpolster of Edinger (parencephalon, prepinealis Zwischenhirndach) exists in this brain, since the velum or origin of the median plexus extends right back to the superior commissure. The latter is a very small band of transverse fibres connecting the two ganglia habenulæ. Immediately behind the superior commissure is the epiphysis cerebri, which consists of a small solid clump of cells (fig. 2, *ep.*) with deeply stained nuclei, lying behind a small recessus pinealis and upon the posterior commissure (*p. c.*). The latter is a broad band of transverse fibres, and is now generally recognised as the limit of the diencephalon.

The constricted anterior pole of each hemisphere is distinguished as an olfactory bulb by the application of the olfactory ganglion to its periphery (figs. 18 and 4, *olf. g.*, *J. g.*).

On tracing the cerebrum caudally in a series of sections, the basal aspect of the olfactory bulb will be found to be continuous with two regions which already present distinct histological features, although there is little superficial indication of any such division. These two regions are the tuberculum olfactorium (figs. 6 and 7, *t. o.*)—a relatively large basal area next to the middle line—and the pyriform lobe, whose surface is covered by the already well-developed "external olfactory radiation" (*e. o. r.*) of Edinger. The tuberculum olfactorium only extends back as far as the lamina terminalis, but the pyriform lobe extends the whole length of the hemisphere (figs. 6—13, *pyr.* and *e. o. r.*). In the adult the pyriform lobe is limited laterally by a well-defined fissure (fissura rhinalis or ectorhinalis of Turner)—figs. 8 and 14, *f. r.*,—and is separated from the tuberculum olfactorium by a deep fissure (fig. 8, *f. er.*)—fissura endorhinalis of Turner. In the fœtus there is no sign whatever of the fissura ectorhinalis, although a shallow endorhinal groove (fig. 10, *f. er.*) is already to be made out. This appears to correspond to what His has wrongly called the rhinal fissure. If this is the case, he has excluded from his "lobus olfactorius" the pyriform lobe, which does not become superficially distinguished from the pallium (Turner) until late in ontogeny. In Notoryctes, even in the adult brain, no rhinal fissure appears to be present, and in Perameles nasuta it is very shallow and imperfect. The rhinal fissure appears late, not only in ontogeny, but also in phylogeny. It appears, therefore—and in this I am supported by His's figures—that the so-called rhinal fissure of the early human fœtus cannot be the ectorhinal—as His believed—but the endorhinal fissure.

The tuberculum olfactorium is not confined to the basal aspect of the cerebrum, but crosses the ventro-mesial angle to become continuous with the "precommissural area of the mesial cortex" (figs. 6 and 7, *p. a.*). In the fœtal brain there is no line of demarcation between these two regions, since they present exactly similar histological features, but in the adult (fig. 8 *) there is a clearly defined boundary line. The "precommissural area" extends from the mesial aspect of the olfactory bulb in front to the lamina terminalis behind (vide figs. 2 and 4, *p. a.*). The tuberculum olfactorium (locus perforatus anticus) and the precommissural area (gyrus subcallosus of Zuckerkandl) correspond to the "posterior olfactory lobule" of His. The whole of the mesial wall of the cerebrum dorsal to the precommissural area forms part of the rudimentary hippocampus (figs. 2, 6, and 7, *hip.*). It will be seen, therefore, that the hippocampus extends as far forwards as the olfactory bulb (the characteristic histological structure may be recognised at a distance of 150 μ behind the olfactory ganglion). The part of the region in immediate relation to the precommissural area is the rudimentary fascia dentata, the dorsal part being the "Anlage" of the cornu Ammonis. As it is traced backwards the hippocampus is found to pass to the dorsal side of the foramen of Monro (fig. 15) and choroid fissure, the ependymal choroid fold being attached to the ventral margin of the "Anlage" of the fascia dentata. The hippocampal rudiment is co-extensive with the fissura choroidea, and forms its dorsal boundary (figs. 9 to 13). In the greater part of its extent this hippocampal "Anlage" is bulged into the lateral ventricle, giving rise to a shallow trough (the "Bogenfurche" of Schmidt, fissura arcuata). To this trough the name "hippocampal furrow" ("Ammonsfurche" of Mihalkovics) may very appropriately be applied. It has an exact morphological significance, being strictly confined to the region which is to become hippocampus. It is clear, therefore, from the relations of the anterior extremity of the hippocampus, that the true Bogenfurche cannot form the "fissura prima" of His.

The position occupied by the hippocampus in this fœtus—entirely dorsal to the foramen of Monro and fissura choroidea—is typical of its true and essential relations in the whole Vertebrate series. The recognition of the homologous region in the sub-mammalian brain constitutes the key to the whole question of the nature of the commissures, because all the commissural fibres arising in this area must belong to the hippocampal or fornix commissure. In the adult Platypus there is no difficulty whatever in recognising the hippocampus, since its histological features, whether studied by aniline blue-black staining or by the methods of Weigert or Golgi, exactly resemble those of the higher mammal (figs. 8 and 14). Upon this fact largely depends the extreme morphological importance of the cerebrum of Ornithorhynchus. For while the topographical relationship of the Prototherian hippocampus resembles that of the Sauropsida, it at the same time presents quite as high a histological differentiation as is found in the Eutheria—a fact which renders its identification quite certain and easy. By comparison it is easy to identify the corresponding region in the fœtal brain, where the simplicity of its histological structure (fig. 15) and the absence of the complicated foldings and inrolling of the adult structure vividly recall the Sauropsidan hippocampus, and at a glance convinces one of the homology. In all adult Mammalia the pallium takes some share in the formation of the mesial cortex (figs. 8 and 14, *p.*), but in the fœtus the hippocampus extends right up to the supero-mesial angle, so as to exclude the pallium from any share in the formation of the mesial wall. Similarly in the reptile the hippocampus forms the greater part of the mesial wall, and extends forwards above the commissures towards the anterior pole of the cerebrum, as Edinger and Meyer have described. Not only does it form the mesial wall, but it extends on to the dorsum of the cerebrum. Herrick, by attempting to draw too close a comparison with the Eutherian brain (where this region is greatly disturbed by the development of a corpus callosum), would limit the hippocampus to the posterior extremity of the hemisphere. This is a gratuitous assumption, utterly unsupported by any evidence.

The whole of the dorsal and lateral aspects of the surface of the hemisphere, from the hippocampus above to the pyriform below, constitutes the pallium (Turner). Both in its ontogenetic and phylogenetic history it continues to increase in extent after the more ancestral hippocampal and pyriform regions have reached their full development, both in size and differentiation of structure. Thus on the one hand it encroaches upon the mesial aspect of the cerebrum, and has a marked influence in the production of the complicated inrolling of the hippocampus; on the other hand, it tends to overlap the pyriform lobe, producing the rhinal (ectorhinal) fissure (fig. 14, *fr.*).

The corpus striatum (fig. 10, *c. s.*) is a large mass, which is closely related ventrally to the tuberculum olfactorium and pyriform lobes. Below the foramen of Monro it is closely connected (fig. 10) with the lamina terminalis, and behind the foramen it is connected with the "Anlage" of the optic thalamus, which lies internal and entirely dorsal to it. The internal capsule is a very insignificant tract, consisting of a few scattered fibres (fig. 11, *c. i.*), which are only to be found in one region. Even in the adult (vide fig. 8) it forms a very scattered and relatively small system, which is indicative of the intermediate position of Platypus between the Sauropsida, which have no proper internal capsule (Meyer), and the marsupials, where it is a well-formed fibre tract.

Behind the foramen of Monro the pyriform lobe (figs. 13 and 14, *pyr.*) is directly continuous with the corpus striatum (*c. s.*), the connecting bridge being the rudiment of the nucleus amygdalæ (*n. a.*), which in the fœtus gives rise to an enormous tænia semicircularis (*t. s.*), or stria terminalis.

The foramen of Monro forms a rounded aperture situated upon the lateral wall of the anterior extremity (Endhirn of His) of the median cavity of the fore-brain, about midway between the roof and the floor (fig. 2, *f. m.*). To be more exact, it opens into the lateral ventricle from a small recess of the third ventricle[1] above the lamina infra-neuroporica, which is bounded anteriorly by the angulus terminalis (fig. 3, *r. n.*) and lamina supra-neuroporica (*l. sup.*), and dorsally by the horizontal extension backwards of that lamina. Into the dorsal aspect of this recess (fig. 15, *a.*) and in front of the foramen of Monro, the paraphysis opens (*par.*). The foramen of Monro is bounded dorsally in the whole of its extent by a

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[1] "Ventriculus communis," "ventricle of telencephalon," "aula."

large mass of neuroblasts (fig. 10, *th.*), the rudimentary optic thalamus. As this mass is traced caudally (figs. 11, 12, and 13) it gradually increases in size, forming a large bulging of the Flügelplatte in the posterior part of the diencephalon. Where it forms the dorsal boundary of the foramen of Monro (fig. 11) this thalamic rudiment consists of three distinct parts—a mesial ependymal layer, an intermediate neuroblastic mass, and a lateral nerve-fibre layer. The connections of the latter cannot be accurately traced, but it appears to be the tænia thalami.

As this thalamic rudiment is traced forwards above the foramen of Monro the neuroblastic mass gradually diminishes in size, until at the extreme anterior limit of the foramen of Monro (fig. 15) it disappears altogether, only the ependymal and nerve-fibre layers being left. The nerve-fibre layer also soon disappears, leaving the ependymal layer only.

The point at which the thalamic rudiment ceases corresponds exactly to the anterior limit of the foramen of Monro, so that the latter is separated from the roof (Deckplatte) by the whole width of the rudimentary optic thalamus.

The foramen of Monro is further bounded above by the epithelial fold which forms the rudiment of the choroid plexus of the lateral ventricle, and which is attached to the ventral border of the fascia dentata (fig. 15, *f. d.*).

Below, the foramen is bounded by the lamina infra-neuroporica (figs. 2 and 10), which here becomes continuous with the corpus striatum (vide fig. 10). Posteriorly the foramen is bounded by the junction of the thalamic rudiment with the corpus striatum (fig. 11). Anteriorly the boundary is formed (vide the right side of fig. 15) by the fusion of the lamina terminalis with the ventral border of the fascia dentata. If, therefore, we leave out of consideration the choroid plexus of the lateral ventricle, it is evident that the foramen of Monro has no immediate relation to the Deckplatte in this brain. Before discussing the relation of the hemisphere to the Deckplatte the paraphysis must be described.

The Paraphysis.

In describing the structures met with in a median sagittal section it was mentioned that the dorsal part of the (actual) anterior wall of the median cavity of the fore-brain was bulged out to form a large sac. The corresponding structure is well seen in the early embryo of Perameles (fig. 16, *par.*). Ventrally it opens into the cavity of the "telencephalon" of His by a narrow neck. Posteriorly its lumen becomes suddenly restricted by two large bulgings from the lateral walls into the cavity. These bulgings are the anterior extremities of the optic thalami (fig. 17). On comparing the appearance of the Perameles brain with that of Ornithorhynchus (fig. 15) the general resemblance is at once apparent, the only essential difference being the presence of a large complicated median fold of the roof of the paraphysis in Platypus. This is the anterior extremity of the "Anlage" of the plexus choroideus medius—(*ch.* 3), the "diaplexus" of Wilder. In the early fœtal brain of Perameles the median choroidal fold of the third ventricle is not yet developed, although that of the lateral ventricle (fig. 16) is well formed, so that the velum and roof of the paraphysis form a simple transverse band. In the Platypus embryo, however (fig. 2), a well-developed choroidal fold extends from the superior commissure to the lamina from which the lateral plexus arises, completely invaginating the paraphysis (figs. 7, 9, and 15) in the middle line. In Platypus the transition from optic thalamus to paraphysis is a very gradual one, so that in examining a series of coronal sections the lateral walls of the diverticulum would seem to be merely the forward continuation of the ependymal layer of the Flügelplatten (fig. 15). This structure has attracted a considerable amount of attention since it was first noticed, and numerous names have been applied to it,[1] and hypotheses

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[1] "Für die vordere Epiphyse, dem Adergeflechtknoten Goettes den Burckhardt in früheren Arbeiten zuerst Plexus choroideus superior, später Conarium genannt hatte, braucht er neuerdings mit Kupffer die von Selenka herrührende Bezeichnung Paraphysis."—Froriep.

advanced to explain it. As yet, however, its significance is veiled in mystery. In this brain it is enclosed in a sheath of dura mater formed by the splitting of the falx cerebri (fig. 7, *fx.*), and it is closely surrounded by a number of very large vessels. From the close relation of the organ to these large vessels, it has been suggested that it may have some nutritive function before the "diaplexus" is developed (Gage).

The Relation of the Roof (Deckplatte) to the Third Ventricle and Foramen of Monro.

In describing the foramen of Monro, it has already been seen that the Deckplatte ("Scheitelplatte" of Burckhardt) is separated from its dorsal aspect by the whole width of the thalamic rudiment. The foramen opens into the small dorsal recess (fig. 15, *d.*) of the third ventricle which is bounded anteriorly by the angulus terminalis and the lamina supra-neuroporica. The latter structure is considered to form part of the Deckplatte, and the continuation backwards of its horizontal part in this specimen (fig. 3) gives rise to the choroid plexus of the lateral ventricle (fig. 15). In fact, it is generally considered that the lateral plexus is a derivative of the Deckplatte (Minot). If this be so, it must be admitted that the foramen of Monro and the hemisphere are in immediate relation to the Deckplatte. If this be so, the different parts of the morphological roof will be seen to be widely separated in the region of the foramen of Monro (fig. 10). Above there is the undoubted roof of the "aula;" whereas laterally, between the thalamic rudiment, and the hippocampal rudiment, is the lateral plexus whose epithelial covering is supposed to be a derivative of the Deckplatte (Minot). If, however, the hemisphere, as is generally supposed, extends up to the Deckplatte, how does the optic thalamus come to occupy the position which is roughly represented in fig. 10, *th.*? Even admitting that the choroid plexus of the hemisphere is a derivative of the roof which has extended backwards, invading, as it were, the mesial hemisphere wall, only two alternatives appear to remain to explain the position of the thalamus in this specimen. Either the hemisphere brain develops from the lateral aspect of the brain-tube on the ventral side of the anterior extremity of the thalamus, or the latter in its growth invades the Deckplatte. All the appearances, both in this brain and in those of all the Perameles and Macropus specimens, are against the latter hypothesis. It would appear that the hemisphere develops on the ventral side of the anterior extremity of the thalamus.[1] The lateral walls of the paraphysis in this specimen look deceptively like anterior extensions of the Flügelplatten.

Taken as a whole, however, the general disposition of parts in the brain under consideration can be harmonised with the account of His. On tracing the pars subthalamica (Forel) or hypothalamus (Waldeyer) forwards in the series of sections, it will be found to become continuous with a large mass lying on the mesial side of the corpus striatum and on the ventral side of the optic thalamus. This mass (fig. 11, *), which forms the lateral wall of the ventral part of the third ventricle, on being traced forwards will be found (fig. 10) to become continuous with the lamina infra-neuroporica. What is this mass? According to the hypotheses of Burckhardt and v. Kupffer it must be considered simply as the anterior extremity of the Grundplatte; whereas, according to His, it must be the anterior end of the Flügelplatte which has become bent towards the base of the brain. In fig. 11 the fibres of the external capsule (*c. e.*) will be seen extending into the mass to cross the middle line (fig. 10) in the lamina infra-neuroporica, so that the mass in question is divided into two parts—a ventral, which in the adult is easily recognised as the tuberculum olfactorium; and a dorsal, which in the adult is corpus striatum. In the adult the anterior extremity of the optic thalamus fuses with the lamina infra-neuroporica ("septum pellucidum") above the anterior commissure, so that the combined mass appears to rest upon the anterior commissure. It is almost impossible

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[1] Without earlier developmental stages no opinion can be expressed concerning these questions (25th April, 1896).

(fig. 8) to draw any line of demarcation between corpus striatum and tuberculum olfactorium. This being the case, this region (fig. 11, *) may doubtfully be homologised with the corpus striatum, as His has done. It will be noted from the figures that the transition from undoubted hypothalamus to this doubtful region takes place at the optic chiasma—the termination of His's "Grenzfurche." If, therefore, it is granted that this doubtful area (*) is corpus striatum, it follows that the hemisphere brain extends down as far as the optic recess, as His has described in the case of the human fœtus.

Having now given a general account of the disposition of parts, there are certain regions which need further consideration.

The Olfactory Bulb.

This part of the cerebrum, whose structure is roughly represented in transverse section in fig. 18, consists of four distinct layers, as Vignal[1] has pointed out. Immediately surrounding the ventricle there is a thick mass of small cells with deeply stained nuclei. This is the ependymal layer (ε). Surrounding it there is a stratum of about the same thickness, but much lighter in appearance—the layer of nerve-cells (δ). Examined with the high power, this is found to consist of a mass of well-formed neuroblasts (fig. 19). Posteriorly this layer is found to be continuous with the essentially nervous part of the cerebral cortex. It is probable that in the adult the neuroblasts which compose this layer mostly develop fibres of the pars olfactoria of the anterior commissure. The most superficial layer is imperfect, consisting of two distinct ganglionic masses, each composed of neuroblasts like the second layer. The larger mass (*olf. g.*) covers the whole inner surface of the bulb, and extends on to the ventral and slightly on to the dorsal aspects of the bulb. In this region the true olfactory nerves terminate. Hence I have distinguished it as the "olfactory" ganglion. On the outer aspect of the bulb there is a second smaller mass (*J. g.*), presenting exactly similar histological features. In this mass the fibres derived from

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[1] Quoted in Minot's 'Human Embryology.'

Jacobson's organ terminate. Hence I have distinguished it as the "ganglion of Jacobson's organ." The further significance of this arrangement I have discussed in the 'Anatomischer Anzeiger.'

Separating both ganglionic masses from the second or nerve-cell layer there is a distinct layer of nerve-fibres (γ), which form the root bundles of the "olfactory [internal and external] radiations" of Edinger. It corresponds to the molecular layer or "Randschleier" of the cortex cerebri.

The surface regions of the hemisphere are already differentiated into two histologically distinct districts, (i) a basal region (comprising the tuberculum olfactorium and the precommissural area), which presents an amorphous and undifferentiated structure; and (ii) a dorso-lateral region—the pallium,—which already exhibits characteristically specialised features. Interposed between these regions on either side there are two districts—the hippocampus and pyriform lobe—which present intermediate or transitional features. These divisions have a further and much wider significance. The undifferentiated basal regions—including not only the precommissural area and tuberculum olfactorium, but also the prosencephalic part of the olfactory bulb, the corpus striatum and lamina terminalis ("septum lucidum")—are the ancient parts of the brain phylogenetically, and develop early in ontogeny. The transition regions appear next in phylogeny—the hippocampus and then the pyriform lobe. The highly differentiated pallium appears last, and continues to increase in size and in histological specialisation long after the other regions have reached the acme of their evolution, or are even in their decline. Thus in the Prototheria the hippocampus and pyriform have already reached the height of their development, whereas the pallium progressively increases in size and complexity in the Eutherian series up to Homo, in whom the lowest stratum—the olfactory—the tuberculum olfactorium and precommissural area are disappearing.

The Pallium.

Five distinct layers are recognisable in the pallium (fig. 20). These are arranged in the following order—proceeding from the surface, and comparing with the layers of the olfactory bulb.

Pallium (fig. 20).	Olfactory bulb (fig. 18).
———	1. The olfactory ganglion (an added layer).
1. The molecule layer *f*)	2. The nerve-fibre layer (γ).
2. The superficial nerve-cell or "mantle" layer (*e*)	3. The layer of nerve-cells (δ).
3. The middle nerve-fibre layer (*d*)	
4. The deep nerve-cell layer (*c*)	
5. The ependymal layer (*a*)	ependymal layer (ε).

The superficial or molecular layer of the pallium forms a clear peripheral band containing only scattered cells and nerve-fibres. It is the rudiment of the molecular layer of the adult cortex, and also appears to correspond to the "Randschleir." In the pyriform lobe and hippocampus (fig. 10) it becomes greatly thickened. In the basal regions it does not exist as a distinct layer.

The superficial nerve-cell layer (*e*)—the mantle layer—consists of a very regular stratum of densely packed neuroblasts, from which the most important constituents of the cortex develop.

The middle nerve-fibre layer (*d*) contains a large number of nerve-fibres and scattered neuroblasts. It appears to be the "Anlage" of the corona radiata, although in the region of the corpus striatum it is separated from the corona proper by a large mass of cells.

The deep nerve-cell layer (*c*)—the Rolando-cell layer of Ludwig Löwe—is more or less intimately joined to the ependymal layer (*a*), but a slight interval (*b*) where the cells are not so closely packed indicates the line of separation. The destiny of this layer is uncertain.

"The Precommissural Area of the Median Cortex."

The general relations of this region have already been described. In a scheme (fig. 5) which indicates the hypothetical arrangement of parts in the anterior wall of the primitive brain-tube it will be seen that the olfactory bulbs (*olf. g*), situated at each lateral angle, are separated by a broad plate of nervous tissue. With the development of the hemispheres this plate becomes bent forwards on either side of the middle line. The lateral part, which now forms a sagittally placed wall (*p. a.*), is the "precommissural area," and the median band connecting the two "areæ" is the lamina terminalis (*l. t.*), which later develops into the septum lucidum. His calls the "precommissural area" part of the "olfactory lobe." In fact, as the homologue of Zuckerkandl's "gyrus subcallosus," it must form part of His's "posterior olfactory lobule." On morphological and histological grounds, however, the precommissural area cannot be separated from the rudiment of the "septum lucidum" (compare figs. 7 and 9), both having equal claims to be considered as parts of the "olfactory lobe" or rhinencephalon.

The Hippocampus.

As the pallium (fig. 15, *p.*) is traced round the supero-mesial angle of the hemisphere the cellular elements will be found to undergo a striking rearrangement. The molecular or superficial layer (fig. 15) will be found to become very much broader than it is in the pallium, and, by comparison with later stages of Perameles, is readily recognised as the homologue not only of the molecular layer, but also of the stratum lacunosum and stratum radiatum of the adult hippocampus. The cells of the superficial nerve-cell layer lose their densely packed arrangement, and the cells of the second, third, and fourth layers become directly continuous with a column of somewhat scattered cells, which produce the pyramidal and polymorphous cells of the hippocampus. As this cell column approaches the margin of the hemisphere the cells become more densely packed again to form the rudimentary fascia dentata (fig. 15, *f. d.*). Since, in the hippocampus, the cells of the fourth layer of the pallium separate from the ependymal layer, the latter appears as a much more sharply defined layer (fig. 15). Between the ependymal layer and the irregular column of neuroblasts there is a relatively wide nerve-fibre layer—the alveus. This is the homologue of and is continuous with the fifth layer of the pallium.

This simplicity of hippocampal formation presents a close resemblance to the corresponding region in the reptile brain. The anterior extremity of the hippocampus in all non-placental mammals maintains this primitive simplicity of structure into adult life (fig. 8). The much-disputed questions of homology will be discussed later on in dealing with the histology of the adult organ.

The fornix system is as yet imperfectly formed, and presents a reptilian-like simplicity of arrangement. Although the descending fibres of the fornix (figs. 7, 9, 15, *d.f.*) are already well formed, there are only a few scattered commissural fibres in the lamina infra-neuroporica.

The Pyriform Lobe.

As the pallium is traced into the pyriform lobe (figs. 6, 7, 9—12) the molecular layer suddenly increases in thickness. This layer contains the fibres of the external olfactory radiation (*e. o. r.*). The superficial nerve-cell layer suddenly becomes more scattered, and loses the regular appearance found in the pallium proper. This layer corresponds to the layer of "double pyramids" (Kölliker) found in the adult pyriform lobe (fig. 8). The other layers of the pallium are represented in the pyriform lobe merely by diffusely scattered nerve-cells. Behind the lamina terminalis the pyriform lobe is continuous mesially with a large mass of diffusely scattered nerve-cells—the nucleus amygdalæ.

The Corpus Striatum and Optic Thalamus.

The corpus striatum (*c. s.*) forms a large mass projecting into the lateral aspect of the lateral ventricle, and lying in the concavity of the external capsule (*c. e.*). Anteriorly it is directly continued into the tuberculum olfactorium (figs. 7 and 8), which Ganser calls the "cortex of the head of the corpus striatum." Posteriorly it is closely connected with the pyriform lobe (figs. 12—14) through the intermediation of the nucleus amygdalæ. Except in the one region immediately behind the foramen of Monro (fig. 11), there is no sign of any division into caudate and lenticular nuclei by an internal capsule.

Histologically the rudiment of the corpus striatum presents numerous well-formed neuroblasts, which give rise to nerve-fibres, whose connections will be described immediately.

The optic thalamus presents in all sections a large mass of neuroblasts, which varies in size and appearance in different sections (figs. 10—13). The only other structure yet differentiated in the thalamic region is the ganglion habenulæ (fig. 13, *g. h.*).

The great thalamic nucleus, which appears to correspond to the "centre mediane de Luys" (Löwe and Minot), is relatively very largely developed in this fœtus, and, as may be seen from fig. 14, this precocious development is an indication of the huge proportions of the adult optic thalamus, whose enormous growth in the lateral direction reduces the corpus striatum in this region to a very thin lamella (fig. 14, *c. s.*).

Connecting the great thalamic nucleus and the corpus striatum there is a huge bundle of fibres (fig. 12) which stands out extremely clearly, since there is practically no internal capsule to obscure it. By means of this fibre tract, which apparently corresponds to Edinger's "radiatio strio-thalamica,"[1] a very intimate connection is established between the corpus striatum and cortex cerebri (pallium) on the one hand, and the "great thalamic nucleus" on the other. A large proportion of these fibres appear to arise from neuroblasts in the corpus striatum. Others appear to spring from the thalamus.

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[1] Only in part.

The following anatomical facts concerning the brain of Platypus appear to be associated with one another :—an enormous trigeminal nerve; a huge development of substantia gelatinosa Rolandi in pons and medulla, and fillet in the mesencephalon; a large and precocious development of the optic thalamus (where in the adult the great bulk of the fillet terminates), and an exceptionally abundant supply of fibres connecting the latter with the corpus striatum and cortex cerebri. The important bearing of this upon the vexed question of the termination of the fillet (lemniscus) will be discussed later on when dealing with the adult. It may be stated here, however, that an examination of the Ornithorhynchus brain clearly shows that the great majority of the fillet fibres terminate by terminal arborisations around the large multipolar cells of the optic thalamus, which, in turn, are connected with the cortex cerebri and corpus striatum.

The huge stria terminalis, which arises from the neuroblasts in the nucleus amygdalæ, extends vertically upwards behind the "radiatio strio-thalamica," and then takes a sudden bend into the horizontal plane (fig. 12, *t. s.*). The picric stain does not permit one to accurately trace its anterior connections.

The account of the optic nerve and its central connections will be deferred until the rest of the brain is under consideration. Before then I hope to examine a series of fœtal Echidnæ, and to be able to supplement these fragmentary and imperfect notes.

Literature.

The last few years have yielded an unusually rich and abundant contribution to the knowledge of the difficult subject of cerebral morphology; and in spite of the different interpretations of the vast mass of data collected, there is, beneath all the conflicting statements, a remarkable degree of uniformity in the essential facts of cerebral development and phylogeny.

No purpose would be served in a descriptive paper such as this in quoting all this bulky literature. In a paper entitled "Die Homologien des Zwischenhirndaches und ihre Bedeutung für die Morphologie des Hirns bei niederen Vertebraten," which appeared in the 'Anatomischer Anzeiger,' Bd. ix, Nos. 5 and 6, p. 152, Rud. Burckhardt began a discussion, which was vigorously carried on in the same journal by Studnicka and Rabl-Rückhard. Before the Anat. Gesellschaft W. His discussed the same subject. His paper was subsequently published in the 'Arch. f. Anat. u. Entw.; 1893, p. 157, "Über des frontale Ende des Gehirnrohres." In the same number His published a paper on nomenclature, "Vorschläge zur Eintheilung des Gehirns."

C. von Kupffer's contribution to the argument is found in his 'Studien zur vergl. Entwickelungsgeschichte des Kopfes des Kranioten,' and also in the report of the Anat. Gesellschaft.

An admirable summary of Burckhardt's views is found in his paper entitled "Der Bauplan des Wirbelthiergehirns" in 'Morpholog. Arbeiten,' hrsg. v. G. Schwalbe, Bd. iv, 1894, p. 131.

Critical digests of the literature will be found in Froriep's paper, "Entwick. des Kopfes" ('Ergebnisse der Anatomie und Entwickelungsgeschichte,' hrsg. v. F. Merkel und R. Bonnet, Bd. iii, 1893); also the papers of Sorenson and Herrick in recent numbers of the 'Journal of Comparative Neurology.'

To Dr. L. Edinger I am indebted for a copy of his paper entitled "Die Faserung aus dem Stammganglion Corpus Striatum" ('Verhdl. Anat. Gesellschaft,' May, 1894), containing an account of the "radiatio strio-thalamica."

EXPLANATION OF PLATE 11.

Illustrating Dr. G. Elliot Smith's paper on "The Brain of a Fœtal Ornithorhynchus."

Fig. 1.—Diagrammatic representation of the brain of fœtal Ornithorhynchus, reconstructed from serial sections × 6. The Zwischenhirn (*di.*), which is shaded, is represented as though the cerebrum were transparent. The oval cerebral hemisphere is seen to slightly overlap the mesencephalon (*mes.*). *b.o.* Bulbus olfactorii. *J.* Jacobson's organ. *n.J.* Nerves from

Jacobson's organ. *n. olf.* Olfactory nerves. *opt. n.* Optic nerve. *n.* 3. Oculo-motor nerve. *G. g.* Gasserian ganglion.

FIG. 2.—Scheme of median sagittal section of the fore-brain, the hemisphere indicated by dotted lines. *b. o.* Bulbus olfactorii. *p. a.* The "precommissural area of the median cortex." *hip.* The rudiment of the hippocampus (including the fascia dentata). *p. c.* Posterior commissure. *e. p.* Epiphysis cerebri (pineal). *s. c.* Superior commissure. *vel.* Velum. *ch.* 3. "Diaplexus" of Wilder. *par.* "Paraphysis" of Selenka. *f. M.* Foramen of Monro. *a. c.* Commissura anterior. *l. inf.* Lamina infra-neuroporica. *r. o.* Recessus opticus of His (præopticus—Burckhardt). *opt. n.* Optic nerve. *r. i.* Recessus infundibuli of His (r. postopticus—Burckhardt). *hyp.* Hypophysis cerebri. *pit.* Pituitary gland.

FIG. 3.—Part of Fig. 2 enlarged.—*l. sup.* Lamina supra-neuroporica of Burckhardt. *r. n.* Recessus neuroporicus (angulus terminalis, lobus olfactorius impar). *f. c.* Fornix commissure.

FIG. 4.—Scheme of horizontal section through a mammalian brain, to show the relation of the "precommissural area" (*p. a.*) to the lamina terminalis (*l. t.*) and olfactory bulb (*b. o.*). *Olf. g.* Olfactory ganglion. *c. s.* Corpus striatum. *th.* Diencephalon (His).

FIG. 5.—Scheme of hypothetical arrangement of the terminal plate of the brain-tube, to show that the precommissural area and lamina terminalis are parts of one structure. Compare with Fig. 4.

FIGS. 6, 7, 9, 10, 11, 12, and 13 are a series of coronal sections of the fœtal Ornithorhynchus brain, each × 12. The hippocampal rudiment (*hip.*) may be seen extending through all the sections, lying in front above the precommissural area (*p. a.*), which in turn is continuous with the tuberculum olfactorium (*t. o.*) and pyriform lobe (*pyr.*), on whose surface is the "external olfactory radiation" (Edinger), *e. o. r.* *p.* Pallium. *c. e.* External capsule.

FIG. 6.—Counting the sections from before backwards (each section being 50 μ thick), this is No. 24. It passes a short distance behind the olfactory bulb.

FIG. 7.—(No. 35.) Just in front of the lamina terminalis. The falx cerebri (*fx.*) splits above to enclose the paraphysis (*par.*) and a number of large vessels. *d. f.* Descending fornix fibres (Reichbundel).

FIG. 8.—Section through the corresponding region in the adult brain. Weigert stain × 3. *p.* Pallium. *h. f.* Fissura hippocampi. *f. d.* Fascia dentata. *d. f.* Descending fornix fibres. *p. a.* Precommissural area. *t. o.* Tuberculum olfactorium. * Line of demarcation between *p. a.* and *t. o.* *f. er.* Fissura endorhinalis (Turner). *pyr.* Pyriform lobe. *e. o. r.* External olfactory radiation. *f. r.* Fissura ectorhinalis. *c. i.* Internal capsule in corpus striatum (*c. s.*). *c. r.* Corona radiata. *alv.* Alveus.

Fig. 9.—(No. 38). Passing just in front of the foramen of Monro on the right side, and through it on the left. References as above.

Fig. 10.—(No. 47.) Through foramen of Monro (*f. M.*). *a. c.* Anterior commissure. *th.* Optic thalamus. *Bf.* The "hippocampal furrow" (Bogenfurche).

Fig. 11.—(No. 51.) Just behind the foramen of Monro. *l. f.* Longitudinal furrow. *r. o.* Recessus opticus. *pit.* Pituitary gland. *G. g.* Gasserian ganglion. *c. i.* Internal capsule.

Fig. 12.—(No. 80.) *g. h.* Ganglion habenulæ. *n. th.* Nucleus thalami (centre mediane de Luys). *r. st.* "Radiatio strio-thalamica" of Edinger. *t. s.* Stria terminalis (running horizontally). *G. g.* Gasserian ganglion. *V. n.* Fibres of fifth nerve proceeding from *G. g.* to the pons.

Fig. 13.—(No. 89.) *n. a.* Nucleus amygdalæ, from which the large stria terminalis (*t. s.*) arises and passes vertically upwards to cross on the dorsal aspect of the radiatio strio-thalamica (*r. st.*). *pons.* The "tuberculum quinti" of the pons Varolii.

Fig. 14.—Section through the adult Ornithorhynchus brain corresponding to Fig. 12 in the fœtus. × 2. References as above. *m. c.* Middle (soft) commissure. *p. subt.* Pars subthalamica (hypothalamus of Waldeyer).

Fig. 15.—Part of Fig. 9 enlarged. *Bf.* Hippocampal furrow (Bogenfurche). *ch.* 3. Median choroidal invagination (diaplexus). *hip.* Hippocampus. *f. d.* Fascia dentata. *p.* Pallium. *c. s.* Corpus striatum. *d. f.* Descending fornix fibres. *l. inf.* Lamina infra-neuroporica.

Fig. 16.—Coronal section through the corresponding region of an early fœtus of Perameles nasuta. *ch. l.* Choroid plexus of the lateral ventricle.

Fig. 17.—Section a short distance behind Fig. 16. *th.* Optic thalamus. *f. M.* Situation of foramen of Monro. *Bf.* Situation of Bogenfurche.

Fig. 18.—*T. s.* Olfactory bulb of fœtal Platypus. × 25. *olf. g.* Olfactory ganglion. *J. g.* Olfactory ganglion into which the nerves from Jacobson's organ are inserted. *j.* Nerve-fibre layer. *d.* Layer of nerve-cells. *t.* Ependymal layer surrounding the ventricle.

Fig. 19.—Neuroblasts (Zeiss D) from *d.* (Fig. 18).

Fig. 20.—Supra-ventricular cortex cerebri (pallium) of fœtal Platypus. × 96. *a.* Ependymal layer. *e.* Deep nerve-cell layer (Rolando-cell layer of Löwe). *d.* Middle fibre layer. *c.* Superficial nerve-cell layer (mantle layer). *f.* Superficial fibre layer (molecular layer).

Figs. 6, 7, 9, 10, 11, 12, 13, 16, 17, and 18 were drawn by means of a camera lucida. Fig. 15 was drawn from a microphotograph, for which I am indebted to Professor Wilson.

On Arhynchus hemignathi, a new Genus of Acanthocephala.

By

Arthur E. Shipley,
Fellow and Tutor of Christ's College, Cambridge, and University Lecturer in the Advanced Morphology of the Invertebrata.

With Plate 12.

ANATOMY.

In the summer of 1894 I received from Mr. Perkins, of Jesus College, Oxford, seven small parasites which he had noticed adhering lightly to the skin around the anus of a species of bird, Hemignathus procerus, which he collected in the island of Kauai, one of the Sandwich Island group. Each of these parasites was divided into three regions,—a head, a collar, and a trunk; and, in fact, they have an almost ludicrous resemblance to a young Balanoglossus with one or two gill-slits (figs. I, II, and III). On investigating their anatomy it at once became evident that the animals belonged to the group Acanthocephala, and, further, that they differed from the other members of the group in the absence of what is perhaps their most characteristic organ,—from which, indeed, they take their name—the hooked proboscis or introvert. The absence of so characteristic a structure, and the fact that the parasites were found outside the body, i.e. not as an endoparasite, but as an ectoparasite, lightly attached to the skin, made me think that perhaps the hooked introvert had been left behind in the intestine of the host, and that the body of the parasite had passed out of the alimentary canal of the bird. However, careful inspection failed to reveal any trace of a scar or mark where the introvert might have been broken off; and although in the absence of hooks and introvert sheath, &c., the anterior part of the body which I have called the head is as unlike the typical introvert as possible, still in its relation to the lemnisci and to the ligament it occupies the position of that organ, and until we can get further information I think the best plan is to regard this part of the body as equivalent to the eversible part of more normal forms.

The second of the three regions into which the body is externally divided is shorter than the head and smaller in diameter; it may be termed the collar. The third or posterior region, which may be called the trunk, is the longest and the most slender of the three; behind it tapers to a point where the orifice of the genital duct is situated, and this end of the animal is always a little turned up (figs. I, II, III, and VII). The exterior of the collar and trunk are smooth or lightly wrinkled, but the head is covered with a number of small depressions or pits which give it a very characteristic appearance, and which are well seen in sections. The head is attached to the collar by a narrow neck, which is surrounded and concealed by the edge of the collar. It is obvious in sections (figs. V and XIII). All the specimens were somewhat shrivelled and apparently distorted. The largest measured 3·5 mm. in length, the smallest 2·5 mm.; had they been fully distended they would probably have been 1 to 1·5 mm. longer. The body-cavity of the head is continuous with that of the neck, and the latter opens freely into the cavity of the trunk (fig. 13). The first-named space is by far the largest. The lumen of the collar region is reduced by the great thickness of the walls of this part of the body, and both here and in the trunk much of the internal space is occupied by the lemnisci and the reproductive organs.

The skin is one of the most characteristic features of the Acanthocephala, and as far as I know is only paralleled by that of the Nematodes, but it possesses certain features not found in the last named group. The whole body is covered by a thin cuticle which does not vary much in thickness in the different regions of the body, and which is invaginated a short distance into the genital pore. Beneath this is the true epidermis, or subcuticle as it is called; this has in my specimens the usual structure met with in the group so well described by Hamann, and consists of a matrix of a fibrillar nature, the fibrils being as a rule arranged radially, in which are embedded a certain number of amœboid nuclei (figs. VI and X). This tissue is much thicker in the region of the collar than elsewhere, and it is thicker in the trunk than in the head. It is pierced in all directions by a series of tubes or lacunæ which have no definite lining, but which seem to be mere splits in the fibrillar matrix. The lacunæ—except in the head—have a general circular direction which is very well marked in the trunk region where each runs into a lateral longitudinal split (fig. X). They contain a small amount of coagulum, the remnant of the fluid which circulates in them; during life this fluid, in other species, holds in suspension fat and coloured oil globules. If these are present in my species they must have been dissolved out in the processes which precede embedding. The circular lacunæ of the trunk not only communicate with one another by means of the two longitudinal lateral lacunæ (fig. XIV), but they open into one another by numerous small branches which have an oblique or longitudinal direction. In the head the lacunæ have a general longitudinal course; they are not, however, straight, but twist in and out between the pits on the surface; they anastomose freely (fig. IV). Thus in a transverse section of the head the lacunæ appear as round holes more or less uniformly arranged in the skin, and the same effect is produced by a longitudinal section of the trunk.

In the collar region the subcuticular tissue is much thickened, and the lacunar system forms a single more or less definite ring which gives off numerous branching anastomosing twigs (fig. V).

Although the above account attempts to give the general course of the lacunæ in the skin, it should be mentioned that there is considerable irregularity in the arrangement, and one is almost inclined to believe that the canals do not remain permanent, but that they sometimes close up and new ones appear. As they have no lining of any kind, such a closing would leave no trace.

As Schneider,[1] Hamann,[2] and Kaiser[3] have shown in the species investigated by them, the lacunar system of the introvert is completely shut off from that of the neck—if it be present—and of the trunk by a fold inwards of the cuticle which cuts the subcuticular tissue in two. I have not been able to find any such cuticular ring in the species in question, but the state of preservation of my specimens does not allow me to say definitely that it does not exist.

The lemnisci are two elongated sac-like prolongations of the subcuticular tissue which are attached anteriorly to the skin at the junction of the head and collar. They extend backwards to the extreme posterior end of the body, and are slightly bent so that a longitudinal section may cut them in two or three places (fig. XIII). Histologically they are composed of the same substance as the subcuticle in direct continuity with which they arise, and they are traversed by a similar system of canals. Physiologically they seem, as Hamann suggests, to act as reservoirs for the fluid of the canal system of the introvert; when the fluid they contain is forced into the spaces of the introvert the latter is everted. It is withdrawn again into the body by special muscles. In most species the canal system of the lemnisci opens into that of the introvert in front of the cuticular ring, and is thus completely independent of that of the trunk. If we assume that the head of my species corresponds with the introvert of other forms which have lost its introvert sheath, the lemnisci open into the same region of the skin as they do in other Acanthocephala.

The nuclei of the subcuticle and of the lemnisci are very remarkable; they correspond in structure with those described by Hamann in Neorhynchus clavæceps, in which species according to this observer both the skin and the lemnisci retain in the adult their embryonic condition. As in Neorhynchus

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[1] 'Arch. Anat.,' 1868, p. 584.

[2] 'Die Nemathelminthen,' Hefte 1 and 2, Jena, 1891 and 1895.

[3] 'Bibl. Zool.,' Heft 7, 1892, p. 1.

the number of nuclei is very small, some twelve to twenty seem to suffice for the whole of the subcuticle, and perhaps two to four for each lemniscus. The structure of the nucleus shows a most striking resemblance to an amœba with rather short pseudopodia (figs. x, xiii, and xiv). No single nucleolus can be detected, but numerous chromatin particles are present, and in some a distinct vacuole can be observed. These nuclei are scattered about in a most irregular fashion; not one may be seen in a number of consecutive sections, and then perhaps three or four may appear, and from their large size persist through several sections. The nuclei lie, as a rule, embedded in the substance of the subcuticle; more rarely they are found in the lacunæ. Although there is no proof, one is tempted to believe that the nuclei wander through the subcuticle and lemnisci in an amœboid manner, and that the small number of nuclei which are found in these tissues is compensated for partly by the large size of each, but more especially by their mobility. Similar amœboid nuclei undoubtedly move about, fuse with one another, and undergo fission in the subcuticle of the larval forms of Neorhynchus clavæceps.

Within the subcuticle and completing the skin on the inner side, is a layer of circular muscles, and still more internally a layer of longitudinal muscles (figs. vi and xv). The muscles of these layers are but a single fibre thick, and they are not very uniformly present. The circular layer is most complete in the region of the trunk, and I have figured a section to show this (fig. xii). The longitudinal layer is even less definite, but scattered fibres can be detected here and there (figs. xiv and xv). Each fibre appears to be spindle-shaped, and in the circular muscles has the striated portion only on its outer face, forming a thin band; the inner half of the fibre consists of vacuolated strands of protoplasm in which is a nucleus. The longitudinal layer of muscles alone is continued over the lemnisci (figs. ix and xiv). These muscles are not covered on their inner side by any layer of epithelial cells, neither does any such layer cover the ligament, but both tissues lie freely exposed to the fluid of the body-cavity.

In the more typical Acanthocephala the anterior end of the body terminates in a hollow eversible portion provided with rows of hooks whose number and shape have a certain systematic value. This introvert can be withdrawn, not into the general body cavity, but into the cavity of the introvert sheath, which is shut off from the general body cavity by a double (Echinorhynchidæ) or a single (Neorhynchidæ) wall. The extrusion of the introvert is believed to be effected by fluid being forced into its lacunæ by the lemnisci. It is retracted by special muscles attached to the inside of its tip; besides these, other retractor muscles run from the outside of the introvert sheath, and these serve to retract the whole sheath and its contents into the trunk. The chief nerve ganglion lies as a rule on the posterior end of the introvert sheath, usually in the middle line, but in the Gigantorhynchidæ it is placed to one side. From the posterior end of the introvert sheath, and having its origin between its two walls when they are present, the ligament runs backward, traversing the body cavity, and ending in the funnel-shaped internal opening of the oviduct in the female and in the vas deferens in the male.

Owing to the absence of an introvert and its sheath, the relations of the ligament in the present species is somewhat altered. It takes its origin from the anterior end of the head, and at first seems to consist of a few strands of muscular fibres which arise from the muscles of the skin (fig. XI). All my specimens but one proved to be mature females, whose ovaries had broken up into the egg masses which are characteristic of the Acanthocephala. These egg masses consist of packets of a dozen or more cells of which the peripheral layer develop into ova at the cost of the central cells which serve them as a food supply (figs. VI, XI, and XIII). These packets coexisted in my specimens with ova in various stages of development, some without any egg shell, whilst others were provided with a thick deeply-staining membrane. The whole lumen of the head was crowded with these ova. In the region of the collar the ova were confined by a thin-walled membrane, and in the trunk there were two such masses of ova, which, however, seemed less mature than those lying in the head. Lying amongst the various organs in the body-cavity were a number of very finely granular masses, which I take to be the masses of spermatozoa (figs. VI and X). Of the complex system by means of which the ova leave the body, little could be made out beyond the fact that a well-marked funnel is present opening into the posterior end of the body-cavity of the trunk (fig. IX). I failed, however, to find a second opening near the narrow end of the funnel such as occurs in other forms, but this may have been due to the poor state of preservation. The funnel leads into a duct which opens on the posterior end of the trunk.

The testes are two in number, and lie one behind the other in the ligament, though owing to its looping both may appear in the same transverse section. The spermatozoa do not escape into the body of the male as the ova do into that of the female, but pass down a duct in the ligament which opens at the end of the body. Traces of accessory glands were seen, but the details were not clear.

The brain lies on or in the ligament just behind its point of attachment to the skin of the head (figs. XI and XIII). Owing to the disruption of the ovaries in my female specimens the ligament could not be traced very far, but in the only male it reached from one end of the body to the other. The brain consists of a few large ganglion cells with a clear homogeneous cytoplasm and deeply-stained nuclei; the divisions between the cells were very sharp and straight (fig. XI). In the females this mass of cells lay in the ligament; in the male, on the other hand, it occupied the centre of the fibrous and muscular strands which compose that body (fig. XV). In the former I could trace no nerves leaving the brain, but in the male two nerves surrounded by muscles pass backward; these obviously correspond with the retinacula of other forms.

Classification.

Until recently the group Acanthocephala included but one genus, Echinorhynchus, which comprised several hundred species. Recently, however, Hamann[1] has pointed out that these species present certain differences which enable him to divide the group into three families, each with a corresponding genus. To these I venture to add a fourth, to include the remarkable form above described. This family may, I think, be called the Arhynchidæ, and the new genus Arhynchus, which name refers to the absence of the eversible introvert; and, inasmuch as it is convenient in naming a parasite to have some indication of its host, I think the specific name may be hemignathi.

If these terms be adopted, the classification of the Acanthocephala will be as follows, the characteristics of each of the first three families being taken from Hamann's papers.

ACANTHOCEPHALA.

I. Family ECHINORHYNCHIDÆ. The body is elongated and smooth. The introvert sheath has double walls, and the introvert is invaginated into it. The nerve ganglion is in the introvert sheath, mostly embedded in it and central in position. The hook papillæ are only covered with chitin at their apex, and the hooks have a process below.

Genus Echinorhynchus, with the characters of the family.

The vast majority of Acanthocephala belong to this family; a few may be mentioned. E. proteus, found in many fishes and varying in size with its host; its larval forms inhabit the Amphipod Gammarus pulex, and are also found in the body-cavity of numerous fresh-water fishes. E. clavula occurs in many fishes and in the intestine of a species of Bufo. E. angustatus is found also in fishes, with its larval form in the Isopod Asellus aquaticus. E. moniliformis is said to attain maturity in the human intestine; its usual host is a mouse, and its larval host the larva of a beetle, Blaps mucronata. E. porrigens invests the intestine of the rorqual and E. strumosus that of a seal. There are many others.

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[1] Loc. cit., and 'Zool. Anz.,' Bd. xv, 1892, p. 195.

II. Family Gigantorhynchidæ. Large forms, whose body is ringed and flattened during life like that of a Tænia. The hooks are like those of a Tænia, the hook-papilla being entirely covered with chitin. There are two root-like processes to each hook. The introvert is muscular, has no lumen and the introvert cannot be retracted into it, but the whole retracts into the body-cavity. The ganglion is excentrically placed to the side, behind the middle of the so-called sheath. The body-cavity is enclosed in a structureless membrane, and is traversed by membranes stretched transversely. The lemnisci are long, coiled, with a central lacuna.

Genus Gigantorhynchus, with the characters of the family.

Hamann includes three species in this family—G. echinodiscus, G. tænioides, and G. spira; and points out that E. gigas agrees with them in all points but that of the external annulation. The first of the above-named species occurs in the intestine of anteaters, and has been found in Myrmecophaga jubata and Cycloturus didactyla. G. tænioides has been found in a species of Cariama, Dicholophus cristatus; and G. spira lives in the king vulture, Sarcorhampus papa. E. gigas in the adult stage occurs in the small intestine of swine, and its larval host is believed to be the grubs of Melolontha vulgaris and Cetonia aurata in Europe and of Lachnosterna arcuata in the United States.[1] It is recorded once from the human intestine.

III. Family Neorhynchidæ. Sexual maturity is reached in the larval state. The introvert sheath has a single wall. A few giant nuclei only are found in the subcuticle and in the lemnisci. The circular muscles are very simply developed, and the longitudinal muscles only present in places.

Genus Neorhynchus, with the characters of the family.

This genus includes but two species, N. clavæceps and N. agilis. They both present interesting cases of pædogenesis, the large embryonic nuclei of the young larva do not break up into numerous nuclei as they do in the com-

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[1] C. W. Styles, 'Zool. Anz.,' Bd. xv, 1892, p. 52.

moner species. N. agilis is found in Mugil auratus and M. cephalus; N. clavæceps in the Carp, Cyprinus carpio, its larva form according to Villot[1] in the fat bodies of the Neuropterous insect Sialis niger; it has also been found in the alimentary canal of the leech Nephelis octocula, and specimens of the water-snail Limnæa have been articially infected with it.

IV. Family Arhynchidæ. Short forms, with the body divided into three well-marked regions,—head, collar, and trunk. The head is pitted, the collar smooth, and the trunk wrinkled, not annulated—in spirit specimens. There is no eversible introvert, and no introvert sheath and no hooks. The sub-cuticle and the lemnisci have a few giant nuclei, and the lemnisci are long and coiled.

Genus Arhynchus, with the characters of the family.

This family in the length and curvature of its lemnisci resembles the Gigantorhynchidæ, and in the persistence of the embryonic condition of the nuclei in the sub-cuticle and the lemnisci, the Neorhynchidæ; but in the shape of the body, its division into three well-marked regions, the absence of eversible introvert, introvert sheath, and hooks, it stands alone, though to some extent nearer to the Neorhynchidæ, in which the introvert is relatively small, the introvert sheath simple, and the number of hooks reduced, than to either of the other families.

The single species Arhynchus hemignathi was found attached to the skin around the anus of a Sandwich Island bird, Hemignathus proceros. This bird is a member of a family Drepanididæ, which is entirely confined to the Sandwich Island group. Professor Newton tells me that it is probable that the "food of Hemignathus consists entirely of insects which it finds in or under the bark of trees;" hence it is probable that the second host of this parasite, if such exists, must be looked for amongst the Insecta.

The Zoological Laboratory, Cambridge;
March, 1896.

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[1] 'Zool. Anz.,' Bd. viii, 1885, p. 19.

DESCRIPTION OF PLATE 12,

Illustrating Mr. A. E. Shipley's paper on "Arhynchus hemignathi, a new genus of Acanthocephala."

In some cases the names of the various structures are written on the figures, in others the following abbreviations have been adopted. *circ. mus.* The layer of circular muscles in the skin. *gen. d.* Genital duct. *gen. p.* The external opening of the duct. *lac.* The lacunæ in the skin. *lat. lac.* The large lateral lacunæ of the trunk. *lem.* The lemnisci. *lig.* The ligament. *long. mus.* The longitudinal muscles of the skin. *mus.* The muscles from which the ligament arises. *nuc.* The amœboid nuclei of the skin and the lemnisci. *sperm.* Coagulated masses of spermatozoa in the body-cavity of the female.

Figs. I, II, and III.—Three views of three different specimens of Arhynchus hemignathi. Each × 20. The division of the body into three regions is well marked. The details are shown in Fig. I. Figs. I and II are rough sketches.

Fig. IV.—A transverse section through the head of a female, crowded with ova and egg-masses; the ligament is shown in section. × 40.

Fig. V.—A transverse section through the same, just below the edge of the collar. In the centre is the neck, which fuses with the collar a few sections further back. The big circular canal of the collar is shown at *lac.* × 40.

Fig. VI.—A transverse section through the trunk of the same. The uppermost lemniscus is cut in two places. The ovary is double, and shows egg-masses as well as eggs; some coagulated masses of spermatozoa are lying in the body-cavity. × 40.

Fig. VII.—A surface view of the external opening of the genital duct. × 40.

Fig. VIII.—Some developing ova, highly magnified.

Fig. IX.—A transverse section through the trunk near the genital pore, taken from the same series as figs. IV, V, and VI. It shows part of the funnel-shaped internal opening of the genital duct, *gen. d.* × 40.

Fig. X.—A transverse section from another specimen taken behind the opening of the genital duct. This shows the arrangement of the lacunæ and their communications with the lateral lacunæ, *lat. lac.*

Fig. XI.—A longitudinal section through the central part of the skin of the head, showing the origin of the ligament and the ganglion cells of the brain, lying in a mass of ova and egg-masses.

Fig. xii.—A small portion of the skin in section, showing the single layer of circular muscle-fibres. × 40.

Fig. xiii.—A median longitudinal section through a female. The whole body-cavity full of ova and egg-masses. The ligament is seen in the head, and the genital duct near its opening in the trunk. The left lemniscus, cut twice, is alone seen. × 30.

Fig. xiv.—A transverse section through the trunk of a male, showing one of the testes. This section shows also the longitudinal muscles on the lemnisci and the large lateral lacunæ, *lat. lac.* × 40.

Fig. xv.—A transverse section through the head of a male, showing the brain in the ligament, and the longitudinal muscle-fibres very well developed. × 40.

Zoological Observations in the South Pacific.

By

Arthur Willey, D.Sc.Lond.,
Balfour Student of the University of Cambridge.

With Plate 13.

In the course of a brief stay in Sydney I had the opportunity of working up for publication some material obtained by me. My warmest thanks are due to Professor W. A. Haswell, who has generously placed space and appurtenances at my disposal in his laboratory at the University of Sydney.

I.

On a New Amphioxus from the Louisiade Archipelago

(Asymmetron caudatum, n. sp.).

(With Plate 13, figs. 1 to 4.)

Last January, as a result of my dredging operations in the magnificent lagoon of the Deboyne groups of islands, of which Panaieti is the largest, I obtained, on two occasions, specimens of the family Branchiostomidæ (a single specimen only on each occasion), which proved to be a new species, nearly related to Asymmetron lucayanum, Andrews.

They were dredged up from a depth of one fathom and seven fathoms respectively, living in clean coral sand. In the same habitat a species of Ophelia is very abundant, and to the casual gaze it bears a striking resemblance to the Amphioxus, with which it is associated. This Ophelia burrows in the sand with its pointed snout, like Amphioxus, but more deliberately, and swims with exactly the same motions of the body as Amphioxus, which is not the case with most other Annelids. At first I thought I was obtaining a fine series of Amphioxus, but the great majority turned out to be Ophelids.

The species now to be described, for which I propose the name Asymmetron caudatum, n. sp., adopting Kirkaldy's system[1] of subdivision of the Branchiostomidæ, is perhaps interesting on account of its geographical distribution relative to other species of Amphioxus, rather than from the possession of novel features.

That it should be entirely distinct from its relatives in Torres Straits, from whom it is removed by a distance of less than six hundred miles, and, on the other hand, closely allied to a species residing in the Bahamas, upwards of eight thousand miles away, on the other side of the American continent, is certainly a noteworthy fact in distribution.

The specific differences between species of Amphioxus are frequently of apparently little moment, but may be of importance when taken in conjunction with geographical distribution. On this principle the Japanese Amphioxus recently described by Andrews[2] should at least be regarded as a marked variety of rather than identical with Amphioxus Belcheri.

As mentioned above, I only succeeded in obtaining two individuals of Asymmetron caudatum, because the unpropitious season of the year, when one is liable to be overtaken by westerly gales, rendered it inadvisable to delay for any considerable length of time in the lagoon.

The larger specimen was an immature female, and measured 29·5 mm.; the other was a mature or submature male, measuring 20 mm. in length. Other differences, particularly in respect of the caudal fin (cf. figs. 1 and 3), occurred between the two individuals; and these differences, combined with the marked contrast in size, would seem to point to a sexual

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[1] Kirkaldy, J. W., "A Revision of the Genera and Species of the Branchiostomidæ," 'Quart. Journ. Mic. Sci.,' vol. xxxvii, 1895, pp. 303—323.

[2] Andrews, E. A., "An Amphioxus from Japan," 'Zool. Anz.,' 1895. This should be named A. Belcheri, var. japonicus.

dimorphism, which, if found to be constant among a large number of individuals, would be a fact of some importance.

My two specimens alone prove that an appreciable sexual dimorphism may occur, whether as a variation or as a fixed property.

The following are all the numerical facts that I have ascertained regarding the two specimens.

1. Female. Length, 29·5 mm.; number of myotomes, 60; formula, 40—9—11; length of tail or urostyloid process behind myotomes, 3 mm.; distance of anus from root of tail, 2·5 mm.; distance of atriopore from root of tail, 6·5 mm.

2. Male. Length, 20 mm.; number of myotomes, 64; formula, 44—9—11; number of gonads, 30, disposed unilaterally on right side.

The characteristic generic features of Asymmetron, exhibited by the new species, are as follows.[1]

The right metapleur is continuous with the ventral fin; the latter has no fin-chambers and no fin-rays; the right and left metapleura pass equally into the rostral fin in front; an intertentacular membrane is present between the ventral buccal cirri; the buccal cirri are plain; and lastly, there is a pair of post-atrioporal, or, better, post-atrial cæca, which are, however, very short, ending abruptly between the posterior lips of the atriopore.

The dorsal fin-spaces become very irregular posteriorly, and cease at about the 54th myotome.

In addition to the length of the body and the number of myotomes, an important specific feature of Asymmetron caudatum is the rostral fin, which is marked off from the dorsal fin by a pronounced constriction of somewhat varying depth (cf. figs. 2 and 4). The rostral fin is indeed a striking feature in the fresh object, but is less marked after preservation.

The caudal fin also varies considerably in the two individuals, its urostyloid portion being much more constricted off from the succeeding portion in the region of the myotomes in the male specimen than in the female (figs. 1 and 3). It is, how-

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[1] I have verified all the points mentioned by sections and preparations.

ever, important to note that in any case there is a distinct caudal fin extending to the posterior extremity, and Kirkaldy's opinion that there is no caudal fin in Asymmetron is somewhat misleading.

From the above description it is evident that A. caudatum comes very near to A. lucayanum, but differs definitely and distinctly from it in size, number of myotomes,[1] and in the possession of a prominent rounded rostral fin, marked off above and below by a constriction.

II.

On the Nepionic Shell of the Recent Nautilus.

(With figs. 5 and 6 on Plate 13.)

While conversing recently with Mr. Charles Hedley, Conchologist to the Australian Museum, Sydney, I had occasion to refer to the very large size of the ovarian ova of Nautilus pompilius, apparently larger than the ova of any other known Cephalopod; while the fluidity of the yolk would lead to the presumption that the ova, when deposited, would be provided with a firm covering, whether horny, coriaceous, or calcareous.

Mr. Hedley then drew my attention to two young shells of N. pompilius in one of the museum cases, in each of which, at the same region in both, there was a very distinct discontinuity in the formation of the shell by the animal, and added that this line of demarcation probably represented the limit reached by the shell at the time of hatching from the egg. As

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[1] The average myotome formula for A. lucayanum as given by Andrews is 44—9—13 = 66, and the average length 13 mm. The maximum length, according to Andrews, is 16 mm. out of a large number of specimens. Kirkaldy gives 19 mm. as the maximum length of specimens sent to Prof. Lankester by Prof. Agassiz.

the size of this young shell behind the line of division between it and the later formed shell-substance seemed to correspond roughly with the dimensions of the ovarian ovum, as stated by me in a former communication,[1] I at once became interested in Hedley's suggestion.

The term "nepionic" was invented by Hyatt in 1890, and embodied by Jackson in his important memoir on the 'Phylogeny of the Pelecypoda,'[2] and has been adopted by Pilsbry in the 'Manual of Conchology.' As I understand it, it is intended to be applied to the larval stages, sensu stricto, of all animals. To quote Hyatt, "This term should be confined to the designation of stages of growth which are immediately continuous with later stages, and parallel or referable in their origin to the adults of allied existing or fossil forms which are not so remote as those from which the embryonic stages are derived."

The nepionic period is succeeded by the adolescent or neologic stages, which "are of as great importance for tracing the genealogy of small groups as are the [nepionic] characters in larger groups."

In the case of those terrestrial Gastropods which lay large hard-shelled eggs full of yolk, the development and growth of the shell take place within the egg until the close of the nepionic period, by which time the shell has in many instances attained a very respectable size. Thus the nepionic shell of the above-mentioned molluscs is that portion of the true shell (as opposed to the embryonic shell) which develops within the egg.

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[1] "Letters on Nautilus, &c.," see *ante*, p. 175.

[2] JACKSON, ROBERT TRACY, "Phylogeny of the Pelecypoda, the Aviculidæ, and their Allies," 'Memoirs Boston Soc. Nat. Hist.,' vol. iv, No. 8, 1890.

PROFESSOR HYATT introduced the term "nepionic" in a foot-note to the preceding memoir as a substitute for the term "silphologic" suggested by him in a previous paper (HYATT, ALPHEUS, "Values in Classification of the Stages of Growth and Decline, with Propositions for a New Nomenclature," 'Proc. Bost. Soc. Nat. Hist.,' vol. xxiii, Part 3, 1887).

I am indebted to Mr. Hedley for these references.

The nepionic shell frequently stands in marked contrast to the post-nepionic or (with the large terrestrial Gastropods) post-natal shell, both by a definite line indicating a temporary discontinuity of growth, and by its different colour and minute sculpturing.[1] In fact, it is obvious that a definite break in the continuity of shell-formation is more likely to occur in those cases in which, after the completion of the nepionic shell, the young mollusc has to go through the operation of hatching, after which it recommences to form post-natal shell-substance. This supposition is, I believe, in accordance with the facts.

With regard to Nautilus, about whose reproduction we are so much in the dark, it is a distinct point gained to know, at least with respect to its shell, at what stage the animal hatches.

The existence of the line of discontinuous growth, at a particular point, in young shells of N. pompilius, might not be regarded as conclusive in itself, but I have since found a precisely similar and constant discontinuity of growth in a number of shells of N. umbilicatus and N. macromphalus.

In the two last-named species the nepionic shell differs from the post-nepionic shell by the presence in the former of a minute plication, and of a peculiar glossy sheen. In N. pompilius the nepionic shell also has a peculiar sheen, and presents a contrast to the post-nepionic shell in the colour of its markings, which are brick-red, those of the latter being crimson.

Fig. 5 (Pl. 13) represents a drawing of the umbilical region of N. umbilicatus, Lam. On looking down into the umbilicus at the first whorls of the shell, it will be seen that after the young shell had completed rather more than one entire whorl, there occurred a sharp and abrupt interruption in the growth of the whorls, and (in the actual specimen, although not shown in the figure) the character of the shell

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[1] Compare Hedley, Charles, "On the Structure and Affinities of Panda atomata," Gray, 'Records Austral. Mus.,' vol. ii, 1892, pls. v and vi.

added after this line,[1] is very distinct from the previously formed shell, as already mentioned. Sometimes there is a visible depression in the shell at the nepionic line.

In the shells of all species of Nautilus there are sometimes to be seen one or several strongly marked lines indicating occasional, but not regularly periodical, interruptions in the growth of the shell,—periods of rest, in fact. These, however, are neither constant in position nor in their occurrence in different individuals. On the other hand, the nepionic line occurs in a constant position in all individuals of a species, although in N. pompilius it cannot be seen beyond a certain stage, owing to the overgrowth of the whorls.

Altogether I have seen the nepionic line in eighteen shells of the three above-named species of Nautilus.

Fig. 6 (Pl. 13) is an outline sketch of a young shell of N. pompilius[2] with still perforated umbilicus, to show the nepionic line marking off the prænatal from the post-natal shell. The following are the measurements of this shell:

(*a*) Length of complete shell (from the anterior free margin to a point directly opposed to it on the posterior convex surface of the shell), 32 mm.; greatest width of complete shell, 19 mm.

(*b*) Length of nepionic portion of shell, 27 mm. (this varies slightly in different individuals from 25 to 27 mm.); greatest width of nepionic portion of shell, 16 mm.

It may be observed that the above dimensions of the nepionic shell of N. pompilius are a good deal in excess of those of the ovarian ovum which I previously described; but not more so relatively, I think, than is the size of other newly hatched Cephalopods to the original size of the freshly deposited ova or of the mature ovarian ova.

Knowing the size and character of the nepionic shell of recent Nautilus, and the size and character of its submature ovarian ovum, I think there is ample justification for the conclusion that the nepionic line marks the period at which the young individual hatches from the egg.

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[1] I shall refer to this in future as the "nepionic line."

[2] The sketch was taken from a specimen in the Australian Museum by kind permission of Mr. Charles Hedley.

There is strong presumptive evidence that the animal of Nautilus at the time of hatching already possesses the main features of the adult, with the possible addition of a yolk-sac. This follows both from the size of the nepionic shell, which comprises a number of chambers, and from the consideration of a very small specimen of Nautilus, which I obtained in New Britain and mentioned in a former publication.[1] I have unfortunately mislaid the shell of this specimen, but it had a perforated umbilicus, through which daylight could be seen, and was at least as small as the shell from which Pl. 13, fig. 6, was drawn.

Jackson (loc. cit.) refers to Hyatt's figures of a young Nautilus Koninckii, in which is indicated "a smooth nepionic period, succeeded by a fluted neologic stage." I have been unfortunately unable to refer to Hyatt's well-known memoir on the "Embryology of Fossil Cephalopoda" ('Bulletin Mus. Compar. Zool. Cambridge, Mass.,' vol. iii, 1872).

In the first part of his "Beiträge zur Entwickelungsgeschichte der fossilen Cephalopoden" ('Palæontographica,' vol. xxvi, 1879–80) Branco figures a number of minute shells of Ammonites, which sometimes, when they measure even less than 1 mm. in diameter, exhibit a deep circular constriction; and this not only in cases in which the adult shell is grooved, but also in many instances in which the latter is not grooved.

If this groove were to be identified or compared with the nepionic line of recent Nautilus, which is itself sometimes depressed, as mentioned above, it would indicate that the ova of the Ammonites referred to were much smaller and poorer in yolk than those of the recent Nautilus. This would be an interesting conclusion if it could be substantiated.

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[1] 'Natural Science,' June, 1895.

III.

On some Variations in the Shell of Nautilus, with Description of a New Variety (N. pompilius, var. Moretoni, nov. var.).

(With figs. 7, 8, and 9 on Plate 13.)

Of the obvious differences that exist between the shell of N. umbilicatus and that of N. pompilius the following may, for my present purpose, be particularly remembered.

1. In N. umbilicatus (see Pl. 13, fig. 5)—

a. The umbilicus is perforated, the shell being so loosely coiled that a small aperture, which can be looked through, is left in the centre of the whorls.

β. The umbilicus is large and open, so that all the whorls can be distinctly seen. This holds good also for N. macromphalus, but here the umbilicus is not perforated.

γ. The free margin of the shell does not merge into the umbilicus, but tends abruptly inwards and downwards, so as to form a prominent shoulder, nearly at right angles to the lateral free margin. It finally fuses laterally with the anterior convexity of the shell, which is pigmented black.

2. In N. pompilius—

a. The umbilicus is imperforate (excepting very young individuals).

β. The umbilicus is practically obliterated through a deposition of callus by the dorso-lateral angles of the mantle.

γ. The free margin of the shell merges directly into the umbilical region.

The different characters tabulated above are usually very distinct, but they may be considerably weakened by variation.

One variety, for instance, of N. pompilius will present all the characteristics of the species with the single exception that the free margin of the shell does not pass directly into the umbilicus, but forms a shoulder.

In another variety the free margin of the shell will pass gradually into the umbilicus, but the latter will be perforated.

Finally, in a third variety the deposition of callus will have been entirely left out and the whorls loosely coiled, so that we shall have the above-mentioned shoulder, a perforated umbilicus, and visible whorls.

The latter variety is not identical with the so-called N. stenomphalus, but is, in a sense, intermediate between the latter and N. umbilicatus. I obtained a single example from New Guinea waters, kindly given to me by the Hon. M. H. Moreton, of Government House, Samarai, British New Guinea. I have pleasure in naming it N. pompilius, var. Moretoni.

In a collection of shells of N. pompilius it may be observed that the extent of deposition of callus over the umbilicus is very unequal; and that while there is usually a thick prominent plug of white callus, sometimes the deposition of the latter has been so deficient as to leave a deep umbilical depression on either side.

A peculiar feature about the variations now being dealt with is that they may occur on one side of the shell only, the other side being more or less normal.

Pl. 13, fig. 7, represents the umbilical region of a variety of N. pompilius, whose umbilicus was only partially perforated. On the right side of the shell (the latter being considered with the convex side downwards, as it is in the fresh condition) there was a deep hole, about a centimetre in depth; on the other side there was a deep umbilical depression, which, however, was closed over with callus, with the exception of a minute pin-hole aperture—perhaps half a centimetre in depth. This latter could only be made out by close inspection, and at first sight the left side of this shell appeared to be practically normal.

It is clear that if this variation were carried a little farther in the same direction, we should have a form possessing the essential features of N. stenomphalus, and there is no reason at present to regard the latter as anything more than a variety of N. pompilius with a persistent perforated umbilicus. In a specimen of N. stenomphalus in the Australian Museum only a portion of the coil was dimly visible, and the free margin of the shell passed directly into the anterior border of the umbilicus without a prominent shoulder.[1]

In Pl. 13, fig. 8, an interesting variation is shown in which the umbilicus was imperforate, yet nevertheless the free margin of the shell did not pass simply into the umbilicus, but bent round in such a manner as to form a prominent shoulder, behind which there was a deep umbilical depression. I have two examples of this variation from New Guinea, and in both cases the above-described shoulder was confined to the left side of the shell, the right side being normal.

It will be found convenient to name these varieties. That first described above, with partially perforated umbilicus, may be called N. pompilius, var. perforatus, nov. var.

The second variety, with the shoulder, may be called N. pompilius, v. marginalis, nov. var.

Now we come to the third variety to be described, namely, N. pompilius, var. Moretoni, nov. var.[2]

In this variety, which is a very well-marked one, there is a prominent shoulder as shown in Pl. 13, fig. 9; the umbilicus is somewhat widely perforated, and a considerable portion of the whorls can be distinctly seen. This shell was symmetrical in every respect. At the first sight of it one might well hesitate whether to regard it as a loosely wound pompilius, or as a closely wound umbilicatus, but the existence of intermediate varieties shows, I think with certainty, that it belongs to the pompilius group.

All the variations described above belong to the category of substantive variations, according to Bateson's nomencla-

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[1] It may be added here that there also seems no reason for regarding N. scrobiculatus as other than a variety of N. umbilicatus. On this view the species of recent Nautilus would be reduced to three,—N. pompilius, N. umbilicatus, and N. macromphalus.

[2] All the varieties described in this paper were obtained in New Guinea, and with one exception from the natives. I have certain evidence of the living Nautilus occurring in New Guinea waters, but the natives know nothing of it, and it is not in a workable condition for the zoologist

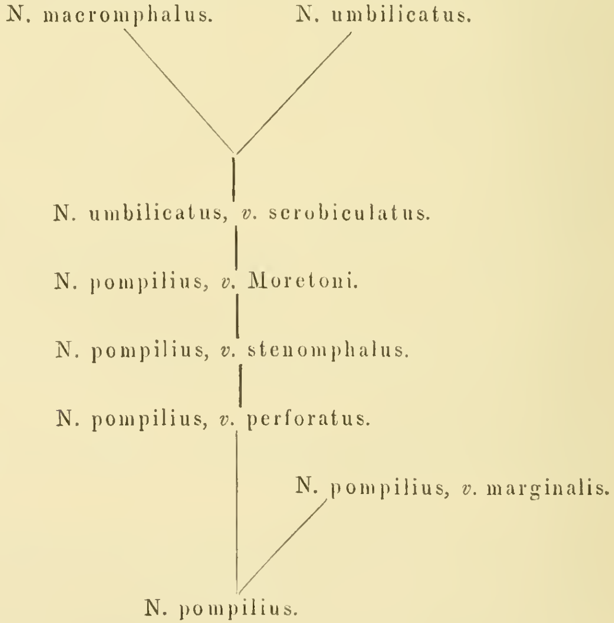
ture,[1] and it is important to notice that they can be arranged in three groups as follows :

1. Single variations, in which the variation affects only a single character, such as the umbilical shoulder or the umbilical aperture.

2. Collective variations, in which a whole group of characters are affected, as in the variety Moretoni.

3. Incomplete variations, as in the two examples of my variety marginalis, where the umbilical shoulder was confined to one side of the shell.

Finally, it may be pointed out that the species and varieties of the recent Nautilus seem to fall naturally into the following scheme, which, however, does not aim at suggesting any particular direction of evolution.



University of Sydney;
May 18th, 1896.

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[1] Bateson, W., 'Materials for the Study of Variation,' Macmillan, 1894.

EXPLANATION OF PLATE 13,

Illustrating Dr. Willey's "Zoological Observations."

Figs. 1—4 refer to Asymmetron caudatum, n. sp. See p. 219.

Fig. 1.—Asymmetron caudatum, n. sp. Posterior extremity of female from right side. *d.* Dorsal. *v.* Ventral. From living object.

Fig. 2.—A. caudatum. Anterior extremity of female from right side. From living object.

Fig. 3.—A. caudatum. Posterior extremity of male from right side. From living object.

Fig. 4. A. caudatum. Anterior extremity of male from left side. From living object.

Fig. 5.—N. umbilicatus. Drawing of umbilical region to show the nepionic line, which is situated a little beyond the first complete whorl of the shell. From right side.

Fig. 6.—N. pompilius. Outline sketch of young shell with perforated umbilicus, to show nepionic line. From right side.

Fig. 7.—N. pompilius, *v.* perforatus, nov. var. Umbilicus partially perforated. The dotted line is merely to indicate the limit of the black pigment on the anterior convexity of the shell. Right side.

Fig. 8.—N. pompilius, *v.* marginalis, nov. var. Umbilical region of left side, to show the umbilical shoulder and depression.

Fig. 9.—N. pompilius, *v.* Moretoni, nov. var. Umbilical region, showing shoulder, perforation, and whorls. From right side.

N.B.—The drawings are placed in such a way that the convex surface of the shell would be directed upwards and the mouth of shell downwards, because it is thought that they would be more intelligible in this position; but the right and left sides are named with the shell considered in the natural position, with the convex surface directed downwards and the mouth upwards.

Chlamydomyxa montana, n. sp., one of the Protozoa Gymnomyxa.

By

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With Plates 14 and 15.

I do not know of any naturalist who has seen the beautiful Chlamydomyxa labyrinthuloides of Archer in a state of "expansion" since he described it in this Journal twenty-one years ago. Mr. Thisleton Dyer, now Director of Kew Gardens, saw it in its active streaming condition when Archer exhibited it at one of the meetings of the Dublin Microscopical Club five-and-twenty years ago. And the other members of that admirable band of naturalists saw it and testify to the correctness of Archer's description and figures.

Some seven years after the publication of his paper Archer sent both to me and (through Prof. Percival Wright) to Mr. Patrick Geddes samples of Sphagnum with the cysts of Chlamydomyxa attached to the fronds of the moss. I kept the specimens which I received in conditions which I hoped would favour the rupture of the cysts and the out-crawling of the Chlamydomyxa-network, but entirely failed to obtain such a result.

Mr. Patrick Geddes made a careful study of the cysts received by him, and wrote a very interesting article on them, accompanied by a coloured plate, in this Journal, vol. xxii, 1882, p. 30. Mr. Geddes especially dwelt upon the remarkable laminated formation of the cellulose cyst-wall, and on the division and multiplication of the encysted mass. He pointed out the importance of Chlamydomyxa for the theory of the vegetable cell-wall and its laminated structure, and he was led to compare the encysted condition of Chlamydomyxa with the encysted condition of such forms as Hæmatococcus and Glœocapsa. He also made important observations on the red-coloured oily substance formed in the cysts.

I frequently searched for Chlamydomyxa in the years following the publication of Archer's paper whenever I found myself in a moorland country with Sphagnum bogs. In the neighbourhood of Lervik, on the Stavanger Fjord in Norway, I searched in vain, as also on Dartmoor. I was, however, rewarded for my continued efforts by at last finding Chlamydomyxa in abundance on August 22nd, 1886, on the surface of Sphagnum gathered in small ditches cut in the bog which occupies clearings in the pine-wood at Pontresina in the Enghadine; and on two subsequent visits to Switzerland at the same time of year, once at Zermatt (1890) and later again in the Enghadine (1892), I found and studied Chlamydomyxa.

On the first occasion when I found Chlamydomyxa, viz. in August, 1886, at Pontresina, I was fortunate in being able to observe and draw specimens which expanded their remarkable networks under the microscope, and I showed such active specimens in the Hôtel Saratz to my friend Ernst Haeckel, who happened to arrive there for a short holiday, and to Sir Edward Fry—a judge not only of legal but of biological matters. My drawings then made are reproduced in Plates 14 and 15, figs. 1—4. I was able to recognise the cysts which accompanied the naked Chlamydomyxa as belonging to the latter, and, indeed, should have recognised them from my previous familiarity with the encysted specimens sent to me by Archer. But I have never seen expanded Chlamydomyxa since that first occasion. At Zermatt and at the Maloja in subsequent years I found only the cysts, and no persuasion which I could offer was sufficient to induce the Chlamydomyxa to leave its cyst. The cysts, however, were always very abundant, and varied in shape and size. It is not at all improbable that the month of August is either too late or too soon for the best chance of observing Chlamydomyxa in the motile condition, and I should recommend other observers in the same locality to try the latter part of June and commencement of July, as affording the best chance of observing Chlamydomyxa in the unencysted condition.

The Chlamydomyxa which I studied in Switzerland, whilst agreeing in essential features with Archer's genus, appears to me to be certainly a distinct species, for which I propose the name Chlamydomyxa montana. The grounds for this distinction will be apparent from the following description.

Mode of Occurrence.—The specimens of Sphagnum which yielded the Chlamydomyxa had a peculiar ruddy-brown appearance and a glistening surface, differing from ordinary healthy growths of the moss. They were old and in a state of incipient decay. I scraped the surface of the leaflets of the moss and teased them on a glass slide, so as to remove and spread as much as possible for observation the matters adhering to the surface.

General Appearances.—I then found, when the preparation was examined with the microscope, numerous olive-brown disc-like or ovoid bodies from the $\frac{1}{200}$ to the $\frac{1}{500}$ of an inch in diameter, which very soon showed a movement of the colourless border by which each was surrounded. The colourless border seemed to open out and spread itself in the form of a network of threads.

The Threads.—The gradual separation and spreading of these threads is a very curious phenomenon, and certainly gives the impression that the threads are pre-formed, closely packed together, and that they gradually separate and straighten out. I am not prepared to assert that such is the case, but I think it very likely. A fully expanded specimen of fair average size is represented in Plate 14, figs. 1 and 2. It is represented in two consecutive phases of expansion, separated by about five minutes, as seen under a high power—No. 10 immersion of Hartnack. If one taps the cover-glass the whole branching and outstretched system of threads suddenly contracts, and forms again a clear colourless "border" to the pigmented disc. But immediately the outpushing of the threads recommences, and seems to proceed by a straightening and disentanglement of the individual threads, which grow in length as one watches them, apparently being extruded from the central mass. The commencement of the process of expansion of the threads is shown in a drawing of another specimen (Plate 15, fig. 4).

In all cases the process of expansion is accompanied by the formation of "vacuoles" in the colourless border-substance (see figs. 1—4), which change their shape and position as the spreading goes on. But they have not the character of the "contractile" vacuoles of Heliozoa, although Archer speaks of such "contractile" vacuoles (perhaps by inadvertent use of the term "contractile") as occurring in his C. labyrinthuloides. Archer also observed frequently solid food particles such as diatoms to be entanged in the substance of the colourless material. I never observed any food particles thus engulfed in C. montana.

The threads are of extreme tenuity, of equal diameter throughout, and appear to me not to undergo any measurable change in dimension. I did not see them shorten and thicken, but they appeared to become flexed and gathered together when a stimulus was applied to them. Further, I never saw any thread either fuse with a neighbouring thread or divide into two. It appeared to me (but the observation is difficult) that when two threads come together they may be very closely apposed, but nevertheless retain their distinctness; and conversely that, where a thread seems to divide into two longitudinally, the case is really one of the separation of two preexisting threads.

My general conclusion is that the threads do not really form either a dendritic branching figure or a network, but are merely apposed so as to form when less expanded, or, to speak more accurately, when less straightened, an apparent meshwork, and when more straightened and separated from one another an apparent tree-like structure, the appearance in both cases being illusive. A gentle to-and-fro swinging movement of an outstretched thread is sometimes seen. Such movement may be due to currents in the surrounding liquid.

As to the further interpretation of the nature of the threads I will say more below.

The Oat-shaped Corpuscles.—Travelling upon the threads and closely packed against one another in those parts of the hyaline border-substance which are, so to speak, not unravelled, are very numerous oat-shaped or fusiform corpuscles. They are represented in figs. 1—4, and one is drawn on a greatly enlarged scale in fig. 5. These corpuscles are described by Archer as leading characteristics of his C. labyrinthuloides, and are compared by him with the nucleated spindle-shaped bodies which travel upon the threads of the Labyrinthula of Cienkowski. In Archer's species of Chlamydomyxa, however, these corpuscles were homogeneous, showing neither an envelope of protoplasm nor a central nucleus. The same is true of the fusiform corpuscles of C. montana. They are structureless. It is important to note that they are very much smaller in C. montana than in C. labyrinthuloides. Archer states that in the latter they are $\frac{1}{4000}$ inch long and half as broad, whereas I find that in C. montana they are not more than the $\frac{1}{12000}$ of an inch or two microns in length. Nevertheless they are perfectly distinct and uniform both in size and shape. I found that they were stained more strongly than the threads by the addition of a solution of iodine; and since neither by this nor by any other method could I detect anything indicating a central nucleus or nuclei in Chlamydomyxa (Archer failed equally), I think that these oat-shaped corpuscles in both species of Chlamydomyxa should be regarded as nuclei, the particles of a fragmented scattered nucleus. In encysted specimens of Chlamydomyxa montana I entirely failed (either by direct examination or by use of reagents) to detect any trace of these oat-shaped corpuscles.

Movement of the Oat-shaped Corpuscles.—The movement of the oat-shaped corpuscles is the most interesting and characteristic feature presented by Chlamydomyxa. It must be distinguished altogether from the straightening and expanding movement of the mass of filaments; at the same time it is not manifested until the filaments have become—some at least of them—straightened and free. Then as such a filament separates itself, and as it were slowly pushes itself forth in a straight line, first one, then another, and finally many of the oat-shaped corpuscles are seen to advance along it. They move slowly in one direction as a rule, stopping sometimes after a considerable advance, and then resuming movement. They do not all travel at the same rate on one filament. I saw on several occasions one corpuscle overtake another and glide over the back (so to speak) of its more slowly moving companion, and advance in front of it. Archer also witnessed this phenomenon in his larger species. Further, the corpuscles do not all travel in one direction on one and the same filament. Some are advancing towards the free extremity of the filament, whilst others are travelling away from it. The corpuscles travelling in opposite directions meet and pass one another, or sometimes on meeting come to a standstill, then after a time the two separate from one another, reversing their previous direction of movement. These movements are not novel in themselves, but similar to the movements of the granules in the pseudopodium of an Actinosphærium or in the threads of the vacuolated cell protoplasm of the Tradescantia hair. What is peculiar in the case of Chlamydomyxa is this, viz. that the moving corpuscles are oat-shaped bodies of definite and uniform size, and that there is no visible coating of streaming protoplasm embedding both them and the filament upon which they move (as there is in the case of the pseudopodium of Actinosphærium).

I am inclined myself, from a careful consideration of my own observations on Chlamydomyxa and Actinosphærium, and of Cienkowski's observations upon Labyrinthula, to adopt the view that the filaments of Chlamydomyxa are inert products of the metamorphosis of its protoplasm, which have a certain amount of durability, but can be rapidly absorbed by the protoplasm which also gives rise to them, as is the case with the axial fibres of the pseudopodia of Heliozoa.[1] The oat-shaped corpuscles also are to be regarded as inert nuclear bodies, inert so far as motility is concerned.

The movement of the oat-shaped corpuscles along the threads is, I believe, produced by an exceedingly delicate coating of hyaline protoplasm. Of the existence of such hyaline protoplasm, which is neither filament nor corpuscle, we have evidence, firstly in the agglutination of the filaments when not extended, and secondly in the movement of contraction and expansion of the mass of filaments. I do not think that it is possible anywhere actually to see as an isolated substance this delicate "varnish" of hyaline protoplasm, but it seems to me reasonable to infer its existence.

Thus I should regard the filaments of Chlamydomyxa as the delicate skeletal supports of a still more delicate streaming protoplasm, in which, as in coarser pseudopodial expansions, parallel currents of different rates or opposed in direction may arise.

The Central Pigmented Corpuscles.—The centre of the disc or irregular body, which is the form taken by Chlamydomyxa montana when in the free motile state, consists, as shown in figs 1—4, of a number of rounded corpuscles closely pressed against one another, and of a yellow-brown colour with a tendency to a greenish tint. There is no doubt that a colourless protoplasmic substance invests each of these corpuscles, and whilst holding the mass together is continuous with the colourless marginal substance or border of the disc. These corpuscles are of fairly uniform size ($\frac{1}{8000}$ of an inch in diameter), and are of viscid consistency. I consider them as identical in character with the green vesicles described by Bourne as forming the bulk of the structure of his Pelomyxa viridis (see this Journal, vol. xxxii ,1891), and I entirely agree with him in separating them altogether from relationship to

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[1] I am inclined to think that such an elastic filament, one-sided in position, must be present also in all cilia and other forms of vibratile protoplasm.

ordinary chlorophyll corpuscles such as those of the leaves of plants.

I consider that these coloured vesicles, which differ from the conception of "corpuscles" or "granules" only in their relatively greater fluidity, are identical with the colourless "Glänzkorper" (Greef) or refringent corpuscles of Pelomyxa palustris, as I have stated in a note to Gould's paper on the structure of that Protozoon, published in vol. xxxvi of this Journal, 1894; and they all, no doubt, have an important chemical function in relation to the surrounding protoplasm. The colouring matters which develop in such vesicles appear to have a special character, and without necessarily agreeing exactly with what is called "chlorophyll," are related to it and to such substances as diatomin, which accompany chlorophyll in other more highly developed organisms. The colouring matter of Professor Bourne's Pelomyxa viridis is clearly not simple chlorophyll, or if such chlorophyll is there it is mixed with other pigmented bodies. The predominant yellow-brown colour of the vesicles (granules or corpuscles) of the disc of Chlamydomyxa montana is suggestive of diatomin. Very possibly it masks chlorophyll. This is probable, because Archer represents his Chlamydomyxa labyrinthuloides as containing vesicles like those in question, but coloured bright green; and further, because after encystation my C. montana undergoes the most remarkable changes in colour, developing a brilliant grass-green tint (in some examples), whilst accompanying this chlorophyll-like colouring matter there are always found in the cysts of C. montana irregular or central droplets of a brilliant crimson oily fluid, soluble in ether (see Pl. 15, figs. 8 and 9).

Encysted Condition.—The cysts of Chlamydomyxa montana closely resemble those of C. labyrinthuloides, as described by Archer and Geddes. The substance of which the cyst-walls are composed yields the blue colour characteristic of cellulose when treated with H_2SO_4 and iodine. The cysts are further remarkable in two features, and unlike the capsules usually termed "cysts" among Protozoa. They have (*a*) a most definite laminated structure, consisting of a series of "shells" or complete coatings of cellulose substance, deposited one within the other, on the surface of the protoplasmic organism. The protoplasmic organism apparently shrinks after the formation of a first cyst, and having grown smaller forms a second deposit, and so on, in some cases to a ninth or tenth. In the second place, (*b*) the living organism enclosed in the cyst appears to be by no means quiescent, but to be undergoing important chemical changes, as shown by its remarkable change of colour (to a bright green) and its development of "droplets" of red-coloured oily material. The activity of the encysted Chlamydomyxa is further and very markedly demonstrated by its movement, change of form, and division into separate masses. The fact that the shells or coatings of cellulose are so freely and abundantly deposited by the living matter enables one to follow these changes in the encysted Chlamydomyxa with certainty. Thus in Pl. 15, fig. 6, we have evidence of division of an original mass of living Chlamydomyxa into three; in fig. 7, part of the cyst at first formed and marked *a* has been deserted, whilst the original outer cysts are much larger than those now occupied by the living material, which has divided into two masses. In fig. 9, three cysts occupied by green-coloured Chlamydomyxa which have given rise also to the red-coloured oil drops, are represented. These three cysts probably originated from the division of one parent mass. The division of the encysted Chlamydomyxa has been described in considerable detail by Professor Patrick Geddes in his paper already referred to.

In reference to differences between C. montana and C. labyrinthuloides, I may point out that I have not seen the body or mass of C. montana when it is in the dendriform streaming condition, to be partly lodged in the ruptured cyst, as Mr. Archer saw and figured that of C. labyrinthuloides. Nor have I seen green pigment (presumably chlorophyll) and red oil drops in that phase, as Mr. Archer describes for C. labyrinthuloides. The dendriform streaming specimens of

C. montana which I observed (in considerable numbers for several days) were always entirely free from any cyst-wall, and, moreover, their central granules or vesicles were of an uniform yellow-brown colour. This may be due to specific difference, but it would be interesting to know what appearance C. montana presents early in the season,—for instance, in June.

The very regular circular cyst drawn in fig. 10 is a fairly common form. As shown in the figure, the cyst contents are yellow in colour, almost bright yellow, with radiating structure resembling yolk-columns. As many as eight concentric laminæ were observed in the cyst drawn in fig. 10.

Affinities of Chlamydomyxa.—I do not think that either the observations made by me on C. montana, or the progress of our knowledge of Protozoa since Archer described C. labyrinthuloides twenty-one years ago, enables us definitely to assign to Chlamydomyxa its position in relation to other Protozoa Gymnomyxa.

I cannot agree with Professor Geddes that it should be regarded as related to the Algæ, since affinities have to be determined by a consideration of all the circumstances, and I cannot see how Chlamydomyxa would fit in with known Algæ.

I fully agree with Archer that the nearest ally of Chlamydomyxa is the Labyrinthula of Cienkowski, and that any consideration of affinities must be based on this alliance. Archer was inclined to regard the "threads" of Chlamydomyxa as protoplasmic, whilst Cienkowski regarded those of Labyrinthula as of a horny nature. I do not think that there is any essential difference between the threads of Labyrinthula and of Chlamydomyxa. I regard them both as a "formed material," differing from streaming protoplasm, and comparable to the axial pseudopodial filaments of Heliozoa. The fusiform travelling nuclei of Chlamydomyxa differ very greatly from the oat-shaped nucleated corpuscles of Labyrinthula both in size and structure. But it seems to me a reasonable view that the condition of Chlamydomyxa is derived from that of Labyrinthula, and that the fusiform nuclei of the former represent the oat-shaped corpuscles of the latter in a reduced condition. The fact that in C. montana as compared with C. labyrinthuloides the fusiform nuclei are still further reduced, being but one third their size, tends to indicate a progressive reduction of these bodies. The protoplasm surrounding the nuclei of the oat-shaped corpuscles of Labyrinthula is represented in Chlamydomyxa by an exceedingly delicate and practically invisible layer, which is also extended over the threads, and is the seat of the movement which is rendered visible by the translation of the nuclei.

The Protozoa which come nearest to Chlamydomyxa and Labyrinthula are certain of the Mycetozoa; but each of the two genera in question differs in its own way from the typical Mycetozoa, especially as to reproduction, and nothing would be gained by sinking them taxonomically in that assemblage.

The most remarkable feature in which Chlamydomyxa differs from Labyrinthula and from all other Protozoa is its "encysted phase." The enclosure of the general protoplasm in a cyst-wall may be compared with the fruit-formation and other cyst-like productions of the Mycetozoa. But the physiological character of the cysts of Chlamydomyxa, the activities of the encysted organism, and the great relative duration and importance of the encysted phase are peculiar to Chlamydomyxa, and may be explained by the fact that this organism is an inhabitant of fresh water, and subjected to the vicissitudes of temperature and evaporation of the inhabited water which we know are frequently associated with special protective structures and aberrant phases of growth and activity.

A point in which both Chlamydomyxa and Labyrinthula agree with the Mycetozoa is their epiphytic habit.

In his paper on Chlamydomyxa labyrinthuloides, Archer draws attention to a terricolous plasmodium (found in a flower-pot) of an unknown Mycetozoon described by Cienkowski. It is not possible to decide from his (Cienkowski's) description whether he had before him Archer's Chlamydomyxa, but it is most probable that he had not, since he does not describe the characteristic structures of that organism. Similarly the Biomyxa vagans described and figured by Leidy, in his large volume on Rhizopoda in the United States Geological Survey of the Territories, 1879, presents some points of agreement with Chlamydomyxa, and was discovered by Leidy upon Sphagnum. Yet inasmuch as neither the delicate filaments nor the fusiform nuclei, nor the central coloured vesicles (granules), nor cellulose laminated cysts are ascribed by Leidy to his Biomyxa, we must suppose that it indicates a distinct organism, not even closely related to Chlamydomyxa.

OXFORD; July 8th, 1896.

EXPLANATION OF PLATES 14 & 15,

Illustrating Professor Ray Lankester's memoir on "Chlamydomyxa montana, n. sp."

All the figures except Fig. 6 are drawn to the same scale.

FIG. 1.—Chlamydomyxa montana, n. sp., in an unencysted expanded condition.

FIG. 2.—The same specimen after an interval of five minutes. Drawn at Pontresina from a living specimen as seen with objective No. 10 immersion of Hartnack, August 22nd, 1886.

FIG. 3.—Another and larger specimen observed and drawn at the same time.

FIG. 4.—A specimen which is beginning to expand its filaments. After five minutes the threads would have a much wider extension.

FIG. 5.—A single fusiform corpuscle (nucleus) greatly magnified, showing its shape and its relation to the filament. The actual length of the corpuscle is $\frac{1}{12000}$ inch.

FIG. 6.—An encysted specimen of C. montana which has divided into three. Pontresina, August, 1886.

FIG. 7.—An encysted specimen of C. montana which has divided into two. Pontresina.

FIG. 8.—An encysted specimen of C. montana which has developed chlorophyll and a crimson oil drop. The cyst-wall is simple. Pontresina.

FIG. 9.—Three similar encysted specimens. Pontresina. These and the last were brought alive to London and drawn there.

FIG. 10.—A spherical cyst with eight laminæ to the cyst-wall and a golden yellow pigment. This last specimen observed and drawn at the Maloja in 1892.

The Constitution and Development of the Society of Termites: Observations on their Habits; with Appendices on the Parasitic Protozoa of Termitidæ, and on the Embiidæ.

By

Professor B. Grassi in collaboration with Dr. A. Sandias.

With Plates 16—20.

The memoir, of which I have made the following translation, was originally published in the 'Atti dell' Accademia Gioenia di Scienze Naturali in Catania,' ser. 4, vols. vi and vii (1893–4), but has become more generally known through the appearance of a separate edition in the former year. But though its value was immediately recognised, the work has not yet become familiar to an extent commensurate with the importance of its contributions to natural science.

The object of the treatise, itself an expansion and completion of certain preliminary papers on Termitidæ by Professor Grassi, is set forth in that author's introduction, and requires no further explanation; but it is perhaps permissible to point out that, over and above the results obtained in the pursuit of that object, the memoir is a signal and instructive example of a class of work but too seldom resorted to—the union of morphological research with an inquiry of the most prolonged and persevering character into the habits and bionomics of the living form. In these latter respects it forms a worthy parallel to the work of such great pioneers in the investigation of the social systems of insects as Smeathman, Huber, and Réaumur. And it is for this reason that no study of an abstract which merely summarises the results obtained can prove as convincing or suggestive as that of the original.

An excellent general summary of the various writings on Termitidæ, which includes references to such facts as have been observed since the publication of the present memoir, is to be found in vol. v of the 'Cambridge Natural History,' by Dr. Sharp. In view of its existence it has been thought unnecessary to make more than a very few additions to the original text; these will be found indicated in the usual way by square brackets.

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To Fritz Müller,
on his Jubilee.
Catania, 1892.

Introduction.

It has been recognised by Darwin, in his immortal work on the 'Origin of Species,' that the existence of insect communities, composed of different castes (kings, queens, workers, soldiers, and the like), furnishes his opponents with a trenchant weapon. Now these communities actually consist not merely of fertile forms (kings and queens), but of sterile forms (workers, soldiers, &c.), distinguished by important modifications of structure and marvellous instincts, none of which are to be found in their parents. The sterile progeny would therefore appear to be uninfluenced by one of the prime factors in the struggle for existence, that of heredity, owing to the impossibility of transmitting to the offspring such modifications of structure or instinct as may be gradually acquired; and Darwin himself admits that it required great confidence in his theory not to renounce it in the face of this objection.

I have had to deal shortly with this question on another occasion with regard to bees, for which I have observed that the cause of their apparent deviation from the normal rule may possibly be found in the existence of workers capable of oviposition, which apply themselves to all the tasks of the colony, and possess the characteristics of true workers, with the single difference that they lay parthenogenetic male ova.

The males which hatch from these eggs would then transmit to the female ova—laid, as we know, by the queen—the characteristic properties of the worker.[1]

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[1] Darwin, however, explains the phenomenon by a very ingenious comparison. "According to M. Verlot," he writes, "some varieties of the double annual stock, from having been long and carefully selected to the right degree, always produce a large proportion of seedlings bearing double and quite sterile flowers; but they likewise yield some single and fertile plants. These latter, by which alone the variety can be propagated, may be compared

As it is probable that the same explanation is equally applicable to other Hymenoptera, I put aside that order of insects to devote myself to another, of remote relationship—namely, the Corrodentia, of which the Termitidæ constitute the typical form. But I found myself here in a much less cultivated field than that of the Hymenoptera, and it took me several years before I was able to see my way.

In the meantime a school has arisen under Weismann, which denies the heredity of acquired characteristics; this has somewhat modified, and perhaps rendered more interesting the general questions which have inspired my particular researches, as I will explain.

It has been known for many years that the same bee larva may develop either into a queen or a worker in accordance with the nutriment it receives. Nutrition, therefore, possesses a most remarkable influence on the bee's generative organs, and on many other characters correlated with their greater or less development (e. g. the faculty of producing wax, or of collecting honey, which is possessed by the worker only, and not by the queen). This would indicate that the environment has a powerful and direct influence on the genitalia, and would therefore tend indirectly to show that the much-disputed inheritance of acquired characteristics is a possibility.

with the fertile male and female ants, and the double sterile plants with the neuters of the same community. As with the varieties of the stock, so with social insects, selection has been applied to the family, and not to the individual, for the sake of gaining a serviceable end." ['Origin of Species,' ed. 6, p. 230. The whole chapter should be consulted.] But it may be objected that the difference between the queen and worker forms is far more profound than that between the simple and double stocks.

Büchner ['Aus dem Geisteslebens der Thiere,' translated under the title 'Mind in Animals,' London, 1881], on the other hand, thinks that the explanation of the phenomenon should be found partly in atavism, and partly—as far, that is, as regards the marvellous instincts—in the instruction which the young receive from the colony. That atavism certainly plays a part in instinct is demonstrated ad evidentiam by a fact discovered by myself. It is known that certain silkworms become pupæ and moths without spinning a cocoon. Now my experiments show that the offspring of such moths may spin perfectly constructed cocoons.

But this argument in its favour would be greatly weakened if the circumstance indicated by me above—namely, the possibility of hereditary transmission by means of oviparous workers—should have played the part which I suppose it to have done.

I determined, therefore, to investigate the origin of the workers and soldiers in Termitidæ,—in forms, that is, whose phylogenetic source is certainly absolutely distinct from that of the social Hymenoptera.[1] Such an inquiry would at least throw light on my hypothesis with regard to the bee, and in any case should lead to results of some utility for the problem I have several times referred to, the heredity of acquired characteristics, and for the subordinate and related question of the direct influence of environment on the generative organs.

The recent researches of Van Beneden, Boveri, O. Hertwig, and others on the ovum and spermatozoon had afforded yet another problem for solution, which would be modified according as to whether there should or should not exist special eggs or spermatozoa for the workers and soldiers of Termitidæ.

In short, the theory of evolution, the disputed heredity of acquired characteristics, and lastly, the theory which postulates the existence in every somatic cell of elements derived from both parents, these alike have all furnished me with motives for regarding the elucidation of the origin of caste forms in the social Termitidæ as a problem of the highest interest. This, then, is the main object of the present memoir, and it has been arrived at only by dint of prolonged observation and preliminary experimentation, the results of which are fully related here as a necessary corollary.

The development of my argument has, so to speak, com-

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[1] It must be recollected that, though we are acquainted with forms which perhaps can be ascribed to the Blattidæ from the Silurian strata, the Termitidæ, according to Scudder (in Zittel's 'Handbuch der Paläontologie,' ii, 772), are absent in all the palæozoic, and appear only for the first time in mesozoic strata. Nevertheless the phylogenetic independence of the Termitidæ and Hymenoptera is indisputable.

pelled me to discuss neoteinia[1] and the simplification and degeneration of forms, and therefore to express my present views on the Thysanura, which for a long time formed the special object of my studies.

In these preliminary remarks I have prominently set forth the fundamental ideas which have directed my work, and now pass at once to the consideration of the Termites.

As yet two species only of Termitidæ, Calotermes flavicollis, Fabr., and Termes lucifugus, Rossi, have been found in Italy. The latter forms the subject of Lespès' admirable monograph,[2] but Calotermes flavicollis is known to us only by a few accounts of merely systematic importance, and not even complete.[3]

However, Fritz Müller has made important investigations[4]

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[1] [The term neoteinia has been introduced by Camerano ('Bull. Soc. Ent. Ital.,' 1885, pp. 89—94) to denote the persistence during adult life of part or all of the characteristics normally peculiar to the immature, growing, or larval stages (e.g. the persistence of gills in the axolotl). It therefore covers much the same ground as is denoted by the term pædogenesis, but appears, so far as can be gathered from Camerano's paper, to include a somewhat wider class of facts than those comprised under the latter term, which would fall under his definition of total as opposed to partial neoteinia. Neoteinia, or the persistence of larval characteristics, does not necessarily imply that anticipation in time of sexual maturity which is usually connoted with the use of the term pædogenesis,—which, moreover, is strictly applied to agamic reproductions.—W. F. H. B.]

[2] "Recherches sur l'organisation et les mœurs du Termite lucifuge," 'Ann. Sci. Nat.' (4), v (1856), pp. 227—282, pls. v—vii.

[3] [Hagen, "Monographie der Termiten," 'Linn. Entom.,' x, 1—144, 270—325; xii, 4—342. The reference to C. flavicollis, op. cit., xii, pp. 54—61, pl. i, fig. 12; pl. ii, fig. 15.]

[4] "Beiträge zur Kenntniss der Termiten," 'Jen. Zeitschr.,' vii (1873). I. "Die Geschlechtstheile der Soldaten von Calotermes," pp. 333—340, pls. xix, xx. II. "Die Wohnungen unserer Termiten," pp. 341—358. III. "'Die Nymphen mit kurzen Flügelscheiden' (Hagen), 'Nymphes de la deuxième forme' (Lespès). Ein Sultan in seinem Harem," pp. 451—463. Id., ix, 1875. IV. "Die Larven von Calotermes rugosus, Hag.," pp. 242—264, pls. x—xiii.

on another species of Calotermes, and these, as will be seen later, are in entire agreement with our observations on the European species.

Nevertheless, as I have already mentioned, the study of Termitidæ in general is as yet very incomplete; and although books of travel certainly abound in notices of these interesting insects, they mostly deal with detached and imperfect observations.

I have repeated Lespès' investigations on Termes lucifugus with particular reference to the so-called "nymph of the second form" which that distinguished naturalist described.

He attributed to it an entirely different significance from that which it really possesses, owing mainly to the circumstance that his period of study was confined to about nine months—from November, 1855, to August, 1856. But how difficult the elucidation of the true function of this nymph of the second form has been the reader will gather from the pages of this memoir; and I may state at once that it has necessitated the removal of many hundred cubic metres of earth and the cutting up of hundreds of trees, a task that has had to be carried out little by little, and has consequently demanded no small amount of patience.

I am indebted to a small but fortunate discovery for the most interesting observations on Calotermes flavicollis, which I have to relate in the present work.

If from three to twenty Calotermes of different ages are placed in a glass tube three to eight centimetres long (Pl. 19, fig. 11), closed with a cork and kept warm—for example, in the waistcoat pocket, unless in summer-time, they continue to live and constitute a family, or better, an independent colony; they rear a fresh king and queen,[1] if orphaned, and they rear soldiers,

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[1] [The statements made on the sexual forms of Termitidæ will be more clearly understood if anticipated by a summary and definition of the terms employed in the course of the work. Sexual or royal forms are of two kinds, true and neoteinic. The true royal forms are imagos, or perfect insects, which acquire a complete development of the wings and

&c., if in want of them. In short, after a certain time the tube will contain a complete little nest, if it did not originally do so. However, the insects do not hesitate to bore through the cork, and, unless they are watched, one is surprised to find some day that they have all made their escape. But frequently they remain in the tube, even though they have made holes putting them into communication with the outer air (Pl. 19, fig. 11).

Some of these little nests can be kept alive for several months, but many die off after a few weeks, though not until they have afforded sufficient opportunity for making numerous observations through the glass walls by aid of a lens. It is desirable to use tubes of various lengths and calibres, because certain points are better seen in a wide than in a narrow tube.

In addition to the insects, the tubes are partly filled with fragments of wood, which should be neither too dry nor too moist. In the former case the insects gradually shrivel, contract, dry up and die; and in the latter case there is a deposit of water vapour on the inner walls, and they are evidently killed by over-dampness. Death ensues more or less rapidly according to the amount of water deposited, and is sometimes almost as sudden as if the insects were suffocated or chloroformed. Slow death due to over-dampness may be accompanied by distinct œdema or reddish discoloration of the

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darkening of the chitin concomitantly with the maturation of the gonads after the last ecdysis. They leave the nest by "swarming." The neoteinic royal forms undergo a premature maturation of the gonads whilst in a late larval or nymphal instar, or that of an immature and pallid imago. This maturation is accompanied by an arrest of development of other parts of the body; the chitin does not darken normally, and the wings do not grow further. They do not leave the nest. The latter class is further subdivided into complementary and substitute royal forms. Complementary forms are not found in Calotermes, but are normal components of the Termes nest, in which they are the only reproductive individuals. Substitute forms are developed to supply the loss of the true royal forms in Calotermes, or the complementary royal forms in Termes. The three varieties of royal examples all comprise kings and queens,—that is, individuals of each sex.]

body; the latter is accompanied by the presence of a bacterium which I have not investigated.

If the wood is too damp the colony may generally be saved by the simple precaution of leaving the cork out of the tube; after a few days the moisture diminishes, and the cork must then be re-inserted, or the opposite extreme of undue dryness is quickly reached. With time and patience an exact estimate can be formed of the amount of moisture necessary, and it can then be easily regulated. The cork must fit closely, and want of oxygen need not be feared. At one time I was accustomed to uncork the tubes three or four times a day, but I subsequently found this to be quite unnecessary; if the Calotermites require change of air, they are able to provide it for themselves by boring through the cork.

When these tiny nests are examined the tube may conveniently be laid flat and left quiet, but an occasional shake is sometimes useful to rouse the inmates to activity.

Unfortunately Termes lucifugus does not flourish in these tubes, but drags on a feeble existence for a week or ten days at most; I have made many but quite unsuccessful attempts to establish a moderately suitable environment for them therein. The species is all the more difficult to study because, in comparison with Calotermes, the members of a colony are smaller and more rapid in movement.

Many as have been the details made out through these glass tubes in my laboratory, there are others which will be more successfully undertaken by anyone who has the opportunity of applying my method to the large exotic species.

Considering that the termites of tropical countries are among the most injurious of insects, I must point out a practical result of my investigations, and one of the highest importance. Contrary to the belief of residents and the accounts of travellers, such as Major Casati,[1] a nest of termites cannot be destroyed merely by killing the king and queen. If there remain alive some eight, ten, or twenty examples, which include any undifferentiated larvæ, or larvæ of perfect

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[1] ['Ten Years in Equatorial Africa,' i, p. 165.]

insects or nymphs, these eight, ten, or twenty will form a new colony, which slowly but surely will become as flourishing as the original stock.

It follows, therefore, that the extirpation of these insects is excessively difficult in practice; and their entry into any situation where they can prove destructive must be prevented. This is the strategy to adopt against them, for when once they have gained admission there is no way of getting rid of them.

The present work has no claim to be a complete monograph of the Termitidæ, and merely furnishes materials for whomsoever will undertake so large a task. It is confined, in short, to the discussion of certain fundamental points.

Before concluding I must express my thanks to Dr. Calandruccio, who has given me no little help in this research. Many observations, particularly those on Calotermes kept in tubes, have been made under my supervision by my pupil Dr. Sandias, and have afterwards been carefully verified by myself.

The Colony of Calotermes flavicollis.

1. Situation and Nest.

As with all Termitidæ, the life of Calotermes is intimately connected with the vegetable kingdom, for it lives exclusively on woody matter. At Catania I have found it only in the stems or roots of living but partially decayed, and therefore, as a rule, old plants, and never in those of which the stem or tap-root measures less than one or two centimetres in thickness. But when once established in a stem or main root it can extend into decayed portions of the branches or side-roots, even if of lesser diameter. Though always absent in entirely sound plants, it can be found in partly decayed examples of many kinds,—of many, but not of all, for I have never met with it in lemon, orange, or Agave americana, &c. It is also relatively scarce in cactus (Opuntia), even though large portions of the plant are dead; but if present, it may infest the rotten phylloclades, which in fact are sometimes the first portions to be occupied.

It is difficult to find a tree with any decayed portion which has not been attacked by Calotermes in Catania and the adjoining provinces, at least in the low country, for I have not searched at a higher elevation than Nicolosi. At Castrogiovanni the species appears to be entirely absent.[1]

As mentioned above, it inhabits still living plants. Should the plant die the Calotermites survive until it has become completely dry, when they perish—a fact that anyone can verify by examination of the vine-stocks annually turned out from old vineyards. If the dead trunk does not dry up, as is the case in marshy situations, the insects continue to flourish.

Lucas and some other writers state that they have found Calotermes flavicollis in buildings. I have never observed this at Catania, but Dr. Sandias has found flourishing colonies at Trapani in the woodwork of verandahs, doors and stairways, &c., ten years old; probably the wood harboured the insects before being worked up for domestic purposes. It should be observed that the climate of Trapani is very damp, so that wood probably dries less there than at Catania.[2]

In order that a plant may harbour Calotermes, it must (necessarily), as I have stated, exhibit some amount of decay, because such decayed portions alone are occupied. To proceed to details, Calotermes never invades the healthy parts, but encroaches at most on their boundaries. If a partly decayed vine-stock is infested, it is usually easy to make out that the healthy tissues are respected; yet should they contain an internal channel of decay barely larger than the body of a Calotermite, the insects can enter and excavate a gallery, which will then present but a very thin lining of decayed matter, and

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[1] [In a foot-note at the end of the original work the authors state that, since it was printed, Signor Giuseppe Corona has discovered the species at Castrogiovanni.]

[2] The Marchese Doria informs me that he has confirmed Dr. Sandias's observation at Genoa, although the climate there is certainly not moister than that of Catania.

will therefore appear to run in the sound structures. But, so far as I have observed, this lining of decayed tissue is never absent.

It is undeniable that the process of decay is hastened by these burrows, particularly because they allow the infiltration of rain-water; but a detailed study of these phenomena would lead too far from the subject.

Calotermes greatly prefers to live in the deepest parts of the dead wood,—that is, the parts nearest the living tissues, and consequently the most recently decayed. Portions which have been long dead are usually too dry for it, and are chosen as a tenement by ants.

Fertile pairs, unaccompanied by eggs or with very few offspring—that is to say, nests in process of formation or recently formed,—are to be found by special search at the places where a plant has been pruned a year or two previously and has subsequently rotted, provided that the pruning has not followed on antecedent decay. This can be easily observed in the fig or vine. Fresh nests, therefore, are usually established where the dead portion is still so limited in extent as not to afford space for a numerous colony, and these situations are rarely preoccupied by other insects, such as ants, beetles, or other Termitidæ, &c. As the colony gradually increases and requires more room, the decayed area spreads, but to all appearance independently of the insects. That this is the case is rendered probable by an examination of progressive decay in a district where Calotermes is absent, such as Lombardy, where the winter is too severe for them.

Turning once more to the formation of the fresh termitaria, I do not wish to deny the possibility of its taking place in trunks in which extensive decay already exists; but such an occurrence is unusual, either because the wood is preoccupied by termites or other insects, or because the royal pairs must traverse parts which are already dry and swarming with enemies (ants), in order to arrive at the required spot where the decay is most recent.

The corks of the tubes are attacked probably because they retain a certain amount of moisture; for if the insects are shut up with nothing but particles of cork they all die in a few days.

To sum up, two conditions are essential for the life and well-being of Calotermes—a suitable temperature and a suitable amount of moisture. But whereas increase of temperature is favorable, at least up to a certain point, the degree of humidity can vary only within very restricted limits.

Owing to the severity of the winter, Calotermes is absent from Lombardy, Piedmont, and Venetia, but it is found in the province of Genoa; its northward distribution is not accurately known. At Catania it is much more sluggish in winter than in summer, the ova do not develop, and the larvæ and nymphs do not moult. The influence of moisture has been repeatedly referred to; it is correlated with the nature of the cuticular structure (chitinous layer), which except in a few regions, such as the mandibles, is very thin, even in the adults and royal pairs, in both of which it is brown in colour. The younger the individual, or the more recent its ecdysis, the thinner is the chitin. In general the rule holds good for Calotermes that white and semi-transparent examples have a thinner cuticle than those which are more opaque and inclined to yellow (very old soldiers or substitute-queens). Young or freshly moulted specimens, usually distinguishable by their greater transparency and whitish or rarely faintly yellow colour, always require more moisture than those which are older or have not cast their skin for some time, and possess a more or less evident yellow tint. The imagos, before or after the loss of their wings, can endure a greater degree of dryness; but even these generally die in a short time if removed from the wood and exposed to the open air.

These conditions of temperature and moisture, naturally with some variation in degree, especially of the latter factor, must hold good for all other species of Termitidæ, and are probably correlated with their limitation to warm countries, their much wider European distribution in epochs when the mean temperature was presumably higher, and with their choice of evening or night, the interval after a shower or a wet day as a swarming-time (Casati).[1]

The nest of the Sicilian Calotermes resembles those of its congeners, which show, as a rule, very little architectural skill. Strictly speaking, they do not build any nest, but content themselves with burrows excavated in wood and never quitted. These burrows vary very much in dimensions, and the same gallery may be narrow in one part and very wide in others. In one of the enlargements, towards the heart of the nest, the royal couple, with a numerous surrounding, is usually to be found. There is never a true royal chamber, such as has been described for many other species. The galleries are very variable in direction, but the widest and longest are generally subparallel with the long axis of the stem. A large number of transverse passages is commonly found, and these are often too narrow to allow room for more than a single individual at a time. According to Fritz Müller,[2] the burrows of Calotermes possess an inner lining of excrement. This appears at first sight really to be the case when they are excavated in rotten and somewhat softened wood. But if they are examined in cork, or in wood which, though dead, is still hard, the absence of such a lining is easily established, and this fact once determined, one can satisfy oneself that burrows made in damp wood are also unlined.

In common with other termites, Calotermes avoids the outer layers of the cortex (as may be readily observed in vine-stocks), and thus protects the nest from the direct action of the atmosphere or infiltration of water.

As previously stated, the colony provides for an increase in numbers by penetrating deeper into the wood. This penetration is also determined by the fact that the superficial wood becomes too dry. The abandoned portion becomes then commonly occupied by ants, the pitiless enemies of Calotermes. The termitarium is separated from the ant-burrows, or from openings caused by wind-cracks or axe-wounds by means of

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[1] ['Ten Years in Equatorial Africa,' i, p. 166.]

[2] ['Jen. Zeitschr.,' vii, p. 343.]

barricades of masticated wood, or more commonly of excrement, which is cemented together by saliva, with or without an admixture of disgorged wood. This disgorgement is normal, and not exceptional, as Fritz Müller believes.[1]

The following facts and other details of interest may be easily observed through the glass tubes.

If some fragments of wood and a few Calotermites are put into a tube and left uncorked, the insects will be found on the following day to have established themselves either in the whole of the space filled with wood, or in its lower portion, at the bottom of the tube. In either case the occupied area is delimited by means of disgorged matter deposited in the interstices between the particles of wood. As far as can be seen the boundary wall is complete, but it lies at different levels and not entirely in the same plane; its margin can easily be made out at the point of contact with the glass, and will be found on revolving the tube to form a complete circle, but with some irregularities of level, obviously due to a selection of the smallest interstices for cementing up without reference to their higher or lower elevation.

[The process of construction can be watched in the tubes; the insect regurgitates a pasty mass, which is spread out, if necessary, by the antennæ, so as to form a rounded pellet on the glass of about a millimetre in diameter, and of the colour of rotten wood.]

The boundary wall is undoubtedly designed for protection against direct contact with the atmosphere; this is proved by its not being constructed if the tube is closed with a cork instead of remaining open.

Such a wall may occasionally be built even in a corked tube, should part of the nest contain any offensive substance. Thus if flour be added to a small tube-nest, after a few days the upper part containing the flour, which will have become mouldy, is found to be cut off in the manner described from the lower portion, in which all the insects have collected.

Sometimes the Calotermites in a tube may be seen to cement

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[1] ['Jen. Zeitschr.,' vii, p. 343.]

together pieces of wood which are unduly loose; but at other times they do not do so, although much incommoded by their mobility. In certain cases they line the lumen of the tube with disgorged matter, so as to form a continuous layer, save for a few irregular patches, but they generally spare themselves this task, or merely begin and immediately abandon it.

It should be added that if the tube is too damp its inner surface may be covered with moisture, to which the insects adhere, particularly when young, and so die. This is guarded against, at least partially, by the lining of disgorged substance.

When the supply of wood in the tube is very small, the Calotermites usually have recourse to the cork, in which they bore one or more galleries a little wider than their body; they gnaw away and hollow out the cork, carrying the débris into the tube, which is soon filled up, as the cork-dust is allowed to remain as a loose mass.

If a corked tube is surrounded with sawdust, some of it can generally be found in its interior, having been carried in through galleries in the cork but little wider than the insects' bodies.

[The corks of tubes kept in the waistcoat pocket are often channelled with burrows leading to the exterior, through which the insects escape and are lost, in the belief that they are enlarging their nest. Sometimes books near which the waistcoat was laid at night were attacked, and the paper was found to be gnawed in places the next morning.]

Burrows made in corks may often be seen to possess a sort of rounded lid at their external opening; this is cut out of the superficial layer of cork, and fits tolerably closely, though it usually falls in a little. It may be hinged to the cork by a more or less wide attachment.

[Calotermites may be frequently seen to carry excrement to the bottom of the tube, and to accumulate it there, mixed up with wood and cork-dust; and sometimes they keep the eggs in the same place.]

If the stopper is too narrow the space between it and the tube is gradually filled up with excrement.

Calotermes flavicollis differs materially from Termes lucifugus in the fact that it confines itself to excavating burrows, and is thus merely a borer; whereas the latter species not only bores, but builds tunnels, in order to connect pieces of wood at a considerable distance apart.

2. Number of Individuals in the Colony.

In these observations a normal development of the colonies is assumed. For should the queen, for example, die before the community has reared a successor, several months pass during which oviposition is suspended and multiplication is consequently brought to a standstill.

A colony of Calotermes rarely consists of more than a thousand members, and is relatively numerous when it contains five hundred. This is correlated with the fact that the queen of our species is very far from attaining the colossal dimensions which are well known to occur in the queen-termites of tropical countries.

After fifteen months of common life the king and queen may be surrounded with fifteen or twenty young, after another year with about fifty, and in the two or three following years the population increases till it reaches a maximum at which it becomes nearly stationary. This is attained when the king and queen have reached the largest possible size.

Eight or ten winged adults may depart from a two-year-old nest, and the number leaving in successive years increases concomitantly with the increase in the population.

At the time of maximum oviposition a queen of three to four years old lays as a rule four, five, or six eggs a day.

3. The Different Castes (Plate 16).

By way of preliminary, it should be stated that for the sake of orderly arrangement a knowledge is assumed in this part of the work of certain conclusions, the demonstration of which is postponed to the succeeding chapter.

A colony of Calotermites contains—

1. Undifferentiated larvæ (fig. 1), capable of becoming

either soldier larvæ, or larvæ of perfect insects,—that is, larvæ possessing the first indications or rudiments of wings.

2. Larvæ of perfect insects (fig. 3), and nymphs (fig. 4) derived from them.

3. Larvæ of soldiers (fig. 2), and soldiers (figs. 5 and 16); the latter derived from the former, and those derived from undifferentiated larvæ, from the larvæ of perfect insects, or from young nymphs.

4. Perfect insects derived from nymphs (fig. 6).

5. A royal couple, properly so called, derived from perfect insects (figs. 7—11).

6. Larvæ of substitute royal forms (fig. 14), and substitute forms (figs. 12, 13, and 25) themselves derived from the former; those in their turn having originated from undifferentiated larvæ with fourteen or fifteen antennal joints, from larvæ of perfect insects, or from nymphs.

To proceed to details: a colony contains newly hatched larvæ about 1 mm. in length,[1] with ten antennal joints of which nine are pilose, and one not. The glabrous third joint is relatively very long, and presents indistinct traces of a tripartite division. These traces soon become more marked, and the separation of the distal joints appears constantly to be clearly defined before that between the middle and the proximal joints, and possibly may actually precede it.

As a result we have larvæ which are a little over 2 mm. in length, and exhibit twelve distinct antennal joints, of which the 3rd, 4th, and 5th are short and bare. In succession the 5th joint, as far as I have seen, becomes pilose and relatively longer; then the 4th and finally the 3rd exhibit the same phenomena.

We thus obtain examples with twelve antennal joints, all pilose; and in the meantime the body increases in size, so that such specimens measure about 4 mm. in length.

The newly born larvæ are all perfectly alike,—that is, they

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[1] In Termitidæ the length of the individual as a rule has only a relative value, as it depends largely on the degree of moisture in the atmosphere, the food supply, &c.

are undifferentiated; but when they have attained an average length of 2 mm. they are divisible into two groups, one with a large head, little narrowed anteriorly (Pl. 16, fig. 2), the other with a small head, more evidently narrowed towards the apex (Pl. 16, fig. 1).

The former have become soldier larvæ, and will ultimately become soldiers. The latter are still undifferentiated; they reach a length of 4 mm. and acquire twelve pilose antennal joints (vide supra); the character of the head either remains unchanged, and continues to be undifferentiated, or becomes modified by an increase in size and in the width of the anterior portion, so that they become soldier larvæ.

Small soldiers (Pl. 16, fig. 16) are to be found which are derived from these very larvæ; they are less than 5 mm. long, and possess twelve pilose antennal joints, with an ill-marked suture between the 4th and 5th.

It may be well to observe at once that soldiers of medium size with thirteen or fourteen pilose antennal joints, and large soldiers (Pl. 16, fig. 5) with fifteen to seventeen pilose antennal joints also exist. Further, the antennæ of many soldiers are evidently mutilated.

Moreover I have often found soldiers with antennæ of twelve, thirteen (Pl. 16, fig. 19), or fourteen all pilose joints, of which the third is in process of division into two, both pilose; sometimes the division is completed in one antenna and hardly indicated in the other. In short, all intermediate stages exist between small, medium-sized, and large soldiers, and the foregoing distinctions have therefore a relative value alone.

For a considerable time I supposed that the soldier of medium size originated from the small soldier, and grew itself into a large soldier; but as I have not succeeded in proving my hypothesis, in spite of long-continued research, I can no longer consider it to be well founded.

Turning to the undifferentiated or small-headed larvæ, we have already seen that they can acquire antennæ of twelve entirely pilose joints, and a length of 4 mm. Subsequently a thirteenth joint is added, and their length increases to 6 mm., when also the thirteenth joint becomes pilose; then a fourteenth joint is developed, and the whole fourteen are always found to be pilose in examples of 7 mm. and upwards in length.

Examples with fourteen joints may exhibit evident traces of wings, which indeed may be already present in individuals with thirteen pilose joints, and a very indistinct rudiment of a fourteenth glabrous joint at the base of the third. But, on the other hand, examples with fifteen joints may be found without trace of wings.

Those which have acquired wing-rudiments may be called larvæ of perfect insects.

Undifferentiated larvæ, with thirteen or fourteen joints, as well as larvæ of perfect insects with thirteen (the fourteenth very imperfect) or fourteen joints may undergo a direct transformation into soldier larvæ with thirteen- or fourteen-jointed antennæ, and from these originate the soldiers of medium size with the same number of antennal joints.[1]

Lastly, undifferentiated larvæ with fourteen joints may either become larvæ of perfect insects without increase in that number, or they may remain unchanged till it has been increased to fifteen, all of which are pilose; and the latter condition may also be reached without change by the larvæ of perfect insects.

Both the undifferentiated larvæ and those of perfect insects with fifteen joints may give rise, without increase in that number, to the same kinds of forms that have been indicated for the larvæ of fourteen joints,—soldier-larvæ, larvæ of royal substitutes, and, provided that they are as yet undifferentiated, larvæ of perfect insects; and the last may acquire a sixteenth joint without increase of the wing rudiments (Pl. 16, fig. 3). As a rule, therefore, the development of the sixteenth joint is accompanied by an increase in the wing-rudiments, so that the larva of the perfect insect becomes a nymph.

I have found no undifferentiated larva with more than fifteen antennal joints; but, as I have said, we may have sixteen

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[1] I have been unable to decide whether the number of joints is capable of increase in the soldier larvæ.

completely pilose joints in the larvæ and nymphs of perfect insects. During this stage both of the latter may undergo the same fate as in the preceding stages, becoming soldier larvæ, larvæ of substitute royal forms, or, if already larvæ of perfect insects, nymphs.

Both the larvæ of perfect insects or nymphs may pass without change to the stage in which the antennæ possess seventeen joints. During this stage both may become larvæ of soldiers or royal substitutes. If this does not happen the nymphs acquire larger wing rudiments, and the larvæ of perfect insects become nymphs (Pl. 16, fig. 4).

Before proceeding further it is desirable to give a fuller definition of the term nymph.

It may be applied to such examples as are 8 or 10 mm. in length, with sixteen or seventeen antennal joints, and with wing-rudiments easily distinguishable by the naked eye. The expression, it must be observed, is incapable of precise definition, inasmuch as there are no characters in insects with an incomplete metamorphosis which distinguish a larva from a nymph, except the wings, which have already begun to develop in larvæ of a certain age. It might possibly be adopted as connoting the earliest rudiments of wings, but this presents the difficulty that they are not easily detected. I therefore follow the terminology of Lespès and Hagen, and conventionally indicate as nymphs those individuals which have the beginnings of the wings readily visible to the naked eye.

From the account just given it follows clearly that large soldiers are derived from the large soldier larvæ, just as the moderate-sized and small soldiers originate from larvæ of corresponding sizes, and that the large soldier larvæ have arisen in their turn from undifferentiated larvæ with fifteen antennal joints, or from larvæ of perfect insects with antennæ of fifteen, sixteen, or seventeen joints, or lastly also from nymphs. The latter, possessing sixteen or seventeen joints, may be transformed into soldier larvæ, and subsequently become large soldiers in which the wing-buds can be distinctly made out with the naked eye (Pl. 16, fig. 26). At a later period these rudiments are reabsorbed until hardly a trace is discoverable with the microscope. This origin of the soldier from the nymph is certainly infrequent.

Nymphs with seventeen antennal joints may become imagos without increase in that number, or with an antecedent addition of one or even two joints; and the perfect insects may thus exhibit antennæ with from seventeen to nineteen pilose joints, a numerical difference which has no relation to sex. Nymphs with seventeen to nineteen joints may be also transformed to royal substitute larvæ, but I do not believe that those with eighteen or nineteen joints can become soldiers, as I have never found so large a number in any example of that caste.

The change from the nymph to the imago is accompanied by the development of pigmented compound eyes, while the wing-rudiments, from being vertical and closely appressed to the sides of the body, become dorso-lateral at their origin, nearly horizontal, and divaricate at the apex.[1] These specimens have at last reached the adult stage (imago), and (Pl. 16, fig. 6) possess fully developed wings; at first white, they gradually become black and capable of flight.

It will be seen from this account that examples with a number of antennal joints varying from twelve to seventeen, and therefore of very different lengths, can be transformed to soldier larvæ, and consequently to soldiers; and that those in which the number of joints varies from fourteen to nineteen may become larvæ of substitute royal forms. The latter larvæ are not easily separable from the others; but in those with from fifteen to seventeen antennal joints the pigmentation of the compound eyes is evident. But it is absent or very scanty in substitute larvæ with fourteen, and some with fifteen joints. Ocular pigment is sometimes present in nymphs with seventeen, and always in nymphs with eighteen or nineteen antennal joints before their metamorphosis into substitute royal larvæ.

The larvæ of perfect insects or young nymphs are customarily selected for development into substitute forms (Pl. 16, fig. 14),

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[1] In these specimens the wings have really reached their full development, but are enclosed in a chitinous sheath.

and the wing-rudiments of the resulting royal examples are therefore absent or very ill-developed. [When a nymph with more evident wing-rudiments is selected for the throne, one or more of these (usually that of the right fore-wing) is bitten off (Pl. 16, fig. 18)].

I have repeatedly stated that the royal forms may originate in two ways; in one case they are derived from perfect black examples, of which the wings are fully developed and become detached along a special line of fissure, so as to leave a short stump (the Schuppe or Squama of authors). These examples constitute the true black or normal kings and queens. In the other case the royal forms are substitutional, and originate from examples which have suffered an arrested development of the wings, and in which the compound eyes are usually but not invariably pigmented[1] (Pl. 16, figs. 17, 25). It is remarkable that the antennæ are never found intact in any king or queen, whether true or substitute, however young it may be. And the majority of royal forms possess a different number of joints, varying from thirteen to six or even four on either side.

A most striking feature of the Calotermite colony is the entire absence of workers, in which this species agrees fully with the American form studied by Fritz Müller.

It may, therefore, be concluded that the kingdom of Calotermes is composed of three castes: that of the soldiers; that of individuals which reproduce without becoming black imagos; and lastly, that of forms which lay eggs after the acquisition of fully formed wings,—that is, after reaching the stage of the perfect insect.

The phenomena related in this section may be recapitulated in the following synthesis.

The normal development of Calotermes up to the perfect stage may undergo deviation at different

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[1] Perfect insects which are still white may also become substitute forms. They do not darken, and the wings are torn off, rarely along the special line, but usually irregularly as in Termes lucifugus (q. v.). These observations were made after the present work was completed.

ages. This deviation may lead to the formation of substitute royal forms, or of soldiers, after passage through the respective larval stages. The soldier larva may originate by modification of examples with from twelve to seventeen antennal joints; and the larva of the royal substitute forms by modification of examples with from fourteen to nineteen antennal joints. Perfect insects which are still white may also become substitute forms.

I can confirm the fact discovered by Lespès[1] in Termes, and by Fritz Müller[2] in Calotermes, that the caste of soldiers is composed of examples of both sexes.

A minute description of all the forms in the different stages of development would be of little interest, and I shall therefore confine myself to a few points which have a special bearing on the problems I have undertaken to solve.

Beginning with the sense-organs:

(1) All trace of eyes is wanting in newly hatched larvæ. The soldiers possess compound eyes, unpigmented and not prominent. The time of their appearance has not been determined; they are present in a rudimentary condition in larvæ of 3—4 mm. in length, with twelve antennal joints—the third glabrous, but they are not clearly distinguishable except in sections. At a later period they are evidently faceted, but remain destitute of pigment. The compound eyes acquire pigment, as previously mentioned, in nymphs about to become imagos and in most examples selected for the dignity of substitute kings or queens. In the perfect insect the eyes become more prominent and abundantly pigmented, and between them is developed an ocellus devoid of any trace of pigment, which I therefore regard as rudimentary.

(2) Sensory hairs (Tastborste), characterised by their shortness and their connection with the nervous system, are very abundant over the antennæ and the whole of the mouth

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[1] 'Ann. Sci. Nat.' (4), v, p. 244.

[2] [Jen. Zeitschr.,' vii, pp. 333—340.]

parts, which possess no other form of nerve-ending, such as cones (Kegel) or papillæ (Zapfen). These hairs are especially numerous on the apex of both pairs of palpi and on the antennæ; on the latter they are most abundant on the apical half of the terminal joints. There appears to be no marked difference between the sensory hairs of the mouth parts and antennæ, and experiment shows that the latter organs are constructed so as to remain functional even when deprived of a certain number of joints.

(3) The tibiæ exhibit the peculiar sense-organs discovered by Fritz Müller,[1] evidently tympanal organs (Pl. 19, fig. 10).

This is shown by the presence of the usual terminal rods, of a characteristic tracheal branch, the lumen of which is not accurately cylindrical, and which opens at either extremity into the main tracheal trunk of the tibia, and lastly, of tympanic membranes.

Tactile hairs are present on various parts of the body, and the so-called abdominal appendices (cerci) also appear to be essentially tactile. These appendices are really identical with the caudal cerci of Thysanura, reduced to a short basilar piece and a long terminal joint, of which the apical extremity is glabrous. The remainder of their surface is covered with very long, fine, and readily vibratile hairs, in addition to others, such as are scattered over the body.

The description just given of them goes to show that they correspond in Calotermes with those found in other insects. All the sense-organs here described, with the aforesaid exception of the eyes, are fully developed at the time of hatching. The visual structures are certainly more or less imperfect except in the adults, and become functional concomitantly with the wings. Their unimportance in other stages is evident from the fact that pigment may be either present or absent in the eyes of substitute royal forms, and that individuals without, or with more or less imperfect eyes, apply themselves equally well to the work of the colony.

[Calotermites move their antennæ freely, and employ them

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[1] [‘Jen. Zeitschr.,’ ix, p. 234, pl. xii, figs. 32, 34.]

just as a blind man does his stick, as Lespès observes. But they are not accustomed to use them in mutual caresses, like other social insects. If the antennæ are cut off at the base the insect becomes inert, stands in a fixed attitude, almost disregards the difference between light and darkness, quivers (vide infra) at rare intervals, and then for a shorter period and less violently than usual. It is not successful in soliciting excrement (vide infra), or does not directly attempt to do so. All these inconveniences are only partially exhibited if the antennæ are detached more or less remotely from their base.]

Fritz Müller's observation[1] that the number of antennal joints in Calotermes rugosus is increased by the successive formation of new joints at the base of the third is well known, and has led to the division of the antenna into two components (base and flagellum), as in other Arthropoda.

I have attempted to determine the origin of the new joints in Calotermes flavicollis, but have not been successful in obtaining a clear idea of the process.

In deciding whether any given joint is the most recent, its smallness, its freedom from hairs, and the indistinctness of the line of demarcation between it and the parent joint must be taken into account. But it will be readily understood that all these criteria are apt to fail.

In the present case, the one which appears most practicable (the presence or absence of hairs) may certainly lead us astray. In fact, antennæ of 13, 14, 15, 16, and 17 joints, with the third and fourth joints glabrous, are to be found, as well as completely pilose antennæ of twelve to sixteen joints (fig. 22). The natural inference is that the third or fourth joint, which was pilose in the latter examples, has become denuded in the former (e.g. for an antenna of fourteen joints, the 3rd and 4th pilose, to become fifteen-jointed (fig. 21) with the 3rd and 4th hairless, one or other of the latter joints must necessarily have lost its clothing); this may have taken place in connection with ecdysis, as we shall see later.

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[1] ['Jen. Zeitschr.,' ix, pp. 246, 247.]

The broad fact remains that individuals exist with from thirteen to seventeen antennal joints, with either the third or fourth (fig. 20) or both joints glabrous, or without a single glabrous joint.

How are the new joints formed? I regard it as certain that the 13th arises by unequal division of the 3rd, at the base of which it appears as a bud. The 15th and 17th appear to arise from the 4th, and the remainder like the 13th (Pl. 16, figs. 20—22). But closer study is necessary before arriving at a conclusion.

It is of fundamental importance to notice that the new joints do not take origin from a zone of embryonic (undifferentiated) tissue, but from already differentiated structures (hypodermis, nerves, &c.).

Calotermes moults periodically, and it is quite untrue that the number of antennal joints increases coincidently with the moult. It is more probable that the latter takes place after the process of joint formation, and in this we may perhaps find the explanation of the just related facts respecting the loss of antennal hairs.

The number of ecdyses cannot be specified; I have found examples of all sizes in process of moulting, and can go no further than to fix it at not less than five. The adults and soldiers do not moult; and the latter are derived from soldier larvæ by an ecdysis, so that while the exuviæ are larval, the new instar is that of a fully-developed soldier.

As with other insects, the operation is accomplished by means of an anterior medio-dorsal fissure, through which are drawn out first the head and thorax, and lastly the abdomen (Pl. 16, fig. 15). In rare cases an example has been seen to be assisted in the operation by his comrades.

Two ecdyses merit special attention. The first is that undergone by the nymph, furnished with wings apparently small in size (really of full dimensions and elaborately folded up under the old ensheathing cuticle), and with genital appendices; from this it emerges with wings of full amplitude, and without appendices should it be a female. The other important ecdysis is that in which the larva of a substitute royal form loses its genital appendices if a female, and this leads us to a detailed consideration of the latter organs.

The genital, often wrongly termed the anal appendices,[1] are homologous with those of the ninth abdominal sternite of Thysanura, and are attached in Termitidæ to what is apparently the eighth, but is really the ninth sternite, the first being fused with the metasternum. They possess hairs which do not differ from the ordinary hairs scattered over the body.

They are present in all sexually immature examples, but in the males only when mature. Further, the sternites differ in the sexes; in the female the true (not the apparent) seventh sternite is strongly developed and semicircular, and the true eighth and ninth are small and possess a median fissure. In the male the true seventh is rather small, as are the true eighth and ninth, in which the fissure is wanting. There is no penis.

I have but little to say about the internal organs. The tracheal system agrees with Fritz Müller's description,[2] and I have likewise observed the stigmata, tracheal trunks, anastomoses, &c. Further, this species exhibits the blind tracheal branches figured by Müller, which I take to be suppressed trunks or tracheal vesicles.

The alimentary canal presents the following features. In newly born larvæ the teeth of the proventriculus are colourless and quite soft,—that is, covered as yet with a delicate cuticle; and the Malpighian tubules are four in number. Four others appear at the epoch when the antennæ possess eleven distinct joints, of which the third and fourth are glabrous, and the former shows traces of division into two; these new tubules require a certain time in which to attain the size of the original four, and I have found them to be still

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[1] [The genital appendices must not be confused with the abdominal appendices or cerci, referred to on p. 268.—W. F. N. B.]

[2] ['Jen. Zeitschr.,' ix, pp. 257, 259, pl. xiii.]

much the smaller when the number of antennal joints has reached twelve, with the fifth joint already pilose, or with the third and fourth alone bare. I may note here that the appearance of intestinal Protozoa (vide infra) coincides with this last stadium, though Joenia is confined to the large-headed larvæ, whereas Monocercomonas is common both to these and the small-headed forms.

The development of the four secondary Malpighian tubules proceeds in such a way that each is placed midway between a pair of the primary tubules; that is to say, the latter are equidistant from each other, and the secondary tubules are intercalated at equal distances between them, so as to produce a series of alternate large (primary) and small (secondary) tubules.

Their mode of development is shortly as follows: they spring from the proctodæum at its junction with the mid-gut, exactly at the same level of the primary series. I have been unable to detect any special layer of embryonic tissue destined to give origin to them, and they may therefore be regarded as a direct derivation from the proctodæal epithelium.

When the antennæ possess twelve joints, all pilose, the difference between the earlier and later Malpighian tubules has ceased to exist.

The salivary glands are highly developed in all castes and at every stage of growth. There is a single pair, as well as a large salivary reservoir, such as Müller has described (Pl. 19, fig. 7).[1] There is an unpaired external opening in connection with the labrum.

[The supra-œsophageal ganglia are situated as in Thysanura, with the olfactory lobes anterior, and the fungiform bodies posterior as in Termes lucifugus (see figs. 27—33*c*, *fung.*). The latter are relatively well developed when compared with those of Embiidæ (fig. 34) or Thysanura; there are two on either side, or four in all, not well separated from each other. As in other insects, they are characterised by

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[1] ['Jen. Zeitschr.,' ix, pp. 256, 257, pl. xii, fig. 42.]

the possession of small cells, of which the nucleus stains more intensely than in the other nerve-cells.

Should a characteristic feature of these organs be sought, by way of contrast with those of less intelligent insects, it will be found in the abundance of these particular small nervous cells.]

The visceral nervous system is well developed, and resembles that of Blattidæ (fronto-labral commissures; frontal and stomato-gastric ganglia, &c.). The salivary glands are supplied (only ?) by branches from the subœsophageal ganglion, coming off from those to the labium or lower lip.

The ventral ganglionic chain possesses six abdominal ganglia, and thus agrees with Lespès' description; the sixth is very large, and is in correspondence with the true seventh and eighth abdominal segments.

At the level of the fourth abdominal ganglion—that is, in the true fifth segment—there open numerous unicellular glands of unknown function. The retro-cerebral gland, which exists in Termes lucifugus,[1] is absent.

Certain features of the different castes and larval forms will now be described.

[Newly born examples are semi-transparent and almost pure white. If the mouth parts are detached the apex of the mandibles and the inner lobe of the maxillæ can just be seen with the microscope to be tinged with yellow, a feature which cannot be made out by examining intact specimens even with a good lens. After a few days these parts acquire a more or less pronounced yellow colour, owing to the thickening of the investing cuticle, and at this time a yellow line, caused by the approximated tips of the mandibles and maxillæ, may be distinguished at the front of the head even with the naked eye, though better with a lens.

This yellow line appears early in forms which develop a large head (soldier larvæ), and is delayed in those of which the head remains small. At the time of its appearance the animal

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[1] [Vide Pl. 16, figs. 28—33, and description.]

is seen to adopt as food a material which is usually of the same dirty yellowish colour as that of more developed examples, and is apparent through the translucent abdomen, so that the general white colour of the body is blotched with yellow. The importance which attaches to this fact will be explained in the subsequent chapter.]

The youngest soldier larvæ are therefore distinguishable by the greater size of the head and the lesser constriction of its anterior portion, as well as by the yellow line in this region; moreover the thorax and the abdomen, which possesses the aforesaid yellowish blotching, appear to be somewhat wider.

The body of small soldiers (5 mm. in length) does not become fully yellow, with exception of the head, which is golden-yellow, and the mandibles, which are brown. Their head is subglobose, and at first sight these small soldiers greatly resemble those of Termes lucifugus, but are distinguishable by the indistinctly marked neck. The relative width of the head and pronotum varies in soldiers of different sizes, as is shown in the plate (Pl. 16, figs. 5, 16).

The body of medium-sized or large soldiers is golden-yellow, much deeper anteriorly, while the mandibles are coloured as in the small soldiers. The head is rectangular, and longer than broad, subquadrate. At the time of differentiation all the soldiers, large and small alike, are white, as I have stated.

True kings and queens (6·5 to 7 mm. in length) of recent development are black, except for the apical portions of the legs and antennæ, which are light yellow, and the anterior three fourths of the pronotum, which are golden yellow. With increase in bulk, at the first moment of the assumption of the definitive habit, the white intersegmental linear spaces become evident, and are most conspicuous when the royal forms have reached the maximum dimensions of which they are capable (Pl. 16, figs. 7, 11). I may note here that a length of 10 mm. for the king and of 14 mm. for the queen is the greatest that I have observed.

These white lines, which are not as yet evident in royal forms as much as two years old (figs. 8 and 9), correspond with the interspaces between the first and second, and in succession to between the sixth and seventh abdominal somites. The second line is usually the widest, but is sometimes similar to the others. They occur alike in both sexes, but as the king increases in bulk less than the queen, they are naturally less marked in the former than in the latter sex at the same age and never ultimately reach the same degree of accentuation.

The substitute king and queen are distinguished not alone by the almost constant presence of pigment in the compound eyes, but also by their pale-yellow colour, which deepens with age to a golden tint.

In these royal forms alike the abdomen becomes enlarged, and I have found examples of both sexes almost equalling the largest true kings and queens in size (Pl. 16, figs. 12, 13). With the natural dilation of the abdomen, certain intersegmental spaces, namely, those which are indicated above for the true king and queen, appear as whitish lines.

I conclude by mentioning that I have looked in vain for any difference between the legs of the various forms. The tarsi are normally four-jointed; and the apex of the tibia possesses three spines, toothed on one side, and common to all the legs (Pl. 16, fig. 24). A plantula is present in the true imagos, but is wanting in all the other members of the colony, including the substitute kings and queens.

These observations probably hold good for all species of the genus Calotermes; I infer this from the many incomplete notes which are scattered in the pages of various writers.

4. Relative Numbers of the Castes.

A nest contains a single king and queen, neither of which can be normally wanting. They may be either true or substitute forms. At times one of the pair, either king or queen, is a perfect and the other a substitute form; and in such cases we have the strange phenomenon of courtship between a black and a yellow example.

The existence of but a single royal couple is an assured fact, but it is not uncommon for two or more nests of Calotermes to co-exist without (at least for us) well-defined limits in the same stem, which therefore appears to contain more than a single royal pair. In connection with this condition are certain facts which prove the existence of the terrible jealousy which is so remarkably shown, e. g., between separate families of the hive-bee. But for the sake of convenience I shall defer them to a succeeding section on Habits.

When a colony is deprived either of king or queen, or of both, it furnishes a certain number of substitute royal forms, of which only one, if a single true form is missing, or two, that is, a pair, if both are absent, is called to the throne.

In every nest, forms of different ages are always to be found; and as a general rule small individuals are more, or not less, numerous than large.

Soldiers are relatively scarce, not more than from two to four being found in nests of from eight to fifteen inhabitants. In large colonies they exist in the proportion of one to very fifteen or twenty examples.

5. Seasonal Variations in the Colony.

It must be recollected, as a general rule, that the development of Calotermes is arrested during the winter months, that is, from the middle of November to the middle of April; and this condition explains the absence of individuals in process of moulting during that period.

In these months the nest contains eggs, sometimes a hundred or more, which are always in the gastrulation stage. Their development remains stationary during the greater part of May, to recommence towards the end of the month, so that newly hatched young are to be found from about the 10th of June till the end of July, a few eggs, from five to ten, hatching every day. In July it is evident that the number of young larvæ increases, so does that of the eggs diminish until their final disappearance. Towards the end of July it is difficult to find a nest which still contains eggs, proving that oviposition is suspended at this time. The same holds good for the interval from November to the middle of May; while the opposite condition exists in the second half of May, in June, September, and October. Consequently oviposition remains suspended during winter and a large part of the summer. At the end of October many eggs are still to be found in the gastrula stage, and it follows from the preceding statements that they remain thus during the winter; but at the same month a certain number can be found in an advanced stage of development. From this, and from the fact that many new-born larvæ are to be found in that month, I can confidently state that the eggs laid in September (and perhaps in the early part of October) develop immediately without need of hybernation.[1]

At all seasons, except from about April to the middle of June, larvæ, with the features of being newly hatched, are to be found in the nests of Calotermes. The larvæ which are born in the second half of October make no progress in development until the following April.

Larvæ in stages of development which succeed those with the characters of recent hatching are to be found at all times of the year.

Nymphs are to be found in every nest during nearly all the year, being absent at most only in August and September.

The perfect insects develop from July to October, a few stragglers appearing in the spring. Their swarming is quite different from that observed in bees, and they leave the nest a few days after they become black. [As development is not simultaneous, they swarm in small groups of at most thirty examples, and occasionally singly or in pairs. A colony may therefore swarm, so to speak, ten or twelve times in all, from July to October.]

This fact explains the existence in many nests of a few winged examples still at the end of the swarming season, that is in October.

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[1] I must admit that there is a certain gap in my observations in the summer months, when I am unable to reside at Catania owing to the excessive heat.

[As a rule a certain number of both sexes become mature at the same time, and the males invariably take flight two or three hours later than the females.] Further details on the subject of swarming will be found in the later section on Habits.

Soldiers and soldier larvæ are to be found the whole year round, but only small soldiers are present in nests under two years old.

6. Duration of Development, of Life, &c.

These matters are very difficult to ascertain, but the following facts are certain:

1. Owing to the interruption of development from November to April, individuals in the same stadium may be of different ages.

2. Eggs which pass the winter in the gastrula stage will give rise in the following summer at most to soldiers with 15-jointed antennæ, or to larvæ with similar antennæ, and with or without very short wing-rudiments. These larvæ become perfect insects and swarm in a later summer.

These conclusions are the result of minute examinations of numerous small or orphaned nests, &c., some of which I shall proceed to record.

By searching in the situations which have been described as the points of origin of new nests, from August to April, some two to twenty perfect insects, with the wings reduced to stumps, may easily be found; the majority are grouped in pairs, male and female, each of which may be accompanied by a few eggs. These pairs are recently formed, and, if originally numerous, are subsequently reduced to one or two (see the succeeding section on Habits).

A pair is established, say, in August, and remains to the end of the autumn with only fifteen or twenty eggs; twelve months later, at the end, that is, of the following autumn, it will be surrounded with fifteen, twenty, or at most thirty young of different ages, the most advanced being large soldiers with at most fifteen antennal joints, or larvæ with a similar number, all pilose, and with a very slight indication of wings.

I must regard certain nests which may be found at the end of October, as having arisen from pairs which had only begun to lay eggs in May of the year following the swarm-period. In these the number of inmates is less than in the nests previously referred to, and no larva possesses more than fourteen antennal joints, the third being glabrous, and the constrictions between the 3rd, 4th, and 5th respectively being ill-marked. The wing-rudiments of these larvæ are not yet discernible, and the soldiers of such nests do not possess more than twelve antennal joints, and are small.

The hypothesis that such nests may have originated from royal pairs disclosed only during the preceding summer, instead of the previous year, and consequently only three or four months old, is quite untenable; as is indicated by the fact that nests are never found to contain only newly hatched or little-grown larvæ at the end of autumn, as must of necessity be the case if young can be born in the year in which the nest is founded. In short, the fact remains that at the end of autumn certain nests are found to possess undeveloped eggs only, whereas others already contain small soldiers, and larvæ with fourteen antennal joints: nests intermediate between these two classes are entirely wanting, though they should be present if the above hypothesis were correct, inasmuch as the swarm-period lasts from the end of July till that of October.

In March, 1891, I observed an absence of nymphs in the examination of several nests orphaned two years previously (occasionally they were present in very small numbers). These nests contained ova and forms in all other stages. It therefore appears that destruction of the royal pair in spring results in the suppression of swarming during July and August of the second succeeding year, but in those months only, because examples in which the wings are only just indicated in March will have become imagines by September and October.

Nests orphaned between February and June sometimes contain no eggs, and usually no new-born larvæ in the following winter.

It is consequently evident that the development of substitute royal forms proceeds very slowly.

The data furnished by orphaned and young nests, and by many other observations which I have made, indicate that perfect and fully winged examples are not obtained before August from eggs laid in July of the preceding year. In short, Calotermes passes part of two years in the larval and nymph stages before taking flight. The soldier may complete its development in the same year in which it is hatched.

It is difficult to say anything about the duration of life. I must deny the existence of any particular season when the soldiers die off, as Lespès has claimed for Termes. The life of the king and queen may be estimated at four or five years at least.

7. Situation of the Different Forms in the Nest.

I have already mentioned that Calotermes does not possess a royal chamber. The king and queen, whether true or substitute, usually remain in close proximity in the heart of the nest, where the inmates are always most crowded. They readily change their situation. The eggs are mostly near them or a little way off, and are never heaped together.

Larvæ, nymphs, and winged forms, if present, are irregularly commingled; but larvæ newly hatched tend to cluster together. The soldiers also are irregularly scattered, but a few are often found in close attendance on the royal couple. The soldiers are generally the first to make their appearance when a nest is opened.

Substitute forms in process of development occur separately, or in groups of two to four in different parts of the nest.

It thus follows that the component members of a Calotermite colony have no special situations in the nest.

8. Certain Habits.

I propose to deal here only with those habits which could not appropriately be dealt with in Section 3.

Calotermites work, feed, and rest indifferently by day or night. When resting, they remain motionless without adopting any special attitude. They are fond of darkness, and when kept in a tube occupy the portions furthest from the light. They certainly work more actively in the dark, but are capable of doing so even when exposed to daylight.

Oviposition continues both by day and night.

Swarming takes place in the morning, usually from 9 to 12; and it must therefore be recognised that Calotermes no longer avoids the light when it has reached the perfect stage.

Before swarming the winged insects collect habitually in a spot which careful observation shows to be in the neighbourhood of an exit-hole, putting the nest into communication with the outer air.

Swarming takes place through this hole. The insects issue by ones or twos, so that the twenty or thirty examples ready to take flight emerge in perhaps a quarter of an hour.

Once outside the nest, they run upwards for a few metres if the locality admits of it, and then only do they take wing. In a room they evidently fly towards the light, and if a wind is blowing they follow its direction. Some soon become tired and settle on the trunks or branches of neighbouring trees; the majority become lost to sight, but many certainly end by alighting on trees. It is here that they group themselves into pairs, the males and females of which must frequently be derived from separate nests, for, as I have mentioned, the sexes swarm separately; this acts as a safeguard by which Calotermes habitually avoids in-breeding.

The winged forms have not been observed to pursue each other in the curious way which will be spoken of under Termes.

I may describe more precisely the manner in which the males and females come together when settled on a tree. The winged forms habitually search for a decayed spot, and when found they dig it out, after losing their wings, in order to bury themselves; it is in this act of excavation that the meeting and subsequent pairing take place.

The wings may be shed, merely by striking against an obstacle, or by becoming damp and adhering to some spot, while the insect continues to move about.

But if not favoured by chance the Calotermite rids itself of its wings, as the following observation shows. Four perfect insects, which had recently left the nest, were captured by hand after flying about a room for some time, and were put under a piece of rotten wood. They had hardly settled down before they began to strip off their wings by resting their tips against some projecting corner of the wood and then moving backwards a little, so that the wings buckled towards the base, broke, and dropped off. When rid of them they began to gnaw the wood, at first along, and then across the grain; each worked by himself and at some distance from his fellows. Subsequently several chance encounters took place between them; they threatened to bite each other, and then ran off in different directions. They were of the same sex. If they had been of different sexes they would certainly sooner or later have copulated.

In the colony of Calotermes all members work for the common welfare. The soldiers serve for defence, but as a rule only when some important enemy has to be combated; at other times nymphs and possibly the older larvæ assume the task.

Cremastogaster scutellaris, Ol., which is abundant here, is one of the most formidable enemies of Calotermes, near which it makes its own nests. This ant enters the termitarium to massacre, whereas its own nest is never invaded by the Calotermite soldiers. If some examples of Cremastogaster are put into a tube containing a Calotermite nest, the following phenomena can readily be followed. The soldiers place themselves with gaping mandibles, waiting for any enemy that may come within reach. They then snap their jaws rapidly, shearing off antennæ and legs, tearing the abdomen, or even cutting the ants in two at the level of the abdominal petiole. The soldier's mandibles are seen to act like extremely sharp shears.

The ants themselves attack the Calotermites indifferently, but habitually avoid the heads of the soldiers, only daring occasionally to attempt to lop off their mandibles. As a rule they attack the soldiers from behind by biting the abdomen, and to protect it the soldiers creep under pieces of wood so as to leave the head alone free.

If a few Cremastogaster and a larger number of Calotermites are put into a tube, peace is usually concluded after about an hour's conflict, with a certain number of dead and wounded on both sides. The ants take up a position in one part of the nest and the Calotermites in another.

[Besides the ants, the soldiers of Termes are terrible enemies, but being small they are easily cut in two through the thorax by the Calotermite soldiers. The workers of Termes are much less dangerous enemies than the soldiers of that species. One, put into a tube-nest of Calotermes with soldiers, was at once placed hors de combat by a nymph, which cut off part of the buccal apparatus. Then sundry large larvæ and other nymphs hurried up, bit off its legs, and tore its abdomen until the viscera protruded. The soldiers took no part except towards the end of the struggle, when one gave it a bite. Similar observations have been made several times, and show, as we said before, that the soldiers purposely reserve themselves for more important foes.

Another Termes worker was put into a Calotermes nest containing no soldiers. The inmates took flight, probably terrified by the knowledge that they were unprotected by soldiers; and the Termes succeeded in throwing the nest into confusion, until after some lapse of time a nymph plucked up courage to bite its abdomen, and thus killed it.

A substitute queen of Termes lucifugus was introduced into another tube containing a Calotermite nest. A soldier promptly despatched her by decapitation, and then only did the nymphs intervene to tear the body. During the rest of the day the soldier never moved from the spot where he had killed the queen.]

Besides protecting the nest the soldiers fulfil other duties, such as that of carrying the young and eggs on their mandibles. These organs are useless for gnawing wood, and their possessors therefore remain idle for hours together, while the rest of the colony is in full activity. Except for these tasks of defence from great dangers and wood-gnawing and consequently excavation of galleries, it is, so to speak, an absolute rule that all labour necessary for the community can be undertaken by any of its members.

Newly hatched larvæ can be seen carrying a fragment of wood heavier than themselves. All forms except the soldiers excavate galleries, provided that their mandibles are sufficiently strong, which naturally is not the case just after birth or after a moult. Both king and queen, whether true or substitute, gnaw up wood and transport excreta, eggs, or wood-meal.

Oviposition appears to be a very laborious process; in one case the egg was not extruded until an hour, and the succeeding egg until half an hour after appearance at the vulva. Once I saw a soldier assist the queen by raising and gently stroking her abdomen, but as a rule she lays without assistance.

Hatching is effected without need of any assistance from inmates of the colony. The chorion is tolerably thick, and the eggs can be kept in a watch-glass without drying up, and the process of hatching observed. Moulting also is accomplished as a rule without assistance.

If the eggs and young are exposed by opening a nest, it is striking to see how the other inhabitants disperse without paying them the least attention, in contrast to the behaviour of ants; and yet one must recognise that the colony is as deeply interested in their welfare as ants are in that of their own offspring, and that it scatters simply because it is panic-stricken. This may be proved by shaking a small nest made of loose pieces of wood in a glass tube or jar. For a moment all the inmates are thrown into disorder by terror, but they quickly recover themselves, become persuaded that it was merely an earthquake, so to speak, and devote themselves to the restoration of order by carrying the eggs back to their place at the bottom of the jar, and removing the young on the mandibles of the soldiers, or in the mouth-parts of their other fellow-inmates.

It must be recognised that Calotermites are perfectly well aware of the presence or absence of the royal pair, and they start about providing fresh ones directly they are orphaned. The following observation is important in this connection. A nest was divided, say, into three smaller nests, in one of which the royal pair was retained; they were put into separate tubes, kept together and uncorked in the same waistcoat pocket. After three or four days larvæ of substitute royal forms were found in them, except in the one containing the royal pair. The colony in the tree from which the original nest was taken had not turned their attention to raising substitute forms, though they were 30 or 40 centimetres distant from any king or queen; whereas those in the tubes, though in close proximity to a royal pair, had at once begun to provide substitutes. It follows that the existence of the royal couple is certainly not perceived by means of any odour which they emit; and this affords us another marked contrast with what is observed in the case of bees.

The copulation of Termitidæ has been extensively discussed; some writers believe it to be accomplished in the open air, but the more general opinion is that the presence of the king in the nest shows that it takes place there, and is repeated from time to time. I regarded the latter supposition as possibly correct directly I found that the king is invariably present in the nest, and that his bulk increases, though to a less extent, concomitantly with that of the queen.

At last, on April 17th, 1891, about 11 a.m., I detected the king and queen in coitu in a glass jar containing a small Calotermes nest. The pair appeared to be about three years old, judging by their size. They stood end to end in a straight line with the tips of their abdomens applied to each other; their attitude was normal, with the dorsum uppermost, except for a slight upward flexure of the apex of the abdomen. After some half-minute they separated, perhaps owing to the exposure to light. The contiguous parts of their abdomen exhibited a white substance which, when the king and queen became detached from one another, remained adhering under the hinder extremity of the queen.

It is therefore certain that connection takes place in the nest and is repeated at intervals; and all my observations satisfy me absolutely that it cannot be accomplished in the open air, and is practicable only after loss of the wings.

[I must regard certain relations which were observed to subsist between two substitute forms still far from maturity, because they were only about a fortnight old, as amatory in nature. One stood still while the other gradually approached, and when sufficiently near brought its antennæ into contact with those of its fellow; it then quickly retired for some distance, and returned later to repeat the pastime. This took place at least four times. On the fifth occasion the one which had been standing still, made movements as if to detain its companion; they then remained together, and very rapidly stroked various parts of each other's body, especially the apex of the abdomen. Their position during the reciprocal palpation of this part was almost that assumed during the act of coitus.]

Several writers have mentioned the convulsive movements characteristic of Termitidæ. These movements or quiverings are easily observed in Calotermes, and may be repeated periodically at very short intervals, almost at the frequency of the pulse-rate.

In the act of quivering the tarsi are held motionless, while the body is shaken forwards and backwards; there may be a simultaneous slight lateral or vertical oscillation. Sometimes an example may stop whilst running, in order to quiver one or more times.

Occasionally these convulsive movements are repeated a few times only, and then stop altogether; but at other times they recur after a few seconds or at most a few minutes' rest, and may thus be continued sometimes for hours with many similar intervals of rest.

In the intervals between successive convulsions the insect remains still or progresses for a short distance only. These movements are executed by all members of the colony except those newly hatched.

I have satisfied myself by careful observation of the phenomena exhibited in tube-nests that these convulsions serve as a cry to summon help or give alarm, or as a lament; in short, as a mode of intercommunication.

When the insects are suddenly annoyed or disturbed by any cause, such as a rough shake of the tube, its change from a vertical to a horizontal position, sudden illumination, or the prolonged effect of too bright a light, all the members of the colony begin to quiver, except those that are running briskly about in search of a better situation. Moribund examples sometimes perform these movements at intervals of a few minutes, in some cases for a couple of hours.

[If a few Termes lucifugus are put into a tube containing the usual little nest of Calotermites, some of the latter, evidently excited by the very rapid movements of the intruders, run off rapidly in the opposite direction, and stop at intervals to quiver with much more energy than usual. This phenomenon is exhibited alike by larvæ, nymphs, and soldiers, but the latter quickly turn back to face the supposed enemy. It seems evident in such a case that those which are first aware of the presence of the Termes quiver violently in order to alarm the population.]

[Sometimes the convulsions of an insect in the neighbourhood of the cork are quickly followed by the exit therefrom of others which have been burrowing inside it. Such cases appear to prove the utility of the action as a mode of signalling.]

Members of the same nest clearly recognise each other. [As a proof, a few examples are removed from the nest and returned after five or six hours. The population is not disturbed or alarmed, and does not scurry about at their re-entry. It is a possible objection that these specimens have immediately recognised the nest, and therefore create no disorder on their return; to meet it a new nest was provided, from which certain individuals were excluded. They were introduced a few hours after the fresh nest was put in order and quiet, but they caused no disturbance although it was unfamiliar to them. As a control experiment, a few strange Calotermites were put into the same nest; the inhabitants took fright at once, and scattered in different directions. But after a little time all became quiet, and no fighting was actually observed. We may therefore conclude that examples taken from different nests readily fraternise; and this applies to the soldiers as well as to the larvæ and nymphs.]

[I should mention with respect to the soldiers that if too large a number is added to a nest, these supernumeraries, as they may be called, are found to be killed or eaten one by one during the next few days.]

[The following observation was made on one occasion. Half a dozen strangers, including a substitute royal example, were added to one of the usual nests in a tube. The royal specimen showed signs of hesitation and remained in the same spot, merely turning round and round, and straightening its legs as much as possible, as though to raise itself above the level of its neighbours. When an inhabitant of the nest approached and touched it, it drew back at once; the other did the same, so that they separated as rapidly as if they were stung. Some hours later the new-comer becâme quiet, and several inmates of the nest approached it to caress the antennæ, &c. I must mention that the nest was orphaned.]

[We have already stated that Calotermites furnish a certain number of substitute forms when deprived of the king and queen. Why then is only a single royal pair to be found? One day one of three substitute forms, which inhabited a small nest, was seen rapidly to pursue another with gaping jaws, with the evident intention of killing it, in which it was unsuccessful. Next day the nest contained only two such forms; very probably the one which was pursued the previous day had been killed.]

[Two true royal forms, a king and a queen, were introduced into one of the usual nests, constructed the day before and containing only nymphs. One of the pair began at first to advance hesitatingly, while the other stood perfectly still; but shortly one after the other gradually moved forwards.

The nymphs then began to scatter in different directions in the endeavour to keep as far away as possible from the royal pair; these gradually retreated to the bottom of the tube, where they were left alone. But now and again a nymph approached with open jaws, and savagely bit one of the pair in the head or thorax, getting bitten with equal fury in return, and consequently retreating.

Next day the royal couple was still left unattended, but was no longer actually disturbed. Then a second similar pair was introduced; at once the nymphs all became greatly excited, attacked them and promptly reduced them both to helplessness by biting off their legs. The second pair was alive two days later, and the queen of the first pair was seen to attack the second king with open jaws; he retreated by dragging himself along the tube, being unable to run through the loss of all his legs. A day later he was dead, and the first queen was observed nibbling the stumps of his legs; on the following day the queen of the second pair was also found dead. Several repetitions of this experiment were made, and always gave similar results. Whenever two or three supernumerary royal pairs are put into a nest, a single pair is all that can be found at the end of a few days.]

I infer from all these facts that Calotermites exhibit those phenomena of jealousy and hostility which are so well known in bees; however, their manifestation is less rapid.

The observations just recorded, and many other facts omitted for the sake of brevity, lead us to the fundamental conclusion that the colony of Calotermes tolerates neither supernumerary royal examples nor supernumerary soldiers. Both one and the other are slaughtered. On the one hand, then, the colony can provide itself with royal forms or soldiers when they are required (vide infra); on the other hand, it rids itself of them when they are over-abundant. These facts imply the possession by Termites of a faculty which may be termed a sense of proportion or numerical sense.

By way of conclusion, I must add that though I have had Calotermites under observation for several years, I may still have failed to detect a great part of their marvellous instincts. This is owing to two circumstances: 1, they are often sluggish; 2, when a nest is opened the population is thrown into such a state of astonishment that it usually does nothing but run away and give signals of alarm. And almost all the observations here recorded are due to the method of employing tube-nests.

The Colony of Termes lucifugus.

1. Situation and Nest.

Several writers, particularly Lespès, have published observations on this subject; but I shall summarise merely my own investigations.

Here in Sicily Termes lucifugus usually inhabits plants, rarely furniture or the wooden beams of buildings. It is most common in plants of which the stem or tap-root measures at least three quarters of a centimetre in diameter; but when it has once entered a stem or large branch it will pass on into the very smallest twigs and roots. It mines irregular galleries, and often avails itself of old beetle-burrows (Bostrychus, &c.); Calotermes does the same thing. Like that species, Termes leaves the outer layers untouched, so that a trunk may be completely mined out and yet appear sound, while the hand can easily be thrust into it by breaking through the thin intact superficial layer.

Owing to the extreme tenuity of this layer in the smallest roots invaded, the galleries may appear at first sight to be tunnelled directly in the ground; but I have never been able definitely to establish the existence of such a mode of construction.

I have never found Termes in the orange, lemon, or vine; but, unlike Calotermes, it is very common in cactus. It continues to live and flourish in perfectly dead and dry wood, even when employed in the construction of roofs, doors, furniture, casks, &c.

It is characteristic that whereas Calotermes confines itself to the original host plant, Termes successively attacks fresh plants or timber, and may thus pass from the furniture of a house to a tree, or the reverse, or from one piece of furniture to another. The following facts are related to this peculiarity:

A few workers of Termes, which are probably explorers, are sometimes found to make a spontaneous appearance in the open air and in broad daylight.

On other occasions Termites travel by availing themselves of natural cracks, e. g. in lava, or by hollowing out small dry rootlets underground, or in reeds by means of the tubular lumen. Frequently they have recourse to galleries, which are quite distinct from the burrows made in wood, because they are fabricated or built up, so to say, by the insects themselves. They are therefore not merely miners, but also builders. These galleries are of two kinds, tubular or D-shaped in section. Galleries are usually constructed in tubular form in the absence of any suitable base on which to build them; if such be present the gutter-shaped gallery (semicircular in section) is resorted to, but even in this case that part of the base which is enclosed between the walls of the tunnel is incompletely cemented over. Galleries of the latter kind are made by preference in the angle of junction of two walls (Pl. 17, fig. 40).

Gutter-shaped galleries may reach the considerable length of eight or more metres. In the choir of the principal church of Pedara I have seen such a tunnel leading from the stalls to a crack in the wall adjoining the wooden ceiling, in which the crack disappeared. The insects travelled between the choir and the ceiling by means of the tunnel and then of the crack, which they made use of apparently without modification. In such cases it is sometimes difficult to distinguish the track of the insects right up to the point where the gallery leaves off.

Similar galleries also occur in the spacious ceiling of the Benedictine church at Catania.

In the building of the Botanical Garden at Catania the Termites have invaded the benches of the school, the bookcases and window-frames, &c. Here I found two gutter-shaped tunnels over 40 cm. in length on the wall of a room; they began from the timber invaded by the insects, and ran along the surface of the wall, to finish at a point where no fissure was discoverable.

The direction of the gutter-shaped galleries may vary as required; they are usually vertical or oblique, less often horizontal, and they may branch in various ways. The tubular galleries are mostly short, rarely exceeding 5 cm., and are narrower than an ordinary pencil. They serve to connect two gutter-shaped galleries or two portions of a nest; and a gutter-shaped gallery may become tubular for part of its course.

On one occasion I found a much flattened tubular gallery about 15 mm. in width, 4 mm. in depth, and 5 cm. in length, and somewhat irregular. This fragile structure was suspended from the ceiling, and contained a certain number of Termites; there were some apertures at its free extremity (Pl. 17, fig. 38). At other times I have found much shorter flattened galleries hanging from the ceiling (Pl. 17, fig. 39; Pl. 18, fig. 15). The purpose of these structures escapes me, but, recollecting the excrescences built on plants by certain tropical Termites, I suspect them to be a rude attempt at a nest. A similar explanation may perhaps be advanced for the galleries found at the Botanical Garden of Catania, which terminated in a free extremity.

Both forms of gallery usually have a diameter from 2 to 6 mm. Their lumen varies at different points, and is generally large enough to allow several insects to pass at once; the internal surface is tolerably smooth, while the outer is irregular and rugged. Their colour is variable, but is usually of a chalky-grey tint. They are composed of fæcal and disgorged matter, and of triturated wood. When connected with a plaster cornice they contain distinct scattered white specks, which are fragments of plaster.

These Termite galleries are invariably very light, porous, and friable. When the Termites meet with large empty spaces while in process of enlarging their nest, they may fill them up by building a complicated labyrinth, as many ants are known to do (Pl. 18, figs. 14, 16); and they readily adapt such projecting pieces of wood as the space may contain to what they are building by covering them over with the materials of construction, or cementing them suitably together.

Excellent specimens of both classes of gallery can be obtained by putting Termites into a glass jar half full of broken-up cactus-phylloclades, and closed with a cork or merely with a sheet of paper (Pl. 18, fig. 17).

If many such nests are formed, one or more can generally be kept alive for six, eight, or more months. I have published elsewhere an account of one of these nests, which I repeat textually.

"For eight months I have kept a colony of Termes lucifugus without king or queen in a jar half full of crushed-up phylloclades of Opuntia, and closed with a sheet of paper tied over the mouth instead of with a bung. The jar holds three litres, and its mouth is wide and polished.

"At the beginning of April the Termites were seen to have settled in the bottom layer only of the rubbish, and the remainder, some 7 cm. in thickness, was quite uninhabited. It was not till the 20th of May that a few specimens appeared in it. Some days later a semicircular gutter-shaped tunnel was found adhering to the walls of the empty part of the jar (the nest material occupying barely a half). This tunnel put the rubbish into communication with the paper cover, which presented a small aperture large enough to admit the body of a Termite at the extremity of the tunnel.

"All kinds of forms in the colony (larvæ, nymphs, soldiers, workers, and winged adults) went backwards and forwards by this gallery, which in its greater part would only allow room for a single individual at a time, but which widened here and there so that two could pass simultaneously. This primary tunnel, as it may be called, was the only one constructed during five days, but it was made to bifurcate by the addition of a lateral branch. This came off at an acute angle from near the middle of the primary gallery, and ran upwards to terminate on the margin of the vessel, where the polished surface began. During the next few days the uninhabited part of the rubbish was tunnelled with numerous burrows, opening on its upper surface by several small holes, some of which were continued upwards by tubular chimney-like galleries of different heights (the largest measured 5 cm.), vertical or oblique in direction, and varying in width, usually just capable of being traversed by a single Termite. The free ends of these chimneys were sometimes closed, sometimes open, and in that case an inmate of the colony would not infrequently peep out as from a watch-tower (Pl. 18, fig. 13).

"Swarming took place on June 1st. On the following days the Termites did very little work, to all appearance. They lengthened a chimney and built another gallery like the first, but not connected with it and not reaching the lip of the vessel; and lastly, they made an incomplete extension of the primary tunnel by carrying it along the junction of the lip and the paper. The latter exhibited two fresh holes at this point.

"One day I destroyed the newly formed section of the primary gallery by taking off the paper, which I purposely put back so that it did not accurately cover the margin of the vessel, but left a gap; next day the primary gallery was continued horizontally outwards for about 1 cm. from the margin of the vessel; this new portion did not run on the surface of the glass, and, like the chimneys, was tubular instead of being semicircular (Pl. 18, fig. 17). A day later it was dismantled and destroyed by the Termites; this did not surprise me, as I had already observed them make and unmake portions of galleries.

"On June 20th the tops of the chimneys and openings were closed up, the galleries were unoccupied, and the whole of the colony had once more retired to the bottom of the vessel."

This colony was unfortunately killed at the end of June by over-dryness.

The structures built before swarming were certainly made chiefly for the purpose of facilitating that procedure. But similar erections, with the exception of the chimneys, can be obtained at a time remote from the swarm-period, or after it has elapsed, as in the case just described, where the Termites evidently found the vessel unsuitable, and attempted to abandon it, but were unsuccessful, and therefore all died.

I state that they endeavoured to quit the jar because on other occasions I have observed a general migration from a vessel which had been inhabited some time, the contents of which were found on examination to be unsuited to their welfare (too damp, mouldy, over-dry, &c.).

Termes does not line the galleries hollowed out of wood with excrement. The wood-meal produced by burrowing varies in colour with the material from which it is derived. Burrows are very easily made in certain cactus-phylloclades which keep their white colour after death, but become very soft; the inner surface of these burrows and the dust removed are both white.

Termites customarily select the softer parts of the wood, but when these are all destroyed they attack the hard parts, and thus form spacious chambers, openings, &c.

Temperature and humidity are as important for Termes as for Calotermes; and as far as is known at present the geographical distribution of these forms coincides.[1] But it must be remembered that the former can flourish at a somewhat lower mean temperature than the latter, so at least I imagine, for the following reasons:

Oviposition commences as early as the beginning of May. In October and November forms in intermediate stages between the nymph and the larva with the earliest indication of wings

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[1] [Termes, however, extends farther north, occurring in France at Toulouse, Bordeaux, Rochefort, and La Rochelle, and in Italy in Tuscany and Venetia, the present writer having lately found a winged example at Venice.—W. F. H. B.]

are very scarce; they begin to appear in December, and become abundant in January and February. The nymphs accomplish the imaginal transformation by April or May. But the fact that examples with the characteristics of those recently born are to be met with in spring, though the nest may have contained no eggs since the month of September, shows that the development of the earliest stages is arrested during the winter, as in Calotermes. Termes, it must be noted, requires a less degree of moisture than Calotermes, and can therefore live with comfort in dry and seasoned timber, and in desiccated portions of trees, &c.

During the warmer months they bury themselves deeper and deeper in dead roots, so that their nests appear to be depleted, and it becomes difficult to procure complementary royal forms, eggs, new-born larvæ, &c., without digging to a great depth.

Termes and Calotermes often share the same tree, but the former habitually confines itself to the dead and drier, the latter to the moister parts. But it will readily be understood that there is no sharp demarcation between these two regions, and therefore none between the two colonies.

2. Number of Individuals in the Colony.

It is practically impossible to make any accurate estimate of the limits of a nest of Termes, as will be seen later. However, a single tree, which certainly does not harbour more than one nest, will contain at times as much as a litre of Termites. As a rule, the offspring of one nest extends to several trees, and the population of a single colony may therefore be reckoned as upwards of two litres—that is to say, very many thousand individuals.

3. The Different Castes (Plate 17).

The society of Termes lucifugus differs widely from that of Calotermes, or of such other Termitidæ as have hitherto been adequately studied.

Its characteristic feature is the invariable absence of a true royal pair,—that is, a pair derived from winged imagos, which have lost their wings (except the stumps). This statement of mine will appear bold, but I have examined thousands of nests during a period of about seven years, and am in a position to make it without the least fear of contradiction. Small colonies, founded by a true royal pair, are to be obtained only by artificially enclosing winged Termes in glass jars partly filled with wood. Nothing of the kind is ever found in nature. On one single occasion I lighted on a true royal pair, though without eggs, in January,—that is, about six months after swarming.

For the present we may leave out of sight these artificial nests in glass jars to consider those found under natural conditions.

The principal differences between the Termes colony and that of Calotermes are as follows:

1. Termes possesses the caste of workers, which is wanting in Calotermes.

2. On the other hand, Termes has no true royal pair, but its place is supplied by a large number of sexually mature individuals, which I term complementary royal forms (Pl. 17, figs. 16, 17, 21). These complementary forms have the characters of larvæ just about to become nymphs—that is, with the wing-rudiments relatively shorter than in the nymph. Their length differs a little, however, in different examples, and occasionally they are entirely wanting.

3. Orphaned nests—that is, nests from which the complementary forms have been abstracted—contain numerous substitute royal forms. These may resemble the complementary forms, but their wings are frequently entirely wanting (Pl. 17, fig. 15), or else developed as in the nymph (id., fig. 23). Sometimes they have the characters of an imago which has become brown in a few places only, and has the wings mutilated (id., fig. 24).

The ordinary nest of Termes may evidently be compared with the orphaned nest of Calotermes, with this difference, that the former is much richer in royal examples, which usually possess some trace of the wings, whereas these are entirely absent in most of the substitute forms of Calotermes.

The orphaned nest of Termes has a still closer resemblance to that of Calotermes, for the royal forms, as I have said, are frequently destitute of wing-rudiments.

In short, in the nest of Termes, as in the orphaned nest of Calotermes, individuals of which the wings have never been fully developed are invariably raised to the throne.

There is a further important distinction: in the Calotermes nest the king is always to be found beside the queen, whereas in numbers of Termes nests examined I have only twice found a single king associated with troops of queens. These kings were observed in the hot season,—that is, at the time when substitute queens are most difficult to find, because then the insects habitually bury themselves deep in the ground. I cannot doubt that I might have found many others if I had been able to continue my investigations in August and September.

The complementary or substitute king is certainly present in the nest about the time when the queens of either kind reach maturity, and he disappears after pairing. The colony must therefore rear fresh kings every year, which become mature in August and September, fertilise the queens, and die. By way of confirming this inference, I may say, in addition to the facts just related, that recently orphaned nests contain as many examples in process of becoming substitute kings as those about to become substitute queens. Complementary kings in process of development can be found from the middle of March onwards, but are always very rare in non-orphaned nests, while developing complementary queens are entirely wanting.

Finally, I may add that all possibility of parthenogenesis is excluded, as will be seen farther on, by the constant presence of abundant spermatozoa in the spermathecæ of the substitute queens.

A nest of Termes contains[1]—

I. Very young larvæ, the head of which is alike in those of equal length (Pl. 17, fig. 1).

They include forms from the smallest (scarcely 1 mm. long, with antennæ of eleven joints, the third bare, the rest pilose) (Pl. 17, fig. 1) to those a little over 2 mm. in length (with antennæ of twelve joints, the third bare, the rest pilose, sometimes with the fourth bare in one antenna only). Larvæ between these two groups are intermediate in length, and have either eleven pilose antennal joints or twelve, the third and fourth bare and the rest pilose. There are four Malpighian tubules in the smaller larvæ (Pl. 18, fig. 11), eight (four large and four small) in the larger (id., fig. 12). I may add at once that the smallest larvæ possess no parasitic Protozoa.

II. Examples 2·25 to 3·75 mm. long, with twelve entirely hairy, or thirteen antennal joints; some with large (Pl. 17, fig. 2), others with small heads (id., fig. 3).

Those with large heads may be regarded as young workers, and may become either adult workers or soldiers.

The smallest members of this group still possess four small [secondary] Malpighian tubules, and may be free from Protozoa (always from Trichonympha).

III. Examples with fourteen antennal joints, 3·75 to 4 mm. in length, with or without very short wing-rudiments.

They fall into the following category:

A. Forms without a trace of wings, with the head relatively large, the abdomen stout and rather short, and the colour of the body less conspicuously white (Pl. 17, figs. 5, 78). These are more or less immature workers, capable of becoming adults, or of transforming into soldiers. They are derived from either the large- or small-headed forms of the preceding stage (II).

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[1] As before, I must assume a knowledge in this section of certain experiments which will be described later.

B. Soldiers with all antennal joints pilose. Derived from large-headed forms of the preceding stage (II).

C. Examples without trace of wings and with a relatively small head (Pl. 17, fig. 4). Derived from small-headed forms of the preceding stage (II).

D. Examples with very short wing-buds (Pl. 17, fig. 6). Also derived from small-headed forms of the preceding stage (II).

IV. Individuals 4 to 6 mm. or more in length, with fifteen or sixteen antennal joints. Some possess very short or partly developed wing-buds, and belong to groups C and D of Stage III (Pl. 17, fig. 9). Others have no trace of wings, and these may be of three kinds: A^2, more or less youthful workers; B^2, soldiers; C^2, larvæ of royal forms, complemental or substitutional, without sign of wings, and with the head small. A^2 are derived from forms A or C of Stage III; B^2 from forms A, possibly also from forms B, C, and D of Stage III; C^2, lastly, from form C of that stage.

V. Individuals with seventeen or eighteen antennal joints, incapable of flight, and infertile, or at least far from maturity.

These may be of five kinds: A^3, soldiers (with not more than seventeen antennal joints, all pilose) (Pl. 17, fig. 14); B^3, adult workers (circa 5 mm. in length) (id., fig. 13); C^3, "nymphs of the first form"[1] (7—8 mm. long), with long wing-pads, the genital organs little developed (id., fig. 10); D^3, "nymphs of the second form"[2] (4—8 mm. long, with more or less short wing-pads, the genital organs well developed) (id., figs. 19, 20, 22); E^3, larvæ of complementary or substitute royal forms, without trace of wings (7—9 mm. in length). As will be seen later, the forms D^3 are also larvæ of royal substitutes. Form A^3 may originate from A^2 of Stage IV, and perhaps from B^2 as well; B^3 is derived from form

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[1] [Lespès, 'Ann. Sci. Nat.' (4), v, pp. 248—251, pl. v, fig. 6.]

[2] [Id., pp. 251—254, pl. v, fig. 7.]

A^2 of Stage IV; C^3 and D^3 from the forms with wing-buds of Stage IV; and lastly, E^3 always from form C^2 of Stage IV.

To this fifth group belong further certain individuals which I regarded as abnormalities before I was acquainted with the facts I have recorded about the soldiers of Calotermes.

They are nymph-soldiers, or nymphs with the buccal apparatus of soldiers. They probably lose their wings and become simple soldiers, as do those of Calotermes.[1]

VI. Perfect insects—that is, with fully developed wings and capable of flight (Pl. 17, fig. 11). The number of antennal joints remains, as in the nymphs, at seventeen or eighteen, but they are always entirely pilose. These specimens are distinguished by a general piceous colour, save for the mouth parts, tarsi, and apices of the tibiæ, which are testaceous. They originate from the nymphs of the first form.

VII. Complementary (Pl. 17, figs. 16—18, 21) or substitute (id., figs. 15, 22, 25) royal forms, sexually mature, or nearly so, but in the guise of the larva or nymph, or else resembling an imago, partly infuscate and with the wings torn.

The latter spring from immature, not fully darkened perfect insects; the others, in the larva or nymph form, arise from the royal larvæ E^3 of group V, or from nymphs of the second form, or finally from nymphs of the first form (fig. 23). The royal forms derived from nymphs of the first form or from not fully darkened perfect insects are all substitute, never complemental forms.

The wing-rudiments may be wanting, or more or less short. The body may be of the whitish yellow of old paper, or may be more or less extensively blotched with brown. The abdomen is much inflated, so that these forms are generally recognisable at a glance.

They exhibit a further characteristic in the possession of

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[1] It now seems to me probable that they should be compared with the egg-hatching workers of the honey-bee.—G. B. Grassi, October, 1896.

longer abdominal hairs than those of the nymphs and perfect insects; these hairs are generally transverse in direction, whereas they point obliquely backwards in the nymphs and imagos.

The number of antennal joints may increase in the adult workers, larvæ of complementary or substitute forms, and perhaps in the soldiers, to the maximum figure stated above.

The general law laid down for the castes of Calotermes is equally applicable to Termes, with the introduction of a slight modification, due solely to the existence of the workers, which are wanting in Calotermes.

It will stand thus:—The regular development of Termes up to the perfect insect may undergo a deviation at various periods of life, which leads to the formation of workers, of complementary or substitute royal forms, or of soldiers; the last passing through the stadium of the young worker. The deviation in question may take place at various periods.

As the anatomical structure of Termes is in general agreement with that of Calotermes, I shall restrict myself to a few very brief remarks thereon.

Turning to the sense-organs, it is noticeable that the soldiers of this genus do not possess compound eyes, nor do the larvæ which become sexually mature, until the wing-rudiments begin to appear. Consequently the complementary and substitute royal forms, which have no trace of wings, are equally destitute of compound eyes. But these are present and pigmented in all the other complementary and substitute forms. The pigment is also acquired by the nymph of the first form when just about to change to the perfect insect.

In the nymph of the second form there is a distinct structure in the neighbourhood of each compound eye, which I interpret as a rudimentary pigmentless ocellus. This may also be easily seen in nymphs ready for the final change and in the perfect insect; but I have been unable definitely to find it in substitute forms (I have not looked for it in sections).

The well-known law of Fritz Müller as to the increase in the number of antennal joints is certainly inaccurate for Termes lucifugus.

The 11-jointed antenna acquires its 12th joint by subequal division of the 3rd, so that it cannot be said whether the resulting 3rd or 4th is the younger. When the number of joints exceeds twelve it is an indisputable rule that the third is the youngest if the number is odd, and the fourth if the number is equal. And when the number of joints is odd no fresh joint develops until its predecessor has become pilose; for I have never found an example with an odd number of joints which were all pilose, while it is easy to find examples with an equal number of joints which are or are not all pilose (Pl. 17, figs. 28—37).

I shall now describe the substitute and complementary royal forms somewhat fully.

They rarely exceed 11 mm. in length, and those without trace of wings probably never attain a length of more than 6 or 7 mm. The only two kings I have found measured about 7 mm. in length. The shape both of the head and thorax in the examples possessing wing-rudiments is exactly similar to that of the nymph, and therefore of the perfect insect. On the other hand, those which have no sign of wings find their parallel in the small-headed larvæ; their pronotum has a characteristic shape, which will be better understood from the figure than from a laborious description, and which distinguishes them from the workers without a shadow of uncertainty (Pl. 17, figs. 26, 27).

The colour of the body, as before mentioned, is generally of the pale yellow tone of old paper, sometimes with an aureous tinge. The head is dull aureous-yellow, with brown compound eyes, which are wanting, as I have said, in the completely wingless forms. Many old examples exhibit large areas which appear brown or sepia-coloured to the naked eye, but are seen under the microscope to be yellow sprinkled with minute black spots. These areas are as follows:

1. The thoracic and abdominal terga (fig. 17). The latter, however, exhibit an immaculate longitudinal median vitta and a similar rounded spot on either side. The vitta may or may not be evident on the metathoracic, and is wanting on the mesothoracic tergite; it is present on the pronotum, where it forms a cruciform mark with a similar transverse vitta towards the apex. As a rule the side margins of the pronotum are also immaculate.

2. The lateral limb of the abdominal sternites; but a few black spots may also be seen to exist over the median portion.

3. The thoracic pleuræ (side-pieces).

4. The basal portion of the legs.

It is important to notice that completely yellow examples may at times have the wing-rudiments more developed than in those with brown markings, although the greater abdominal development, or their known history, may show the latter to be the older.

The wing-pads are dirty white and exhibit abundant tracheæ, arranged as in the fully formed wing.

Hairs are distributed everywhere except on the intersegmental spaces. As I have already said, those on the abdomen are longer and transversely directed (figs. 17 and 18), and thus distinguish these forms from those in which the wings are fully developed (fig. 12). The genital appendices are always absent in the female.

The abdominal hairs and black maculation furnish characteristic points of difference from the fully winged forms. The latter are found to become black by uniform darkening,—that is, without first presenting the black spots peculiar to the complementary or substitute examples.

The number of antennal joints in this latter group of royal forms is variable, and may differ on each side of the head; it may be 14, 15, 16, or 17; but the last number is exceptional. In no case are the antennæ intact, as the examination of the last joint as well as the third and fourth shows (Pl. 17, fig. 29). I have found queens without indication of wings and with sixteen-jointed antennæ, which were obviously truncated at the apex; and the condition of the third and fourth joints being pilose, led me to infer that eighteen would have been present if they were intact. But this is never the case in these forms.

There remain for description those substitute forms which are derived from perfect insects which have not become black, and have the wings torn off (Pl. 17, fig. 24). They measure about 6 mm. in length, and possess the customary long outstanding hairs. The dark compound eyes are conspicuous, and the ocelli can also be made out. The antennæ are curtailed as usual, and the wings are rarely torn off exactly along the hind margin of the squama, but so as to leave an additional portion of varying, usually small size, the laceration following a very irregular course, as if the wing had been gnawed off.

The body is generally of a yellow colour, and is not spotted with black, but the margin of the pronotum, especially the posterior, and the hind margins of the meso- and meta-notum are of a uniform brown, even when seen through the microscope.

Occasionally the head and the entire meso- and meta-notum are brown; frequently, also, the thoracic pleuræ and the outer face of the basal portion of the legs. In some examples the apex of the abdomen is brownish. In some the wings are of a uniform dirty white, but in many others the squama, the costal margin, and perhaps part of the torn edge are brown.

The genital appendices are present in the male, but are wanting in the female, as in other complementary and substitute queens.

The stages of growth of substitute or complemental forms with longer or shorter wing-buds are important, and require notice. They are to be found by selection of the examples with seventeen or eighteen antennal joints and rudiments of the wings. According to Lespès' classical researches, these examples are of two kinds, with the wing outgrowths respectively strongly and feebly developed. The former (fig. 10) are his "nymphs of the first form;" the latter (figs. 19 and 20), his "nymphs of the second form," are further characterised by the bulkier and more ovoid abdomen. The eyes of the latter group begin to become pigmented and prominent, and their ocelli are visible. Their antennæ are intact, and the hairs resemble those of the nymphs of the first form.

These nymphs of the second form become complementary royal forms by a moult in which they acquire the characteristic direction of the abdominal hairs and, if of female sex, lose the female genital appendices.

They exhibit a marked development of the genital organs which will be subsequently described.

In the examples, previously mentioned, of which the head begins to enlarge, much the same development of the mandibles and maxillæ takes place as in Calotermes flavicollis.

With respect to the general colour of the inmates of the colony, I should add that the workers are normally dirty white or yellowish, and the soldiers more distinctly yellow; freshly moulted or very small specimens, and most undifferentiated forms, or those destined for sexual maturity, are pure white.

The legs are alike in all the forms; the anterior tibiæ possess three, the others two apical spines.

Adult and fully winged examples exhibit the well-known sexual differences of the seventh, eighth, and ninth abdominal sternites, viz.—1. The seventh (the apparent sixth) is strongly developed and semicircular (with the rounded edge posterior in the female), very short in the male. 2. The eighth is reduced to two lateral lobes in the female, and is small and entire in the male. 3. The ninth nearly resembles the eighth. A similar disposition is found in the mature substitute and complementary forms. As in Calotermes, the ecdyses are rather numerous in Termes lucifugus, and do not bear the supposed relation to the increase in the number of antennal joints.

4. Relative Numbers of the Castes.

It is impossible to indicate the relative numbers of the different forms with any degree of certainty, owing to the excessive difficulty of fixing the limits of a colony. But, as before, the soldiers of Termes are far less abundant than the other forms. The workers occur in enormous numbers; the young and larvæ are also very numerous, the "nymphs of the first form" relatively much less so.

Examples in process of development into royal forms are common only in trees which, though densely populated, contain no or very few royal forms. Nevertheless a certain number of male "nymphs of the second form" can easily be found from March to June, especially in trees containing complementary or substitute queens.

Complementary forms occur in 6 or 8 per cent. only of trees invaded by Termes, but in these there may be upwards of a thousand, though the number usually oscillates between fifty and two hundred.

Substitute royal forms, varying in number from about ten to two hundred, are confined to those nests which have been partially or completely orphaned, either by destruction of the complementary kings and queens, or by cutting down a tree and removing it a kilometre or so away from its original situation.

In the nests which I have mentioned as having been obtained in glass jars, a single true royal pair was found.

5. Seasonal Variations in the Colony.

The colony differs very much at different times of the year. Eggs are present in May, June, and July, and, in all probability, in August and September as well.

The youngest larvæ are never present in April and May.

Nymphs of the first form are not met with in June and July. Forms with tolerably well-marked wing-buds, and with fourteen to sixteen antennal joints, are absent or very scarce in October and November; they increase in number in December, to become abundant by January or February.

Winged imagos occur from the beginning of April to the middle of June (a few stragglers being exceptionally found as late as September).

The remaining forms are present, as a rule, all the year round, except the kings, or incipient royal forms of either sex.

The latter have already been repeatedly referred to, and must receive further notice in the following chapter.

Lastly, I must not omit to mention that nymphs of the first form are absent in some years from certain nests, which have probably been orphaned at a previous period.

6. Duration of Development, Life, &c.

The eggs hatch fifteen or twenty days after they are laid.

Many observations lead me to conclude that the very young larvæ found in the winter do not develop farther than the nymph of the first form in the following summer, and therefore must certainly live through a second winter before acquiring wings; e.g. larvæ born in October, 1889, will not have the wings fully developed until April, 1891.

Thus, too, the complete or almost complete absence in October and November of examples with 14—16-jointed antennæ and distinct wing-buds compels me to believe that those hatched in May have become nymphs already, or else that they do not yet possess fourteen antennal joints. The latter hypothesis is correct; for if the former were, a much larger number of nymphs ought to be found in particular nests than is actually the case.

A small colony obtained in a glass jar was furnished with a number of fully winged individuals in the early part of May; on the 20th of December it contained, beside the other inhabitants, five workers with 12—14-jointed antennæ.

Several orphaned nests were placed in large glass jars in January; next October they still contained small specimens with 13—14-jointed antennæ, while no substitute forms had developed.

These further facts agree sufficiently with the hypothesis which I regard as correct.

In conclusion, a lapse of eighteen to twenty months may be estimated to take place between the times of hatching and of reaching the perfect state. The workers and soldiers probably require a much shorter time, and both can apparently be developed by the autumn from eggs laid in May of the same year.

The duration of life of single specimens cannot easily be estimated. The soldiers and workers certainly do not die off about the middle of June, as Lespès pretends. The king, whether complementary or substitute, does not live more than a couple of months after reaching sexual maturity, whereas the corresponding queens will live for several years.

7. Situation of Different Forms in the Nest.

The fertile or nearly fertile royal forms usually live in a very remote part of the nest, often collected together in a deep root or in the heart of a large trunk.

The only two mature kings I have found accompanied the queens; the latter may be surrounded with numerous new-born larvæ and clumps of 30 or 40 to 100 eggs.

Eggs and larvæ can be carried long distances, as is shown by the occasional presence of numerous young larvæ and sometimes of eggs as well in trees destitute of queens.

The larvæ, nymphs, winged forms (if present), soldiers, and workers all occur mingled together, both in the midst of the queens and elsewhere. Recently invaded situations contain, as a rule, chiefly workers and soldiers; and isolated workers, which one is tempted to look on as explorers or pioneers, may sometimes be found under stones, or in reeds, &c. Certain parts of the nest often contain principally workers and soldiers; others larvæ with wing-rudiments and nymphs.

[I would add further that when a nest is opened certain parts will contain nothing but soldiers in the neighbourhood of the egg-clumps. It is a mistake to regard this as a normal state of things; the disturbance and noise of opening the nest have put all the other inhabitants to flight, while the valiant soldiers alone remain to protect the eggs.]

VIII. Certain Habits.

The swarming will be first described.

A swarm was observed on May 14th, 1891. A host of Termites issued in groups of two to five from a single crack in a tree-trunk, rose on the wing for about three metres, and then followed the direction of the wind. Many fell on the neighbouring plants, and others were seized by ants as they emerged. The swarm began at 10 a.m., and lasted for more than two hours.

This incomplete observation was made by the laboratory servant, who chanced to see a similar occurrence on May 24th, 1891. In the second case the winged forms were seen to issue from several holes, at which a few soldiers and workers also appeared. The imagos were all destroyed, at first by two lizards, which remained on watch near the nest and devoured them directly they appeared. When the lizards were driven off the insects were seen to come out in groups of six or eight, run a certain distance, spread their wings, and then take flight. At first they rose a certain height, and then followed the direction of the wind (a light scirocco). A few struck against branches and fell to earth, but they quickly got up again. This swarm lasted from about 9.30 to 11 a.m. When it was over the nest was opened, and found to contain many imagos ready for swarming about half a metre from the exit-holes. These were all females, as were those (twenty-six) collected during the swarm.

Sinilar swarms were observed on various other occasions. One of special interest took place in the laboratory from the nest in a glass jar, which I have previously described, mentioning its occurrence on June 1st. The details are now given.

Towards the end of April I examined the nest at the bottom of the jar, and observed the appearance of perfect insects, some brown, others still white, but becoming brown in the course of a few days. After May 20th, suspecting that swarming would take place soon, I covered the vessel with a wider and taller glass bell-jar. Both were placed on a pane of glass, and the jar was not completely closed, because the paper did not accurately fit its mouth.

On June 1st, about 9 a.m., I found a number of winged forms with a few soldiers and workers on the part of the sheet of glass which lay between the two jars; the poor little animals had taken advantage of the spaces left by the ill-fitting paper to emerge, and were then vainly trying to escape from the bell-jar. Nothing was disturbed, and twenty-four hours later no change had taken place, except that the winged forms were more numerous, and some were moribund.

I then decided to liberate them, and removing the bell-jar I put them by means of a quill pen into a receptacle containing suitable materials for a nest—but without success, for they all died in less than forty-eight hours. No more winged examples could be detected through the walls of the glass jar; it was replaced unopened on the pane of glass, and once more covered with the bell-jar. Twenty-four hours later a large number of larvæ and several soldiers were again found on the pane. They were then returned to the nest by means of a quill, and did not escape again.

The observation here recorded was made some years ago, and though imperfect is not wanting in significance.

Another swarm was observed on a May morning of the present year (1892). There happened to be a small level place in front of the holes from which the perfect insects issued, and on this they ran to and fro before taking wing. They were accompanied by soldiers and workers which had emerged into daylight, evidently to protect the swarm.

Several writers have recorded that black Termites, when ready to fly, perform certain movements which can be best followed by putting the insects on a sheet of paper; these are the so-called love passages, often described, and especially by Fritz Müller.

They are not exhibited by Calotermes, but may easily be observed in Termes lucifugus.

The majority of examples dispose themselves after the loss of their wings in pairs, one behind the other. More exactly, the one in front attempts to run away from the other, which pursues it and palpates the extremity of its abdomen, and sometimes the sides as well. In some cases the pair is composed of a wingless individual in front and a winged one behind; or a male in front and a female behind; or the opposite; or both may be of the same sex, whether male or female.

If a few workers are put among the imagos, one of the latter may often be seen to pursue a worker in the same manner. And occasionally three examples, instead of merely a pair, may be seen, one following the other.

I believe that the meaning of these supposed amorous displays is entirely different from that usually assigned to them, and that the pursuer wishes to solicit the dejecta of the one pursued; this will be explained in the following chapter.

I have said that the adults lose their wings (the persistence of the squama being understood) (Pl. 17, fig. 12), and I must now explain more minutely how this occurs. Suppose that the wings of a specimen are accidentally allowed to touch the moist walls of the glass jar, they stick to it, and readily break off as soon as the owner tries to run away.

[The insects perform various movements on their own account in order to tear off the wings. I have seen one raise and lower them, and at the same time put the hind leg over them so as to hold them down to the surface on which it was standing. Another example got rid of them by violent fluttering; and a third, which had only one wing left, tried to tear it off at first by forcible flapping, and then succeeded by holding it firmly with one of the hind legs.]

It often happens that the imagos lose their wings while still in the nest, but they nevertheless abandon it, as do those of Calotermes.

In fact, the perfect insect has an imperious craving to quit the nest in which it develops.

Winged examples artificially enclosed in a corked tube quickly gnaw through the cork and escape. This happens even if the wings have fallen off.

It will be recollected that the two sexes swarm at different times. This is demonstrated by—

1. The fact that all members of a swarm are found to be of the same sex.

2. The presence in many nests, late in or at the end of the swarm-period, of black winged forms, which are all males or all females only (by a rare exception a single male may be found to every twenty or thirty females), whereas nests in which the imagos are still white contain a male to every two or three females.

The convulsive movements spoken of under Calotermes are exhibited alike by Termes, and are common to all members of the colony except the newly born, and have the same significance. Moreover the soldier is able simultaneously to produce a special crepitus (creaking), which arises whenever the head is held horizontally during the act of quivering by friction between the hind margin of the occiput and the anterior margin of the pronotum. But whenever the head is held in the normal position during the act—that is, somewhat deflexed—no perceptible sound is produced, owing to the absence of friction.

The soldiers, therefore, possess two distinct modes of communication; and it is noticeable that those of Calotermes always hold the head obliquely deflexed when quivering and produce no sound.

I may add that this characteristic crepitus may be heard at very short intervals by applying the ear to a trunk containing a nest of Termites. This proves that the quivering motions are a constant feature in normal and undisturbed nests, in which they are therefore not employed to give indications of alarm or distress; and I conclude that, besides these significations, the convulsive movements must also have the value of ordinary speech; that they constitute, in short, a means of intercommunication. The same conclusion holds good for Calotermes; and I imagine that the quivering of both species produces a sound which is perceptible to the tympanal organ of the tibia, but is inaudible to the human ear.

Termites, moreover, may communicate by means of the antennæ. Thus, if a few are placed on a table, they usually arrange themselves in single files, which circle round the objects standing thereon; and, in such a case, if two Termites moving in opposite directions chance to meet, they reciprocally touch their antennæ and then continue each on its own course (vide also previous statements).

Tasks necessary for the common welfare, with a few exceptions, are undertaken by all the inmates of the colony; but the soldiers are unable to gnaw wood, owing to the great elongation of their mandibles.

Substitute or complemental royal forms have never been seen to prepare wood-meal, or to transport it, or ova, &c. Yet all these duties are carried out by the perfect insects with fully developed wings, before or after they have been shed. Newly-born larvæ may easily be found carrying about wood powder.

[The soldiers serve for defence, like those of Calotermes. Two soldiers, one a Termite, the other a Calotermite, were put together in a small glass vessel. They accidentally came into contact and began to fight. The Termite, having the advantage of great quickness in movement, whereas Calotermes is sluggish, bit off some of its enemy's legs, and was proceeding to further hostilities, when the other seized an opportune moment and cut its head off. On other occasions the soldiers of Calotermes tore the abdomen of the soldiers of Termes to pieces.

The soldiers' mandibles may appropriately be likened to a powerful pair of shears. Termite soldiers become formidable when put into one of the customary little nests of Calotermes deprived of soldiers, rapidly cutting off the antennæ of numerous examples, and biting them in various places. But if they are few in number, the Calotermites eventually reduce them to helplessness by shearing off their mandibles, and then pursue, tear, and kill them.

A fight is invariably provoked by putting soldiers of both species into a jar; if large larvæ or nymphs of Calotermes are introduced into a colony of Termes they are usually left alone by the soldiers, which probably fear them; whereas Calotermites (see p. 283) always kill any workers or nymphs of Termes which have been added to their nest. Termes soldiers fraternise, and do not fall out, even when taken from different nests.

If triturated wood, soldiers, workers, and young of Termes are put together in a jar, the soldiers are soon seen to post themselves on the top of the rubbish, evidently on guard.

Sometimes inmates of the same nest (soldiers and workers, or the latter inter se) come to blows, and wound each other ferociously in the thorax or abdomen, and do not stop unless others interfere to separate them. These internecine battles can be provoked, e. g. by overturning the contents of a nest, and are perhaps due to each individual imagining that his neighbour is the cause of the disturbance.

Termites shun the light, and prefer to collect in the darkest parts of a vessel.]

(To be continued.)

EXPLANATION OF PLATES 16—20,

Illustrating Professor B. Grassi's and Dr. A. Sandias's paper on "The Constitution and Development of the Society of Termites: Observations on their Habits; with Appendices on the Parasitic Protozoa of Termitidæ, and on the Embiidæ."

The first number after the explanation of each figure indicates the ocular, the second the objective of the microscope employed. Kor. = Koritska microscope, with the tube in. Hart. = Hartnack microscope, with the tube in. T. = Termes lucifugus. C. = Calotermes flavicollis.

Instead of the expression that a given individual possesses, e.g. seventeen, antennal joints, the abbreviation "with seventeen joints" is employed.

PLATE 16.

Calotermes flavicollis.

Fig. 1.—Small-headed larva, with twelve joints. The third, fourth, and fifth indistinct; the former not pilose; the fifth with short hairs (distinguishable with a higher amplification only).

Fig. 2.—Large-headed larva, with thirteen joints. The third short, and not pilose.

Fig. 3.—Small-headed larva, with sixteen joints. The third and fourth scarcely indicated, and not pilose. Wing-rudiments distinctly present, but very short, and visible only with higher amplification.

Fig. 4.—Nymph, with seventeen joints. The third pilose, the fourth not.

Fig. 5.—Large soldier.

Fig. 6.—Perfect insect, with fully developed wings.

Fig. 7.—True queen, in the fourth year of maturity.

Fig. 8.—Outline of a true king or queen, in the second year of maturity.

Fig. 9.—Outline of a true queen, in the third year of maturity.

Fig. 10.—Outline of a true king, in the fifth year of maturity.

Fig. 11.—Outline of the abdomen of a true queen, in the fifth year of maturity (drawn approximately to the same scale as Fig. 10).

Fig. 12.—Young substitute queen.

Fig. 13.—Outline of the abdomen of a substitute queen, in the third year of maturity (drawn to the same scale as Fig. 11).

Fig. 14.—Developing royal substitute form, with fifteen joints; the third the shortest, and not pilose.

Fig. 15.—Exuviæ of a developing substitute form.

Fig. 16.—Outline of the body of a small soldier (the antennæ are omitted).

Fig. 17.—Outlines of the hind angle of (*b*) the mesonotum and (*a*) the metanotum of a substitute queen, with very slight traces of the wing-outgrowths. 3, 4, Kor.

Fig. 18.—Outline of the right half of the meso- and metanotum of developing substitute form. The anterior wing-rudiment is torn off.

Fig. 19.—Antenna of a small soldier. 3, 4, Kor.

Fig. 20.—Base of a fifteen-jointed antenna. 3, 4, Kor.

Fig. 21.—The same in a different stage, but still fifteen-jointed.

Fig. 22.—The same after development of a sixteenth joint.

Fig. 23.—Ovary and oviduct of a soldier. 3, 4, Hart.

Fig. 24.—Posterior leg of a young nymph.

Fig. 25.—Old substitute queen, with wing-rudiments.

Fig. 26.—Half of the thoracic terga, exhibiting wing-rudiments, in a young soldier. 3, 5, Hart.

Termes lucifugus.

Fig. 27.—Brain of a worker, by transmitted light. 3, 5, Hart.

Figs. 28 to 33.—Series of horizontal sections of the brain of a young nymph, to exhibit the fungiform bodies (interpreted as psychic centres). They are represented by the darker and more closely dotted portions (which possess small, deeply staining nuclei).

Fig. 28 represents the most superficial section, and is followed by the others in numerical order.

Fig. 34 represents, by way of comparison, a similar section through the brain of Embia, at the point where the fungiform bodies attain the maximum dimensions. *gl.* Retro-cerebral gland. [This gland of unknown function exists (only ?) in the nymph of the first form, the perfect insect, and the soldier. It eliminates a transparent secretion, which can be spirted out for some distance.]

PLATE 17.

Termes lucifugus.

Fig. 1.—Larva, with eleven joints, the head undifferentiated.

Fig. 2.—Large-headed larva, with twelve pilose joints.

Fig. 3.—Small-headed larva.

Fig. 4.—Small-headed larva, with fourteen joints, the fourth not pilose.

Fig. 5.—Diagram of a similar but large-headed larva. The hair-lines between 2 and 3, and between 4 and 5, apply to each of the two figures.

Fig. 6.—Larva similar to 4, but larger and with wing-rudiments.

Fig. 7.—Larva similar to 5, but equal in size to that of Fig. 6.

Fig. 8.—Anterior portion of a larva similar to that of Fig. 7, but with a somewhat larger head; probably a soldier larva.

Fig. 9.—Larva, with fifteen joints; the third alone not pilose, and with evident wing-rudiments.

Fig. 10.—Nymph, with long wing-pads.

Fig. 11.—Fully winged perfect insect.

Fig. 12.—Perfect insect after shedding the wings.

Fig. 13.—Adult worker.

Fig. 14.—Soldier.

Fig. 15.—Young wingless substitute queen.

Fig. 16.—Old wingless complementary queen.

Fig. 17.—Old complementary queen, with slight rudiments of wings.

Fig. 18.—The same, with more distinct rudiments.

Fig. 19.—Male nymph of the second form (March 1st).

Fig. 20.—Outline of a male nymph of the second form (April 11th).

Fig. 21.—Young complementary queen, derived from a nymph of the second form.

Fig. 22.—Thorax of a nymph of the second form, with the wings more developed than those of the example in Fig. 21.

Fig. 23.—Substitute queen, derived from a nymph of the first form.

Fig. 24.—Substitute queen, derived from a perfect insect; partly infuscate, and with the wings torn (the infuscation is not shown).

Fig. 25.—Posterior extremity of a very old substitute queen, without sign of wings.

Figs. 1 to 25 are all drawn by the camera lucida to an equal scale, with exception of Figs. 16, 17, and 21, which are somewhat more enlarged.

Fig. 26.—Pronotum of a worker. 3, 4, Kor.

Fig. 27.—Pronotum of a completely wingless substitute queen. 3, 4, Kor.

Fig. 28.—Antenna of a nymph of the second form. 3, 4, Kor.

Fig. 29.—Antenna of a complementary queen. 3, 4, Kor.

Fig. 30.—Base of a twelve-jointed antenna.

Fig. 31.—Base of a thirteen-jointed antenna.

Fig. 32.—Base of a fourteen-jointed antenna.

Fig. 33.—Base of a fifteen-jointed antenna.

Fig. 34.—Base of a sixteen-jointed antenna.

Fig. 35.—Base of another sixteen-jointed antenna.

Fig. 36.—Base of a seventeen-jointed antenna (nymph of the first form).

Fig. 37.—Base of an eighteen-jointed antenna (nymph of the first or second form).

The figures 30 to 37 are all copied by the microscope, 3, 4, Kor., with the tube drawn out.

Fig. 38.—Flattened tube constructed by T., and suspended from a plaster cornice. The lower end (to the right of the figure) was open; the upper end is broken.

Fig. 39.—A similar flattened tube—short, enlarged and flask-shaped. A small portion of the cornice to which it was suspended is represented.

Fig. 40.—Portion of a gallery formed by T. in the angle of a wall; seen from the inside.

PLATE 18.

Termes lucifugus.

Fig. 1.—Ovary of a perfect insect before loss of the wings. 3, 6, Kor.

Fig. 2.—Ovaries of a nymph of the second form. 3, 4, Kor.

Fig. 3.—Ovary of a very old complementary queen. The tubules are evidently atropied, and the spermatheca was empty. 1, 4, Kor. *Por. ant.* = anterior portion.

Fig. 4.—Left ovary of a nymph of the first form. 3, 4, Kor.

Fig. 5.—Testis of a perfect insect before loss of the wings. 3, 6, Kor. (Spermatozoa are present in the vas deferens.)

Fig. 6.—Testis of a nymph of the second form. 3, 4, Kor.

Fig. 7.—Testis of a nymph of the first form. 3, 4, Kor.

Fig. 8.—Testes, vasa deferentia, and vesicula seminalis (the two latter not containing spermatozoa) of a perfect insect before loss of the wings. 3, 4, Kor.

In the above eight figures, and in some on the following Plate, the efferent ducts are partly shown, in addition to the generative glands.

Fig. 9.—Developing spermatozoa, in the fresh state. The one indicated with the letter *a* is fully developed. 4, $\frac{1}{12}$ Kor.

Fig. 10.—Oviduct (*tu.*), uterine portion (*ut. ov.*), spermatheca (*spt.*), sebaceous (colleterial) glands (*gl. seb.*) of a complementary queen. 3, 4, Kor.

Fig. 11.—Portion of the intestine at the origin of the four Malpighian tubules in a newly-born larva. 3, 4, Kor.

Fig. 12.—Similar portion, with four large and four small tubules. 3, 4, Kor.

Fig. 13.—Superficial portion of a nest of T. constructed in a jar, with exit-holes and chimneys for swarming.

Fig. 14.—Portion of a termitarium found in a bench in the church Pesara.

Fig. 15.—Tubular gallery, similar to that of Fig. 39, Pl. 2, but not flask-shaped.

Fig. 16.—Portion of a partly excavated and partly built nest, found in a large cavity in the root of a cactus swarming with T.

Fig. 17.—Galleries constructed by T. kept in a glass jar; D-shaped, except the one projecting over the lip, which is tubular. The shading at the bottom indicates the rubbish which harboured the colony.

PLATE 19.

The left side of the plate refers to Calotermes flavicollis, except Fig. 6, which refers to Termes lucifugus; the right side refers to Embia.

Left Side (Calotermes).

Fig. 1.—Ovary and colleterial gland of a true queen in the second year of maturity. 3, 4, Kor.

Fig. 2.—Ovaries of a very bulky queen, enlarged about three diameters (the tubes do not actually lie in one plane as in the figure). *ext. ant.* = anterior extremity.

Fig. 3.—Colleterial glands of a true queen. 3, 4, Kor.

Fig. 4.—Left testis (*test.*), vas deferens (*con. def.*), and vesicula seminalis (*ves. sem.*) of a true king. 3, 6, Kor.

Fig. 5.—Testis of a substitute king, several years old. 3, 6, Kor.

Fig. 6.—Portion of the spermatheca, showing the ducts and orifices of the underlying glands (fresh). (Termes lucifugus.)

Fig. 7.—Salivary glands of a small larva. *res.* = reservoir. 3, 8, Kor.

Fig. 8.—Relations of the hinder part of the chylific ventricle and intestine. The former contains a blackish, the latter a yellowish detritus. Their junction is indicated by the insertion of the Malpighian tubules.

Fig. 9.—Stomodæum (*int. ant.*) and part of the chylific ventricle (*int. med.*). *inv.* = invagination of the former into the latter.

Fig. 10.—Tympanic organ in the fresh state. 3, $\frac{1}{12}$, Kor.

Fig. 11.—Tube-nest. Large portions of the glass are obscured by disgorged matter. The cork is riddled with burrows, and is represented separately on the right.

Fig. 12.—Spermatozoa from the spermatheca, in the fresh state. 5, $\frac{1}{12}$, Kor.

Right Side (Embia).

Fig. 1.—Ventral ganglionic chain; L. 1 = anterior, L. 2 = middle, L. 3 = posterior leg.

Fig. 2.—Dorsal view of the tracheal system (the stigmata are numbered).

Fig. 3.—Alimentary canal. *gl. sal.* = salivary glands. *int. ant.* = œsophagus and proventriculus. *int. med.* = chylific ventricle. *int. post.* = intestine.

Fig. 4.—Ovarian tubes and oviducts (*ovd.*). *seg. med.* = segment médiaire (the successive abdominal segments are numbered).

Fig. 5.—Male generative organs.

Fig. 6.—Posterior extremity of the male. *proc. dext.* = right, *proc. sin.* = left apophysis. *cer. dext.* = right cercus.

Fig. 7.—Labium and labial palpus of one side.

Fig. 8.—Maxillary lobes and palpus.

Fig. 9.—Anterior tarsus (seen obliquely from the side).

Fig. 10.—Middle tarsus (idem).

Fig. 11.—Posterior tarsus (idem).

PLATE 20.

Parasitic Protozoa of Termitidæ.

The figures are all drawn with a Koritska microscope, ocular 5, objective $\frac{1}{16}$, Leitz. The dotted lines represent the continuation of the unbroken lines on the remote face.

Fig. 1.—Trichonympha agilis, in optical section, nearly corresponding with the middle plane of the body.

Fig. 2.—The same, at a somewhat different level.

Fig. 3.—The same, in a superficial plane.

Fig. 4.—The same, partly schematic, to show the arrangement of the flagella.

Fig. 5.—The same, to give an idea of the complicated arrangement of the spicules in some examples.

Fig. 6.—Joenia annectens.

Fig. 7.—Idem.

Fig. 8.—Idem.

Fig. 9.—Endoskeleton and nucleus of a very large example of Joenia in optical section.

Fig. 10.—Microjoenia hexamitoides.

Fig. 11.—Dinenympha gracilis.

Fig. 12.—Idem.

Fig. 13.—Idem.

Fig. 14.—Idem.

Fig. 15.—Idem.

Fig. 16.—The same, with spirilla attached to one extremity.

Fig. 17.—The same, covered with spirilla.

Fig. 18.—Pyrsonympha flagellata (the majority of the flagella are omitted).

Fig. 19.—The same, in superficial view.

Fig. 20.—The same, exhibiting the nucleus and rodlets.

Fig. 21.—Holomastigotes elongatum (the majority of the flagella are omitted).

Fig. 22.—The same, in superficial view.

Fig. 23.—Plan of the lines of origin of the flagella on both faces of Holomastigotes elongatum.

Fig. 24.—The same, in another individual.

On Ctenoplana.

By

Arthur Willey, D.Sc.

With Plate 21.

THE discoverer of the remarkable genus Ctenoplana, which presents affinities both to the Ctenophora and to the Turbellaria, was, as is well known, Professor Alexis Korotneff, who obtained only a single specimen off the west coast of Sumatra, and described it in the 'Zeitschrift für wissenschaftliche Zoologie'[1] for 1886.

Korotneff found his specimen drifting in a current of the sea, in the company of a large number of Porpita. It was distinguished by its deep red or crimson colour, and was named C. Kowalevskii in honour of the discoverer of Cœloplana.

Since 1886 no second record of the occurrence of the genus has been made.

In January of this year (1896), while cruising among the islands which form the Eastern Archipelago of British New Guinea, in pursuance of zoological work, I was fortunate enough to pick up a cuttle-bone which had evidently been afloat for a long time, and was being carried along by the current off the group of the islands named on the chart the Conflict Group.[2] On the cuttle-bone were numerous minute

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[1] Vol. xliii, pp. 242—251, Taf. viii.

[2] These islands surround a magnificent lagoon.

organisms, including young green-tinted Polychætes, young Planaria, Anthozoan larvæ, young Cirripedes in the Cypris stage, and four specimens of Ctenoplana. Three of the last were of a pronounced green colour, and the fourth was crimson.

The green Ctenoplana, both on account of its colour and its shape, is an entirely new kind, and I shall name it C. Korotneffi. The crimson variety may or may not be specifically identical with C. Kowalevskii; but as my sketches of the external form differ somewhat from Korotneff's figures, I think it will be well to give it a provisional name with the object of engaging the attention of any zoologists who may have future opportunities for studying the genus. I propose, therefore, to call my crimson specimen C. rosacea.

As I had no chance of getting ashore, I had to make the best of the limited accommodation supplied by a small cutter, in order to observe the appearances presented by the living animals and their movements. Although I omitted to make accurate measurements of the living expanded animals, their average diameter would correspond closely in length with that of C. Kowalevskii, which, as stated by Korotneff, measured 6 mm.

Many of the external features of Ctenoplana were correctly described and figured by Korotneff, but his specimen appears to have been not very active; and although, as he says, he had it under observation in the living condition for three to four hours, it did not once extrude its tentacles, so that he only became aware of their existence in section. The consequence of this was that Korotneff was completely wrong in localising the plane of the tentacles. He placed them in the plane at right angles to that in which they actually occur.

At the ends of one of the principal diameters of the disc-shaped body of Ctenoplana the margin of the body is incurved. Korotneff, without the smallest hesitation, describes these marginal bays as anterior and posterior in position, while, according to him, the tentacles were situated along the diameter at right angles to the "antero-posterior" diameter—that is to say, in what would correspond to the transverse plane. This, however, is quite wrong.

As will be seen later on, I agree with Korotneff in his identification of the antero-posterior axis (in comparison with bilateral animals), but it is along this axis that the solid tentacles lie.

Furthermore, Korotneff's specimen did not give him an exhibition of its swimming powers, so that he could not observe the movements of the ctenophoral plates, and the result was that he formed the opinion that these plates had become altered as to their function, and that they hardly appeared to serve for the progression of the body. This is a curious repetition of the old error with regard to the means of locomotion of the Ctenophores, as set forth in Chun's monograph. As a matter of fact, when Ctenoplana swims, the ctenophoral plates are its sole means of locomotion.

I now pass on to a systematic account of my own observations.

1. Shape and Movements of the Body.—Like the Planarians, the body of Ctenoplana comprises a thickened median ridge-like area and two lateral thin skirt-like areas, the "Seitenfelder" of Lang. In the attitude assumed when crawling, the body is nearly round with the exception of the above-mentioned marginal bays, from which I observed the muscular pinnate tentacles being constantly protruded and retracted while the animal was crawling (fig. 1). As also observed by Korotneff, Ctenoplana crawls with one of the rounded margins of the body directed forwards as a rule. The tentacles thus appear remarkably like transversely paired structures, and one would naturally at first describe them as such. But it must be remembered that the terms anterior, posterior, and transverse, as applied to bilateral animals, are not applicable to Ctenoplana.

The tentacles, when extruded, are found to be white structures, thus making a marked contrast to the green or red colour of the body. They are provided with small secondary tentacles or pinnæ, arranged somewhat irregularly, but in a single series. Like the tentacles of Cœloplana, described by Kowalevsky, they are strictly comparable with the tentacles of a Cydippid. Both the tentacles and their pinnæ are quite solid, being completely filled up with a muscular core. Within the body each tentacle is enclosed within a hollow sheath which opens to the exterior at the end of a small papilla at the base of the marginal bay. When retracted, therefore, the tentacles form a median axial skeletal support for the body, interrupted in the middle region of the body by the aboral sense-organ.

The aboral surface of the body may be at once called the dorsal surface, and the oral the ventral surface.

The possession of a relatively wide Planarian-like skirt not only permits Ctenoplana to crawl about on firm surfaces, but enables it also to attach itself, in a highly characteristic manner, to the surface-film of water by its ventral surface. In this position it greatly resembles Planarians, which are also fond of assuming the same position. When lying thus attached to the surface of the water the round central oral opening can be seen. The mouth can be protruded so as to form a slight cone.

When swimming, Ctenoplana brings the two halves of the skirt together so as to form a bell-shaped, or better, a Pilidium-shaped structure which progresses very rapidly by means of the ctenophoral plates. In swimming, the aboral pole is directed forwards as it is in the Ctenophora.

The ctenophoral apparatus consists of eight small oval plates, placed four on each side of the tentacle axis.[1] Across each plate run six or seven shallow grooves, from which the long cilia arise (figs. 1 and 5). The cilia of each groove appear in section to be united usually for some distance from their base, and then to separate out into the individual cilia (fig. 5). The ctenophoral plates alternate with the lobes of the central gastric system (figs. 1—3). I only had a fleeting view of the

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[1] The line joining the bases of the tentacles may be called the "tentacle axis."

peripheral anastomosing ramifications of the gastric system, and have not indicated them in the sketches of the external form.[1]

When Ctenoplana wishes to sink from the surface to the bottom it doubles itself up in the usual way, and so sinks apparently without employing the combs. This was also observed by Korotneff.

2. The Aboral Sense-organ.—As already described by Korotneff, the aboral sense-organ consists essentially of an otolithic mass, suspended by stiff processes from adjacent cells in a cupule, and surrounded by a ring of ciliated tentacles. Korotneff figures the latter in the form of a simple circlet. This, however, is not the case. The circlet of sensory tentacles surrounding the otolith consists of two distinct and separate halves, with about nine tentacles in each half. The one half is placed on one side, and the other on the opposite of the tentacle axis (fig. 1).

This is perhaps the most important observation that I was able to make on the living animal, and it is a crucial one for deciding upon the homologies of the axes of Ctenoplana with those of bilateral animals. The division of the circlet of sensory tentacles into two portions was remarkably distinct and unequivocal. The sensory or apical tentacles (as distinguished from the muscular or terminal pinnate tentacles) are usually carried extruded (figs. 2 and 3), but they can be completely retracted.

3. Cilia.—I cannot confirm Korotneff in his statement as to the general distribution of cilia over the surface of the body. The places where I have observed cilia (apart, of course, from the ctenophoral plates) are as follows: (i) on the sensory tentacles, (ii) on the cells lining the sheaths of the pinnate tentacles, and (iii) over a large area of ventral surface (fig. 5). I must deny the presence of cilia on the general dorsal surface.

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[1] As Ctenoplana is semi-opaque, it is difficult to discern much of the internal structure in surface view.

4. Gastro-vascular System.—The central main portion of the gastro-vascular system presents the lobed appearance shown in the figures, the lobes being paired about the tentacle axis. The middle and largest pair of lobes belong to the stomach, and thus serve to mark out the stomachal plane (Magenebene of Chun). The stomachal plane, therefore, as in the Ctenophores, lies at right angles to the plane of the tentacles, which corresponds to the funnel plane (Trichterebene) of Ctenophores.

My identification of the stomachal plane in Ctenoplana is just the reverse of Korotneff's, who erroneously placed it in the true tentacular plane.

From the two opposed sides of the stomach a narrow median canal leads into the two terminal end-lobes of the central gastric cavity (cf. the schematic fig. 11). The two end-lobes are in open communication with the peripheral canal-system.

I do not find such definitely circumscribed peripheral canals as those figured by Korotneff, but they appear to me in section merely as the spaces partitioned off by the dorso-ventral trabeculæ, which Korotneff describes as dorso-ventral muscles (fig. 5).

The median funnel-vessel was correctly figured by Korotneff. It arises from the stomach immediately opposite to the mouth, and, proceeding aborally, embraces the sense-organ without opening to the exterior. It is very clearly shown in section.

5. Tentacle Sheaths and Musculature.—The tentacle-axis is occupied by the sheaths of the tentacles, which are hollow tubes lined by ciliated cells lying immediately beneath the dorsal surface, and completely separated from one another by the aboral sensory complex. The muscles of the tentacles form part of the voluminous musculature, which, so far as I can make out, effects the retraction of the aboral sense-organ and of the ctenophoral plates, which can be completely withdrawn into the body (cf. fig. 5). The tentacles were retracted in my preserved specimens, and so it was impossible for me to

analyse this very complicated longitudinal musculature. The musculature[1] on one side of the stomachal plane is completely separated from that on the other side; so that in sections parallel with the stomachal plane, passing through the region of the sense-organ, no muscles are visible. But at a short distance on either side of the median stomachal plane the sections in contracted specimens are almost entirely occupied by the convoluted bundles of muscles. Again, beyond the region of the ctenophoral plates the sections merely show the dorsally placed muscular tentacle lying in its sheath (fig. 10).

6. The Gonads.—By the discovery of the male genital organs of Ctenoplana I have brought a welcome additional piece of evidence as to the adult character of the organism.[2] The testes are placed at the bases of the two end-lobes of the main portion of the gastro-vascular system. Their position is indicated by crosses in fig. 1. They thus consist of two pairs of organs, paired about the tentacle axis. They may be either simple or lobed and subdivided. They may contain practically nothing but mature spermatozoa as in fig. 7; or they may contain both mature and developing spermatozoa as in fig. 9. Finally, they may possess one or several ducts opening to the exterior on the dorso-lateral surface of the body below the level of the ctenophoral plates.

The male genital ducts are merely tubular extensions of the tunica propria which encloses each testis.

In the centre of that portion (always the ventral portion) of the testis in which the immature sperm-cells (spermatogonia and spermatocytes) occur there is usually to be observed a cavity surrounded by large clear cells exactly like those which line the cavities of the terminal gastric lobes; and, in fact, I have traced this cavity into communication with the gastro-vascular system (cf. figs. 5, 6, and 9).

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[1] I do not include the dermal musculature described by Korotneff, about which I am at present in the dark.

[2] Unfortunately I can say nothing about the female reproductive organs. It seems unlikely that Ctenoplana should be unisexual. More probably it is a protandric hermaphrodite.

These central cavities in the immature testes may therefore be called the genital cæca, and the genital products appear to arise as proliferations of the walls of the cæca (figs. 5 and 6).

What is very puzzling is the fact that similar proliferations occur on the walls of the terminal gastric lobes themselves (fig. 5). On the dorsal walls of the terminal gastric lobes the cells of these proliferations appear to assume the properties of chloragogenous cells, and numerous yellowish refringent concretions occur in and amongst them. Somewhat similar refringent particles are to be seen in the cells of the subjacent true endoderm. Finally, in connection with this subject I can only mention the fact that as the median walls of the neighbouring terminal lobes fuse together on nearing the median canal which connects them with the stomach, the minute cellules which compose the greater part of the proliferations in question are replaced by long pyramidal cells which compose a compact gland, having a radiating structure due to the peculiar arrangement of the cells. I will call this a gastric gland, and hope that at some future date light may be thrown upon its nature.

What distinguishes the genital proliferations from the above-described gastric proliferations, apart from their different topographical relations, is the fact that the nuclei of the cellules of the former are of different sizes (fig. 9). The larger nuclei I interpret as belonging to spermatogonia and the smaller to spermatocytes. Unfortunately I am unable to make out any nuclear structure in my preparations, although they are otherwise well enough preserved.

The spermatozoa form dense clusters with characteristically deeply stained heads and unstained tails. The tails are directed both outwardly and mesially. When a testis contains only mature spermatozoa there is no longer any trace of the genital cæcum (fig. 7).

With regard to the ducts in one individual, I counted no less than twelve ducts, which were distributed equally between the four testes. Of these ducts 1 was able to see the actual opening to the exterior in six. In another individual I counted seven ducts altogether.

It should be added that the above description of the male gonads applies exclusively to C. Korotneffii, all three specimens of which possessed them.

7. Axial Relations—Comparison of Ctenoplana with Planaria and Ctenophora.—As already known from the work of Korotneff, Ctenoplana agrees with the Ctenophora in the possession of a main axis(Hauptachse) which connects the aboral pole with the oral pole, the mouth with the sense-organ, and that this main axis forms the line of junction of the two principal planes—namely, the tentacular plane and the stomachal plane.

Ctenoplana presents remarkable Planarian affinities in respect of its dorso-ventrally flattened body, in the possession of a definite dorsal surface, and a definite ventral or locomoter surface, in its habit of creeping, and especially in its habit of attaching itself to the surface-film of water.[1] This enumeration, to which may be added the partial ciliation of the ectoderm, nearly exhausts the list of its strictly Planarian affinities.

Besides the coincidence of the main axis and principal planes of Ctenoplana with those of the Ctenophora, the chief points of affinity are the possession of two pinnate tentacles which are each retractile within a sheath, the possession of the eight ctenophoral plates, and the presence of the median funnel vessel.

The two series of sensory tentacles placed on opposite sides of the otolith, whose epithelium is directly continuous with the epithelium of the cupule of the otolith, are directly comparable with the polar plates (Polplatten) as described by Chun in the Ctenophores. In the first place they agree with the latter in lying in the stomachal plane, in so far that they are paired about the tentacle axis. This is the most important point of agreement morphologically, but they also agree in

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[1] According to the remarkable observations of Chun, some Ctenophores possess this power, effecting it by spreading out the wall of the stomach,—sometimes, as in Lampetia Panceri, nearly everting the stomach as far as to the origin of the peripheral vessels.

some details. The relation to the otolith-bearing portion of the sense-organ is identical in both cases. The polar plates of Ctenophores are ciliated, as are the sensory tentacles of Ctenoplana. Moreover in the Beroidæ, according to Chun, the thickened margin of the polar plates does not form a simple ridge, but is raised up into a series of lappets. This is a very remarkable correspondence, and after my observation of the double, paired character of the sensory tentacles of Ctenoplana I think there can be no doubt that the latter are homologous with the polar plates of Ctenophores.

The comparison of the gonads of Ctenoplana with those of other forms is not such a simple matter. They agree with those of the Ctenophora in being developed about the walls of diverticula of the gastro-vascular system, and with those of the Polyclades in being enveloped in a tunica propria. But they differ from both in the possession of ducts opening directly to the exterior. In the Ctenophora the genital products fall into the meridional vessels, and are discharged through the mouth; while in the Polyclades, according to Lang, the tunicæ propriæ which envelop the innumerable testes open into a system of intra-cellular genital capillaries which eventually convey the sexual products to the vas deferens on each side, by which they are ultimately led to the ventrally placed external genital pore.

We now come to the critical consideration of the axial relations of Ctenoplana. The problem to be solved is the following:—To what do the planes of the tentacles and of the stomach respectively correspond in bilateral animals? Does the tentacle plane of Ctenoplana (Trichterebene of Ctenophores) correspond to the sagittal plane of bilateral animals or to the transverse plane?

We shall find, if it has not already appeared evident in the foregoing pages, that Ctenoplana unequivocally proves, as I think, that the tentacle plane or funnel-plane of it and the Ctenophores corresponds to the sagittal plane of bilateral animals, and not to the transverse plane.

At present there exist two interpretations of the axial relations of the Ctenophores, namely, that of Chun[1] and that of Lang.[2] These may be briefly tabulated as follows.

According to Chun—

1. Tentacle or funnel-plane of Ctenophores = Sagittal plane of Bilateralia.
2. Stomachal plane of Ctenophores = Transverse plane of Bilateralia.
3. Main axis of Ctenophores[3] = Longitudinal axis of Bilateralia.

According to Lang—

1. Tentacle or funnel-plane of Ctenophores = Transverse plane of Polyclades.
2. Stomachal plane of Ctenophores = Sagittal plane of Polyclades.
3. Main axis of Ctenophores becomes bent (geknicht) in Polyclades.

From the above it will be seen that, as regards the tentacle and stomachal planes, Lang's interetation is the exact reverse of that of Chun; and yet it is singular that there is no mention of such a fundamental discrepancy in Lang's monograph.

Selenka (quoted by Lang) held the view that the anterior end of a Polyclade corresponded to the aboral pole of the Ctenophore, and the posterior end of the former to the oral pole of the latter. Lang says he himself formerly held this view, but afterwards gave it up as being erroneous. It would, however, necessarily follow if the main axis of the Ctenophores corresponded to the long axis of Polyclades as stated by Chun. The latter view, however, is irreconcilable with Chun's own identification of the tentacle plane of Ctenophores with the sagittal plane of Bilateralia, and, in fact, it may be dismissed, once for all, as erroneous.

Chun's other homologies, however, in respect of the tentacle[4] and stomachal planes are fully confirmed by the conditions

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[1] Carl Chun, 'Die Ctenophoren des Golfes von Neapel,' 1880.

[2] Arnold Lang, 'Die Polycladen des Golfes von Neapel,' 1884.

[3] Carl Chun, "Die Verwandtschaftsbeziehungen zwischen Würmern und Cœlenteraten," 'Biol. Centralblatt,' Bd. ii, 1882–3. In this paper Chun intimates that the main axis of Ctenophores becomes the long axis of Polyclades; but I cannot find out how he reconciles some of the views here expressed with the previous statements as to the homologies of the planes contained in his monograph.

[4] Chun denominated the plane in which the tentacles of Ctenophora lie the Trichterebene, because there are no tentacles in the Beroidæ.

observed in Ctenoplana. Chun was at first in doubt as to the criterion by which to homologise the planes of Ctenophores with those of Bilateralia, as the axes passing through these planes in Ctenophora were equipolar (gleichpolig).

The way by which he finally arrived at the conclusion that the tentacle plane corresponded to the sagittal plane was so remarkable that I will give a free translation of his description.

"Naturally," says Chun, "we must disregard all accidental conditions of asymmetry by which one of the axes (Kreuzachsen) becomes inequipolar. For example, one seldom finds a Cestus veneris in which the two band-like halves of the body are equal in length. . . . Should, however, one of the axes prove to be inequipolar in such a way that constantly an essential organ-complex failed to develop on the one half of the axis, then we should have a transition to bilateral symmetry which would enable us to speak of a dorsal and a ventral surface. . . . How surprised was I to find a larva which presented a remarkable axial disturbance in the funnel-plane [*i. e.* the tentacle plane] ! I give it the provisional name of Thöe paradoxa, as I have not succeeded in associating it with certainty with any adult Ctenophore. It possesses, in fact, only a single tentacle apparatus and tentacle [Fangfaden]. Only in the course of the later development is a second tentacle apparatus differentiated at the other pole of the axis, so that the original disturbance becomes gradually levelled out."

In Ctenoplana the tentacle axis and the stomachal axis are equipolar; but if we consider about which axis the paired structures are situated, we are simply forced to acknowledge that the plane of the tentacles corresponds to the sagittal plane,—in other words, that the tentacle axis of Ctenoplana and Ctenophora corresponds to the longitudinal axis of Bilateralia.

Lang's theory of the origin of Polyclades from Ctenophores rests in the first instance on the assumption that the pinnate tentacles of Ctenophora and Cœloplana are homologous with the sensory tentacles of Polyclades; and his above-quoted interpretation of the axial relations is framed in accordance with this assumption.

In the first place the fact should be emphasised that under no circumstances and from no point of view are the tentacles of Ctenoplana bilaterally disposed, but they are biradially disposed.

As mentioned above, it cannot be denied that, in the creeping attitude, the tentacles of Ctenoplana present to the onlooker the appearance of ordinary transversely paired structures, and it may seem difficult to imagine an ancestor of bilateral animals with an unpaired tentacle in front and an unpaired tentacle behind. But the point is that we have not got to imagine this, because in the animals with which we are dealing there are no such relations as anterior and posterior, right and left.

As regards the particular homology of the pinnate tentacles (Greiftentakel) of Ctenophores with the nuchal tentacles of Polyclades, so strongly and, it must be added, plausibly upheld by Lang, I venture to think that my observations on Ctenoplana, especially as to the double character of the aboral circlet of sensory tentacles, justifies me in frankly denying its accuracy. From their close relation to the central sensory apparatus, and the fact that they are paired about the tentacle axis, which I regard as equivalent to the longitudinal axis of Polyclades, I suggest that it is much more probable, from their relations and function, that the paired multiple sensory tentacles of Ctenoplana and the polar plates of Ctenophora are homologous with the sensory nuchal tentacles of Polyclades, than that the latter are homologous with the pinnate tentacles of Ctenophora, whose chief function is that of seizing objects for food.

Moreover, from their structure and function, their extreme retractility within definite sheaths, and their worm-like mobility, it would appear that the pinnate tentacles of Ctenoplana and Ctenophora belong to a category of structures totally different from that of the nuchal tentacles of Polyclades. They belong, namely, to the same category of structures as the proboscis of Nemertines and of certain Rhabdocœle Planarians.

Finally, we may recapitulate the organs in Ctenoplana which are paired about the tentacle axis (cf. fig. 1). There are four pairs of ctenophoral plates, three pairs of gastric lobes, two pairs of gonads with their ducts, and one pair of multiple sensory tentacles.

From what has been said I regard it as proved that—

1. The tentacle axis of Ctenoplana = the longitudinal axis of Planarians.
2. The stomachal axis of Ctenoplana = the transverse axis of Planarians.
3. The main axis of Ctenoplana = according to Lang, the primary main axis of Planarians, which becomes bent as the ganglion is shifted towards the anterior end of the body.
4. The main axis of Ctenoplana and Ctenophores = the dorso-ventral axis of Bilateralia.

8. Synopsis of Species of Ctenoplana.

(i) C. Kowalevskii, Korotneff.—Colour crimson, body in swimming attitude shaped like a truncated pyramid; median dorsal surface concave; free margin of skirt frilled. Habitat, west coast of Sumatra.

(ii) C. rosacea, n. sp.—Colour crimson; body in swimming attitude of a quadrilateral form; median dorsal surface convex; free margin of skirt plain. May be merely a variety of preceding species. Habitat, Eastern Archipelago of New Guinea.

(iii) C. Korotneffi, n. sp.—Colour green; body in swimming attitude roof-shaped; median dorsal surface upraised with two upright end-knobs; free margin of skirt slightly frilled. Habitat, Eastern Archipelago of New Guinea.

In Korotneff's fig. 13 there are only eleven sensory tentacles figured for C. Kowalevskii,[1] while C. rosacea had

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[1] Korotneff describes an aperture to the exterior on each side in the neighbourhood of the tentacles in C. Kowalevskii which leads into a "system of canals which branch in the body parenchyma." Korotneff himself says that after he had preserved his specimen in sublimate he was unable properly to orientate it. I have already shown that he completely misplaced the tentacles. The apertures in question are obviously the openings of the

about eighteen. But I should hesitate to insist upon this as a specific difference.

9. General Conclusions.—With regard to the systematic position of Ctenoplana, which we now know to be an adult animal, I am strongly of opinion that it is an ancestral form, and not, as some zoologists seem to suppose, a highly modified creeping Ctenophore. By ancestral form I simply mean a primitive archaic form belonging to an ancestral type, and of course I do not imply that it is the actual ancestor of anything in the world. That the Planarians and Polyclades in particular have close affinities with the Ctenophora there can be no doubt, but it is very much open to question whether the former are derived from the latter. The view that the Polyclades are so derived seems a reversal of the natural order of events, which point to the littoral fauna as the origin both of the pelagic and of the abyssal fauna.

Are we to regard the immediate ancestors of the Turbellaria as amorphous forms, like Trichoplax, or forms without any kind of symmetry, like Planulæ or the Mesozoa? Or, on the contrary, are we not rather to regard their immediate ancestors as forms with some kind of radial symmetry?

Having regard to the complete bilateral symmetry of the flat-worms, and more particularly their well-developed nervous system, with cerebral ganglion in even the lowest forms, I cannot imagine them to be derived directly from amorphous organisms, but rather from animals which possibly, like Ctenoplana, possessed a biradial symmetry.

Ctenoplana approaches more nearly to a condition of bilateral symmetry than the Ctenophores do, in that it possesses very clearly differentiated dorsal and ventral surfaces. And this is exactly what we should expect to find in the littoral or sublittoral ancestor of such purely pelagic forms as the Ctenophora, the pelagic habit, as is well known, often tending to produce a more or less radial symmetry.

tentacle sheaths, and the "system of canals" are the sheaths themselves, which do in fact send off occasional diverticula, possibly due to the contraction of their walls during preservation (cf. figs. 5 and 10).

On the other hand, a biradial form, like Ctenoplana, possesses the potentiality of assuming a strictly littoral life, in which the ventral surface is the permanent locomotor surface, such an existence leading to a condition of bilateral symmetry, according to well-understood physiological principles.

The ctenophoral plates must have put in their appearance for the first time in some form or other; and although it is at present beyond the limits of our knowledge to explain how they arose, yet it is not right to conclude that the ctenophoral plates of Ctenoplana are degenerate or reduced structures merely because they are smaller than the ctenophoral rows of the Ctenophora.

It is a groundless assumption to say that Cœloplana and Ctenoplana are modified creeping Ctenophores. Ctenoplana is an expert crawler, it is expert at hanging on to the surface film of water, and it is indeed an expert swimmer. Everything it attempts it does well in the old primeval fashion, and there is nothing degenerate about it.

If Cœloplana and Ctenoplana are neither Ctenophores nor Planarians, what are they? I think it is necessary to create a new order of Plathelminthes for their reception; and I propose to call the new order the Archiplanoidea, and to regard it as equivalent to the orders Turbellaria, Trematoda, Cestoda, and Nemertina.

Furthermore, I should look to the Archiplanoidea for the ancestors of all the Plathelminthes (including the Nemertines) on the one hand, and of the Ctenophora on the other.

The resemblance in form and shape, however superficial, between Ctenoplana and the Pilidium larva of Nemertines should not pass unnoticed; and it is a remarkable fact that the main axis of Pilidium passes through mouth and apical sense-organ as in Ctenoplana.

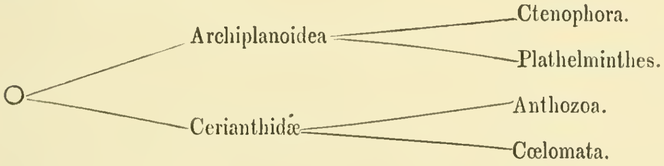
In the Archiplanoidea, therefore, we have organisms presenting a transition from radial to bilateral symmetry.

In the Cerianthidæ, as we know especially from the works of Carl Vogt[1] and Éd. van Beneden,[2] we have also forms belonging to the category of radial animals, which are undoubtedly physiologically radial, and nevertheless present a pronounced bilateral symmetry.

Van Beneden's views are clearly set forth in the following quotation from his memoir above quoted:—"Je partage entièrement l'opinion de Sedgwick et de Caldwell d'après laquelle le disque qui porte la bouche et les tentacles, chez les Actinozoaires, répond morphologiquement à la face neurale des Annéles, des Arthropodes, et des Chordés. Je pense, comme ces auteurs, que la bouche des Cnidaires est homologue à la fente blastoporique des Arthrozoaires. Les diverticules cœlomiques qui sont, ontogéniquement parlant, la cause de la segmentation, répondent aux loges mésenteriques des Anthozoaires et les cloisons intersegmentaires sont anatomiquement équivalentes aux sarcoseptes."

If we accept these conclusions side by side with those derived from the study of Ctenoplana, we are compelled to frame the hypothesis, which I believe to be highly probable, of the diphyletic origin of Bilateralia.

The following scheme will make this view clear, and will save a long discussion:



I believe this view will be found to be a natural one in every respect; and if it be regarded by morphologists as substantiated, it will certainly relieve the science of morphology of several burdens. For instance, Hubrecht's original speculations as to a relationship between the Nemertines and the Chordates, as well as Bateson's comparison of the Nemertines with Balano-

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[1] Carl Vogt, "Des Genres Arachnactis et Cerianthus," 'Arch. de Biol.,' t. viii, 1888.

[2] Ed. van Beneden, "Recherches sur le développement des Arachnactis," ibid., t. xi, 1891.

glossus and many other such like theories, which at the time no doubt appeared to be logical necessities, will be quite ruled out of the field of possibilities.

The descendants of the Archiplanoidea have no cœlom and no præoral lobe. The descendants of the Cerianthidæ have a cœlom and also a præoral lobe (excluding the Anthozoa).

It is an interesting parallelism that the criterion for the antero-posterior axis, both in the Cerianthidæ and in the Ctenophora (Thöe paradoxa), was provided by what may be called a directive tentacle. It may, indeed, be something more than a mere parallelism.

10. Summary of Principal Results.—(1) Discovery of one very distinct new species of Ctenoplana, and of another somewhat doubtful new species.

(2) Observation of the movements and of the pinnate tentacles of the living Ctenoplana.

(3) Accurate localisation of the pinnate tentacles.

(4) Discovery of the double character of the circlet of sensory tentacles surrounding the otolith.

(5) Discovery of the male genital organs and ducts of Ctenoplana, thus proving that Ctenoplana is an adult animal.

(6) Description of the tentacle sheaths.

(7) Account of the genital cæca of the gastro-vascular system, about whose walls occur the genital proliferations.

(8) Chloragogenous tissue and gastric gland.

(9) The tentacle axis of Ctenoplana corresponds to the longitudinal axis of Planarians, the stomachal axis of the former to the transverse axis of the latter, and the main axis of the former to the dorso-ventral axis of the latter.

(10) The solid pinnate tentacles of Ctenoplana are not disposed bilaterally, but biradially.

(11) The ctenophoral plates, gastric lobes, gonads, gonaducts, and aboral sensory tentacles are paired about the tentacle axis.

(12) The aboral sensory tentacles of Ctenoplana are homologous with the polar plates (Polplatten) of Ctenophora, and with the nuchal tentacles of Polyclades.

(13) The testes of Ctenoplana are enclosed within a tunica propria.

(14) The pinnate seizing tentacles (Greiftentakel) of Ctenoplana and Ctenophora, retractile within definite sheaths, belong to the same category of structures to which the proboscis of Nemertines and certain Rhabdocœle Planarians belong.

(15) Creation of a new order, the Archiplanoidea, for the reception of Cœloplana and Ctenoplana. The order will thus contain two families, the Cœloplanidæ and the Ctenoplanidæ.

(16) Hypothesis of the diphyletic origin of Bilateralia.

In conclusion, as I am about to leave Sydney, I wish to repeat my thanks to Professor W. A. Haswell for his kindness and hospitality to me.

SYDNEY; June 29th, 1896.

EXPLANATION OF PLATE 21,

Illustrating Mr. Arthur Willey's paper "On Ctenoplana."

N.B.—My material was preserved in sublimate and in a sublimate-acetic mixture, and stained with alum-cochineal.

FIG. 1.—Ctenoplana rosacea, n. sp., from dorsal aspect. The two pinnate tentacles are extended, the ctenophoral plates alternate with the gastric lobes, the two middle large gastric lobes mark the stomachal plane; in the dorsal centrum is seen the otolith, surrounded by an incomplete circlet of ciliated sensory tentacles paired about the tentacle axis; the spots round the margin of the skirt represent crimson pigment spots. From living specimen. N.B.—The crosses indicate the positions of the male genital organs.

FIG. 2.—C. rosacea. In swimming attitude. From living specimen. Tentacles retracted. *t. o.* Opening of tentacle sheath.

FIG. 3.—C. Korotneffi, n. sp. In swimming attitude. The space indicated by dotted line below the aboral sense-organ was dimly seen through the body, and probably represents the space into which the sense-organ is withdrawn on retraction, although it might represent the funnel vessel.

From living specimen. Tentacles retracted. *t. o.* Opening of tentacle sheath.

Fig. 4.—Sketch of Ctenoplana as it may be seen when attached to the surface-film of water. In the centre is seen the mouth. The two end-lobes of the central gastric system show up white.

Fig. 5.—C. Korotneffi. Section parallel to stomachal plane (i. e. transverse to tentacle axis) to show the origin of the genital cæcum, &c. The section is somewhat oblique. *cil.* Ciliated epithelium of ventral surface. *cæ.* Genital cæcum. *ch.* Chloragogenous cells. *c. p.* Ctenophoral plate, retracted. *d. e.* Dorsal spongy vacuolar non-ciliated epithelium, with mucous granules at external surface. These cells would seem to be comparable to the so-called "Glanzzellen" of Ctenophora. *ent.* Cœlenteron. *ep.* Digestive epithelium, nuclei placed near free end of cells. These are clear faintly staining cells with indistinct cell outlines, and with a sharply defined non-ciliated free margin. *gen.* Genital proliferation on the wall of the genital cæcum. *g. p.* Gastric proliferation. *mes.* Mesenchymatous tissue. *t. o.* Opening of tentacle sheath. *t. s.* Tentacle sheath with its ciliated epithelium; the tentacle itself is retracted further back. *v. e.* Non-ciliated glandular epithelium of the ventral surface.

Fig. 6.—The same. Succeeding section to preceding through gonad to show the conversion of the genital cæcum into a canal. *cæ.* Genital cæcum. *s.* Genital proliferation broken up into polygonal groups of sperm mother-cells.

Fig. 7.—C. Korotneffi. Section through the region of the gonad of another individual to show the testis full of mature spermatozoa and the opening of the genital duct. *d.* Tangential section of portion of duct. *d. e.* Dorsal epithelium. *g. o.* Genital aperture. *t. p.* Tunica propria with flattened nuclei in its walls.

Fig. 8.—The same. Succeeding section to preceding to show junction of genital duct with tunica propria.

Fig. 9.—Section through a gonad of same individual as that from which fig. 5 was taken, to show subdivision of the testis. *cæ.* Genital cæcum. *d.* Genital duct. s^1. Spermatogonia. s^2. Spermatocytes. s^3. Spermatidia. s^4. Spermatozoa. *t. p.* Tunica propria.

Fig. 10.—Section through tentacle and its sheath. *c. s.* Cavity of sheath. *s.* Wall of sheath composed of ciliated epithelium. *t.* Tentacle with peripheral nuclei and central muscle-fibres. In the centre of the tentacle runs a core of mesenchyme-cells, *mes.* *p.* Branch or pinna of the tentacle.

Fig. 11.—Schematic figure to explain connections of the lobes of the central portion of the gastro-vascular system. *f.* Position of funnel vessel.

An Attempt to deduce the Vertebrate Eyes from the Skin.

By

H. M. Bernard, M.A.Cantab., F.L.S.

With Plate 22.

In the February issue of the 'Annals and Magazine of Natural History' I published an outline sketch of a new theory of vision. It was suggested that eyes arose as local modifications of tissue induced by the excessive crowding of pigmented granules at spots most frequently and brilliantly illuminated, and that this crowding of the pigmented granules might be made to explain both the origin of the eye as a structure and its functions as an organ. I now propose, as time and opportunity allow, to compare a few eyes with the tissues out of which they have, or according to the theory they should have, arisen, in order to ascertain how far such comparisons support the theory.

I take the Vertebrata first, not only because the general facts of the structure and development of the eyes in this class are most widely known, but because of the paramount interest attaching to any questions relating to our own highest sense.

Now, according to the theory alluded to, eyes must have developed out of that tissue in which, under the action of light, pigment accumulates. That tissue is the skin; hence the eyes in the Vertebrata must have arisen as modifications of the skin. There are two kinds of eyes in the Vertebrata; the more or less vestigial "pineal" eye, and the Vertebrate eye proper. These eyes are constructed on different plans, and must either, according to the theory, be different modifications of the same kind of skin, or else modifications of two different types of skin. I shall endeavour to show that the latter assumption best accords with the facts; that the change which undoubtedly took place in the character of the skin as the Vertebrata arose out of their Invetebrate ancestors is sufficient to explain the difference between these two types of eye.

Following the lines of the theory, I make two assumptions:—(1) The retina is but a specialised portion of the epithelial layer of the skin, between the cells of which the pigment granules from the subjacent chromatophoral layer stream outwards under the action of light. (2) The retina and the chromatophoral layer must have been in intimate and inseparable association through all the stages of the evolution of the eye. I have, then, to try to show how far the facts relating first to the structure, and secondly to the development of the Vertebrate eyes can be harmonised with these assumptions; how far, indeed, it is possible to deduce the Vertebrate eyes directly and continuously from the skin.

A glance at the diagrams (Plate 22) shows that a striking parallel between the eyes and the skins, out of which I assume them to have arisen, can be easily instituted, but the details are by no means easy to work out, and still more difficult to demonstrate. The greatest difficulty, of course, lies in the fact that, according to their ontogenetic histories, the eyes either wholly or partly developed from the brain. It is true that no one has yet succeeded in elucidating these embryological records; nevertheless they hold the field, even though amounting to little more than bald assertions that the eyes developed from the brain and not from the skin. Before critically examining this adverse testimony I propose to marshal all the available facts which seem to connect the eyes directly with the skin, and to suggest possible explanations of the various modifications and specialisations of the tissues of which our eyes are constructed. Only after having shown that it is possible to deduce the eyes as continuous structural modifications of the skin shall we examine the embryological records, and endeavour to show that the facts are, in the main, in harmony with the argument based upon structure.

I take the pineal eye first, in spite of the disadvantage involved in this choice, arising out of the many debatable details concerning this organ. Its claim even to be an organ of sight at all has been disputed. Assuming it, for the present, to have been an eye, we are, it seems to me, justified for many reasons, which will be more apparent later on, in regarding it as having preceded in course of time the Vertebrate eyes proper. Its place in this discussion is, therefore, that which is suggested by its history as here interpreted.

The close resemblance of the pineal organ to an eye of the Invertebrate (Molluscan) type was first pointed out by de Graaf.[1] The suggestion has not been accepted, for reasons chiefly embryological, nevertheless I am convinced that it is correct. If the pineal organ ever was an eye—and all the evidence points that way,—it should, according to our theory, have developed directly from the skin. With this hypothesis it entirely agrees, its structural relationships being precisely those which they should be had it arisen simply as an invagination of a skin of the Invertebrate type, i.e. of a skin consisting of an external palisade layer supported internally by a layer of connective tissue (Diagram I). Regarding its structure alone, then, and this is the only point that at present concerns us, there is no difficulty in believing that the pineal eye developed first as an optic pit from the skin of the ancestors of the Vertebrata, before that skin had assumed the Vertebrate type, i.e. before the palisade layer had become protected externally by the mucous and horny layers.

Dealing with the development of the pineal eye more in detail,—according to the theory, the retina arose by a secondary multiplication of the epithelial sensory cells for the appreciation of the variations in intensity of irritation caused by the movements of the pigmented granules towards the exterior; while the dioptric apparatus was due to the accumulation

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[1] 'Zool. Anz.,' 1886.

at the surface of slime wholly or partially produced by the excessive discharge of the pigmented granules. This refractive mass, at first probably lying merely at the surface, would eventually be enclosed in an invagination, a phenomenon so common (e.g. in the formation of glands) that a discussion of the mechanics by which it might be brought about need not here detain us.

The formation of a lens, the definite structure of which is now perhaps only indicated by the lengthening of the palisade cells as shown in the diagram, brought the pineal eye as an organ of sight to a high functional level. From this it has steadily declined, until it persists as a vestige which, in many cases, can no longer function in any way for the appreciation of variations of light intensity.

In support of this interpretation of the morphology and physiological origin of the pineal eye, I would call attention to Spencer's figures,[1] a study of which leaves no doubt whatever that the pigmented cells are streaming from the connective-tissue capsule round the eye through the retina, just as in the rest of the skin they stream out from the cutis through the palisade layer of the epidermis. In the series of sections of Hatteria, kindly lent me by my friend Mr. Martin Woodward, in addition to the pigmented cells, there are others making their way alike through the retina and the palisade layer of the epidermis. These are cells containing enormous vacuoles which force the nuclei to one side. On reaching the horny layers these cells flatten out, and their vacuoles form flat spaces which give the cuticle a sort of false lamination.

A still closer parallel between the pineal eye and the skin is observed in Uromastix, for the loan of sections of which I am again indebted to Mr. Woodward. Streaming through the cutis are innumerable cells laden with concretions which are black by transmitted, white by reflected light. They remind one of the guanin granules found in the tissues of Arachnids. Now, while the cells containing these white concretions do not seem to be able to pass through the palisade layer, but stop

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[1] 'Quart. Journ. Micr. Sci.,' xxvii.

short within the cutis beneath it, the cells which contain the red pigmented granules pass freely on, and are seen everywhere forcing their way into the epidermis, and, I believe, helping to build up the horny layer.

On turning to the pineal eye, what do we find? A close network of cells filled with similar white matter enveloping the eye externally. The white matter here also fails to climb up into the retinal cells, just as in the skin it fails to climb up into the epidermis, while on the other hand passing up between these cells are others laden with red pigment, which makes its way into or between the retinal cells, just as the pigment from the cutis passes between and into the palisade cells of the epidermis.[1]

In addition to the pineal eyes of Hatteria and Uromastix, I have examined this organ in Petromyzon planeri, ammocœtes of which I obtained near Jena and fixed in corrosive sublimate. As is now well known, there is no black pigment in these eyes; they appear to me to have become a receptacle for concretions similar to those already noted in the cutis of Uromastix.[2] The condition of the eye itself appears to indicate extreme degeneracy. Having sunk below the skin it

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[1] Comparison of the pineal eye and skin of Uromastix reveals another fact of some importance for the theory of light sensation which I have ventured to put forward. The pigment granules are in this case much larger and more clearly defined in the eye than in the skin. It is a noticeable fact that in eyes in general the pigment grains are much more sharply and distinctly granular, and also apparently not seldom rather larger than are the pigment granules in the rest of the body. This fact is certainly in favour of my suggestion that their passage up and down between the rods of the retina causes a mechanical stimulation.

[2] I therefore doubt the wisdom of Gaskell's description of this matter as "white pigment." It is worth noting also that the white concretions, which have no definite shape in the cutis, are pointed and fusiform in the cells round the eye in Uromastix. The guanin granules have the same or a very similar shape in the argentea of fishes. I have seen similar white long-oval plates in the eyes of spiders. These facts suggest the possibility of associating these last-named granules with the guanin "crystals" found in such quantities in the bodies of these as of other Arachnids. (On their origin cf. 'Journ. Roy. Micr. Soc.,' 1893, p. 427.)

seems no longer in a position to have much pigment pass outwards through it, and, if any travels through, it probably passes right through without being even temporarily arrested, presumably because the resistance of the retina to the passage of the pigment which in the functional eye is, according to the theory, the cause of the irritation and resulting sensation has ceased. In the same way the resistance of the retina to the entrance of the white matter observed in Uromastix has also ceased, so that it streams outwards through the cells in single shapeless or angular granules [which are of very different sizes, and have no resemblance to true pigment granules either in appearance or distribution], to accumulate at the distal ends of the degenerate retinal cells. Beyond this point they seem unable to travel. I know of no evidence which would lead me to believe that the coagulum in the cavity of the eye is due to any transformation of these granules; on the other hand, it is quite possible that it may result from the occasional passage and conversion into slime of true pigment.

With regard to Leydig's doubts[1] as to whether the pineal eye was ever an eye at all, his objections are based upon the very facts which, it seems to me, establish the point beyond dispute. He appeals to the presence of pigment in the lens. But this is exactly what we might expect in an eye going out of function. The pigmented cells ball together as they reach the free spaces among the retinal cells outside the palisade layer; then streaming through the retina they ball again on reaching the cavity of the eye, and may accumulate as globular masses against and within the lens.[2] For some reason or other, as the eye ceased to function, the pigmented granules ceased to clarify on reaching the cavity of the eye, as they appear to do, say, in the eyes of molluscs, of Petromyzon (see below), on passing into the vitreous humour through the

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[1] 'Abh. Senk. Nat. Gesch.,' xvi, 1890, p. 531.

[2] In some cases the pigment seems (in Spencer's figures, l. c.) to be forcing its way between the lens cells; this we should imagine would be the most natural. It is not easy to understand why, in other cases, the cells should ball together in the heart of the lens.

cells in the pars ciliaris retinæ of Vertebrate eyes (see below), and as they certainly do in the rete mucosa of the Vertebrate skin. That they formerly clarified in the cavity of the pineal eye also we have some evidence in another of the facts which Leydig adduces as a reason for disbelieving the original ocular function of these structures. The remains of the homogeneous clear substance which I assume once filled the cavity of the eye still here and there persists, as Leydig himself has shown. It appears in some cases as bristle-like streaks or threads of clear matter streaming outwards from the surface of the retina, or even in a thick layer like a cuticle. That this substance ever formed a definite system of rods turned towards the cavity of the eye, such as has been suggested by Gaskell,[1] I think somewhat doubtful, although it is quite possible that here and there some such differentiation may have taken place (cf. the "rods" of the Cephalopod eye).

Summing up this brief sketch of the pineal eye, we note that structurally (its embryology will be discussed later on) it is quite explicable as a simple invagination of a skin of the Invertebrate type, and may well have arisen in the manner suggested by our theory, while our ancestors still possessed such an undifferentiated epidermis.

An eye arising in this way would necessarily be what is known as a direct vision eye,—that is, the nerves would end in the retina without any bending back upon themselves.

The Vertebrate Eye Proper.—In process of time the skin lost the simple character it possessed when, according to the foregoing, the pineal eye arose. Cells budded off from the palisade layers, while others (e. g. pigment-bearing cells) migrated through the palisade layer, and these together, the

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[1] 'Quart. Journ. Micr. Sci.,' vol. xxxi. At the same time it is obvious that the interpretation of the facts here adopted is hardly reconcilable with the deduction of Vertebrates from the Arthropods; a chitinous exoskeleton does not lend itself to such simple invagination as we have here assumed. I do not think the depression in the centre of the retina of the pineal eye of Petromyzon planeri at all justifies Gaskell's comparison of that eye with the eye of the Acilius larva. A comparison with other pineal eyes shows that that depression is hardly primitive; it may even be a result of degeneration.

former being the more important element, built up a layer of cells, the outermost of which typically harden into horny scales. We thus get the Vertebrate type of skin as shown to right and left of Diagram II. The cutis is richly provided with blood-vessels (shown diagrammatically as loops), the chromatophores are numerous, and those which have reached the epidermis are seen forcing their way up between the palisade cells. Lastly, the ultimate ramifications of the integumentary nerves no longer end, as in the primitive skin, in or among the palisade cells, but, penetrating that layer, terminate among the cells of the rete mucosa.

In this change in the character of the skin we can perhaps find, on the one hand, a partial explanation of the degeneration of the pineal eye, and, on the other, a clue to the chief differences between that eye and the Vertebrate eye proper.

The pineal eye, sunk below the palisade layer and no longer in organic connection with it, would probably suffer by any change such as that described in the character of the outer skin. The separation of the ocular vesicle from the palisade layer would hamper its control over the development of that layer, which might or might not run a course favourable to the eye as an organ of vision. As far as we can see, the secondary thickening of the outermost layers by stratification from the palisade layer was not calculated to benefit the pineal eye. It would impede its function, and therefore cause it to degenerate. A still more important factor making for degeneration is probably to be found in the rise and development of the skull. A review of the available facts relating to these eyes involuntarily suggests that they—there were, it seems, originally two[1]—succumbed, first one and then the other, before the advancing edges of the bony plates which developed to protect the ever-enlarging brain. This degeneration would be hastened if new and perhaps more efficient eyes developed to replace and more than compensate for the loss of the old.

The eyes which appear actually to have replaced the pineal

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[1] Owsianikow, 'Mem. Akad. St. Petersburg,' 7, xxxvi, 1888; also Locy, 'Anat. Anz.,' 1894, p. 169.

eye (or eyes) would again, according to our theory, have developed out of the skin; but, inasmuch as the character of the skin had changed, the type of eye would differ from that of the pineal eye. The same physiological principle would, however, come into play; the cells of the palisade layer would be irritated by the variation in the pressure of the pigmented matter travelling between them under the action of light, and these cells could become sensory cells by association with the nerve-endings now found among the cells of the rete mucosa. The new eye might thus from the first be, as indicated in Diagram II, an inverse eye, i. e. the nerve-fibres (*n*), passing outwards towards the surface, would have to bend back on themselves in order to become associated with the palisade-retinal cells.

The gradually thickening nerve-strands of this hypothetical epidermal eye may be assumed to have ultimately passed in a group through the palisade layer at the (? posterior) edge of the new specialised sensory area (see diagram). This ever-thickening and broadening nerve-strand appears to have carried through with it one or more loops of the vascular system of the cutis, together with strands of connective tissue.

The specialisation of a portion of the palisade layer to form the retina of a purely epidermal eye such as that figured in the diagram would, in course of time, prevent that portion from yielding any mucus or horn cells towards the exterior, more especially as the palisade cells of the retina must be supposed to have early specialised into cuticular rods. The deficiency caused by this more or less effective barrier to the free passage of pigment granules through the retina towards the surface would have to be made up somehow, not only to form a dioptric apparatus, but also for the protection of the retina. It was a long time before I could see how the palisade cells surrounding the retina could cover it over with a horny layer. The solution to the problem suggested in the diagram was arrived at by working backwards from the lens of the definitive eye (cf. Diagrams IV, III, II). The palisade cells round the periphery of the primitive retina appear to have lengthened greatly, and bent over the specialised area somewhat in the manner indicated. These long cells would therefore be merely a modification of the ordinary prickle-cells. By the detachment and death of their distal portions they would be able to yield a succession of horny cells, so as to maintain a continuous hard covering over the retina. This covering appears eventually to have formed a primitive surface lens, moved by fibrils from the intrusive connective tissue.

The next stage in the development of this hypothetical epidermal eye was probably an invagination of the whole of the modified portion of the skin, including the lengthened palisade or lens cells. This invagination is shown in Diagram III. Two factors may have helped to bring it about. 1. The retina becoming bulged inwards by the great accumulation of slimy fluid in the cavity of the eye, the tendency of the surrounding skin would be to constrict off the vesicle so formed. 2. The lens being attached by fibrils to the place of entrance of the optic nerve, and probably slightly moveable, would tend to be drawn in with the retina. Any way, if the eye started at all as we have suggested, we are justified in assuming an invagination such as that described, for that alone appears able to explain the arrangement of the tissues, among which I would call attention to the loops of the vascular system of the cutis, which, diagrammatically represented, assume the positions shown by faint dotted lines in Diagram III.[1] Further, the remains of the neck of such an invagination may still perhaps be seen in the fibrous ring which persists after the formation of the aqueous chamber as the ligamentum annulare (fishes) or ligamentum pectinatum (other Vertebrates), and which, it is important to notice, connects the iris (and not the lens) with the cornea (*lig. an.*, Diagram IV).

If we picture to ourselves the change of shape which the spoon-shaped retina shown in Diagram II would have to undergo in passing to the form shown in Diagram III, the origin of the choroidal fissure is at once apparent. As the

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[1] In this I am following the familiar diagrams of the blood-vessels of the Vertebrate eye to be found in text-books.

retina bulged further and further inwards, the nerve-strand connecting it with the brain shifted down towards the base of the cup. It is quite indifferent whether we speak of the nerve-strand cutting down the sides of the ever-deepening retinal cup, or of the sides of the cup growing up on each side of the nerve. The vascular and connective-tissue elements which accompanied the nerve (see Diagram II) would now protrude into the cavity of the eye. In the completely invaginated eye (shown in Diagram III) it is obvious that the choroidal fissure could originally only have extended from the edge of the long palisade or lens cells to the entrance of the optic nerve.

In Diagram IV I have indicated some of the adaptations which would be necessary to complete the Vertebrate eye. The lens had to be isolated, and its long cells rolled under it from all sides. We need not assume that the earliest isolated lens had its fibres arranged in the highly specialised manner characteristic of the higher Vertebrates; any folding of the long palisade cells under the more hardened central portion would be sufficient. The freedom of the lens and folding under of its long cells could, it seems to me, be brought about if the lens itself, under the action of contractile fibres intruding with the optic nerve into the cavity of the eye, was so far moveable that its axis deviated through small angles from the optic axis of the eye.

With regard to this method of accounting for the isolation of the lens, the following considerations are worth notice. The eye itself would have been immoveable through all the earliest stages of its evolution, but the Vertebrate eye is, as we know, a highly moveable structure. We are justified in concluding that its present powers of movement are but more perfect ways of attaining ends which, in its earliest stages, it must have striven to attain. It is not unlikely, therefore, that the connective-tissue strands which entered the eye in its earliest stages became attached to the edges of the primitive surface lens, and effected some simple movements. As the retina bulged inwards, these simple lens movements might be supplemented by slight movements of the whole eye,—these double movements probably playing some part in bringing about the invagination depicted in Diagram III, an invagination which, as above insisted upon, must have included the lens. Whether the eyeball formed by this invagination ever moved with any degree of freedom under the cornea may be doubted; the fibrous connection persisting in the ligamentum annulare was almost certainly strong, and may well have been rigid from the first. Certain it is that the movements of the eye as a whole, i. e. of the ocular invagination together with the skin above it (cornea), not only gave rise to the conjunctival folds by which the eye is suspended in the skin, but also rendered the directive adjustment of the lens by contractile fibrils unnecessary. As is well known, fibrils for the movement of the lens ("m. retractor lentis"—Beer) still persist in the eyes of the bony fishes, not only for the adjustment of focus, but also, according to Beer,[1] for slight changes in the direction of the line of vision. It is in keeping with these facts that the eyeball itself in the fishes is much less moveable, and in this respect also more primitive, than it is in the higher Vertebrates. We shall have presently to note other primitive features connected with the eyes in the bony fishes.

On the isolation of the lens and the consequent abstraction of a large portion of the palisade layer from the front of the ocular globe, we may assume that this layer was regenerated, as shown by dotted lines in Diagram IV.

The aqueous chamber developed as a space among the fibrous tissue forming the neck of the invagination: it would thus be morphologically a lymph space in the cutis. I have indicated the splitting apart of the fibres in this place in Diagram III. The aqueous chamber would thus from the first be quite distinct from the vitreous chamber, which was primarily a cleft in the epidermis (see below).

The iris could be developed by the thinning away of the fibrous substance above the lens, and its radial contraction away from the optic axis. This contraction may be supposed to have given rise originally to the ciliary processes, as shown

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[1] 'Pflüg. Arch.,' Bd. liii, 1894.

in the diagram. These are, however, now secondarily specialised.

It was an integral part of my theory, not only that the accumulation of pigment granules in the illuminated spots gave rise to the sensory visual areas in the epithelium by the irritation caused by their passage between the epithelial cells, but also that the excessive discharge of such granules supplied or helped to supply the refractive matter for a dioptric apparatus. This supposition entirely harmonises with this suggested deduction of the Vertebrate eye directly from the epidermis.

When a certain area began to form a retina, i. e. in the earlier stages of the condition shown in Diagram II, the excess of pigment would pass out between the sensory cells, and would supply so much matter to the epidermis cells outside the retina; here it would be clarified, as the pigment is typically clarified in the epidermis, and added to the thickness of the refractive layers. As the sensory cells multiplied, and were further cuticularised as rods, and the relation between them and the irritating chromatophores became more specialised, the way to the exterior would be barred, and the necessary material would have to be brought in from the circumference of the retina.

We have probably to look to the long cells depicted in the diagram for the bringing of the matter used in forming the harder refractive portions of the primitive lens. But, in addition, pigmented cells would almost certainly travel into the cavity of the eye along the connective-tissue strands which accompanied the nerve and blood-vessels. The rapid clarifying of this pigmented matter in the fluid contained in the space between the lens and the retina would give rise to a slimy mass, the rudiments of the vitreous body. The derivatives of this intrusive connective tissue would be found in the processus falciformis and pecten, which still convey pigment into those eyes that retain such structures. As the eye advanced in specialisation, and this important channel for conveying pigment into the eye to supply material for the vitreous humour was almost entirely lost (Diagram IV), compensation would be found in the great increase of the inner surface of the eye, the posterior half of which alone could function as retina; the other, anterior half, consists of the undifferentiated palisade epithelium, which allows the pigment to pass through as slime into the vitreous humour. It is also probable that some material for the same purpose finds its way along the optic nerve into the cavity of the eye.

This suggested origin of the vitreous humour, viz. that it is largely due to pigment granules passing into the eye cavity and dissolving into slime, is not only in accord with our homology of the retina with the epidermal palisade layer which gives rise to the mucus layer, but it is also supported by certain facts. In sections of the eyes of embryo chickens, dendriform exudations of slime, obviously forming the vitreous humour, are seen coming from the ciliary portion of the retina. The vitreous body is known to be easily detachable from all parts of the interior of the eye, except the ciliary region and the place of entrance of the optic nerve. The pigment granules are known to pass from the pigmented epithelium into the palisade layer in the iris, and the process can be seen beginning before the lens is reached. The actual microscopic appearances in fortunate sections are all in favour of their supplying slime for the vitreous humour. In my series of sections of the larva of Petromyzon planeri the retina is only in contact with the pigmented epithelium in the axis of the eye, only here are any rods and cones found; where the retina is not in contact with the pigmented epithelium, not only are no rods and cones developed, but the pigment does not accumulate in the choroid epithelium. It appears as if, there being no layer of rods and cones to hinder its advance, the pigment granules pass freely through, and form masses of semi-clarified granules within the space between the retina and epithelium. In the ciliary region of the retina, where the two layers—the retina (without rods) and the epithelium—come gradually into contact, all the appearances are as if the pigment granules are streaming through the retina into the vitreous humour. The eye is, however, so immature that this latter is not yet a clear slimy fluid, but a dense mass of fine granules, quite referable, as far as microscopic appearances go, to pigment granules only partially dissolved and clarified.[1]

This, in brief, is the way in which it is possible to conceive that the eye might have been developed directly from the skin, as our theory demands. That it actually has developed in this way is perhaps difficult to prove in face of the very different history suggested by its embryology; still, when the evidence is summed up, it appears to be of considerable weight.

I claim, for instance, that by this method of deriving the eye, the arrangement and character of all the more important tissues are fully accounted for.[2]

As examples I may draw attention to the following points:

1. The pigmented epithelium is not an ordinary epithelium, but rather a close layer of chromatophores, some of which are large ten-sided cells with two nuclei,[3] which latter feature is not infrequent in chromatophores.

2. The presence of the stellate chromatophores in the choroid would be a vestige of the dense chromatophoral layer that seems to have been very generally present in the cutis of many pre-mammalian Vertebrates.

3. The fibrous connection between the front surface of the iris and the cornea, specially pronounced as the ligamentum annulare of fishes, might well be the remains of the neck of the assumed invagination. It is attached to the iris and not to the lens, which is of significance for this method of deducing the eye from the skin.

4. The difference between the vitreous and aqueous humours

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[1] I propose to enlarge on this subject in an illustrated paper dealing specially with skins and pigments.

[2] I have omitted all mention of the sclerotic because I believe its development was concerned with that of the conjunctival folds, and of the specialised muscles for the movement of the eye, which latter did not come within the range of the inquiry.

[3] Boden and Sprawson, 'Quart. Journ. Micr. Sci.,' vol. xxxiii.

is also accounted for. A comparison of the diagrams shows at a glance that, while the latter is simply a lymph space (cf. Fuchs's diagram of the lymphatics of the eye[1]) arising within the connective tissue of the cutis, the former is an epidermal space, and is accordingly filled with slimy matter, presumably identical with that which gradually turns the cells of the rete mucosa into the horn cells.

5. The shape and curious arrangement of the cells forming the lens, the gradual loss of their nuclei, and their progressive transformation into hard refractive matter as the centre is reached are simply explained by regarding them as the prickle and horny cells which formed at one time a primitive surface-lens, subsequently engulfed in the invagination. That these fibres are closely comparable with epidermal prickle-cells can be demonstrated under the microscope;[2] they have all the known characters of such cells, in addition to their gradual decay and conversion into hard refractive matter. The pigmented granules of the iris on the one hand and the vitreous humour on the other could obviously supply them with abundance of slimy matter for this purpose.

6. I may be allowed again to allude to the arrangements of the blood-vascular loops as shown in the diagrams; to the ciliary process, which is accounted for as a simple mechanical result of the formation of the iris (cf. Diagrams III and IV); and to such structures as the pecten and processus falciformis, and the intra-bulbar blood-vessels still persisting in different eyes among the lower Vertebrates.

In addition to the weighty evidence afforded by these purely morphological arguments, it is worth noting that the recent discovery of Wolff,[3] fully confirmed by Müller,[4] as to the regeneration of the lens in Triton from the iris, is in the main in accord with Diagrams III and IV. The details as given by these authors are, however, very curious. The outer of

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[1] Reproduced in Morris's 'Treatise on Anatomy,' 1893, p. 889.

[2] Cf. the first note, p. 357.

[3] 'Archiv für Entwick. Mechan.,' i, 1895.

[4] Eric Müller, 'Arch. f. micr. Anat.,' p. 23, 1896.

the two inner pigmented layers of the iris, viz. that continuous with the pigmented epithelium, becomes the lens epithelium on the distal face of the lens, while the inner yields the long lens-cells. This naturally raises the question whether the lens epithelium may not be the homologue of the pigmented epithelium, the lens fibres alone representing the palisade layer. It may be that this regenerative process is strictly recapitulatory, and that this is the right explanation of the facts. On the other hand, the lens epithelium passes so gradually into the lens fibres round the equator of the lens, that it is difficult to believe that the whole structure is not the result of the folding of a single continuous epithelium. Again, the lens in the Vertebrate eye can hardly be such an entirely new structure, dating, as in the case of the lens of the pineal eye, simply from the time of the invagination, which this new suggestion would compel us to believe. It seems to me far more probable that it was an early modification of the external horny layers of the epidermis, which, as illustrated in the diagrams, became involved in an invagination. A comparative study of lenses, including those in degenerate eyes, might throw further light on this subject. The embryological development of the lens is, according to our view, so purely adaptive that it can hardly help us.

It is obvious, further, that this method of deducing the Vertebrate eye from the skin has the advantage that this organ need no longer be any exception to the rule which obtains in the animal kingdom, that organs of sense develop directly and continuously out of the skin. Lastly, we must not forget the significance of the fact that the change of type which can be seen to have taken place in the Vertebrate eyes is easily referable to the change which we know must have taken place in the character of the skin from the Invertebrate to the Vertebrate type.

Having, then, shown that it is possible physiologically and morphologically to deduce the Vertebrate eyes from the skin, the pineal eye from the skin in its Invertebrate condition, the definitive eye from the skin in its Vertebrate condition, we have to face the embryological histories of these eyes and the interpretations usually put upon them.

Taking the definitive eye first, it is found to arise ontogenetically by the union of two distinct structures. The "primary optic vesicle," as it is called, develops as an invagination of the brain towards the skin. This collapses into itself so as to form a cup or spoon, open towards the skin, and joined to the brain by a stalk or handle. The anterior wall, lining the hollow of the cup or spoon, becomes the retina and retinal palisade layer; the posterior wall, forming the outside wall of the cup or spoon, becomes the pigmented epithelium in contact with the palisade layer. Into this cup there dips down from the outer skin an invagination which becomes constricted off and forms the lens. The outer rim of the cup or spoon grows over the lens so as to form, with other elements, the iris.

The question we have to try to answer is, are these processes even approximately historical, or are they purely embryological adaptations in order to obtain a desired end by a series of short cuts? The answer must depend entirely upon the weight of the evidence. It must be remembered that we have no direct evidence whatever. Our sole guides are inferences to be drawn from known facts, and these we are only roused up to use when discussing some proposed clue to the right understanding of the said facts. In the present instance a theory of light sensations compels me to assume that the Vertebrate eyes have developed from the skin, and in the foregoing pages I have endeavoured to show that the known facts of structure and function are explicable on this assumption. The morphology and physiology of the eye, as the latter is interpreted by the theory, go throughout hand in hand. When we turn to the embryological development our connected story is thrown into confusion. Some of the details, it is true, are in most satisfactory agreement, as we shall presently see; but the most essential processes, viz. those just described, differ entirely from our scheme.

In the face of this serious difficulty, are we to withdraw or boldly to examine the embryological processes in order to ascertain (1) whether any plausible phylogenetic explanation can be given them? and (2) whether they cannot be more simply explained as adaptations? With regard to the former test, I confess at the outset that it seems to me almost waste of time to discuss the possibility of these complicated infoldings and fusions of separate parts indicating the history of such a singularly compact organ as the eye, especially if we are to assume, what we are justified in assuming, an unbroken continuity of function from the earliest rudiments to its most complicated development. We are, in the first place, precluded from believing that the functional eye developed continuously from the brain towards the skin which then formed a lens, as we should have no explanation of the bending back of the nerve-fibrils. In order to get over this difficulty it is suggested that the primary optic vesicle, i. e. the invagination from the brain, may represent a primitive eye of the type known as an "optic pit." It is true that, according to our interpretation of the facts, we have evidence in the pineal eye or eyes that such structures did at one time exist on the heads of the ancestors of the Vertebrata. If a pair of such eyes were caught and eventually folded in by the medullary groove, they might, it is thought, give rise to these "primary optic vesicles," with the retinæ in the right position to become the retinæ of the paired Vertebrate eyes. And, at first sight, there seems to be some possibility of deducing the Vertebrate eyes from a pair of engulfed, and therefore vestigial, and for the time being functionless eyes, which may have started into life once more by coming into contact on each side with some thickening, or perhaps glandular invagination, of the ectoderm. This latter, by condensing the light upon the pigment still present in these buried eyes, might once more set it in regular movements, which would record the variations in the intensity of the light. Some such hypothesis, it is claimed, would explain what is called the inversion of the eye, for the light would now shine through what was formerly the under side of the retina.

The closer, however, this suggestion is examined, the more unworkable it becomes. Whence, for instance, came the optic nerve of such an eye before it was engulfed in the medullary groove? If from some primitive ganglionic centre, how came it to be transferred to the definitive centre formed by the medullary groove? How did this optic nerve manage to coincide with the stalk of the invagination? Further, it is not easy to deduce in this way the specialised association of the chromatophoral layer with the retinal layer. The actual evidence against the primary optic vesicles having been mechanically forced in by the lens is very strong, quite apart from the difficulty of imagining why a lens-like body should crush in the optic vesicle, and, as if by a happy accident, create a highly organised eye. Why, again, was the pigment confined to the (originally) external hemispheres of these buried optic pits? Lastly, we do not know to what extent the medullary groove is historical. Nervous systems usually develop from thickenings of the ectoderm; and if a large amount of material is required, the thickening may easily become an invagination or a groove, and it is by no means necessary to suppose that such invagination has any phylogenetic signification at all; it may be purely an adaptive process for the supply of formative tissue. Indeed, in the Cyclostomata and bony fishes, which are very low down in the Vertebrate phylum, the central nerve-strand actually arises as a solid thickening. But, admitting for the present that the medullary groove may have some historical value, eyes are not very likely to let themselves be tucked in so as to be functionless, unless there is some obstacle to prevent them from shifting. According to our theory, the pigment will always be drawn in the direction of the strongest illumination, and on changes taking place in the form of the body the eyes will shift—through this attractive action of the light upon the pigment—into the positions in which they can best function as organs of sight.[1] This

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[1] Perhaps one of the most remarkable instances of the power of the eyes to follow light is that recorded by Carl Chun ('Biologisches Centralblatt,' xiii, 1893). Certain Crustaceans have luminous organs which throw light upon the ground beneath them. This light has actually drawn down a portion of

renders any theory of the infolding of a pair of functional eyes into the medullary groove, to my mind at least, highly improbable.

Indeed, I think it will be freely admitted that it is not easy to find any plausible interpretation of the embryological processes as recapitulatory of the actual evolution of the eye. We turn, therefore, to ask whether they can be better explained as adaptations?

At the outset it is obvious that the second assumption with which we started, that the pigmented epithelium must have been from the first in intimate and inseparable association with the retina, compels us to assume that the primary optic vesicle, in which the retinal half only secondarily comes in contact with the pigmented half, is simply a developmental adaptation.

Let us see whether the hypothetical history of the eye above sketched offers any interpretation of this optic vesicle. The great importance of the eye in the economy of the organism, leads to its development earlier and earlier in the embryo, each shift back admitting of shorter cuts for the attainment of the desired end. This may well have been the rule, even when the eye was at the simple stage shown in Diagram II, in which the retina was spoon- or ladle-shaped, with the nerve representing the handle. The most necessary requirement for the eye at this stage was undoubtedly the rapid formation of the specialised retina involving a great increase of nerve tissue, and its intimate association with the chromatophoral layer. Secondary infoldings of ectodermal tissue in order to supply by a short cut the great increase of sensory cells required in the formation of retinæ is a well-known phenomenon in the development of other eyes, which are more obvious modifications of the skin than are the Vertebrate eyes. I may mention the larger eyes of scorpions and spiders, the specialised retinæ of which develop embryologically as invaginations in a plane

the eye on each side, so as to look at the ground illuminated by the animals themselves. All stages occur; in some animals the eyes are only elongated downwards, in others a piece of each eye has become detached so as actually to form a separate pair of eyes.

more or less at right angles to the optic axis of the definitive eye, the two layers of the invagination becoming applied to form the more specialised elements of the organ. This is what we may assume to have been the first adaptive embryological process in the evolution of the Vertebrate eye. Its end was not to produce the definitive eye, but the hypothetical eye at the stage shown in Diagram II. Hence the primary optic vesicle may have originally been a simple ectodermal invagination apart from the central nerve system.

The earlier this retinal invagination is laid down, the more chance it would have of being involved in the medullary groove. Connection between them could be found, first of all, in the rudiments of the optic nerve, which would have been laid down as an ectodermal thickening joining the optic invagination with the central medullary invagination. A further shortening of the process might soon lead to the primary optic invagination developing as a lateral offshoot from the medullary groove.[1]

We are not altogether without evidence to support this interpretation of the origin of the primary optic vesicle, as an adaptation for the production of the eye when it was in a primitive condition,—such, for instance, as we have depicted in Diagram II. I have already called attention to what, according to the history of the eye here described, are certain very primitive features in the eyes of fishes. I refer to the accommodation of the eye by means of the m. retractor lentis (Beer), to the persisting power of moving the lens so as to vary the direction of sight, to the slight powers of movement of the eye itself as a whole, to the small development of the iris, and to the persistence of a prominent ring of tissue—the ligamentum annulare—further forward on the iris than is the homologous ligamentum pectinatum of higher Vertebrates, which represent, according to the foregoing, the neck of the ocular invagination (Diagram III). Now it is surely of some

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[1] The arrangement sometimes found, in which the optic vesicles only grow out after the groove has closed over, can be easily regarded as a secondary specialisation.

significance to find that, in these same animals, not only does the nervous system arise as a solid strand of ectoderm, but the eye and the optic nerve arise "quite high up on the side of the brain,"[1] and only sink down later into the ventral position (with respect to the medullary axis) typical of the higher Vertebrates. It seems to me that these facts belong to one another, and may be claimed as primitive features retained by these lowly Vertebrates.[2]

It is, I am aware, usual to regard this development of the medullary axis as a solid strand as secondary, but the arguments are not conclusive. For the reasons above given, I am inclined to believe that the solid medullary axis in these cyclostomes and bony fishes is a direct inheritance from their Invertebrate ancestors; and that, conversely, the widely open medullary groove is a secondary specialisation for the purpose of supplying a still larger quantity of material as the nervous axis of the Vertebrates became more and more pronounced.[3]

According, then, to our interpretation of the facts, the

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[1] Hoffmann, 'Arch. mik. Anat.,' xxiii, 1883, p. 45.

[2] Evidence of this secondary connection of the optic invagination with the brain has, further, been recently deduced from a study of the developing brain itself. Waters, from a study of the primitive segmentation of the brain ('Quart. Journ. Micr. Sci.,' vol. xxxiii, 1892, p. 457), arrives at the conclusion that the optic nerve was once serial with the other segmental nerves. The fact that the larger proportion of the nerve fibrils develop from the retina towards the brain [Assheton, 'Quart. Journ. Micr. Sci.,' 34 (1892), p. 85; Robinson, 'Journ. Anat. Phys.,' 30, 1896, p. 319] may perhaps represent the enormous secondary multiplication of the retinal sensory cells.

[3] The presence of a medullary plate in forms which appear to be still lower in organisation than the Cyclostomes is perhaps a difficulty, but the very diversity of their specialisations, Urochorda, Cephalochorda, Hemichorda (see Lankester's article "Vertebrata," 'Encyc. Brit.'), suggests that they have wandered off in different directions—all, however, towards degeneration—from some more typical Vertebrate form. The lowness of their organisation may perhaps be paralleled by that of the Copepods, which are apparently simpler than the form Apus, which has the best claim to rank as primitive among the Crustacea. I would suggest a similar explanation for both cases, viz. the fixation and subsequent specialisation of larval forms. I have suggested the same also to account for the Acarina, which in many respects are simpler than I believe the ancestral Arachnid could well have been.

"primary optic vesicle" reproduces the retina and specialised chromatophoral layer of the eye when it was at the stage shown in Diagram II. This would account for the fact that the lens, though it appeared, as I think, in the epidermal stage of the eye, does not appear ontogenetically with the primary optic vesicle, but has to develop separately.

Some confirmation of this view will be found if we compare the shape of the optic cup with the retina at the first hypothetical stage. The primary optic vesicle never apparently forms a true cup; it is far more spoon- or ladle-shaped, the sides gradually folding up over the handle or stalk. The stalk itself tends to fold, and where the sides of the spoon meet, just over the handle, the choroid fissure arises. This is an almost exact reproduction of the retina shown in Diagram II. As the primitive retina expanded, the optic nerve entering from the edge may have been wide and fan-like. As then the retina bulged deeper into the body, and its sides folded steeply up, the optic nerve would also fold with it near its junction with the spoon-shaped retina. This folding would be more marked if the point where the nerve joined the retina left the level of the skin and travelled inwards towards the base of the invagination. I claim, therefore, that we have here direct embryological evidence of the former existence of a ladle-shaped retina almost exactly corresponding with that sketched in Diagram II, i.e. without a lens in organic connection with it.

The ontogenetic development of the lens takes place, as is well known, by an invagination of the ectoderm; this obviously does not and cannot repeat the evolutionary process as depicted in the diagrams. It is, perhaps, probable that the embryological invagination which forms the lens may be some faint attempt to repeat the invagination shown in Diagram III. Any way this method of lens formation would clearly have to be adaptive if the account above given of the origin of the "primary optic vesicle" is approximately correct. As far as I can remember, nothing similar to this suggested complication has been recorded, although if we knew enough we should probably find it to have been very common. We have the slow and uniform development of an organ, viz. the eye, through the lapse of time. Its ontogenetic development cannot possibly repeat the evolutionary process, because, when the eye was in the earliest stages, the embryo early acquired the habit of producing the organ in that primitive stage by a short cut. This short cut the embryo has never given up, and it has thus lost all chance of being able to repeat the subsequent evolutionary processes. The development, therefore, of all these later specialisations must necessarily be almost purely adaptive.

With regard to the pineal eye, somewhat the same explanation of its ontogeny is suggested. The rudimentary optic invaginations, situated close to the median line, early became involved in the developing medullary axis. They were, however, not adaptive structures, but the actual optic pits. Again, in this case also, the connection between the developing optic pit and the medullary axis or groove would be found in the optic nerve. The most serious objection to this suggestion is probably to be found in the fact that the epiphysis seems to appear later than the first rudiments of the Vertebrate eyes, whereas it ought, perhaps, to appear earlier. As a matter of fact, very little reliance can be laid upon the order of appearance. The functional eyes, whether pineal or definitive, seem to be hurried on the scene almost before anything else. As soon as the pineal eye became functionless or of less importance than the definitive eyes, there would be no hurry in its development, and the definitive eyes might appear first, although historically much later developments than the pineal eyes.

It may be objected that there is not the same difficulty in supposing the pineal eye to have developed from the brain, it being but a single vesicle with a simple nerve-stalk, so that its ontogeny might repeat its historical evolution. Spencer, who assumes the embryology of the eye to be in the main recapitulatory, compares the epiphysis with the tunicate eye, but does not believe that it began as an eye. In order to get over the difficulties in the way of deducing the pineal eye structurally from the tunicate eye, the possibility of which had been assumed by Lankester, he suggests that the same structure which, at an early stage of its development, formed the tunicate eye developed into the pineal eye only after it had grown out into a long stalked vesicle. The inherent objections to this supposition seem to me to be as great as those which it was intended to avoid. On the other hand, however, the facts appear to me to be all in favour of the account given above, the parallel between the retina with the retinal pigment and the palisade layer with its subjacent accumulation of pigment cells, between the connective-tissue capsule of the eye, with its chromatophores and other wandering cells, and the cutis—the fact that the eye is still embedded in the thickened cutis in many forms, and that the skin above the eye is frequently found transparent,—all seem to indicate the skin, and not the brain, as the real mother-tissue of the eye.

Given, then, the possibility of explaining the embryology of the pineal eye as adaptive, there seems to me to be no valid reason why we should not accept the teachings of comparative morphology, and recognise the pineal eye as a relic of the simpler type of skin of our Invertebrate ancestors.

The suggestion that the pineal eye arose out of detached portions of the paired primary optic vesicles, I think, defies all attempts to work out in detail. Beard's explanatory diagrams, it seems to me, cease to be manageable if, instead of single layers of epithelial cells, we try to marshal functional eyes in the same way.

In the foregoing pages I have endeavoured to show how the Vertebrate eyes admit of being deduced directly from the skin, as my theory of the origin of sight requires. My object has been not only to remove a possible objection to the theory arising from the embryological development of these eyes, but also to show how they might be made even to bear testimony in its favour. It must be borne in mind that the arguments here adopted are not so strong as they might be. They would have

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[1] Beard, "The Parietal Eye of Cyclostomes," 'Quart. Journ. Micros. Sci.,' vol. xxix, pl. vi, figs. A, B, C.

been greatly strengthened if it had been possible to incorporate some of the more direct evidence in favour of the theory from which they start. This evidence is, however, cumulative; and in endeavouring, first, to show that the chief types of eye are both morphologically and physiologically explicable by this theory, I merely begin with that portion of the evidence which came readiest to hand.

In selecting eyes for analysis in subsequent contributions to this subject I shall not follow any systematic order; my primary object not being any comparative study of eyes, but merely the detailed working out of the observations which I have made, which seem to me to afford evidence of the truth of my theory of the origin of light sensations.

EXPLANATION OF PLATE 22,

Illustrating Mr. H. M. Bernard's paper, "An Attempt to deduce the Vertebrate Eyes from the Skin."

Fig. 1.—Diagrammatic representation of a pineal eye regarded as an invagination of a simple palisade epithelium. The pigmented contents of the chromatophores of the cutis find their way in the skin to the surface, where they form a layer of slime (yellow), and in the eye into the cavity of the invagination, where they form a slimy vitreous humour.

Fig. 2.—Hypothetical early stage in the evolution of the Vertebrate eye proper. Externally the palisade layer of the skin has budded off layers of cells, which as "prickle-cells" absorb the pigment and other matter passing through the palisade cells, and, dying, become horny scales. The nerves of the skin (*n.*) no longer end in the palisade layer, but among the prickle-cells. Hence, when the palisade cells become retinal cells stimulated by the passage of the pigmented granules, the nerves have to bend back. The retinal palisade cells early become cuticularised, apparently in order to oppose more effectively the outward streaming of the pigmented granules. The nerves are already grouped into a solid strand, and form a kind of handle to the spoon-shaped retina which is being bulged in by the accumulation of slimy matter in the epidermal cleft which has arisen above the retina. Into the

cavity thus formed, blood-vessels and connective tissue conveying chromatophores intrude, and help to supply the matter for the vitreous humour. The horny covering of the retina is supplied by specially long "prickle-cells," which form a kind of surface lens.

Fig. 3.—Hypothetical stage following that shown in Fig. 2, the retina having bulged still further into the body, and the optic nerve (*o. n.*) having sunk more towards the base of the invagination, the whole eye, including the surface lens, has been invaginated below the skin. In the stalk of the invagination, composed of cutis, lymph-spaces commence to appear in the optic axis of the eye. The intruding blood-vessels and connective tissue are shown entering the cavity of the eye with the optic nerve, and radiating strands towards the lens for the movements of the same are diagrammatically indicated.

Fig. 4.—Shows the changes which would be required to complete the sensory and dioptric apparatus of the Vertebrate eye. The lymph-spaces are specialised into the aqueous chamber; the stalk of invagination persists as the ligamentum annulare (or pectinatum). The radial contraction of the tissue to form the iris gave rise to a fold—the rudiment of the ciliary processes. The lens has become isolated by the rolling round (as indicated by arrows) of the palisade layer of the distal portion of the eye. The portion of the palisade epithelium thus given up to the lens is represented as having been regenerated (dotted lines).

The Reproduction and Metamorphosis of the Common Eel (Anguilla vulgaris).[1]

By

G. B. Grassi,
Professor in Rome.

Four years of continual researches made by me in collaboration with my pupil, Dr. Calandruccio, have been crowned at last by a success beyond my expectations,—that is to say, have enabled me to dispel in the most important points the great mystery which has hitherto surrounded the reproduction and the development of the Common Eel (Anguilla vulgaris). When I reflect that this mystery has occupied the attention of naturalists since the days of Aristotle, it seems to me that a short extract of my work is perhaps not unworthy to be presented to the Royal Society of London, leaving aside, however, for the present, the morphological part of my results.

The most salient fact discovered by me is that a fish, which hitherto was known as Leptocephalus brevirostris, is the larva of the Anguilla vulgaris.

Before giving the proofs of this conclusion I must premise that the other Muræenoids undergo a similar metamorphosis. Thus I have been able to prove that the Leptocephalus stenops (Bellotti), for the greatest part, and also the Leptocephalus morrisii and punctatus belong to the cycle of evolution of Conger vulgaris; that the Leptocephalus haeckeli, yarrelli, bibroni, gegenbauri, köllikeri, and many other imperfectly described by Facciola, and a part of the above-named Leptocephalus stenops of Bellotti, belong to the cycle of evolution of Congromuræna mystax; that the Leptocephalus tænia, inornatus, and dia-

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[1] From the 'Proceedings of the Royal Society,' November, 1896.

phanus belong to that of Congromuræna balearica; that under the name of Leptocephalus kefersteini are confounded the larvæ of various species of the genus Ophichthys; that the Leptocephalus longirostris and the Hyoprorus messanensis are the larvæ of Nettastoma melanurum, and that the Leptocephalus oxyrhynchus and other new forms are larvæ of Saurenchelys cancrivora, and that finally a new little Leptocephalus is the larva of Muræna helena.

The form known as Tylurus belongs to Oxystoma, of which we unfortunately know nothing more than a figure by Raffinesque. I have not been able to find the Leptocephalus of Myrus vulgaris, of which I have had only a single individual, in which the transformation was already far advanced. Neither have I found the Leptocephalus of Chlopsis bicolor, a very rare form, which is related to Muræna and to Murænichthys. As the result of these observations, the family of the Leptocephalidæ has been definitely suppressed by me; the various forms of that family are, in fact, the normal larvæ of the various Murænoids.

In regard to the greater part of the above-named species, the control has been threefold, namely:

Firstly, anatomical. I have compared the various stages in all their structures, and have made the due allowance for the changes brought about by the metamorphosis at the close of larval life.

Secondly, natural. I have found in nature all the required transitional stages.

Thirdly, experimental. I have followed, step by step, the metamorphosis in aquariums.

Therefore the hypothesis of Günther that the Leptocephali are abnormal larvæ, incapable of further development, must be rejected. All this is related by myself at length, with all historical details which concern the question, in a large memoir which is about to appear in the journal edited by Professor Todaro.

Until now all these facts have been unknown, because normally they can only be observed in the abysses of the sea at a depth of at least 500 metres. Fortunately, along a part of the coast of Sicily strong currents occur, which must be ascribed to the tide, producing very large displacements of the water in the narrow Strait of Messina. I shall give further details concerning these currents in my large memoir. In consequence of the strong currents sometimes—I say sometimes because there is no regularity, and one may have to wait for a year without obtaining any material—not only many deep-sea fishes, but also all stages of the development of the Murænoids are met with in the surface-water. To these currents we owe all the captures of Muræna helena with ripe eggs, which is in accordance with what I had already argued from other facts, namely, that the reproduction of the Murænoids takes place at great depths of the sea.

Before I proceed to speak of the common eel, I must premise that Dr. Raffaele has described certain pelagic eggs as belonging to an undetermined species, putting forward the suggestion that these eggs belong to some Murænoid. This matter has been investigated by myself, and I have shown that the newly hatched larvæ (called "præ-larvæ" by me) derived from these eggs have essentially the character of Leptocephali.

The life history of the Murænoids, leaving aside for the present the common eel, is as follows:—Females can only mature in very profound depths of the sea, that is to say, at least a depth of 500 metres. This fact I established by finding well-known deep-sea fishes together with Leptocephali, ripe Murænæ, and quite ripe eels (see below). The females of those species which do not live at this depth must therefore migrate to it. The male, however, can mature at a smaller depth, and therefore they migrate into the greater depth when they are already mature. Fertilisation takes place at great depths: the eggs float in the water; nevertheless they remain at a great depth in the sea, and only exceptionally, for unknown reasons, some of them mount to the surface.

From the egg issues rapidly a præ-larva, which becomes a larva (Leptocephalus) with the anus and the urinary opening near the tip of the tail. The larva then becomes a hemi-larva, the two apertures just named moving their position towards the anterior part of the body, which becomes thickened and nearly round. By further change the hemi-larva assumes the definitive or adult form. The larva, as well as the hemi-larva, shows a length of body much greater than that exhibited by the young Murænoid of adult form into which they are transformed. By keeping specimens in an aquarium I was able to establish a diminution of more than 4 cm. during the metamorphosis. With regard to the greatest length which the larva can attain in a given species, and the amount of diminution which accompanies metamorphosis, there are great individual variations.

The history of the common eel, to which I am now about to refer, is very similar to that given above for the other Murænoids. The common eel (Anguilla vulgaris) undergoes a metamorphosis, and before it assumes the definitive adult form it presents itself as a Leptocephalus, which is known as Leptocephalus brevirostris. This Leptocephalus was discovered in the Straits of Messina many years ago. A specimen was also captured by the "Challenger," and another specimen was taken by the Zoological Station of Naples in the Straits of Messina. This form is occasionally carried to the surface by currents. By exception, in the month of March, in the year 1895, we captured several thousands of them in one day; but the best way to secure this Leptocephalus (and a very easy one) is to open the intestine of the Orthagoriscus mola, a fish which is common in the Straits of Messina, and in it one is certain to find a very large number of specimens. It must be observed that Orthagoriscus mola is a deep-sea fish. The specimens of Leptocephalus brevirostris found in the intestine of Orthagoriscus are more or less altered by digestion. Those specimens of Leptocephalus brevirostris which are taken near the surface in the open sea are in a better state of preservation, but, unfortunately, these also frequently have the epidermis injured so that they cannot maintain their life in an aquarium for more than a few days; they live long enough, however, to allow us to observe that it is their habit to conceal themselves in the sand or in the mud as the common eel (Anguilla) does. Here it is to be noted that the various forms of Leptocephali have habits resembling those of the Muræenoids to which they belong, i.e. they dig into the sand or abstain from doing so according as the adult form has or has not this habit.

I now pass on to the characters of Leptocephalus brevirostris. I give them here in the same order as I shall use in my larger memoir. The length varies from 77 to 60 mm., the same extent of variation as observed in other Muræenoids. The caudal fin tends to assume the form which it has in the Elver[1] or young Anguilla. It is to be noted that in other Leptocephali the caudal fin also tends always to exhibit the adult form. The lower jaw projects sometimes more than the upper jaw, as in Anguilla. The margin of the mouth is wide, as in Anguilla. The tongue is free, as in Anguilla. On the other hand, the youngest elvers which I have observed have smaller eyes than Leptocephalus brevirostris, and this need not surprise us, since we know that in other species of Muræenoids the diminution of the eyes occurs during the metamorphosis. The nostrils are separated from one another, the anterior tubes are relatively at a considerable distance from the tip of the snout and from the rim of the mouth. They are in a position in which they are observed in many other Leptocephali, which are destined to transform themselves into adult forms having the anterior nostrils in nearly the same position as in the common eel. The posterior nostrils, on the contrary, are not tube-like, and are in the same position as those occupied in the adult Anguilla. It is worth remarking that in other Leptocephali also the posterior nostrils have already assumed the adult position when the anterior ones are still far removed from it. In L. brevirostris I find a larval dentition which resembles that of the other Leptoce-

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[1] The word "Elver" is used in this paper in its strict sense, viz. for the young form of Anguilla vulgaris as taken when ascending rivers in vast numbers.

phali. In correspondence with the small size of Leptocephalus brevirostris the number of larval teeth is small. Researches founded, firstly, on the enumeration of the myomeres; secondly, upon the enumeration of the dorsal and ventral arches of the vertebræ of the caudal extremity (hypurals); and thirdly, upon the enumeration of the posterior spinal ganglia, lead with great certainty to the conclusion that the Leptocephalus brevirostris is the larva of a Murænoid, the number of whose vertebræ must lie between 112 and 117, most probably 114 or 115. Such a Murænoid is the Anguilla vulgaris. The Murænoid indicated cannot be any other of those occurring in the Mediterranean, because they all have a number of vertebræ higher than 124.[1] Counting the myomeres in Leptocephalus brevirostris, one finds generally only 105 complete, five others incomplete, and all the others in a state of transparency and incomplete formation. These latter are fortunately at the posterior extremity, where other criteria come to our assistance, namely, the spinal ganglia and the vertebral arches. To show how I arrive at the number of vertebræ which must be possessed by the adult Individual, corresponding to a given Leptocephalus brevirostris, I quote the following example:—I assume that three vertebræ develop themselves in correspondence to the first four incomplete myomeres, and that 105 must develop themselves in relation to the 105 complete myomeres,—that is to say, between the fourth and fifth myomeres, between the fifth and sixth, and so on until we reach the 105th vertebra lying between the 104th and 105th myomeres. I further conclude that seven other vertebræ are developed at the caudal extremity, as indicated by the number of vertebral arches and the spinal ganglia in that region. We count, therefore, in all 115 vertebræ, and this is the number which can be easily seen in many specimens of Anguilla vulgaris.

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[1] Murænesox savanna is said to have 109 vertebræ, but it is doubtful whether it really occurs in the Mediterranean. The position of its nostrils and the number of its branchiostegal rays render its association with Leptocephalus brevirostris impossible.

Here I must particularly insist that I have ascertained in an absolute manner that during the metamorphosis of the Muræenoids the number neither of the myomeres, nor of the vertebral arches, nor of the spinal ganglia is subjected to any change. The hypurals of Leptocephalus brevirostris are precisely the same as in the elver of Anguilla vulgaris. The last hypural which is fused with the urostyle may present itself as a single piece, or may be more or less cleft. These are variations which are met with also in the elver. Just as in the elver, the last hypural but one is always extensively cleft, or, if the expression is preferred, doubled. To the last hypural correspond five rays, whilst four correspond to the last but one, and one to the last but two, the whole structure being identical with that found in the elvers of Anguilla vulgaris. Of these ten rays, the eighth, seventh, and sixth are bifid, both in Leptocephalus brevirostris and in the elvers of Anguilla vulgaris. In the pectoral fin of Leptocephalus brevirostris the definitive rays can be observed, and these are of the same number as in the elvers of Anguilla vulgaris. Leptocephalus brevirostris is transparent, and has colourless blood. The red corpuscles are wanting, but there are present so-called "blood-plates" ("Blutplättchen" in German) similar to those of the inferior Vertebrates. The bile is also colourless. This fact is observed in all the other Leptocephali. Leptocephalus brevirostris is, however, the only one which is free from all pigmentation. Correspondingly, the common eel is the only species of Muræenoid which at the close of metamorphosis (i.e. in the youngest elvers) is devoid of all trace of larval pigmentation. It was this observation which first led us to the discovery of the relations between Leptocephalus brevirostris and Anguilla vulgaris.

In making transverse sections of Leptocephalus brevirostris I found other characters which confirm the relation between it and the common eel; for instance, the branchiostegal rays are ten to eleven in number, as is also observed in the elvers of Anguilla vulgaris. In the common eel the well-known lateral branch of the fifth pair of the cranial nerves exists. It is also found in Leptocephalus brevirostris. This lateral branch could not be found by Dr. Calandruccio in the other common Muræenoids of Sicily, and is wanting also in the other Leptocephali.

The mucous canal-system (sensory canals) in the head are already developed, partially in Leptocephalus brevirostris, and are incompletely developed in the elver. As in the elver, so in Leptocephalus brevirostris, the pyloric cæca are wanting. The blind extremity of the stomach and the incompletely developed swim-bladder, which is as yet free from contained gas, are present both in Leptocephalus brevirostris and in the elver of Anguilla vulgaris. The pronephros is in active function, as in the other Leptocephali. The Malpighian glomerules of the kidney (mesonephros) are lobed as in the eel, and their number corresponds with that observed in the Helmichthys stage, of which I will speak further on. The genital gland, not yet sexually differentiated, is almost identical with that of the same stage. In short, it may be said that the whole organisation of Leptocephalus brevirostris corresponds with the organisation of the common eel, if we make allowance for those changes which are observed in the metamorphosis of the other species of Muræenoids, such as reduction of the pancreas and of the liver, disappearance of the protoskeleton, complication of the musculature, increase in size of the cerebellum, loss of the larval teeth, development of the definitive teeth, &c.

From the description of these Leptocephali I must pass on briefly to speak of the stages nearer to the condition of the elver. I am, however, obliged to leave a break in the series, which, however little its significance, yet certainly will make some impression on the minds of those who do not realise with what caution I have formed my conclusions. I must confess that since I have learnt how difficult it is to procure an entire series of the development of a Muræenoid, I am more astonished at being able to recognise a single stage in the development of a given species than at not finding the whole series. I must point out that the break in my series of the development of Anguilla vulgaris would have been much smaller if I could have persuaded myself to kill and preserve one of the hemilarvæ which I happened to meet with at the end of the year 1892. They were really transitional stages between Leptocephalus brevirostris and that stage which I shall describe further on. I published this fact in a preliminary note in the month of May, 1893. They were transparent with almost colourless blood, without any trace of pigmentation except at the eyes, and had lost all the larval teeth, whilst they possessed already very few and very minute teeth of the definitive series.

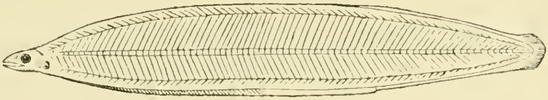

Fig. 1.

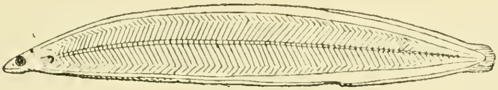

Fig. 2.

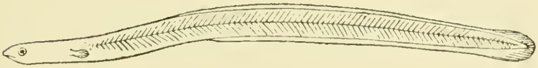

Fig. 3.

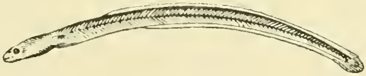

Fig. 4.

Fig. 1.—Leptocephalus brevirostris. Natural size.
Fig. 2.—Leptocephalus brevirostris. Later stage. Natural size.
Fig. 3.—Anguilla vulgaris. Transition stage. Natural size.
Fig. 4.—Anguilla vulgaris. Definitive habit (Elver). Natural size.

The body was thickened, and already showed the cylindrical form. They measured little less than 8 cm. In short, they were Leptocephalus brevirostris on the way to transformation into Anguilla vulgaris. As a matter of history they actually did transform themselves in my aquarium with the usual diminution in their dimensions, and subsequently proceeded to increase in bulk.[1] The metamorphosis took place, as usual, without the animal taking in any nourishment whatever. The resumption of growth was accompanied by a resumption of feeding. Unfortunately I had no other individuals of this stage.

The stage which I now pass on to describe (fig. 3) can be obtained during the winter in the sea. I have never found them at the mouths of rivers. The length varies from 54 to 73 mm. Most individuals measured about 65 mm. The body is relatively longer than in the elver. It is also relatively deeper, as in Leptocephalus. We are reminded of Leptocephalus also by the pigment of the eye, the vitreous transparency of the body, the swim-bladder being indistinguishable in the living animal, and the absence of all larval pigmentation. The blood is slightly coloured, and the bile is already green. Slight pigmentation can be seen along the central nervous system, and at the middle part of the caudal fin. This commencement of the definitive or adult pigmentation in the regions named before it occurs in any other part is also seen in other Muræenoids. The definitive teeth are very minute, and few in number. The intestine contains no food. After what I had observed in the other Muræenoids, the simple observation of the barely indicated teeth, and of the absence of aliment in the gut, would have been sufficient to convince me that the stage now under notice must be preceded by a Leptocephalus phase. Indeed, if we did not admit such a preceding history, we could not understand how this little fish could have attained such a size with-

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[1] The fact that I actually have obtained in an aquarium the transformation of L. brevirostris into Anguilla vulgaris is of prime importance. The time occupied was one month.

out acquiring well-developed teeth, and without nourishing itself.

In conclusion, no one would hesitate, even not knowing Leptocephalus brevirostris, to refer the stage now under discussion to a Muræenoid about to complete its Leptocephalus metamorphosis, were it not for the fact that there has been so much question concerning the reproduction of the common eel, and that so many capable observers have failed in dealing with it, that every new observation is received with scepticism. The stage of which I am now speaking, in the hands of a pure systematist, would probably be described as a Helmichthys, a genus established for certain forms of Leptocephali far advanced in transformation.

The next forms to which I have to refer are captured in the course of migration from the sea into fresh water. When kept in an aquarium they assume the characters of the elver, diminishing more or less in volume, and without nourishing themselves. The elvers of the common eel can present themselves in stages differing little from that last described, as well as in a form which has already developed the full pigmentation of the adult. Even those which most resemble the preceding stage always have a character which distinguishes them easily, namely, the presence of a definitive pigment, more or less superficially placed on the head, and not to be confounded with the pigment round the posterior extremity of the brain, which latter is already present in the preceding stage. In specimens taken at the mouths of rivers this more or less superficial pigment was, so far as I could ascertain, always present.

As the pigmentation develops itself, the little eel gradually undergoes a diminution in all its dimensions. It results from my measurements, that the fully pigmented elver has an average length of 61 mm., while for the more or less colourless elver the average length is 67 mm. I found pigmented elvers which were reduced in length to 51 mm., a size which I never observed in those elvers in which the development of pigment had not taken place.

The facts which I have stated demonstrate that the eel goes through a metamorphosis, and that Leptocephalus brevirostris is its larva. Some further considerations remain to be given, although I believe that zoologists will not consider the question still an open one after the record of facts given above—facts which any one may verify by examining the material which is preserved in my hands. Many to whom I have related my discovery of the history of the common eel have objected that eels are found almost everywhere, whilst Leptocephalus brevirostris is limited to Messina. In reply, I must say that, first of all, it is not true that Leptocephalus brevirostris is limited to Messina; secondly, that at Messina there are special currents, which tear up the deep-sea bottom which everywhere else is inaccessible; thirdly, although it is true that on the coasts of many countries where Anguilla vulgaris is found, no one has ever seen a Leptocephalus brevirostris; it is also true that in no country, not even in those where eels are abundant, has anyone ever seen an eel of less than 5 cm. in length. Since it has to be admitted that no one knows the eel before it arrives at the length of 5 cm., there is no greater difficulty in supposing that during this unknown period the eel passes through a Leptocephalus stage than in supposing that it does not do so. The critical study of the literature of this subject, and a great many continued observations, have occupied me for many years, and have been undertaken just in those places where young eels are to be found. They enable me, from my own studies, to affirm with assurance that young eels with the definitive adult form do not exist of less than 5 cm. in length.

From the study of the memoir of Raffaele on pelagic eggs, I have come to the conclusion that the eggs of his undetermined species No. 10, having a diameter of 2·7 mm., and differing from all the others in the absence of oil-globules,[1] must belong to the Anguilla vulgaris, because from them Dr. Raffaele

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[1] Renewed researches have convinced me that this egg is that of Anguilla vulgaris. There is, however, another egg belonging to an undetermined Murænoid which is devoid of oil-drops, and can easily be confused with the true eggs of Anguilla.

obtained præ-larvæ which had only forty-four abdominal myomeres. I endeavoured for two years in vain to study these eggs at the Zoological Station of Naples. I found only a few of them, and these died prematurely.

In another point my researches have yielded a very interesting result. As a result of the observations of Petersen, we know now that the common eel develops a bridal coloration or "mating habit," which is chiefly characterised by the silver pigment without trace of yellow, and by the more or less black colour of the pectoral fin, and finally by the large eyes. Petersen inferred that this was the bridal coloration from the circumstance that the individuals exhibiting it had the genital organs largely developed, had ceased to take nourishment, and were migrating to the sea. Here Petersen's observations cease and mine begin. The same currents at Messina which bring us the Leptocephali bring us also many specimens of the common eel, all of which exhibit the silver coloration. Not a few of them present the characters described by Petersen in an exaggerated condition,—that is to say, the eyes are larger and nearly round instead of elliptical, whilst the pectoral fins are of an intense black. It is worth noting that in a certain number of them the anterior margin of the gill-slit is intensely black, a character which I have never observed in eels which had not yet migrated to the sea, and which is wanting in the figures and in the originals sent to me by Petersen himself. Undoubtedly the most important of these changes is that of the increase of the diameter of the eye, because it finds its physiological explanation in the circumstance that the eel matures in the depths of the sea. That, as a matter of fact, eels dredged from the bottom of the sea have larger eyes than one ever finds in fresh-water eels I have proved by many comparative measurements, made between eels dredged from the sea bottom and others which had not yet passed into the deep waters of the sea. Thus, for instance, in a male eel taken from the Messina currents, and having a total length of 34½ cm., the eye had a diameter, both vertical and transversal, of 9 mm. and in another eel of 33½ cm. the same measurement was recorded. In a female eel, derived from the same source and purchased in the market, whose length was 48½ cm., the vertical diameter of the eye was 10 mm., and the transversal diameter rather more than 10 mm. These are not the greatest dimensions which I observed, and I conclude from these facts that the bridal habit described by Petersen was not quite completed in his specimens, and that it becomes so only in the sea and at a great depth. In relation to these observations of mine stands the fact that the genital organs in the eel taken in the Messina currents are sometimes more developed than in eels which have not yet entered the deep water. Thus it has happened that male individuals have occurred showing in the testes here and there knots of spermatozoa. These spermatozoa are similar to those of the Conger vulgaris, and must be considered as ripe. As is well known, so advanced a stage of sexual maturity has never before been observed in the common eel. This appears to be due to the fact that the males hitherto examined had not yet migrated into the deep water of the sea.

Eels with big eyes taken from the depths of the sea were, before the above facts were known, described as a distinct species under the name of Anguilla bibroni (Kaup) and of Anguilla kieneri (Kaup), not to be confounded with Anguilla kieneri (Günther), which is a synonym of Lycodes kieneri.

In certain cloacæ of ancient Rome which to-day are disused and contain pure water, remarkable eels are found of a length of from 20 to 30 cm., of a grey colour, without trace of yellow, of male and female sex, with enormous eyes, and with more or less rudimentary genital organs. They are individuals which, confined in a place without light, have acquired prematurely one of the characters of the bridal habit without a corresponding development of the genital organs. These individuals are probably incapable of ulterior development, as the condition of their genital organs seems to demonstrate.

Under the name Anguilla kieneri (Kaup) there have probably been included some individuals which had acquired big eyes under conditions similar to those described for the eels of these Roman cloacæ. From these and similar observations it clearly results that all the European eels must be included under a single species; and this is an important fact from another point of view, namely, that it destroys an objection which might be raised against my conclusion with regard to the development of Anguilla vulgaris from Leptocephalus brevirostris, namely, the objection that Leptocephalus brevirostris belongs not to Anguilla vulgaris, but to Anguilla kieneri, or to Anguilla bibroni.

To sum up, Anguilla vulgaris, the common eel, matures in the depths of the sea, where it acquires larger eyes than are ever observed in individuals which have not yet migrated to deep water, with the exception of the eels of the Roman cloacæ. The abysses of the sea are the spawning-places of the common eel: its eggs float in the sea water. In developing from the egg it undergoes a metamorphosis, that is to say, passes through a larval form denominated Leptocephalus brevirostris. What length of time this development requires is very difficult to establish. So far we have only the following data:—First, Anguilla vulgaris migrates to the sea from the month of October to the month of January; second, the currents, such as those of Messina, throw up, from the abysses of the sea, specimens which, from the commencement of November to the end of July, are observed to be more advanced in development than at other times, but not yet arrived at total maturity; third, eggs, which according to every probability belong to the common eel, are found in the sea from the month of August to that of January inclusive; fourth, the Leptocephalus brevirostris abounds from February to September. As to the other months, we are in some uncertainty, because during them our only natural fisherman, the Orthagoriscus mola, appears very rarely; fifth, I am inclined to believe that the elvers ascending our rivers are already one year of age, and I have observed that in an aquarium specimens of L. brevirostris can transform themselves into young elvers in one month's time.

Changes in the Cell-organs of Drosera rotundifolia, produced by Feeding with Egg-albumen.

By

Lily Huie,
Physiological Laboratory, Oxford.

With Plates 23 and 24.

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INTRODUCTION.

THE subject of this research was suggested to me by Dr. Gustav Mann, with the view of throwing some further light upon the functions of the nucleus and nucleolus, and to test whether his views were correct,—namely, that the chromatin segments are organs for the elaboration of food; that the nuclear chromatin is not the essential element, inasmuch as it only represents partly elaborated material; that the nucleolus is a storehouse for some elaborated matter, &c.[1] By

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[1] Gustav Mann, "The Functions, Staining Reactions, and Structure of Nuclei," 'Proc. British Association,' Section D, 1892, Edinburgh meeting.

the kindness of Professor Gotch I have been permitted to work in the Histological Department of the Physiological Laboratory at Oxford, under the guidance of Dr. Mann.

Literature.

Numerous as have been the papers published on the Droseraceæ since Charles Darwin's classical treatise upon 'Insectivorous Plants,' comparatively few have dealt with cytological changes induced by functional activity of the glands; and these few have been mainly devoted to the observation and elucidation of the "Phenomenon of Aggregation of Protoplasm," a term applied by Darwin[1] to the following phenomena:

"If a tentacle is examined some hours after the gland has been excited, ... the cells instead of being filled with homogeneous purple fluid, now contain variously shaped masses of purple matter, suspended in a colourless or almost colourless fluid. The little masses of aggregated matter are of the most diversified shapes, often spherical or oval, sometimes much elongated, &c. . . . These little masses incessantly change their forms and positions, being never at rest. A single mass will often separate into two, which afterwards reunite. Their movements are rather slow, and resemble those of amœbæ or of the white corpuscles of the blood. We may, therefore, conclude that they consist of protoplasm."

Cohn, in his review of 'Insectivorous Plants,'[2] threw doubts upon Darwin's inference that the aggregated masses consisted of protoplasm, and called them "Zusammenballungen" of the red-cell sap.

Francis Darwin,[3] who studied the phenomenon in the cells of the stalks of the tentacles, reasserted the view of his father

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[1] 'Insectivorous Plants,' London, 1875, p. 39.

[2] 'Deutsche Rundschau,' 1876.

[3] Darwin, F., "On the Process of Aggregation in the Tentacles of Drosera rotundifolia," 'Quart. Journ. Micr. Sci.'

that the aggregated masses were "protoplasm." He states the two opposing theories thus:

I. "My father's view, that the aggregated masses consist of protoplasm, and that their movements are simply due to their own contractility, excited by various external agencies."

II. "Professor Cohn's view, which appears to be that the aggregated masses consist of condensations of cell-sap, and as a necessary corollary that the movements are impressed on the masses by some kind of protoplasmic action external to the masses."

That the latter view is the correct one was proved by Schimper, Gardiner, and De Vries, all of whom subsequently studied the phenomenon, and came to the conclusion that it is the contents of the vacuoles, and not the protoplasm, which give rise to the phenomenon described by Darwin.

Schimper[1] compared the condition of the cells before and after stimulation in Sarracenia, Drosera, and Utricularia, and found that the protoplasm under the influence of the stimulation gains an increased power of imbibition. Water is withdrawn by it from the cell-sap, and in Sarracenia and Drosera the tannin with which the cell-sap is laden becomes concentrated, and gives rise to the appearance Darwin called "Aggregation."

De Vries[2] describes the movements thus:

1. An increase in the rapidity and vigour of circulation in the peripheral layer of protoplasm.

2. A division of the vacuole into several smaller vacuoles, which are each surrounded by part of the original vacuole wall.

3. A very marked diminution of the volume of the vacuole, because some of its original constituents are expelled through the vacuole wall, and collect between this and the circulating protoplasm. The expelled fluid has, at least approximately,

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[1] Schimper, A. J. W., "Notizen über insektfressende Pflanzen," 'Bot. Zeit.,' 1882, Nos. 14 and 15.

[2] De Vries, H., "Ueber die Aggregation im Protoplasma von Drosera rotundifolia," 'Botanische Zeitung,' 1886.

the same attraction for water as the remaining contents of the vacuole, but possesses a different chemical composition. The colouring-matter, the tannin, and certain unknown albumins, precipitable by ammonium salts, are retained inside the vacuole. The grape-sugar and vegetable acids are probably, in part at least, expelled. Turgor is almost the same in stimulated as in unstimulated tentacles; it takes, e.g., a solution of between 2 per cent. and 3 per cent. KNO_3 to produce plasmolysis in unstimulated tentacles. The author finds that aggregation takes place first in the cells nearest the glands, and that division of the vacuoles occurs also in the gland-cells themselves, although no protoplasmic circulation is to be seen. When stimulation ceases the cells return gradually to their original condition, while the vacuoles increase in size, and ultimately fuse again into a single one.

This author describes further a similar but distinct phenomenon. Under certain conditions, especially when stimulated by salts of ammonia, by free ammonia in weak solution, by iodine, by osmic acid, and even sometimes by stimulating a fresh leaf with albumin, or by slowly killing a tentacle by drying, the albumins dissolved in the sap of the vacuole are precipitated; first in the form of a fine granulation, afterwards fusing into larger globules equalling in size the little vacuoles formed by aggregation, when it is not easy to distinguish between this appearance and that resulting from aggregation. But that they are different phenomena may be shown by first inducing normal aggregation, and then treating the aggregated cells with 1 per cent. ammonium carbonate.

The ammonia salts did not penetrate the thick cuticle of the tentacle stalks, but entered at the cut places and also by the gland-cells of the tentacle, and the little mammilla-shaped glands situated on the stalk of the tentacle.

A year previous to the appearance of De Vries' papers, Gardiner[1] published an account of "The Phenomena accom-

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[1] Gardiner, W., "On the Phenomena accompanying Stimulation in the Gland-cells of Drosera dichotoma," 'Proc. Roy. Soc. London,' 1885, p. 229.

panying Stimulation in the Gland-cells of Drosera dichotoma," in which he described the phenomenon of aggregation in living stalk cells, much as Darwin had done. He also noticed the phenomenon produced by the action of carbonate of ammonia, and called it "passive aggregation." A spindle-shaped or acicular body in the stalk cells and epidermal cells of the leaf called a "rhabdoid" is also described, which, as well as the elongated nuclei of the stalk cells, tends to become spherical after long stimulation.

Gardiner studied also the changes in the appearance of the gland-cells themselves after stimulation. His methods were as follows:

Leaves stimulated from five minutes to seventy-two hours by feeding with flies, or small pieces of frog's muscle, were examined fresh, or after fixing in alcohol, picric acid, or osmic acid. The best results were got with specimens treated for twelve hours with 1 per cent. or 2 per cent. solution of chromic acid. He describes a typical resting gland-cell thus:—"The protoplasm is arranged in a network or reticulum. The meshes of this reticulum are excessively close around the nucleus, which is situated at the base of the cell; but towards the free surface they are much more open, the close and more open arrangement merging the one into the other. The meshwork extends through the whole cell-cavity, and the interstices between the meshes are occupied by a pink cell-sap, and the whole is bounded by a structureless ectoplasm. In neither of the three layers of cells covering the tracheidal cells of the head could any obvious movement of the protoplasm be detected."

After stimulation for twenty-four hours the following histological changes were observed:

"A gland mounted in water exhibited a mottled appearance, such mottling being caused by a vacuolation of the most peripheral portions of the protoplasm of the gland-cells. In section, such a cell showed that in the course of secretion there had been a using up of the cell contents, and instead of the meshwork occupying the whole of the peripheral portion of the cell, so as to give a fairly homogeneous appearance, large spherical cavities had appeared in the reticulum here and there, such cavities being occupied by the cell-sap. The sap had, moreover, a much darker pink tint. Thus a breaking down or destruction of some part of the reticulum has taken place. After some seventy-two hours' stimulation this breaking down of the reticulum had reached to such an extent that in the peripheral portion before referred to, all the central core of the meshwork had for the most part disappeared, and replacing it was a single large vacuole filled with cell-sap. The cytoplasm had, moreover, contracted from the upper or free surface of the cell-wall. In no case does the destruction and consequent vacuolation extend to the base of the cell, where the nucleus is situated. The nucleus is always surrounded by dense protoplasm; and there are grounds for believing that after very long stimulation, when all the secretion has been poured out, and before absorption begins, an active growth of the protoplasm takes place around the nucleus, and in the more basal portion of the cell."

"The view here taken (which is supported by certain of the staining reactions) with regard to secretion is that in the gland-cells the more peripheral network consists of protoplasm, together with a formed substance derived from it, and that the outpouring of the secretion is caused by the repeated breaking down (owing to stimulation) of the protoplasm into this formed substance, which is of a mucous nature, and which rapidly attracts water and escapes as the secretion to the external surface."

Gardiner does not mention what the staining reactions are. The paper I quote from is called a "Preliminary" one. I believe the author has never published a more complete account; and, as far as I know, no one has with modern histological methods worked out the minute cytological changes which occur in the gland-cells, especially with regard to the nucleus and nucleolus and the staining reactions of the protoplasm.

EXPERIMENTS.

With the view of observing the minute histological changes induced by functional activity in the gland-cells of Drosera rotundifolia experiments were made as follows.

I. In Perthshire, Scotland, in the beginning of September, 1895, leaves were fed with the white of a soft-boiled egg, cut into pieces approximately 5 mm. in length by 1 mm. in breadth and thickness. The leaves were fixed after the following intervals of time:—one hour, twenty-four hours, forty-eight hours, seventy-two hours. These intervals were chosen in order that the leaves might be fixed at the same time of day in each case to avoid all variations due to diurnal changes. Young vigorous leaves, which showed no trace of having had a previous meal, were likewise fixed at the same times, and the whole experiment was conducted while the plants were growing in their native habitat, an open moor.

II. Another series of experiments was made in May, 1896, in Berkshire, England, where the leaves were again fed without being removed from their natural habitat, and fixed at intervals of from one minute up to the time when the leaves had again fully expanded and appeared to have regained their normal condition, which varied with the vigour of the leaf from four to seven days.

III. Repetition of experiment in August, 1896, in Scotland, to determine changes induced by an insoluble tissue, namely, boiled pieces of cork.

IV. A number of plants were removed for convenience to a cool greenhouse, and their leaves were fixed at various intervals after feeding.

In each set of experiments 15—20 leaves were used for each period of time, e. g. twenty leaves to determine changes after one minute, twenty leaves to show alterations after two minutes, &c.

The results of the four sets of experiments coincided on the tissues being examined by the methods about to be detailed; but none of my drawings have been taken from material of the fourth series, because plants kept for a few days in a greenhouse frequently show, as Darwin pointed out, a loss of the bright red colour peculiar to them under natural conditions, and they are therefore affected to some extent by their artificial surroundings.

METHODS.

I used the four following fixing fluids:

1. One per cent. chromic acid solution, as recommended by Gardiner.[1]
2. Absolute alcohol.
3. Mann's picro-corrosive alcohol.[2]
4. Mann's weak watery picro-corrosive fluid.

The effects of these fluids were very different.

The chromic acid caused the controls (unfed leaves) to close up as if powerfully stimulated; and on subsequent histological examination the glands presented the appearance of having been stimulated for a short time,—for example, the nuclei of the third layer of gland cells had become amœboid, or irregular in form. The whole tissue was cloudy, and stained with no precision.

The two alcoholic fixing agents preserved the control leaves in a beautifully expanded condition, but instantly made the glands white and transparent-looking, as if some substance had been extracted. Sections of such glands showed more or less distortion or slight collapse of the cell walls, and great vacuolation of the contents of the apical gland-cells. By the picro-corrosive alcohol, however, the large chromatin bodies

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[1] Gardiner, W., "On the Phenomena accompanying Stimulation of the Gland-cells of Drosera dichotoma," 'Proc. Roy. Soc. London,' 1885.

[2] Mann, G., "On a Method of preparing Vegetable and Animal Tissues for Paraffin Embedding, with a few Remarks as to Mounting Sections,' 'Trans. Bot. Soc. Edin.,' vol. xviii.

of the later stages of stimulation were specially well fixed, and they stained with great precision.

Mann's watery picro-corrosive fluid is in every way satisfactory, especially in its action upon control leaves. It both keeps the leaves expanded and preserves the dark colour of the glands. Though it causes some shrinkage of the protoplasmic body from the cell wall, it does not destroy any of its characters, and the points of attachment that remain in spite of the shrinkage serve to bring into evidence the fact that the protoplasmic bodies of neighbouring cells are intimately connected with the cell wall at corresponding places, and so are probably in connection with each other. Further, material fixed in the watery fluid takes the stains with most satisfactory precision.

The formula for this fixing fluid is as follows:—Saturated $HgCl_2$ in $\frac{3}{4}$ per cent. NaCl, 1 part. Saturated solution of picric acid in Aq. Dest., 3 parts. This fluid has a specific gravity of 1020.

The material was left in this for twelve hours, then transferred for twelve hours to a saturated solution of corrosive sublimate in normal saline, and afterwards dehydrated in alcohol of gradually increasing strength, being placed in 50 per cent. alcohol for four hours; 60 per cent., four hours; 70 per cent., about ten hours (i.e. all night); 80 per cent., five hours; 90 per cent., five hours; absolute alcohol, ten hours; then next day into two further changes of absolute alcohol. Chloroform was next introduced into the bottom of the vessel with a pipette. An hour was allowed to elapse after the tissue had sunk in the chloroform; the fluid was then all poured off, and fresh chloroform substituted, and this was changed once more after six hours. Paraffin of 52° melting-point was next added in small pieces, until saturation at a temperature of 30° C. was reached. The tissue was then placed in a warm chamber heated to the melting-point of the paraffin, a little more melted paraffin added, and then the chloroform was allowed to evaporate slowly. Sections were cut 5·08 μ thick by a Cambridge rocking microtome, fixed on glass slips in ribbons by Mann's[1] egg-albumen method, and stained either by M. Heidenhain's iron-alum hæmatoxylin (with or without previously staining in Bordeaux red), which gives very good results for the merely morphological aspects; or by Mann's[2] eosin and toluidin blue method, for the study of the alkaline and acid reactions. In every stage of stimulation the staining reaction was controlled by having on the same slide a row of sections of unfed material. The method of staining with eosin and toluidin blue is as follows:—Free the sections from paraffin by xylol; remove the xylol by alcohol; place the sections in Gram's iodine solution (double strength) for five minutes; wash out the greater part of iodine with alcohol.

Wash in water till the sections are quite white; place in 1 per cent. watery solution of water-soluble eosin (Grübler) for fifteen minutes; rinse in water; place in 1 per cent. solution of toluidin blue for five minutes; rinse in water; decolourise in absolute alcohol till the control sections upon the slide appear as on fig. 1, or pale blue to the naked eye. It is very essential that the absolute alcohol is pure, or otherwise the blue colour will be extracted too rapidly by the lime which is used in the distillations of alcohol. Further, do not allow the alcohol to drop on the slide, because this causes unequal washing out; but always immerse the whole slide in a vessel filled with absolute alcohol; clear in xylol by immersing the slide, and mount in turpentine or xylol balsam.

General Structure of the Glands.

In the heads of the tentacles of Drosera rotundifolia, D. dichotoma, &c., we may distinguish between glandular and non-glandular elements (see the accompanying figure). The latter consist of a group of large tracheids forming the

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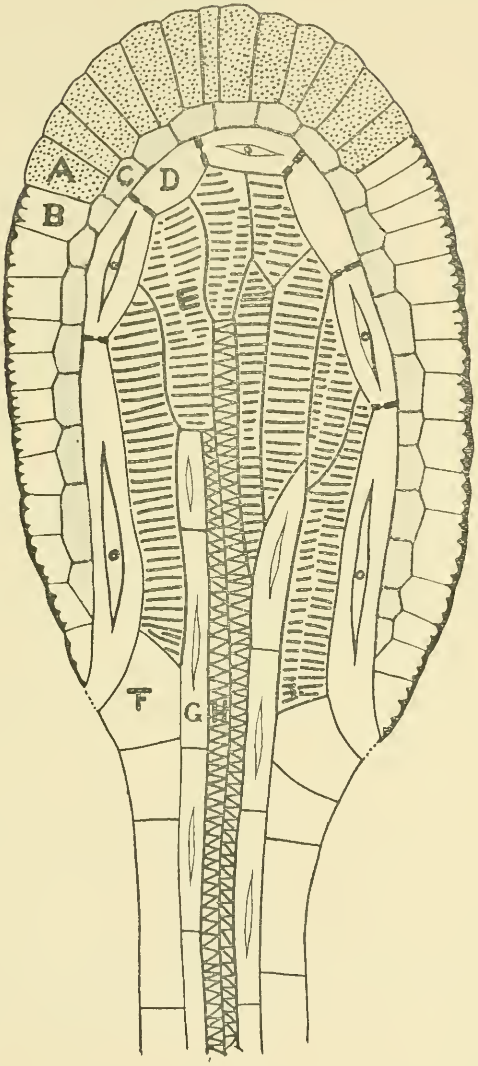
[1] Mann, G., "A New Fixing Fluid for Animal Tissues," 'Anat. Anzeiger,' viii Jahrg. (1893), Nos. 12 u. 13, p. 442.

[2] Mann, G., 'Zeitschrift f. wiss. Mikrosc.,' xi, 1895, p. 489.



Tentacle of *Drosera rotundifolia* constructed from serial sections:—A = apical gland-cells; B = lateral gland-cells; C = second layer of gland-cells; D = third layer of gland-cells; E = tracheids; F = dermatogen; G = periblem; H = plerome of stalk of tentacle.

core of the head, and varying in number with the size and vigour of the leaf, and in the centre of which terminates a fibro-vascular bundle (consisting of one or two spiral vessels, of small lumen, and an accompanying sheath of long narrow starch-containing cells) which springs from the vascular system of the leaf, and traverses the stalk of the tentacle. These non-glandular elements presumably function as a channel for the transference of fluids.

The glandular elements consist of three bell-shaped layers of gland-cells covering the tracheids. The external layer is composed of cells of two kinds. Those at the apex are thin-walled elongated cells, numbering in a longitudinal section 12—14. The lateral cells of the outer layer are shorter, and possess thick walls. Their external walls have tooth-like internal projections of cellulose.

The cells of the second glandular layer resemble closely the lateral cells of the superficial layer, but their walls have no projections.

The third layer is composed of comparatively few, but very long cells, which are remarkable for the large amount of tannin in solution contained in their cell-sap, and for the strong cuticularisation of those walls, both longitudinal and transverse, which separate them from one another. The transverse walls are worthy of special attention, because they are composed of two projections, one from each side. The projection from the outer side is strongly cuticularised; that from the inner side (next the tracheids) is lignified. Between the two there is a minute space through which intercellular communication is permitted. This layer of cells is also epidermal in its origin, and arises from a zone of epidermal cells immediately below that forming the initial cells of the lateral external layer. Each cell of this zone elongates inwards and then subdivides.

The entire tentacle head is cuticularised superficially. I do not understand how Gardiner[1] comes to describe the glands

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[1] Gardiner, W., "On the Phenomena accompanying Stimulation in the Gland-cells of Drosera dichotoma," 'Proc. Roy. Soc. London,' 1885.

of Drosera dichotoma as without cuticle, and Goebel[1] to say that the apical gland-cells are not cuticularised. Like those of Drosera rotundifolia, the gland is covered with cuticle. After prolonged treatment by iodine and sulphuric acid all that is left undestroyed of the median longitudinal section of a gland of either of these species is the continuous outline of cuticle and the cuticularised walls of the third layer of gland-cells.

A method for readily seeing the cuticular envelope in comparatively large pieces is to take an entire leaf that has been blanched in alcohol, to soak it in water, then to leave it for some minutes in strong iodine solution, to lift it out and wash off the superfluous iodine in water. A few of the tentacles should then be cut off and laid upon a glass slip; a drop of concentrated sulphuric acid be placed upon them, and a cover-glass laid over them; and when the reagent is seen through the microscope to have taken effect by the usual coloration being produced, the cover-glass is to be pressed gently so as to rupture the apices of the gland and squeeze out the contents. The cuticular envelope of the gland usually remains attached at its base, and floats out as a semi-transparent membrane stained yellow by the iodine.

Gardiner[2] describes the gland-cells as "remarkably pitted on their upper or free surface; and Goebel[3] states that the outer walls of the apical gland-cells are dotted. I have examined pieces of cuticle obtained in the manner just described, with a 1/12 apochromatic oil immersion object-glass by Zeiss with oculars Nos. 8 and 12, but have found no well-defined pores. I have equally failed on examining sections. The internal cellulose protuberances of the thickened outer walls of the lateral cells of the external glandular layer often produce the appearance of enclosing large deep pits; but it is a deceptive appearance, as a little careful study shows. There is no

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[1] Goebel, 'Pflanzenbiologische Schilderungen,' Theil i, p. 198.

[2] Gardiner, W., "On the Phenomena accompanying Stimulation of the Gland-cells of Drosera dichotoma," 'Proc. Roy. Soc. London,' 1885,

[3] Goebel, 'Pflanzenbiologische Schilderungen,' Theil i.

such appearance in the apical cells. The secretion must, of course, leave the apical gland-cells somehow, and the albumen pass somehow into the tentacle, but how it is impossible as yet to say quite definitely. Silver nitrate enters the tentacles most readily through the lateral gland-cells, and clefts appear between the apices of the apical gland-cells a few minutes after stimulation, and the albumen seems to pass in through these clefts, as will be shown later on.

As Charles Darwin pointed out,[1] the extreme marginal tentacles of some leaves of D. rotundifolia differ from the other tentacles in exhibiting a unilateral development. Their heads are very much elongated, and bear the glandular surface on the ventral side only. The plan of structure is, however, the same as in ordinary tentacles, all the elements being present, and the unilateral development appears to be merely the result of pressure during early growth in the bud.

Results of Histological Examination of Material fixed in Watery Picro-corrosive Sublimate, and stained with Eosin and Toluidin Blue.

Before describing these results, it may be well to explain the names applied to the nuclear organs.

Chromosomes are the organs which show the well-known affinity for alkaline dyes, and which are situated at the periphery of the nucleus.

Nuclear Plasm is the material which in the resting state forms the main bulk of the nucleus, and is neutrophile in character; it corresponds to what is frequently called the nuclear sap.

Nuclear Sap is the more watery fluid inside the nucleus, in which is suspended the nuclear plasm, the latter being precipitable by $HgCl_2$ and other reagents.

Nucleolar Chromosomes or Nucleoli are the spherical organs which show a special affinity for acid dyes, and have a more or less central position.

Endonucleoli are spaces inside the nucleolus.

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[1] Darwin, C., 'Insectivorous Plants,' p. 7.

Apical Gland-cells.

The Resting State as seen in Unfed Leaves used as Controls. Fig. 1, Plate 23.

The Cell Wall stains pale blue. The free wall of the cell by shrinkage has sometimes become slightly concave, but otherwise appears turgid.

The Cytoplasm has retracted from the cell walls except in the lower basal third, where it either remains entirely in contact with the cell wall, or is attached to it by strands, which are in line with similar strands in neighbouring cells. The general appearance is suggestive of communication in this region between the apical gland-cells themselves, and also between them and the cells of the second layer. The cytoplasm is apparently homogeneous, and arranged in a foam-like manner. It stains pure blue, and contains a coarse granulation embedded in it which stains a deeper blue, and represents some zymogen. The constant position of the nucleus is just below the middle of the cell, and the cytoplasm between it and the outer wall is generally densest in the middle third, being more vacuolated towards the free surface and in the immediate vicinity of the nucleus. Surrounding the nucleus, and partly hiding this looser arrangement, is a more finely granular mass of protoplasm which often shows a slight affinity for the red stain. This zone gradually merges over into the general plasm, but shows a number of distinct radiations passing both outwards from the nucleus and towards the basal attachment of the cell. The plasm, where retracted from the cell wall, sometimes shows minute dark blue granules, which frequently also occur on the margins of the vacuoles. Compared with the lateral cells of the outer layer and with the cells of the second layer, the cytoplasm of the apical gland-cells is much deeper in colour, because of its greater abundance in these cells.

The Nucleus is situated just below the middle of the cell. It may be spherical or oval.

The nuclei vary in size, being generally smaller in the cells nearest to the apex. They are remarkably plump, exhibiting a full and rounded contour. They stain of a purplish tint.

Whether a definite nuclear membrane exists is doubtful, but in mid-focus the nucleus is sharply defined against the cytoplasm, partly because of the difference in tint, and also because of the peripherally placed dark blue chromatin granules.

The Nuclear Chromosomes are very minute granules, apparently shaped like diplococci, each coccus being slightly flattened, and attached to its neighbour by its broad side. They stain an intense blue without any reddish tint.

The Nuclear Plasm is granular and always very dense in controls. Sometimes the granules appear to radiate from the nucleolus, and in other cases their arrangement produces a sponge-like appearance; or, again, the granules are too closely packed to show any definite arrangement. They stain of a purplish tint.

The Nucleolus is embedded in the nuclear plasm. One, sometimes more, very distinct deep red nucleolus is always present, surrounded by a narrow Frommann's clear zone. If there is only one nucleolus, it is large; it may be in any part of the interior of the nucleus, but is generally about one quarter to one-third of the diameter of the nucleus, removed from its periphery.

It always presents a perfectly smooth spherical outline, and contains one or more distinct endonucleoli.

Effects of Stimulation for One Minute on the Apical Gland-cells. Type 1. Fig. 2.

The Cell Wall shows no evidence of diminished turgor, there being no collapse. It stains purplish. Between the apical thirds of neighbouring cells a very distinct reddish material is to be noted, staining, in colour and intensity, exactly like the semi-fluid egg-albumen in contact with the head. In tentacles stimulated with pieces of boiled cork this red material is always absent. We are dealing, therefore, with a substance (albumen ?) which is passing in between the cells, and not with a substance which is being excreted by the cell.

The cytoplasm in this specimen has retracted from all the walls equally.

It is very difficult to distinguish in colour between the cytoplasmic granulation and its matrix. The general tone is of a deep-blue purple, and the matrix seems to be paler than the granulation. Fully half the cell is occupied by very large vacuoles filled with a fluid which stains pale blue. The walls of the vacuoles are lined, to a great extent, with deep blue granules which show no trace of purple or red. The vacuoles are largest in the upper third of the cell, but usually one or two large ones lie also near the base. The cytoplasmic granulation is extremely dense round the nucleus, and stretches between the vacuoles in radiating amœba-like processes.

Characteristic of this stage is the presence in the cytoplasm of one (occasionally two) very apparent blue "corpuscles," about twice the size of the nucleolus, and having a dark blue granular periphery. The explanation I should like to offer for this appearance is as follows :—In the unstimulated cell some substance is freely distributed, which helps to give rise to the affinity for the blue stain. On stimulation this substance is withdrawn from the cytoplasm (which now takes a purplish stain), and is collected in vacuoles of various sizes. By mordanting the cytoplasm surrounding the vacuoles an affinity for the blue dye is established, and the deeply stained cytoplasm will give rise to the appearance of a distinct wall to the vacuole. The smaller vacuoles, because seen in their entirety, appear of a deeper colour than the large ones which are seen in section, and could easily be mistaken for definite corpuscles. The substance acting as a mordant is in this case probably tannic acid.

The Nucleus maintains its normal position in the cell, its normal size, shape, and outline. There is no sign of a collapse, it being still plump and well filled out. It stains exactly the same depth and tint as the cytoplasm, but is distinctly marked off from it by its dark blue periphery.

The Nuclear Chromosomes are in no way different from those of unfed specimens.

The Nuclear Plasm appears very indistinctly granular, as if the granules had swelled and fused, but is still extremely dense.

The Nucleolus stains a purple-red. It is still full and spherical, and frequently appears even enlarged. It is surrounded by a broad Frommann's circle, and does not show the endonucleoli as distinctly as in the resting condition.

Effect of Stimulation for One Minute on the Apical Gland-cells. Type 2. Fig. 3 (slightly more advanced than Fig. 2).

The Cell Wall is pinkish purple, as in the last specimen, and there is the same appearance of some reddish material between the apices of the cells.

The Cytoplasm is shrunken from the walls, but attached in one place to the basal wall, and in two places to one lateral wall. Its matrix and granulation are indistinguishable from each other. The plasm is very red round the nucleus for a distance equal to two thirds of the diameter of the latter. Beyond this it is deep blue-purple, as in the last specimen, and the apical fourth of the cell is entirely occupied by a network of vacuoles, the reticulum between them containing masses of the deep blue granules which line the vacuoles as in the last specimen. The same granules are distributed, apparently in strings, through the thick granulation occupying the middle of the cell. A pseudo-corpuscle is present, as in the last specimen.

The Nucleus is normal as to position, size, and shape. It is of the same reddish tint as the cell-plasm surrounding it, but is clearly defined by its dark blue periphery, and still maintains its plumpness.

The Nuclear Chromosomes are like those of unfed specimens.

The Nuclear Plasm is of the same tint and general appearance as the granulation surrounding the nucleus.

The Nucleolus is dark reddish purple, and is surrounded by Frommann's clear zone. The endonucleoli in all the cells are much less distinct than in unfed specimens.

Effect of Stimulation for Five Minutes on Apical Gland-cells. Fig. 4.

The Cell Wall is coloured as in specimens fed for one minute. The specimen from which fig. 4 was taken had been only lightly touched by the egg-albumen, but in specimens in contact with large masses of the albumen the same appearance of a pink substance between the apices of the apical gland-cells is seen as in the former specimen.

The Cytoplasm has retracted from the walls, but remains in contact at one or two points with the basal wall and the lower parts of the lateral walls as usual. The coloration generally resembles that of fig. 2, though there is less of the scattered dark blue granulation. The blue corpuscle-like vacuoles are generally present in cells of this stage, though absent in the one from which the drawing was taken, which, in fact, shows scarcely any vacuolation, perhaps because its contact with the albumen used as food was comparatively slight.

The Nucleus is, with regard to position, size, and shape, normal. It is of the same red tint or slightly redder than the surrounding cytoplasm, and its dark blue periphery is less definite and regular than formerly, as if broken at intervals, which may perhaps be due to a change in the nuclear membrane, the latter no longer staining with the blue.

The Nuclear Chromosomes.—The individual granules have become larger and more conspicuous. The gland from which the drawing was taken was, however, the only one in the material examined at this stage which showed this development.

The Nuclear Plasm is as dense as in unfed specimens, but the granular structure has fused, as already described in material after one minute's stimulation.

The Nucleolus is as in specimens fed for one minute.

Effect of Stimulation for Ten to Twenty Minutes on the Apical Gland-cells. Fig. 5.

The Cell Wall is in some specimens the same as in the last description, while in others no penetration of albumen between the cells can be made out.

The Cytoplasm shows, as regards vacuolation, great variety in material of this stage. The specimen from which the figure (5) was drawn is more vacuolated than most of the cells, which latter rather correspond in this respect to earlier stages already described. All other details remain as in the earlier stages (figs. 4 and 2), except that there are no blue granules, and the blue "corpuscles" are rare.

The Nucleus becomes less distinctly defined in outline. Other details remain as in the last specimen described.

The Nuclear Chromosomes are distinctly larger and more conspicuous than in unfed specimens.

The Nuclear Plasm shows enlarged pale spaces which, combined with the less full and rounded contour, give to the nucleus a slightly attenuated appearance as compared with unfed specimens. In colour it resembles the earlier specimens.

The Nucleolus is unchanged from earlier stimulated specimens.

Effect of Stimulation for Twenty Minutes to One Hour on the Apical Gland-cells. Fig. 6.

Note.—It is extremely difficult to decide which is the sequence of the three types next to be considered. They are all characteristic of glands which have been active for periods intermediate between twenty minutes and four hours, and it is by no means certain that the order here adopted is the correct one. The type shown in fig. 6, which was taken from a tentacle stimulated for one hour, was seen also in a tentacle fed for only twenty minutes. I have, therefore, placed it before the other two.

The Cell Wall is pale blue-purple. In many cells the walls appear less turgid than in controls, being often somewhat crooked or uneven; this is especially the case in the lateral walls.

The Cytoplasm shows considerable vacuolation, especially in the outer third of the cells, but not more so than in some previously described earlier stages. Round the nucleus the cytoplasm is dense. The entire cytoplasm stains red, except that at the apex of the cell there is a trace of blue. A few deep blue granules adhere to the exterior of the apical wall, a condition which I leave unexplained. Whether in figs. 6, 7, and 8 there is not more protoplasm than in cells stimulated 1—5 minutes is difficult to say. Probably, as the result of stimulation, a temporary increase in the amount of cytoplasm occurs.

The Nucleus is shrunken, leaving a clear white zone between it and the surrounding cytoplasm.

Nuclear Chromosomes appear as large granules, and are brought into close proximity to each other by the shrinkage of the nucleus.

The Nuclear Plasm is the same colour as the surrounding cytoplasm, but appears deeper because of its greater density.

The Nucleolus stains the same tint as the surrounding nuclear plasm, and therefore is difficult to see. In the specimen figured it is invisible, hidden probably by the enlarged nuclear chromosomes.

Effect of Stimulation for One to Four Hours on the Apical Gland-cells. Fig. 7.

The Cell Wall is very pale blue. The apical cells appear frequently to overlap each other, an appearance due to loss of turgor.

The Cytoplasm is stained of a purple-red, becoming bluer in the apical fourth, where it is greatly vacuolated. There are very marked red granular aggregations in contact with the nucleus on its basal aspect.

The Nucleus is somewhat swollen. Its position is normal.

The Nuclear Chromosomes are larger than in unfed leaves.

The Nuclear Plasm is shrunken to form a dense central mass, attached at fairly regular intervals to the nuclear periphery, so as to present a stellate outline. The vacuoles thus formed appear slightly blue. The nuclear plasm, because of its density, stains more deeply than the cytoplasm, but of the same tone of colour.

The Nucleolus is undiscernible. It is, however, probably present, as in other material, also, showing this retracted condition of the nuclear-plasm, I have been able to reveal it by Heidenhain's iron-alum hæmatoxylin.

Effect of Stimulation for One to Four Hours on the Apical Gland-cells. Fig. 8.

The Cell Wall is very pale blue.

The Cytoplasm is greatly vacuolated. The main body of the plasm is red, shading to blue round the vacuoles.

The Nucleus is spherical and swollen. Its outline is very indistinct, and its periphery undefined.

The Nuclear Chromosomes are deep blue. They show a tendency to be displaced or arranged irregularly.

The Nuclear Plasm is purple. It appears thin because spread out over a larger space than before. White spaces occur in it here and there.

The Nucleolus is small and pale red.

Effect of Stimulation for Twenty to Thirty Hours on the Apical Gland-cells. Figs. 9A and 10.

Note.—The state about to be described is characteristic of glands that have been active for twenty to thirty hours, but is sometimes reached in twelve hours.

The Cell Wall is pale blue. It presents the same appearance of loss of turgor as noticed in specimens fed for one to four hours.

The Cytoplasm is an extremely scanty network staining red, or with a trace of blue here and there in the parts furthest from the nucleus.

The Nucleus is normal as to size and outline, or is shrunken so as to form an oblong body with its long axis at right angles to that of the cell.

Nuclear Chromosomes now consist of eight large dark blue segments. They are remarkably distinct and conspicuous in unshrunken nuclei, and appear to be V- or U-shaped, reminding one of the well-known stages in karyokinesis. In shrunken nuclei they are brought very close together, and help to give the nucleus a dark purple appearance.

The Nuclear Plasm is red. It is vacuolated in the unshrunken nuclei. It is dense purple-red in the shrunken nuclei, which are therefore much darker than the cytoplasm.

The Nucleolus is pale red, inconspicuous, sometimes very small in the unshrunken nuclei. It is undiscernible in the nuclei that have shrunken. Endonucleoli are indistinguishable, owing to the paleness and transparent appearance of the nucleoli.

Fig. 9B is a nucleus from an apical gland-cell of a leaf that had been fed with yolk of boiled egg, and which after thirty hours was fixed in Mann's picro-corrosive alcohol. It is remarkable for the large size of the chromosomes, which seem to be approximately V-shaped. It is also remarkable for the absence of nuclear plasm. The cytoplasm is in the same condition as is shown in figs. 9 and 10.

In those experiments where pieces of cork were laid on the leaves to produce stimulation, complete exhaustion of the cell, similar to fig. 10, resulted as regards the cytoplasm; while the nucleus, although shrivelled and shrunken, stained a pure red, there being not a trace of blue colour in the chromosomes. This peculiar behaviour of the chromatin segments I have also seen, though not frequently, in leaves which had been fed twenty to thirty hours previously with egg-albumen. I mention this fact because there may be some analogy between this affinity for red dyes as seen here, and also met with during the middle period of mitosis—a view which seems to be supported by figs. 9A and B, where one of the features of mitosis is reproduced.

The Apical Gland-cells Two to Three Days after Feeding (the Leaf beginning to reopen). Fig. 11.

The Cell Wall is pale blue.

The Cytoplasm shows the usual general retraction and basal attachments. It is extremely dense and granular round the nucleus, forming a well-defined zone which occupies the middle third of the cell, so that cells of this stage can be easily recognised with low powers. The thick granulation stains a deep purple. The matrix appears to stain the same colour, but fainter. Below the nucleus are one or two very large vacuoles. Above it the space is either occupied by one or two large vacuoles, or, as in the cell figured, a protoplasmic network traverses the upper third of the cell, enclosing numerous smaller vacuoles in its meshes.

The Nucleus is in position, size, and shape as in unfed specimens. It stains of the same tint as the cytoplasm, and therefore lacks the clear definition which is characteristic of the resting state.

The Nuclear Chromosomes are in the form of numerous granules of slightly larger size than in the resting state. They have a somewhat undefined appearance, and want of clearness of outline.

The Nuclear Plasm is granular. It resembles very closely the cytoplasmic granulation in every way; so that the nucleus appears to be only a portion of the cell-plasm enclosed by a broken ring of chromatin granules.

The Nucleolus is either very pale and transparent, and usually very small, or is quite undiscernible.

Apical Gland-cells, Seven Days after feeding (the Leaf thoroughly opened up, and glistening with exuded drops). Fig. 12.

The Cell Wall is pale blue.

The Cytoplasm has retracted as a whole from the cell walls, but is attached in the basal third at various points, as is the general rule, both in controls and fed leaves. It is densest near the nucleus and below it. In the rest of the cell it is largely vacuolated. In structure and colour it is exactly like that of unstimulated glands. The vacuoles are large and numerous, and their contents are perfectly homogeneous, and are unstained; though usually the vacuoles appear to have a bluish tinge in mid-focus, caused by underlying or overlying plasm.

The Nucleus is in position, size, and shape as in unfed specimens. They also agree with the resting nuclei in their general appearance of plumpness and turgor.

The Nuclear Chromosomes are peripheral granules which are either equally small or very slightly larger than those of specimens that have never been fed. They stain the same deep blue, and are similar in shape and arrangement.

The Nuclear Plasm is granular. Its general arrangement produces a sponge-like appearance, and is therefore similar to the least dense specimens among controls. It shows affinity for both dyes, as does the nuclear plasm of controls.

The Nucleolus is exactly as in controls,—that is, very evident, with distinct endonucleoli.

LATERAL SUPERFICIAL GLAND-CELLS.

The Resting State, seen in Unfed Leaves used as Controls. Fig. 13, Plate 24.

The Cell Wall is turgid, and stains pale blue.

The Cytoplasm is either not retracted at all from the cell wall, or is retracted as in the apical cells, except at certain points where it is applied to the basal wall and to the lower parts of the lateral walls. It is always attached by strands to the projections from the external wall.

The Cytoplasm is exactly similar to that of the apical cells in its structure and staining properties, but frequently appears paler because it is less dense. It is very dense round the nucleus, but the more peripheral parts are largely vacuolated. A reddish tint such as sometimes occurs in apical cells round the nucleus is hardly ever seen in lateral cells.

The Nucleus is placed in the centre of the cell or slightly below it. It is similar to the nuclei of the apical gland-cells, though sometimes slightly paler owing to the nuclear plasm being somewhat less dense.

Nuclear Chromosomes are like those of the apical cells, or sometimes the granules are slightly larger.

The Nuclear Plasm resembles that in the apical cells, or occasionally is less dense.

The Nucleolus is as in the nuclei of the apical cells.

The Effect of Stimulation for One Minute on the Lateral Superficial Gland-cells. Type 1. Fig. 14.

The Cell Wall is pale purplish pink. Its turgor is unchanged.

The Cytoplasm is attached to the basal and lateral walls, but shrunken towards the apex. The distribution is like that of unfed specimens. Its coloration is pinkish purple, and fairly uniform throughout the cell. A blue "corpuscle" is usually present in the cell-plasm.

The Nucleus is normal as to position, size, and shape. It is slightly deeper in colour than the cytoplasm surrounding it.

The Nuclear Chromosomes are as in unfed specimens.

The Nuclear Plasm is unchanged in structure, but shows slightly more affinity for red than in unfed specimens.

The Nucleolus is deep purple-red, and is surrounded by Frommann's zone. The endonucleoli are less distinct than in unfed specimens.

Note.—The lateral superficial gland-cells at the base of this tentacle-head show a much redder coloration than the other cells of the layer, and therefore resemble fig. 15.

Effect of Stimulation for One Minute on the Lateral Superficial Gland-cells. Type 2. Fig. 15.

The Cell Wall is extremely pale purple. There is no red coloration between the cells.

The Cytoplasm is retracted from the basal and lateral walls, but not from the apical to which it is closely applied. The general distribution of the cytoplasm is like that of controls. In colour it is like that of the apical cells,—that is, red round the nucleus, becoming bluer towards the periphery. The blue "corpuscles" are present as a rule.

The Nucleus is normal as to position, size, and shape. It is of the same shade of colour as the cytoplasm surrounding it, or sometimes rather bluer, but is sharply defined by its dark blue periphery.

The Nuclear Chromosomes are as in unfed specimens.

The Nuclear Plasm is less distinctly granular, though as dense as in unfed specimens.

The Nucleolus is deep purple-red, and is surrounded by Frommann's zone. The endonucleoli are not distinct.

Effect of Stimulation for Five Minutes on the Lateral Superficial Gland-cells. Fig. 16.

The Cell Wall is pale pinkish purple in the specimen figured. In other specimens more densely surrounded by the albumen used as food, the external walls, and the upper part of the lateral walls are very red.

The Cytoplasm has apparently not diminished in mass, or only slightly so. Its coloration is as in apical cells of this stage. A blue "corpuscle" is frequently present.

The Nucleus is normal as to position, size, and shape; but its blue periphery is more or less irregular.

The Nuclear Chromosomes are like those of the apical cells, appearing as large, conspicuous, generally distinctly double granules.

The Nuclear Plasm in general arrangement is as in unfed specimens. In some cases it is slightly less dense. Its colour is like that of the surrounding cytoplasm.

The Nucleolus is unchanged from the one-minute stage.

Effect of Stimulations for Ten to Twenty Minutes on the Lateral Superficial Gland-cells. Fig. 17.

The Cell Wall, as in the last case, stains either pale purple or red. In the specimen chosen the walls are pale purple.

The Cytoplasm is in general aspect, bulk, distribution, and coloration similar to that seen in specimens fed for shorter periods.

The Nucleus and Nuclear Chromosomes show no change since the stage last described.

The Nuclear Plasm is less dense than formerly. Its colour is like that of the surrounding cytoplasm.

The Nucleolus is unaltered from the last stage described.

Effect of Stimulation for Twenty Minutes to One Hour on the Lateral Superficial Gland-cells. Fig. 18.

Cell Wall is pale purplish blue. The walls of these cells do not show the same loss of turgor that is seen in the apical cells. Owing to their greater thickness they are more resistant.

The Cytoplasm is reddish purple. It seems to cover as great an area as in control leaves, but is everywhere much less dense. There is no shrinkage from the cell wall. The peripheral layer is very blue. A blue corpuscle-like vacuole is sometimes present.

The Nucleus is swollen, and its outline is very indistinct. The periphery is apparently broken, and there is no trace of a nuclear membrane.

The Nuclear Chromosomes are in the form of a great number of irregular granules larger than in unfed specimens, but somewhat indistinct in outline, and staining a less intense blue.

The Nuclear Plasm is less dense than formerly, because of the increased size of the nucleus. In it there are large white spaces. It stains a bluish purple, and so gives the nucleus a bluer tint than the surrounding cytoplasm.

The Nucleolus is pale red. Frommann's clear zone is not seen. The endonucleoli are not well defined, or are absent.

Effect of Stimulation for One to Four Hours on the Lateral Superficial Gland-cell. Fig. 19.

The Cell Wall is very pale blue.

The Cytoplasm is red or reddish purple.

The Nucleus may be said to be perfectly wanting in outline. It is chiefly defined from the cytoplasm by its distinct blue chromosomes upon their light background of sparse nuclear plasm, and large white spaces.

The Nuclear Chromosomes appear as a few large segments. They are fewer and larger than those of the apical gland-cells. They stain a pure deep blue.

The Nuclear Plasm is very scanty, and of the same tint as the cytoplasm, but large white spaces occupy most of the interior of the nucleus, which has therefore a washed-out, empty appearance.

The Nucleolus is small.

Note.—It seems as if the lateral superficial cells and the cells of the second layer in this case were in advance of the apical cells; for the collection of the chromatin into a few large segments, and the vacuolation of the nucleus, are characteristic of more advanced stages of glandular activity.

Effect of Stimulation for One to Four Hours on the Lateral Superficial Gland-cells. Fig. 20.

The Cell Wall is pale blue.

The Cytoplasm is red, shading to a bluer tint towards the periphery of the cell. The red colour is deepest close to the nucleus, but there are no such well-defined masses of red material as are seen in the apical cells of the same gland (fig. 7). A blue "corpuscle" is sometimes present.

The Nucleus, Nuclear Chromatin, and Nuclear Plasm are the same as in the apical cells.

The Nucleolus is small, and also indistinct because it resembles in colour the surrounding nuclear-plasm. Fig. 20 may be an earlier stage than fig. 19, because the nuclear chromosomes have not as yet aggregated into eight big segments.

Effect of Stimulation for Twenty to Thirty Hours on the Lateral Superficial Gland-cells. Figs. 21 and 22.

The Cell Wall is pale blue.

The Cytoplasm is as in the apical Cells.

The Nucleus is represented by the two types found in the apical cells. The unshrunken nuclei are in all respects similar to those of the apical cells of a corresponding period. The shrunken nuclei differ somewhat in the two layers. In the lateral cells they seldom, if ever, become elongated, but remain approximately spherical.

The Nuclear Chromosomes, the Nuclear Plasm, and the Nucleolus resemble those of the apical cells of same period, the formation of eight chromosomes being again very evident.

The Lateral Superficial Gland-cells Two to Three Days after Feeding. Fig. 23.

The Cell Wall is pale blue.

The Cytoplasm exhibits a granulation resembling that of the apical cells (fig. 11), but is scarcer, and therefore paler; it surrounds the nucleus, and stretches away from it, especially towards the base of the cells. Cytoplasmic strands also run out from the nucleus towards the apical peripheral layer, intersecting the cell and dividing the space into large vacuoles.

The Nucleus resembles those of the apical cells, but is here somewhat darker, because relatively denser than the surrounding cytoplasm.

The Nuclear Chromosomes resemble those of the apical cells, or are slightly larger; they are apparently spreading out to form less compact bodies than in figs. 21 and 22.

The Nuclear Plasm and Nucleolus resemble those of the apical cells of the same period.

The Lateral Superficial Gland-cells Seven Days after Feeding. Fig. 24.

The Cell Wall is pale blue.

The Cytoplasm is exactly like that of controls, or is somewhat less abundant, with larger vacuolated spaces.

The Nucleus, Nuclear Chromosomes, Nuclear Plasm, and Nucleolus resemble those of the apical cells of same gland and those of controls.

THE SECOND LAYER OF GLAND-CELLS.

The Resting State, seen in Unfed Leaves used as Controls.

The Cell Wall is pale blue.

The Cytoplasm is very scanty compared to cells of the outer layer.

A thin peripheral plasmic layer always remains applied to the wall of the cell. Cytoplasmic strands suspend the nucleus in the middle of the cell, and radiate from it to the peripheral layer lining the wall. Large vacuoles occupy the spaces between these radiating strands. The structure and staining properties of the cytoplasm are exactly the same as in the apical and lateral gland-cells of the superficial layer. A reddish tint round the nucleus is sometimes (though rarely) seen.

The Nucleus, Nuclear Chromosomes, Nuclear Plasm, and Nucleolus are like those of the lateral superficial gland-cells.

The Effects of Stimulation for One Minute to Twenty Minutes upon the Gland-cells of the Second Layer.

All the cytological changes correspond to those of the lateral superficial cells, except that the cell walls are always pale purple, never red.

Effect of Stimulation for Twenty Minutes to One Hour on the Gland-cells of the Second Layer.

The Cell Wall and Cytoplasm are like those of the superficial cells stimulated for a slightly longer period.

The Nuclei of the cells below the apical gland-cells have shrunken in the same way as the apical nuclei, while the lateral cells of the second layer have their nuclei in the same condition as the lateral superficial cells, or only very slightly shrunken.

The subsequent changes in the cells of the second glandular layer agree in all respects with those of the lateral superficial gland-cells.

GLAND-CELLS OF THE THIRD LAYER.

The Resting State, seen in Unfed Leaves used as Controls. Fig. 25A, Nucleus seen in longitudinal section; 25B, the same in transverse section.

I have only figured the nuclei of this layer, because the cells are very large, and the cytoplasm is too scanty to show any characteristic changes, except those of the staining reaction. In tentacles fixed in absolute alcohol, however, a dense plasm is seen filling the cell, and resembling mucus.

The Cell Wall.—The outer wall of a longitudinal section stains pale blue. The inner wall next the tracheids stains deep blue. The cuticularised parts do not stain at all.

The Cytoplasm is merely a thin peripheral layer, slightly granular, staining pure blue. The layer lining the wall next the tracheids generally shrinks away from it to the centre of the cell, which it traverses like a cord, attached at its ends to the point in the transverse wall between the cuticularised portion and the lignified projection. As this is the case in all the cells of the layer, a cord, or rather a lamella, appears to stretch continuously from cell to cell.

The Nucleus is spindle-shaped. Its position is peripheral. It lies either in the layer of cytoplasm lining the external wall, or in that which lines the internal wall. Should the cytoplasm shrink to the centre of the cell, the nucleus is taken with it. Its long axis corresponds to the long axis of the cell.

The Nuclear Chromosomes are minute granules which generally appear to be double. They stain deep blue. They are peripherally placed, and their arrangement frequently suggests that they are disposed like beads upon invisible threads, which describe a wide-meshed reticulum.

The Nuclear Plasm is granular; and the granules appear more or less distinctly to be arranged in chains, or to form a kind of open network with the spaces occupied by a homogeneous substance. Both granules and spaces stain blue, without any reddish or purple tinge, thus differing from the nuclei of the other gland-cells. This is the general rule; but in leaves taken in autumn the nuclei of this layer occasionally correspond in tint with those of the other gland-cells.

The Nucleolus.—There is one large nucleolus, or two smaller ones. They stain deep red, and contain one or more distinct endonucleoli.

Effect of Stimulation for One Minute on the Cells of the Third Glandular Layer. Type 1. Fig. 26A, Nucleus seen in longitudinal section; Fig. 26B, in transverse section.

The Cell Wall is pale purple; deeper in tint and bluer on the side next the tracheids.

The Cytoplasm is as in unfed specimens, except that it stains pinkish purple. The occasional presence of a blue "corpuscle" is doubtful.

The Nucleus is normal as to position and size. It shows no alteration in shape, except that it is slightly less pointed at the ends. Its general tint is pinkish purple; and it shows more affinity for the red stain than the majority of the nuclei of the other gland-cells.

Nuclear Chromosomes are as in unfed specimens.

The Nuclear Plasm is of a reddish-purple tint. It is distinctly granular, and is arranged in an open network in the meshes of which is a pale purple homogeneous substance.

The Nucleolus is dark purple-red. The endonucleoli are indistinct or absent.

Effect of Stimulation for One Minute on the Cells of the Third Glandular Layer. Type 2. Fig. 27.

The Cell Wall stains pale blue-purple, showing a much bluer tint than the walls of the other gland-cells.

The Cytoplasm is pale pink, but otherwise is like that of unfed specimens. There is no blue "corpuscle" present.

The Nucleus is normal as to position and size. It is less finely pointed at the extremities than in controls. It exhibits a strong affinity for the red stain. This affinity is markedly greater than in the nuclei of the other gland-cells.

The Nuclear Chromosomes are apparently as in controls.

The Nuclear Plasm is distributed as in unfed specimens, but the granules stain red. The substance which occupies the meshes of the reticulum is also red.

The Nucleolus stains dark crimson. The endonucleoli are badly defined.

Effect of Stimulation for Five Minutes on the Cells of the Third Glandular Layer. Fig. 28.

The Cell Wall and the Cytoplasm resemble those last described.

The Nucleus has become much broader and shorter, and shows an intense affinity for the red stain.

The Nuclear Chromosomes are very distinctly double. They stain very dark blue.

The Nuclear Plasm stains red. It is a very open reticulum, composed distinctly of granules strung together in a moniliform manner.

The Nucleolus resembles those of specimens stimulated for one minute.

Effect of Stimulation for Ten to Twenty Minutes on the Cells of the Third Glandular Layer. Fig. 29.

The Cell Wall and Cytoplasm resemble those of specimens fed for one minute.

The Nucleus has become still shorter and broader. It shows the same affinity for the red stain as the last type.

The Nuclear Chromosomes have slightly increased in size, but in other respects they are like the Nuclear Plasm and Nucleolus as in the last type.

Effect of Stimulation for Twenty Minutes to One Hour on the Cells of the Third Glandular Layer. Fig. 30.

The Cell Wall.—The external longitudinal wall stains pale blue; the wall next the tracheids dark blue.

The Cytoplasm stains very pale bluish purple.

The Nucleus is almost spherical, and stains very pale blue-purple.

The Nuclear Chromosomes are conspicuous deep blue granules of various sizes, and considerably larger than in the control.

The Nuclear Plasm stains reddish purple, and is gathered together in the centre of the nucleus, instead of being distributed in chains. It is still apparently granular.

The Nucleolus is pale red, and much smaller than in the control (fig. 25).

Effect on the Cells of the Third Glandular Layer of Stimulation for One to Four Hours. Fig. 31.

The Cell Wall and Cytoplasm are as in the last type.

The Nucleus is oval, spherical, or irregular in shape. It stains a more or less intense blue, sometimes very deeply.

The Nuclear Chromosomes are conspicuous dark blue granules.

The Nuclear Plasm is scanty and granular, staining reddish purple. It is collected to form a little cloud round the nucleolus.

The Nucleolus stains purplish red. It has a transparent appearance, and contains one or more endonucleoli.

Effect of Stimulation for One to Four Hours on the Cells of the Third Glandular Layer. Fig. 32.

The Cell Wall, Cytoplasm, Nucleus, Nuclear Chromosomes, and Nuclear Plasm as in the last description.

The Nucleolus is purple-red, and is indistinct because it agrees in colour with the granules which closely surround it. One or more endonucleoli are present. In the figured specimen the endonucleolus is large.

Effect of Stimulation for Twenty to Thirty Hours on the Cells of the Third Glandular Layer. Fig. 33.

The Cell Wall.—The external wall is pale blue; the internal wall is deep blue.

The Cytoplasm is very scanty. It stains a very pale blue, thus differing in a very marked manner from that of the other gland-cells. Sometimes there is a trace of red, or an appearance of a few red granules here and there.

The Nucleus is irregular in shape, and stains pale pinkish purple, and apparently quite homogeneous.

The Nuclear Chromosomes consist of a number of dark blue granules of varying size which are peripherally placed.

The Nuclear Plasm is altogether absent, at least no granulation can be made out, only a diffuse stain.

The Nucleolus is pale red and transparent-looking. It possesses one or more endonucleoli.

Cells of the Third Glandular Layer Two to Three Days after Feeding. Fig. 34.

The Cell Wall.—The external wall is pale blue, the internal wall deep blue.

The Cytoplasm stains pale blue.

The Nucleus is irregular in shape, slightly oval, and stains blue.

The Nuclear Chromosomes occur as a number of scattered granules, each apparently double.

The Nuclear Plasm consists of blue granules, arranged in rows. It is rather scanty, and stains much less deeply than the nuclear chromosomes.

The Nucleolus is large, stains purplish red, and contains one or more endonucleoli.

Cells of the Third Glandular Layer Seven Days after Feeding. Fig. 35.

The Cell Wall is pale blue.

The Cytoplasm is pale blue and somewhat granular, as it is in leaves that have never been fed.

The Nucleus is spindle-shaped in some tentacles, but not drawn out at the ends into such fine acicular points as in controls. The spindle-shaped nuclei are coloured blue like those of controls. Nuclei like fig. 34 are also common.

The Nuclear Chromosomes are exactly as in specimens that have never been fed.

The Nuclear Plasm consists of blue granules like those of control specimens, arranged in moniliform rows. In some nuclei the appearance is most suggestive of a spiral arrangement of these chains of granules round the nucleolus.

The Nucleolus is large and deep red as in controls, with clear endonucleoli, and surrounded by Frommann's clear zone.

In general appearance the cells, as a whole, are very like those in the control specimens.

Summary and Concluding Remarks.

As the result of an appropriate stimulation of the gland-cells of Drosera by food, it is seen that the basophile cytoplasm becomes used up, and is represented ultimately by a very scanty eosinophilous plasm. The restoration of the cytoplasm is brought about by the nucleus absorbing food material, metabolising it, and then excreting it into the cytoplasm, as is proved by—

(1) The great increase in the bulk of the basophile nuclear chromosomes during a period preceding the restoration of the cytoplasm.

(2) The scanty amount of eosinophilous nucleolar chromatin, and small size of the nucleolar organ during the same period.

(3) By the neutrophile cytoplasm first appearing immedi-

ately round the nucleus; and this extra-nuclear plasm corresponding in colour reactions (chemically) and in size of granules (morphologically) with the intra-nuclear plasm.

(4) By the diminution of the nuclear chromatin, and increase in the amount of nucleolar chromatin, whenever the cytoplasm has been restored.

That the extra-nuclear plasm undergoes a further change on its own account seems to be proved by the purple colour gradually being changed into blue.

Whether the nuclear or the nucleolar chromatin is the primary product of metabolism; whether they are formed simultaneously by the nuclear or nucleolar organs respectively; whether the one or the other plays the part of a ferment-secreting organ in relation to nuclear metabolism, are questions only to be answered after further investigation.

The aggregation of the nuclear chromatin into a definite number of V̄-shaped segments—eight in Drosera—proves that such a change is not a feature characteristic of mitosis, but simply a sign of great activity in the nuclear organs.

I intend continuing my research on Drosera with the view of determining whether food materials which differ chemically will produce characteristic changes in the gland-cells.

DESCRIPTION OF PLATES 23 and 24,

Illustrating Lily Huie's paper, "Changes in the Cell-organs of Drosera rotundifolia produced by feeding with Egg-albumen."

All the figures were drawn with Zeiss's camera lucida, Zeiss's $\frac{1}{12}$ apochromatic oil immersion objective, and No. 8 compensating ocular. The tube of the microscope was drawn out to its full extent, and the drawing-paper was laid on the table. The figures of the lateral superficial cells, and those of the cells of the third glandular layer, were almost invariably taken from the same gland, as the corresponding figures of the apical gland-cells.

Figs. 1—12 show the cytological changes in the apical gland-cells, produced by feeding with egg-albumen :

Fig. 1. The resting condition.
Fig. 2. One minute after feeding.
Fig. 3. One minute after feeding. Slightly more advanced.
Fig. 3 A. Appearance of semi-boiled white of egg, fixed in picro-corrosive and stained exactly like the sections. No blue colour visible. Granulation much finer than in the cells.
Fig. 9 B. Nucleus from cell, fed for thirty hours on yolk of egg.

Figs. 13—24 show the cytological changes in the lateral superficial gland-cells.

Fig. 13. The resting condition.
Fig. 14. One minute after feeding.
Fig. 15. One minute after feeding. Somewhat more advanced.

Figs. 25—35 show the changes in the nucleus of the cells of the third glandular layer.

Fig. 25 A. Nucleus cut longitudinally.
Fig. 25 B. Nucleus cut transversely.
Fig. 26 A. Nucleus cut longitudinally.
Fig. 26 B. Nucleus cut transversely.

Observations upon the Development and Succession of the Teeth in Perameles; together with a Contribution to the Discussion of the Homologies of the Teeth in Marsupial Animals.

By

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and

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With Plates 25—32.

Part I.—Introduction.

Recent years have witnessed a noteworthy revival of interest in the morphological interpretation of the facts of mammalian dentition. This renewed interest is traceable to the more systematic and thorough-going application of the methods of embryological study to the distinctively morphological, and no longer merely to the histogenetic aspects of the phenomena of tooth development. These methods have yielded a valuable supplement to the work of the systematist and palæontologist, and have provided a very necessary basis for a critical estimate of views arrived at by investigators working along such different lines of research.

As a result of the fresh activity to which we have alluded there has sprung up a pretty copious literature, which, added to that previously existing, renders the study of the problems of dentition at the present day by no means a light one.

It is not, however, the object of the writers to attempt to give any comprehensive sketch of the evolution of the problems met with in such a study. Nor do they profess to supply anything like a complete and adequate discussion, even of the present position of these problems. Their aim has from the outset been a much more limited one, and they feel absolved from making any such attempt all the more that general literary surveys of the kind referred to, along with sufficient bibliographical data, have been published comparatively recently by more than one distinguished authority in this department of science. Special reference may here be made to the address by Professor H. F. Osborn at the American Association in August, 1893, specially important from the palæontological side, to the masterly résume given by Professor Gustav Schwalbe in an address to the "Anatomische Gesellschaft" at Strassburg in May, 1894; to the brief but lucid and interesting account by Mr. M. F. Woodward in 'Science Progress' for July, 1894; and, lastly, to that given by Professor W. Leche in his recent important monograph on "mammalian tooth-development in the 'Bibliotheca Zoologica,' 1894–5.

But although in the following pages no effort is made after historical completeness, abundant reference must necessarily be made to the various phases of scientific opinion upon the most important dentitional questions, and we trust that our statement of these questions will be found to be not only accurate, but sufficiently detailed for the purposes of discussion.

In spite of the substantial enlargement of our knowledge of the mammalian dentition attained of late years, it must be admitted that no final settlement of some of the more important issues has yet been arrived at. On the contrary, certain of the more novel phenomena recently brought to light have so far served rather to complicate than to simplify the problems involved.

No mammalian order has called forth more discussion in respect of its tooth equipment than the Marsupialia. Primarily, no doubt, this is owing to the inherent peculiarities of the dentition in this order. But in part also it is due to the fact that the more or less peculiar characteristics of the dentition in the Metatheria (and, a fortiori, in the Prototheria) have, on account of the usually accepted zoological position of the group, been approached with a quite special interest, as likely to afford important clues to the phylogenesis of the teeth in Mammalia generally. A consideration of the literature of this branch of the subject might indeed suggest that something like unanimity has been attained upon several important matters, e.g. the serial homology of the deciduous premolar of Marsupials with the more anterior premolars. As will appear in the sequel, however, it is the opinion of the present writers that, even on the points referred to, the discussion is very far from being finally or satisfactorily concluded. As regards several other weighty questions, no pretence of agreement is made by various investigators; and in not a few instances the accounts of what are obviously identical phenomena reveal actual discrepancies of observation, as well as very diverse interpretations of those facts in regard to which their observations do coincide. It has accordingly appeared to the authors highly desirable that the body of fact and observation available for the construction of adequate hypotheses concerning the marsupial dentition should be further supplemented from the developmental side; and, being comparatively favorably placed for obtaining suitable material, they have been induced to undertake the task of, at least, providing further reliable records of observations upon tooth development in Marsupials. With this object the polyprotodont genus Perameles was chosen in the first instance, and P. nasuta has throughout furnished the major part of our material, and formed the basis of most of the descriptive part of this paper. Other forms, however, have been examined with reference to particular points, e.g. Dasyurus viverrinus, Phascologale cristicauda, Trichosurus vulpecula, and Macropus ruficollis.

Perameles was specially chosen as our type for study and description as representing a fairly generalised marsupial type which has not hitherto been made the subject of any complete or extended investigation, though several authors (Röse [1], Woodward [2], and Leche [3]) have made reference to observations made by them on isolated individual stages of its development.

The series of specimens at our disposal has been a fairly complete and satisfactory one, and in its collection we are indebted to the following gentlemen for material generously placed at our disposal:

The Trustees of the Australian Museum, Sydney; Professor W. A. Haswell, University of Sydney; Professor W. Baldwin Spencer, University of Melbourne; Messrs. C. W. De Vis, Brisbane Museum; A. G. Hamilton, George Masters, A. M. Lea, and Dr. R. Broom.

Review of Past and Present Opinion.—Whilst we have disclaimed any attempt after historical completeness, we nevertheless deem it expedient, or even imperative, before attempting to set forth our own observations, to make such reference to past and present views as may be necessary to provide a basis for the future discussion of our own observations.

In 1867 the law of the succession of the teeth in the Marsupialia was definitely formulated by Flower (4).

This author claimed to show by means of his own researches and those of others that, wherever a tooth-change can be shown to occur in marsupial animals, such tooth-change involves only one tooth—the last of the premolar series.

This view being accepted, the question naturally arose—"to which set of teeth in non-marsupial Mammals do the non-changing antemolar teeth of Marsupials correspond?" Flower concluded that they answered to the permanent or successional teeth of higher Mammalia, and that thus only one true milk-tooth was present in any Marsupial. This interpretation, taken along with the more primitive character of the marsupial organisation in other respects, led him to suggest that "the milk or deciduous teeth may rather be a set superadded to supply the temporary needs of Mammals of more complex dental organisation" (4, p. 639).

The views of Flower were subsequently adopted and extended by Oldfield Thomas (5), who adduced in their support certain important palæontological facts.

Upon the relation of the Eutherian to the Metatherian stocks, Thomas is notably explicit. He considers that "the change from Metatherian to Eutherian" occurred, "in all probability," within the limits of the family Dasyuridæ. His conclusions, therefore, that "the rudimentary tooth-change of Marsupials represents an early stage in the first formation" of a complete change, and that the Marsupials are "still in a backward condition out of which the Eutheria have long since passed," are of quite fundamental significance in his interpretation of the phenomena of the dentition of Mammals generally.

The general argument in favour of Flower's view of the primitive character of the single tooth-change in Marsupials, derived from the zoological position of the order, is expressed thus by Thomas:—"When we consider that in every character of their organisation the Marsupials are infinitely behind and at a lower stage of evolution than the placental Mammals, it would appear to be a total subversion of all the ordinary rules to suppose that in this one character of their dentition they should have passed on in advance of all the other Mammals, and, having gone through the condition in which the latter now are, should have again nearly evolved away that process of tooth-change which is to its placental possessors so evidently advantageous" (5, p. 450).[1]

A more special argument is also derived from the fact "that five out of the six families of Marsupials, natives both of Australia and America, have, with the comparatively unimportant exceptions already noted as occurring among the Dasyuridæ, arrived at precisely the same stage of tooth-change"—a circumstance which would be unlikely to occur if

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[1] It may be remarked that this is precisely what has actually occurred in Dasyurus and Sarcophilus in relation to other Dasyuridæ, according to Thomas himself, i. e. after first evolving a tooth-change (single, of course), they have next proceeded to get rid of it.

the modern tooth-change were a remnant of a fuller one, for then " we should naturally expect that, under the very various conditions of the struggle for existence, equally various degrees of reduction would have been attained to." It may be pointed out that the cogency of this argument would entirely disappear if it could be shown to be probable that the (hypothetical) reduction was dependent upon conditions of life common to, and peculiar to, the entire group.

In professing his firm adherence to Flower's view that the teeth of Marsupials in front of the last premolar represent the permanent teeth of other Mammals, Thomas states that he was led to that opinion by " finding the impossibility of working out the general homologies of the teeth on the basis of the opposite view," and by very extended observations of specimens.

It is perhaps unnecessary to follow Mr. Thomas through his somewhat elaborate and rather far-fetched doctrine of a retardation which ought to have occurred in Marsupials if their teeth had formerly possessed milk predecessors which were subsequently lost,—a retardation parallel to that which occurs in the case of the last permanent premolar; and which he alleges as also occurring in the case of the first incisor in a number of Marsupials, probably by way of preparation for the acquirement of a milk-tooth. Thomas himself remarks upon " the difficulties in the way of understanding how the ordinary processes of evolution " could first have " brought about such a preliminary retardation,"—a remark with which his readers will readily agree.

The above views have now an interest for us which is largely historical, since Thomas has explicitly surrendered the main point of his position in view of later discoveries.

The views of Flower, prior at least to Thomas's advocacy of them, had not as a whole received general approval. His identification of the non-changing antemolar teeth of Marsupials with those of the permanent series of Placentals was, indeed, practically universally received. The view, however, that the seemingly almost complete monophyodontism of

Marsupials was a primitive condition, and that the original mammalian stock was actually monophyodont, had not met with general acceptance previous to the publication of Thomas's paper in 1887. Notably Winge (6)[1] maintained, as against Flower, that in all probability the condition in Marsupials was secondary, and due to an almost complete loss of the milk dentition in that group; and this opinion of Winge possessed many adherents.

The emphatic reiteration of the views of Flower by so eminent an investigator as Oldfield Thomas, upon the grounds of his own extensive researches, seems to have served as a stimulus to renewed consideration of the subject of marsupial dentition, especially from the developmental point of view. The first-fruits of the latter research appeared in December, 1891, in the form of a paper by Kükenthal (7) on tooth development in Didelphys.

In his introductory remarks Kükenthal indicates the Flower-Thomas theory of the primitive character of the single tooth-change in Marsupials as the prime consideration with reference to which his investigations were directed. Thomas had admitted that a discovery of successional germs accessory to the non-changing marsupial (antemolar) teeth would be fatal to the theory in question, and the result of Kükenthal's examination of Didelphys was to reveal the presence, at the lingual sides of nearly all the developing teeth in that animal, of epithelial ingrowths of the primitive dental lamina. These ingrowths he naturally interpreted as rudimentary enamel-germs of successional teeth, in series with the undoubted enamel-germ of the actual successional premolar ($p\,\frac{3}{3}$, i.e. *pm.* 4 of Thomas).

Kükenthal thus believed that he had established on a perfectly secure basis, the view that the existing teeth of Marsupials in front of the last premolar are in reality milk-teeth in series, not with the persisting last premolar, but with its milk

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[1] We have been unable to consult Winge's original paper, and have had to rely for our knowledge of his views upon the accounts of Kükenthal and Leche.

predecessor. Kükenthal's claim was promptly admitted by Thomas himself (8) as apparently incontrovertible, and he therefore no longer refuses to subscribe to the view of a primitive diphyodontism of mammals, "probably in direct succession to the irregular polyphyodontism of their reptilian ancestors,"—a diphyodontism which "may even have existed in what were in other respects members of the latter class." Nevertheless Thomas is far from admitting that the whole problem of the phylogeny of the dentition in Mammalia is thereby cleared up. He regards, e. g., the fact that the Mesozoic Triconodon changed a single tooth only, as rendered inexplicable by the newer theory. Still he definitely adopts the latter, merely passing on to a criticism of Kükenthal's views upon other issues, i. e. the homologies of the individual premolars, and the questions of the nature and mode of origin of the molars.

An important and elaborate memoir on the development of the human teeth by Carl Röse was published in 1891 (9), and apparently independently of Kükenthal, and contemporaneously with him, Röse had also worked out the tooth development of Didelphys as well as of several other marsupial forms. The results of this work were published in September, 1892 (1).[1]

As regards the question of the presence of rudimentary enamel-germs of successional teeth, Röse largely confirms the observations of Kükenthal upon Didelphys,[2] and he showed that lingual ingrowths of the dental lamina, similar to those found in Didelphys, were present in all other Marsupials he examined.

During 1892–3 Röse continued to publish the results of an active investigation into the phenomena of tooth development in a number of other forms, both mammalian and reptilian.

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[1] Röse's views upon the marsupial dentition were, however, outlined in his paper on tooth development in Edentata, published in July, 1892 (34).

[2] An unfortunate error in Röse's paper, subsequently acknowledged by him, was his mistaking the enamel-organ of the deciduous premolar for that of the first molar.

Röse has also pushed boldly into the realm of theory, and has presented hypotheses to account not only for the more divergent types of mammalian dentition, but for the derivation of the latter from that of polyphyodont and homodont ancestors. We cannot avoid the feeling that in his views upon these matters the quantity of theorising is somewhat disproportionate to the extent of the basis of fact and observation. His schematic representation (29), for example, of the mode of derivation of the human dentition from a lowly reptilian-like type appears to us to be a rather striking instance of a highly ingenious but a somewhat uncritical exercise of the scientific imagination.

Röse's contributions to our knowledge of tooth development are, however, both extensive and of very great interest and importance, and his interpretations are, as a rule, entitled to the utmost respect.

As regards the mammalian dentition, Röse is a powerful advocate (*a*) of the primitive diphyodontism of the mammalian stock, (*b*) of the doctrine that the multituberculate teeth of the heterodont dentition originated by a process of fusion of several individually distinct and simple conical members of a homodont dentition.

In these views Röse has, of course, had many predecessors, Kükenthal among others, but Röse's attempts to further establish the validity of these propositions deserve special recognition.

As regards the marsupial dentition in particular, Röse's general conclusions may be thus summed up :—That dentition, like that of mammals generally, was originally diphyodont: "Allein die Thatsache, dass hinter allen Zähnen zeitweilig eine zusammenhängende, bandförmige Zahnleiste verläuft, beweist uns, dass die Beuteltiere von diphyodonten Säugern und weiterhin von polyphyodonten reptilienähnlichen Vertebraten abstammen" (34, p. 508). And again: "Das Milchgebiss der Säugetiere ist nicht eine Neuerwerbung, sondern eine phyletische Vererbung und ist entstanden durch zusammendrängen mehreren reptilienähnlichen Zahnserien in eine Einzige" (ib., p. 509). Thus it is held that during phylogeny the Marsupials have suffered loss of all the teeth of the "permanent" series in front of the last premolar, with, indeed, the doubtful exception, according to Röse, of the last upper incisor in some forms.[1]

In this connection Röse remarks upon the "noteworthy constancy of the group with reference to the single tooth-change from Mesozoic up to modern times—a constancy which had seemed to Thomas so inexplicable,—and he offers the following explanation:—"Die Beuteltiere sind aber bei der Reduktion des vielfachen Zahnwechsels der reptilienähnlichen Vorfahren der heutigen Säuger gleichsam über das Ziel hinausgeschossen und haben sich in eine Sackgasse verrannt, aus der kein Rückweg möglich ist" (1, p. 705). He also suggests that such a reduction could only be serviceable if at the same time the milk-teeth came to grow from persistent pulps,—a condition which, he remarks, is attained only by the wombat.

Röse agrees with Kükenthal in referring the molars to the same series as the other teeth, i. e. to the milk or first dentition, if they are to be referred specifically to one or other of the two series represented by the antemolar teeth. Into his later view respecting the possibility of the molars representing "end-members of separate dentitions" we need not now enter.

In 1893 a highly interesting and important paper was published by Röse (11) on the subject of tooth development in Phascolomys. We are of opinion that the full significance of the observations therein recorded has been apprehended neither by subsequent writers nor by the author himself, though the latter undoubtedly attached considerable importance to them.

The results of Röse's research (for which unfortunately only one pouch specimen, of 19 mm. body-length, was available) would seem to tend towards a confirmation of a long discredited statement of Owen's (15), to the effect that the incisor teeth and the first molar are changed in the young animal. It appears from Röse's investigation that at a comparatively early

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[1] This view regarding the nature of the last polyprotodont incisor has received no confirmation whatever from any later observer.

stage in its tooth development the wombat possesses rudiments of teeth entirely unrepresented in the adult dentition; and that, further, certain of these teeth are precociously calcified, and, according to the author, obviously belong to a generation antecedent to that to which the permanent teeth of the animal belong. In addition to this he finds, in a position in the jaw corresponding to that occupied later by the single adult premolar, a single pointed, precociously calcified tooth, provided with a large and "bulbous" lingual germ ("Ersatzleiste"), which latter he regards as the true germ of the permanent premolar; the rudimentary but well-formed calcified tooth beside it being the deciduous predecessor to which Owen apparently referred.

In summing up his results Röse first emphasises the fact of the possession by the wombat of two typically distinct dentitions "ganz ähnlich wie die placental en Säuger." Of these two incomplete series he points out that all the members of the first, and several of those of the second, must be resorbed in early life.

He then proceeds to put the important question, "which of the two tooth-series of wombat corresponds to the milk series of other Marsupials?" And just here he finds himself involved in some little difficulty. For, while he finds it easy to homologise the posterior elements of the series with those found in other Marsupials by reckoning the "Ersatzleiste" of the small calcified "premolar" as the germ of the persisting one, he feels almost compelled to identify the calcified and precocious germs of the first generation in the anterior segment of the jaw with the "milk" (persisting) dentition of other Marsupials. He is thus led to postulate a fundamental difference in homology between the teeth of the anterior and posterior segments of the jaw respectively, and thus also between the anterior persisting teeth of wombat and those of other Marsupials. "Während die Schneidezähne der polyprotodont Beutler zur ersten oder Milchzähnserie gehören, rechnen diejenigen vom Wombat zur zweiten oder bleibenden." He adds, however, that it is not improbable that the condition found in wombat may ultimately be found characteristic also of some other diprotodont Marsupials.

It will be noted that if the view for which Röse indicates his preference be correct, the acceptance of it implies at least a partial surrender of what we may call the Kükenthal-Röse position in relation to the marsupial dentition generally.

In his recent work (3, pp. 100, 101), Leche has definitely adopted that interpretation of Röse's observations which Röse himself somewhat reluctantly put aside, and has thus attempted to conserve in its integrity the ruling modern theory of the marsupial dentition as a true "milk" series.

The solution which Leche confidently advocates involves the interpretation of the prematurely calcified teeth of wombat, not as homologues of milk-teeth, but as vestigial remains of a "prelacteal" series inherited from the polyphyodont ancestors of the Mammalia.

It will appear in the sequel that the present writers are very strongly inclined to adhere to that interpretation of these rudimentary teeth which Röse decides to accept in the paper under consideration. But in so doing it will appear that they also advocate a much wider extension of the hypothesis involved in that interpretation than was contemplated by Röse.

In the 'Proc. Zool. Soc.,' May 2nd, 1893, there appeared a paper by Mr. M. F. Woodward (2) on "The Development of the Teeth of the Macropodidæ," in which the author gave an account of his discovery in certain members of that family of a number of small calcified teeth supplementary to the proper rudiments of the adult dentition.

Thus in the upper jaw of Petrogale he found, in addition to the germs of the three adult incisors, three "minute calcified rudimentary (or rather vestigial)" teeth. So, again, in the case of the lower jaw he found two vestigial teeth in addition to the enamel-germ of the permanent lower incisor. From his facts Mr. Woodward draws certain conclusions regarding the relations of the dentition of Macropods to that of Polyprotodonts and primitive Marsupials, with which we are not here concerned. It is to be noted that the author refers the adult incisors of Macropods to the first dentition, accepting, as he does, the criterion which had seemed sufficient to Kükenthal and Röse. He says, "If these various and often minute cord-like downgrowths of the dental lamina (lingually to the enamel-germs of the adult incisors) are to be interpreted as representing rudiments of teeth, as seems probable from comparison with the known rudiments of the first or second dentition in other mammals, then we find that in the kangaroos the incisor teeth all belong to the first dentition, that the relations of the canines are uncertain," &c. &c. Again, on account of the presence of a "distinct but small" lingual downgrowth by the side of the enamel-germ of the foremost upper vestigial tooth, Woodward referred that tooth to the first dentition equally with the germs of the adult teeth; and he extends the same determination to the other two, partly from their general analogy to the first, and partly on account of certain observations as to their relative position in reference to the dental lamina, and to the enamel-germs of the neighbouring adult teeth.

Similar reasonings prevailed with him in regard to the lower incisors, and accordingly he is led to interpret the vestigial incisors simply as decadent members of the same series to which the adult teeth belong.

Mr. Woodward's paper constitutes the earliest publication in which were recorded observations upon the presence of undoubted embryonic vestigial teeth in Marsupials. Röse's paper, dealing with such structures in wombat, was not published till 4th August, 1893.

On the same day there appeared in the 'Morphologisches Jahrbuch,' Bd. xx, a paper (12) by Professor W. Leche, which bore the date January, 1893. This contribution was supplementary to his paper (13) in the preceding volume on the subject of mammalian tooth-development, and it contains an account of his researches into the development of the teeth of Myrmecobius, to which in his previous paper he has referred as still in progress.

In Myrmecobius Leche had discovered the presence of calcified structures connected with the dental lamina, and placed labially with reference to it and to the enamel-germs of the adult teeth. These calcified tooth-remains, though less perfectly formed, or perhaps we should say more completely degenerated, than those described by Mr. Woodward, bear a striking general resemblance to his, both in respect of their topographical relationships and of their structural features. Leche's interpretation of them was, however, widely different from that given by Woodward in the case of the Macropod vestigial teeth, for he viewed the calcified structures as the sole remains of an entire "prelacteal" dentition which had otherwise become suppressed. To this view Leche still adheres in his latest work (3), where he claims that both Woodward's and Röse's observations just referred to are to be explained along similar lines.

Woodward himself (14) has accepted Leche's notion of a "prelacteal" dentition, so far at least as Myrmecobius is concerned, and he believes that he has obtained confirmation of the view through a similar discovery in Phascologale.

By far the most important recent contribution to the literature of this subject is the comprehensive monograph by Professor W. Leche already referred to (3).

In addition to a rich collection of observations copiously illustrated, this book contains a systematic discussion of all the more important issues raised by a study of the ontogeny of the mammalian dentition. In the latter portion of this paper Leche's views are dealt with in detail in so far as they have a bearing upon the subject-matter of this work. Meanwhile we may remark that one of the most important features of Leche's contribution is his criticism of the commonly prevalent but loose and unreliable notion as to what really constitutes a morphological tooth-germ.

Such a critical determination is urgently needed if any further progress is to be made in investigation of the dentition along the lines of embryological research. In the development of our own views we have been largely stimulated and aided by Leche's masterly essay.

GENERAL ACCOUNT OF THE LEADING CONCLUSIONS FROM OUR OWN INVESTIGATION.

In approaching the subject of our own researches one or two matters call for special remark.

In the first place it is necessary or desirable that we should indicate the general grounds upon which we have felt compelled to depart from the now usually accepted views of the marsupial dentition. The attitude we have felt bound to adopt practically implies a return to Winge's views on the main question involved; but with the notable corroboration of that theory derived from our interpretation of the so-called "prelacteal" vestigial teeth as remains of the true milk series, which, according to Winge, had been entirely lost from the marsupial dentition, except in the case of the deciduous last premolar.

At the time our research was begun, and for some time afterwards, we were fully persuaded of the truth of the Kükenthal-Röse theory, and found no reason to question Leche's identification of his vestigial teeth in Myrmecobius as "prelacteal," to which category we felt, with Leche, strongly disposed to refer the vestigial calcified teeth discovered by Woodward in the Macropodidæ.

We were accordingly highly delighted to (apparently) confirm the accepted views by the further discovery in Perameles of a number of quite similar "prelacteal" rudimentary teeth.

The examination of the earlier stages of tooth development in Perameles, however, forced upon us irresistibly the conviction that the deciduous premolar in that animal must belong to the same series as the so-called "prelacteals."

For in Perameles the deciduous premolar is differentiated from the dental lamina contemporaneously with the so-called "prelacteal" teeth, and at a period prior to the differentiation of any other tooth of the adult dentition. This early formation of the deciduous premolar is not peculiar to Perameles. It is important to note that it occurs also in Didelphys.

But its precocity cannot be explained in Perameles, as it usually has been in Didelphys, by a reference to the future size of the tooth, since, as is well known, it is in Perameles by far the smallest of the whole cheek-tooth series, and, indeed, is absolutely a small-sized tooth. Neither can the early development be explained by its position in the jaw. Indeed, from its relatively posterior position in the young and developing jaw, quite the contrary, i. e. a retardation, might have been expected, such as affects the hinder (molar) elements of the dental series. The discussion of this important matter will be resumed further on in this paper. So much it was essential to state at the outset to render our position intelligible.

It was only with great reluctance that we arrived at this apparently inevitable conclusion that the deciduous premolar was a member of the "prelacteal" series, and although it seemed impossible to interpret the facts in the case of Perameles in any other way, it seemed doubtful whether we should be able to reconcile this view satisfactorily with the facts observed in the case of other Marsupials, more particularly in Didelphys. At least, it seemed difficult to do so in a way that would carry conviction to those whose views on the marsupial dentition were moulded upon the conditions represented in Didelphys. In that animal it has indeed been shown (cf. Kükenthal [7]) that the deciduous premolar is, at the first, the most advanced of all the teeth; but the subsequent course of its development, resulting in the production of a relatively large molariform tooth, seemed anything but favorable to a theory according to which it must be regarded as belonging to an otherwise degenerated "prelacteal" order of teeth.

It may now appear somewhat curious that the very obvious possible explanation of the whole difficulty did not dawn upon us at the very outset. But so completely were we under the influence of the ruling theory of the homology of the permanent marsupial dentition to the milk dentition of higher Mammals, that it was some little time ere it occurred to us even to call in question the grounds of this identification, and at the same time the "prelacteal" character of the vestigial teeth so frequently met with in Marsupials. But we very soon saw that, could the lacteal theory of the permanent marsupial dentition be successfully impeached, all difficulties would be at once removed from the theory we felt bound to advocate from a consideration of the condition in Perameles, where the deciduous premolar and the so-called "prelacteals" evidently belong to one and the same dentitional series. This series would of course no longer be regarded as "prelacteal," but as the true homologue of the milk series of the higher Mammalia.

It was while in this mental attitude to the question that we were first appealed to by Leche's sceptical critique (**3**, pp. 132, 136, &c.) of the criteria usually relied upon as sufficient to determine whether or not any given lingual downgrowth of the dental lamina is morphologically the enamel-germ of a replacing tooth. For the fuller elaboration of our final attitude to the questions thus suggested, and for the evidence upon which our conclusions are based, we must refer to the subsequent sections of this paper. Here it is only necessary to say that we have been led to reject the presently prevailing opinion regarding the more or less swollen downgrowths formed at the lingual sides of the developing marsupial teeth. It is our emphatic opinion that these are not the representatives of the replacing teeth of higher mammals, nor, indeed, are they actual individual tooth-germs at all, but mere residual appendages of the lamina, though they may, in a sense well recognised by Leche, contain the "promise and the potency" of a possible tooth-generation. But the adult teeth in front of the last premolar are the genuine homologues of the replacing teeth of higher mammals, and the milk-teeth of the latter are represented, in front of the deciduous premolar, by the so-called "prelacteal" vestiges, of which, as we shall have occasion to notice, there are abundant remains in Perameles.

We are convinced that this view is amply justified by the considerations set forth in this paper, and that, when deliberately weighed, it will at once be found agreeable to all the facts of development of the marsupial dentition, and to afford a far more natural and unstrained explanation of these facts than the hypotheses heretofore dominant. We cannot but believe that the enormous simplification which would be effected by the adoption (if satisfactorily demonstrated) of the view we now advocate must be appreciated on every hand. In its light the peculiarities of the marsupial dentition may be rendered easily intelligible, and the difficulties of interpretation hitherto associated with these peculiarities forthwith disappear.

In particular the new view would seem to afford the only adequate explanation of Röse's highly interesting discoveries in the wombat. We have already seen how this observer felt bound to interpret the rudimentary teeth he found in his fœtal specimen as belonging to a milk series; and although Schwalbe and Leche have both subsequently expressed the opinion that these rudiments are to be interpreted as "prelacteal," we are of opinion that this view presents many difficulties which are obviated by the simpler and more natural view we feel bound to advocate on the grounds of our own observations. We at least find it now impossible to adopt any different conclusions on the points in question, respecting the morphology of the marsupial dentition, than the following:

1. The permanent teeth of Marsupials are the homologues of the permanent or replacing teeth of higher mammals.

2. The deciduous premolar is a true milk-tooth, and it is not the sole representative of the series to which it belongs, since the so-called "prelacteal" teeth are in reality milk-teeth which have undergone reduction, and have well-nigh wholly disappeared, under the operation of influences unfavorable to their development.

3. The lingually situated downgrowths of the dental lamina

by the sides of the developing teeth are no rudimentary enamel-germs. They are merely portions of a quite indifferent "residual dental lamina" becoming liberated on differentiation of the permanent teeth from the parent lamina. The swelling of the distal portion of the downgrowth is a mere thickening of the free border of the residual lamina, and exhibits no differentiation which is really characteristic of the production of actual enamel-organs.

It is possible that its presence is to be explained in terms of a continued formative activity on the part of an unexhausted dental lamina, an activity which might conceivably issue in the production of enamel-germs of a third series, such as Leche has shown exceptionally to occur amongst other mammals. We are, however, unaware of any single instance in which a differentiation genuinely characteristic of the formation of an enamel-organ of a third dentition has been observed among the Marsupialia.

We may here touch upon one other strong point in the primâ facie case we have been attempting to set forth in favour of the serial homology of the deciduous premolar with the so-called "prelacteal" teeth. This is brought to light in the investigation of those marsupial forms in which the deciduous premolar is inconstant in its presence or altogether absent from the normal dentition. Thus in Dasyurus viverrinus, in spite of the absence in the adult of any representative of the last premolar, either deciduous or successional, we find the deciduous premolar to be constantly present in the young mammary fœtus as a small and precociously calcified vestigial tooth (figs. 80 and 81). It is indeed considerably larger than the vestigial "prelacteal" teeth met with elsewhere, as in Perameles, or even in Dasyurus itself (see $di\,\frac{3}{}$, fig. 23). But in all other essentials it agrees with the "prelacteals," e. g. in time of differentiation, relative situation, and in the fact of its absorption during fœtal life.

An essentially similar condition we find in Phascologale cristicauda, in which also no trace of any milk premolar appears in the adult. This form, however, differs from

Dasyurus in the presence in the adult upper jaw (though only occasionally, according to Baldwin Spencer, **23**, pp. 23 and 26) of the successional last premolar as a "minute and tubercular" tooth (i. e. "p. 4," cf. **22**, p. 276). This tooth is, however, absent from the adult lower jaw.

Thylacinus offers a still more advanced phase of development, for in it the successional premolar is now a well-developed tooth, larger than the second premolar ("p. 3" of Thomas), and is preceded by a milk premolar, though that is still only a minute and rudimentary one, and is shed during infancy (**22**, p. 255).

In these respects Perameles may be regarded as standing just above Thylacinus, for while the last permanent premolar is well developed in both forms, its deciduous predecessor in Perameles is a well-formed though still relatively a small tooth, and is not extruded by the eruption of *p.* 3 (Thomas's "p. 4") until the animal has attained about three fourths adult size. The condition in Perameles may thus be regarded as itself intermediate between that in Thylacinus and that in Didelphys, where the deciduous premolar is a very large and multicuspidate molariform tooth.

It is beyond question that these several conditions represent stages in a process of reduction affecting first the deciduous, and then the successional premolar, until the Dasyurinæ condition is reached.

Is it not in the highest degree probable that in this series we have to recognise, as it were going on under our eyes, the same process of reduction which, at an earlier epoch, has brought the other antemolar milk-teeth down to the condition of mere calcified vestigial structures—the so-called "prelacteal" rudiments? In other words, the deciduous premolar is simply the hindmost member (so far as we know) of a dental series exhibiting various stages of a retrogressive process, some of the more anterior members of the series being represented by various "prelacteal" rudiments.

The Question of Nomenclature of the Premolars.

After careful consideration we have not thought it well to adhere to Thomas's (5) numerical determination of the teeth in the premolar region. That is doubtless an attractive theory, which aims at enabling us to homologise the premolars of modern Marsupials with those of the higher mammals; but we are as yet unconvinced that the case has been sufficiently made out.

Admitting the probability that one of the premolar series has been lost in the ancestors of modern Marsupials, we cannot regard Thomas's contention that it is *p.* 2 which has disappeared as placed beyond all reasonable doubt. Thomas's case for the homology of the last premolar of modern Marsupials to *p.* 4 of other mammals is made up of the following factors:

(*a*) The existence of variations in the way of an occurrence of the hypothetically missing *p.* 2; to which may be added—

(*b*) The alleged occurrence in ontogenetic development of a possible rudiment of an enamel-germ in the position of Thomas's "p. 2."

(*c*) The probable phylogenetic relation of Triconodon to modern Marsupials.

The present writers are, however, of the opinion that there are too many uncertainties connected with each of these factors to warrant our basing any system of nomenclature upon a theory so conditioned.

With regard to the first of these, Bateson (21) has well shown how indecisive is the evidence derived from a study of tooth-variations in determining individual homologies of teeth. In Bateson's judgment "the system elaborated by Thomas breaks down; not because there is any other system which can claim to supersede it, but because the phenomena of variation are not capable of this kind of treatment," because "it is not possible to apply any scheme based on the conception that each tooth has an individual homology which is consistently respected in variation." It will be noted that these contentions do not necessarily affect our belief that the normal teeth are individually homologous in different forms; but only lead to the belief that the facts of variation do not yield reliable evidence in favour of such an homology in any given case. If this be so, then the first and a very important support for Thomas's theory gives way.

Even less weight can be attached to the second consideration adduced in support of Thomas's theory. Röse does indeed mention a possible rudiment of Thomas's "pm. 2" in Didelphys. But for this Kükenthal sought in vain, and, as a result of a later and more extended research on Didelphys and other marsupial forms, Leche formulates his judgment upon the matter in the following passage:

"In diesem Zusammenhange möchte ich ausdrücklich hervorheben, dass die ontogenetischen Untersuchungen bisher keinen Aufschluss über die Homologien der einzelnen Zähne der Beuteltiere und derjenigen der Placentalier gegeben habe. Auch die von Thomas versuchte Homologisirung der Prämolaren der Beuteltiere gewinnt durch die ontogenetischen Befunde keine Stütze" (3, p. 107).

Woodward, however, has recorded his discovery in Macropus giganteus (2, p. 463) of "numerous small enlargements and irregularities" in the diastema between the canine and the "third" premolar of the upper jaw, "some of which may possibly represent the missing premolars." This is vague enough. But he goes on to say, "In the lower jaw, however, there is a very distinct vestige of a tooth in the form of an irregular enamel-organ with enamel epithelium and pulp (fig. 14). This, from its proximity to the third premolar, must represent pm. 2." Since, however, there is another typical marsupial premolar to be accounted for somewhere in this situation, it seems to us not a little rash to pronounce the enamel-organ in question—merely on account of its proximity to *p*. 3—to be "pm. 2," a tooth admitted to be otherwise entirely absent from the marsupial dentition.

Like Kükenthal and Leche, we have sought in vain for any confirmation (in Perameles) of the view that Thomas's "pm. 2" is present in the developing marsupial jaw.

We must therefore hold with Leche that embryological investigation yields no support to the theory of the presence of this hypothetical element of the marsupial dentition; and though its absence may not be conclusive against that theory, it forms an additional difficulty in the way of entertaining a system of homologies based upon the ideal existence of such an element.

Only the third consideration quoted above in support of Thomas's nomenclature remains for consideration, viz. that derived from the dental formula of Triconodon. This would certainly seem to render it highly probable that the ancestors of Marsupials were possessed of four premolars. Thomas's argument rests upon the usually accepted close phyletic or even phylogenetic relationship between Triconodon and modern Marsupials, but it also requires the identification of the last premolar in the latter with "pm. 4" in the former. Now both of these propositions may doubtless be justified as highly probable, but neither, surely, can so far be regarded as scientifically certain. And, in particular, we hold that the evidence so far brought forward is insufficient to determine which premolar, if any, has disappeared in the course of evolution.

On the whole we believe it to be safer in the meantime to designate the premolars simply numerically in the order of their occurrence in the modern marsupial type, instead of founding a system of nomenclature upon the condition of Mesozoic forms whose precise zoological relationships can only be inadequately determined.

And, in adopting in this paper the older method of numeration, we do so the more readily that Thomas's system has not as yet gained general acceptance among Continental writers.

MATERIAL AND METHODS.

For the purposes of our research we have had at our command fourteen different stages of Perameles young. Among these stages P. obesula was represented by three specimens, while the remainder of the material was furnished by P. nasuta.

The youngest was an intra-uterine specimen of P. obesula, and from this early condition onwards we possess a pretty complete series of stages.

The material representative of the more important stages has been sufficiently abundant to enable us to obtain complete series of sections in different planes.

Decalcification was effected chiefly by means of nitric alcohol; sections were cut in paraffin except in a few cases where celloidin was preferred. The stains used were Grenacher's borax-carmine, hæmatoxylin, hæmatoxylin and eosin, hæmatoxylin and picric acid; the hæmatoxylin stains were chiefly used, and are greatly to be preferred, especially the double stains named. We find a very dilute solution (very faintly claret-coloured) of Renaut's hæmatoxylic glycerine to give the best results. The stain should be light if to be followed by eosin, and deep (i.e. of considerably longer duration) if to be followed by picric acid. The latter (as also the eosin) is used in a weak solution in 90 per cent. alcohol. Sections were generally stained on the slide, being fixed by Mayer's, or latterly by Mann's albumen method.[1]

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[1] Owing to the enormous number of serial slides we had to work with, each slide containing very numerous sections, it was rather important to have a short and convenient method of designating any particular section in our notes and descriptions. We have found it exceedingly useful to employ a formula thus:—$\frac{18}{6-\mathrm{III}-\mathrm{E}}$. Here the figure above the line indicates the number of the section in any given row, counting from the left-hand end. The Arabic numeral below the line refers to the number of the particular row of sections on the slide, counting from the top. The Roman numeral indicates the number of the slide in the series; and the capital letter specifies the series itself. For ordinary work the last may often be omitted. The

PART II.—DESCRIPTION OF STAGES.

Stage I.—Perameles obesula: intra-uterine embryo.

Length from anterior convexity of head to curved hinder
extremity of body . . . . 8·75 mm.
Coronal and sagittal series examined.

This stage is that in which an allantoic placenta has been described by one of us (H., 30).

The margins of the gap are not yet soldered together to form the "Saugmund."

As regards its tooth development, this stage appears to correspond pretty closely to that described and figured by Röse as his earliest stage in Didelphys (1, p. 641, fig. 1).

The structure referred to by Röse as "einer leicht ins Kiefermesoderm eingesunkenen Epithelwucherung," and labelled "z. l." in his fig. 1, is present in our specimens in both upper and lower jaws. In the upper jaw a very shallow groove like that shown in Röse's figure appears abruptly a little behind the anterior end of the jaw. This faintly indents the surface of a slight thickened ingrowth of the oral epithelium into the mesoderm. Both groove and solid cellular ingrowth when traced backwards gradually fade away, the superficial groove disappearing sooner than the solid proliferating band of epithelial cells.

In coronal sections of the lower jaw a lens-shaped thickening of the oral epithelium is first met with anteriorly. Soon a shallow groove appears over this, and the thickening then dips more deeply into the mesoderm, becoming almost triangular in cross-section. Further behind, the groove becomes

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description of a slide is thus easily condensed into a series of notes, each prefaced by a formula expressive of the individual section to which the note refers. Frequently one wishes to refer to a number or groups of sections at one time. This is obviously to be accomplished by extending the upper line of the formula thus:—$\frac{18-26}{6-\text{III}-\text{E}}$. Here a group of eight sections in the sixth row of the third slide of series E is conveniently indicated. This method is specially useful for reference from drawings to the sections figured.

slightly deeper and opener, the ingrowth at the same time becoming thicker. Finally the groove opens out and disappears, leaving only the thickened ingrowth, again lenticular on cross-section, which in turn disappears a few sections further back.

Röse's fig. 1 (1) sufficiently illustrates the condition found by us in this early stage.

Stage II.—P. nasuta: mammary fœtus.

Length from vertex to root of tail	17 mm.
Head length	7·5 „

Transverse (coronal) and sagittal series studied.

The dental lamina is already pretty fully developed, though the differentiation from it of enamel-organs has not progressed very far, so that only a very few enamel-organs can be recognised as such, and there are relatively long stretches of quite undifferentiated lamina. The latter is relatively thick (fig. 1, *dl.*), especially at its so-called "neck." In other words, the groove in the mesoderm occupied by the elongated mass of ectodermal cells forming the lamina is a widely open one, its lips not yet being approximated so as to thin out the lamina towards its connection with the deep surface of the oral epithelium.

Upper Jaw.—In the upper jaw the dental lamina extends anteriorly almost, but not quite, to the mesial plane: mesially it is separated by an interval from the lamina of the opposite side. In this anterior incisor region the structure is best studied in sagittal sections, for in the sagittal plane we obtain nearly true transverse sections of the lamina for some distance outwards. Fig. 6 shows a sagittal section parallel with the mesial plane which just shaves the margin of the orifice of Stenson's duct (*S. d.*), and cuts the dental lamina (*dl.*) transversely to its axis some distance in front of this. The lamina is seen to be surrounded by young connective tissue, and the whole is capped by an imperfect dome-shaped roof of bone—the commencing alveolar portion of the premaxilla (*pmx.*). This dome-shaped roof in turn causes an upward inflection of the cartilage of the nasal floor (*al.*) in this its most anterior portion. The upward inflection of the cartilage of the nasal floor is visible also in coronal sections some distance in front of the naso-palatine foramen. In serial sagittal sections, as one traces them outwards from the mesial plane, the dental lamina soon after its commencement is seen to become distinctly thickened and enlarged. This enlargement extends outwards for some distance, and occupies a considerable portion of the anterior transversely lying portion of the lamina. This we take to be the representative of the first upper incisor, although there is as yet no differentiation of an enamel-organ distinct from the dental lamina, and therefore the tooth, as a distinct organ, cannot yet be said to have come into existence.

(It may not be out of place here at the outset to remark that, where we have given interpretations of the facts and phenomena observed [as distinguished from simple records of observations], these interpretations are expressions of judgments arrived at after careful collation of the facts, not only in the stage under notice, but in those both preceding and succeeding. An explanation may thus occur which would not be warranted by the facts noted in the immediate context alone.)

Laterally to the swelling mentioned the lamina is again shallower and less bulky for a short distance. Soon, however, it again swells out to form an enlargement of considerably less transverse extension than the first. This we believe to be the representative of the second incisor. It is developed about the point where the lamina begins to bend backwards in a sagittal direction, as a comparison of coronal and sagittal sections indicates. Immediately external to it (or behind it) the lamina bends much more acutely, and assumes definitely the general sagittal direction which it maintains during the remainder of its course backwards. And just at this acute portion of its curve the lamina expands rather suddenly into a large swelling, oval on cross-section, which is evidently representative of the third incisor tooth. This swelling is of considerable interest, because in connection with it we have a most important and striking feature present. This consists in the differentiation, towards its anterior end, of a shallow but quite definite mesodermal papilla, which indents its labial side, forming the rudiment of the true milk predecessor of the permanent third incisor, whose Anlage forms the bulk of the swelling.

The series of drawings (figs. 1—5) completely illustrates the characters of this milk rudiment ($di^{\underline{3}}$) and its relations to the swollen portion of the dental lamina representing the Anlage of the permanent tooth ($i^{\underline{3}}$).

Thus fig. 1 shows the lamina (*dl.*) in advance of the $i^{\underline{3}}$ region destitute of any differentiation. In the next succeeding section, fig. 2, the labial outgrowth ($di^{\underline{3}}$) has appeared very abruptly growing out from the "neck" of the lamina. In the following section (fig. 3) the milk enamel-organ ($di^{\underline{3}}$) is broader, and its relation to the lamina is slightly modified. The connective tissue on its labial aspect promises to form a papilla (*mp.*), and there is a slight tendency to cupping of the enamel-organ itself. As yet the main portion of the dental lamina exhibits very little modification, but from this point backwards it swells considerably, so that in fig. 4, three sections further back, it is decidedly more massive, whilst at the same time its differentiation from the milk enamel-organ is hardly visible, being indicated only by the arrangement of the nuclei of the constituent cells. Still the milk papilla ($mp.\ di^{\underline{3}}$) is distinct though very shallow. Three sections still further back (fig. 5) the milk enamel-organ has wholly disappeared, leaving, however, a much-thickened dental lamina, representing the hinder and main portion of the Anlage of the permanent third incisor ($i^{\underline{3}}$).

The precise position of the milk-tooth rudiment on the antero-lateral aspect of the entire third incisor Anlage is definitely established, not merely by an examination of the serial sections figured, but by comparative study of sagittal series, which affords complete corroboration of the statements just made.

It will be shown in connection with the description of the next stage that the milk enamel-organ just described undergoes a rapid but most imperfect differentiation, and that in later stages (from Stage IV onwards) it has entirely disappeared. At no time is there any formation of hard dental tissues in connection with it. Comparison of the present stage (II) with the next (III) proves that the labially placed papillary indentation now described has nothing to do with the formation of the papilla of the permanent third incisor.

Behind the site of $i^{\underline{3}}$ the dental lamina is again much reduced in size for a few sections, but presently it enlarges slightly in the succeeding ones and again decreases. This almost certainly indicates the site of the future $i^{\underline{4}}$. Behind this the lamina again enlarges, its cross-section becoming swollen and rounded, and after continuing thus through a number of sections it changes its shape, but without decreasing in sectional area, so as to form a figure elongated in cross-section. This gradually undergoes still further enlargement and elongation by a markedly deeper ingrowth of the lamina: this enlargement we have definitely ascertained to be the canine rudiment. Whether the shallower thickening of the lamina continuous with it in front has any significance as the Anlage of $i^{\underline{5}}$ we cannot be certain, though probably it may be thus interpreted.

The shape of the canine rudiment is quite distinctive in early stages, for already the part of the dental lamina answering to it manifests that tendency to disproportionately deep ingrowth into the surrounding connective tissue which is indicative of the future deep-seated position of the differentiated tooth. Its development may be followed with ease through all the stages from this onwards.

But, as now differentiated, the markedly enlarged canine moiety of the dental lamina is not to be regarded as merely the rudiment of the permanent canine. Subsequent stages, especially that immediately succeeding, prove that from the present Anlage a rudimentary deciduous (milk) tooth ($d^{\underline{c}}$) is also formed. Indeed, the formation of a $d^{\underline{c}}$ is already foreshadowed by the existence of a labially directed outgrowth (vide fig. 7) from near the basal portion (i. e. the "neck") of the elongated laminar ingrowth. A comparison with fig. 13, which shows the exactly corresponding structure in the case of the lower canine rudiment, will sufficiently demonstrate the first steps in that evolution which results in the interesting condition so beautifully shown in the next stage, where we have the well-formed miniature enamel-organ of a deciduous canine tooth above and below (figs. 20 and 37).

On account of the deep extension of the canine Anlage it forms a prominent feature in sagittal sections which pass through its plane, all the more that a long extent of the dental lamina behind it, though quite continuous throughout, is relatively very shallow and insignificant. This latter portion of the dental lamina, representing the whole of the premolar region between the canine and the deciduous premolar, is at the present stage absolutely void of any special structural differentiation. It is, as already said, comparatively shallow (though a "neck" is slightly indicated), and extends backwards through very many sections to the region of $dp\frac{3}{}$.

Here it again deepens considerably, its deeper part or fundus becomes swollen, and ere long it is seen to be deeply indented on its labial aspect by a large papilla, giving it the typical form of a cup-shaped enamel-organ. This is represented in fig. 8, in which it is to be noted that the process of formation of a cup-shaped enamel-organ has gone on without any trace, so far, of the emancipation of the developing organ from the parent lamina. An early stage of the latter process may, however, be recognised in fig. 9 (*rdl.*), which represents the corresponding organ in another embryo from the same pouch. (For the more advanced stage of the same process compare the next stage as illustrated in fig. 24.)

Special attention may once more be called to the fact that although $dp\frac{3}{}$ in Perameles is never other than a small and insignificant tooth compared with the other functional members of the dental series, yet nevertheless at this early stage it is already large and well advanced in its development as an enamel-organ; and it is the only antemolar tooth-rudiment, amongst those which subsequently attain maturity, which as yet exhibits the least trace of papillation. The precocious character of its development is well illustrated in fig. 10 ($dp^{\underline{3}}$), showing in sagittal section its relation to the oral epithelium (*o.e.*) and to the molar portion of the dental lamina (*dl.*) behind it, which is cut vertically in the sagittal plane of the section.

The molar portion of the dental lamina is massive and well developed for quite a considerable distance behind $dp^{\underline{3}}$, as may be seen in fig. 10. At first it is merely flask-shaped on transverse section, but soon its cross-section alters in shape by its distal margin bulging out obliquely in a labial direction.

This constitutes the Anlage of $m^{\underline{1}}$, and is seen in fig. 11 to exhibit a very slight depression at its fundus. . . . Opposite this depression the connective-tissue cells are aggregated to form the very earliest Anlage of a dermal papilla ($mp.m^{\underline{1}}$). Both in front and behind, the swollen Anlage gradually diminishes in thickness. It is worthy of special remark that here we have the very youngest stage in the differentiation of a separate molar enamel-organ, and that in this there is not the slightest indication of a composite character of the dermal papilla whose earliest stage of evolution is here exemplified. It is, from the first, single and individual. In the next succeeding stage we shall find that this incipient enamel-organ has rapidly attained a typical cup-shaped or even "bell-shaped" ("glockenförmig") character, and has "caught up with" $dp^{\underline{3}}$ in its progress towards full differentiation.

Behind the Anlage of $m^{\underline{1}}$ the molar lamina gradually diminishes in size, and finally comes to a rather abrupt termination in a somewhat truncated hinder extremity.

It will be evident from fig. 10 that at least the major portion of the dental lamina in the molar region is directly continuous with the deep surface of the oral epithelium. If the third succeeding section of this series were also figured, it would be seen that this continuity of the lamina with the oral epithelium extends right up to the very hindmost end of the molar lamina. It is thus evident that the dental lamina in the molar region at the present stage has arisen by direct proliferation and ingrowth of the cells of the Malpighian layer of the oral epithelium, as is the case in front of the molar region.

An examination of later stages proves that the line of continuity between the oral epithelium and the molar lamina grows backwards, for some time, pari passu with that rearward progress of the lamina itself which accompanies the gradual elongation of the jaw.

At the present stage the entire dental lamina has retained its connection with the oral epithelium.

In a very young mammary fœtus of Dasyurus the molar dental lamina does not end abruptly, but, after somewhat suddenly becoming shallower, undergoes a further very gradual diminution in depth, until it fades away into a thickening of epithelium, lens-shaped in cross-section, like that which has been described by Röse as constituting the earliest trace of the dental lamina in the anterior region of the jaw.

Lower Jaw.—The armature of epithelium on the oral surface of the lower jaw near its tip is only moderately thick, and at first it thins slightly as it is traced backwards; then suddenly on each side a localised thickening of epithelial cells appears, which invades the underlying connective tissue, and suggests the character of an extremely thick, broad, and somewhat shallow dental lamina. In reality, however, the definitive dental lamina appears abruptly a short distance behind as a further downgrowth from the thick cell-mass in question. (The precise significance of the latter is doubtful. As it is traced further back it becomes largely continuous with the corresponding mass of the opposite side. Further back still, the fused structure is seen to be absolutely continuous with the epithelial cell-mass forming the tip of the tongue, which is thus firmly glued to the upper surface of the lower jaw. As the tongue is traced backwards it gradually frees itself from the latter, and the thickening of the jaw epithelium is then seen to have largely disappeared.) The dental lamina itself, springing abruptly as aforesaid from the deep surface of the epithelial armature of the jaw, becomes almost at once somewhat enlarged, and forms a swelling whose outer aspect is somewhat flattened, while its fundus is more rounded and is somewhat mesially inflected. The outer, more flattened portion now comes to project labially, and is seen to consist mainly of cells, the chromatin of whose nuclei is evidently in the active phase. This feature causes this portion of the mass to appear pretty definitely differentiated with a hæmatoxylin stain. Some sections further back the labial projection of the lamina is deeply indented by a dermal papilla (fig. 12), so as to form a labially directed enamel-organ ($di_{\overline{1}}$) in the cup-shaped stage. This is as yet incompletely differentiated from the common mass of the swollen dental lamina. The entire enlargement of the lamina in this situation corresponds to the region of the first incisor, and the labially cupped enamel-organ, in process of differentiation, is the Anlage of the first milk incisor ($di_{\overline{1}}$). This rudimentary tooth is shown in subsequent stages to undergo a precocious though imperfect development into a minute calcified tooth.

Opposite the papilla of $di_{\overline{1}}$ the main mass of the dental lamina has become considerably enlarged, and the increase in bulk continues behind the rudiment of the milk-tooth. Part of this posterior thickening doubtless represents the hinder part of $i_{\overline{1}}$, but the more posterior portion must provide the material for the development of $i_{\overline{2}}$. This is rendered certain by comparison with the succeeding stage (III), for in both stages the dental lamina makes an abrupt turn outwards and runs transversely for a very short distance, instead of antero-posteriorly. Now in Stage III it becomes certain that $i_{\overline{3}}$ is developed at the postero-external limit of this transversal part of the lamina, and $i_{\overline{2}}$ at its antero-internal extremity. Further, in the present stage the short transversely running part of the lamina commences immediately posterior to the thick part of the lamina which lies behind $di_{\overline{1}}$; whilst at the outer end of the same short transverse part of the lamina appears a new thickening. This, as we shall see, is the only other swelling in front of the canine, and it corresponds exactly in position to $i_{\overline{3}}$ in Stage III.

The posterior limit of this rudiment of $i_{\overline{3}}$ may be recognised by a marked diminution in the sectional area of the lamina, which continues back quite small until it again expands into the typically elongated canine Anlage. The lamina in this region is relatively much elongated on transverse section. It does not, however, penetrate the deeper tissues in a vertical direction, but is diverted rather mesially, parallel with, and pretty closely adjacent to, the deep surface of the oral epithelium. In it a very interesting step in differentiation may be observed in the shape of a very slight but unmistakable attempt at the formation of the enamel-organ of the milk canine (fig. 13, $d._{\overline{c}}$). This is just on the point of becoming cup-shaped, and the dermal papilla ($mp.d_{\overline{c}}$) is beginning to form. In the succeeding stages this Anlage will be followed through the course of its evolution. Here, as in the other examples of milk Anlagen, the structure is first developed not only on the labial aspect of the common canine enlargement of the dental lamina, but opposite its anterior part, the swelling attaining its maximum development just behind the milk rudiment.

As is the case in the upper jaw, the premolar portion of the lamina behind the canine Anlage is small and presents no local differentiation until we reach the region of the last premolar ($dp_{\overline{3}}$). Here the dental lamina becomes much enlarged in all its dimensions, and the bulbous mass becomes indented labially by the large dermal papilla of $d.p._{\overline{3}}$ (the "milk molar"). Its characters are so closely similar to those of the corresponding organ in the upper jaw that the figures of the latter may suffice for both (figs. 8 and 9). Fig. 14, however, illustrates the appearance seen in sagittal section.

The molar region of the dental lamina is in a precisely similar condition to that exhibited in the upper jaw. There is only a slight indication of the differentiation of the first molar enamel-organ. For the most part the molar lamina forms simply a slab-like lamina of considerable dimensions, extending backwards, and continuous in front with the milk premolar.

It is throughout in direct connection with the deep surface of the oral epithelium, as serial sections, sagittal and transverse, show most definitely. But as in the upper jaw, so also here, there is found at a short interval behind $dp._{\overline{3}}$ an outward projection or bulging of the labial aspect of the lamina entirely comparable to that which in the upper jaw serves to broaden the lamina transversely. Here, however, it is placed much nearer to the "neck" of the lamina, and throws a very slightly cupped surface, with the rudimentary papilla in relation to it ($mp.m_{\overline{1}}$), more distinctly on to the labial aspect of the Anlage. Fig. 15 illustrates the condition described, and may be advantageously compared with the figure of the lower canine Anlage (fig. 13).

Behind the Anlage of $m_{\overline{1}}$ the labial projection disappears, and the lamina is left as a simple but fairly thick band lying parallel with the oral epithelium, to which it is attached by a "neck" curved almost at right angles with the dorso-ventral axis of the lamina. As in the upper jaw, this disappears altogether with considerable abruptness.

Our readers will thus observe that in following the development of the dental lamina in Stage II we have been able to trace what to all appearances are the earliest steps in the direction of individual tooth-differentiation. During this period the dental lamina still includes the Anlagen of all the future teeth; none of these have as yet been emancipated from it, and the great majority of the Anlagen have as yet little or no claim to be considered as individualised tooth-germs.

Regarding the morphological interpretation of our observations, especially in the way of the determination of tooth Anlagen, we believe that in the case of a number of these there can be difference of opinion. It has already been indicated that the justification of our interpretation in certain other cases depends to some extent upon our observations in subsequent stages of development. A fuller discussion of these more disputable points must therefore be reserved till later.

Stage III.—P. obesula: mammary fœtus.

Length from vertex to root of tail . . .	22 mm.
Head length	9 „

Studied in coronal and horizontal series.

The examination of this stage reveals features of uncommon interest and importance.

Although our specimen representing this stage is not specifically identical with those of the stages immediately preceding and succeeding, we are confident that this difference is of no consequence, and does not in the least prejudicially affect the conclusions arrived at. So far as it is possible to ascertain and to judge, the condition presented by the stage answers exactly to what one would expect to find, intermediate between Stages II and IV. The correspondences, indeed, are throughout unmistakable.

Here for the first time the great majority of the permanent teeth are sufficiently differentiated to be recognisable as distinct and individual enamel-organs. Most of these, however, as we shall see, are in a very early stage of their individual differentiation, and are not yet emancipated from the dental lamina. The latter structure is relatively massive and absolutely continuous throughout. Its line of attachment to the oral epithelium (proximal margin or "neck") is, however, in parts considerably attenuated; and in a few places, for a section or so, it is just possible to recognise a discontinuity between these structures. This is doubtless due to the commencement of the process of resorption which Röse has shown (9) to produce fenestration of the lamina.

With these extremely rare and slight interruptions the attachment to the Malpighian layer extends up to the posterior end of the molar part of the lamina.

Upper Jaw.—In the incisor region the extreme anterior end of the dental lamina (fig. 16, *dl.*) is directed somewhat mesially, but it no longer lies so distinctly in a transverse direction as in the preceding stage.

The Anlage of the first permanent incisor (fig. 16) is indicated close to the anterior extremity of the lamina by the presence of a subglobular outgrowth ($i^{\underline{1}}$), bulging in an antero-lateral direction, i.e. at right angles with the axis of the lamina (*dl′.*) in this situation. The lamina itself is here plump and swollen, so that on section the two together form a bilobed mass. The labial lobe, however ("$i^{\underline{1}}$"), is merely a localised swelling, while the lingual (*dl.*), becoming more attenuated behind, is continued for some distance onwards to connect with the second incisor region.

It will be remembered that, in the preceding Stage II, $i^{\underline{1}}$ was represented by a mere uniform enlargement of the dental lamina. The outgrowth of the labial mass we have now described constitutes therefore the next step in the differentiation of the enamel-organ of the first incisor. And the growth of this labially projecting mass involves the development, between it and the main body of the lamina, of a depression. This is seen both in front, behind, and especially above, where it is somewhat more pronounced. The surrounding capsule of connective tissue, where that is in relation with the depression in question, exhibits distinct though slight evidences of cellular differentiation. Fig. 16 shows a horizontal section of the first incisor region with the sulcus extending on to the anterior face of the Anlage. Here the connective tissue is less fibrous, and its cells are more closely aggregated together to form what is in all probability the Anlage of the dermal papilla. The latter indeed projects slightly into the sulcus.

The formation of the labial lobe above referred to, and the associated production of a depression between it and the main portion of the dental lamina, are of great importance. We find that when the earliest stage of the process of cupping of an enamel-organ can be traced, that process is commonly, if not invariably, initiated by an overgrowth of the cells of the dental lamina so as to form a projection on the labial aspect; and that the future cup-like depression into which the dermal papilla subsequently fits is foreshadowed by such a sulcus as we have above described. And when the cupped enamel-organ is at length evolved by this process, the outer part of the rim of the cup is constituted by the labially outgrowing lobe, and the inner part of the rim of the cup is formed by the main body of the dental lamina itself. It will be observed that this explanation is essentially in agreement with the idea expressed in Röse's simile regarding the relation of the cupped enamel-organs to the dental lamina, when he says they are arranged "like swallow-nests on a board." Our present stage illustrates the condition found just prior to the actual "swallow-nest" stage of differentiation of the enamel-organs. At this stage, indeed, "sulcus" is the term which more adequately expresses the character of the depression corresponding to the future cup of the enamel-organ. It is open both fore and aft, because it owes its first formation to a mere labial outgrowth of somewhat inchoate character. It may be noted further that this sulcus may be very shallow, or even absent, if the outgrowth of cells takes place near to the free margin of the lamina and extends simply outwards. Thus in the figure given (fig. 11) of the first upper molar Anlage in Stage II the labial prominence is so wide, and extends so near to the free margin of the lamina, that the intervening sulcus is broad and extremely shallow. The cellular condensation indicative of the future dermal papilla is, however, unmistakable. So also, with some difference, in the Anlage of $m\frac{1}{}$, Stage II (fig. 15).

The definitive cupping of such a bilobed enamel-organ of course involves the subsequent appearance of a margin or rim to the cup both in front and behind, in consequence of the more pronounced local limitation of the processes of enamel-organ formation,—processes which at first operate along a stretch of dental lamina indefinitely limited fore and aft.

As may be gathered from Röse's "swallow-nest" comparison, the lingual wall of the cupped enamel-organ is formed at first simply by the dental lamina,—the "board" against which the "swallow-nests" are placed. But by-and-by, as we shall see hereafter, this dental lamina undergoes further differentiation, whereby a proper and distinct inner wall is contributed to complete the enamel cup, leaving a more or less liberated dental lamina independently of the enamel-organ, and situated at its inner or lingual side. This we term the "residual dental lamina."

After this somewhat necessary digression—partly anticipative of what we shall have to point out in detail later on—we may return to the description of the lamina in Stage III.

Behind the posterior limit of the Anlage of $i^{\underline{1}}$ the dental lamina becomes itself progressively reduced in sectional area until it approaches the region of the second incisor, its axis being directed somewhat outwards as well as backwards to reach the latter.

Here it quickly increases both in height and in thickness, and is seen to form the lingual portion ($dl^{\underline{2}}$) of another bilobed mass (fig. 17), comparable to that in the region of $i^{\underline{1}}$. To this bilobed swelling a similar interpretation must be given as that employed in the case of the first; i. e. its lingual portion is simply the enlarged dental lamina ($dl^{\underline{2}}$), while the labial portion of the main mass projecting outwards ("$i^{\underline{2}}$") is the outer or labial portion of the enamel-organ of $i^{\underline{2}}$. Here again the lobes are separated by a groove (fig. 17) passing over the summit of the Anlage, and reaching its anterior and posterior aspects.

In fig. 18 "II" represents a horizontal section of the whole epithelial mass in the region of the second incisor. Here $dl^{\underline{2}}$ indicates the lingual lobe of the mass corresponding to the swollen continuation of the dental lamina itself. This horizontal section is taken above the level which would show the continuity anteriorly of $dl^{\underline{2}}$ with $dl^{\underline{1}}$ in fig. 16, and about the level indicated by the line *ab.* in fig. 17, which shows a coronal section through the same region. (It will be remembered that between the developing teeth the dental lamina is considerably lower than opposite them.) In this figure of a horizontal section there is seen to project from the labial aspect of $i^{\underline{2}}$ a small epithelial mass ($di^{\underline{2}}$), which we believe to be the representative of the enamel-organ of the second milk incisor. The same projection is visible in fig. 17, showing a transverse (coronal) section of the same region.[1] The backward recurvature of this small labially projecting cell-mass, seen in fig. 18, must not be mistaken for an indication of commencing papillation from behind forwards. The series of sections proves that the projection in question is simply being gradually pinched off from the main body ($i^{\underline{2}}$). Higher up, the horizontal sections show only the two lobes of the Anlage of $i^{\underline{2}}$ ($dl^{\underline{2}}$ and "$i^{\underline{2}}$"). It will presently appear that all these features are still better marked in connection with the region of the third incisor, which is partly illustrated in the same drawing (fig. 18, "III").

Horizontal sections taken at a lower level than fig. 18 show the dental lamina ($dl^{\underline{2}}$) in the region of the second incisor to be prolonged backwards into continuity with $dl^{\underline{3}}$ in the third incisor region.

Horizontal sections passing through the upper part of the third incisor-mass closely resemble those through the upper part of the second—viz. in each case we have lingually the lobe formed by swollen dental lamina, and labially the lobe formed by the differentiating labial moiety of the incisor Anlage. As in the cases of the two more anterior tooth-germs, the two lobes are separated by a slight groove or sulcus, and, corresponding to this, over the summit of the Anlage the connective tissue shows a slight cellular aggregation indicating the commencement of the dermal papilla.

Horizonal sections taken a little lower down begin to show a narrow labial projection in a position corresponding to that of $di^{\underline{2}}$ in the second incisor region. Still lower there suddenly appears, closely external to the last-named outgrowth, an isolated mass of epithelial cells. In sections taken still more inferiorly, as shown in fig. 18, "III," this cell-mass ($di^{\underline{3}}$) is found to be really connected with the labial aspect of the main mass of $i^{\underline{3}}$ by a narrow neck (*cb.*). This labial cellular out-

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[1] The single coronal section here figured might seem to suggest that the $di^{\underline{2}}$ projection simply forms the lower limit of a papillated depression on the labial aspect. This is a merely accidental resemblance, as a study of the neighbouring sections in the series amply proves.

growth is further seen to be the seat of retrogressive processes, for in neighbouring sections it shows invasion by connective tissue, partially breaking it up into smaller cell-groups.

This cell-mass is incontrovertibly the serial homologue to the projection figured under "$di^{\underline{3}}$" in the region of the second incisor in figs. 17 and 18, though plainly it is in a more advanced phase of evolution, as its greater isolation from the main mass and condition of degeneracy testify. We are satisfied that this cell-mass can be regarded as none other than the degenerating remains of that very early, labially placed enamel-organ, which we have described and figured above (p. 454, and figs. 2, 3, and 4) in connection with a prominent swelling of the incisor region of the dental lamina in the preceding Stage II. It will be remembered that the localised thickening of the dental lamina was set down as the Anlage of $i^{\underline{3}}$, and the labially developing enamel-organ, imperfectly approximating to the cupped stage, was regarded as that of $di^{\underline{3}}$. The judgment there expressed on the strength of our observations upon the differentiation of the dental lamina in that stage, is now seen to be borne out by the degree of development subsequently attained by the presumably homologous structures.

It is interesting to note that in the present stage, as in the preceding, the third incisor Anlage as a whole is still the most bulky of the incisor series, although the disproportion between it and the other incisor Anlagen is now greatly diminished.

It must be noted in regard to fig. 18 that, in a longitudinal section passing so near to the base of the dental lamina in the $i^{\underline{3}}$ region as that figured, it is only the basal portion of the Anlage of $i^{\underline{3}}$, and the vestigial remains of $di^{\underline{3}}$, which are recognisable. It is only at higher planes that the differentiation of the Anlage of $i^{\underline{3}}$ into labial and lingual lobes is as recognisable as it is, e. g. in the case of $i^{\underline{2}}$ in the same section. Lower down in the case of the latter region, indeed, the labial portion of the Anlage of $i^{\underline{2}}$ similarly disappears from the section as a distinct lobe, leaving only the common lamina plus the labial projection of $di^{\underline{2}}$.

The structure of the differentiating dental lamina in the third incisor region will be rendered further intelligible by a reference to fig. 19, which illustrates a coronal section through this region. Here again the bilobed character is only obscurely manifested, but in the next succeeding section it is as plainly seen as in $i^{\underline{2}}$ in fig. 17, and the cellular aggregation at the site of the future papilla is also clearly seen. The line *ab.* shows the approximate level of the horizontal section in fig. 18. Here the almost isolated remains of the enamel-organ of $di^{\underline{3}}$ are well shown.

In this figure (19) it will be observed that the attachment of the whole mass to the oral epithelium is already narrowed. The deep notch between oral epithelium and dental lamina on the lingual side represents the result of the process of pinching off from the oral epithelium which is now in progress. Originally the attachment no doubt corresponded to the whole breadth of the base of the mass lingually. As a result of the pinching off, the primitive continuity of the dental lamina on its lingual side with the oral epithelium is now obscured.

The plane of the horizontal section through the region of $i^{\underline{3}}$ (fig. 18) is such that although it does not shave the upper free border of the low dental lamina between the low-lying $i^{\underline{2}}$ and $i^{\underline{3}}$, it does cut the lamina between $i^{\underline{3}}$ and $i^{\underline{4}}$, obliquely for a certain distance (fig. 18 $dl^{\underline{4}}$). The fourth incisor Anlage itself, however, lies wholly at a higher level.

It is unnecessary to enter upon a detailed description of the Anlagen of the fourth and fifth incisors. The following statements will suffice. The dental lamina is continuous throughout, both in its own extent and with the oral epithelium. It has undergone enlargement at two places corresponding respectively to the fourth and fifth incisors. These localised enlargements are for the most part of a general character, though bulging mainly to the labial side, except that in each case there is already to be found, projecting labially from near the base of each rounded swelling, a somewhat attenuated epithelial process, precisely comparable in general appearance, structure, and relations to that marked "$di^{\underline{?}}$" in figs. 17 and

18. And as in the latter case, so here, we take these rudimentary labial outgrowths of epithelial cells to represent the abortive enamel-germs of true milk incisors, $di^{\underline{4}}$ and $di^{\underline{5}}$.

It is, however, when we come to deal with the canine rudiment in this stage that we really obtain the most emphatic testimony to the validity of the interpretation which we have given of these interesting vestiges.

From the fifth incisor the dental lamina, though small, is continued back without interruption, and very soon it exhibits that great vertical enlargement which we find to be characteristic of even the earliest canine rudiments in both upper and lower jaws.

In fig. 21 we show a horizontal section which in front passes through the upper part of the fifth incisor mass ($i^{\underline{5}}$). This is seen to bulge out labially (but this is quite above the level of rudimentary $di^{\underline{5}}$). From the inner or lingual part of the Anlage of $i^{\underline{5}}$ the dental lamina is continued backwards for a short distance, to lose itself, in this sectional plane, in a broad area of epithelium (*o.e.*). This, as may be learnt from the drawing, is simply the deep layer of buccal epithelium sliced parallel with its free surface. A section or two higher this epithelial patch disappears, giving place to the prolongation backwards of the narrow dental lamina. Still higher in the series the lamina is seen to undergo enlargement so as to form the most inferior portion of the canine swelling of the lamina (cf. fig. 20). This enlargement markedly increases in thickness as it is followed upwards through the horizontal series. But although the lamina is so definitely enlarged, the differentiation of the permanent tooth has hardly yet set in; certainly no distinct outgrowing labial lobe is apparent, like that observable in the anterior incisor germs. It seems highly probable, however, that the upper and labially deflected portion (marked "*c*" in fig. 20) of the whole Anlage is really equivalent to the labial lobe of the bilobed incisor masses, and is thus about to form the labial portion of the cupped enamel-organ of the permanent canine. If this be so, then the proper morphologically distal margin of the dental lamina is formed by the elbow-like projection marked "*c.dl.*" in the figure, and the flattened surface between *c.dl.* and the apical point of the whole enlargement would represent the site of the future enamel cup. However this may be, the one specially striking and important feature of this general canine Anlage is the presence, near its "neck," of a very perfect miniature enamel-organ in the cup-shaped stage. This structure projects directly outwards in a labial direction from the proximal portion of the dental lamina, and in it we recognise, in accordance with the views we have set forth in the Introduction, the true rudimentary "milk" canine (fig. 20, $d^{\underline{c}}$).

In fig. 22 we have shown another horizontal section through the upper jaw of this stage, through the same region as, but at a higher level than, the section illustrated in fig. 21. In this section we remark the canine thickening of the dental lamina $^{\underline{c}}$, and its more attenuated prolongation backwards into the premolar region ($p^{\underline{1}}dl.$). Beside the thickened canine portion, the enamel organ of $d^{\underline{c}}$ is seen. Further important reference will be made to this figure later on. In the meantime we would draw attention to the fact that the minute, and up to this stage perfect, enamel-organ described above is entirely homologous in position and relations with those small lobular outgrowths of the epithelium of the dental lamina situated labially from the Anlage of the four hindmost incisors, which we have interpreted as representatives of enamel-organs of deciduous incisors. And it is not materially diverse from these in regard to its chronological position.

Now if the serial homology with the incisor vestiges be granted—and we think it is impossible to avoid such a concession—this at once establishes the title of these vestiges to be regarded as true representatives of the enamel-organs of a tooth-generation preceding the permanent teeth. And in our opinion this generation is homologous to the milk series of Eutheria.

So far as we can ascertain, there is not to be discovered either in the present or in the preceding stages any such differentiation in the first incisor region as might be taken to represent there the rudiment of a true milk-tooth, i.e. one which belongs to a tooth generation preceding that to which the first permanent incisor belongs. Nevertheless there is some reason for the belief that traces of an attempt at the production of such a tooth do appear at some time during the development of the teeth in Perameles. And if any such rudiment does occur, then the cell material of which it consists must be derived by outgrowth from the labial side of the base of the mass we have described as constituting the Anlage of the first incisor. It has been stated above that in its size and degree of differentiation (including that of a "milk" rudiment) the third incisor Anlage is the most developed member of the upper incisor series at the present stage. The second is less developed, but yet exhibits features similar to those in the third. So also in the case of the fourth and fifth incisor Anlagen. Although, therefore, no such labial remains occur in connection with the first incisor Anlage in Stage III as we have been able to show associated with the incisors behind it, and more especially in the canine region, we consider ourselves justified in the belief that certain cellular processes situated on the labial side of the root of the dental lamina in the first incisor region of the next stages (IV and V) may possibly represent the remains of the missing rudiment of a $di\frac{1}{}$. In the present stage we may suppose that the latter is not structurally defined from the basal portion of the common first incisor Anlage.

In further corroboration of our views upon the incisor development in Perameles it may not be inappropriate to refer to the condition we have found in another polyprotodont Marsupial, Dasyurus viverrinus. Among our series of stages of development of this form we possess one which, in respect of the third incisor, exhibits a general stage of development intermediate between the present stage (III) and the following stage (IV) of Perameles.

As in Perameles, but in much more marked degree, the third is the largest and most advanced in its development among the upper incisors. Here (fig. 23) the definitive cupping of the enamel-organ of $i^{\underline{3}}$, has at last been effected, and a well-marked dermal papilla (*mp.* $i^{\underline{3}}$) formed, while at the same time the main body of the dental lamina has undergone such differentiation that the mass of cells forming the lingual portion of the cupped enamel-organ is now becoming distinct from the rest of the dental lamina. The latter is, in fact, in process of liberation as a "residual" dental lamina (*rdl.*). (In an antecedent stage the Anlage of $i^{\underline{3}}$ is found to be differentiated to exactly the same extent as the corresponding Anlage in Stage III of Perameles.) A remarkable feature in this section is the rudimentary $di^{\underline{3}}$. Whatever may be said in detraction of the claims of the structure we have described in connection with $i^{\underline{3}}$ in Perameles, to figure as a vestigial enamel-organ, it is impossible to deny that here in Dasyurus we have an indubitable vestigial predecessor to $i^{\underline{3}}$. It seems to us impossible to gainsay the homology testified to by this comparison between Perameles and Dasyurus. And it is superfluous to point out that an admission as regards the identity of the structure labelled $di^{\underline{3}}$ in Perameles with the vestigial tooth in Dasyurus involves the admission of a similar homology for the structures in Perameles in series with "$di^{\underline{3}}$." Here in Dasyurus (fig. 23) $di^{\underline{3}}$ is not simply a degenerate cell-mass, but has assumed specific dental characters by the precocious evolution of a small but thick dentine cap, which again is covered by a hood of regularly arranged enamel-cells. Instead of forming a projection from the rest of the incisor mass, the vestigial tooth rather lies embedded in the labial aspect of the latter near its base. Perhaps this may be explained by a reference to the great labial outgrowth of the Anlage of the permanent incisor which must have occurred to bring about the condition figured, together with the later stationary and unprogressive character of the calcified vestigial $di^{\underline{3}}$.

The examination of an earlier stage of Dasyurus has shown us the third milk incisor at a stage prior to its calcification as a deeply cupped enamel-organ structurally comparable to the enamel-organ of $d^{\underline{c}}$, figured by us in Perameles (fig. 20). Thus we have shown that, in Dasyurus, the rudimentary enamel-organ of $di^{\underline{3}}$, does not undergo the rapid degeneration which is exhibited by $di^{\underline{3}}$, in Stage III of Perameles, but passes into the regular cup-shaped stage which we have seen in the upper jaw of Perameles to be attained only by $d^{\underline{3}}$.

A thoughtful comparison of the following series of figures will render it easy to understand the derivation of the conditions found in the third incisor region of Dasyurus from the earlier condition illustrated in Stage II of Perameles:

Cf. Perameles, Stage II, $i^{\underline{3}}$ and $di^{\underline{3}}$ in figs. 3 and 4.
„ „ III, $i^{\underline{2}}$ in figs. 17 and 18.
„ „ „ $i^{\underline{3}}$ in figs. 18 and 19.
„ „ „ c and $d^{\underline{c}}$ in fig. 20.

In fig. 21 it is seen that the dental lamina is continued backwards, diminished but unbroken, from the region of the canine (marked "*o. e.*") to a point where it somewhat suddenly expands to form the Anlage of the first premolar ($p^{\underline{1}}$). It will be evident from the figure that, though this enlargement appears as a general expansion of the lamina, the addition or increase of cell material is towards the labial side, so that the bulging is in that direction. On coronal section, indeed, one obtains an appearance not far removed from that exhibited in this same stage by $i^{\underline{1}}$, although it can hardly be said that a definite furrow has appeared between the labial bulging and the main body of the dental lamina. Both in figs. 21 and 22 the stretch of dental lamina extending from the canine to the first premolar is recognisable.

In the first-named figure, however, the section passes along the more constricted basal portion or "neck" of the lamina. In the second figure the section passes through the lamina near its free margin or "fundus," where that reaches a high vertical extension in the neighbourhood of the canine. Further back the lamina disappears from the section by becoming vertically shortened, the horizontal section thus cutting it obliquely. The hinder part of this obliquely cut portion of the lamina, as shown in fig. 22, does to some extent coincide with the anterior part of the first premolar swelling in fig. 21. It constitutes, indeed, as coronal sections prove, the lingual portion of the latter mass. The labial bulging of the Anlage is lower down, and is not cut through at this level (cf. fig. 21).

The interval between the tapering ends of the Anlagen of the first and second premolars is a comparatively short one. Here the dental lamina, although quite continuous, appears low and relatively insignificant.[1] This is especially interesting, as it is just here that one might expect some trace of Thomas's hypothetical "$pm^{\underline{2}}$."

A glance at fig. 21 is sufficient to show how far forward the anterior tapering end of the second premolar enlargement of the lamina extends. This enlargement is, indeed, of very considerable antero-posterior extent. Anteriorly its cross-section is rounded, but posteriorly it is much more vertically extended, gradually narrowing at the same time, to be continued on as the vertically elongated but otherwise unmodified lamina, which is found in the region between the second and third premolars (cf. text Fig. 1, A—G).

Fig. 22, representing a horizontal section taken at a higher level than fig. 21, shows the higher hindmost portion of $p^{\underline{2}}$ cut somewhat obliquely, and gradually passing back into continuity with the freed dental lamina on the lingual side of the well-developed milk premolar, $dp^{\underline{3}}$.

On the labial side of the basal margin or "neck" of the

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[1] The lamina looks lower than it really is because it is somewhat folded in its length, so that in cross-section the long axis (being attached to free margin) is not straight, but crooked. Such bending of the lamina near the neck is a common enough phenomenon, and here it is strongly marked. An outwardly projecting elbow in cross-section thus produced may easily enough be mistaken for a true outgrowth of cells in some cases, and such an error must be carefully guarded against. The separation of the lamina from the oral epithelium frequently leaves such an elbow projecting freely, and this may form another source of error in interpretation.

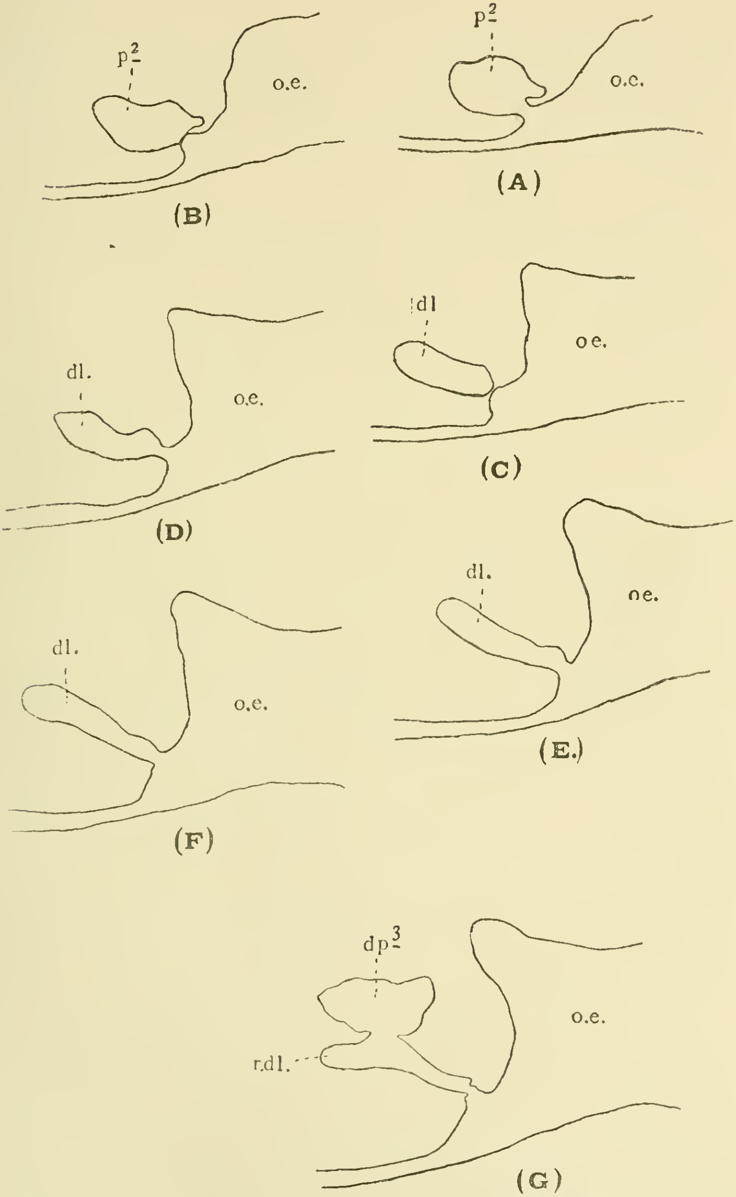

Fig. 1.—A—G. Series of coronal sections (each three sections apart) from premolar region of upper jaw of Stage III, and passing through dental lamina (*d. l.*) between p^2 and dp^3. (× 90 diameters.)

dental lamina, opposite the anterior half of $p^{\underline{2}}$, there is to be seen through several sections a small mass of cells projecting. It is possible that this is representative of $dp^{\underline{2}}$. If so, it is very degenerate, and there is no similar structure beside the Anlage of $p^{\underline{1}}$, though a similar small cell-mass is present in the lower $p^{\underline{2}}$ (see below).

The epithelial projection in question is at all events not due to a bending of the lamina, whose "neck" is short, straight, and perfectly preserved in the region referred to.[1]

It will be remembered that in the preceding Stage II no trace of localised thickening or other differentiation was observable in the premolar region of the dental lamina in front of the site of the third premolar, but that here a tooth Anlage in the cup-shaped stage was already present. And whilst in the present stage the rudiments of the two anterior premolars ($p^{\underline{1}}$ and $p^{\underline{2}}$) are sufficiently defined as such by localised enlargement of the dental lamina, the Anlage of that premolar tooth which was already cup-shaped in the preceding stage is now still further advanced, showing differentiation of the stellate reticular tissue of the enamel-organ (figs. 22 and 24).

Furthermore it is to be remarked that the process of liberation of $dp^{\underline{3}}$ from the lingually-placed dental lamina, which was stated to have just set in the preceding stage, has progressed considerably, so that the freed dental lamina (fig. 24, *rdl.*) now forms a partly independent epithelial ingrowth by the lingual side of the tooth rudiment. The latter is still seen (fig. 24) to be somewhat broadly attached to the labial aspect of the liberated lamina at some distance from its apex, or, strictly speaking, from its free distal margin, and extending nearly to its attached proximal margin or "neck."

A careful investigation of the earliest stages of premolar tooth-differentiation has thus served to show that this third in order among the premolars is not differentiated at all contemporaneously with the

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[1] The question of the significance of certain outgrowths of the dental lamina on its labial side is discussed below in connection with the molar problem.

other premolar germs. On the contrary, it is comparatively far advanced in structural differentiation by the time there appears any trace at all of the anterior premolars, or more than very slight traces of the formation of the enamel-organs of any permanent tooth whatever.

The vertical elongation of the cross-section of the dental lamina just anterior to $dp^{\underline{3}}$ has been referred to. Just in front of the plane at which the enamel-organ of the latter tooth comes into view the dental lamina is higher than at any more anterior part of the premolar region, and as high as it is at the canine thickening. This height is retained by the residual lamina opposite to $dp^{\underline{3}}$. Towards the hinder part of the tooth the lamina becomes separated off from the oral epithelium.

A couple of sections or so behind the disappearance of the last trace of the enamel-organ of $dp^{\underline{3}}$, the free margin of the dental lamina undergoes an abrupt further elongation, i.e. it suddenly penetrates considerably deeper into the connective tissue to be prolonged into the rudiment of $m^{\underline{1}}$, which forms immediately behind as a large cup-shaped enamel-organ. This is not visible in fig. 22, since the plane of that section passes altogether beneath $m^{\underline{1}}$. Fig. 25, however, represents a section taken at a higher plane, where the extreme upper or basal portion of $dp^{\underline{3}}$ is cut through, along with its associated residual lamina (*rdl.*). The latter is seen to be continued backwards into the first molar, and the lower face of the enamel-organ of this tooth ($m^{\underline{1}}$) is seen to be shaved through.

Fig. 26 shows a still higher plane, where therefore the continuity with the lamina in the premolar region is not visible, but where the lamina ($m^{\underline{2}}$ *dl.*), ascending posteriorly, and becoming freed from the hinder part of the developing tooth, is continued backwards into the region of the future second molar. Here the first molar is seen to be a deeply indented ("glockenförmig") enamel-organ (cf. fig. 27), which in its degree of maturity now rivals $dp^{\underline{3}}$. It will be remembered that in the preceding stage the enamel-organ of $m^{\underline{1}}$ had only just become recognisable as a distinct Anlage, though $dp\frac{3}{}$ was already a cup-like enamel-organ.

Figs. 28 and 29 represent coronal sections through $m\frac{1}{}$, rather behind the middle of the tooth, and through the posterior part of the tooth, respectively. In these the process of differentiation of the tooth Anlage from the parent lamina is seen to be well advanced, so that the residual dental lamina (*rdl*). which remains, after separation from it of a tooth rudiment, appears with its free distal margin or fundus somewhat swollen, and freely projecting by the side of the first molar Anlage.

As the residual lamina is traced backwards from the region of $m\frac{1}{}$ (cf. figs. 25 and 26) it retains for a time on its labial face some irregular projections over the area corresponding to that occupied further forwards by the differentiated enamel-organ of $m\frac{1}{}$. A comparison of figs. 29 and 30 (the latter being the tenth section behind the former) will serve to explain this statement. It will also appear that the residual dental lamina of the first molar region has very slightly increased in thickness. Here, of course, it simply constitutes the primitive and undifferentiated lamina intermediate between the region of the first and second molars.

Fig. 31, taken some little distance further back, shows considerable broadening of the lamina at its free margin, after somewhat the same fashion as we have seen to characterise the Anlage of the first molar in the preceding Stage II.

Here, again, the thickening of the fundus appears to be chiefly due to a proliferation of the cells at the labial lip of the free margin of the lamina.

Fig. 32 shows a section immediately in front of the plane at which the molar lamina abruptly terminates.

In the last three sections (cf. especially figs. 30 and 31) the prominent labially directed process (*l.o.*) near the base or attached margin of the dental lamina is the cross-section of a continuous secondary lamina in this region ($m\frac{1}{}$ to $m\frac{2}{}$), whose significance will be discussed below in connection with the questions of molar homology (vide Part III).

Lower Jaw of Stage III.—The phase of tooth development exemplified in the lower jaw is on the whole a little in advance of that found in the upper. This is more notable in some regions than in others. During the period of development which intervenes between Stages II and III, rapid advancement has been made in the differentiation of the first lower incisor Anlage. An attentive comparison of our figures of sections through this region in the two stages (figs. 12 and 33) will chiefly show that the early papillated Anlage of di_1 in Stage II has rapidly passed through the succeeding stages of its development up to and including the development of a perfect, though thin, dentine cap for the papilla. No enamel has been formed, but the enamel-organ—apparently arrested in its evolution—has become separated from the main mass of the dental lamina by a considerable interval, remaining connected with it only by a delicate and disintegrating strand of epithelial cells forming a "Verbindungsbrücke" (fig. 33, *cb.*).

It may be noted that the position of $di_{\overline{1}}$ relative to the Anlage of $i_{\overline{1}}$ appears to have altered during the transition from Stage II to Stage III. In the former the rudiment of $di_{\overline{1}}$ occupied the labial aspect of the more anterior portion of the swelling corresponding to $i_{\overline{1}}$. Here, however, the differentiation and segregation of $di_{\overline{1}}$ have allowed of a growth forward of the bulky Anlage of $i_{\overline{1}}$, unhindered by the presence of any more anterior dental element. Hence, in the present stage, the vestigial $di^{\underline{1}}$ has come to lie opposite the more posterior moiety of its large morphological successor. The relative forward extension of the latter appears to continue at least up to a period represented by our Stage IV (see fig. 56).

We have in the next place to point out that, in the present stage (III) the dental lamina, which was almost wholly undifferentiated from the enamel-organ of $di_{\overline{1}}$ in Stage II, has gone on to form the large papillated dental germ of $i_{\overline{1}}$ (fig. 33). But as yet there is no trace of differentiation of a residual dental lamina from the Anlage of $i^{\underline{1}}$. In the succeeding Stage IV, however, a residual lamina, with its free marginal portion distinctly swollen, is exceedingly well developed (fig. 55) along the whole extent of the tooth ($i_{\overline{1}}$) so that the latter has come to appear as a huge appendage of the liberated lamina.

In the present stage no such differentiation has occurred, and the whole of the large dental lamina remaining over after the differentiation of $di_{\overline{1}}$ appears for the present totally converted into an enamel-organ for $i_{\overline{1}}$. Thus the sequence of phenomena observable in this series of three stages (II, III, and IV) in the case of this particular region goes far to illustrate and support our contentions as to the nature and conditions of occurrence of a residual dental lamina, the so-called "Ersatzleiste" of Röse.

As the papillated Anlage of $i_{\overline{1}}$ is traced backwards it gradually diminishes in sectional area, becoming at the same time more consolidated by loss or marked reduction of the looser epithelial cells in its interior, which become the stellate tissue. When the last trace of papillation has disappeared posteriorly, the structure is seen to be again a mere undifferentiated dental lamina transitional from the first to the second incisor region. In the latter situation it swells out again, and at the same time becomes slightly indented below. There is also a somewhat denser aggregation of connective-tissue cells in relation to this indentation than elsewhere in the fibrous capsule, and the cellular accumulation forms a faint elevation, corresponding to the indentation of the enamel-germ.

This condition of affairs corresponds to what we have already noted in connection with the upper incisors. Beyond the Anlage of $i_{\overline{2}}$ the dental lamina runs for a short distance almost transversely outwards, and then swells into the Anlage of $i_{\overline{3}}$. This relationship is very striking. At first we were puzzled by the appearance of the coronal sections in this region, for both $i_{\overline{2}}$ and $i_{\overline{3}}$ appear in the same section (fig. 34), and the relation of the intervening part of the dental lamina seems obscure. A casual examination would suggest the idea that the Anlage of $i_{\overline{3}}$ is morphologically in the same transverse segment of the dental lamina as $i_{\overline{2}}$, and is therefore related to it as belonging to a labial or elder generation. Its superficial position would almost seem to lend support to this view. But it is absolutely negatived by the facts elicited by more careful study. The true explanation was arrived at by following the dental lamina forwards and backwards in the coronal series, by careful collation with the appearances seen in the corresponding locality in coronal series in Stage II, and above all with those found in the examination of horizontal sections of Stage III itself. By means of such observations we have been able to determine with certainty that the longitudinal continuity of the dental lamina is maintained nearly in the antero-posterior direction from $i_{\overline{1}}$ to $i_{\overline{2}}$, then almost transversely outwards for a short distance between $i_{\overline{2}}$ and $i_{\overline{3}}$, and then again backwards and rather inwards into the canine region.

In other words, $i_{\overline{3}}$ is situated upon the dental lamina posteriorly, in the morphological sense, to $i_{\overline{2}}$, and not morphologically on its labial side, as a coronal section by itself might suggest.

In illustration of these facts, fig. 34 of a coronal section through $i_{\overline{2}}$ and $i_{\overline{3}}$ may be compared with figs. 35 and 36 of horizontal sections. These latter are taken at slightly different levels, six sections intervening. In fig. 35 the swollen Anlagen of $i_{\overline{2}}$ and $i_{\overline{3}}$ are seen connected by the outwardly directed dental lamina. The peaked anterior extremity of the $i_{\overline{2}}$ swelling indicates the continuation forwards of the dental lamina (cut obliquely) into the first incisor region. The rounded hinder end of the Anlage of $i_{\overline{3}}$ is seen to end abruptly at this level, but this is only because the plane of section prevents its backward continuation from appearing. In fig. 36, which is closer to the oral epithelium, the lamina is seen to be prolonged back as a well-marked band, from the hinder end of the upper part of the $i_{\overline{3}}$ swelling, through the canine region, to reach the first premolar Anlage ($p_{\overline{1}}$).

The swollen Anlage of $i_{\overline{3}}$ exhibits the same kind of indentation of its fundus as that of $i_{\overline{2}}$, and there is similar evidence of preparation for the formation of a dermal papilla. It forms a shallower Anlage than $i_{\overline{2}}$ besides being placed at a higher level.

In one or two sections we find close under the oral epithelium, and placed in the angle between the latter and the labial side of the enamel-organ of $i_{\overline{3}}$, a somewhat flattened mass of epithelial cells surrounded by condensed connective tissue. This appears to represent a rudimentary *d*$i_{\overline{3}}$. In the following stages its form and relations become still more manifest, though it never undergoes calcification. It does not appear in the section shown in fig. 34.

No such rudiment is observable in connection with $i_{\overline{2}}$.

Behind $i_{\overline{3}}$, the dental lamina, which is there considerably displaced outwards from the mesial plane, now bends slightly inwards again (cf. fig. 36), and becomes markedly reduced in height. After continuing for a short distance as an extremely shallow and insignificant structure, its cross-section rather suddenly undergoes marked elongation, penetrating further and further into the surrounding connective tissue, not vertically but rather mesially, in a direction almost parallel with the deep surface of the oral epithelium. At the same time it swells out markedly at its free distal margin or fundus, and at its point of maximum development exhibits some flattening, or even slight depression, towards its labial side (fig. 37). There is present also just the faintest trace of the differentiation of the connective tissue foreshadowing the growth of the dermal papilla, though as yet there is no papillary projection whatever in this situation. The proximal or attached portion of the lamina (or "neck") is elongated and much constricted, and is pretty closely appressed to the deep surface of the oral epithelium. Close to its point of continuity with the latter is attached the small but deeply cupped enamel-organ of *dc.* (fig. 37), which has been figured in its earlier stage of differentiation in Stage II (fig. 13).

The superficial resemblance between fig. 34, showing relation of $i_{\overline{3}}$ to $i_{\overline{2}}$, and fig. 37 showing the relation of $d_{\overline{c}}$ to $_{\overline{c}}$ is somewhat striking; but, as has been pointed out, the fundamental relationships are totally distinct in the two cases. The appearance is explained by the kink in the lamina which has been described.

In fig. 36 the dental lamina is seen continued back as a well-marked band from the hinder end of $i_{\overline{3}}$ through the canine region to the first premolar Anlage. The intermediate part of this elongated portion of the dental lamina really consists of the thinned-out "neck" portion of the dental lamina, where that constitutes the canine Anlage. Its topographical relation to the vestigial milk canine $d_{\overline{c}}$ is well shown.

Behind the canine region the dental lamina is again reduced in size, until it is continued, as may be seen in the horizontal section figured (fig. 36), into the Anlage of $p_{\overline{1}}$. Here it attains considerable bulk, and, unlike the corresponding Anlage in the upper jaw, it shows slight but distinct indentation at its base, and the usual indication of the earliest commencement of a dermal papilla, in the form of a deeply stained cellular aggregation opposite the depression in the enamel-germ, and slightly projecting into it.

Beyond $p_{\overline{1}}$ the dental lamina becomes attenuated before it once more enlarges to constitute the Anlage of $p_{\overline{2}}$. This closely resembles $p_{\overline{1}}$, but is even more distinctly though still only slightly cupped (fig. 38). As $p_{\overline{2}}$ is traced backwards the labial lobe, which forms the outer boundary of the shallower depression of the enamel-organ, disappears, but the main body of the dental lamina continues backwards, uniformly plump and well developed, for a very considerable distance; nor, indeed, does it lose its character, but merely undergoes further vertical elongation at its continuation into the residual dental lamina, which now exists in a well-developed condition by the side of the highly developed enamel-organ of $dp_{\overline{3}}$. Here it is longer, and, though a little less thick, it is still markedly swollen in its marginal portion, so that upon cross-section it appears like a large bud-like lobe (fig. 39, *rdl.*), and this is surrounded by a capsule of condensed connective tissue.

The development of $dp_{\overline{3}}$ so closely resembles that of the corresponding tooth in the upper jaw that little special description need be given. It is indeed just a little in advance of its opponent. In particular we find that in the hinder part of its enamel-organ an important differentiation has set in, of which no trace is as yet visible in the upper tooth. Fig. 40 shows that the cup-like cavity of the enamel-organ is now in process of subdivision into two, and that, corresponding to this the dermal papilla exhibits two very slight pointed projections. Here plainly we have the earliest stage in the production of more than one cusp in the case of an enamel-organ which, at the previous stage of its development, was a perfectly simple cup, with a correspondingly simple papilla. The figure represents, in fact, an appearance which has been already claimed by Röse as illustrating the earliest and most primitive condition of a multicuspidate tooth. In the case of the deciduous premolar in Perameles, it can be proved that such is not the case; and that here, at least, cusp-formation is a secondary complication, introduced at a period subsequent to the formation of the primitive dermal papilla.

As in the upper jaw, the dental lamina behind $dp_{\overline{3}}$ is the prolongation of the residual lamina in the region of the latter, and some distance behind it is continued into the Anlage of the first molar. There is not the same sudden elongation here as in the upper jaw, and it can therefore be plainly seen that the inner lip of the most anterior part of the cupped enamel-organ of $m_{\overline{1}}$ is the direct continuation of the dental lamina, the rest of the enamel-organ having plainly arisen by outgrowth from the labial surface of the lamina, as we have seen to be the case in other tooth rudiments. On the other hand, the residual dental lamina has not liberated itself from the first molar Anlage in the lower jaw as in the upper, except in so far that the enamel-organ gradually diminishes posteriorly, and finally disappears as a mere labial excrescence of a thickened lamina. The latter is continued backwards, and very shortly behind it develops another laminal excrescence, which when followed is seen to form the labial boundary of the cup of the papillated enamel-organ of $m_{\overline{2}}$ (fig. 41). This tooth now exhibits a much more advanced condition than does the corresponding Anlage in the upper jaw.

The labial portion of $m_{\overline{2}}$ in turn disappears rather abruptly (see fig. 42), leaving a simple elongated dental lamina (*dl.*). The latter has now become separated from the oral epithelium, and soon disappears entirely from the section, without having given any indication of the future formation of the third molar.

Stage IV.—P. nasuta: mammary fœtus.

Length from vertex to root of tail . . .	34 mm.
Head length	16 „

Coronal, horizontal, and sagittal sections examined.

The transition from Stage III to Stage IV represents a greater advance in development than that from Stage II to Stage III.

Upper Jaw.—The dental lamina (fig. 43, *dl.*) begins some distance in front of the anterior end of the first incisor, as a downgrowth from the lingual angle of a broader epithelial invasion of the connective tissue (*ca.*). The possible significance of this will be adverted to in the sequel. In fig. 44, $i^{\underline{1}}$, is seen to be connected with the dental lamina by a bridge of cells (*cb.*), or "Verbindungsbrücke" of Röse. This structure alone bears witness to the earlier condition manifested in Stage III, where the enamel-organ of $i^{\underline{1}}$ was still an integral portion of the dental lamina. Beyond the attachment of the connecting bridge (*c.b.*) the "residual" dental lamina (*rdl.*) extends as a free laminar ingrowth.

Springing from the labial angle of the broad epithelial ingrowth above referred to may be seen (fig. 44) a hooked cellular process (*ep.*). And, between this and the proper dental lamina itself, the surface of the broad epithelial ridge is beset with irregularities. In many sections, indeed (cf. fig. 46, *cp.*), completely isolated epithelial cell groups may be seen in the connective tissue to the labial side of the "Verbindungsbrücke" of $i^{\underline{1}}$, i.e. between the latter and the irregular edge of the broad epithelial mass which forms the basis from which the proper dental lamina springs. In other sections somewhat similar epithelial cell-masses are seen still connected with the Malpighian layer of the epithelium.

We cannot give a positive opinion respecting the significance of these more or less isolated cell-groups. Either they are partially strangled epithelial ingrowths, such as we shall later on have occasion to refer to as dipping more or less deeply into the connective tissue from the deep surface of that lamina which forms the Anlage of the lip-furrow (labio-alveolar furrow); or else they may have to be interpreted as degenerated remains of the connections of a first milk incisor. If the latter, then the irregular area with which they are related must be interpreted as forming, morphologically, a part of the labial surface of the original dental lamina, whose basal part has, as it were, opened out towards the mouth cavity. We think that consideration of the appended figs. 43—46 will support this as at all events a plausible explanation.

It will be remembered that in Stage III no rudiment of $di^{\underline{1}}$ was found. But the connection of the dental lamina (at its first incisor enlargement) with the oral epithelium was a very broad one, and, in the reduction to its present dimensions, it might well have left cellular vestiges of a rudimentary $di^{\underline{1}}$, stranded, as it were, on the labial side of the now relatively constricted base of the proper dental lamina.

In fig. 45 the residual dental lamina (*rdl.*) in the region of $i^{\underline{1}}$ is well seen. Its fundus is distinctly enlarged ("kolbig"), but it is merely the thickened free margin of the continuous lamina seen in front in fig. 43 and the succeeding figures. Behind this point, indeed (i. e. fig. 45), it loses its independence for a few sections, when it is more intimately fused with the side of the enamel-organ of $i^{\underline{1}}$ (fig. 46), but almost immediately it again extricates itself as a free but less prominent residual lamina. Shortly behind this again, opposite the posterior part of $i^{\underline{1}}$, the lamina is practically suppressed altogether. Traces of its former presence remain in the shape of slight and inconstant cellular projections from the oral epithelium, and from the lingual aspect of the enamel-organ of $i^{\underline{1}}$, respectively.

Soon after the appearance of $i^{\underline{2}}$ in the sections the lamina completely reappears and relates itself to that tooth in a manner similar to that observed in the case of $i^{\underline{1}}$, a residual dental lamina, " bud-like " on cross-section, being present here also.

The enamel-organ of $i^{\underline{1}}$ is relatively shallow, having only attained cup-like form, while $i^{\underline{2}}$ is deep and bell-shaped, with pointed apex. In neither case are hard dental tissues present.

We have been rather surprised to find that the enamel-organ of $i^{\underline{3}}$ in the present stage is less advanced in development than that of $i^{\underline{2}}$. It is even a trifle less mature than $i^{\underline{3}}$.

In the two previous stages it was the largest of the incisors, and, at least in Stage II, the most advanced. Now it is found to lag behind as a much shallower cup-shaped enamel-organ. It is, however, somewhat deeply placed, and is attached near to the distal end of a dental lamina which is, as a whole, more massive here than in front.

Another evidence of relative immaturity is found in the fact that the residual dental lamina, though distinctly indicated, is only as yet imperfectly liberated by differentiation from the enamel-organ.

Opposite the hinder end of $i^{\underline{3}}$ the deep and bulky dental lamina abruptly diminishes in depth, and is prolonged backwards into the less deeply situated $i^{\underline{4}}$, with the lingual part of whose cupped enamel-organ it is directly continuous, much as was seen to be the case with the second lower molar of Stage III.

Behind $i^{\underline{4}}$ the dental lamina relates itself in like manner to the closely similar cupped enamel-organ of $i^{\underline{5}}$. Neither of these Anlagen as yet exhibits any traces of a residual dental lamina, i. e. they are as yet destitute of "Ersatzleisten." They are decidedly less advanced in development than the anterior incisors.

No trace of a milk predecessor is now found in connection with any of the incisors, with the doubtful exception of the first. We have seen above that the vestiges of such present in Stage III were already retrogressive, that of $di^{\underline{3}}$ being in process of invasion and dispersion by connective-tissue ingrowth.

The canine calls for little remark. It is a large and deeply cupped enamel-organ (fig. 47), and its future residual dental lamina is only very partially indicated as a somewhat bulky projection from the side of the enamel-organ. The drawing, however, contains a highly interesting feature in the shape of an attenuated cord of cells ($d^{\underline{c}}$) with a slightly clubbed termination, springing from the labial side of the dental lamina near where it is continuous with the oral epithelium. This appears in only a very few sections, abruptly disappearing fore and aft, and is without doubt the retrogressive vestigial representative of the perfect miniature cupped enamel-organ of the milk canine figured in Stage III (fig. 20 $d^{\underline{c}}$). Since this is all that is left of such a perfect rudiment as that in Stage III, it is not surprising that the much more rudimentary milk incisor structures seen in Stage III should have wholly disappeared.

Behind the canine the dental lamina, losing much of its depth, but still remaining pear-shaped on cross-section, is continued bodily into the first premolar Anlage.

Both the first and second premolars are now deeply cupped enamel-organs of an equally advanced stage of development to that of the canine (fig. 47), which they now much resemble. In the case of each a residual dental lamina is just being differentiated. In this respect, but not otherwise, $p^{\underline{1}}$ is just a little in advance of $p^{\underline{2}}$.

At its hinder end $p^{\underline{2}}$ tapers away into the undifferentiated dental lamina, which here remains tolerably thick and club-shaped on cross-section. On its being traced backwards, there soon appears by the side of the dental lamina, but at a considerable distance from it, the enamel-organ of the deciduous premolar. This is not only placed labially, but is situated low down, i. e. close to the oral epithelium. It has now attained some degree of complexity. One can easily distinguish a protocone, deep and pointed, from the shallower and less pointed paracone and metacone, in front and behind.

The inner epithelium is elongated and cylindrical, especially at the apex of the protocone, where the cells are about as long again as elsewhere, and their inner halves are pale and unstained, the nuclei forming an outer marginal band. Covering the tip of the papilla of the protocone there is an exceedingly thin dentine cap, the only one hitherto encountered in the upper jaw (fig. 48). Outside the inner enamel epithelium the stratum intermedium forms a very distinct layer of cubical or flattened cells, and outside this again the stellate enamel tissue is reduced to a comparatively narrow layer.

As it is traced backwards into the region of $dp^{\underline{3}}$, the dental lamina increases in thickness, and opposite the paracone it begins to exhibit remarkable modifications of its swollen free marginal portion in the shape of alternate constriction and enlargement, the constrictions being due to ingrowth of connective tissue on the labial aspect of the lamina. The thickest portion of the lamina is opposite the protocone (fig. 48, *rdl.*), where also the connection between $dp^{\underline{3}}$ and the swollen dental lamina becomes apparent.

Fig. 49 represents a horizontal section through the region between $p^{\underline{2}}$ and $m^{\underline{1}}$; the level is too high to show the very lowly situated $dp^{\underline{3}}$ at all well, it is indeed only shaved through near its higher or basal limit.

The tapering of $p^{\underline{2}}$ into the dental lamina, and the prolongation of the latter by the sides of $dp^{\underline{3}}$ and $m^{\underline{1}}$, is strikingly shown; also the peculiar modification of the lamina which has been referred to as taking place opposite $dp^{\underline{3}}$.

It can hardly be gainsaid that here we have the earliest promise of the specific differentiation of $p^{\underline{3}}$. But we are not at all clear as to the significance to be attached to the constricting ingrowths of connective tissue described and figured. They are also present in similar shape in Stage v (fig. 50). At first sight they suggest papillæ, but not only are they histologically entirely unlike the Anlagen of papillæ (for instead of being cellular growths they are fibrous bands), but an examination of much later stages shows that they disappear as such, and that the enamel-organ of $p^{\underline{3}}$, when finally elaborated, is a simple and single rounded cup-like structure.

A comparison of sagittal series with the horizontal and coronal of this stage proves that the ingrowths of connective tissue shown in the horizontal section are neither mere pits nor simple cross-furrows, but that they are circular furrows surrounding, and partially isolating, two rounded projections of the labial face of the lamina marked *a* and *b* in fig. 49. How these two knobs—for such they are definitely proved to be—are related to the process of formation of $p^{\underline{3}}$, we are not in a position to say. That they are no mere accidental outgrowths is shown by the fact that they are present, under only slight modification in form, in the next stage (v, fig. 50). Nevertheless, in still later stages the regularity of the arrangement is lost, and the lamina simply appears irregularly thickened, until finally out of this thickening a quite simple and normal cup-like enamel-organ arises.

A superficial criticism, having regard only to our fig. 49 of the present stage and fig. 50 of the next, Stage v, might be disposed to claim the indentations there represented as examples of supposed primitive papillæ whose fusion would constitute $p^{\underline{3}}$. It is just remotely possible that here we do have phenomena that ought to be interpreted by some fusion hypothesis, though we are strongly inclined to think otherwise. In any case if we do here meet with a case of fusion the structures that are fused are not dermal papillæ, for the structures which in some sections are suggestive of papillæ are merely cross-sections of the fibrous connective tissue occupying certain circular grooves which circumscribe knob-like prominences of the dental lamina near its fundus.

We may further point out that so far, and after careful study, especially of these earlier and plastic stages, we can (with Leche) find no support for Woodward's statement that $p^{\underline{3}}$ (i. e. the successional tooth) takes its origin from the dental lamina morphologically in front of $dp^{\underline{3}}$ (i. e. the milk molar), and is therefore probably in series with it.

In his paper already referred to Mr. Woodward makes the following statement:—"It is interesting to note that in Perameles the large supposed successional tooth is quite distinct in origin from the small fourth premolar which is shed [*dp.*$^{\underline{3}}$]; it is, in fact, formed from the dental lamina situated immediately behind *pm* 3 [$p^{\underline{2}}$] and morphologically in front of the fourth premolar [$p^{\underline{3}}$]" (2, p. 467). It is unfortunate that Mr. Woodward makes this statement without amplifying it by a more detailed description or illustrating it by drawings (for Perameles).

From our own minute and detailed study in Perameles of the region of the dental lamina concerned we are convinced that Mr. Woodward has misinterpreted the appearances there met with. We do not deny that the latter may sometimes seem to suggest the view that Woodward adopts, but upon further examination it becomes untenable. In the absence of any figures the readers of Woodward's description would necessarily suppose that in Perameles one meets with just such an enlargement of the dental lamina between $p^{\underline{2}}$ and $dp^{\underline{3}}$ (his "*pm.* 3" and "*dpm* 4") as is represented in the wax model of the corresponding region of Petrogale figured by him. But this is by no means the case. In connection with the description of Stage III of Perameles we have drawn attention to the fact that the dental lamina behind $p^{\underline{2}}$ gradually tapers backwards from the thickening which represents the enamel-organ of the latter tooth, and that, as it approaches the region of $dp^{\underline{3}}$, it becomes somewhat more slender, but at the same time distinctly more elongated vertically. (See text, Fig. 1, A—G.) There is no localised enlargement whatever of the stretch of lamina between $p^{\underline{2}}$ and $dp^{\underline{3}}$. It is true that it is plump and well developed, but this does not specially distinguish it at the stage in question from stretches of the lamina between other tooth Anlagen.

We have already pointed out that in fig. 22 the apparent swelling of the dental lamina in front of the region of $dp^{\underline{3}}$ is due merely to its plane of section. To understand it properly the gradual vertical elongation of the lamina behind $p^{\underline{2}}$ must be borne in mind. The plane of the section lies too high to intersect the main mass of $p^{\underline{2}}$, which is relatively low and transversely elongated. Still the obliquely cut anterior portion of the segment of the lamina figured really corresponds to the tapering posterior end of $p^{\underline{2}}$, which is higher (deeper) than the rest of the Anlage. In like manner the narrowing of the dental lamina, seen in the figure as occurring towards $dp^{\underline{3}}$, is to be explained not as an actual diminution of the sectional area of the lamina, but only of its width at this horizontal level. And if sections through exactly the same region but in a higher horizontal plane be examined, it will be found that, when the fundus of the free dental lamina close beside $dp^{\underline{3}}$ is cut through, its sectional outline is quite comparable to that seen further forwards. There is, in short, just such a gradual heightening of the lamina, when it is traced backwards into the $dp^{\underline{3}}$ region, as there is in front of the premolar region when the lamina is traced forwards from $p^{\underline{1}}$ towards the canine.

It has already been shown that a residual dental lamina is liberated by the side of $dp^{\underline{3}}$ at a very early period, and that this soon becomes thickened at its margin and "bud-like" on cross-section. It is from this liberated lamina that $p^{\underline{3}}$ takes its origin in Perameles.

Even in Petrogale, upon which Woodward chiefly founds his case, we cannot allow that the conclusion that $p^{\underline{3}}$ (his $p^{\underline{4}}$) is morphologically in front of $dp^{\underline{3}}$ (his $dp^{\underline{4}}$) is at all so inevitable as he regards it. The proofs drawn from the mere appearance of the dental lamina in transverse sections are, in our opinion, of very little value. A quite similar development of the deeper part of the dental lamina, and an identical development of loose and stellate-like epithelial tissue in its interior, may frequently be met with where there is no question of the presence of a tooth at all.

It is only the definite localised elevation, sharply limited fore and aft, figured in the drawing of a wax model of this region of the lamina in Petrogale which seems to us at all a formidable evidence of the view put forward. And even this we cannot regard as conclusive. For, according to Mr. Woodward's statement and figures, the enamel-organ of $dp^{\underline{3}}$ (his $dp^{\underline{4}}$) at the stage referred to has not yet differentiated itself as an organ distinct from the dental lamina. The whole lamina in the $dp^{\underline{3}}$ region appears as if converted into the enamel-organ, as is commonly the case in the earlier stages of tooth development. This phase of development is, however, only a passing one. By-and-by the separation of the enamel-organ from the lamina which gives it birth is indicated, and the resulting appearance of a residual lamina or "Ersatzleiste" we regard as the first condition of the appearance of a successional tooth.

This first condition is as yet absent in the early stage of Petrogale under notice. Mr. Woodward in effect maintains that in its absence we must forthwith accept the presence of an enlargement of the lamina in front as the true Anlage of $p^{\underline{3}}$ (his $p^{\underline{4}}$). We hold, on the contrary, that until we are in a position to trace the fate of the residual lamina, which will assuredly manifest itself by the lingual side of $dp^{\underline{3}}$, it is premature to decide upon what constitutes the earliest germ of $p^{\underline{3}}$ ("$p^{\underline{4}}$"). If the evolution of the swelling figured by Woodward can be clearly traced up to the formation of the enamel-organ of $p^{\underline{3}}$ ("$p^{\underline{4}}$"), without suspicion of a confusion with the subsequent evolution of a true "Ersatzleiste" of $dp^{\underline{3}}$, then Mr. Woodward's case for Petrogale will have been made out.

We therefore insist that it is necessary to have recourse to somewhat later stages for corroboration, or otherwise, of Woodward's view. And what is the result of such a reference? We shall quote Mr. Woodward's own words. "In a slightly older embryo the same condition was observed, but owing to the development of the third and fourth premolars, especially of the latter, they somewhat overlap the lamina connecting the two, and it in consequence becomes displaced to the inner side of these structures. So much does the fourth premolar grow forward with age that it appears as if this lamina was a downgrowth from the inner side of the enamel-organ of $pm^{\underline{4}}$ [the spaced type is ours]; this, however, is really not the case; the lamina is morphologically in front of that tooth, and only attains a secondary connection with it" (2, p. 458). Now, if we disentangle the statement of facts from the accompanying explanatory hypothesis, we recognise that in the later stage, i.e. when $dp^{\underline{3}}$ has become thoroughly differentiated, a free dental lamina is found by its lingual side appearing "as if this lamina was a downgrowth from the inner side" of its enamel-organ.

But this is precisely the condition we find in Perameles, where the appearance of such a laminar "downgrowth" is most assuredly not due to any process of overlapping or disproportionate growth of any kind. Nor is there in that form any antecedent enlargement of the lamina in front of the $dp^{\underline{3}}$ region. We infer from his language that Mr. Woodward found some slight difficulty in explaining the fact of an actual connection between $dp^{\underline{3}}$ and the lamina by its lingual side, on his theory of a forward growth producing overlapping, since he denominates such a connection as "secondary." Now we are firmly convinced that no truly secondary connection is ever developed between a dental lamina and an enamel-organ which has previously been differentiated off from the lamina. It is, a priori, most unlikely that any such secondary connection should be established. And we believe that, wherever a connecting bridge is present, it will be found necessary, and not very difficult, to interpret it as a remnant of the original primary connection between enamel-organ and parent lamina. We must believe that Mr. Woodward's method of explaining away the importance of the connection he found in his later stage of Petrogale rests upon an erroneous interpretation of the facts. We hold that in all probability he is wrong in supposing that the part figured in the earlier stage in front of $dp^{\underline{3}}$ is the same as the part found in the later stage by the side of that tooth. The latter part is simply the free dental lamina of the region of $dp^{\underline{3}}$ itself, now liberated by a more complete differentiation of the enamel-organ of the latter; and it is from it, and not from the lamina morphologically in front of $dp^{\underline{3}}$, that $p^{\underline{3}}$ is subsequently developed. We have put our re-interpretation of Mr. Woodward's facts in frankly dogmatic form for the sake of clearness. There is too much unavoidable uncertainty about any question of this kind to encourage a genuinely dogmatic attitude in regard to it. And we may, indeed, with Leche, admit after all the possibility of $dp^{\underline{3}}$ arising in front of $p^{\underline{3}}$ without concluding, with Woodward, that the teeth so arising belong to the same series. At the same time the facts in Perameles do not permit us to entertain any doubt with regard to the origin of $dp^{\underline{3}}$, however it may be in the case of Petrogale. Nor do our investigations in Marsupials lead us to side with Leche in his view that the germs of the permanent teeth do arise in front of those of the milk-teeth. Judging from the observations already detailed with regard to the position of the early rudiments of the vestigial milk incisors, we must believe that the Anlagen of the permanent teeth arise side by side with those of the milk-teeth, though the latter are placed rather opposite the anterior portions of the former. This we have already seen to be originally the case in the region of the first lower incisor of Perameles. Nevertheless at a comparatively early period the vestigial milk enamel-organ comes to lie opposite the hinder end of the permanent tooth, so that here the primitive relation comes to appear reversed.

Woodward calls attention to the anomalous eruption of $p^{\underline{3}}$ in Perameles rather in front of its "supposed" predecessor $dp^{\underline{3}}$.

But, after all, the point of eruption of a tooth is of secondary importance, and we find, on the other hand, that not only at its first appearance, but during the very long latent period which precedes its elaboration as a cupped enamel-organ, the germ of $p^{\underline{3}}$ is placed, not in front of, but opposite to $dp^{\underline{3}}$.

It would be difficult to draw any other conclusion from our fig. 48, and here we are in a position to state that there is absolutely not the slightest scrap of evidence tending to prove that any such "secondary attachment" has been entered upon as Woodward has imagined to take place in his parallel case. We are perfectly confident that our interpretation is the correct one for Perameles.

From the description of $dp^{\underline{3}}$ given above, it will be observed that it is still in a more advanced phase of evolution than the two anterior premolars. But the difference is rapidly becoming less marked. The comparatively rudimentary character of the deciduous premolar of Perameles is now expressing itself in a much less rapid increase in size, so that it is now being rapidly overhauled in its progress by the enamel-organs of $p^{\underline{1}}$ and $p^{\underline{2}}$. In consequence of this fact, the very striking discrepancy in the periods of appearance of the enamel-organs of $dp^{\underline{3}}$ and of the anterior premolars respectively, is, from now on, less and less apparent. It is thus quite easy to understand how observations upon a series of stages which did not include any younger than the present (Stage IV) might lead to the conclusion that these teeth were serially homologous.

The appearance of the upper first molar in Stage IV is represented in fig. 51. Here, as in $dp^{\underline{3}}$, a thin dentine cap is present over the summit of the protocone. A well-marked residual dental lamina (*rdl.*) is present, whose significance will be discussed in connection with the general question of molar homology. This figure alone is sufficient to disprove Woodward's view (2) that "lingual downgrowths of the dental lamina" do not occur in connection with the molar teeth.

Two drawings (figs. 52 and 53) are given of the enamel-organ of $m^{\underline{2}}$ from distinct series of sections (and not quite at corresponding points). In each case a well-marked swollen ("knospenförmig") "Ersatzleiste" or residual dental lamina (*rdl.*) is visible.

There is also a small labial "sprout" or "outgrowth" (*l.o.*) opposite a knee-like bend or "Knickung" of the lamina, the significance of which is elsewhere discussed.

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[1] Woodward has apparently given up this view, so far at least as certain rodents are concerned (cf. **18**).

After the enamel-organ of $m^{\underline{2}}$ disappears from the serial sections, the dental lamina continues on, still for the most part in connection with the oral epithelium, and by-and-by it becomes swollen to form the undifferentiated Anlage of $m^{\underline{3}}$ (fig. 54). In this its hinder portion the lamina preserves the kink or flexure above referred to, as well as the (laminar) labial outgrowth (*l.o.*) from this. The latter has, we are convinced, nothing to do with tooth production (cf. p. 564 et seq.).

Lower Jaw.—In the lower jaw the dental lamina arises somewhat abruptly a little distance in front of the first incisor region. Here it is fairly thick and plump. This portion must be regarded as having been produced by a slight extension forwards of the lamina since the period represented by Stage III, occurring pari passu with the continued elongation of the jaw. When the region of $i_{\overline{1}}$ is reached the lamina is seen to be continued on into a thickened residual dental lamina by the lingual side of $i_{\overline{1}}$ (fig. 55, *rdl.*). The enamel-organ of the latter is large and well developed, and is connected with the lamina by a thin epithelial connecting bridge. Further back the latter is lost, while the lamina itself has become much elongated and thinned, and here (fig. 56) is found attached to its neck a delicate strand of cells (*cb.*) forming a "Verbindungsbrücke" for the small vestigial calcified $di_{\overline{1}}$. Only a faint trace of a dentine cap is found at the apex of $i_{\overline{1}}$ in spite of the large size of the tooth.

Behind the first incisor region the very deep and thin lamina is continued on, and soon the enamel-organs of $i_{\overline{2}}$ and $i_{\overline{3}}$ appear almost simultaneously in the coronal series as a result of the peculiarity in the topographical relations of these teeth referred to in connection with the earlier stages. $i_{\overline{3}}$ is placed more superficially and labially, and it would have been impossible from an examination of this stage alone to have rightly interpreted the appearance presented (fig. 57). In this figure there will be observed a distinct labial outgrowth ($di_{\overline{3}}$) from the root of the dental lamina. Adjacent sections show it better as a thickened cell-mass attached to the root of the lamina by a thinner connecting bridge, and they also prove that it is related more intimately to $i_{\bar{3}}$ than to $i_{\bar{2}}$, as might be suggested by fig. 57. We can only interpret this as a vestige of a $di_{\bar{3}}$, of which a trace was found in Stage III in the form of a flattened mass of epithelial cells labially to the Anlage of $i_{\bar{3}}$.

As $i_{\bar{2}}$ and $i_{\bar{3}}$ disappear posteriorly, the dental lamina is greatly reduced in depth for some distance, and then gradually deepens again, becoming more and more elongated and swollen as the canine region is approached. Here (fig. 58), but still some distance in front of the actual canine enamel-organ, we find the vestigial $d_{\bar{c}}$ attached to the lamina by a delicate epithelial strand (*cb.*).

It is of interest to note that in one of our series of sections of this stage this is a precociously calcified tooth like $di_{\bar{1}}$ (fig. 58), while in another series it exists in the form only of a loose and degenerating epithelial mass.

The identification of this vestigial tooth as $d_{\bar{c}}$ is rendered easy by a comparison of its relations in the earlier stages where no possible doubt could be felt, and where its present relative dislocation is evidently in progress.

The lower permanent canine has not progressed very rapidly during the period intervening between Stages III and IV. Although it has attained considerable dimensions, its papilla is still very rudimentary, and its enamel-organ is only slightly cupped. Furthermore it is not yet differentiated off from the lamina, so that the residual lamina has not yet come into existence. Only a short stretch of lamina intervenes between the last trace of the canine and the commencement of the first premolar ($p_{\bar{1}}$). The latter tooth is more advanced in development than the canine, though not greatly so. It is deeply cupped by a prominent papilla, and the differentiation of the residual dental lamina has begun.

The second premolar is in a precisely similar condition to that of the first, tapering away at its posterior end into a fairly deep and thick dental lamina, which is continued back into the third premolar region. In this situation $dp_{\bar{3}}$ comes into view, placed away to the labial side of the lamina. Since the appearance of this tooth (except that it as yet shows no calcification) and its relations to the liberated lamina are exactly as described and figured in the upper jaw, no further particulars need be given.

Behind the third premolar region the lamina (still continuous throughout with the oral epithelium) undergoes further deepening and becomes continuous with the large enamel-organ of the first molar, which is larger and more complicated than the corresponding upper tooth. Here the dental lamina is for some distance separated off from the oral epithelium. A residual dental lamina is well developed, as in the upper jaw, and its freely projecting margin is moderately swollen. Towards the posterior end of $m_{\overline{1}}$ the dental lamina, now unconnected with the tooth, is also for the most part separated off from the oral epithelium, and is continued into the region of the second molar. Here again it shows a labial connecting strand ("Verbindungsbrücke") joining it to the enamel-organ of $m_{\overline{2}}$; whilst its free marginal portion forms a large residual dental lamina, just as in the upper jaw. Towards the hinder end of $m_{\overline{2}}$ the dental lamina again becomes connected with the oral epithelium, exhibiting near its point of connection a somewhat elongated labial laminar outgrowth. Further back the lamina entirely loses its connection with the oral epithelium, becoming more deeply placed among the connective tissue of the jaw. Its distal portion is converted into the papillated enamel-organ of $m_{\overline{3}}$, whose posterior end forms the present termination of the lamina. The liberation of a residual dental lamina by the side of $m_{\overline{3}}$ has already been partially effected.

Stage V.—P. nasuta: mammary fœtus.

Length from vertex to root of tail . . .	37 mm.
Head length	17 „

Coronal and horizontal series examined.

This stage represents only a slight advance on the preceding.

Upper Jaw.—All three first incisors are now well developed, the third especially showing a distinct advance from the preceding stage. It is now triangular and pointed in coronal section, and possesses a distinct dentine cap, as also do the first and second.

The dental lamina is definitely interrupted between $i^{\underline{1}}$ and $i^{\underline{2}}$, but otherwise it is continuous, though often greatly reduced in size, throughout the rest of the incisor region, and it retains its connection with the oral epithelium.

Towards the anterior part of the first incisor region irregular epithelial cell-processes spring from the oral epithelium close to the root of the dental lamina, similar to those mentioned in connection with the corresponding region in Stage IV (figs. 43—46).

The residual dental lamina is still clearly marked by the sides of $i^{\underline{1}}$ and $i^{\underline{2}}$, but it is now considerably reduced in size, absolutely as well as relatively to the tooth-germs. The residual dental lamina in the region of $i^{\underline{3}}$ has become definitely established, and indeed it now closely resembles that of $i^{\underline{1}}$ and $i^{\underline{2}}$. In each case, though forming a distinct and freely projecting laminar downgrowth beyond the connecting stalk of the tooth-germ, it is already a somewhat attenuated and insignificant structure. We should certainly not be warranted in following Leche by reading any special importance into its persistent presence at this stage. It is plainly steadily disappearing.

The fourth and fifth incisor enamel-organs are in a much less advanced stage than those in front. They are still relatively shallower and cup-like, with rounded papillæ, much as they were in Stage IV. They still appear as modifications of the dental lamina which is directly continuous with the lingual lip of their cup-like body, and no residual lamina has as yet differentiated itself from them. As one might expect, the portion of the lamina with which they are continuous is bulkier, i. e. less reduced, than it is in regions where tooth-germs have attained a more advanced stage of development.

The lamina behind $i^{\underline{5}}$ passes directly and with a somewhat abrupt deepening into the canine lamina. This, with the associated tooth-germ, is shown in fig. 59. Behind the canine the lamina is abruptly shortened, and is continued after a short interval into the bell-shaped enamel-organ of $p^{\underline{1}}$, whose papilla is destitute of any dentine cap.

The differentiation of the residual dental lamina has set in by the lingual side of the enamel-organ.

The second premolar exhibits a condition precisely similar to that of the first, except that the faintest trace of a dentinal cap to the pointed papilla may be observed. The residual dental lamina is fairly developed.

Behind $p^{\underline{2}}$ the dental lamina becomes gradually larger on cross-section, the germ of $dp^{\underline{3}}$ soon appearing in the coronal series. By the side of the latter tooth the dental lamina exhibits precisely the same kind of modification as was seen in the preceding stage in the corresponding situation (cf. fig. 49).

Fig. 50 shows a horizontal and fig. 60 a coronal section of the structures concerned. It will be noted that in this stage also the relative development of $dp^{\underline{3}}$ is considerably retarded as compared with that exhibited in earlier stages. Its dental cap is only a trifle in advance of that of $p^{\underline{2}}$. From its present condition alone it would be quite impossible to arrive at that conclusion with regard to its serial homology which we find it necessary to adopt in view of the earlier characters, both of the tooth itself and of the rest of the dentition.

In the molar region the connection of the dental lamina with the oral epithelium is frequently interrupted.

The first two molars are large and well developed. Lingually from each there is a large and well-developed residual lamina comparable to that figured for the last stage. The Anlage of the third molar is slightly more bulky than in Stage IV, but is still represented by a mere distal swelling of the lamina, as represented in fig. 61. In this figure the projection marked "*cb.* $m^{\underline{2}}$" is seen by comparison with the anterior sections to correspond to the root of the laminar connection ("Verbindungsbrücke") with $m^{\underline{2}}$.

Lower Jaw.—The dental lamina in front of the region of the first incisor shows some further antero-posterior extension since the period represented by Stage IV. This anterior segment of the lamina now exhibits an attenuation of its "neck," while its fundus shows a very definite oval enlargement, which disappears as the anterior plane of $i_{\overline{1}}$ is reached. Here, as in the preceding stage, the lamina is continuous with the "residual" lamina by the lingual side of that tooth.

The first incisor is a large pointed germ, with a fairly thick dentine sheath to the papilla. The milk incisor, *d*$i_{\overline{1}}$ (fig. 66 A) is present as a strongly calcified miniature tooth, placed at the labial side of the apex of $i_{\overline{1}}$. It has a small but distinct dermal papilla, and the dentine shell is surrounded by a sheath of small epithelial cells, which is attached by a laminar connection to the root or attached border of the dental lamina beside $i_{\overline{1}}$.

As in the preceding stages, $i_{\overline{3}}$ occupies a markedly labial position, and owing to the kink of the lamina, whose occurrence has been already described, its anterior portion has come to lie opposite the posterior end of the large $i_{\overline{1}}$. Posteriorly it occupies a similar position with reference to nearly the whole of $i_{\overline{2}}$. Indeed, in a few sections all three germs are visible in the same coronal plane. Both $i_{\overline{2}}$ and $i_{\overline{3}}$ possess dentine caps, and end behind in nearly the same coronal plane, though $i_{\overline{2}}$ extends a trifle more posteriorly than $i_{\overline{3}}$. The continued dental lamina is, however, placed beside $i_{\overline{3}}$, the morphologically posterior member of the series.

A long though attenuated residual lamina appears by the lingual side of $i_{\overline{1}}$, projecting far beyond the connecting bridge between the latter and the dental lamina (fig. 66 A, *rdl.*). The residual lamina is also present beside $i_{\overline{2}}$ and $i_{\overline{3}}$, but, owing to the dislocation of $i_{\overline{3}}$, the lamina has undergone corresponding dislocation and is partly interrupted. As already indicated, it is resumed beside the posterior end of $i_{\overline{3}}$, from which it extends backwards.

A delicate epithelial lamina is to be seen springing from the root of the dental lamina (i. e. from its attachment to the oral epithelium) opposite $i_{\overline{2}}$ and $i_{\overline{3}}$, and extending labially to $i^{\underline{3}}$. This ends in a minute mass of cells, and it persists through a considerable number of sections, and evidently answers to the labial outgrowth figured in connection with Stage IV (fig. 57) as a vestigial $di_{\overline{3}}$. It is now in process of absorption, and apparently has never shown any sign of calcification. From its first appearance in Stage III it has never attained the dignity of tooth-like differentiation of structure.

Behind the third incisor region the dental lamina again deepens, though its connection with the oral epithelium is interrupted for a time. Its free margin thickens, and is continued directly into the canine Anlage, but very soon is partially freed from it, being prolonged as a residual dental lamina. The canine enamel-organ is now bell-shaped, and as yet is uncalcified.

In the anterior premolar region the oral connection of the dental lamina is frequently interrupted ; $p_{\overline{1}}$ is slightly calcified, while $p_{\overline{2}}$ has as yet developed no dentine.

The deciduous premolar and its relations to the Anlage of $p_{\overline{2}}$ resemble those in the upper jaw, except that the $p_{\overline{3}}$ thickening does not exhibit the peculiar indentations present in the upper jaw, and that $dp^{\underline{3}}$ is distinctly less advanced and is still uncalcified ; in fact, it appears slightly less mature than in the preceding stage.

The molar region shows an advance upon the condition in the lower jaw of Stage IV, in that $m_{\overline{3}}$ is now a fairly large and deeply papillated tooth showing traces of differentiation of cusps. A well-developed residual dental lamina is present on the lingual side of each molar, and extends far beyond the epithelial connection with the enamel-organ.

Stage VI.—P. nasuta: mammary fœtus.

Length from vertex to root of tail . . .	44 mm.
Head length	24 ,,

Lips now separated to form the "definitive Mundspalte."

This stage exhibits a marked advance upon the last in regard to tooth development. In it we may be said to encounter for the first time throughout the adult form of the various teeth, except in the most posterior molar region all the teeth are well calcified, and have now attained such size relatively to the jaws that, especially in the incisor region, a good deal of overlapping occurs in both jaws.

Further, in Stage v the dental lamina, though frequently interrupted and generally exhibiting signs of reduction and commencing resorption, was, on the whole, fairly complete. In the present stage (vi), on the other hand, the lamina is exceedingly imperfect and scrappy; and even where it appears it usually displays much attenuation and irregularity of form from the operation of the degenerative process.

Upper Jaw.—Beside the first incisor of the upper jaw only comparatively slight traces of the dental lamina are visible, and these are now quite unconnected with either the tooth or the oral epithelium. It is impossible to distinguish any specific remains of the residual dental lamina as such. Beside $i^{\underline{2}}$ it is just possible to recognise portions of lamina corresponding to "Ersatzleiste" and "Verbindungsbrücke" in a few places; while in the region of $i^{\underline{3}}$ no residual lamina can be identified.

The fourth and fifth incisors are now well calcified, though smaller than the anterior ones. Their more juvenile character is perhaps evidenced by the persistence, in more regular form, of the dental lamina with its residual prolongation. But these latter also persist to a large extent in connection with the canine, as shown in fig. 62 (*rdl.*), which represents the anterior portion of that tooth (and therefore does not show the pointed and strongly calcified character of its apex).

In the region of the anterior premolars the dental lamina is scrappy, but vestiges of the free residual lamina remain here and there, as well as portions of the rest of the lamina and of the epithelial connecting bridge.

The lamina becomes more regular and complete behind $p^{\underline{2}}$, and in the region of $dp^{\underline{3}}$ its marginal portion is swollen, forming the Anlage of $p^{\underline{3}}$ as shown in fig. 63. In adjacent sections here and there it exhibits some indentations, but of irregular character. In this its swollen portion it is surrounded by markedly condensed connective tissue.

The thickening of the residual lamina becomes even more sharply accentuated than in fig. 63 in sections further back. The deciduous premolar is a well-calcified tooth having a sharply pointed chief cusp, while the anterior portion through which the section passes in fig. 63 shows a low and flattened crown.

Behind $dp^{\underline{3}}$ the continued dental lamina becomes more uniform in thickness. In the region of $m^{\underline{1}}$ traces of the connection with the latter tooth are discernible, as also in region of $m^{\underline{2}}$. A residual lamina is present in both regions.

Towards the end of the region of the second molar the well-marked dental lamina becomes gradually more highly developed, still retaining a well-marked laminar projection towards $m^{\underline{2}}$—the remains of its original connection with the dental lamina (fig. 68, *cb*, $m^{\underline{2}}$). Then, somewhat abruptly, the residual lamina beyond (distal to) the 'Verbindungsbrücke' develops a marked labial bulging, so that it appears as a knobbed swelling, flattened or even slightly concave distally, forming the Anlage of $m^{\underline{3}}$ (fig. 68 A). The connective tissue exhibits a very evident condensation and cellular accumulation where it is in relation with the flattened or slightly concave surface—the rudiment of the papilla of $m^{\underline{3}}$.

Lower Jaw.—The undifferentiated segment of dental lamina in front of the first incisor is again in evidence, and its swelling is now more marked than in the preceding stage, though, as in the latter, it tapers away and becomes more flattened and attenuated before being continued into the residual dental lamina beside $i_{\overline{1}}$. This residual lamina is now greatly reduced in thickness, and no longer exhibits traces of its former connection with $i_{\overline{1}}$.

Beyond the progressive enlargement and perfecting of the three incisors there is little further to note. The vestigial $di_{\overline{1}}$ is still present as a strongly calcified toothlet on the labial side of $i_{\overline{1}}$ near the oral surface. Its outer dentine layer apparently forms now a complete shell surrounded by a layer of deeply staining cells. The central nuclei appear altered and degenerated.

The canine is not so far advanced as the incisors. It is smaller, and its dentinal covering much thinner.

Beside $p_{\overline{1}}$ a trace of the free residual portion of the dental lamina is still to be seen. This tooth is further advanced than the canine, for both its dentinal and enamel layers are thicker.

Beside $p_{\overline{2}}$ there is a small but distinct residual lamina projecting beyond the point of attachment of the connecting bridge. The tooth is somewhat less advanced than $p_{\overline{1}}$.

The third premolar region is similar to that in the upper jaw. In one place there is a very distinct indentation of the thickened lamina on the lingual side of $dp_{\overline{3}}$. This indentation persists through a considerable number of sections, and is filled by loose connective-tissue cells, the whole being surrounded by a condensed connective-tissue capsule (fig. 64). This represents the earliest trace of the definitive papilla of $p_{\overline{3}}$.

In the posterior molar region the anterior cusp of $m_{\overline{3}}$ is now calcified. The tooth is still attached to the persistent lamina, which is prolonged beyond the point of attachment as a residual lamina.

Stage VII.—P. nasuta: mammary fœtus.

Length from vertex to root of tail . . .	56 mm.
Head length	25 „

The incisor region of this stage derives some special interest from comparison with the previous stage. On the whole the teeth are somewhat larger, indicating greater maturity. But $i^{\underline{5}}$ forms an interesting exception. Here it is not yet calcified, although it was quite strongly calcified in Stage VI. It is, in fact, only slightly ahead of the condition in Stage V. Furthermore its topographical relations differ from those seen, not only in Stage VI, but also in Stages V and VIII, all of which agree with each other.

Prior to our Stage V there is no overlapping of the posterior incisors, which are small; and $i^{\underline{4}}$ is simply placed in front of $i^{\underline{5}}$. But in later stages the enlargement of the upper incisor teeth relative to the size of the jaw causes very considerable overlapping, and in Stages V, VI, and VIII the arrangement is a determinate and identical one. It is briefly as follows:

$i^{\underline{2}}$ appears above the posterior portion of $i^{\underline{1}}$, but on a slightly more lateral (labial) plane.

$i^{\underline{3}}$ appears directly above the posterior portion of $i^{\underline{2}}$.

$i^{\underline{4}}$ appears below the posterior end of $i^{\underline{3}}$, but in a slightly more lateral plane.

$i^{\underline{5}}$ appears mesially to, and on a higher plane than, $i^{\underline{4}}$.

Now in Stage VII the above arrangement is departed from in that $i^{\underline{4}}$ appears not below but above $i^{\underline{3}}$, as well as laterally from it, and $i^{\underline{5}}$ appears directly below $i^{\underline{4}}$ instead of being over it.

We are unable to explain these differences (i.e. the weak development of $i^{\underline{5}}$ and the aberrant position of $i^{\underline{4}}$ and $i^{\underline{5}}$) and can only set them down as instances of individual variability.

Fig. 59 A represents the canine of the upper jaw, and may be compared with fig. 59, showing the same tooth in Stage V. These figures are especially intended to illustrate the gradual reduction of the dental lamina, including its "residual" prolongation. Along with them may be taken fig. 59 B from Stage VIII, showing a still more advanced condition of resorption and degeneration. The figures are introduced apropos of Leche's reiterated and emphatic insistence upon the long persistence and large size of portions of the residual dental lamina. We do not find these to be at all remarkable, though we have chosen for illustration the case of the canine, which provides one of the best marked and most persistent residual laminæ amongst the anterior teeth. The three figures given simply show a progressive, if not very rapid, degeneration of the superfluous epithelial residua of the dental lamina.

A residual dental lamina beside $p^{\underline{1}}$ and $p^{\underline{2}}$ is now very distinct. Beside $dp^{\underline{3}}$ the Anlage of $p^{\underline{3}}$ is labially knobbed, and at its fundus is present a distinct dermal papilla (cf. succeeding stages). Well-marked residual laminæ are present by the lingual sides of the first two molars; and $m^{\underline{3}}$ closely resembles the corresponding tooth-germ in Stage VI (fig. 68 A).

Lower Jaw.—The dental lamina begins only a very short distance in front of the anterior plane of $i_{\overline{1}}$, so that the anterior segment of the dental lamina referred to in the preceding stages is greatly foreshortened.

Fig. 65 represents a coronal section passing through the dental lamina which just shaves the forwardly directed apical part of the first incisor. The dental lamina in this situation now shows a fairly well differentiated epithelial enamel-germ (*r. e. o.*), which we are inclined to interpret as that of a lost incisor in front of $i_{\overline{1}}$. The facts relating to this important structure are deserving of very careful attention, and are as follows:

During the period which elapses between Stage III on the one hand and Stages V and VI on the other, the dental lamina in front of $i_{\overline{1}}$ appears to undergo an elongation from behind forwards. This anterior segment of the lamina exhibits, in Stages V and VI, a very well-marked thickening, which decreases posteriorly where it is continuous with the residual lamina of $i_{\overline{1}}$.

In Stage VII the anterior growth of the large $i_{\overline{1}}$ has encroached upon the region in question, and accordingly the latter portion of the dental lamina is both relatively and absolutely shorter, antero-posteriorly, than it was in the immediately preceding stages. At the same time, however, it has become much more definitely thickened, and now seems to form the rudiment of a distinct enamel-organ with a flattened or slightly concave base (fig. 65).

This enamel-organ now appears as if formed by the most anterior extremity of the residual dental lamina of $i_{\overline{1}}$. At this stage posterior sections of the rudiment in question would certainly suggest the idea that it is related successionally to $i_{\overline{1}}$. But a consideration of the antecedent conditions of this structure, arising as it does entirely independently of and quite in front of $i_{\overline{1}}$, seems to us sufficient to dispose of such an interpretation in view of the very ample grounds, both general and special, for maintaining the truly successional nature of $i_{\overline{1}}$

itself. No one viewing our fig. 33 can doubt that $i_{\overline{1}}$ is in some sense successional to our vestigial $di_{\overline{1}}$, as there illustrated.

It must be borne in mind that the first lower incisor of the adult is a large and forwardly growing tooth. We have already seen that its Anlage is at first placed behind that of its small and rudimentary milk predecessor, but that subsequently the latter appears as if displaced backwards, owing to the anterior extension of the large permanent tooth. In like manner, we believe that this forward growth of $i_{\overline{1}}$ accounts for the noteworthy change in the later topographical relations of $i_{\overline{1}}$ to the rudimentary enamel-germ produced from a segment of the dental lamina, which in earlier stages is entirely in front of it.

We think it most probable that the rudiment in question really represents an incisor which has been lost, in front of $i_{\overline{1}}$, and which appears in imperfect form, and for a short time only, during ontogeny, before the very great forward extension of $i_{\overline{1}}$ wholly prevents its further development. Its continuity posteriorly with the residual lamina of $i_{\overline{1}}$ according to our views proves nothing one way or another with regard to its successional character, for everywhere we find that it is the residual lamina in the region of a tooth which is the true morphological continuation of the undifferentiated dental lamina in front or behind it.

It is interesting to compare the condition in Perameles with that described by Mr. Woodward for Petrogale (2). In that form he found two small calcified vestigial incisors. The anterior of these was entirely in front of the large permanent lower incisor, which latter he therefore regarded as really an $i_{\overline{2}}$.

In connection with his vestigial first incisor (regarded by him as belonging to the first dentition) he describes and figures a lingual downgrowth of the dental lamina showing clearly the papillated enamel-germ of a successional tooth (see his fig. 10). Now we have shown (see our fig. 33) that our vestigial $di_{\overline{1}}$ is related thus, not to a rudimentary successional tooth-germ, but to the adult $i_{\overline{1}}$. It is evident, therefore, either that $i_{\overline{1}}$ of Perameles is not homologous to the adult permanent lower incisor of Petrogale, or that our vestigial $di_{\overline{1}}$ is not homologous to the first vestigial incisor of Petrogale. May it not be that an anterior milk incisor in Perameles has been entirely suppressed, and that its successful germ, serially homologous with $i_{\overline{1}}$, attains a development in front of the first lower incisor, comparable to that of the successional germ connected with the first vestigial incisor of Petrogale?

And may it not be that Woodward's second vestigial incisor (his $i_{\overline{3}}$), to which he was unable to recognise any successor, is really the homologue of our $di_{\overline{1}}$ whose legitimate successor is Woodward's $i_{\overline{2}}$, the almost certain homologue of our "$i_{\overline{1}}$" of the adult Perameles?

An interesting modification in the relations of the vestigial first incisor ($di_{\overline{1}}$) is seen in this stage. In the early stages it was seen to be attached intimately and directly to the neck of the main dental lamina opposite its connection with $i_{\overline{1}}$ (see fig. 33). In Stage v (fig. 66 A) its attachment to the neck of the dental lamina is being, as it were, stretched away labially, thus tending towards the acquisition of an apparently independent attachment to the oral epithelium. This may be explained as effected, either figuratively or literally, by an opening out upon the deep surface of the oral epithelium of the most superficial part of the common lamina. In the present stage this process has been completed, and in fig. 66 the vestigial $di_{\overline{1}}$ is seen to possess an independent lamina of attachment to the deep surface of the oral epithelium labially from the line of attachment of the main lamina.

It is such a process of opening out and labial dislocation as this, which we have already suggested as explaining the peculiar downgrowths on the labial side of the root of the dental lamina present in the first upper incisor region in Stages IV and V (figs. 43—46 and p. 485). The present instance is an absolute proof of the possible occurrence of just such a dislocation of the primitive connection of a labial and more superficial member of the dental series.

In this stage may be noted for the first time the differentiation of the posterior secondary cusp of $i_{\overline{3}}$. Both in $i_{\overline{2}}$ and $i_{\overline{3}}$ the anterior part of the tooth is most strongly calcified. The former tooth has the thickest dentine cap, and it extends, though somewhat thinned out, practically to the posterior limit of the papilla of the tooth. But in $i_{\overline{3}}$ the dentine cap does not yet cover the posterior part of the papilla. In both teeth ($i_{\overline{2}}$ and $i_{\overline{3}}$) the very large and pointed papilla is seen to become less pointed as it is traced backwards, until its summit becomes flattened, and this flattening persists in $i_{\overline{2}}$ till the hinder boundary of the papilla is reached. In the case of $i_{\overline{3}}$, however, the papilla, after remaining flattened for some sections, quite abruptly shoots up a second pointed apex, which, however, at this stage is destitute of any dentinal covering. This second point to the papilla is merely superimposed upon the massive basal part of the papilla common to the entire tooth, and is a mere outgrowth of the primary papilla.

There are, in the incisor region of our series of Stage VII, considerably richer remains of the dental lamina than in Stage VI. Indeed, in the former there is still a very well-developed residual lamina beside $i_{\overline{1}}$, which retains its connection nearly all along with the oral epithelium, and extends into the region of $i_{\overline{2}}$ and $i_{\overline{3}}$.

This relative immaturity also characterises the more posterior teeth in the lower jaw, including $dp_{\overline{3}}$, the dentinal covering of whose papilla is much thinner than that of the same tooth in Stage VI. We have already seen that in respect of the upper jaw the present stage exhibits some anomalous features.

The Anlage of $p_{\overline{3}}$ is large—even bigger than in Stage VI—and, as in the latter, exhibits a distinct indentation with rudimentary papilla.

In the molar region $m_{\overline{3}}$ is a large enamel-organ. As in Stage VI the anterior cusp alone as yet is provided with a dentinal cap. The dentinal lamina on its lingual side is deeply placed and quite unconnected with the oral epithelium. Before it terminates posteriorly it becomes markedly thickened. Opposite the anterior part of the tooth it forms a residual lamina for $m_{\overline{3}}$, but posteriorly it becomes free from its connection with the tooth.

Stage VIII.—P. nasuta: pouch specimen.

Length from tip of snout to root of tail . .	82 mm.
Head length	38 „

Upper Jaw.—The incisors are all strongly calcified. Their relations to one another are much the same as in Stages v and vi, only $i^{\underline{4}}$ is practically in the same horizontal plane as $i^{\underline{3}}$ and placed labially. The fifth incisor, however, as in the stages mentioned, appears distinctly on a higher plane as well as lingually from $i^{\underline{4}}$. There is a hiatus between $i^{\underline{5}}$ and $^{\underline{c}}$ in which no tooth appears in the coronal sections. Here the dental lamina is present in a disintegrating condition. Its deepened character becomes apparent as it approaches the canine, and its distal portion is somewhat swollen but quite irregular in outline, due to invasion by connective tissue assisting in its disintegration. Occasionally traces of its original connection with the Malpighian layer may yet be seen.

The second premolar and the first molar have become so approximated that they partly overlap. The deciduous premolar occupies a position labially and superficially to the hinder part of the former and directly superficial to the anterior end of the latter, all three teeth appearing together in a number of the coronal sections. The Anlage of $p^{\underline{3}}$ is strongly developed by the lingual side of $dp^{\underline{3}}$, especially opposite its posterior part. The residual dental lamina, of which it forms the deepest part, has lost its superficial connection with the oral epithelium, though traces of such a connection here and there appear. The greater part of the superficial moiety of the lamina shows the extreme irregularity of outline due to progressive disintegration, and a number of rounded cell-nests or "epithelial pearls" are developed in connection with it. The deeper (distal) portion, forming the Anlage of $p^{\underline{3}}$, is very thick, and is found to develop quite abruptly a labial lobe. A few sections behind, this is seen to form the labial boundary of a cupped depression filled with connective-tissue cells. The whole Anlage is surrounded by an envelope of condensed connective tissue, and is separated by a bony lamella from the overlying hinder part of $p^{\underline{2}}$. No drawing is given, but the condition may be understood by reference to fig. 67 (Stage IX) and fig. 73 of Stage X. The deciduous premolar persists in the sections for some distance behind the point of disappearance of $p^{\underline{2}}$ and beneath the rapidly enlarging $m^{\underline{1}}$.

In the region of the first two molars traces of the dental lamina persist, sometimes as small irregular groups of epithelial cells, and sometimes as large and rounded "epithelial pearls." The lamina, however, assumes more definite form posteriorly opposite the hinder end of $m^{\underline{2}}$.

The third molar is still very much in the condition it exhibited in the immediately preceding stages (fig. 69), i. e. it shows commencing papillation, somewhat more marked than formerly; but the more superficial (more proximal) part of the lamina now exhibits a number of irregularities in place of the simple labial projection corresponding to the root of the laminar connection for $m^{\underline{2}}$. These irregularities are secondary developments, probably degenerative in character, but they might easily be taken for evidences of plurality of papillæ were their history not accurately traced. The connective tissue is condensed around the proper Anlage of $m^{\underline{3}}$, and shows a true rudimentary dermal papilla filling the basal depression of the Anlage. No such condensation of papillary differentiation is present in relation to the pseudo-papilliform modifications of the proximal part of the lamina referred to above (fig. 69).

Lower Jaw.—In the series at our disposal the region in front of $i_{\overline{1}}$ was not available. The anterior region of $i_{\overline{1}}$ itself was also injured. Abundant traces of a fairly bulky residual lamina undergoing disintegration were, however, discernible, and these are continued into the region of $i_{\overline{2}}$.

The deciduous first incisor $di_{\overline{1}}$ is still in evidence as a small and strongly calcified toothlet. The second incisor now extends forwards some distance in front of $i_{\overline{3}}$. The base of $i_{\overline{1}}$

extends backwards for a considerable distance below both the succeeding teeth, and the third now extends considerably behind the second incisor.

The deciduous premolar is now calcified right down to its root. The Anlage of $p_{\overline{3}}$ exhibits a distinct but small and simple dermal papilla, while the proximal ("neck") part of the lamina is irregular and contorted from the operation of degenerative processes. The three anterior molars are well-formed calcified teeth, and the dental lamina towards the posterior end of $m_{\overline{3}}$ becomes well developed as a residual lamina for that tooth, and then exhibits the differentiating Anlage of $m_{\overline{4}}$.

Stage IX.—P. nasuta: pouch specimen.

Length from tip of snout to root of tail . .	91 mm.
Head length	40 „

Upper Jaw.—The incisors are now more elongated and relatively narrower than in the preceding stages. Each appears, in coronal sections, above the hinder part of the tooth in front, overlapping the latter considerably. The relation of $i^{\underline{5}}$ to $i^{\underline{4}}$ is similar to that of $i^{\underline{4}}$ to $i^{\underline{3}}$, &c.

The tips of all the incisors lie near the oral epithelium. The canine appears above the hinder part of $i^{\underline{5}}$, overlapping it; $p^{\underline{1}}$ occupies a similar relation to $^{\underline{c}}$, and $p^{\underline{2}}$ to $p^{\underline{1}}$.

Up to the premolar region the dental lamina is represented only by fragmentary and degenerated remains in the shape of broken-up and isolated groups of epithelial cells, which are best marked beside $i^{\underline{3}}$ and $^{\underline{c}}$. In the anterior premolar region these degenerated remains continue to appear, though very sparsely in the region of the anterior part of the second premolar. After $dp^{\underline{3}}$ appears in the section the remains of the residual dental lamina become more definite, and soon are arranged in definite laminar form, but are deeply placed and quite unconnected with the oral epithelium; the relations of $dp^{\underline{3}}$ to the hinder part of $p^{\underline{2}}$ and to the residual dental lamina with the Anlage of $p^{\underline{3}}$ are illustrated in fig. 67. The most anterior sections of $dp^{\underline{3}}$, which cut the apical part of the tooth somewhat obliquely, show that it has already cut the gum. As it is traced backwards the crown recedes from the surface, and its crown assumes the appearance shown in the figure (fig. 67).

More posteriorly it is narrower than in the drawing, but is still much elongated. In this stage $dp^{\underline{3}}$ is seen to be a very much smaller tooth than the anterior premolars. It does not appear in the sections until behind the plane of the maximum development of $p^{\underline{2}}$, but nevertheless the posterior part of $p^{\underline{2}}$ extends backwards slightly behind it, being still visible when $dp^{\underline{3}}$ has totally disappeared.

The character of $m^{\underline{3}}$ is shown in fig. 70. It exhibits only a very slight advance on the preceding stages of the same tooth.

Lower Jaw.—In sections passing through the anterior tip of $i_{\overline{1}}$ the same rudimentary enamel-organ is encountered as was noted in Stages IV—VII. It is, however, more irregular than in Stage VII, and is evidently undergoing resorption, without having shown the least trace of calcification.

The tip of $i_{\overline{2}}$ has now grown far forward by the labial side of $i_{\overline{1}}$, and has insinuated itself between the latter tooth and its vestigial milk predecessor $di_{\overline{1}}$. This is a clear case of relative displacement of $i_{\overline{2}}$ similar to that which we have shown to occur in the case of $i_{\overline{1}}$ with reference to the rudimentary enamel-organ morphologically in front of it. $i_{\overline{3}}$ at this stage shows the now calcified posterior secondary cusp very distinctly. $di_{\overline{1}}$ is in statu quo as regards its structural characters, only its relative topographical position is slightly altered by forward growth of $i_{\overline{2}}$. $i_{\overline{3}}$ appears further back by the labial side of $i_{\overline{2}}$. It bears the same topographical relation to $i_{\overline{2}}$ as the latter does further forward to $i_{\overline{1}}$, so that all trace of the early peculiarities in the relative situation of these teeth is now lost.

The basal part of $i_{\overline{1}}$ may be traced far back, lingually to, and in a deeper plane than, $i_{\overline{2}}$ and $i_{\overline{3}}$, all three appearing together in the sections throughout a considerable extent of the anterior part of the jaw.

$dp_{\overline{3}}$ is now a narrow tooth much elongated vertically, which has cut the gum. Its residual lamina first becomes discernible opposite its anterior end.

The Anlage of $p_{\overline{3}}$ is now more bulky than in preceding stages. It is placed opposite the hinder part of $dp_{\overline{3}}$, and though of larger size exhibits only a very slight depression answering to the cupping of the enamel-organ; and here its papilla can hardly be said to exist as such, though the connective tissue is evidently tending towards its formation by local cellular accumulation opposite the depression.

In the posterior molar region the dental lamina ends as a free laminar mass by the lingual side of $m_{\overline{3}}$, and in front of the middle of that tooth. The Anlage of $m_{\overline{4}}$ does not seem to have made progress in the interval which separates this from the preceding stage.

Stage X.—P. nasuta.

Length from tip of snout to root of tail . .	118 mm.
Head length	50 „

This stage is distinctly further advanced on the whole than the preceding one, but the deciduous premolars are only just cutting the gum, while in Stage IX they had already protruded somewhat.

In the upper jaw no teeth have undergone eruption save $dp^{\underline{3}}$, but in the lower jaw the lower incisors have broken through in addition to the deciduous premolar.

In the region of the canine there are still to be found abundant remains of the residual dental lamina in the shape of detached cell-masses, embedded in the fibrous connective tissue lingually from the well-developed canine. These disappear and reappear frequently in the serial sections, and, in various sections widely separated from one another, one of the detached cell-masses assumes a very definite pear-shaped form, and is surrounded by a distinct connective-tissue capsule (fig. 72). This pear-shaped mass is always the deepest mass present, and obviously corresponds to the fundus-portion of the residual lamina. Its appearance is highly suggestive of the "knospenförmig" tooth-germs of other writers. But the fact that such appearances occur intermittently throughout nearly the whole extent of the lengthy canine region seems sufficient to negative this idea. We can point to quite a number, no less than seven, absolutely separate and distinct "bud-like enamel-germs" of this sort, existing in antero-posterior series by the side of the canine of this stage. Each of these is fairly bulky, pear-shaped, and concentrically encapsulated. It is beyond doubt that they are nothing more than portions of the swollen free distal margin of the residual lamina which persists for some time after the antero-posterior continuity of that margin has been interrupted by regressive processes. It is equally difficult to imagine a production of several rudimentary "bud-like enamel-germs of replacing teeth" by the side of the single canine, or to imagine a primitively single "bud-like" germ subdivided at intervals into a lengthy longitudinal series of bud-like masses.

Let it be specially noted that in the case before us we have presented the phenomenon of "knospenförmig" cell-masses, long persistent, and distinctly encapsulated by the surrounding connective tissue, i.e. offering the only credentials to which Leche appeals for the determination of such structures as true tooth-germs. The demonstration of their multiplicity in such a case as the present seems to us to be the reductio ad absurdum of the replacing-enamel-germ theory.

It seems to us that the presence of these structures at a comparatively advanced stage of the canine tooth development is largely explicable by reason of the considerable bulk of the entire canine Anlage, to which attention has frequently been called in these pages. The notable size of the canine lamina is doubtless associated with a higher degree of formative activity, which is longer in being exhausted here than elsewhere. In any case we can attach no special morphological significance to the continued presence at this period of even such definite epithelial structures as those described.

The two anterior premolars are large pointed teeth, and cause marked projection of the gum. Vestiges of the residual lamina are here and there discernible by the lingual side of the teeth as in the canine region, but on a smaller and less impressive scale. Here and there the form of the residual lamina (pear-shaped, with long stalk) is preserved, but for the most part the vestiges—generally absent altogether—are in the form of scattered minute epithelial cell-groups.

The deciduous premolar is in the act of cutting the gum with the most anterior part of its crown.

The process of eruption is very clearly seen to be attended by the flattening out of the enamel epithelium covering the tooth crown and its conversion into squamous epithelium with concomitant formation in it of epithelial "nests" or "pearls" close to the tooth cusps. This nest-formation also proceeds in the oral epithelium over the tooth. Eventually the epithelial pearls become placed quite near the surface, and they then undergo rupture and disintegration, their cores of concentric epithelial cells being lost and the tooth crown exposed. These different stages can be plainly followed in this one case by tracing $dp^{\underline{3}}$ backwards from its point of actual eruption towards the posterior more deeply placed part of the tooth, where the preparations for eruption are proceeding. The cell-nests here noted as forming in the enamel epithelium are in all probability similar to those epithelial nodules noted by Poulton (25) as appearing in the "most superficial part of the middle membrane of the enamel-organ immediately over the apex of each chief cusp of the large broad posterior tooth" of Ornithorhynchus (see his pl. ii, figs. 4, 5, 11, and 12, and pl. iii, fig. 6). It may be noted, however, that in this stage of Perameles the tooth is very much more advanced than those figured by Poulton in Ornithorhynchus, and the middle stratum of the enamel epithelium can no longer be distinguished as such. All we can say is that in the midst of the epithelial investment of the tooth-crown, formed by the now flattened enamel epithelium (as well as in the neighbouring oral epithelium), these cell-nests are formed, and that the process of eruption of the tooth under notice is accompanied and so far conditioned by their denudation and disintegration.

It is noteworthy that, in respect of its enamel formation, $dp^{\underline{3}}$ in Perameles displays a striking degeneracy. At no time do the cells of its inner enamel layer attain any great degree of elongation as compared with those of other teeth, and the layer of enamel actually formed is a very thin lamella indeed.

The Anlage of $p^{\underline{3}}$ with its distinct though small papilla is well represented in fig. 73.

In the molar region the residual dental lamina has practically disappeared from the first molar, but it is present by the sides of $m^{\underline{2}}$ and of $m^{\underline{3}}$, in which latter situation it is shown in fig. 71.

This section passes through the plane of the hinder end of $m^{\underline{2}}$, which lies considerably to the labial side of the part figured. It will be observed that the connective tissue shows a definite concentric arrangement around the residual dental lamina in this figure. Such an arrangement persists throughout the whole extent of the residual lamina, though it is only considerably behind the plane figured that it constitutes the Anlage of $m^{\underline{4}}$.

Lower Jaw.—The first two incisors have already completely broken through the epithelium at their apices. The anterior primary cusp of $i^{\underline{3}}$ is just in process of eruption, and here there may be observed at its tip a follicular or nest-like arrangement of epithelial cells which is in the act of opening out on the surface by disintegration, as was noted in the case of $dp^{\underline{3}}$ in the upper jaw.

$di_{\overline{1}}$ is still observable, but it is now more degenerate in character, merely consisting of a solid dentinal nodule, in which no trace of a papilla or cellular core can be recognised.

$dp_{\overline{3}}$ is in process of eruption, and this is associated with cell-nest formation between the surface and the erupting tooth point. The Anlage of $p_{\overline{3}}$ resembles that of the upper jaw pretty closely.

The fourth molar is a simply but deeply papillated enamel-organ with the middle layer of stellate tissue well developed. A residual dental lamina has already appeared lingually as a result of the differentiation of the anterior part of $m_{\overline{4}}$; the hinder part of the tooth is not yet constricted off from the parent lamina.

Stage XI.—P. nasuta: pouch specimen.

Length from tip of snout to root of tail	127 mm.
Length of skull	43 „

This stage is only slightly, if at all, older than Stage x. Indeed, in certain respects development is less advanced, for in the upper jaw no teeth have yet broken through the gum, though the canine and premolars are causing very marked projection of the latter.

Both the deciduous premolar and the Anlage of $p^{\underline{3}}$ closely resemble those of the preceding stage. The proximal part (or "neck") of the residual lamina, where that forms the Anlage of $p^{\underline{3}}$, offers a very striking example of cell-nest formation as a comcomitant of the process of disintegration of the lamina. Here we have the papillated Anlage of $p^{\underline{3}}$ borne upon an attenuated lamina, whose proximal border towards the oral epithelium exhibits a number of large globular epithelial swellings showing the concentric arrangement of the constituent cells characteristic of epithelial "pearl" formation.

The molars resemble those in Stage x.

In the lower jaw $di_{\overline{1}}$ is in the same degenerate condition as in Stage x, but the dentinal nodule representing it is even smaller. Otherwise the lower jaw presents no noteworthy features.

Stage XII.—P. obesula: pouch specimen.

Length from tip of snout to root of tail	120 mm.
Length of skull	43 „

The lower jaw only of this specimen was studied. Though its dimensions do not exceed those of Stage xi, it represents a decidedly older stage. This is explainable by difference in specific characters.

The Anlage of $p_{\overline{3}}$ still shows a rudimentary papilla projecting into the slightly cupped enamel-germ. The whole Anlage has an irregular appearance in many sections, owing to the presence of irregular appendages derived from the "neck" portion of the dental lamina.

Stage XIII.—P. nasuta: pouch specimen.

Length from tip of snout to root of tail	180 mm.
Length of skull	56 „

It will be seen from fig. 75, representing the upper jaw of this stage, that all the antemolar teeth (except $p^{\underline{3}}$) have cut the gum, and most of the general characters of the adult dentition are recognisable. Of the molars two in the upper jaw and three in the lower have broken through. The very small $dp^{\underline{3}}$ is seen occupying the slight interval between $p^{\underline{2}}$ and $m^{\underline{1}}$.

The Anlage of $p_{\overline{3}}$ in the lower jaw is shown in section in fig. 74. It is now a well-developed cupped enamel-organ, and, in one of the two series cut, the dermal papilla is much larger than in the section figured, filling up the whole of the somewhat deeper cup of the enamel-germ.

In the latter the stellate tissue of the middle layer is now well developed. In fig. 74 it will be observed that the enamel-organ is now in process of constriction off from the lamina, whose free end is already beginning to project as a new residual lamina (*rdl.*). That this interpretation is the correct one is proved by reference to Leche's figs. 140 and 142 (herewith reproduced for comparison as figs. 76 and 77), showing the corresponding enamel-organs of $p\frac{3}{3}$ in Phascolarctus. In connection with the latter a very evident and swollen residual dental lamina has anew developed itself by the side of $p\frac{3}{3}$. This, according to Leche, provides for the possibility of the production of a tooth of the third (his "fourth") dentition. We believe that this possibility must not be lost sight of, but in the meantime we prefer to point out that the regular development of such an Anlage as has been discovered and figured, both by Leche and by ourselves, by the lingual side of $p\frac{3}{3}$, serves in the most striking way to confirm our view of the homology of $p\frac{3}{3}$ to the other adult antemolar teeth, whose residual dental laminæ ("Ersatzleisten"—auct.) are therefore merely equivalent to that which later develops beside the third permanent premolar.

It may be noted that in Phascolarctus $p\frac{3}{3}$ appears to differentiate at a much earlier period than does the corresponding tooth in Perameles; for though the stage figured by Leche is considerably less advanced in its general development, and as regards the rest of its dentinal characters, than the present stage of Perameles, yet the Anlage of $p_{\overline{3}}$ has attained a somewhat higher degree of organisation.

Stage XIV.—P. nasuta: dried skull of a young adult about three quarters grown. (See figs. 78 and 79.)

Skull length . . . . . 70 mm.

Here (fig. 78) in the upper jaw the fourth molar is in course of eruption, and the premolar tooth-change is now almost completed. The third permanent premolar, $p^{\underline{3}}$, has broken through, and its crown has nearly attained the level of the anterior premolars. By the eruption of its posterior portion it is displacing the small $dp^{\underline{3}}$. On the right side the latter tooth is missing, but may have been accidentally lost. On the left side $dp^{\underline{3}}$ is still present, lodged in the slight hollow over the posterior end of $p^{\underline{3}}$. In the lower jaw (fig. 79) the eruption of $p_{\overline{3}}$ is not so far advanced, but the relations are otherwise entirely similar to those on the upper jaw. The crown of $dp\frac{3}{3}$ is worn and flattish or slightly hollowed. In this connection we may note that Flower (4, p. 635, and Pl. XXX, fig. 1) describes and figures the tooth-change in Perameles in an animal not quite full grown. His description of the condition is as follows:—"The permanent incisors, canines, and two anterior premolars are in place. Behind these in each jaw is a very minute, rather compressed tuberculated tooth, succeeded posteriorly by the true molars of the permanent series. In the alveolus above this minute tooth, which is the temporary or deciduous molar, is lodged the germ of the posterior permanent premolar, a tooth having a large compressed, pointed, triangular crown, with small anterior and posterior basal tubercles." (Pl. XXX, fig. 1.)

PART III.

DISCUSSION OF GENERAL PROBLEMS OF THE MARSUPIAL DENTITION IN THE LIGHT OF THE FOREGOING OBSERVATIONS.

Our own conclusions may, perhaps, be most conveniently introduced in the course of a discussion of the views of previous writers—already partly outlined in the introductory portion of this paper. And in order to focus the discussion, and to set forth its issues more clearly and definitely, we have thought it useful to formulate certain leading questions, and to define the attitude which has been assumed towards these by other observers whose views are related to our own either by way of agreement or contrast. In the formulation of these questions we have pretty closely followed the lines, and even in part the language, of writers who, like Thomas, Schwalbe, and Leche, have so greatly advanced the intelligent discussion of the subject of mammalian dentition.

I. "Do the existing teeth of Marsupials in front of the last premolar correspond to those of the milk or of the successional dentition of higher mammals?"

It will presently appear that the discussion of this question involves a consideration of those criteria which may enable us to determine a given embryonic structure as the germ of a successional tooth.

II. How are we to explain the single tooth-change or succession (i. e. in the case of the last premolar), hitherto almost universally recognised as the sole instance of tooth-change among Marsupials?

III. To which dentition belong the molars of Marsupials and of mammals generally? and—

IV. What is the nature of that generally admitted process of evolution by which multicuspidate teeth have been derived from a primitively simple unicuspidate type?

I. Homology of Antemolar Teeth of Marsupials.

In reference to the first question, it has already been pointed out that Flower (and formerly Thomas) held that the non-changing antemolar teeth of Marsupials answered to the permanent or successional teeth of the Eutherian orders. This determination was adopted with great unanimity up till the period of publication of Kükenthal's discoveries, even by those who dissented on other fundamental points from the Flower-Thomas hypothesis regarding the dentition of Metatheria.

But from the time that Kükenthal first recognised the persistence of somewhat swollen ("kolbig") downgrowths of the dental lamina at the lingual sides of the developing teeth of Marsupials, these downgrowths have on every hand been regarded as the true equivalents of the Eutherian successional series, and the entire theory of the marsupial dentition has accordingly been remodelled to suit the newer interpretation. Up to the present, so far as we know, not a single investigator has ventured to proclaim his dissent from the latter-day creed in this respect.[1]

If, then, we proceed to inquire upon what foundation this belief is based, we find that it rests solely on the occurrence, in Marsupials, of the epithelial downgrowths referred to, taken along with the similarity of the latter (*a*) to the earliest known rudiments of successional enamel-germs in other mammals, and (*b*) to the earliest stage of the one successional tooth admittedly existing in the marsupial jaw. But the question cannot, we believe, be thus summarily disposed of. It must be subjected to a much more thoroughgoing criticism, such as is embodied in the very weighty and thoughtful discussion of the entire subject by Professor Leche in his recent monograph (3).

In that work Leche has pointed out that, in order to decide in any given case whether a tooth belongs to one or other dentition, certain criteria have been employed whose worth and validity are of very different degrees. He attempts to

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[1] But see addendum, p. 581.

determine which of these may legitimately be utilised in arriving at such a decision.

(1) The Criteria of Serial Tooth Homology as set forth by Leche.

We propose first of all to summarise Leche's treatment of this fundamental problem. After reviewing his position the extent of our agreement and difference with him will become apparent in the course of discussion.

In the first place Leche discusses (*a*) the significance of the occurrence of epithelial downgrowths of the dental lamina lingually to developing enamel-organs.

That the presence of swollen epithelial downgrowths internal to the enamel-organs of mammalian teeth was sufficient to stamp the latter as belonging to the milk dentition, no one apparently, until Leche, had thought of questioning.

Woodward (2), indeed, is somewhat guarded in his language when he writes, "If these various and often minute downgrowths of the dental lamina are to be interpreted as representing rudiments of teeth, as seems probable from comparison with known rudiments of the first or second dentition in other mammals," &c.; but, nevertheless, he appears to accept in their entirety those dentitional theories which depend wholly upon the determination in question.

Leche, however, enters fully into the question of the validity of the assumption that Kükenthal's swollen downgrowths actually represent successional enamel-germs; and his conclusions are by no means decisive in favour of that assumption. The following passages will serve to illustrate his attitude:—"Da, wie bereits erwähnt, die Differenzirung des Schmelzkeimes ausschliesslich oder doch vorzugsweise an der labialen Fläche der Schmelzleiste erfolgt, so ist auch von vorneherein zu erwarten, dass das tiefe Ende der Schmelzleiste lingualwärts vom Schmelzkeim auftritt. Ist also jene 'Knospe,' welche von demselben verdichteten Mesodermgewebe welches das Zahnsäckchen bildet, umgeben ist (figs. 9, 10), nichts anderes als das zuerst sichtbare Product des Abschnürungsprocesses des Schmelzkeimes von der Schmelzleiste, so legt schon diese Thatsache den Schluss nahe, dass die 'Knospe' nicht, wie noch mehrfach auch von denneuesten Autoren angegeben wird, an und für sich identisch mit einem Schmelzkeim, respective einer Zahnanlage sein kann. Dieses giebt auch daraus hervor, dass, wie die vorstehenden Untersuchungen lehren, die Entstehung einer 'Knospe' nicht an eine bestimmte Dentitionsreihe gebunden ist: sie tritt nicht nur neben den typischen Milchzähnen sondern auch neben solchen Zähnen auf, die in der Regel ohne Nachfolger sind wie die Ersatzzähne (figs. 55, 78, 79, u.a.) und die Molaren (text—fig. 2)."

The substance of this criticism is frequently repeated by Leche, thus (3, p. 133):—"Steht es somit fest, dass das Auftreten einer 'Knospe' zunächst nur den beginnenden abschnürungsprocess des Schmelzkeimes von der Leiste kennzeichnet, ohne dass dadurch unbedingt ein neuer Zahn zu Stande kommt," &c.; and again (3, p. 136), "Das Vorkommen einer 'Knospe' d. h. das mehr oder weniger frei hervortretende Schmelzleistenende neben einen Schmelzkeime keineswegs beweist, dass der letztere zur ersten Dentition gehört. Ja, wir können weiter gehennicht einmal die weiterbildung dieser 'Knospe' zu einem wirklichen Schmelzkeime berechtigt zu dem Schlusse, dass der mit einer solchen Zahnanlage ausgestattete ältere Schmelzkeim unbedingt der ersten Dentition angehört, da, wie wir aus den obigen Untersuchungen wissen, auch lingualwärts von typischen und unbestrittenen Repräsentanten der zweiten Dentition solche knospenförmige Schmelzkeime vorkommen können, welche sich in einigen Fällen zu vollständigen Zähnen ausbilden."

Having thus provisionally disposed of the assumption that the mere presence even of a "bud-like" lingual downgrowth of the dental lamina is sufficient to establish the "milk" homology of the tooth beside which it is found, Leche goes on to pass in review other criteria which might be taken as affording the necessary test of a supposed serial homology. He dismisses (b) "simultaneousness of function" as affording quite incompetent evidence of serial homology between individual teeth, on the ground that in some mammals (notably in Erinaceus) certain of the milk-teeth function along with successional teeth.

Again, (c) the different depth at which one enamel-germ springs from the dental lamina compared with another can, in Leche's view, afford no reliable criterion of serial homology. Thus in Erinaceus the dental lamina in the situation of several of the antemolar teeth is markedly shallowed, and is wholly transformed into an enamel-organ very superficially placed. But it is found that the dental lamina, at the places referred to, has to produce only one tooth, and the anomalous position of the enamel-germ is held to be explained merely by the absence of tooth-change in that particular segment of the jaw.

While agreeing in general with the judgment expressed above, we are bound to add that the reasoning appended to it is not conclusive to us, for the absence of a tooth-change will not account for discrepancies of situation in many cases, e. g. the striking depth of the upper canine Anlage frequently referred to in this paper may be contrasted with the relative shallowness of the enamel-germs of the two anterior premolars which are without doubt serially homologous with the canine. On the other hand, we have found that enamel-organs which at first are close under the oral epithelium, and which have (as in Leche's description) no dental lamina or only a very short one, superficial to them, do afterwards exhibit quite a well-marked dental lamina, and from this by-and-by a residual lamina is differentiated. This is what happens in the case of the anterior premolars of Perameles, though they never attain the great depth of the canine Anlage.

We are of opinion that the relative depth of the various enamel-organs depends upon several factors, partly, perhaps, intrinsic to the lamina itself, and dependent upon the degree of its formative activity as an epithelial mass; and partly extrinsic, and dependent upon its topographical relations to various other structures.

(d) The time of development of a tooth, in so far as this takes account merely of the attainment of maturity and of the period of eruption of a tooth, fails, in Leche's judgment, to provide the necessary evidence, and constitutes a quite unreliable test of the serial identity of different teeth.

This test is, however, constantly relied upon by Röse, apparently without any misgivings as to its validity. Thus, concerning the last premolar and third incisor of Phalangista Cookii, he says (**1**, p. 702), "Diese Zähne sassen noch tief in ihren Alveolen, die Farbe und Dichtigkeit ihrer Schmelzkappe wies darauf hin, dass sie von bedeutend jüngerer Bildung sind als ihre Nachbarn. Von einem Zahnwechsel, d. h. der Resorption eines Zähnes der ersten Reihe konnte auch hier keine Andeutung angefunden werden. Es scheint mir sehr wahrscheinlich, dass auch bei Phalangista Cookii nicht allein der letzte Prämolar, sondern auch der dritte Incisivus des Oberkiefers aus der zweiten Zahnreihe entsteht," &c.

(e) But, on the other hand, the time of development of a tooth taken in a different sense furnishes a test which Leche recognises as of the highest importance, if not of paramount authority. Its value depends upon the validity of the following generalisation:—"Die Anlagen der zu derselben Dentition (Zahngeneration) gehöhrigen Zähne differenziren sich gleichzeitig oder nahezu gleichzeitig an der Schmelzleiste" (**3**, p. 137).

To this law of contemporaneousness of origin of the members of the same dentition Leche does indeed attach certain qualifications, but it nevertheless remains for him the most valid criterion in the determination of the serial homologies of the different teeth.

(2) The Serial Homology of the Marsupial Antemolar Teeth as tested by Appropriate Criteria.

We may now turn to the results of Leche's application of his critical method just expounded to the general question under discussion, viz.: Are the existing teeth of Marsupials in front of the last premolar homologous to the first or to the second dentition of higher mammals? And it is noteworthy that Leche's conclusions are to a very large extent negative as regards the value of just those developmental features upon which alone Kükenthal and Röse relied to establish the "milk" homology of the non-changing antemolars of Marsupials.

It had simply been assumed by Kükenthal and Röse that the presence of a residual lamina ("Ersatzleiste" of Röse), more or less swollen, by the lingual side of an enamel-organ gave sufficient assurance of the "lacteal" character of the latter. Leche's weighty and, as we believe, entirely valid contentions have, at any rate, opened the door to scepticism with regard to this doctrine. It remains to be seen upon what grounds Leche after all gives in his adhesion to a view which has been rendered assailable with the weapons he has himself provided.

The Nature and Morpologieal Value of a "Residual Lamina."

In one of the numerous passages in which he discusses the morphological value attachable to the liberated residual dental lamina, Leche utters his opinion as follows:—"Das durch die Emancipation des Schmelzkeimes freigewordene Schmelzleistenende bildet an und für sich nur die Voraussetzung für die Entstehung einer Zahnanlage: je bedeutender dieser Schmelzleistentheil ist, desto grösser ist die Prädisposition für die Bildung eines neuen Zahnes. Und wir können hinzufügen: ist dieses Schmelzleistenende wirklich kolbenoder knospenförmig angeschwollen und von einem Zahnsäckchen umgeben erst dann ist diese Möglichkeit als realisirt zu betrachten, erst dann können wir von einer (knospenförmigen) Schmelzkeimanlage reden, einerlei ob diese Anlage sich später weiter entwickelt oder nicht" (3, p. 134).

It will be remarked that this passage is by itself quite indecisive. It merely expresses the author's view that any free end of the dental lamina swollen (i. e. "kolbig" on section), and surrounded by an investment of condensed connective tissue, has a right to be regarded as an enamel-germ, though it may be an abortive one. And, since the author holds that such abortive germs are at least occasionally met with beside the true successional teeth of higher mammals, it is evident that we are not enabled by their mere presence to determine which tooth generation, if any, they represent.

Elsewhere, however, in a very important passage Leche explicitly sums up the argument in favour of the true "successional" character of the lingual downgrowths beside the various marsupial teeth in the following words:

"Charakteristisch für die Beutelthiere sind also sowohl das constante Vorkommen und die scharfe Ausprägung dieser Schmelzkeime und ihre Uebereinstimmung mit dem Schmelzkeim des p. 3, als auch ihre lange Permanenz, welche Eigenschaften diese Gebilde nicht unwesentlich von den lediglich durch die Emancipation der Zahnanlagen von der Schmelzleiste entstandenen 'Knospen' unterscheiden, ein Punkt, den ich hier ganz besonders betonen möchte. An einigen dieser Schmelzkeime sind deutliche Zahnsäckchen vorhanden" (3, p. 103).

Now we cannot but feel that if Leche's criticisms detailed above be well grounded, and if the sceptical lesson he repeatedly inculcates have taken hold upon the reader, the latter will find it difficult to discover in the summary quoted anything at all sufficient to reassure him of the certainty of that identification which the author advocates.

It is difficult to understand how "constancy of occurrence" —"a sharply stamped character"—and "long persistence" can possibly constitute a "not unessential" difference. To us there appears nothing at all "essential" about such distinctions, and thus far we must hold that Leche's own verdict ought to have been, at most, "not proven."

In one of the passages just quoted from Leche (on p. 103) we find him asserting that whenever the free end of the (residual) dental lamina is actually swollen in a "kolben" or "knospenförmig" manner, and when in addition we can recognise the presence of an investment of condensed connective tissue to form a "tooth-sac," then we have a right to speak of the structure as an "enamel-germ," whether it develops further or not.

With regard to the first of these two alleged guarantees of identity as genuine enamel-germs, it is held by the present writers that undue importance has been attached to the distinction between the free end of the dental (residual) lamina while in the condition of a mere prolongation beyond the developing enamel-organ, and the same prolongation when it has undergone some slight enlargement. With most writers, it is true, that distinction is not a very prominent one. Indeed, it would appear that, to the majority of them, practically any lingual prolongation of the dental lamina beyond its point of connection with a developing tooth is to be regarded as an "Ersatzleiste," and therefore as the homologue of a successional tooth. In Kükenthal's earliest reference to the marsupial condition (24) we find him basing his view of the "milk" homology of the marsupial incisors upon the possession by them of an "Ersatzleiste" with a swollen ("kolbig") free end. On the other hand, neither Röse nor Woodward lay any particular stress upon the enlargement of the free end of the residual laminal downgrowth. They do not ignore its frequent occurrence, but neither do they seem to regard that feature as a sine quâ non of its title to consideration as an enamel-organ. The passage already quoted from Woodward (p. 525) will sufficiently bear out this statement as far as that writer is concerned.

But according to Leche a mere lingual prolongation of the dental lamina beyond the point of attachment of the enamel-organ of a tooth gives of itself no certain promise of future tooth formation, or perhaps one should say, no reliable evidence of its morphological value as an enamel-organ of a succeeding tooth generation. Leche is thus forced to base a fundamental morphological distinction in large part upon that swollen ("kolben" or "knospenförmig") character which is held to distinguish the residual dental lamina beside the teeth of Marsupials. It may be quite true that such thickening of the free end of the residual lamina is an invariable antecedent to the first formation of a true successional tooth. But it is not equally permissible to assert, conversely, that wherever such a feature is perceptible there we must recognise the presence of a rudiment of an enamel-organ belonging to a definite tooth generation. The fact is that under nearly all the discussions touching the "swollen" residual lamina or "Ersatzleiste" of Marsupials—not even excluding Leche's more critical remarks—there appears to us to lurk an assumption which is traceable to the use of somewhat ambiguous descriptive terms. Thus the term "bud" ("Knospe") seems to us wholly misleading as descriptive of the somewhat thickened downgrowth (our residual dental lamina) so frequently met with by the sides of the developing enamel-organs in the marsupial jaw. The word "bud-like" ("knospenförmig") may indeed describe the outline appearance of the lingually prolonged lamina as seen in a cross-section, but it is thoroughly inapplicable to the actual solid form which that downgrowth really possesses.

We must therefore raise a most emphatic protest against the use of a phraseology such as that employed by Leche in the following sentence:—"Zunächst ist zu betonen, dass bei den Beutelthieren die Schmelzkeime der zweiten Dentition sich meist länger als die Schmelzleiste erhalten, also ganz wie bei einer Anlage, aus der ein Zahn sich wirklich entwickelt: hätte die Zahnanlage jede Bedeutung eingebusst, so ist schwer einzusehen, wesshalb sie als knospenförmiger Schmelzkeim sich länger als ihr Mutterboden, die Schmelzleiste erhalten sollte" (3, p. 105). Here the distinction assumed between "enamel-germs of the second dentition" and the "dental lamina" is a most unjustifiable one. The idea that, during disintegration of the latter, we can distinguish "bud-like enamel-germs" which are preserved longer than "the parent structure—the dental lamina" is a wholly fanciful one, dependent upon the confusion of the outlines of cross-sections with those of solid extended structures.

In his recent criticism of Leche's general attitude towards the question of marsupial teeth (27) Kükenthal employs the same objectionable form of expression—"bud-like enamel-germs": "Es sind nun, wohlgemerkt, nicht etwa die Enden der frei endigenden, einfachen Zahnleiste, die nach innen von den durchbrechenden Zahananlagen der Beuteltiere liegen" [but they are really nothing more], "sondern knospenförmige, teilweise von verdichtetem Bindegewebe umgebene Schmelzkeimstadien," &c. (27, p. 655).

Localised serial swellings of the continuous dental lamina in its liberated or residual phase, such as we can justifiably speak of as separate enamel-germs, do not exist, either distinguished from, or as integral parts of, the residual lamina aforesaid.

An exception to this statement must of course be made in favour of *p.* 3, which arises in the first place as a localised thickening of the residual lamina by the side of *dp.* 3. But *p.* 3, as we shall attempt to prove more conclusively below, is serially homologous with the enamel-organs of the other antemolar teeth of the adult, and not with the residual lamina developed by their sides.

We cannot insist too strongly on the laminar character of the residual lamina. As we have again and again shown in the course of our description of stages, it arises as a result of the constriction process whereby the permanent enamel-organs are differentiated from the main dental lamina. And, when thoroughly established, it is in perfect morphological continuity with the undifferentiated dental lamina fore and aft, intermediate between the region of one tooth and those of the next in front and behind. This is well brought out in our fig. 82, which is a combination drawing from several successive horizontal sections of the upper jaw of our Stage v. The complete antero-posterior continuity of the dental lamina in the anterior premolar region could not be demonstrated in a single section, but in the combination figure no violence has been done to any essential relationship. And the figure will be sufficient to illustrate the manner in which the free residual lamina by the lingual side, say, of $p\frac{1}{}$, simply forms the direct continuation of the undifferentiated dental lamina before and behind, which, in turn, is continued into the residual laminæ of $^{\underline{c}}$ and of $p^{\underline{2}}$. (We have carefully verified the planes of section, and have definitely determined that they correspond to the free portion of the epithelial [residual laminar] downgrowth. But, indeed, the view here expressed is supported by the whole body of our observations.)

The merest glance at our figure will serve to show that, at least in this region, the term "bud-like" applied to the residual laminar downgrowth is ludicrously inappropriate. The swollen "bud-like" outline seen on cross-section is due to a general and continuous thickening of the free marginal portion of the lamina.

It may with justice be contended that a perfectly similar marginal thickening of the primary dental lamina may be noticed prior to the differentiation from it of the earliest enamel-organs (though then the whole structure is much fuller and plumper than is the residual lamina of later stages), and that the later recurrence of such a condition may well be taken as heralding the advent of a new dentitional series. To this we reply that that general and continuous marginal thickening of the lamina, primary or residual, of itself signifies nothing at all in the way of tooth differentiation.

It is possible, indeed, to affirm—but this is equally true of a non-swollen residual dental lamina destitute of any tooth-sac—that the epithelial residuum is the potential equivalent of further successional teeth. But in our view there is no more reason to identify the residual dental lamina with any one tooth generation than there is to identify the primary and undifferentiated dental lamina of a higher mammal specifically with the "milk," to the exclusion of the "permanent" series of mammalian teeth.

We regard the lingually placed "epithelial downgrowths" beside the normal adult enamel-organs merely as portions of a dental lamina not yet wholly exhausted of its formative activity, and therefore possibly still capable, exceptionally, of providing material for the production of teeth homologous with a third Eutherian dentition (fourth dentition of Leche).

The hypothetical product of the residual dental lamina may perhaps be represented as tooth-series to the *n*th power, rather than as any definite series. Kükenthal (24) aptly remarks—and in this he is following the lead of Baume (26)—that the two mammalian dentitions are sisters whose mother is the undifferentiated dental lamina. This is true on the whole, but according to our theory it requires the further comment that the "Ersatzleiste" in Marsupials is analogous to the mother after the second parturition (the product of the first pregnancy having been early aborted), and ought not to be mistaken, as heretofore, for the younger daughter. The theoretical possibility of the occurrence of a third pregnancy need not be excluded. Leche has shown that occasionally in mammals such an event does actually occur; but so far as our experience goes the formal possibility or promise of a third dentition has been absolutely unfulfilled in Marsupials. In this connection we may ask the reader to compare Leche's figures (e. g. his figs. 106, 113, 115, 116, 118, 121, 124, and 137) of residual laminar downgrowths in various marsupials, which he labels as "knospenförmig," or even actually as "Schmelzkeime," with his figures (e. g. figs. 28—30, 74, 84, 94, and 95) of residual downgrowths of the lamina by the lingual sides of the true permanent or residual teeth of certain other mammals, and also with the two figures (our figs. 76 and 77) we have reproduced from his figs. 140 and 142, showing the similar appendage to $p\frac{3}{3}$ in Phascolarctus. It will be seen that no structural differences serve to distinguish the downgrowths in these different cases.

In view of the foregoing discussion the term "knospenförmig" will be seen to be thoroughly out of place as applied to the slightly thickened laminar downgrowths figured in cross-section in Leche's figs. 137 and 140.

It has been shown in connection with our Stages II and III that the first rudiments of the enamel-organs of the individual teeth arise as localised enlargements of the primary lamina especially in the form of labial outgrowths therefrom. And if it could be shown that the continuous residual lamina of Marsupials does actually develop regular localised enlargements, bud-like or other, by the lingual sides of the enamel-organs of the adult teeth,—of similar character to that which we have seen to constitute the first rudiment of $p\frac{3}{3}$, then the modified views of Leche would receive some support. But such is not the case. Of definite and regular "bud-like" swellings, other than expressions of that general and continuous marginal enlargement to which we have already alluded, we find no trace, unless indeed the production of isolated groups of cells and the formation of epithelial "pearls" and "cell-nests" during the final disintegration of the residual lamina were to be reckoned as such. And in the latter event we have shown that no less than seven rudimentary successional germs must be held to be present in the region of the upper canine of Perameles.

It is true that the residual lamella is not absolutely even thoughout its entire extent, but presents various slight irregularities and inequalities, both in contour and in the thickness to which its free marginal portion attains here and there.

These, however, never amount to localised swellings, which could possibly be spoken of or regarded as in any sense differentiated from the lamina. (The mode of origin of *p.* 3 will receive special attention.) Where local variations may be recognised they are extremely indefinite, and their only semblance of regularity of arrangement results from the fact that the level of the free distal edge of the residual lamina is to some extent affected by the depths of the enamel-organ, beside which it lies; hence, e. g., it is much deeper opposite the canine than beside the last incisor. These differences have an obvious and easy mechanical explanation. Nothing further issues from the structural condition thus brought about, except perhaps a slightly longer persistence of degenerating remains of the deeper lamina.

The view here set forth is not only borne out by our own pretty extensive observations, directed with special reference to this point, but also by examination of Röse's figures of his models of the developing dentition in Didelphys (**11**; cf. especially his fig. 12). In none of the stages there represented do we get any indication of "bud-like" or partially isolated structures arising from differentiation of the residual lamina, which is there quite clearly shown (cf. his figs. 12 and 15) as a continuous band. It is true that the contour of the latter, whilst plain and fairly even in parts, is in other places crooked and irregular; but the latter condition is obviously attributable, chiefly if not entirely, to the overcrowding of the developing teeth (cf. especially the incisor region of his fig. 12).

In Röse's models of the early stages of the human dentition (**9**) there may be followed the process of formation of a residual dental lamina, which up to a certain point exhibits characters very similar to those we find in the case of the residual dental lamina of the marsupial jaw. But the structural similarity between the indifferent stage of the human residual lamina and that of Marsupials really yields no evidence either for or against their actual and strict homology. For Leche has clearly proved[1] that residual laminæ may be developed by the side of the enamel-organs of the second (permanent) dentition of higher mammals. And indeed, as already pointed out, he has figured a residual laminar downgrowth by the side of the one undoubted successional marsupial tooth in Phascolarctus (figs. 76 and 77), an observation which we have to a large extent been able to confirm for Perameles (cf. p. 521 and fig. 74).

It is, to say the least of it, very suggestive that just in Phascolarctus, where the deciduous premolar is very rudimentary, and where, therefore, we may suppose the formative activity of the dental lamina to be less exhausted than in other

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[1] See especially his notes on the third incisor and canine of Erinaceus (G) on pp. 25, 26 of his monograph (**3**), and his illustrative figures, 28—30. Cf. also fig. 74 showing residual lamina ("Schmelzkeimähnliche") beside p. 1 in Phoca; fig. 94 showing same in Desmodus; and fig. 97 showing a similar condition of residual lamina beside $i^{\underline{1}}$ of the same animal. Cf. also Marett Tims' researches on the dentition of Canis (**37**).

forms, we find, by the lingual side of the early maturing *p.* 3, a well-formed residual lamina as figured by Leche. So also the preservation of the dental lamina in Desmodus and Phoca, referred to and figured by the same author, is doubtless due to the weaker development of both tooth series, i. e. there is more formative material left over than in other cases.

Connective-tissue Condensation around a Supposed Enamel-organ.

Leche, as we have seen, attached considerable importance to the occurrence of a "rudimentary tooth-sac," in the shape of a condensation of the connective tissue around a supposed enamel-germ. But while he utilises it for diagnostic purposes, he is yet by no means blind to its equivocal character. "Dass jene Verdichtung des Mesoderms an sich durchaus nicht immer die Anlage einer Zahnpapille oder eines Zahnsäckchens zo sein braucht, dass sie vielmehr das rein mechanische Produkt des Eindringens des Ektoderms ist, geht ausser aus den obigen Thatsachen auch aus dem Umstande hervor, dass, wie schon Baume (p. 66) beobachtet hat nicht nur der Schmelzkeim sondern auch die Schmelzleiste, falls sie genügend tief in das Mesoderm eindringt, von verdichteten Mesoderm-gewebe umgeben ist" (**3**, p. 15). And again:—"Sowohl aus Baume's als meinen Untersuchungen geht hervor, dass die Schmelzleiste überall da, wo sie genügend tief in das Mesoderm eindringt, eine Verdichtung in diesem hervorruft. Wie ich oben (p. 15, figs. 4 and 5) näher ausgeführt habe, ist also diese Verdichtung und Abplattung der Mesodermzellen durchaus nicht immer die Anlage eines Zahnsäckchens oder einer Zahnpapille, sondern vielmehr als das rein mechanische Product des Eindringens der Ectodermleiste aufzufassen. An den Stellen, wo die Schmelzkeime entstehen, schreitet durch den verstärkten Druck, welchen diese auf die umgebenden Mesodermzellen ausüben, die Verdichtung und Abplattung der letztern weiter zur Bildung von Zahnsäckchen und Zahnpapille, während durch die Rückbildung der Schmelzleiste in den Zwischenräumen zwischen den Schmelzkeimen die von jener hervorgerufene Differenzirung im Mesoderm wieder ausgeglichen wird" (3, p. 131).

These quotations from Leche are sufficient to dispose of the claim that a mere dermal condensation around an epithelial downgrowth can give any reliable guarantee of its nature. Our own observations have fully convinced us of the worthlessness of this feature as a test character. Connective-tissue condensation, in which the cells become flattened and concentrically arranged around an epithelial downgrowth or enamel-organ, is beyond doubt simply the response to the stimulus supplied by the continued proliferative activity of the epithelium. Naturally such condensation will precede tooth formation, but it will also accompany every other continued growth of the epithelial lamina to whatever cause it is due; and, as a matter of fact, it is most markedly seen around those proliferating epithelial masses or cell-nests which so frequently appear during the absorptive and retrogressive metamorphosis of the dental lamina.

Even on the ground of his own admission, then, we may put aside as incompetent that test of the genuineness of an enamel-germ which Leche bases upon the presence or absence of a rudimentary tooth-sac. And there remains only the swollen ("kolbig" or "knospenförmig") character of the epithelial downgrowths of the dental lamina, already criticised at some length.

That Leche should find it necessary to appeal to the "constancy of occurrence," "sharply stamped character," and "long persistence" of the supposed successional germs seems to us to indicate some mistrust of the judgment founded upon their structural features. But if the latter are insufficient to suggest that theory of their homology which he espouses, we are at a loss to see how the theory can be strengthened by the appeal to the vague characteristics referred to. Nor have the characteristics themselves greatly impressed us. The structures in question do, doubtless, "constantly occur," but they are no more "sharply stamped" in character than the fact of their mere existence would demand; nor do they "persist" beyond a period consistent with the general process of disintegration of the dental lamina of which they form parts.

Worthlessness of Proof from Agreement of Development of p. 3 with that of Supposed Enamel-germs.

In the passage quoted above from Leche (p. 198) it will be found that in discussing the residual laminar downgrowths he mentions their agreement with the enamel-germ of p. 3 as tending to establish their claim to be regarded as themselves rudimentary enamel-organs.

It is doubtless true that in its evolution *p.* 3 arises out of the residual dental lamina of *dp.* 3, and that that lamina at an early period exhibits the same developmental phase exhibited by the residual lamina subsequently developed by the lingual sides of the other enamel-organs. But in view of our previous contentions the fact of this general agreement can carry no weight as a proof of true serial homology.

Application of the Criterion of "Contemporaneousness of Origin."

Leche in the next place passes on to apply in this connection his favourite criterion of serial homology, viz. that of Contemporaneousness of origin of the different Anlagen from the dental lamina (cf. p. 528).

Remarking that the centre of gravity of the whole question of the homology of the persisting antemolar teeth of Marsupials lies in that of the relations of *dp.* 3 and *p.* 3 to the other antemolar teeth, Leche proceeds to apply to this question the above-mentioned test. And instead of obtaining a clear and unquestioned verdict in his favour on this head he finds himself from the first involved in a difficulty, which has to be obviated by an important qualification of his doctrine of "contemporaneousness." He finds, in fact, that the Anlage of *dp.* 3 is, after all, not contemporaneous in its first differentiation with the Anlagen of the other antemolar teeth with which he is attempting to demonstrate its serial homology, but is really in advance of the latter. The further hypothesis invoked in explanation of this is that the stage of differentiation of the Anlagen is conditioned by the future size and grade of development of the teeth concerned. And just in so far as this contention is valid, the value of Leche's paramount test is of course discounted. The author's own words in this important connection may be quoted : " Nun ergiebt sich sowohl aus dem von Röse (vi, fig. 4) abgebildeten Modelle eines 15½ mm. langen Didelphys-Jungen als auch aus der Untersuchung meines Stadium B (17 mm. lang), dass alle Zahnanlagen dieselben Beziehungen zur Schmelzleiste zeigen, dass aber die Entwicklungsstufe der verschiedenen Anlagen—und dies geht auch aus Kükenthal's Mittheilungen (I, pag. 662) hervor—schon auf diesen zeitigen Stadien der Künftigen Grösse und Ausbildung des betreffenden Zahnes entspricht. So ist der grösste von ihnen, namlich Pd. 3,—ich sehe naturlich von den Molaren ab,—auch Zugleich der am weitesten entwickelte, dann kommt der nächstgrösste (Cd.), welcher weiter entwickelt ist als die schwächeren Pd. 1, Pd. 2, und die Schneidezähne. Man hat daher ebensowenig Recht, dem Pd. 3 seiner höheren Entwicklungsstufe halber, einer älteren Dentition Zuzuzählen, wie wenn man aus demselben Grunde in Frage Stellen wollte, dass der Eckzahn zu derselben Dentition gehört wie die übrigen Zähne (Pd. 1, 2, und Schneidezähne). Bei dem etwas alteren Stadium C von Didelphys (siehe oben pag. 88) finden wir sogar, dass Pd. 3 weniger entwickelt ist als z. B, Pd. 2. Es bildet also dieser Umstand eine Stütze für die Zurechnung des Pd. 3 zu derselben Dentition wie die persistirenden Ante-Molaren " (3, p. 102).

Now it may be quite true that the future size of a tooth does, to some extent, influence the period of the differentiation of its Anlage from the dental lamina, i. e. the mere bulk of the lamina in a given position may determine the more hasty evolution of a tooth-Anlage in that situation. We may further point out that yet another factor does, at least in the case of the molars, determine the order of appearance of the Anlagen of teeth of the same series, viz. the relative position in the jaw. And it is at least possible that this factor may have some influence in the case of the antemolar teeth, seeing that the first formation of the dental lamina itself progresses from before backwards. But the significantly early differentiation of the enamel-organ of *dp*. 3, which we have shown to occur in the case of Perameles, obviously cannot be explained either by position in the jaw or by future size of the tooth. It will be remembered that *dp*. 3 in Parameles is the smallest of all the (functional) teeth in that animal. And yet it is differentiated from the dental lamina before any of the enamel-germs of the adult dentition have taken origin. Leche has been misled in the case of *dp*. 3 through the accident of its large size in Didelphys. Had he been conversant with the facts of development as we have ascertained them in Perameles, he could not have rested satisfied with his suggested explanation.

The relatively early differentiation of the adult canine Anlage, to which Leche refers in Didelphys in order to illustrate the law that future size influences period of differentiation, is not to be remarked in Perameles in our, for this purpose, most critical Stage III.[1] On the other hand, it is a fortunate circumstance that just in this stage we possess a perfect example of the differentiation, in connection with the canine Anlage of an enamel-organ which is truly synchronous with the enamel-organ of *dp*. 3, and which cannot, in our judgment, be regarded as other than that of a genuine canine "milk" tooth. This fact will, however, be more fully discussed in the sequel.

The fact, to which Leche several times refers, that in somewhat later stages of Didelphys (e. g. his Stage C) *dp*. 3 is less advanced than, e. g., the second premolar (p. 2), is of no avail in diminishing the importance of the fact of its early appearance.

So also in Perameles we have found that *dp*. 3 in its

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[1] In our Stage II the common canine Anlage is certainly very large, but it is yet in an indifferent phase. In the lower jaw it may be seen that an enamel-organ is in process of differentiation from its labial surface, but it is not that of $\frac{\ }{c}$, but of $d\frac{\ }{c}$.

subsequent evolution and maturation lags behind the neighbouring and more juvenile teeth, and is finally outstripped by them in its developmental progress. But Leche has himself, as we have seen, shown the worthlessness of the criterion of period of maturity, and we cannot follow him in his virtual application of that criterion in the passage above quoted. The subsequent behaviour of a developing tooth does not cancel, or otherwise alter, the significance of its first appearance, and we have shown that the latter cannot be disposed of in the way Leche suggests. We are far from affirming the all-sufficiency in every case of Leche's test of synchronicity as applied to the earliest differentiation of enamel-organs. No doubt other considerations, such as those above referred to, must in many cases be taken account of. Here, however, we believe that we have a case in which the value of the criterion of contemporaneousness is clearly illustrated; and it teaches, in our view unmistakably, the doctrine that *dp.* 3 is not serially homologous with the other antemolar members of the adult dentition.

This decision is of course the key of the whole position involved in the question under consideration, viz.:—"Do the existing teeth of Marsupials in front of the last premolar correspond to those of the milk or of the successional dentition of higher mammals?"

It can hardly be denied by anyone that the deciduous premolar of Marsupials is homologous to the milk-teeth of other Mammalia.[1] A recognition that *dp.* 3 is not homologous with the other antemolar teeth, but belongs to an "earlier" category, practically implies the serial homology of these teeth with the successional *p.* 3, and therefore their true homology with the successional teeth of higher mammals.

The view that *p.* 3 is in series with the teeth in front of it may at first appear, when viewed in isolation, an improbable one. But we think it may be taken as established by the facts before us, and at the very least estimate it agrees better with the facts in Perameles than the alternative theory.

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[1] But see above, p. 441.

Kükenthal, who laid special emphasis upon the precocious differentiation of *dp.* 3 in Didelphys, held that the early liberation of the residual dental lamina entailed by the constriction off of the enamel-organ of *dp.* 3 could only be conceived as the differentiation of the first Anlage of the successional tooth (7). It will be plain from the views we have enunciated throughout this paper that we cannot assent to this interpretation. The residual lamina beside *dp.* 3 is not to be conceived as actually at its first appearance a rudimentary enamel-organ. It is at first indifferent. But it is not long before a definite and progressive localised thickening and enlargement sets in (cf. Stage III) similar to that which constitutes the earliest rudiments, say, of the other premolars. With the latter, indeed, the rudiment of *p.* 3 is in direct serial continuity. We may therefore very well consider the rudiment of *p.* 3 as appearing tolerably early in development, though its further structural evolution is greatly delayed by the development beside it of its predecessor *dp.* 3.

II. Interpretation of the Tooth-change in Marsupials.

In reference to the second question formulated, it will be borne in mind that all recent authors are agreed that in those Marsupials whose dentition has been satisfactorily investigated, one tooth only is replaced by a successor, and that this tooth is invariably the last premolar.

The statement of Owen (15) that in Macropus, and also in wombat, the milk incisors are shed during the mammary fœtal stage, has never been confirmed by any subsequent observer, and has been universally discredited, the more readily that the statement is made without any definite indication of the details of such a process having been actually observed. It is, nevertheless, hard to believe, as Woodward (14) has pointed out, that such an accurate observer should hazard a statement of this kind absolutely without evidence. And in view of the discoveries of Woodward and Röse regarding the presence of vestigial teeth in the forms named, it may yet be found that phenomena in the way of shedding or absorption of rudimentary teeth actually do occur, such as might naturally be interpreted by Owen as cases of ordinary, if precocious, tooth-succession.

As yet, however, we can only deal with the one undoubted manifestation of tooth-change admittedly occurring in Marsupials. Is such tooth-change to be regarded as the survival of an originally more complete succession? With the single exception of Professor Leche all the recent authorities would seem to adopt the affirmative answer to this question, thus taking their stand upon the primitive diphyodontism of Marsupials, and inferentially of mammals generally. We have already seen how Mr. Oldfield Thomas (8) definitely, if rather reluctantly, gave in his adherence to this theory as a consequence of Kükenthal's researches. Any hesitation he exhibits is confessedly due to the difficulty he finds in explaining upon this hypothesis the striking fact that Triconodon already in Mesozoic times exhibited just the same fulness (or meagreness) of tooth-change which to-day characterises the marsupial group. But after all it does not appear that the peculiar fact mentioned (even if Triconodon is admitted as really of marsupial organisation, as seems probable) is easier of explanation on any alternative hypothesis. Surely it is just as difficult to account for the fact that a new acquisition of milk-teeth (as supposed by the older Flower-Thomas hypothesis) should have stopped short with Triconodon in the marsupial group, as to believe that the process of degeneration (supposed by the newer hypothesis) should have been suspended as far back as the Mesozoic age. For any secondary condition capable of accounting for the former suspension, such as the peculiar nutritional conditions of Marsupials, may without much difficulty be applied so as to account for the latter.

Leche has more recently come forward as an advocate of the alternative hypothesis that the tooth-change in the case of the last premolar is not the remnant of a more complete change, but the first appearance of a new dentition foreign to the primitive marsupial organisation. His theory, however, is markedly distinct in other respects from the original view of Thomas and Flower, for it is framed in full view of the presence of those ingrowths of the dental lamina which, in common with Kükenthal, Röse, and others, he regards as rudimentary enamel-germs. These, however, he interprets not as the retrogressing vestiges of an older, but as the products of a progressive evolution heralding the advent of an entire new dentition, which among the Eutheria has arrived at a condition of greater or less completeness. We have seen, too, that Leche's theory is widely different from that of Flower and Thomas in that he holds fast the homology of the marsupial teeth to the milk dentition of Eutheria; in his opinion it is the "second" dentition, not the "first," which is in process of acquisition.

In supporting his theory Leche refers to the difficulty which, as we have already seen, was experienced by Thomas in reconciling the condition observed in Triconodon with Kükenthal's theory of the vestigial character of the second dentition in modern Marsupials, and he claims that the difficulty vanishes when his theory is adopted, since he is able to point to the peculiar adaptation of the marsupial mouth to the sucking function as a cause adequate to account for the prolonged failure to develop a second dentition in the anterior region of the jaw.

Leche would thus figure as a supporter of the original monophyodontism of Marsupials, were it not for the considerations introduced by his highly significant discovery of calcified vestigial teeth. These he interprets as belonging to a "prelacteal" dentition, since they are evidently antecedent in development to the existing adult teeth in these animals.

Leche's Denial of the Vestigial Character of the Supposed Second Dentition of Marsupials.

If the theory of the persisting teeth of Marsupials, which is held by Leche in common with every recent investigator, be conceded, it is not easy to follow Leche in his opposition to the Kükenthal-Röse doctrine of the vestigial character of the supposed successional enamel-germs. It is true he simply refuses his assent until further proof. But the reasons he urges in support of the alternative theory do not appear to us to be of a very convincing character. Those sceptical arguments which alone appear to us to be specially cogent as applied to the theory of Kükenthal and Röse, and which we owe largely to the logic of Leche himself, appear to us to be almost equally destructive of the presuppositions of his own position.

Leche first calls attention to the long persistence of the so-called "enamel-germs of the second dentition." We have already adversely criticised the idea, common both to Leche and his opponents, that genuine and actual successional enamel-germs are present. But even supposing that such are really in evidence, we cannot see that their "long persistence" is any argument against their vestigial character. On the contrary, if they are really vestiges of teeth which have been lost, it is precisely these remnants of structures which formerly persisted throughout a considerable part of the life of the animal which will retain the strongest tendency towards durability.

Again, the occasional occurrence in other mammals (e. g. Erinaceus and Phoca) as discovered by Leche of teeth of a third dentition, developed from outgrowths of a residual dental lamina by the lingual sides of teeth of the second dentition, does no doubt establish the capacity of the dental lamina—after partial exhaustion by the production of a first and a second dentition—to once more liberate itself as a free residual lamina, from which in rare cases there may actually be generated members of a third and entirely new dentition.

But just in so far as this argument is relied upon for Leche's purpose his case is weakened for the establishment of the homology of the supposed potential enamel-germs of Marsupials to the Eutherian second dentition, a case which is, at its best, in our opinion an exceedingly weak one. In fact, we may say that if the production in some mammals of teeth of a third dentition, from "enamel-germs" similar to those of Marsupials, be admitted, this may fairly be claimed as at least establishing, on Leche's own premises, the possibility of a true morphological correspondence between the similar structures in the forms compared, and thus as tending to overthrow that homology of the adult marsupial teeth to the Eutherian milk dentition which Leche accepts as definitely fixed.

To this deduction from Leche's reasoning we have already given in our complete adherence, and we are thus after all at one with Leche in denying that the so-called "enamel-germs" are vestigial remains of fully developed successional teeth, since we deny that they are "enamel-germs" at all.

In further opposition to the interpretation of the residual laminar downgrowths as vestigial in character, we may cite the fact of the non-occurrence, in any single case, of occasional more advanced stages of tooth development, such as might legitimately be expected to crop up as the result of atavistic tendencies. That such an expectation is not without warrant is shown by the fact that in cases where undoubted vestigial teeth are found, as in the case of the so-called "prelacteal" teeth of Leche (our "milk" teeth), these frequently, if not generally, exhibit a prematurely advanced and "abbreviated" developmental condition.

Denying then, as we do—with Leche—the vestigial character of the supposed rudimentary enamel-germs in Marsupials, and—against Leche—their character as successional enamel-germs, we have to make the attempt to homologise the marsupial dentition with the typical mammalian upon totally different lines. Such an attempt can, we believe, be quite satisfactorily carried out, with the help of material in the way of facts and observations, of which some of the earliest and most significant were contributed by Leche himself. These facts and observations concern the existence of representatives of an undoubtedly vestigial tooth-series, whose imperfect development precedes the evolution of the persisting adult teeth.

Concerning the So-called "Prelacteal" Teeth.

Vestigial representatives of this earliest "prelacteal" tooth generation have been described by Leche in Myrmecobius, and, as indicated in our introductory sketch, he has interpreted the discoveries by Woodward and Röse of similar vestigial teeth as demanding an identical explanation.

If now it be admitted, on the strength of our previous contentions, that the doctrine of the homology of the existing antemolar teeth of Marsupials to the Eutherian milk dentition rests upon very slender grounds, surely the discovery in Marsupials of vestiges of a dentition preceding the adult one may well give us pause before adding, with Leche, a theoretical third to the two dentitions already recognised as the typical mammalian heritage. We do not think that due consideration has yet been given to the question whether these discoveries alone do not enable us to decide upon the precise value to be attached to the supposed rudimentary enamel-germs, in whose determination as such Leche has at least taught us to exercise a very cautious and even sceptical criticism, and which he himself after all accepts rather as potential than as actual "enamel-germs."

If these problematical germs can be dispensed with, the view of their successional homology proving to be ill-founded, the theory of the marsupial dentition may be reduced to very simple terms. The whole of the adult marsupial antemolar teeth (except *dp.* 3) could then simply be recognised as homologous to the permanent or successional teeth of other mammals; whilst the homologues of the Eutherian milk-teeth would be found in the deciduous premolar, together with any vestigial so-called "prelacteal" teeth which may be recognisable.

This now proposed explanation of the marsupial dentition has not been wholly ignored by Leche. Thus, in reference to the supposed "prelacteals" of Myrmecobius, he says, "Entweder stellen die fraglichen rudimentären Zähne die erste (Milch) Dentition dar, welche bis auf diese Reste verschwunden ist, während die zweite Dentition, welche die erste während der Phylogenese gänzlich ihrer Funktion enthoben und verdrangt hat, durch die persistirenden Zähne repräsentirt wird. Oder, die persistirenden Zähne entsprechen bei Myrmecobius wie bei den andern Beutelthieren der ersten Dentition, so dass die erwähnten rudimentären Zähne nichts anderes als Reste einer Dentition, welche der ersten Dentition vorangegangen ist, darstellen können" (3, p. 91). The arguments used by Leche to dispose of the first view seem to us exceeding weak. "Gegen die erste alternative spricht nun zunächst der Umstand dass dieselbe ohne jegliche Analogie bei den übrigen Beutelthieren ist, denn bei diesen entspricht ja, wie die neusten Untersuchungen übereinstimmend darthun, das persistirende Gebiss der ersten Dentition der placentalen Säugethiere. Und da gerade Myrmecobius in Bezug auf die Anzahl der Backenzähne die primitivste Form unter den lebenden Beutelthieren ist, würde, falls wir diese Alternative acceptiren wollten, das Myrmecobius-Gebiss durch das Vorkommen einer ganzen Reihe von Zähnen der zweiten Dentition zugleich höher als die übrigen Beutelthiere entwickelt sein-eine Annahme, welche durch ihren Mangel an wahrscheinlichkeit von selbst fällt" (3, p. 91).

It is plain that the "general acceptance in Marsupials of the homology of the persisting teeth to the milk-teeth of Placentals" simply goes for nothing in the present connection, seeing that it is just the validity of this "general acceptance" that is challenged, partly on the grounds of the existence of the "prelacteals." To determine the latter as morphologically "prelacteal" on the grounds of the accepted "milk" homology of the persisting marsupial teeth appears to us like reasoning in the very narrowest of circles.

And with regard to the second argument from the condition in Myrmecobius we are at a loss to perceive its bearing upon the question at issue. Granting for the present, at least, that Myrmecobius is the most primitive marsupial form, are we in the least bound to assume that even the most primitive mammal should exhibit partial monophyodontism, or at least incompleteness of its successional series? To make such an assumption is again to beg one of the most important questions at issue. Why, we ask, should it not simply be held that the most primitive mammals possessed both a milk and a successional tooth series, but that the former had undergone almost total suppression amongst the ancestors of the modern Marsupials (? Triconodon). We have already pointed out that the retention of the single tooth-change from Mesozoic times to the present offers neither more nor less difficulty than any other mode of explaining the Triconodon condition (cf. also Leche [28], p. 273).

The only argument used by Leche in this relation which appears to us to require serious consideration is his statement respecting traces of true "prelacteal" tooth-rudiments labially from the milk enamel-organs of higher mammals.[1] But when we examine the descriptions and figures upon which Leche bases this startling statement, we find that the indications referred to are of the very feeblest and most inconclusive kind (see his figs. 3 and 5′). We have ourselves met with structural indications in the pig (cf. figs. 83—85; text-figs. 2 and 3) which at first tend to suggest, even more strongly than Leche's, an interpretation such as he has given. But they are really to be explained in a quite different manner, as we hope to show incidentally later on when dealing with the question of molar homology (cf. p. 567, *et seq.*).

It is unnecessary here to recapitulate our own observations upon the so-called "prelacteal" vestigial teeth in Perameles, which, in accordance with our theory, we have constantly designated as "milk" or deciduous teeth. It is sufficient to say that we have recognised what we believe to be vestiges of these teeth in connection with at least four, and perhaps all, of the upper incisors, at least two lower incisors, and both upper and lower canines. Of these, $di\frac{3}{}$, $di\frac{1}{}$, and $d\frac{c}{c}$ have been traced in the cupped and papillated stage, while $di\frac{}{1}$ becomes strongly and $d\frac{}{c}$ weakly calcified.

In our examination of these interesting rudiments we very early became convinced of their serial homology with the tooth *dp.* 3. As we have stated in the introductory part of this paper, this conviction at first compelled us to take up the

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[1] The argument from the topographical relations between those portions of the dental lamina connected with the rudimentary and persisting teeth, respectively, may be passed over as unimportant. The various stages we figure of vestigial teeth in Perameles quite sufficiently explain any peculiarity in the late stages of the vestigial teeth, alone studied by Leche.

novel and revolutionary view that the deciduous tooth of Perameles, and probably of other Marsupials, was a member of a supposed degenerate "prelacteal" series. But ere long we were led, first to call in question, and then confidently to reject the "prelacteal" theory of this earliest tooth-series, as a violation of that principle of parsimony which should govern our procedure in the construction of explanatory hypotheses. For if *dp.* 3 and the supposed "prelacteals" be regarded as representatives of an otherwise suppressed milk series of marsupial teeth, we shall have before us a workable hypothesis which we believe to be free from the difficulties and complications which beset that more generally current, and which offers no insuperable difficulties of its own.

In preceding pages we have dwelt upon the application of Leche's criterion of the contemporaneousness of origin of the tooth-Anlagen from the dental lamina. We have shown that, judged by this test, *dp.* 3 belongs to a different category than that of the other persisting antemolar teeth. The identification of *dp.* 3 and the "prelacteals" as members of one and the same tooth-series may be designated as a positive result of the application of the same criterion. The investigation of our Stages II and III has yielded the most striking evidence of the validity of such a conclusion.

Thus in Stage II the enamel-organs of the future permanent antemolar teeth are in abeyance, or are represented only by localised undifferentiated thickenings of the dental lamina. But already $dp\frac{3}{3}$ and $di^{\underline{1}}$ show well-marked cupping (figs. 8, 9, 14, and 12), while $di^{\underline{3}}$ shows a slighter degree of it (figs. 2, 3, and 4), and the enamel-organ of $d^{\underline{c}}$ is, at least, in process of differentiation from the main mass of the canine Anlage (fig. 13).

But it is in connection with Stage III that the most striking pictures are obtained. The horizontal series from this stage was of especial use to us during our period of transition. Specially would we refer to our fig. 22, as affording a most instructive comparison between the canine "prelacteal" enamel-organ, so-called (our *dc.*), and the deciduous third premolar, *dp.* 3.

The position of the latter with regard to the neighbouring dental lamina is seen to correspond—not to that of the other adult teeth—but most accurately with that of the canine "prelacteal" enamel-organ, which is well seen in the section; $dp^{\underline{3}}$ and $d^{\underline{c}}$ are both seen to project labially so as to lie in a sagittal plane distinct from that occupied by the developing enamel-germs of the permanent teeth. This relation is also very evident, if slightly less striking, in coronal sections through the same Anlagen; we have only to imagine the bulk proportions of the respective parts in figs. 20 and 24 to be somewhat altered in order to realise the most complete correspondence between the two.

It is of the greatest interest to compare Röse's fig. 1, representing the dental condition of a fœtal Phascolomys (11, p. 752) with that just described. There, in the wombat, it appears that *dc.* is comparatively large and calcified, but is evidently of precisely the same order as the smaller calcified cheek-tooth marked D, whose homology with *dp.* 3 cannot, in our opinion, be doubted (cf. also his fig. 3). Here, therefore, the bulk proportions of *dc.* and *dp.* 3 are altered from what we find in Perameles, but otherwise the condition presents a remarkable similarity.

The very marked labial situation occupied by $dp\frac{3}{3}$ in all the entire series of our stages is most striking, and must not be confounded with such a lateral displacement of enamel-organs as may ensue as a result of over-crowding of the jaw. This latter occurs more especially in the incisor region, and its effects are well illustrated in the figures of Röse's models of Didelphys already referred to. But the distinction in the orientation of the enamel-organ of *dp.* 3 is established from its very first appearance. It is most striking when the germs of the anterior premolars begin to appear, and long before any displacement through encroachment on their part could be imagined. Thus both in serial position and in period of differentiation the enamel-organ of *dp.* 3 relates itself to the so-called "prelacteals," and not to the permanent antemolar teeth.

Along with these considerations may be borne in mind the tendency, so often illustrated amongst Marsupials, for this same tooth to share the fate of its fellows and to become vestigial. We have referred in the introduction to its condition in Dasyurus and Phascologale, and here we need do no more than refer to our figures of the tooth in the first-named of these forms (figs. 80 and 81).

On the grounds, therefore, both here and elsewhere detailed, we can have no hesitation in affirming that *dp.* 3 ought to be regarded as a member of the same series which includes the vestigial canines and incisors, and that this series corresponds to nothing else than the normal mammalian milk-series, which in Marsupials has been profoundly modified in the way of suppression.

Primitive Diphyodontism and "Suppression."

Along such lines of reasoning we thus reach the standpoint of the primitive diphyodontism of mammals—a position already occupied, though, as we believe, on erroneous grounds, by Kükenthal, Röse, and others. We believe that we are justified in seeking for the cause of the almost total suppression of the milk-teeth in front of the last premolar, in the modified condition of the mouth in marsupial young in consequence of its peculiar adaptation to the sucking function. This would seem to be a more natural employment of this factor than that of Leche, who has already suggested it. For he seeks by it to explain the non-appearance of an entirely new series of replacing teeth. Surely such an organic modification would more immediately tell upon an existing milk dentition in the way of suppression, rather than—merely through delay of such dentition—affect the subsequent development of successors.

In fact, Leche himself, in opposing the view that the second dentition has actually once been present and has since disappeared, contends in so many words that, according to the principle of "abbreviation," the suppression should affect the first rather than the second dentition. "Ferner falls wirklich jemals eine vollständige zweite Dentition ausgebildet gewesen wäre, ist es kaum zu erklären, wesshalb z.B. bei Didelphys, wo durchaus keine Ursache zu einer Reduction oder retrograden Entwicklung des Zahnsystems als Ganzen vorliegt und actisch auch keine Reduction eintritt, die zweite und nicht vielmehr die erste, im allgemeinen schwächere Dentition unterdrückt wurde—etwas, das ja auch nach dem Princip der Abkürzung der Entwicklung zu erwarten gewesen wäre" (**3**, p. 105. See also **28**, p. 372 [2]).

We note also in this connection the admission of the same author, "Wo aber sonst innerhalb der Klasse der Säugethiere Monophyodontismus auftritt, spricht der zur Zeit vorliegende Thatsachenbestand zu Gunsten der Annahme, dass die erste Dentition verschwunden ist und die zweite persistirt" (**3**, p. 143). Leche finds in Erinaceus an illustration of this view. He has come to the conclusion—we believe justly—that in this form those antemolars which are subject to no tooth-change are members of the second dentition which have hastened their time of development, and that Erinaceus represents "a transition form from the diphyodont to the monophyodont stage." Thus suppression in Erinaceus is interpreted in a totally different way from that occurring in Marsupials, so that three different mammalian conditions may be recognised: (*a*) the lowest or marsupial being characterised by an almost complete monophyodontism, from failure to develop successional teeth; (*b*) the typical mammalian condition, where complete duplicate sets of antemolar teeth—milk and successional—are developed; and (*c*) a still more advanced condition, attained in Erinaceus, Bradypus, and Pinnipedia, which again approaches monophyodontism, but this time through defect of the first (milk) or historically older dentition. An elaborate hypothesis like this, to explain what are essentially very similar conditions as regards suppression in Erinaceus, &c., and Marsupials, seems to us to bear its condemnation upon its face. We think the proofs are overwhelming that in Marsupials, as in the other forms referred to, but to an even greater extent, the suppression has affected the milk dentition and not the successional, and that we may extend to Marsupials generally the conclusion of Röse, that "Phascolomys Wombat ganz ähnlich wie die placentalen Säuger zwei typische gesonderte Dentitionen besitzt" (**11**, p. 745).

In a paper upon the milk dentition of the Rodentia (**18**) Woodward has discussed the occurrence of vestigial teeth in certain members of that order, and has shown that, in the forms dealt with, these vestigial teeth are representatives of the milk dentition. It may be noted that this conclusion is reached in the case of the mouse in spite of the fact that "there is present at one stage in the development of the large lower incisors a slight downward prolongation of the dental lamina on the posterior side of the enamel-organ of that tooth." This is, of course, simply a repetition of the ordinary marsupial condition. Upon it he comments:—"This might be regarded as presenting an indication of a permanent tooth, the large incisor being referred to the milk dentition, while the vestigial incisor in front might represent the pre-milk dentition. On the other hand, if this very slight prolongation of the dental lamina has any morphological value at all, I should be inclined rather to consider that it represented that supposed fourth dentition, as described by Kükenthal and Leche for the Seals" (p. 626). Here, then, we find Woodward applying to the vestigial teeth of the mouse precisely that mode of interpretation which is claimed by us to be alone capable of affording a satisfactory solution of the marsupial problem.

In Kükenthal's latest utterances (in reply to Leche) upon the problems of the mammalian dentition (**27**) we have a convenient summary of his views, which have undergone little if any change from those of his earlier papers.

He adheres firmly to the view that both the ordinary dentitions of mammals were inherited from sub-mammalian ancestors, but apparently admits as established the assertion that "traces of two other extinct dentitions are occasionally still present embryonically."

But it is extremely difficult to follow Kükenthal in his explanation of the manner in which suppression has been brought about in different groups. He first formulates a "law of reduction," stipulating that the tendency to suppression has constantly affected the first dentition most strongly. Thus he explains the suppression of the supposed "prelacteal" series. So far all is intelligible. But when he comes to explain suppression as witnessed within the mammalian class itself the case is much ess clear. "Bei den niederen Säugetieren dominirt die erste Dentition, die zweite kann wohl ausgebildet sein (Edentaten),[1] oder aber sie fällt aus besonderen Gründen—secundären Anpassungen—dem Rudimentärwerden anheim (Beutler, Cetaceen).[2] Bei den höheren Säugetieren verliert die erste Dentition an Bedeutung, und die zweite kommt mehr zur Geltung. Wenn jetzt gewisse Lebensbedingungen einen Zahnwechsel ungünstig sind, wird nicht die zweite Dentition unterdrückt werden, sondern die erste eine raschere Entwickelung und ein früheres Ende nehmen." (The last sentence expresses the corollary from the previously enunciated "law of reduction," and formulates precisely what we believe to have happened in the case of Marsupials.)

In view of this startling exception of Marsupials from the ordinary operation of the law of reduction, it is rather strange to find Kükenthal going on at once to say that "ein einheitliches Gesetz beherrscht also die Dentitionen aller Wirbeltiere" (p. 657). But why should Kükenthal ask us to make a special exception of the Marsupials from the operation of his own "law"? Why should he expect us to assent to the idea that while "conditions of life unfavorable to tooth-change," amongst mammals generally, should tend towards suppression of the milk dentition, yet nevertheless the

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[1] Upon this statement with regard to the Edentata, as well as upon the entire passage, Leche's rejoinder (**28**, p. 275) may be consulted.

[2] We are constrained to avoid special discussion of the Cetacean condition because we are disposed to hold with Leche that the homology of the persistent teeth of Cetacea must still be left as an open question (**28**, pp. 274–6).

"secondary adaptations" which have operated amongst the marsupial group have resulted in the well-nigh complete extinction of the successional dentition?

We have little doubt that the answer to these queries ultimately resolves itself into this,—that Kükenthal has not been able to bring himself to question the validity of the prevalent judgment which has stamped mere secondary or residual laminar downgrowths—sometimes thickened marginally—as veritable enamel-germs of successional teeth.

We are quite unable to sympathise with Kükenthal's final protest against Leche's views as calculated "to disturb anew the now clear conception" of the dentitional problem. In our opinion Leche's systematic criticism has been most timely, and if he has not gone the whole length in carrying out his criticisms to what we believe to be their logical conclusions, yet to him belongs the credit of having first introduced systematic critical criteria into the discussion of the developmental aspects of the problems of dentition.

III. Serial Homology of the Molars.

The question concerning the serial homology of the molars is not altogether separable from the fourth question, which deals with the origin of multicuspidate teeth in general.

For a connected historical sketch of the state of opinion on these points we may simply refer the reader to Leche's monograph (**3**, pp. 145–8). A succinct account may also be found in Woodward's paper (**14**), and a more extended discussion of the subject in Schwalbe's address (**16**). The principal views held may be shortly summarised as follows:

(*a*) The molars belong to the first or milk dentition (Owen, Beauregard, Kükenthal [earlier view], Röse [earlier view], Osborn, Hoffmann, Leche).

(*b*) The molars belong to the second or "replacing" dentition (Lataste, Magitot, Woodward).

(*c*) The molars are not homologous to any single series, but to two or more dentitional series, either by actual fusion of the tooth-germs of the latter, or of the material from which such tooth-germs would have been formed (Schwalbe, Kükenthal).

(*d*) The molars are the lateral end-members of separate dentitions: thus, in man, the dentition of which *m.* 1 is the end-member lies between the first and second dentitions (Röse [later view]).

The arguments mainly relied on by Leche for the establishment of the "milk" affinities of the molars largely hinge upon that interpretation of the development of the antemolar teeth with which we are now sufficiently familiar.

The presence of a residual dental lamina—when its distal portion is somewhat swollen, and especially when the surrounding connective tissue is somewhat condensed—has been liberally drawn upon by him to furnish proofs of the milk homology of the antemolar teeth. And, having been accepted as practically sufficient for that purpose, it is now utilised in establishing a like homology for the molars.

There can be no doubt that the molar segment of the dental lamina in Marsupials does very constantly develop a well-marked and often thickened residual laminar downgrowth opposite each tooth as a consequence of its differentiation from the parent lamina. Here, as elsewhere, however, the residual lamina is in each case directly and serially continuous, fore and aft, with the intermediate undifferentiated parent lamina; in other words, the residual laminar downgrowth does not exhibit discrete swollen portions, but is an elongated continuous band, more or less uniformly thickened towards its free distal margin.

Value of the Molar Residual Lamina.

No secure basis for the establishment of the dentitional value of the molars is afforded by the presence of this residual lamina. It might be hastily concluded that, with our definite opinion of the "successional" character of the persisting antemolar teeth, we are bound to attach the same value to the molars. But we are by no means compelled to do so. If the molars are to be regarded as homologous with any one dentition, as is likely enough, they may very well be equivalent to the milk series, as represented, e.g., by *dp.* 3. For the production of a residual dental lamina, during the differentiation of the enamel-organ of a tooth from the parent lamina, for us neither involves nor excludes the belief that successors may or do arise from that residual lamina. In other words, the production of a residual dental lamina by the lingual side of a milk tooth-germ in itself does no more than guarantee the possibility of the origin from it of a true successional tooth, just as its presence by the side of the Anlage of a successional tooth involves the potentiality of the origin from it of a tooth of a post-successional dentition.

We may, perhaps, advantageously refer once again to the condition of the first molar in the early stages (II and III) of Perameles. It will be remembered that in Stage II that enamel-organ is already recognisable as such, and its stage of development, though slightly less advanced than *dp.* 3, is fairly on a par with that of the anterior milk-teeth ("prelacteals"). Its papilla is just indicated.

In Stage III the resemblance between *dp.* 3 and *m.* 1, both in their stage and manner of development, is worthy of note. At the very least it may be urged that there is no primâ facie case for assigning *m.* 1 to a different series from *dp.* 3.

Woodward at first (2, p. 460) seems to have based his belief in the successional character of the molars upon his inability to discover in Didelphys, in the Macropodidæ, and some other mammals "rudimentary enamel-germs" or "Ersatzleisten" at their lingual sides. And he attempted to explain away what he regarded as a "suggestion" of such structures in Lepus and Talpa by a critical distinction which, thoroughly carried out in reference to marsupial developmental features, leads directly up to the main thesis of this work. Woodward in a subsequent paper (18) has fully recognised the existence of such lingual growths of the molar dental lamina in certain Eutherian forms, and in that connection reconsiders the question of molar homology. He still inclines strongly to the theory of their successional character, though, of course, no longer upon the grounds of the absence of what he regards as rudiments of possible successors. But the latter he would prefer to relegate to the category of Leche's fourth (post-successional) dentition. His reasons for such a decision are largely of a speculative character.

But there is one feature of his case which is by no means merely theoretical, but is based directly upon observation of structure. We refer to the presence of alleged rudiments of a molar dentition older than the existing molar series. We shall recur to this subject presently.

We have examined several series of sections of early Macropus embryos, and, like Woodward, we there find that the large and deeply cupped molar enamel-organs are as yet indistinguishable from the dental lamina, the latter appearing for the time being to have been wholly converted into the cup-like enamel-organs. But this is precisely what we find to be the case with the milk enamel-organs of the incisor and canine teeth in embryo pigs of 20 mm. head-length, where of course successional teeth arise later on. It is entirely a question of the stage of advancement of the developmental processes. And however it may be in Macropodidæ, there is not the slightest doubt that lingually placed "residual" prolongations of the dental lamina (and with swollen free distal margin) do occur constantly in Perameles during the development of every one of the molars, as shown in our descriptions and figures. Thus fig. 27 shows the tolerably early appearance (Stage III) of the residual lamina by the side of $m^{\underline{1}}$. Here there can be no possible confusion with the Anlage of $m^{\underline{2}}$ which is seen in the horizontal sections (figs. 25 and 26) to be just developing further back. That the evidence derived from these horizontal sections is not to be gainsaid becomes apparent in the examination of Stage IV. There $m^{\underline{2}}$ is a well-developed cupped enamel-organ, and has itself developed a definite residual lamina with a swollen fundus (fig. 52), while beside $m^{\underline{1}}$ the residual dental lamina is seen persisting as a typical "Ersatzleiste," and appears on cross-section as a swollen and "bud-like" ("knospenförmig") downgrowth (fig. 51).

And with the development of each successive molar a similar condition is brought about.

It would certainly appear that the evolution of the macropod molar proceeds less rapidly than it does in a polyprotodont form like Perameles.[1] In any case it becomes quite certain, from examination of our consecutive stages, that a residual dental lamina with thickened margin comes to project freely by the lingual side of the molars, just as in the case of the antemolar teeth.

Concerning the Significance of Labial Outgrowths of the Lamina in the Molar Region.

Holding such views as we do of the comparatively trifling significance to be attached to the occurrence of a residual dental lamina (even when "knob-like" or "bud-like" ["kolbig" or "knospenförmig"] on cross-section), it becomes the more important for us to come to a decision with regard to the real character of those labially directed outgrowths of the dental lamina in the molar region noticed by Woodward. These, as has been mentioned above, have been interpreted by him as possible or even probable vestigial remains of predecessors of the existing molar teeth.

In such vestiges he is inclined to believe (**2**, pp. 460 and 470, and cf. **18**, p. 630) we have the true serial homologues of the antemolar milk-teeth.

It is plain that, from our point of view, a discovery of vestigial remains of teeth preceding the functional molars would tend to place the latter in the same category with, say, the permanent canine of Perameles, where, as has been shown, a pretty large residual dental lamina is differentiated alongside the Anlage of the permanent canine at a time when a mere vestige of the milk canine (*dc.*) alone remains (fig. 47).

Woodward describes as "present on the outer side of the enamel-organ (in Petrogale) a conspicuous outgrowth of its cells, extending down into the gum at right angles to the

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[1] Probably the future large size of the macropod molar has something to do with the relative delay in the process of its differentiation.

swollen portion of the dental lamina." He goes on to remark that "we can only interpret these appearances on the grounds that the functional molars belong to the second or replacing dentition, and that this downgrowth on their outer sides represents the rudimentary, or rather vestigial, milk or first dentition."

We can fully confirm the observations of Woodward in regard to the existence of such labial projections as he has thus described (and figured in his figs. 25, *a* and *b*, and 26). The like are constantly seen in Perameles in certain regions, and at first we were inclined to interpret them in the same manner as Woodward has done.

We have, however, been led to entertain grave doubts as to whether such a construction can legitimately be placed upon the facts observed by Woodward and ourselves. In the first place it may be observed that the whole labial surface of the dental lamina often presents considerable irregularity as compared with the lingual surface, and the irregularities not infrequently constitute actual outgrowths or processes. This condition is specially noticeable in those parts of the lamina in front of or behind the enamel-organ of a molar tooth (cf. fig. 30, "*d*"). And even opposite the tooth-germ cellular projections may be observed upon the labial aspect of the "neck" of the dental lamina, proximal to the place of attachment of the enamel-organ, as in figs. 28 and 29 ("a"). This kind of process appears to consist of cellular material, originally forming part of the enamel-organ, which has been left attached to the main stem or "neck" of the lamina during the process of constriction off by which the enamel-organ is liberated from the lamina; and it is very probably comparable to those villus-like projections which not infrequently occur upon the outer surface of the developing enamel-organ itself. Indications are shown in fig. 29, "c," and especially in fig. 28, "c," of such villous irregularities over the general surface of the enamel-organ of $m \cdot \underline{1}$ towards its hinder end. In some sections, several (as many as three) labial projections from the neck of the dental lamina of the character indicated in figs. 27, 28, and

29 (" a") may be recognised, one above the other. It is plain that, whatever be the real meaning of these, it is impossible to regard them as vestigial representatives of teeth. This form of labial projection must therefore be excluded. Again, it may be found that a projection on the labial side of the dental lamina is traceable to the point of severance of the lamina from the oral epithelium.

Thus in the section shown in fig. 27, an outgrowth of this character (" b ") appears to be the direct prolongation of the proximal margin of the dental lamina, which has just been separated from the oral epithelium though it is still in contact with it. If a comparison of this figure be made with that of $dp^{\underline{3}}$ in fig. 24, it will become evident that the condition in the former is easily derived from that of the latter. We have only to imagine that the freed margin of the lamina in the region of $m^{\underline{1}}$ has become shifted, or has actually grown, labially from its late point of attachment (or later point of severance). Such an explanation may possibly apply not only to the case quoted, but to that represented in Woodward's fig. 26, *m′* (cf. also his fig. 20, *d. l.*).

On the other hand, neither of the explanations suggested above appears sufficient to account for the appearance shown in his figs. 25 *a*, and 25 *b*. These represent a form of outgrowth or projection with which also we are familiar in Perameles. Thus in figs. 30 and 31, passing through the lamina just behind $m^{\underline{1}}$ in Stage III, and where the last trace of the enamel-organ of that tooth is disappearing from the sections, we find that a labial process (*l. o.*) of very distinct and definite character manifests itself, springing from the neck of the dental lamina. This becomes established, not as a mere localised projection, but as a continuous secondary lamina extending right back to the place where the entire dental lamina ends abruptly in the Anlage of $m^{\underline{2}}$ (figs. 25–6).

The structure described cannot, we believe, be explained by either of the modes of interpretation already put forward as applicable to some other cases. It cannot in any sense be a consequence of disintegration or severance, and its constancy and persistent continuity in the hindmost molar region forbid our regarding it as a more or less accidental or capriciously developed villous outgrowth or process. But at the same time the fact that it does not constitute any mere knob-like excrescence, but that it really extends longitudinally backwards as a flattened laminar or ridge-like outgrowth, seemed to us upon closer consideration to be unfavorable to its claims to be regarded as of rudimentary or vestigial dental character.

On examining the next succeeding stage (IV), where $m^{\underline{2}}$ is a well-developed enamel-organ, and $m^{\underline{3}}$ has attained a degree of development comparable to that of $m^{\underline{2}}$ in Stage III, we find that the secondary labial ridge or lamina aforesaid has now disappeared opposite $m^{\underline{1}}$ and up to near the hinder part of the now developed $m^{\underline{2}}$. Its disappearance is associated with the disappearance in most of the sections of the connection between the dental lamina and the oral epithelium, i. e. with the onset of disintegration of the proximal portion of the dental lamina.

But towards the hinder end of the now well-developed $m^{\underline{2}}$ the secondary labial laminar outgrowth again comes into view (figs. 52 and 53, *l. o.*), this time extending backwards from near the hinder end of $m^{\underline{2}}$ to the posterior limit of the dental lamina with its thickened Anlage of $m^{\underline{3}}$ (fig. 54, *l. o.*).

We see, therefore, that the conditions which formerly obtained further forwards are exactly repeated here at the progressively growing segment of the dental lamina. Here again, however, there is nothing to suggest a vestigial dental character. The continuous laminar character, indeed, is an indication to the contrary.

We may sum up these and further observations in this direction by affirming that, towards the hinder end of the dental lamina (which in the molar region is the growing end, and is thus ontogenetically younger than the parts of the lamina in front of it), there is constantly to be found, in addition to the main stem or axis, as it were, of the dental lamina a secondary offshoot or lateral leaf-like outgrowth, directed labially, nearly at right angles with the stem, as shown in figs. 30 and 31 (*l. o.*) and in Woodward's figs. 25 *a* and 25 *b*.

The definiteness, constancy, and longitudinal extension of this form of labial projection markedly distinguish it from those other kinds of outgrowths on the labial side of the dental lamina to which we have alluded above.

No satisfactory explanation of the meaning of this structure seemed forthcoming until, after some incidental study of serial sections of pig embryos, the conclusion was forced upon us that this secondary labial laminar projection really represented the continuation of the labio-dental, or, better, labio-alveolar epithelial lamina (precursor of the lip-furrow or labio-alveolar groove) which the researches of Röse (9) in the human teeth have shown to arise from a common Anlage with the dental lamina proper.

This identification seems to us so important and so unexpected, as applied to structures so far back in the molar region, and especially in marsupial animals (in which, at least anteriorly, the lip-gum furrow is long suppressed), that we find it necessary to exhibit in some detail the facts upon which our conclusion is based.

It must be admitted that the explanation offered seems far-fetched and improbable, nor do figs. 30 and 31 seem to lend much countenance to it. Nevertheless we hope to show good reason for the belief that the labial laminar outgrowth is, at least, an epithelial lamina which is largely independent of the dental lamina proper.

In the first place we must state that in respect of the mode of extension backwards of the dental lamina in Marsupials, our observations are so far at variance with those of Röse upon human molar development. There can be no doubt that in the animals examined by us the greater part of the molar lamina grows posteriorly by extending backwards its continuity with the oral epithelium, and not merely by extending back freely into the mesoderm beneath the epithelium as Röse has described it. The anterior, greater part of it appears to be as much the product of direct ingrowth from the oral epithelium as is the dental lamina in the antemolar region. That this is the case as far as the entire molar lamina in Stage II is concerned we have already pointed out, but we may here at once state that we have observed the extension backwards of the dental lamina in continuity with the oral epithelium in other stages as far as the region of the third molar inclusive in the upper jaw, and just short of this region in the lower. In fact, it may be stated that this continuity with the oral epithelium exists just as far back as the oral epithelium overlies the molar Anlagen. The most posterior molars appear to originate precociously from a backward free prolongation of the lamina before the lengthening of the jaw permits a co-extensive prolongation backwards of the oral epithelium.

In pig embryos of 20 mm. head-length, we also find the connection of the dental lamina with the oral epithelium maintained right up to the hinder end of the molar region, or within a couple of sections of it.

We are, therefore, little surprised to find that in the pig the labio-dental or labio-alveolar lamina (i. e. the epithelial Anlage of the lip-furrow which is formed anteriorly) is continued back into the molar region as the Anlage of what we may here call the gum-cheek-furrow. And at the extreme posterior end of the proper dental lamina the latter is seen to be fused near its basal or attached margin with the labio-alveolar lamina, the two structures forming parts of a common Anlage, as Röse has shown to be the case at first in the anterior region of the jaw. Fig. 83 illustrates the condition met with close to the posterior end of the molar lamina in the upper jaw of such a pig embryo. The lamina stops rather abruptly a few sections further back.

The section figured passes close behind the posterior end of the molar Anlage,—in fact, partly shaves it. Projecting labially from the neck of the lamina near the oral epithelium there is seen in cross-section a laminar projection (*l. o.*) of the kind whose significance we are discussing, and which is proved, by examination of the series, to be neither more nor less than a continuation backwards of the labio-alveolar lamina or Anlage of the "lip-furrow."

The accompanying figures in the text are outlines of the identical epithelial structures in the lower jaws of the same

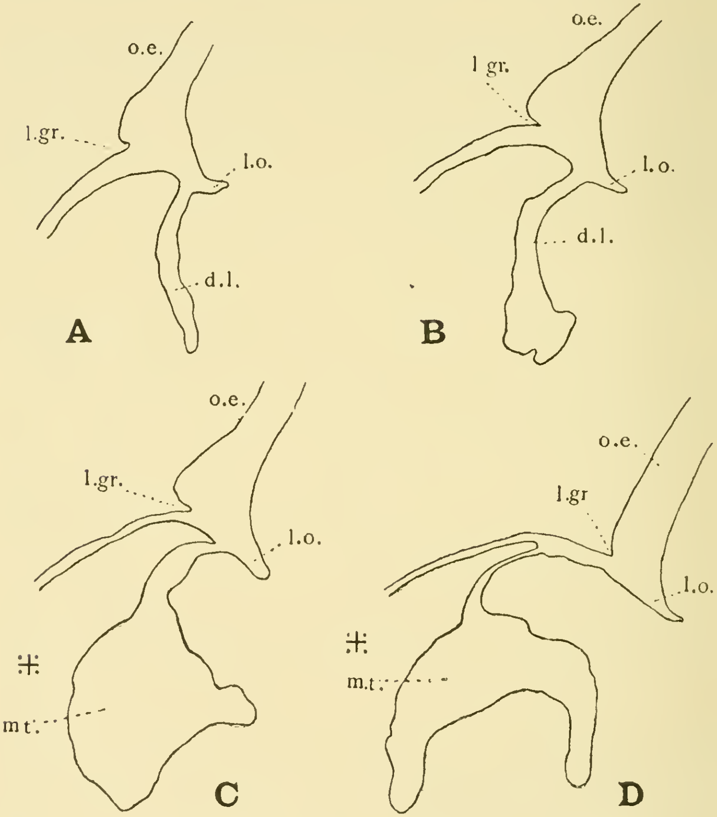

Fig. 2, A—B.—Pig embryo of 20 mm. head-length. Four serial coronal sections through the molar region of the lower jaw. A. Some distance behind $m_{\overline{1}}$. B. Two sections in front of A. C. Through posterior part of $m_{\overline{1}}$. D. Through middle region of $m_{\overline{1}}$. *l. o.* = labial laminar outgrowth. *l. gr.* = lip groove. × 45.

series. (The lower jaw was chosen as affording a better series of gradations of otherwise exactly similar conditions.)

Text-fig. 2 (A) shows the common laminar Anlage attached to the oral epithelium (which exhibits on its oral surface a trace of the actual furrow). This section corresponds exactly in its relation to the molar lamina with that shown in fig. 83 from the upper jaw, and shows only a very slight variation therefrom in form. The next three outlines (text-fig. 2, B, C, D,) are from sections taken at intervals of a few sections further forwards. Of these, D shows the definitive separation of the labio-alveolar Anlage from the proper dental lamina by an increase of the connective-tissue basis of the alveolus.

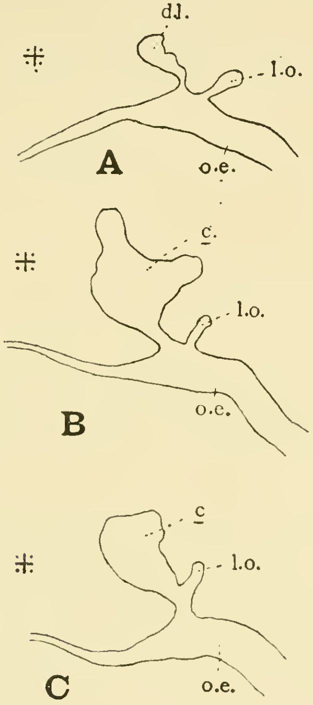

FIG. 3, A—C.—Pig embryo of 20 mm. head-length. Three serial coronal sections, upper canine region. A. Just in front of $\underline{c}$. B. Through middle region of $\underline{c}$. C. Through posterior region of $\underline{c}$. × 45.

The remaining figures (text-fig. 3, A, B, and C, and figs. 84 and 85) from the pig are taken, not from the molar region, but from much more anterior parts of the jaws, in order to show the striking appearances in the way of labial processes which are produced at certain stages of the differentiation of the common Anlage of labio-alveolar groove and proper dental lamina. Attention may be especially directed to the transitional forms of the labial projections in the upper and lower jaws figured in figs. 84 and 85. It must be mentioned that every one of the labial projections figured has actually been traced into continuity with the definite lip-furrow Anlage as clearly as in the case of the series shown in the first four outline figures (text-fig. 2) taken from the molar region. With regard to the latter it may be remarked that, as might be expected from the fact that the more immature portion of the molar lamina is the posterior, the primitive connection of the Anlagen of labio-alveolar and proper dental lamina is recognisable behind, and in proceeding forwards in the molar region a transition to a state of mutual independence of the two structures occurs. The fact that again, anteriorly, there is a return to the status of a common Anlage is doubtless conditioned by other developmental factors.

Comparison of fig. 83 and text-fig. 2 of the molar lamina in the pig, with figs. 30 and 31 of Stage III, and 52—54 of Stage IV of Perameles, and also with Woodward's figs. 25 *a* and 25 *b* of Petrogale, will hardly fail to carry conviction of the essential identity of the structures therein represented.

From a careful investigation of these labial appendages in the molar region we therefore conclude that while such appendages may not be uniformly homologous, yet those which alone are definite, and irreducible to the results of unimportant incidents of development, require a different mode of interpretation from that suggested by Woodward. We must accordingly dismiss the idea that any structural features occur in the development of the marsupial molars which can fairly be interpreted as vestiges of degenerate "milk" predecessors.

We are thus thrown back upon the already noted resemblance between the development of $dp^{\underline{3}}$ and $m^{\underline{1}}$ in the early stages. Such resemblance as has been adverted to cannot, of course, by itself prove that an actual serial homology exists between the two teeth. It may indeed establish a primâ facie case for such an homology. But, however we may decide the special problems of the distinctively marsupial dentition, the serial homology of the molars must remain as a general question of mammalian dentition, whose decision must yet be regarded as a separate and largely independent issue.

The theories of molar homology set forth under (*c*) and (*d*) on page 558 still remain to be dealt with. Of these the latter has not as yet been supported save by its author, and may, we believe, be regarded as a mere speculation. The former, which is supported by both Kükenthal and Schwalbe, may best be discussed in connection with the next question, which primarily concerns the mode of origin of multicuspidate teeth, but which raises the general question of fusion of originally distinct dental units.

IV. THEORIES OF DENTAL FUSION AND THE ORIGIN OF MULTICUSPIDATE TEETH.

The results of the present research do not, any more than Woodward's, lend countenance to the view once advocated by Kükenthal, that molars are a result of the fusion of germs of more than one dentition, in the sense in which fusion has been supposed to occur between tooth-germs of the same series. But Kükenthal's present position in regard to this question is rather less simply expressed. He holds "dass die echten Molaren im Wesentlichen zur ersten Dentition gehören, dass sie aber ein Verschmelzungsproduct der Anlagen erster Dentition mit dem Material, aus dem sonst die zweite Dentition entsteht, darstellen" (**20**, p. 112, and **27**, p. 659).

Against this view both Woodward (**14**, p. 447) and Leche (**3**, p. 146) have pointed out that it ignores the fact, upon which Kükenthal had himself insisted, that a residual dental lamina does normally develop by the lingual side of the first molar. To this criticism Kükenthal has omitted to reply during the course of his criticism of Leche, embodied in his latest publication on this subject—'Zur Dentitionenfrage' (27). And we find him towards the close of this last paper simply reiterating the opinion in the course of his remarks in reply to Hoffmann.

We confess that Kükenthal's view is still very far from being clear to us. When he speaks of the molars as representing "ein Verschmelzungsproduct der Anlagen erster Dentition mit dem Material, aus dem sonst die zweite Dentition entsteht," are we to understand that the enamel germs of a first dentition are first of all differentiated from certain residual "material" representing enamel-germs of a second dentition, and that, having been differentiated from one another, these are subsequently fused together? If this be what is meant, then certainly the facts of marsupial development give no countenance to such an idea. Indeed, the mode of origin, preservation, and gradual disintegration of the molar residual lamina prove that certain "material" remains over which is not fused or taken up during molar development.

But if Kükenthal's words are not to be understood in the sense referred to, and if we are to believe that he does not conceive of a morphological separation or form-differentiation ever having been effected between the material of the first dentition and the material representing the second (as, indeed, his employment of the term material would seem to imply), then we can only say that, so far as we can see, his view differs but slightly, if at all, from Hoffmann's idea of "physiological" fusion.

The opinions of the last-named author are thus approvingly summed up by Leche in a passage which deserves special comment:—"Will man aber den Begriff der Verschmelzung umbedingt beibehalten, so kann man, wie Hoffmann richtig bemerkt, und wie auch ich bereits oben (p. 142) hervorgehoben habe, sich vorstellen, dass das Schmelzleistenmaterial, welches bei den niederen Wirbelthieren zur Ausbildung einer Ganzen Anzahl von Zahnserien verwendet wird, bei den Säugethieren zur Ausbildung von bedeutend wenigeren, dafür aber komplicierteren Zähnen benutzt wird" (3, p. 155).

Concerning such a view we would remark that it amounts simply to a surrender of the idea of the fusion of morphological structures as such. The aggrandisement of one morphological structure at the expense of the material required for the development of another, whereby the survivor is enabled to launch out into a further structural differentiation, may be a justifiable conception, but it ought not to be confused with a case of morphological concrescence. True morphological homology deals with the identity of organic forms, not with that of the mere "material" organised under such forms. In fact, it may be questioned whether the identity of organic material, as distinguished from that of the form under which it is organised, is at all a fruitful or even valid biological concept.

In any case, until Kükenthal has disposed of the objection based upon the presence by the side of the molars (e.g. of Marsupials) of a residual lamina entirely comparable to that found beside other admittedly simple teeth, his theory of homology of the molars must be regarded as untenable.

A still more fundamental question underlies the preceding discussion, i.e. whether the multicuspidate form of the modern mammalian molar has originated by the concrescence of several originally distinct and simple tooth-germs, or by the gradual evolution of cusps as outgrowths of a single simple conical tooth.

In favour of the latter view are ranged the majority of palæontologists (cf. especially Cope [10] and Osborn [34]), who have elaborated a most plausible scheme showing the steps in the supposed evolution of the complex mammalian molars from a primitive conical type of tooth, through a very early tri-tubercular condition.

The fusion theory, on the other hand, has taken shape chiefly at the hands of a few embryological investigators—notably Kükenthal and Röse.

Röse has described the appearance, at a very early period of the development of a molar enamel-organ, of several mesodermal papillary upgrowths prior to any marked differentiation of the enamel epithelial germ. These upgrowths he confidently interprets as the homologues of the originally distinct denticles of which, in his view, a complex tooth is really built up (cf. **29**, fig. 1).

Woodward has remarked upon Röse's attempt to prove his theory in the case of the chameleon, "where the back teeth are each composed of three cones, which, according to him (Röse), arise independently of one another," to the following effect:—this is true to a certain extent, but these cusps develop under a common enamel-organ, and there is no indication of their ever having possessed independent organs, as would have been the case if they were distinct teeth, there being merely a differentiation of the cylindrical enamel-epithelium over each cusp, which Röse considers sufficient evidence in favour of his view" (**14**, p. 446).

We have occasionally come across appearances which at first seemed to suggest multiple papillary upgrowths in connection with the developing molar lamina. Thus in fig. 69, though the whole of the surrounding connective tissue has not been represented, it is plain that the irregularities of the labial surface of the dental lamina might (if the connective tissue were all filled in) suggest multiple papillation. But, as we have already shown in our previous references to this figure, this view would be quite erroneous. The true and only papilla of $m^{\underline{3}}$ is marked "*mp.*" Fig. 69 may be compared with figs. 68A and 70. So far as our observation and experience go a truly multiple papillary character is never found in the earliest stages of development of a marsupial molar. At its first differentiation as such the molar enamel-organ is as simple, single, and uncomplicated in form as any incisor enamel-organ. And as certainly we find that we can watch the ontogenetic evolution of the marsupial molar cusps by a gradual differentiation of the primitively simple cup-shaped or bell-shaped enamel-organ.

It would appear, however, that such a statement as the latter is by no means regarded, at least by Kükenthal, as inconsistent with the doctrine of phylogenetic concrescence of dental germs. Replying to Hoffmann, he observes, "Der Backzahn eines heutigen Säugers is ein so complicirtes plastisches Gebilde, welches im Laufe seiner Stammesgeschichte einer solchen Summe von Veränderungen unterworfen worden ist, dass ich nie daran gedacht habe, dass seine Entwickelung uns über die ersten Stammesgeschichtlichen Vorgänge, die in die Uebergangsperiode von Reptilien zu Säugern fallen, würde Aufschluss geben können, und ich habe schon früher . . . . die wenig glückliche Idee Röse's, dass die Ausbildung einzelner kegelförmigen Schmelz- und Dentinkappen an der spitze von Backenzahnanlagen für die Verschmelzung spricht, als nicht beweiskräftig zurückgewiesen" (27, p. 658).

Certainly the crude theory here disclaimed will not stand even a very superficial criticism. But the differentiation of the molar dental lamina in Marsupials does not in the least suggest the occurrence of a fusion-process of any kind. And we are in a position to add that even the teeth of Ornithorhynchus[1] are to be found, at a stage considerably anterior to that described by Poulton (25), still in the condition of quite simple deeply-cupped enamel-organs, from which the advancing complication of form shown in Poulton's figures, and well known in the fully developed teeth, is derived by differentiation in the way of mere inequality of growth.

There can be no doubt that the advocates of the fusion-hypothesis, instead of being aided by ontogenetic considerations, will have to face the fact—perhaps not necessarily fatal, but at least disconcerting—that, in a series of comparatively primitive mammalian forms, the cusp-development of a complicated molar can be traced out as a mere growth-differentiation of a primitively smooth and simple bowl-shaped enamel-organ, just as, according to Osborn (34, p. 206), we can be "in at the birth of every successive cusp" in phylogenetic development.

[1] We hope ere long to make our observations in this direction the subject of a special paper.

It may be conceived, of course, that prior to the simple cup-shaped enamel-organ, there is a stage like that alleged to exist by Röse, in which several mesodermal papillæ beneath a common enamel-germ represent the future tooth. But the evidence for the existence of such a condition is as yet so extremely meagre and inconclusive that we cannot admit that a serious case for it has been made out.

Schwalbe's observations in favour of fusion, referred to by Kükenthal, cannot be regarded as necessarily possessing any great phylogenetic significance. The fusion referred to (**16**, p. 21) of the upper milk incisor with the precociously developing crown of the successional tooth need not be taken as possessing either more or less morphological importance than, e. g., syndactyly in the human subject. Like the latter, the condition might even be to some extent hereditary, but its interest and importance are probably pathological rather than morphological. Were it not for the undeniable importance of Kükenthal's observations on the process of division of the cheek-teeth of whales into single conical teeth (**19**),[1] and of the further statement of the same author that he has been able actually to detect a fusion as taking place between molar enamel-germs in the case of the walrus (**20**), we should be disposed to regard the fusion theory as a very shadowy hypothesis indeed. And even with the support alluded to we cannot regard its claim to acceptance as at all a strong one. There is plenty of room for sceptical criticism. Thus, concerning Kükenthal's fig. 89 (**19**) Woodward has remarked (**14**, p. 447) that the condition illustrated and described (**19**, p. 411) appears "rather indicative of the formation of a cusp by outgrowth from a simple conical tooth" than of the fusion process supposed.

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[1] Osborn has pointed out (**34**, p. 199) that "even by Kükenthal's hypothesis the typical Mesozoic mammal could not furnish as many teeth as are found in some of the dolphins;" and he suggests as a likelier explanation that "as the jaws were elongated the dental fold was carried back and the dental caps were multiplied."

PART IV.

Concluding Remarks.

Before concluding this discussion it may not be wholly out of place to ask the question whether our observations and the conclusions deducible therefrom can be made to throw any light upon the more general problem of the affinities of Marsupials with other mammalian groups.

Hasty generalisation is certainly to be deprecated, and it is only with the greatest diffidence that we even approach the discussion of such a weighty question with the equipment of our own partial and imperfect knowledge, more especially of the palæontological aspects of the problem.

There are, however, one or two more or less obvious deductions from the views which have been advocated in the foregoing pages, and partially summarised in the introductory section of the paper (p. 441).

It is plain that, if our view of the "milk" homology of the so-called "prelacteal" teeth be admitted, we are bound to believe that the marsupial order as a whole—if not derived from truly Eutherian ancestors, as seems unlikely from the general type or organisation exemplified—is at least an offshoot from a diphyodont stock common to both Metatheria and Eutheria.

Following upon the publication of Kükenthal's and Röse's researches upon marsupial teeth, Osborn (**34**, p. 204) has remarked that "the discovery of the complete double series seems to have removed the last straw from the theory of the marsupial "ancestry of the Placentals." And the adoption of the conclusions of the present paper in no whit weakens the general purport of this criticism, since it still leaves untouched the important fact that one of the two typical mammalian dentitions has been lost during the evolution of the Marsupialia. In respect of their tooth-equipment then, the Metatheria are degenerate mammals.

With this view it is interesting to correlate such speculations as inevitably arise in consequence of the discovery by one of us (H., **30**) of a true allantoic placenta in Perameles. It is obvious that this discovery admits of only a limited number of alternative explanations. It implies either (*a*) that an allantoic placenta has been quite independently evolved within the limits of the Metatherian and Eutherian groups, thus affording a quite remarkable instance of parallelism in development;[1] or (*b*) that the Eutheria have inherited their allantoic placenta actually from polyprotodont marsupial ancestors closely allied to the modern Peramelida; or (*c*) that both the Metatheria and the Eutheria have sprung from an earlier mammalian proto-placental stock.

If the latter alternative were adopted (and we believe that it alone will in the end commend itself to the judgment of morphologists), then we should be in a position to define the common mammalian ancestors of the Metatheria and Eutheria as both placental and diphyodont.

The much-debated question as to whether or not this early mammalian stem was also marsupial in its organisation may, in view of developmental researches upon the mammary organs during recent years, admit of a not unsatisfactory reply. For the researches of Gegenbaur (**36**), Klaatsch (**32**), and others appear to have established the fact of the possession of rudiments of "mammary pouches" ("Mammartaschen") by embryo Eutherians. Such mammary pouches (to be distinguished from a true Marsupium) are, in ruminants, according to Klaatsch, converted into the tubular teat-cavity.[2] Bonnet expresses Klaatsch's view in this connection as follows:—"Wo aber die Mammartasche unverändert bestehen bleibt, wie bei den Wiederkaüern und den Equiden macht er den Anschluss dieser Formen an ganz niedere Zustände, die gar kein Marsupium ausgebildet haben, wahrscheinlich" (**31**, p. 628).

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[1] But in such case Perameles, contrary to all previous belief, would exhibit a more advanced or specialised condition than any other known Marsupial.

[2] The contrary opinions of Rein, though accepted by Minot in his 'Human Embryology,' have been subjected to severe criticism by Klaatsch, and the views of the latter observer have been adopted by Bonnet (**31**).

It would appear probable that we must be prepared to entertain favorably Klaatsch's suggestion that the "Placentals" have originally all passed through a kind of marsupial stage, "ein Form, die jederseitz zwar eine Mammartasche, aber keinen Beutel besass." He denominates the animals which exhibited this form "Taschentiere" or "Bursalia."

Such a rudimentary or primitive condition must have been a characteristic of the common stock of both Meta- and Eutheria, and was only a marsupial one in the sense in which Echidna is now marsupial.

Klaatsch has recently pointed out (**33**) what strong reason there is for the surmise that the evolution of mammary pouches, such as Echidna possesses, is probably an even older trait of mammalian development than the evolution of the mammary glands themselves. Its existence in the oviparous Echidna proves that it is a much older mammalian characteristic than any form of placental connection can possibly be. We cannot follow Hubrecht (**35**) in his assumption that the Protamniote ancestors of the Promammalia (and of the Sauropsida) must have been viviparous.

In our view the Monotremes must be taken to represent a quite distinct offshoot of a common Promammalian (Hypotherian) stem, which was originally both oviparous and "bursal" (in the sense of Klaatsch), and in which both hairs and mammary glands were gradually developed. We do not believe that in the long run it will be found possible to maintain the essential dissimilarity of the mammary glandular organ in Monotremes (**36**, and cf. Minot, l. c., pp. 565–6).

After the separation of the Monotreme phylum we must suppose the placenta to have appeared, constituting the stock protoplacental. At all events, the existence of a placenta in the marsupial order seems to indicate that the primitive pouched common ancestors (Bursalia) of the Meta- and Eutheria, long after losing their oviparous character, developed an allantoic placental connection between the embryo and the uterine wall. At the same time the mammary function, already evoked during the oviparous period for the nourishment of the immature young as in Monotremes, became further and more perfectly developed. We may further suppose that now one branch of the stock thus circumstanced, i. e. the Eutherian, went on to further exhaust the nutritive possibilities implied in the acquirement of a placental connection; retaining, however, and at the same time elaborating, the function of lactation in relation to more advanced stages of development. Another branch,—the Metatherian,—neglecting, from some cause or other, the opportunities offered by the original formation of a placental connection, may be supposed to have gone on developing the latent capabilities of the mammary function for the provision of adequate means of nutrition for the immature young. These capabilities included the replacement of the primitive mammary pouches by a true Marsupium, partly at least derived from the latter. The original pouched condition is thus to be carefully distinguished from the derivative or truly marsupiated condition of the Marsupialia, which is as much a secondary development along one line as, e. g., the ruminant mammary condition is along another.

And the character of the marsupial dentition as we interpret it renders it very highly probable that the secondary evolution of a true Marsupium has all along been accompanied by a retrogressive development or degeneration from the normal early mammalian diphyodont dentition. Indeed, as Leche has pointed out, the functional adaptation of the mouth of the marsupial young to the peculiar suckling conditions prevalent in the order has no doubt conditioned the almost entire suppression of one of the two dentitions. The dentition suppressed is, according to Leche, the second (his third); but in our view it is, beyond all doubt, the first or milk dentition which has degenerated.

University of Sydney, N.S.W.;
July 4th, 1896.

ADDENDUM.

Reference has been made in a foot-note in the body of this paper to a contribution by Dr. Marett Tims (37) of "Notes on the Dentition of the Dog," published in February in the 'Anatomischer Anzeiger.' Since our research was completed and the bulk of our work written up before Dr. Tims' paper came into our hands, we have found it easier to leave its consideration for this special note.

From his observations upon tooth-development in the dog, Tims has arrived at certain conclusions with regard to the mammalian dentition with which our work will be found in general agreement. And although this writer has apparently not carried on special researches on the teeth of Marsupials, his own work upon the dog has led him to foreshadow in some degree the views independently arrived at by the present writers on the grounds of a somewhat extensive and prolonged series of observations.

Dr. Tims' further confirmation of the common occurrence of a residual dental lamina beside the permanent teeth of Eutheria is a very welcome one.

The conclusion from his paper with which we are most particularly concerned is the following:—"That there is not sufficient evidence for believing in the existence of a pre-milk dentition even in a rudimentary condition in the Mammalia of the present day." And a corollary, drawn in part from this proposition, is that if Tims' view be accepted, "the teeth of Marsupials would once more appear to belong to the permanent series."

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EXPLANATION OF PLATES 25—32,

Illustrating Messrs. J. T. Wilson's and J. P. Hill's paper, "Observations upon the Development and Succession of the Teeth in Perameles; together with a Contribution to the Discussion of the Homologies of the Teeth in Marsupial Animals."

All sections drawn were outlined by means of Zeiss's camera lucida.

List of Common Reference Letters.

C. S. Coronal Section. *H. S.* Horizontal Section. *S. S.* Sagittal Section. *U. J.* Upper Jaw. *L. J.* Lower Jaw.

cb. Connecting bridge. *dl.* Dental lamina. *mp.* Dermal papilla. *rdl.* Residual dental lamina. *cm.* Meckel's cartilage. *l. o.* Labial laminar outgrowth. *o. e.* Oral epithelium. *t.* Tongue. $i^{\underline{1}}$, $^{\underline{c}}$, $p^{\underline{2}}$, &c. First upper incisor, upper canine, second upper premolar, &c. $i_{\overline{2}}$, $_{\overline{c}}$, $p_{\overline{3}}$, &c. Second lower incisor, lower canine, third lower premolar, &c. $di_{\overline{1}}$, $d^{\underline{c}}$, $dp^{\underline{3}}$, &c. First lower milk incisor, upper milk canine, third upper milk premolar, &c.

The lingual side of the figure of each coronal and horizontal section is indicated by a cross.

Stage II.

Figs. 1—5.—Serial coronal sections, *U. J.*

Fig. 1. In front of third incisor region.

Figs. 2 and 3. Next succeeding sections through enamel-organ of $di^{\underline{2}}$, attached to "neck" of dental lamina, and showing earliest formation of dermal papilla.

Fig. 4. Third section behind Fig. 3, showing di^3 merging posteriorly in common dental lamina.

Fig. 5. Third section behind Fig. 4, through Anlage of i^3.

All × 210 diameters.

Fig. 6.—*S. S.* Cutting the anterior portions of the upper and lower dental laminæ transversely, not far from the mesial plane. *al.* Alinasal cartilage. *ch.* Choanal passage. *cm.* Meckel's cartilage. *J. O.* Organ of Jacobson. *J. c.* Cartilaginous capsule of Jacobson's organ. *mx.* Maxillary palate. *n. e.* Epithelium of nasal cavity. *pmx.* Premaxilla. *rh.* Olfactory bulb. *S. d.* Stenson's duct. *t.* Tongue. × 25.

Fig. 7.—*U. J., C. S.* Canine Anlage. × 210.

Fig. 8.—*U. J., C. S.* Milk premolar (dp^3). × 210.

Fig. 9.—*U. J., C. S.* Milk premolar (dp^3) in another embryo from same pouch, with commencing liberation of the residual dental lamina. × 130.

Fig. 10.—*S. S.* dp^3 and molar segment of dental lamina (*dl.*). × 50.

Fig. 11.—*U. J., C. S.* Anlage of m^1 with commencing papilla-formation ($mp.\, m^1$). × 130.

Fig. 12.—*L. J., C. S.* Anlage of di_1. × 230.

Fig. 13.—*L. J., C. S.* Canine Anlage. × 210.

Fig. 14.—*S. S.* dp_3 and molar dental lamina (*dl.*). × 50.

Fig. 15.—*L. J., C. S.* First molar Anlage. × 130.

Stage III.—P. obesula.

Fig. 16.—*U. J., H. S.* Anterior end of dental lamina, showing the labial portion of the Anlage of i^1 as a lobe projecting at right angles from the main dental lamina (*dl.*), and the continuation backwards of the latter (*dl'.*) towards the region of i^2. × 140.

Fig. 17.—*U. J., C. S.* Second incisor mass, showing the labial portion of the Anlage of i^2 projecting from the swollen lamina, and the representative of di^2. × 180.

Fig. 18.—*U. J., H. S.* Second and third incisor masses (II and III), with rudiments of di^2 and di^3. The level of the section is indicated by the dotted lines *a* . . . . *b* in Figs. 17 and 19. × 180.

Fig. 19.—*U. J., C. S.* Third incisor swelling, showing the narrow "neck" attaching the mass to the oral epithelium and the remains of the enamel-organ of di^3. × 180.

Fig. 20.—*U. J., C. S.* Canine mass, showing the as yet undifferentiated Anlage of the permanent canine, with the cup-shaped enamel-organ of the milk canine (d^c). *c. dl.* The morphologically free edge of dental lamina. *c.* The probable equivalent of the labial lobe of the incisor masses. × 210.

Fig. 21.—*U. J.*, *H. S.* Cutting the oral epithelium at the point marked *o. e.* × 90.

Fig. 22.—*U. J.*, *H. S.* At a somewhat higher level than Fig. 21. × 90.

Fig. 23.—*U. J.*, *C. S.* Through the third incisor ($i^{\underline{3}}$) of an early fœtus of Dasyurus viverrinus. × 330.

Fig. 24.—*U. J.*, *C. S.* $dp^{\underline{3}}$. × 130.

Fig. 25.—*U. J.*, *H. S.* Molar region at a higher level than Fig. 22. × 90.

Fig. 26.—*U. J.*, *H. S.* $m^{\underline{1}}$ at a higher plane than Fig. 25. × 90.

Fig. 27.—*U. J.*, *C. S.* Middle region $m^{\underline{1}}$. × 130.

Fig. 28.—*U. J.*, *C. S.* $m^{\underline{1}}$ in the third section behind Fig. 27. × 130.

Fig. 29.—*U. J.*, *C. S.* Posterior region of $m^{\underline{1}}$. × 120.

Fig. 30.—*U. J.*, *C. S.* Dental lamina just behind $m^{\underline{1}}$. × 120.

Fig. 31.—*U. J.*, *C. S.* Dental lamina five sections behind Fig. 30. × 120.

Fig. 32.—*U. J.*, *C. S.* Dental lamina in region of future $m^{\underline{2}}$, and just in front of its termination. × 120.

Fig. 33.—*L. J.*, *C. S.* $i_{\overline{1}}$ and $di_{\overline{1}}$. × 230.

Fig. 34.—*L. J.*, *C. S.* Anlagen of $i_{\overline{2}}$ and $i_{\overline{3}}$. × 120.

Fig. 35.—*L. J.*, *H. S.* Anlage of $i_{\overline{2}}$ and $i_{\overline{3}}$. × 90.

Fig. 36.—*L. J.*, *H. S.* Nearer the oral epithelium than Fig. 35. × 90.

Fig. 37.—*L. J.*, *C. S.* Anlage of permanent $_{\overline{c}}$, with deeply cupped enamel-organ of $d_{\overline{c}}$. × 210.

Fig. 38.—*L. J.*, *C. S.* Anlage of $p_{\overline{2}}$. × 150.

Fig. 39.—*L. J.*, *C. S.* $dp_{\overline{3}}$. × 230.

Fig. 40.—*L. J.*, *C. S.* $dp_{\overline{3}}$, seven sections behind Fig. 39, showing the differentiation of cusps. × 130.

Fig. 41.—*L. J.*, *C. S.* $m_{\overline{2}}$. × 120.

Fig. 42.—*L. J.*, *C. S.* Dental lamina behind enamel-organ of $m_{\overline{2}}$. × 120.

Stage IV.

Fig. 43.—*U. J.*, *C. S.* Dental lamina in front of $i^{\underline{1}}$. *ca.* Common Anlage of lip-groove and dental lamina proper. × 120.

Fig. 44.—*U. J.*, *C. S.* $i^{\underline{1}}$. *ep.* Epithelial ingrowths (see text). × 120.

Fig. 45.—*U. J.*, *C. S.* $i^{\underline{1}}$ three sections behind Fig. 44. × 120.

Fig. 46.—*U. J.*, *C. S.* $i^{\underline{1}}$ five sections behind Fig. 45. × 120.

Fig. 47.—*U. J.*, *C. S.* $^{\underline{c}}$ with remains of $d^{\underline{c}}$. × 100.

Fig. 48.—*U. J.*, *C. S.* $dp^{\underline{3}}$ passing through the protocone. × 130.

Fig. 49.—*U. J.*, *H. S.* Through the region between $p^{\underline{3}}$ and $m^{\underline{1}}$. For ex-

planation of the projections from the dental lamina marked "*a*" and "*b*" see text. × 100.

FIG. 50.—(STAGE V.) *U. J., H. S.* Region between $p^{\underline{2}}$ and $m^{\underline{1}}$. × 100.

FIG. 51.—*U. J., C. S.* $m^{\underline{1}}$ passing through its protocone. × 80.

FIG. 52.—*U. J., C. S.* $m^{\underline{2}}$. × 80.

FIG. 53.—*U. J., C. S.* $m^{\underline{2}}$ in another series, and nearer its posterior end than Fig. 52. × 80.

FIG. 54.—*U. J., C. S.* Anlage of $m^{\underline{3}}$. × 80.

FIG. 55.—*L. J., C. S.* $i_{\overline{1}}$. × 100.

FIG. 56.—*L. J., C. S.* $i_{\overline{1}}$ some distance behind Fig. 55, showing $di_{\overline{1}}$. × 100.

FIG. 57.—*L. J., C. S.* $i_{\overline{2}}$ and $i_{\overline{3}}$. × 50.

FIG. 58.—*L. J., C. S.* Dental lamina in front of $_{\overline{c}}$ with $d^{\underline{c}}$. × 210.

STAGE V.

FIG. 59.—*U. J., C. S.* $^{\underline{c}}$. × 50.

FIG. 59 A.—(STAGE VII.) *U. J., C. S.* $^{\underline{c}}$. 50.

FIG. 59 B.—(STAGE VIII.) *U. J., C. S.* $^{\underline{c}}$. × 50.

FIG. 60.—*U. J., C. S.* $dp^{\underline{3}}$ and dental lamina in region of future $p^{\underline{3}}$. × 165.

FIG. 61.—*U. J., C. S.* Anlage of $m^{\underline{3}}$. × 220.

STAGE VI.

FIG. 62.—*U. J., C. S.* $^{\underline{c}}$. × 50.

FIG. 63.—*U. J., C. S.* $dp^{\underline{3}}$ with Anlage of $p^{\underline{3}}$. × 50.

FIG. 64.—*L. J., C. S.* $dp_{\overline{3}}$ with Anlage of $p_{\overline{3}}$. × 120.

STAGE VII.

FIG. 65.—*L. J., C. S.* Passing through the forwardly directed apex of $i_{\overline{1}}$, and showing the enamel-germ of an incisor (*r. e. o.*) which arises from the dental lamina in front of $i_{\overline{1}}$. × 210.

FIG. 66.—*L. J., C. S.* Through $i_{\overline{1}}$, showing $di_{\overline{1}}$ independently attached to the oral epithelium. × 150.

FIG. 66 A.—(STAGE V.) *L. J., C. S.* Through $i_{\overline{1}}$, showing $di_{\overline{1}}$ becoming attached to the oral epithelium labially from the neck of the dental lamina. × 150.

FIG. 67.—(STAGE IX.) *U. J., C. S.* $dp^{\underline{3}}$ with Anlage of $p^{\underline{3}}$. × 30.

FIG. 68.—(STAGE VI.) *U. J., C. S.* Posterior portion of $m^{\underline{2}}$. × 120.

FIG. 68 A.—(STAGE VI.) *U. J., C. S.* Some distance behind Fig. 68, showing Anlage of $m^{\underline{3}}$. × 120.

FIG. 69.—(STAGE VIII.) *U. J., C. S.* Enamel-germ of $m^{\underline{3}}$. × 120.

Fig. 70.—(Stage IX.) *U. J., C. S.* $m^{\underline{3}}$. × 120.

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Fig. 72.—(Stage X.) *U. J., C. S.* Passing through $^{\underline{c}}$, showing one of the enlargements of the residual dental lamina surrounded by a connective-tissue capsule. × 230.

Fig. 73.—(Stage X.) *U. J., C. S.* Enamel-germ of $p^{\underline{3}}$. × 120.

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(After Leche, Taf. xvi, figs. 140 and 142.)

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