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PROCEEDINGS

OF THE

ROYAL PHYSICAL SOCIETY

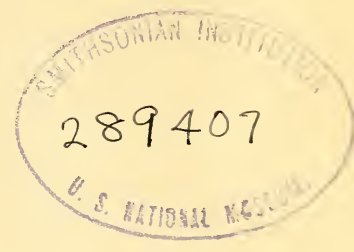
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1915-1923.



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MCMXXIII.

ROYAL PHYSICAL SOCIETY.

Instituted 1771.

Incorporated by Royal Charter 1788.

Council for 1923-1924.

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JOURNAL OF PROCEEDINGS.

OCTOBER 1915 — MARCH 1923.

SESSION CXLV.

Monday, 25th October 1915.

1. The Moulting of the King Penguin. (Illustrated by lantern slides from photographs by Miss MACKENZIE.) By Professor J. COSSAR EWART, M.D., F.R.S.
 2. SPOLIA AUSTRALIENSIS. (III.) The Fresh-water Fauna. By J. H. ASHWORTH, Esq., D.Sc., F.R.S.E.
 3. Some Observations on the Habits and Biology of the Common Wasp. (Illustrated by lantern slides.) By the SECRETARY.
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Monday, 22nd November 1915.

1. The Utility of the Useless. By the Retiring President, Principal O. CHARNOCK BRADLEY, M.D., D.Sc., F.R.S.E.

The Annual Reports of the Secretary, Librarian, and Treasurer were submitted for the Session 1914-15.

The following Office-Bearers for the Session were elected:—

President—Professor ARTHUR ROBINSON, M.D., M.R.C.S.

Vice-Presidents—PERCY H. GRIMSHAW, Esq., F.R.S.E., F.E.S.; Professor D'ARCY W. THOMPSON, M.A., C.B., D.Litt.; J. H. ASHWORTH, Esq., D.Sc., F.R.S.E.

Secretary—JAMES RITCHIE, Esq., M.A., D.Sc.

Assistant-Secretary—JAMES A. S. WATSON, Esq., B.Sc., F.R.S.E.

Treasurer—WM. WILLIAMSON, Esq., F.R.S.E.

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Councillors—HUGH MILLER, Esq., F.Z.S.; MALCOLM LAURIE, Esq., B.A., D.Sc.; J. KIRKE NASH, Esq., L.D.S.Ed.; B. N. PEACH, Esq., LL.D., F.R.S.L. & E., F.G.S.; J. F. GEMMILL, Esq., M.A., M.D., D.Sc.; JOHN RENNIE, Esq., D.Sc., F.R.S.E.; D. C. M'INTOSH, Esq., M.A., D.Sc., F.R.S.E.; Principal O. CHARNOCK BRADLEY, M.D., D.Sc., F.R.S.E.; WM. EVANS, Esq., F.F.A., F.R.S.E.; Professor T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E.; T. H. GILLESPIE, Esq.; Professor D. C. MATHESON, F.R.C.V.S., D.V.S.M.

Monday, 20th December 1915.

1. The Bionomics of the Tiger Beetle, *Cicindela campestris*, with exhibition of specimens. By Miss LILY H. HUIE.
2. Exhibition of three rare Scottish Beetles. By J. KIRKE NASH, Esq., L.D.S.Ed.

3. Note on the Occurrence of two Generations of the Nudibranchiate Mollusca *Lamellidoris bilamellata* and *Archidoris tuberculata* in the course of a year. By LOUIS P. W. RENOUF, Esq., B.A.
4. Further notes on *Lamellidoris bilamellata*. By LOUIS P. W. RENOUF, Esq., B.A.
5. Remarks on *Hermæa dendritica*, and other Nudibranchs from the shores of the Forth, with exhibition of living examples. By WM. EVANS, Esq., F.F.A., F.R.S.E.

Monday, 24th January 1916.

1. A brief Analysis and Criticism of the Board of Agriculture's Report on "Isle of Wight" Bee Disease. By JOHN ANDERSON, Esq., M.A., B.Sc., Lecturer on Bee-keeping, North of Scotland College of Agriculture.
2. Observations and Experiments bearing on "Isle of Wight" Disease in Bees. By JOHN RENNIE, Esq., D.Sc., and JOHN ANDERSON, Esq., M.A., B.Sc.

Monday, 28th February 1916.

1. Exhibition of Sheep-maggot Flies and other Insects from Australia. By J. H. ASHWORTH, Esq., D.Sc., F.R.S.E.
2. Exhibition of two living Geckos from the Seychelles. By T. H. GILLESPIE, Esq.
3. Some uncommon Insects from Scotland. By WM. EVANS, Esq., F.F.A., F.R.S.E.
4. Observations on Colour-preference in the Winter Gnat. By the SECRETARY.

Monday, 27th March 1916.

1. Letter from Mr W. DENNISON ROEBUCK, Hon. Recorder of the Conchological Society, 259 Hyde Park Road, Leeds, requesting the co-operation of Fellows in completing the Census of Land and Freshwater Mollusca of Scotland.
2. Exhibit of two living Geckos, *Phelsuma madagascariensis*, from the Seychelles. By T. H. GILLESPIE, Esq.
3. Observations on Colour-preference in the Winter Gnat. By the SECRETARY.
4. Some points in the Cytology of the later spermatogonial and first meiotic nuclei of *Distomum hepaticum*. By Miss MONICA TAYLOR, S.N.D., B.Sc. (Communicated by Professor J. GRAHAM KERR, F.R.S.)
5. Notes on *Trypanophis grobbei* as observed at Naples. By J. F. M. FLOYD, Esq., M.A.

SESSION CXLVI.

Monday, 23rd October 1916.

1. A peculiar type of Segmentation and Blastula formation, with Illustrations. By J. F. GEMMILL, Esq., M.D., D.Sc.
2. The Marine Leech, *Calliobdella nodulifera* (Malm. 1863). By W. HAROLD LEIGH-SHARPE, Esq., B.Sc.(London). (Communicated by Dr GEMMILL.)
3. Exhibition of a Land Nemertean (*Geonemertes*) and luminous Cephalopods. By J. H. ASHWORTH, Esq., D.Sc.

Monday, 27th November 1916.

1. A History of the Study of British Diptera or Two-winged Flies. By the retiring Vice-President, PERCY H. GRIMSHAW, Esq., F.R.S.E., F.E.S.

The Secretary, Treasurer, and Librarian submitted reports for the Session 1915-16.

The following Office-Bearers for the Session were elected:—

President—Professor ARTHUR ROBINSON, M.D., M.R.C.S.

Vice-Presidents—Professor D'ARCY W. THOMPSON, C.B., M.A., D.Litt., F.R.S.; J. H. ASHWORTH, Esq., D.Sc., F.R.S.E.; JAMES RITCHIE, M.A., D.Sc., F.R.S.E.

Secretary—Miss MARION I. NEWBIGIN, D.Sc.

Assistant-Secretary—JAMES A. S. WATSON, Esq., B.Sc., F.R.S.E.

Treasurer—WILLIAM WILLIAMSON, Esq., F.R.S.E.

Librarian—LIONEL W. HINXMAN, Esq., B.A., F.R.S.E.

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Monday, 18th December 1916.

1. Exhibition of a remarkable Saturnid Cocoon from Northern India. By PERCY H. GRIMSHAW, Esq., F.R.S.E., F.E.S.
2. The Genus *Hylastes*, Er., and its importance in Forestry: A Study in Scolytid Structure and Biology. By JAMES W. MUNRO, Esq., B.Sc. (Communicated by WM. EVANS, Esq., F.F.A., F.R.S.E.)
3. Exhibition of Abnormal Eggs of British Wild Birds. By J. KIRKE NASH, Esq., L.D.S.Ed.

Monday, 22nd January 1917.

No Meeting was held on this date.

Monday, 26th February 1917.

1. Letter from Mr W. DENNISON ROEBUCK, Hon. Recorder, Conchological Society, Leeds, requesting the co-operation of the Fellows in completing the Census of the Land and Freshwater Mollusca of Scotland.
2. The Holly Tortrix Moth (*Eudemis naevana*): Its Biology and Economic Importance. By Miss LILY HUIE, F.E.S.
3. Body-Colour as affected by Blood-Colour in Amphipods and Isopods, with some remarks on a Bacterial infection of *Gammarus*. By JOHN TAIT, Esq., M.D., D.Sc. (Communicated by Dr ASHWORTH.)

iv Proceedings of the Royal Physical Society.

4. Exhibition of Anatomical Preparations of Bees and other Insects. By Miss ELSIE HARVEY. (Communicated by Dr JOHN RENNIE.)
 5. Exhibition of Stereographs of Living Insects. By HUGH MAIN, Esq. (Communicated by Miss HUIE.)
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Monday, 26th March 1917.

1. Lantern Demonstration of the formation of the Corona Radiata in Mammalian Ova. By Professor ARTHUR ROBINSON, M.D., M.R.C.S.
 2. Lantern Demonstration on Segmentation and Germ Layer Formation in *Tealia*. By JAMES F. GEMMILL, Esq., M.A., M.D., D.Sc.
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SESSION CXLVII.

Monday, 22nd October 1917.

1. The Significance of the Physical Characteristics of Race in Man. By the SECRETARY.
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Monday, 26th November 1917.

1. The Nautilus and other Shells. By Professor D'ARCY W. THOMPSON, M.A., C.B., F.R.S., D.Litt., the retiring Vice-President.

The Secretary, Treasurer, and Librarian submitted reports for the Session 1916-17.

The following Office-Bearers were elected for the Session 1917-18:—

President—Professor ARTHUR ROBINSON, M.D., M.R.C.S.

Vice-Presidents—J. H. ASHWORTH, Esq., D.Sc., F.R.S.; JAMES RITCHIE, Esq., M.A., D.Sc., F.R.S.E.; Professor DAVID WATERSTON, M.D., F.R.S.E.

Secretary—Dr MARION I. NEWBIGIN.

Assistant-Secretary—OLIVER H. WILD, Esq., M.B.O.U.

Treasurer—WM. WILLIAMSON, Esq., F.R.S.E., F.L.S.

Librarian—LIONEL W. HINXMAN, Esq., B.A., F.R.S.E.

Councillors—WM. EVANS, Esq., F.F.A., F.R.S.E.; Professor T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E.; T. H. GILLESPIE, Esq.; Professor D. C. MATHESON, F.R.C.V.S., D.V.S.M.; PERCY H. GRIMSHAW, Esq., F.R.S.E., F.E.S.; Miss LILY HUIE, F.E.S.; Professor T. H. BRYCE, M.A., M.D.; R. ELMHIRST, Esq., F.L.S.; B. N. PEACH, Esq., LL.D., F.R.S.; Professor D'ARCY W. THOMPSON, M.A., C.B., F.R.S.; Professor J. ARTHUR THOMSON, M.A., LL.D., F.R.S.E.; JAMES A. S. WATSON, Esq., B.Sc., F.R.S.E.

Monday, 17th December 1917.

No Meeting was held on this date.

Monday, 28th January 1918.

1. Demonstration of some Peculiar Teeth. By Professor ARTHUR ROBINSON, M.D., M.R.C.S., F.R.S.E.
 2. Note on the Jelly-masses found in East Lothian in September 1917. By J. H. ASHWORTH, Esq., F.R.S.
 3. A Criticism of Reibisch's Otolith-method of estimating the Age of the Plaice. By H. CHAS. WILLIAMSON, Esq., M.A., D.Sc. (Communicated by Dr JAMES RITCHIE.)
 4. *Limnaea glabra* as a Scottish Species. By W. DENNISON ROEBUCK, Esq., M.Sc., F.L.S. (Communicated by Mr WM. EVANS.)
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Monday, 25th February 1918.

1. The Red Deer in Scotland; an Illustration of the Influence of Man on Animal Life. By JAMES RITCHIE, Esq., M.A., D.Sc.
-

Monday, 25th March 1918.

1. Exhibition of living specimens of *Stegomyia fasciata*. By J. H. ASHWORTH, Esq., F.R.S.
 2. (a) Further Observations of Tiger Beetles in Captivity;
(b) Methods of preparing insects as Microscopic Objects. By Miss L. H. HUIE, F.E.S.
 3. Giant Cuttle-fish in British Waters, with special reference to a recent Scottish Example. By JAMES RITCHIE, Esq., M.A., D.Sc.
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SESSION CXLVIII.

Monday, 28th October 1918.

1. War-time Collections from various Fronts.
 - i. *Mesopotamian Front* :—
 - (a) Specimens of Eggs of the White-tailed Lapwing and other Birds.
 - (b) Beetles and other Insects. Collected by W. EDGAR EVANS, Lieut., R.A.M.C. Exhibited by WM. EVANS, Esq., F.F.A., F.R.S.E.
 - ii. *Western Front* :—
 - (a) Beetles from ARRAS. Collected by Major H. M. VICKERS, M.B., Ch.B. Exhibited by Professor T. HUDSON BEARE, B.A., B.Sc.
 - (b) Miscellaneous Insects, especially Hymenoptera and Diptera. Collected by Major H. M. VICKERS, M.B., Ch.B.
 - iii. *Salonika Front* :—
 - Diptera. Collected by JAMES WATERSTON, Lieut., R.A.M.C. Exhibited by J. H. ASHWORTH, Esq., F.R.S.

FRANCIS COWAN, Esq., C.A., was elected Hon. Auditor in succession to the late Mr RICHARD BROWN, C.A.

Monday, 25th November 1918.

1. Preliminary Accounts of the Development of (a) the Sea-anemone *Bolocera tuediae* and (b) *Melicertidium octocostatum* (Sars.), a Leptomedusa with a theca-less hydroid Stage. By J. F. GEMMILL, Esq., M.A., M.D., D.Sc. (With lantern slides.)
2. Some Observations on *Pleurocystis cutanoi*, Hesse, 1909; a Coelozoic Parasite of the Earth-worm. By W. HAROLD LEIGH-SHARPE, Esq., B.Sc. (Communicated by J. F. GEMMILL, Esq., M.A., M.D., D.Sc.)
3. Note on the Collection and Culture of *Amoeba proteus* for Class purposes. By Miss MONICA TAYLOR, S.N.D., D.Sc. (Communicated by JAMES RITCHIE, Esq., M.A., D.Sc.)

The Secretary, Treasurer, and Librarian submitted reports for the Session 1917-1918.

The following Office-Bearers were elected for the Session 1918-1919.

President—J. H. ASHWORTH, Esq., D.Sc., F.R.S., F.R.S.E.

Vice-Presidents—JAMES RITCHIE, Esq., M.A., D.Sc., F.R.S.E.; Professor DAVID WATERSTON, M.D., F.R.S.E.; Professor T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E.

Secretary—Dr MARION I. NEWBIGIN.

Assistant-Secretary—OLIVER H. WILD, Esq., M.B.O.U.

Treasurer—Wm. WILLIAMSON, Esq., F.R.S.E., F.L.S.

Librarian—LIONEL W. HINXMAN, Esq., B.A., F.R.S.E.

Councillors—PERCY H. GRIMSHAW, Esq., F.R.S.E., F.E.S.; Miss LILY H. HUIE, F.E.S.; Professor T. H. BRYCE, M.A., M.D.; R. ELMHIRST, Esq., F.L.S.; B. N. PEACH, Esq., LL.D., F.R.S.E.; Professor D'ARCY W. THOMPSON, C.B., D.Litt., F.R.S.; Professor J. ARTHUR THOMSON, M.A., LL.D., F.R.S.E.; JAMES A. S. WATSON, Esq., B.Sc., F.R.S.E.; Principal O. CHARNOCK BRADLEY, M.D., D.Sc., F.R.S.E.; T. CUTHBERT DAY, Esq., F.C.S., F.R.S.E.; Miss AUGUSTA LAMONT, B.Sc.; Professor ARTHUR ROBINSON, M.D., M.R.C.S.

Monday, 16th December 1918.

1. Observations on *Amoeba proteus*, Pallas. By Miss LUCY A. CARTER, B.Sc., S.N.D. (Communicated by Dr JAMES RITCHIE.)
2. Butterflies from Coll. Exhibited by FRANCIS COWAN, Esq., C.A.
3. Spontaneous repair of Fractures in Birds and Mammals. Exhibition of Specimens by Principal O. CHARNOCK BRADLEY, M.D., D.Sc.

Monday, 27th January 1919.

1. Exhibition of Heart and Blood of Dog showing *Filaria immitis*. By J. H. ASHWORTH, Esq., F.R.S.
2. The Brain and Cranial Nerves of *Acanthias vulgaris*, Risso, with some remarks on those of *Galeorhinus galeus* (Linn.) and of *Pristiurus melanostomus*, Günther. By G. L. PURSER, Esq., M.A.(Cantab.). (Communicated by L. P. W. RENOUF, Esq., B.A.) With lantern slides.
3. Notes on Photography in Scientific Research. (With lantern illustrations.) By T. CUTHBERT DAY, Esq., F.C.S., F.R.S.E.

Monday, 24th February 1919.

1. The Nestling Tail of Ducks and Geese. By Professor J. COSSAR EWART, M.D., F.R.S.
 2. Some Insects from the Oriental and Australasian Region. By PERCY H. GRIMSHAW, Esq., F.E.S., F.R.S.E.
 3. A simple piece of Apparatus for setting Insects. By Major H. M. VICKERS, M.B., Ch.B.
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Monday, 24th March 1919.

1. Some Diptera of Medical and Veterinary Importance in Mesopotamia. By Major W. S. PATTON, I.M.S.
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SESSION CXLIX.

Monday, 27th October 1919.

1. Some Aspects of Scottish Animal Life. Address by JAMES RITCHIE, Esq., M.A., D.Sc., F.R.S.E., Retiring Vice-President.
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Monday, 24th November 1919.

1. Lice and Trench Fever. By A. D. PEACOCK, Esq., M.Sc., Captain, R.A.M.C. (T.), Entomologist to the American Trench Fever Commission. (With lantern slides.)

The Secretary, Treasurer, and Librarian submitted reports for the Session 1918-19.

The following Office-Bearers were elected for the Session 1919-20 :—

President—J. H. ASHWORTH, Esq., D.Sc., F.R.S., F.R.S.E.

Vice-Presidents—Professor DAVID WATERSTON, M.D., F.R.S.E.; Professor T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E.; Professor J. F. GEMMILL, M.A., M.D., D.Sc.

Secretary—Dr MARION I. NEWBIGIN.

Assistant-Secretary—OLIVER H. WILD, Esq., M.B.O.U.

Treasurer—WM. WILLIAMSON, Esq., F.R.S.E., F.L.S.

Librarian—JAMES A. S. WATSON, Esq., B.Sc., F.R.S.E.

Councillors—B. N. PEACH, Esq., LL.D., F.R.S.E.; Professor D'ARCY W. THOMPSON, M.A., C.B., F.R.S.; Professor J. ARTHUR THOMSON, M.A., LL.D., F.R.S.E.; Principal O. CHARNOCK BRADLEY, M.D., D.Sc., F.R.S.E.; T. CUTBERT DAY, Esq., F.C.S., F.R.S.E.; Miss AUGUSTA LAMONT, B.Sc.; Professor ARTHUR ROBINSON, M.D., M.R.C.S.; EDWARD B. BAILEY, Esq., B.A.; JAMES W. BOWHILL, Esq., B.A.; WM. EVANS, Esq., F.F.A., F.R.S.E.; JAMES RITCHIE, Esq., M.A., D.Sc., F.R.S.E.; Professor L. A. L. KING, M.A.

Monday, 15th December 1919.

1. The Down of Penguin Chicks and other Birds. By Professor J. COSSAR EWART, M.D., F.R.S.

Monday, 26th January 1920.

1. The Organisation of a Campaign against Sleeping Sickness. By Captain BASIL SPENCE, R.A.M.C., M.B., C.M., of the Sudan Sleeping Sickness Commission. (With lantern slides.)
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Monday, 23rd February 1920.

1. Exhibition of specimens of some British Ants found in Scotland, with notes on their Life-histories, Distribution, etc. By Professor T. HUDSON BEARE, B.A., B.Sc.
 2. On Hermaphroditism in the Anura, with a report on four new cases in the genus *Rana*. By F. A. E. CREW, Esq., M.B., Ch.B.
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Monday, 22nd March 1920.

1. Notes on the Biology of the Ephyrae of *Aurelia*:
(a) Mode of capturing food; (b) Ciliation; (c) Variation. By Professor J. F. GEMMILL, M.A., M.D., D.Sc. (With lantern slides.)
 2. Variation in the Ephyrae produced by single Strobile of *Aurelia*. By JAMES W. LOW, Esq., B.Sc., Assistant Nat. Hist. Department, Univ. College, Dundee. (With lantern slides.)
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SESSION CL.

Monday, 25th October 1920.

1. Demonstration of Microscopic Preparations of Mouth-parts of Blood-sucking Diptera. By Miss LILY HUIE, F.E.S., with explanatory photo-micrographs by Mr CUTHBERT DAY, F.C.S., F.R.S.E.
 2. Nuclear Division in the Dinoflagellate *Oxyrrhis*. By J. S. DUNKERLY, Esq. (Communicated by Professor GRAHAM KERR, M.A., F.R.S.)
 3. An Investigation into the Life-history of the Wheat-bulb Disease Fly. By Professor J. F. GEMMILL, M.A., M.D., D.Sc. (With lantern slides.)
 4. The Ptarmigan of Spitsbergen. By Dr W. S. BRUCE and Mr R. I. MAPLETON.
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Monday, 22nd November 1920.

1. The Myrmecophilous Coleoptera of Great Britain; true guests, hostile persecuted lodgers, indifferently treated lodgers. Exhibition of examples of the three classes and notes on their life-history. By Professor T. HUDSON BEARE, B.A., B.Sc., F.E.S.
2. Exhibition of Living Case-bearing Beetle Larvae, inhabiting ants' nests. By O. H. WILD, Esq., M.B.O.U.
3. Orthoptera (Locusts, Mantids, etc.) from Mesopotamia. By WM. EVANS, Esq., F.F.A., F.R.S.E.
4. An Early Embryo of *Myrmecophaga jubata*. By Miss SHEINA M. MARSHALL, B.Sc. (Communicated by Professor GRAHAM KERR, M.A., F.R.S.)
5. *Rhabdamocha marina*. gen. n. et sp. n. By J. S. DUNKERLY, Esq., B.Sc. (Communicated by Professor GRAHAM KERR, M.A., F.R.S.)

The Secretary, Treasurer, and Librarian submitted reports for the Session 1919-20.

The following Office-Bearers were elected for the Session 1920-21 :—

President—J. H. ASHWORTH, Esq., D.Sc., F.R.S., F.R.S.E.

Vice-Presidents—Professor T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E.; Professor J. F. GEMMILL, M.A., M.D., D.Sc.; Lieut.-Col. WARDLAW RAMSAY.

Secretary—Dr MARION I. NEWBIGIN.

Assistant-Secretary—OLIVER H. WILD, Esq., M.B.O.U.

Treasurer—WM. WILLIAMSON, Esq., F.R.S.E., F.L.S.

Librarian—JAMES A. S. WATSON, Esq., B.Sc., F.R.S.E.

Councillors—T. CUTHBERT DAY, Esq., F.C.S., F.R.S.E.; Miss AUGUSTA LAMONT, B.Sc.; Professor ARTHUR ROBINSON, M.D., M.R.C.S.; EDWARD B. BAILEY, Esq., B.A.; JAMES W. BOWHILL, Esq., B.A.; WM. EVANS, Esq., F.F.A., F.R.S.E.; JAMES RITCHIE, Esq., M.A., D.Sc., F.R.S.E.; Professor L. A. L. KING, M.A.; Professor DAVID WATERSTON, M.D., F.R.S.E.; THOS. CAMPBELL, Esq., M.A., M.B., C.M., K.I.H.; G. LESLIE PURSER, Esq., M.A.; Miss LILY HUIE, F.E.S.

Monday, 20th December 1920.

1. Variations in the Afferent Branchial Arteries of the Skate. By Miss AUGUSTA LAMONT, B.Sc.
2. Notes on some Littoral Oligochaeta of the Clyde. By JOHN STEPHENSON, Esq., M.B., D.Sc., F.R.S.E.
3. A Spirochaete from the Pancreas of the Skate. By G. LESLIE PURSER, Esq., M.A., F.R.S.E.

Monday, 24th January 1921.

1. The Prehistoric Find at Piltown. By Professor DAVID WATERSTON, M.D., F.R.S.E., retiring Vice-President. (With lantern slides.)

Monday, 28th February 1921.

1. Remarks on some South Indian Hemiptera, with exhibition of Specimens. By THOMAS CAMPBELL, Esq., M.A., M.B., C.M., K.I.H.
2. Some Asiatic Lake Faunas. By NELSON ANNANDALE, Esq., B.A., D.Sc. (With lantern slides.)

Monday, 21st March 1921.

1. A Disease of the Fat Body of the Larva of *Tipula*. By JOHN RENNIE, Esq., D.Sc. (With exhibition of specimens.)
2. Mites from Hive Bees and Hives. By JOHN RENNIE, Esq., D.Sc., and Miss ELSIE HARVEY, B.Sc.

SESSION CLI.

Monday, 24th October 1921.

1. Crustacea from the Mergui Archipelago, Lower Burma, and from the Arimba Archipelago, Portuguese East Africa: (i.) Stomatopoda. By ALEXANDER PATIENCE, Esq.
2. Exhibition of (i.) the earliest known stages of the Common Freshwater Eel, and (ii.) preparations illustrating the Food of the Red Grouse and other Game Birds throughout the Year. By JAMES RITCHIE, Esq., M.A., D.Sc. F.R.S.E.
3. Multipolar Spindles in the Oöcytes of the Guinea Pig. By G. LESLIE PURSER, Esq., M.A.

Monday, 28th November 1921.

1. On the Moulting of the Lobster. By R. ELMHIRST, Esq., F.L.S.
2. The Banana Fly (*Drosophila ampelophila*) and the modern Chromosome Theory of Heredity. By F. A. E. CREW, Esq., M.B., Ch.B., D.Sc.

The Secretary, Treasurer, and Librarian submitted reports for the Session 1920-1921.

A Resolution was unanimously adopted, that Section IV. of the Society's Constitution be modified to read as follows:—

“IV. The following Fees shall be payable by Fellows, viz. :—

- “1. Ordinary Fellows shall pay an entrance-fee of 10s. 6d., and an Annual Subscription of 17s. 6d., and shall be entitled to receive the *Proceedings* of the Society.
- “2. They shall be entitled at any time to compound their Annual Contributions by a single payment of Ten Guineas, or of Six Guineas in the case of Fellows permanently resident abroad.”

The following Office-Bearers were elected for the Session 1921-1922 :—

President—Professor D'ARCY W. THOMPSON, C.B., M.A., D.Litt., F.R.S.

Vice-Presidents—Professor J. F. GEMMILL, M.A., M.D., D.Sc.; EDWARD B. BAILEY, Esq., B.A., M.C.; Principal O. CHARNOCK BRADLEY, M.D., D.Sc.

Secretary—Dr MARION I. NEWBIGIN.

Assistant-Secretary—OLIVER H. WILD, Esq., M.B., Ch.B.

Treasurer—WM. WILLIAMSON, Esq., F.R.S.E., F.L.S.

Librarian—JAMES A. S. WATSON, Esq., B.Sc., F.R.S.E.

Councillors—JAMES WM. BOWHILL, Esq., B.A.; WM. EVANS, Esq., F.F.A., F.R.S.E.; JAMES RITCHIE, Esq., M.A., D.Sc., F.R.S.E.; Professor L. A. L. KING, M.A.; Professor DAVID WATERSTON, M.D., F.R.S.E.; THOS. CAMPBELL, Esq., K.I.H., M.A., M.B. C.M.; G. LESLIE PURSER, Esq., M.A., F.R.S.E.; Professor J. H. ANSWORTH, D.Sc., F.R.S., F.R.S.E.; Prof. T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E.; F. A. E. CREW, Esq., M.B., Ch.B., D.Sc.; JOHN RENNIE, Esq., D.Sc.; H. MAXWELL VICKERS, Esq., M.B., Ch.B.

Monday 19th December 1921.

1. The Beetle Fauna of the Upper Spey Valley. By Professor T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E., D.L., retiring Vice-President.

Monday 30th January 1922.

1. Exhibition of Mollusca from the Mediterranean and Puget Sound, and of a Land-Crab from Christmas Island, with remarks thereon. By Professor J. H. ASHWORTH, D.Sc., F.R.S.
2. Demonstration of specimens from the Animal Breeding Research Department of Edinburgh University. (Communicated by F. A. E. CREW, Esq., M.B., Ch.B., D.Sc., Director.)
 - i. Abnormalities of the Reproductive System in the Pig (by Miss H. B. FELL) and the Goat (by M. R. V. PANIKKAR, Esq.).
 - ii. The Thyroid of a monstrous Calf. By E. J. S. GLASS, Esq.

Monday, 27th February 1922.

1. Exhibit of Products of an early Tertiary Desert Climate in the Island of Mull. By E. B. BAILEY, Esq., B.A., M.C.
2. Homing in the Honey Bee. By JOHN ANDERSON, Esq., M.A., B.Sc. (With lantern slides.)

Monday, 27th March 1922.

1. Exhibit of Cross-bred Chicks showing sex-linked Inheritance :—
 - (a) From the Poultry Department, Edinburgh College of Agriculture. By Miss H. F. NEWBIGIN. (Communicated by Dr MARION I. NEWBIGIN.)
 - (b) From the Animal Breeding Research Department, University of Edinburgh. By F. A. E. CREW, Esq., M.B., Ch.B., D.Sc., Director.
2. Exhibition, with remarks, of *Cryptohypnus riparius*, one of the Click-beetles, and its larva or "Wire-worm," from Agricultural Land round Edinburgh. By WM. EVANS, Esq., F.F.A., F.R.S.E.
3. Æstivation of *Protoperus*, with exhibition of specimen. By G. LESLIE PURSER, Esq., M.A.

SESSION CLII.

Monday, 23rd October 1922.

1. Exhibition of Living Example of the Carnivorous Snail-slug *Testacella heliotidea*, from an Edinburgh Nursery-garden. By JAMES RITCHIE, Esq., M.A., D.Sc.
2. Metamorphosis in the Axolotl through Pituitary administration, with exhibition of specimens. By L. T. HOGGEN, Esq., M.A., D.Sc. (Communicated by F. A. E. CREW, Esq., M.B., Ch.B., D.Sc.)
3. Exhibition of section of timber from the roof of Westminster Hall damaged by *Xestobium tesellatum*. By R. STEWART MACDOUGALL, Esq., M.A., D.Sc.

Monday, 27th November 1922.

1. Obituary Notice of Mr WM. EVANS. By Dr JAMES RITCHIE.
2. The Nuptial Flight of the Ghost Swift Moth (*Heptalus humulus*), with special reference to Sexual Dimorphism and Polygamy in this Species. By H. M. VICKERS, Esq., M.B., Ch.B.
3. Exhibit of hide of Ox showing damage due to *Hypoderma bovis*, with notes thereon. By G. B. WALLACE, Esq., B.Sc. (Communicated by Dr STEWART MACDOUGALL.)
4. Specimens of Wood and Bark showing the workings of *Hylesinus fraxini* and *H. crenatus*, with notes on distribution. By W. P. LEGERWOOD CAMERON, Esq. (Communicated by Dr STEWART MACDOUGALL.)

The Secretary, Treasurer, and Librarian submitted reports for the Session 1921-22.

The following Office-Bearers were elected for the Session 1922-23:—

President—Professor D'ARCY W. THOMPSON, C.B., M.A., D.Litt., F.R.S.

Vice-Presidents—EDWARD B. BAILEY, Esq., B.A., M.C.; Principal O. CHARNOCK BRADLEY, M.D., D.Sc., F.R.S.E.; JAMES RITCHIE, Esq., M.A., D.Sc., F.R.S.E.

Secretary—Dr MARION I. NEWBIGIN.

Assistant-Secretary—H. MAXWELL VICKERS, Esq., M.B., Ch.B.

Treasurer—THOS. CAMPBELL, Esq., K.I.H., M.A., M.B., C.M.

Librarian—Professor J. A. SCOTT WATSON, B.Sc., F.R.S.E.

Councillors—Professor DAVID WATERSTON, M.D., F.R.S.E.; G. LESLIE PURSER, Esq., M.A., F.R.S.E.; Professor J. H. ASHWORTH, D.Sc., F.R.S., F.R.S.E.; Professor T. HUDSON BEARE, B.A., B.Sc., M.Inst.C.E., D.L.; F. A. E. CREW, Esq., M.D., D.Sc.; JOHN RENNIE, Esq., D.Sc.; Professor J. F. GEMMILL, M.A., M.D., D.Sc.; J. F. M. FLOYD, Esq., B.A.; DOUGLAS GUTHRIE, Esq., M.D., F.R.C.S.; J. KIRKE NASH, Esq., L.D.S.Ed.; Professor ARTHUR ROBINSON, M.D., M.R.C.S.; WM. WILLIAMSON, Esq., F.R.S.E., F.L.S.

Monday, 18th December 1922.

1. Observations on *Rhinosporidium*. By Professor J. H. ASHWORTH, D.Sc., F.R.S., Presidential Address.

Monday, 22nd January 1923.

1. On the Extension of the Breeding Ranges of certain Birds in Scotland. By Miss EVELYN V. BAXTER, H.M.B.O.U.
2. Some notes on the Hawfinch (*Coccothraustes coccothraustes*), with exhibition of bird, nest and eggs. By J. KIRKE NASH, Esq., L.D.S.Ed.
3. Exhibition of nest and varieties of eggs of Weaver Bird (*Hyphantornis cucullatus*) from the Gold Coast. By J. M. DALZIEL, Esq., M.D.
4. Exhibition of Specimens of Human Cervical Ribs. By Professor ARTHUR ROBINSON, M.D.

Monday, 26th February 1923.

1. The Biology of the Wheat Bulb Fly: A Study in Economic Zoology. By Professor J. F. GEMMILL, M.A., M.D., D.Sc., Retiring Vice-President. (With lantern illustrations.)

Monday, 26th March 1923.

1. The Infertility of Domestic Races and the Intersterility of Wild Species. By Dr MARION I. NEWBIGIN.
2. Exhibit of wind-rounded Sand-grains from the shore of the Chalk-sea, Morven. By J. SIMPSON, Esq.
3. Exhibition of two Specimens of Maize-heads illustrating the effects of Cross-fertilization, from a Canadian plant-breeding station. By JAMES RITCHIE, Esq., M.A., D.Sc.

ELECTION OF FELLOWS.

The following were elected Ordinary Fellows :—

<i>Name of Fellow.</i>	<i>Date of Election.</i>
JAMES F. M. FLOYD, B.A.; JOHN ANDERSON, M.A., B.Sc.	25th Oct. 1915.
LOUIS P. W. RENOUF, B.A.	22nd Nov. 1915.
Miss AUGUSTA LAMONT, B.Sc.	20th Dec. 1915.
Miss ELSIE HARVEY	26th Feb. 1917.
THOMAS CAMPBELL, M.A., M.B., C.M.; THOMAS W. M. CAMERON; F. A. E. CREW, M.B., Ch.B.; R. FAIRLIE; F. W. FLATTELY; DOUGLAS GUTHRIE, M.D., F.R.C.S.; ROBERT K. S. LIM, M.B., Ch.B.; G. LESLIE PURSER, M.A.; CHARLES W. SANDERSON; W. S. TAYLOR	15th Dec. 1919.
JAMES W. LOW, B.Sc.; Miss AGNES CAMPBELL, B.A.; W. E. AGAR, B.A., D.Sc.	26th Jan. 1920.
J. S. DUNKERLY, B.Sc.; Miss SHEINA M. MARSHALL, B.Sc.; JOHN STEPHENSON, M.B., D.Sc.; Rev. J. M. McWILLIAM	20th Dec. 1920.
Miss JANET C. W. BANNERMAN; Miss HONOR B. FELL	24th Jan. 1921.
P. F. KENDALL, B.Sc.	21st Mar. 1921.
W. J. A. COLDSTREAM; Major F. CRAGG, I.M.S.; Miss ELSIE I. MACGILL, B.Sc.; H. MOSTYN LEWIS; Major W. S. PATTEN, I.M.S.	19th Dec. 1921.
Miss JANET S. S. BLYTH, B.Sc.; EDWARD J. V. GLASS; M. R. V. PANIKKAR	27th Mar. 1922.
E. LEONARD GILL, M.Sc.; Professor J. RUSSELL GREIG; L. T. HOGBEN, M.A., D.Sc.	27th Nov. 1922.
Surgeon Rear-Admiral J. H. STENHOUSE, R.N.; T. GRAHAME, M.R.C.V.S.	18th Dec. 1922.

The following was elected a Corresponding Fellow :—

Professor A. MURRAY DRENNAN, M.D.	18th Dec. 1916.
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The following were elected Honorary Fellows :—

W. CARRUTHERS, F.R.S.	21st Mar. 1921.
B. N. PEACH, LL.D., F.R.S.	28th Nov. 1921.
LIONEL W. HINXMAN, B.A., F.R.S.E.	18th Dec. 1922.

DONATIONS.

The following have been specially gifted to the Society's Library :—

<i>Title.</i>	<i>Presented by</i>
1. The Book of Butterflies, 3 vols., 1832, by Capt. Thomas Brown. (Written during his Presidentship of the Roy. Phys. Soc.)	Dr John Rennie.
2. Vols. III. to IX. of the Aberdeen University Zoological Studies	Univ. Aberdeen.
3. The Subantarctic Islands of New Zealand, Vols. i. and ii.; Index Faunæ Novæ Zelandiæ. By F. W. Hutton, F.R.S.	Phil. Inst. Canterbury, Christchurch, N.Z.
4. Plants, Seeds, and Currents in the West Indies and Azores. By H. B. Guppy, M.B., F.R.S.E.	The Author.
5. Le Volvox; Sur la Phylogénèse de l'Orthobionte; Note Préliminaire sur l'Oeuf du Volvox globator. Par Charles Janet	The Author.
6. <i>Amphipoda montagui</i> ; The Spawning and Exuviation of Arenicola; On the Herring in Captivity, and on an effect of the Environment on the Structure of the Fish. By H. Chas. Williamson, M.A., D.Sc.	The Author.
7. The Fauna of the Clyde Sea-area. By James Chumley, F.R.G.S.	The Author.
8. A criticism of Reibisch's Otolith-Method of Estimating the Age of the Plaice. By H. Chas. Williamson, M.A., D.Sc.	The Author.
9. From Darwinism to Kaiserism. By Robert Munro, M.A., M.D., LL.D., F.R.S.E., F.S.A.Scot.	The Author.
10. Memoirs of the Wernerian Society, 7 Vols.	O. H. Wild, M.B.O.U.
11. The Biology of the Sea-shore. By F. W. Flattely and C. L. Walton, M.Sc.	F. W. Flattely, Esq.
12. <i>Proceedings</i> of the Royal Physical Society, Vols. viii. to xvi.	J. Martin White, Esq.
13. Liostephanina and its Allies. By F. W. Payne, B.A.	The Author.

The following Framed Portraits have been added to the Collection representing Past Presidents of the Society :—

Portrait of

Principal O. CHARNOCK BRADLEY, M.D., D.Sc., President 1912-15.

Principal Sir WILLIAM TURNER, K.C.B., President 1863-66 and 1885-88, after the painting by Sir JAMES GUTHRIE.

DAVID GRIEVE, Esq., President 1874-77.

STEVENSON MACADAM, Esq., Ph.D., President 1865-68.

HUGH MILLER, Esq., President 1851-54.

OBITUARY.

Apart from Mr WM. EVANS, of whom a notice appears in this issue on p. 281, the Society has lost by death during the period 1915-23 many distinguished and active Fellows, among others the following:—

Ordinary Fellows.

Dr J. A. HARVIE BROWN a former President and a Scottish naturalist of wide repute [July, 1916].

Mr RICHARD BROWN, who for 25 years acted as Hon. Auditor [May, 1918].

Dr. W. S. BRUCE, who by his expeditions, especially in the "Scotia," did much to increase our knowledge of the fauna of Polar seas [Oct., 1921].

Mr C. T. CLOUGH, geologist [Sept., 1916].

Mr JOHN J. DAGLEISH, an ornithologist who made large collections of birds' eggs [1922].

Dr ROBERT MUNRO, a distinguished archæologist [July, 1920].

Lt.-Col. WARDLAW RAMSAY, ornithologist and student of bird life [April, 1921].

Mr WILLIAM TAYLOR, who discovered new fossil reptiles in the Triassic beds of Elgin [June, 1921].

Sir WILLIAM TURNER, a great anatomist who was for 58 years a Fellow of the Society and also acted as its President [Feb., 1916].

Sir GERMAN SIMS WOODHEAD, noted for his studies on pathogenic bacteria [Dec., 1921].

Hon. Fellows.

Dr WM. CARRUTHERS [1922]; Canon A. NORMAN [1918]; Professor LAPWORTH [1920].

LIST OF FELLOWS

At 1st October 1923.

*Those marked * are Life Members.*

Date of
Election.

1915. Anderson, John, M.A., B.Sc., 17 Beaconsfield Place, Aberdeen.
1905. *Anderson, T. J., B.Sc., Nairobi, British East Africa.
1901. *Annandale, Nelson, B.A., D.Sc., The Museum, Calcutta.
1902. *Ashworth, Prof. J. H., D.Sc., F.R.S., Zoological Department,
University, Edinburgh.
1907. *Bagnall, R. S., 15 Grey Street, Newcastle-on-Tyne.
1904. Bailey, Edward B., B.A., M.C., H.M. Geological Survey, 33 George
Square, Edinburgh.
1921. Bannerman, Miss Janet C. W., 11 Strathearn Place, Edinburgh.
1885. Barbour, A. H. F., M.A., B.Sc., M.D., 4 Charlotte Square, Edinburgh.
1904. Beare, Professor T. Hudson, B.A., B.Sc., M.Inst.C.E., J.P., D.L.,
University, Edinburgh.
1880. *Beddard, Frank E., M.A., D.Sc., F.R.S., Zoological Gardens,
London, N.W.
1881. *Berry, W., Tayfield, Newport, Fife.
1912. Blackwood, G. G., M.C., F.F.A., 1 Blackness Crescent, Dundee.
1921. Blyth, Miss Janet S. S., B.Sc., Animal Breeding Research Department,
High School Yards, Edinburgh.
1906. *Bowhill, Jas. Wm., B.A., Morelands, Grange Loan, Edinburgh.
1892. Bowhill, Thomas, F.R.C.V.S., 1445 6th Avenue, Fairview, Van-
couver, British Columbia (c/o Messrs Thos. White and Park,
66 George Street, Edinburgh).
1893. *Bradley, O. Charnock, M.D., D.Sc., F.R.S.E., Royal (Dick)
Veterinary College, Edinburgh.
1904. Brown, R. N. Rudmose, D.Sc., The University, Sheffield.
1876. *Bruce, W. P., Kinleith Mill, Currie.
1907. Bryce, Professor T. H., M.A., M.D., F.R.S., No. 2, The University,
Glasgow.
1910. Caird, Wm. J., School House, Sandhaven, Fraserburgh.
1919. Campbell, Thomas V., K.I.H., M.A., M.B., C.M., 30 Comiston
Drive, Edinburgh.
1920. Campbell, Miss Agnes, B.A., Hampton, Malvern, Jamaica.
1876. *Carmichael, His Excellency Lord, of Skirling, 13 Portman Street,
London, W. 1.
1921. Coldstream, W. J. A., University Union, Edinburgh.
1902. Cowan, Francis, C.A., Westerlea, Murrayfield, Edinburgh.
1919. Crew, F. A. E., M.D., D.Sc., 40B George Square, Edinburgh.
1894. Day, T. Cuthbert, F.C.S., F.R.S.E., 36 Hillside Crescent, Edinburgh.
1895. Douglas, Wm., 9 Castle Street, Edinburgh.

Date of
Election.

1910. Elmhirst, R., F.L.S., Superintendent, Marine Biological Station, Millport.
1883. Ewart, Professor J. Cossar, M.D., F.R.S., University, Edinburgh.
1919. Fairlie, R., 7 Ainslie Place, Edinburgh.
1921. Fell, Miss Honor B., 26 Pitt Street, Edinburgh.
1884. *Ferguson, James A. E., M.B.,
1885. Ferguson, James Haig, M.D., F.R.C.P.E., 7 Coates Crescent, Edinburgh.
1919. Flattely, F. W., Zoology Department (University of Durham), Armstrong College, Newcastle-on-Tyne.
1915. Floyd, James F. M., B.A., Natural History Department, University, Glasgow.
1911. Gemmill, Professor J. F., M.A., M.D., D.Sc., University College, Dundee.
1922. Gill, E. Leonard, M.Sc., Royal Scottish Museum, Chambers Street, Edinburgh.
1913. Gillespie, T. H., Director-Secretary, Zoological Park, Corstorphine, Edinburgh.
1922. Glass, E. J., University Union, Teviot Place, Edinburgh.
1909. Gordon, Mrs Ogilvie, D.Sc., Ph.D., F.L.S., White Lodge, 34 Abbey Road, London, N.W. 8.
1922. Grahame, T., M.R.C.V.S., Dalnacraig, Aberdour, Fife.
1909. Gray, Mrs Elizabeth, 59 George Street, Edinburgh.
1922. Greig, Professor J. Russell, Royal (Dick) Veterinary College, Edinburgh.
1877. Grieve, Somerville, 21 Queen's Crescent, Edinburgh.
1886. Grieve, Symington, 11 Lauder Road, Edinburgh.
1893. Grimshaw, Percy H., F.E.S., F.R.S.E., Royal Scottish Museum, Chambers Street, Edinburgh.
1913. Gumpert, Eugene, Ph.D., 15 Heathfield North, Twickenham, Middlesex.
1893. *Guppy, H. B., M.B., F.R.S.E., E.M.A.,
1919. Guthrie, Douglas, M.D., F.R.C.S., 4 Rothesay Place, Edinburgh.
1917. Harvey, Miss Elsie, c/o Flatters and Garnett, Oxford Road, Manchester.
1899. Hay, Wm. Peach, M.B., C.M., 555 Lincoln Road, Peterborough.
1883. Henderson, J. R., M.B., C.M., F.L.S., C.I.E., 14 Murrayfield Avenue, Edinburgh.
1899. Heslop, Charles, 75 Branstone Road, Burton-on-Trent.
1922. Hogben, L. T., M.A., D.Sc., Physiological Department, University, Edinburgh.
1878. Horne, J., LL.D., F.R.S., F.G.S., 20 Merchiston Gardens, Edinburgh.
1883. Hoyle, W. E., M.A., D.Sc., F.R.S.E., National Museum of Wales, City Hall, Cardiff.
1911. Hutton, W. Kilpatrick, M.D., Queen Margaret College, University, Glasgow.
1904. *Ingram, B., F.R.C.S.E., Balfour, Tasmania.
1903. Jamieson, E. B., M.D., Anatomy Department, University, Edinburgh.
1895. *Johnston, Colonel Henry Halcro, D.Sc., M.D., F.L.S., late Army Medical Service, Orphir House, Orphir, Kirkwall, Orkney.

- Date of
Election.
1869. *Kennedy, Rev. J., M.A., D.D., 9 Hartington Place, Edinburgh.
 1892. Kerr, Professor J. Graham, M.A., F.R.S., University, Glasgow.
 1878. Kidston, Robert, LL.D., F.R.S., 12 Clarendon Place, Stirling.
 1908. King, Professor L. A. L., M.A., 48 University Avenue, Glasgow.
 1904. *Kinnear, Norman B., M.B.O.U., Bombay Natural History Society,
 Apollo Street, Bombay.
 1910. Kenneth, John H., University Union, Edinburgh.
 1921. Kendall, P. F., B.Sc., Edinburgh and East of Scotland College
 of Agriculture, George Square, Edinburgh.
1915. Lamont, Miss Augusta, B.Sc., 73 Falcon Road, Edinburgh.
 1912. Laurie, Malcolm, B.A., D.Sc., Rothamstead Experimental Station,
 Harpenden, Herts.
 1907. Lee, G. Wharton, D.Sc., H.M. Geological Survey, 33 George Square,
 Edinburgh.
 1902. *Leigh, J. Hamilton, F.L.S., F.Z.S., Bindon, Wellington, Somerset.
 1921. Lewis, H. Mostyn, Penucha, Caerwys, Flintshire.
 1861. Logan, A., The Hollies, Colinton, Edinburgh.
 1920. Low, James Wotherspoon, B.Sc., Birkbeck College, Breams Buildings,
 London, E.C.4.
1886. M'Cracken, Professor, Englesea House, Crewe.
 1896. *MacDougall, R. Stewart, M.A., D.Sc., F.R.S.E., 9 Dryden Place,
 Edinburgh.
 1922. MacGill, Miss Elsie J., B.Sc., 9 Ormelie Terrace, Joppa.
 1913. MacGregor, Murray, B.Sc., 33 George Square, Edinburgh.
 1904. Mackie, N. Alex., 13 Barnton Terrace, Edinburgh.
 1920. M'William, Rev. J. M., Wellpark House, Craigmore, Bute.
 1920. Marshall, Miss Sheina M., B.Sc., Marine Laboratory, Millport,
 Buteshire.
 1914. Matheson, Professor Donald C., 3 Lockharton Crescent, Edinburgh.
 1889. *Millar, Robert C., C.A., 30 York Place, Edinburgh.
 1898. Miller, Hugh, F.Z.S., Zoological Laboratory, 18 Bristo Street,
 Edinburgh.
 1898. Morton, Kenneth J., F.E.S., 13 Blackford Road, Edinburgh.
 1911. Murray, Gilbert James, Homewood, Barnton Avenue, Davidson's
 Mains.
 1889. Musgrove, Professor James, M.D., LL.D., F.R.C.S., Swallowgate,
 St Andrews.
1904. Nash, J. Kirke, L.D.S.Ed., 1 Inverleith Row, Edinburgh.
 1909. Newbigin, Miss Marion I., D.Sc., 2 Chamberlain Road, Edinburgh.
1922. Panikkar, M. R. V., 11 George Square, Edinburgh.
 1910. Patience, A., 140 London Street, Glasgow.
 1921. Patton, W.S., Major, I. M. S., Zoology Department, University,
 Edinburgh.
 1919. Purser, G. Leslie, M.A., Natural History Department, University,
 Edinburgh.
1915. Ramsay, John Maclean, 10 Merchiston Gardens, Edinburgh.
 1909. Rennie, John, D.Sc., 60 Desswood Place, Aberdeen.
 1915. Renouf, L. W. P., B.A., National University, Cork.

- Date of Election.
1911. Rettie, Theodore, D.Sc., 12 Ann Street, Edinburgh.
1913. Richey, J. E., B.A., M.C., 33 George Square, Edinburgh.
1907. Ritchie, James, M.A., D.Sc., Royal Scottish Museum, Chambers Street, Edinburgh.
1909. Robinson, Professor Arthur, M.D., University, Edinburgh.
1919. Sanderson, Charles William, Birnicknowe, Cockburnspath.
1900. Schäfer, Professor Sir E. A., LL.D., M.D., Sc.D., F.R.S., University, Edinburgh.
1902. *Simpson, Professor J. Y., D.Sc., F.R.S.E., 25 Chester Street, Edinburgh.
1886. *Somerville, Professor Wm., M.A., D.Sc., F.L.S., F.R.S.E., 121 Banbury Road, Oxford.
1922. Stenhouse, Surgeon Rear-Admiral J. H., R.N., 12 Dalkeith Street, Joppa.
1920. Stephenson, John, M.B., D.Sc., F.R.S.E., Zoological Department, University, Edinburgh.
1900. *Tait, David, H.M. Geological Survey, 33 George Square, Edinburgh.
1919. Taylor, W. S., 20 Morningside Place, Edinburgh.
1893. Terras, James A., B.Sc., 40 Findhorn Place, Edinburgh.
1910. Thompson, Professor D'Arcy W., C.B., D.Litt., F.R.S., University, St Andrews.
1911. Thomson, A. Landsborough, O.B.E., M.A., D.Sc., 9 Addison Gardens, Kensington, London, W. 14.
1887. Thomson, Professor J. Arthur, M.A., LL.D., F.R.S.E., University, Aberdeen.
1876. *Thomson, John,
1906. Thomson, R. B., M.B., Ch.B., Aliwal North, South Africa.
1905. Troup, Capt. R. D. R., The Grove, Wembdon, Bridgwater, Somerset.
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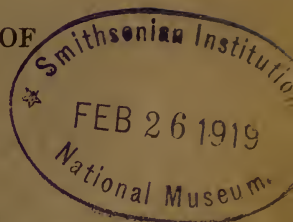
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PROMOTION OF ZOOLOGY AND OTHER BRANCHES OF
NATURAL HISTORY.

SESSION 1915-1916.



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PROCEEDINGS
OF THE
ROYAL PHYSICAL SOCIETY

SESSION CXLIII.

I.—The Bionomics of the Tiger-beetle (*Cicindela campestris*).
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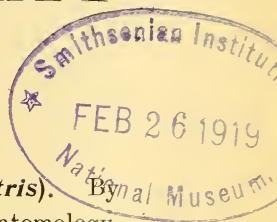
(Read 20th December 1915. MS. received 22nd December 1915.)

GENERAL OBSERVATIONS.

“THE egg-laying habit of the Tiger-beetles is not yet known.” So writes Kellogg in his fine book on “American Insects,” and this statement supplied the initial stimulus for the following observations on the habits and life-history of *Cicindela campestris*.

This is a well-known and conspicuous British beetle. It attracts attention by its brilliant green colouring, and its habit of appearing in considerable numbers on bright sunshiny days from April onwards, making short, rapid flights, or running actively on dry white roads, or sandy banks. It is common in the West Highlands, where the observations that follow were made.

The larva, though so often figured in books of Entomology, is not in its native haunts so generally familiar as is the adult. But in localities inhabited by the adult the grub may easily be found burrowing in sand-banks, in peat, or even in the borders of sandy roads. It has been described as ugly and misshapen, but its shape gives it certain very distinct advantages. The great head and jaws together with a semi-circular plate on the pro-thorax form the mud-coloured disc which, trap-door-like, closes the mouth of the hole. The back curves to a hump, on which on the 8th segment behind the head are a pair of strong hooks directed forwards. These serve to anchor the larva in its burrow when catching its prey, which it does by a sudden outward spring at a passing insect. Further, the larva lives in a burrow deeper than the length of its body, and it uses the hooks to support itself in the upper part of the burrow while waiting for prey.



The approach even of the shadow of any creature big enough to be dangerous causes the larva to withdraw instantly into its hole, and it is often just this movement which catches the eye of the observer and betrays the presence of the grub. If the earth round the burrow be much disturbed or upheaved, as for instance by the insertion of a knife-blade, the inhabitant, especially if young and small, will leave in alarm and seek a securer situation; where, using its mandibles for excavation and its head as a shovel, it soon makes itself a new "dug-out." In arranging the inside of a burrow to its liking, a larva will often be head downwards, with its tail-end protruding from the top of the hole. A convenient way of watching operations is to fill a tumbler with damp sand, and make with a slender pencil a rough burrow close to the glass—a plan also employed by Mr F. Enoch. A fair-sized larva put into this hole will at once set to work, and though it will insist on plastering up the window as often as one may clear away the sand, still a good view of its methods may often be obtained. The burrow is always smooth-walled, and is never such a tight fit as to preclude turning movements. The orifice is perfectly circular with its edges smoothly rounded off. By this the entrances to these burrows can be distinguished from those of bee-burrows, which often occur in the same situation. The bee-burrows, further, slope inwards for some distance, while those of *C. campestris*¹ are more perpendicular to the surface of the soil.

A full-grown larva measures rather under an inch in length, and its burrow usually exceeds three inches in depth, and rarely exceeded four in the district where these observations were made. The diameter of a large burrow at the entrance measures 5 to 6 mm.

SPECIAL OBSERVATIONS.

My own observations on *Cicindela* began in Argyllshire in July 1912. In the district larval burrows were numerous wherever there was a sandy, peaty soil open to the sun for many hours daily. They were specially common on old sandy dykes, and on the hillsides where cattle tracks had worn away the heather. The majority of the larvæ were remarkably uniform in size—about half-grown. Fully-grown larvæ were extremely rare. A peat containing five burrows was taken to Edinburgh for observation. At the end of August the larvæ plugged the openings with earth and did not re-open them. Unfortunately, shortly afterwards, the peat was thrown away by mistake.

In mid-July of the next year (1913) the locality was again visited. There were now everywhere to be found larvæ with burrows 5 to 6 mm. in diameter. Again the uniformity in size was general. These large larvæ were still

¹ Other species of *Cicindela* show slight differences in the nature of their burrow.

feeding, and their favourite prey seemed to be blow-flies. A big blue-bottle might often be seen caught by the head and sticking out of a larval burrow. In this position its soft internal tissues would be extracted, and next day the empty integument might be found cast away at some distance from the hole.

LARVÆ KEPT IN CAPTIVITY.

Sixteen large burrows having been marked to facilitate observation on a later occasion, sods containing eight others were dug up and taken to Edinburgh at the end of July 1913. Soon afterwards the inhabitant of one of these closed its hole by plugging the entrance with earth. A second larva closed its burrow on 25th August, another on 31st August, and a fourth on 1st September, and by 7th September all the burrows brought to Edinburgh had been closed. At the time it was conjectured from the size of the larvæ that the burrows were closed for pupation, but this surmise afterwards proved to be wrong. The larvæ were preparing for hibernation. The sods containing the burrows were kept in ordinary flower-pots placed at the base of a wall with a southern exposure, where they were subjected to the usual rigours of winter. From September 1913 till April 1914 the larvæ remained hibernating in their closed burrows. On 19th April 1914, it was noticed that all the burrows save one had been re-opened. Next day this last one opened, and all the larvæ were given a meal of raw meat. On the following day, 21st April 1914, one of them closed its burrow again. This time the retirement was for pupation, and before 8th May all the burrows under observation in Edinburgh had been re-closed.

On 17th May 1914, the burrow which had been closed on 21st April 1914 was examined by carefully splitting the sod. The larva was at the bottom of its hole and had not yet pupated. The two halves of the sod were joined together with as little dislocation as possible, and the sod was left undisturbed until 28th July 1914, when it was again opened up, and the adult beetle was found in the burrow. This beetle was transferred to a breeding-cage, and though torpid at first soon became quite active. On the following day (29th July 1914) two other burrows, which had been closed at the end of April 1914, were examined and found to contain pupæ. It was possible to preserve one of these burrows without its walls crumbling away, yet admitting a view of the pupa within. On 9th August this pupa had changed to an imago, but it was still quite white and remained in the burrow. Next day its thorax had become green. On the third day the beetle was coloured all over, though with a bluer tinge than maturer insects exhibit. In this state it was placed with the other beetle, which, instantly recognising its soft

condition, pounced upon it and devoured it. The remaining sods were left undisturbed, it being practically certain that each now held an adult Tiger-beetle, or a pupa about to become one.

PARALLEL OBSERVATIONS IN THE OPEN.

On 3rd September 1913, a short visit to Argyllshire was made. Of the sixteen burrows that had been marked in July, four were found closed up for hibernation. Two of these were opened for examination, and the larvæ were discovered at the bottom. When taken out the grubs showed themselves quite active, and readily made new burrows for themselves, closing the entrance as before. The sixteen burrows were re-marked in order that they might be found again in the following spring.¹

On 27th April 1914, Argyllshire was again visited. The larval burrows had been re-opened, and some of those marked in autumn were found again, and their inmates accepted a meal of meat, though blue-bottles and green-bottles were about, and a species of *Bibio* was very numerous. Four of these burrows were removed to Edinburgh, where one was closed by the larva for pupation on 2nd May, one on 3rd May, and the other two two or three days later. On 9th August 1914, I opened three of these burrows, and in each case a beetle was found. These three beetles and the beetle of the original stock obtained on 28th July were put into a breeding-cage, placed out of doors in a sunny situation.

On 25th August 1914, another short visit to Argyllshire was made. Four of the marked burrows were found, and were now all closed. They were opened for examination, and in each was found a beetle head upwards in the burrow. All the beetles when first exposed were semi-torpid, and remained so for some little time, only moving when touched. Two of them were placed at once, without being roused, in small specimen tubes plugged lightly with cotton wool and kept in darkness, to ascertain if possibly the beetles might thus pass the winter. They remained alive for some weeks, moving slightly if touched. Eventually, however, they died, probably from lack of moisture. The two other beetles were placed in the breeding-cage beside the four already mentioned.

The cage measures a cubic yard, and is roofed half by glass and half by zinc gauze, which admits the entrance of sufficient rain for that season of the year. The east and west sides being of zinc gauze permit constant ventilation, while the sides to the north and south are of glass. The north side is

¹ It will be noted that, compared with the larvæ being kept at Edinburgh, these in the West were later in closing their burrows for hibernation.

somewhat protected by a high wall at about three yards distant from the breeding-cage. The whole of the south side of the cage can be opened as a hinged door, but food was always put in, and refuse taken out, through a sliding-panel formed by the glass part of the roof. The cage was set on a prepared sandy soil which with a few peats formed its floor.

BEHAVIOUR OF BEETLES PREMATURELY TAKEN FROM THE PUPAL CHAMBERS.

The beetles ran about actively on sunny days, making also little flights, eating blue-bottles that were given them, or morsels of raw meat. Towards sunset they sought holes in the ground which they improved to their liking, using the mandibles to excavate, while holding on to the earth behind them with their long hind legs. When a hole was satisfactorily prepared the beetle would retreat into it backwards, its eyes and jaws remaining for some time visible from the outside. On dull days the beetles would so remain, usually quite hidden. They showed no inclination to pair.

As the autumn days became shorter and colder the beetles became more retiring, though on fine days they would still come out and eat. As flies became scarce they were fed mainly on raw meat, given in small pieces. They would suck these white. They also relished blow-fly maggots which were bred specially for them. A beetle would seize one of these by one end, and run about with it sticking cigar-like from its mouth. But a blue-bottle was always the favourite food. The lucky possessor would scurry off to seek a quiet corner where to enjoy the prize in peace, but generally two or three covetous comrades would give chase, and there would ensue a tug of war, resulting in the partition of the fly. In the beginning of October 1914 the beetles ceased to come out of their holes.

The first beetle to re-appear after hibernation was noticed on 6th March 1915. It moved about but little, refused food, and in the early afternoon retired again. It behaved thus every day for a week, and then disappeared completely for another week; but by the end of April 1915 five of the six beetles artificially removed from their pupal chambers in autumn had re-appeared, and were running about in the breeding-cage.

BEHAVIOUR OF BEETLES ALLOWED TO EMERGE NATURALLY FROM THEIR PUPAL CHAMBERS.

At this time also (April 1915) adults were emerging from the six burrows that, having been left undisturbed, had never been opened up since closed by their inhabitants for pupation at the beginning of May 1914. These six burrows, I may recall, had been closed by their larvæ for hibernation by 7th September 1913. By 20th April 1914 they had been opened again by

the larvæ, which were then fed. By 6th May 1914 these burrows had been all permanently closed for pupation of the now full-fed larvæ, and remained closed throughout the following summer, autumn and winter. 25th April 1915 was brilliantly sunny, and two beetles were observed in the act of emergence. One had been partially uncovered on the previous day by a shower of water, but in the case of the other the whole process was watched. First the tips of the mandibles were seen working through the earthen plug, and gradually a hole was made through which the head emerged. After looking about for a time the beetle withdrew again, and so remained for about an hour when it came finally forth. By 30th April 1915 all six of these burrows had been opened up by the emerging adults, and I had a total of eleven beetles running actively about in the breeding-cage. Five of these were males and six females.

SEX DISTINCTIONS.

The males of *C. campestris* are somewhat smaller than the females, and may further be distinguished by the first three tarsal joints of the front legs being somewhat flattened laterally, and clothed on the under surface with bristle-like hairs. The females, besides being larger, may be recognised by bearing on the elytra, in addition to the pale yellow spots possessed also by the male, a pair of black dots, one on each elytron, near the scutellum.

PAIRING.

Not till the end of May was any inclination towards pairing exhibited, though the beetles were very active on bright days, and ate with avidity what was given to them. On dull days they seldom appeared, and showed no desire for food.

In the last week of May 1915 another visit to Argyllshire was made. Tiger-beetles were very numerous. Half a dozen were caught and put for observation in a small portable breeding-cage. In the sunshine they paired readily, they also ate voraciously. On dull days they remained almost inert.

There was a remarkable scarcity of larvæ in the district. One sandbank where they had chiefly abounded was searched from end to end and only a single specimen found.

THE EGG-LAYING HABITS.

In the early days of June it was noticed that some of the captive females were ovi-positing. They, however, suffered a great deal of disturbance from the other females in the cage. These would deliberately annoy the egg-layer, by running up against her, nipping her in the face, pulling her legs or seizing her round the body. Two ovi-positing females

were therefore isolated, and each was placed along with one male, in a small breeding-cage thickly sanded at the bottom. Here the egg-laying habits could be watched conveniently. Eggs were never laid on cold, dull days, but in sunny weather the female beetles would extend their ovi-positors, feel the ground for a suitable spot, and commence to bore, breaking up the earth with two pairs of curved horny points, with which the tip of the ovi-positor is provided. One or two pits so commenced were usually for some reason abandoned, before an entirely satisfactory spot was found. Such pits persist and are visible for weeks in fairly firm soil or turf. When the egg has been deposited the beetle carefully fills up the hole again, and lastly rakes over the surface with her curved picks. The whole process of ovi-position occupies from 15 to 25 minutes. On one occasion during a period of constant watching a beetle was seen to ovi-posit five times between 9 A.M. and 2 P.M. on a sunny June day. Later in the day the weather became cloudy and no more eggs were laid. But repeated observation went to show that the activity of this beetle was by no means exceptional. Indeed it would seem that under the stimulus of sunshine a beetle feels impelled to get rid of her eggs, though the rate of ovi-position is restrained by the careful and deliberate manner in which it has to be performed. If a beetle is so disturbed in the act of ovi-position that she withdraws her ovi-positor at the critical moment from the pit she has made, and the egg gets laid on the surface of the soil, she will turn round excitedly and devour her egg. Several of the harassed beetles mentioned above carelessly dropped their eggs anywhere; the other beetles showed no disposition to eat the dropped eggs of their companions, and if such an egg was not devoured by the female herself, as it sometimes was, it would remain untouched.

In July (1915) observations were made in the open in Argyllshire which confirmed in all particulars those already made on the egg-laying habits of these beetles. In a little clearing among the heather of a hillside a female was surprised egg-laying. She ran off into the heather, but, perfect stillness being observed, she came back and re-commenced operations. Extending her ovi-positor she felt about over the soil surface, and after rejecting one or two spots eventually excavated her pit, ovi-posit and covered up the place. The ground was dry, and breaking it up with the horny points at the end of the ovi-positor was unmistakably hard work. As the hole deepened the beetle raised herself on her front legs till her body assumed an almost perpendicular attitude, and not only the ovi-positor, but the posterior part of the abdomen itself became sunk in the earth. A pause in the exertions indicated the passage of the egg, and then the work of filling up began. This also was done slowly and carefully, and lastly the

surface was raked over, till a few grains of loose sand alone marked the spot. After a pause another ovi-position was made in the same careful and deliberate manner.

THE EGG.

The eggs are 2 mm. in length, oval, yellowish when first laid, with smooth surface. When first deposited the eggs are coated with a viscid substance that makes them adhere more or less to the earth, sand or peat in which they are deposited. As the eggs mature they become white and somewhat swollen. Still riper eggs exhibit the two pairs of eyes of the larva, clearly seen through the egg-membrane. In a clod of very adhesive sand that was examined, the eggs and newly-hatched larvæ were found each at the bottom of a pit 4 or 5 mm. in depth, of which the sides were quite firm, though loose sand filled in the top. However, eggs experimentally buried in a new place hatched in due time, and the emerging grubs fashioned their burrows as easily as those hatched from undisturbed eggs.

THE YOUNG LARVÆ.

Eggs had been laid in the sandy floor of a small breeding-cage between 12th and 20th June. The cage was kept under constant observation, and the sand was daily watered, and freely exposed to the sun. The first larva appeared on 11th July, and the rest of the eggs continued to hatch-out successively through the remainder of July. Newly-hatched larvæ are quite white save for the eyes, and adhering to them may be seen the cast-off egg-membrane. One that was watched darkened in little over an hour. Beginning at the antennæ the colour spread from the anterior to the posterior end of the body. In structure a newly-hatched larva resembles a grown one, except that the abdomen is unextended. As the small wooden breeding-cage did not contain much depth of sand, the little grubs were, after about a fortnight, gently dislodged from their burrows, and sixteen of them were successfully transferred to a wide flower-pot filled with sand. This was done because young larvæ very soon increase the depth of their burrows. A grub of 5 mm. in length may have a burrow $1\frac{1}{2}$ inch deep. Other eggs were hatching-out in the peats contained in the large breeding-cage. Further, a visit to Argyllshire made at this time (July 1914) showed that the sandy bank which a month before had been searched almost in vain for the larval burrows of *Cicindela*, now exhibited numbers of minute burrows containing larvæ measuring 3 to 5 mm. in length. On the sand-dykes and on the hill paths it was the same. Everywhere, where in 1912, 1913 and 1914 half-grown or large larvæ had first abounded and later disappeared, numberless little burrows could now be found.

The little larvæ in captivity were fed on small caterpillars and maggots. When about six weeks old they closed their burrows. Those that did so before the end of August (approximately) re-opened in about 10 days, having accomplished a moult. Their heads were now much larger than before, and the diameter of the burrows was correspondingly increased. The newly-moulted grubs were always anxious to feed, and were sometimes successful in catching small flies for themselves. Three of the newly-moulted larvæ gave the following measurements. One was slightly over half an inch long, another measured $\frac{2}{3}$ of an inch, and the third $\frac{7}{16}$. Throughout September the larvæ were fed mainly on the mining maggots of the chrysanthemum fly. These were offered them almost daily, but were not always accepted. If the maggots were dropped bodily into the burrows this was resented, and the intruder promptly ejected. In the first half of September there was much sunshine, and small flies abounded, some of which fell a prey to the Tiger larvæ. The latter half of the month was cold and sunless, and the larvæ began to close their burrows for hibernation. No more freshly moulted individuals appeared; those which had retired as for ecdysis remaining in retreat. One of these was dug up for examination, and found to have moulted. The youngest burrows were the last to close. By 8th October all the burrows had been closed up.

ADULTS IN CAPTIVITY.

During all these observations the adults remained perfectly healthy in captivity. They were supplied with flies, maggots and caterpillars, as well as small bits of raw meat. These last were particularly relished if dipped in water and presented wet. In hot weather the sand on the floor of the cages was watered daily, and the beetles eagerly sucked up the water. They might be seen lying with their mandibles thrust into the wet sand, or into water drops. It sometimes appeared as if the beetles were capable of learning through experience. When, for instance, a new form of food was given them, the first time they would take it with hesitation—experimentally as it were; but the second time they would at once recognise it, and jump at it (literally) with avidity. In the small breeding-cages, also, they became quite indifferent to being closely approached and watched, the females even continuing their egg-laying perfectly undisturbed by the nearness of an observer. On the other hand, a beetle newly imprisoned from the hillside would for some days be too excited to settle down. Pairing and ovi-position continued to take place all summer, and even in the first half of September in warm sunshine. After that the beetles became more and more retiring, moving but little when they did appear, and showing no eagerness for food; though, occasionally, when

a live maggot was placed in front of one of them, the movements of the larva seemed to incite the beetle to seize and devour it. Eventually one beetle after another ceased to appear.

On 7th December, when the beetles had been hibernating for about two months, and after there had been a fortnight of frosty weather—the temperature on some nights sinking as low as 13° F. below freezing-point—two beetles, a male and a female, were taken from their retreats into a warm temperature. Both became quite active. One had been simply hibernating under a turf, and the other in a hole it had dug out for itself in the ground. Appearances, therefore, favour the expectation that the adult of *C. campestris* may live through a second winter.¹

The foregoing observations show that the life-cycle of a Tiger-beetle extends over several years. Whether these years be four or more depends chiefly on the amount of prey the larva is able to capture.

Thus in my observations eggs that were laid between 12th and 20th June hatched out between 11th and 30th July. The resulting grubs, which were supplied with as much food as they could consume, had reached a length of half an inch when six weeks old. They then closed their burrows for moulting and re-appeared about ten days later. They continued to feed and make a little more growth till the second half of September when they closed for hibernation, the most mature closing first. When they re-open in April (1916) they may be slightly over half an inch long, and less than half the thickness of a mature larva; that is, they may be approximately one quarter of the full size.

According to the foregoing notes larvæ first observed in their natural habitat in July 1912, when they were about half-grown, did not become egg-laying beetles till June 1915. My own grubs, from eggs laid in June 1915, will re-open in April 1916 measuring approximately one quarter the full size. These may possibly attain half size by July 1916, and from the foregoing data may be expected to reach full reproductive maturity in June 1919, giving a life-cycle from egg to egg of exactly four years. A typical life-cycle might therefore be made up as follows:—

Egg stage, about one month, say from mid-June to mid-July 1915.

Larval stage, nearly three years, from mid-July 1915 till June 1918.

Pupal stage, six or seven weeks, from early or mid-June till late July or early August 1918.

¹ Since the above was written an adult female has re-appeared above ground (April 1916) after hibernating during the winter 1915-16. It is now (May 1916) thirteen months since this adult emerged from the pupal chamber.

- Adult stage* (a) within the pupal chamber, eight to nine months, from early August 1918 till near the end of April 1919.
- (b) from emergence from pupal chamber till egg-laying, about six weeks.

It was noticed that in the main there is each year a general uniformity in the age of the *Cicindela* population of the locality in which these observations were made. Every fourth year (approximately speaking) a beetle year occurs, and the intervening years each exhibit larvæ in a stage of development characteristic of the year. But though this is true in the main, it is obvious that owing to the unequal start in life given to young larvæ of the same year, some being hatched as early as May, others as late as September, and to other causes, no year will be without both adults and larvæ, and in the year of large larvæ, small ones will always be found.

I have pleasure in here recording my thanks to Dr Stewart MacDougall for his constant kindly encouragement throughout the foregoing investigations.

(Issued separately, 14th September 1916.)

II.—Note on the Occurrence of Two Generations of the Nudibranchiate Mollusca *Lamellidoris bilamellata* (Linn.) and of *Archidoris tuberculata* (Cuvier) in the course of a year. By L. P. W. Renouf, B.A., the Bute Laboratory and Museum, Rothesay.

(MS. received 15th December 1915. Read 20th December 1915.)

SYSTEMATIC observations, extending from February to October 1915, on the fauna of a short stretch of shore on the eastern side of the Isle of Bute, have discovered *Lamellidoris bilamellata* (Linn.) and *Archidoris tuberculata* (Cuvier) to be two of the commonest forms of nudibranchs in that region. Of these *bilamellata* far outnumber *tuberculata*, but the latter has a wider distribution.

L. bilamellata was observed from 11th February 1915, when the observations began, until 28th April, and again from 27th July; *A. tuberculata* was seen from 2nd March until 4th April, and again from 27th July. The latter was found in abundance also on 3rd May about half a mile from the former locality.

L. bilamellata was in abundance and spawning freely from 2nd March to 29th March, after which date it decreased in numbers until 28th April. Between this date and 28th June it was unrepresented by either spawn or individuals. Absence from Bute made it impossible to make observations between 28th June and 27th July, but by this latter date *bilamellata* was again present in abundance, many individuals being in pairs, whilst a few were spawning. On 8th August, 10th September, and 11th October very large numbers were observed, a large proportion of them spawning. On 9th August this species was seen in abundance on the lower piles of Rothesay Pier, some two miles from the former locality, both in pairs and spawning.

A. tuberculata was seen in abundance from 10th March to 29th March. No spawn was seen on the former occasion but pairs were common, whilst on 15th and 29th March both pairs and spawn were abundant. On 28th April only a few small individuals and a single coil of spawn were seen, but on 28th May many large individuals and abundant spawn were found about half a mile from the former locality.

On 25th June this species was quite unrepresented, but on each of the dates 27th July, 16th August, and 10th September a few small individuals were seen, and on 11th October one was found in the act of spawning.

All the winter specimens of *L. bilamellata* and their spawn-spirals were

of large size, the former averaging 26 mm. by 17 mm., the latter 17 mm. by 85 mm. The specimens found from 27th July to 10th September were all of small size, 7 mm. by 4 mm. to 15 mm. by 10 mm., and their spawn-spirals of proportionate size, 4 mm. by 24 mm. to 6 mm. by 60 mm. On 11th October large individuals were abundant as well, but none of them showed any signs of breeding. On this occasion *L. bilamellata* showed a much wider distribution than heretofore, being plentiful from the upper Fucus zone to the ordinary spring-tide low-water line, whereas its previous range was from the latter to the upper Laminarian zone only.

A. tuberculata showed a corresponding difference in size: the winter individuals were large and laid large spawn-spirals, whilst the summer and autumn forms were small, and the one spawn-spiral found during October was of a proportionate size.

The very great difference in size between the larger winter-spring and the smaller summer-autumn forms points to the latter being the offspring of the former, and as the latter were breeding there seems no doubt that during this year, at any rate, two generations of *L. bilamellata* and of *A. tuberculata* have been produced.

If these phenomena are of normal occurrence, it would appear that *bilamellata* breeds twice during the first year of its existence but only once a year afterwards.

The summer-autumn material of *tuberculata* is insufficient to allow of any definite inferences being drawn, but what there is points to the same state of affairs as has been inferred for *bilamellata*.

Alder and Hancock remark that there is great disparity in size in *bilamellata*, but they give no indications as to whether the smaller and larger forms were found simultaneously or at different times of the year, though they do hint at a double-breeding period. They also mention the occurrence of forms of intermediate size, thus giving the hint that the larger is merely an older stage of the smaller form, though they do not bring out this point.

Note on the Nudibranchiate referred to above as Lamellidoris bilamellata (Linn.).—The forms referred to above as *Lamellidoris bilamellata* (Linn.) seem to be intermediate between the two forms described by Alder and Hancock as *Doris bilamellata*, Linn., and *Doris pilosa*, Müll.

In habitat and size these two species closely resemble each other, the former being found "on and under stones between tide marks," the latter "in shallow water and between tide marks"; whilst the size of the former is from $\frac{1}{2}$ in. to $1\frac{1}{4}$ in. by half as broad, of the latter $\frac{1}{2}$ in. to nearly $1\frac{1}{4}$ in. All the Bute specimens were found between ordinary tide marks

and, for the most part, on the underside of stones and boulders, none being found so deep as the line of low spring-tides, and none being obtained in the dredge. From this they would appear to be *bilamellata* rather than *pilosa*. In size the winter-spring specimens measured on the average $1\frac{1}{20}$ in. by $\frac{7}{10}$ in.

L. bilamellata is described as being "elliptical, nearly equally rounded at both ends," its cloak "covered with stout, not much crowded, clavate, strongly spiculose tubercles," and with the underside "slightly granulated." *D. pilosa*, on the other hand, is "ovate, very convex, and semi-transparent," its cloak "covered with soft, slender, conical, pointed papillæ," with the underside "veined in white and usually spotted."

Our forms combine these characters, for most of them are rounded at both ends, convex (some of them very convex) and semi-transparent, whilst the cloak is covered dorsally with both "stout, clavate, strongly spiculose tubercles," and "soft, slender, conical, pointed papillæ," and its underside is both "granulated" and "spotted." The branchial plumes resemble those of *bilamellata* in both structure and number, and the masticatory apparatus contains the erect, ear-shaped membranous fold of that species.

Alder and Hancock found *bilamellata* breeding in February, March, April, May and June, and August and September, chiefly in February and August; *pilosa* they found in April, May, June and as late as September, chiefly in May and June. Hence they suggest the probability of the former having two breeding periods, the one early in spring, the other late in summer. They do not say whether *pilosa* was found breeding between June and September, so that it is not quite clear whether this species is credited with two breeding periods or with but a single extended period.

As stated in the preceding note our forms appear to have two distinct breeding periods, with the maxima during March and September-October, in this respect resembling *bilamellata* rather than *pilosa*.

Regarding the spawn Alder and Hancock say of *bilamellata*:—"The spawn forms a compressed coil of one, or occasionally two volutions; spreading at the top, and often a little curved outwards, so as to give it a vase-like outline. That of a large individual measured $\frac{1}{4}$ in. in height, and $\frac{1}{2}$ in. in diameter at the top; usually, however, it is not above half that size." Of *pilosa* they say:—"The spawn . . . is of a pretty, cup-like form, with the margin turned outwards, and in some cases a little flounced." The spawn of our specimens resembles that of *pilosa* in arrangement and in size, for it is distinctly "flounced," and is of even larger dimensions than the spiral figured by Alder and Hancock, whilst the spirals of even the small summer-autumn forms much exceed in size those described as being typical of *bilamellata*.

Alder and Hancock make no mention of *bilamellata* in captivity, but of *pilosa* they say that it is difficult to keep owing to its propensity of crawling out of the water. This propensity was exhibited by all our forms, but, nevertheless, the larger forms spawned in captivity, the process of ovi-position was observed, and some of the spawn was hatched.

Thus our specimens appear to combine the characters of *bilamellata* and *pilosa*, sharing features of general conformation with both of them, whilst they resemble the former as regards their branchial and masticatory organs and their double breeding period, but the latter in the size and disposition of their spawn spirals.

(Issued separately, 14th September 1916.)

III.—The Connection of *Nosema apis* with Isle of Wight Disease in Hive Bees. Remarks on the evidence submitted in the Board of Agriculture Reports of 1912 and 1913. By John Anderson, M.A., B.Sc., Lecturer in Bee-keeping to the North of Scotland College of Agriculture.

(Read 24th January 1916. MS. received 5th February 1916.)

I. HISTORICAL AND INTRODUCTORY.

ISLE OF WIGHT Bee Disease was reported from the island after which it is named in the year 1904, and it was at first stated that it did not appear on the mainland till 1909. It is now, however, believed that "the trouble was not unknown on the mainland prior to the Isle of Wight outbreak."¹

It was in 1906 that bee-keepers became really alarmed, and Mr A. D. Imms, B.A., M.Sc., was requested by the Board of Agriculture to proceed to the Isle of Wight to investigate. He found the disease prevalent over practically the whole of the Island, and he collected much information from the bee-keepers as to the symptoms and course of the disease, the ways in which they believed that infection was conveyed, and the remedies they had experimented with. He dissected a number of bees, and made smears of the gut contents, fixing and searching these for bacteria.

Imms' description of the symptoms is as follows: "The earliest noticeable symptom of the disease is the inability of the affected bees to fly more than a few yards without alighting. As the disease progresses the bees can only fly a few feet from the hive, and then drop and crawl about aimlessly over the ground. They are often to be seen crawling up grass stems, or up the supports of the hive, where they remain until they fall back to the earth from sheer weakness, and soon afterwards die. In a badly infected stock great numbers of bees are to be seen crawling over the ground in front of the hive, frequently massed together in little clusters, while others remain on the alighting board. . . . Affected stocks examined in early spring show symptoms similar to those of dysentery. The bees discharge their excrement over the combs and on the sides, floor, and alighting board of the hive. . . . The bee-keepers state that this condition is only present after the winter confinement within the hive. . . . After the winter is over and the bees are all on the wing, no dysentery is noticeable, and all the diseased bees that have been dissected showed the opposite condition of distension of the gut. . . . The colon and adjacent part of the rectum are enormously distended

¹ Board of Agriculture Report, 1912, p. 13.

with a congested mass of material, consisting primarily of pollen grains. . . . Some amount of a dark-coloured fluid is present very often in the chyle-stomach, but it is not distended with it."

Mr Imms suggested no theory to account for the disease, but he recommended destruction of the affected stocks, with thorough disinfection of the hives and appliances.

Dr Malden's researches were carried out during 1908, and his report was published in February 1909. He made a systematic bacteriological examination of the alimentary canal of the bee. All bacteria observed were separately investigated, and it was found that no one type was characteristic of the disease. With the exception of one form, all the bacteria found in diseased bees were found also in healthy bees, and just as commonly. A type, called by Malden *Bacillus pestiformis apis*, was, however, present in 60 per cent. of the affected bees, so he made pure cultures and fed these to healthy bees. The bacillus was transmitted but the disease was not produced, so Dr Malden concluded that *Bacillus pestiformis apis* could not be the cause of the trouble.

The third and largest report, issued in May 1912, was the joint production of five workers. This report extends to 143 pages, is very comprehensive, and claims to contain everything of value in the earlier reports of Imms and Malden. From the point of view of this paper the most important sections are IV., V. and VI., because these deal with the alleged connection between Isle of Wight Bee Disease and the parasite *Nosema apis*. The succeeding sections of the report lose a considerable part of their significance if it can be shown that *Nosema apis* is not responsible for the disease.

It was in 1906 that Drs Fantham and Porter discovered in diseased bees from the Isle of Wight a protozoan parasite which has been stated to be invariably present in bees suffering from Isle of Wight Bee Disease. In 1907, E. Zander in Bavaria had independently discovered the same parasite, had named it *Nosema apis*, and had declared that it produced in bees a disease which he called "malignant dysentery." (Imms states, however, that dysentery is not a characteristic symptom in Isle of Wight Disease.)

Drs Fantham and Porter have worked out the life-history of *Nosema apis* with much care and in very minute detail. Their monograph, contained in Section V. of the report, is illustrated by many drawings on a large scale. The organism produces a characteristic spore, oval, highly refractive, easily distinguished, being 2 to 4 μ in diameter, and 4 to 6 μ in length. In badly infected specimens almost every cell in the chyle-stomach of the bee appears to be a mere bag of spores. The ripe spores escape into the colon, are discharged by the bee in flight, and are ingested by other bees when they

sip the dew on the grass. When the chyle-stomach of the new host is reached, an amœba escapes from the spore, penetrates one of the cells of the gut-lining, and starts to grow at the expense of the cell. Two or more parasites may enter the same cell, but even one by repeated subdivision may fill the cell with spores.

II. SOME EXPERIENCES IN LEWIS, OUTER HEBRIDES.

Specimens were first sent to Cambridge from Lewis in October 1911, at the time of the second outbreak of disease in the Island. The specimens were from two stocks, and these are Nos. 54*a* and 54*b* in the table on page 47 of the 1912 report. Dr Graham-Smith examined these himself and reported "many young stages" of *Nosema*. Destruction of both stocks was advised, but they were watched for a few days longer, and only one was killed. The other, a colony of American Golden Bees, completely recovered, wintered in excellent order, and never again displayed crawling symptoms. A stock which "crawled" during the following January was found by Dr Graham-Smith to contain *Nosema* in all stages. It was allowed to die out, and became extinct on 29th February. In the summer of 1912 another stock displayed "crawling" in a very marked degree. Specimens were sent to Dr Graham-Smith, and finally, in July, the remnant of the stock, with combs, was despatched to Cambridge. They were kept for some time there, and in those which died Dr Graham-Smith found "nothing very special."

In June 1913, there was in Stornoway a very typical case of Isle of Wight Disease. The stock affected was at full strength, crowding ten standard combs, and fully occupying a section crate of the usual size. The crawling bees could be found all over the garden on a fine day, and the other symptoms of the disease were very marked. A number of the "crawlers" were examined for *Nosema*, but no spores were found. Specimens ("crawlers") were sent as usual to Dr Graham-Smith. Dr Porter, who had now been entrusted with the work, made the following report with regard to the specimens sent: "The bees examined contained some young stages of the parasite. One had a very few spores. There is no doubt that *Nosema* exists in them, at any rate in some, which act as parasite carriers."

I was much interested to learn from this report that *Nosema* could not always be found in "crawling" bees, because this agreed with my experience in Lewis. By this time I had examined a large number of bees for spores of *Nosema*, and the result had been surprising. I had no difficulty in getting the spores, but these were found in bees which appeared perfectly healthy rather than in bees which were displaying symptoms of Isle of

Wight Disease. There were two stocks in particular from which I could procure spores at almost any time, yet these stocks showed only the normal death-rate, and could not at any time be said to display symptoms of disease. The theory that *Nosema* was the cause of Isle of Wight Disease did not seem to fit the facts as observed in Lewis. It might, therefore, be profitable to examine the results of the Cambridge investigation to see how far the main conclusion is warranted.

III.—CRITICISM OF THE CONCLUSION THAT NOSEMA IS THE CAUSE OF ISLE OF WIGHT DISEASE IN BEES.

1. If *Nosema* were the cause of the disease then *Nosema* ought to be demonstrable in every bee suffering from the disease. But Dr Porter was unable to find any stage of *Nosema* in some of the "crawling" bees which I sent her in June 1913. On page 41 of the 1912 report is an account of 66 cases investigated jointly by Drs Graham-Smith, Fantham and Porter. *Nosema* was not found at all in 13 cases, spores were found in only 29 cases, and so-called young stages in other 24 cases. The authors discount three cases in which the bees arrived dead, though it is quite easy to find spores in bees that have been dead for months. They claim, therefore, to have found *Nosema* in 53 out of 63 cases, or in 84 per cent. of the cases examined.

If *Nosema* is present in every case of Isle of Wight Disease, it is somewhat surprising that it was not noticed by Imms or Malden in 1907 and 1908. Both were searching for bacteria, and Dr Malden in particular claims to have exhausted this field. *Nosema* as compared with the average bacterium is relatively large, and one has difficulty in believing that Malden could have failed to notice it if it were actually present.

2. If *Nosema* be the cause of Isle of Wight Disease, the presence of the parasite, at any rate in quantity, should always produce the disease. But there is much evidence to show that *Nosema* may be present without producing the characteristic symptoms of Isle of Wight Disease. Two such cases in Stornoway have been mentioned above. We still have one of these stocks under observation, and we can get spores of *Nosema* from it almost at any time. I have frequently picked up bees entering this hive with pollen on their legs, or nectar in their honey-sacs, yet on examination they displayed heavy infection of *Nosema* in the spore stage. On page 50 of the 1912 report we read: "Spores in small numbers were found, however, in specimens from several stocks in one apiary in Scotland. No symptoms of the disease had previously been noticed, and none have appeared since."

Maassen, writing in 1911,¹ states that *Nosema* can be found in most

¹ *Mitteil. a. d. K. biolog. Aust. f. Land. u. Fortswirtschaft*, 1911, p. 50.

stocks in Germany, and that stocks containing the parasite winter well, and display no signs of dysentery or May-pest. He admits that *Nosema* may be pathogenic, but believes that disease makes its appearance only when the stocks are weakened by unfavourable conditions. In the season 1909-10, he carried out an experiment with 30 stocks of bees all strongly infested with *Nosema*. In the spring three colonies showed dysentery; two had a heavy loss of bees; one died outright, apparently from starvation. The three dysenteric colonies recovered. The remaining 24 stocks wintered well and developed normally in spring, except that some of the colonies displayed "*Maikrankheit*" without great loss. It was easy to prove the presence of *Nosema* in all the colonies, and at times the parasite was present in enormous numbers. Only the bees newly hatched were at all times free from infection. The stocks with May disease got over it and became prosperous in summer. Heberle, discussing this experiment in the *American Bee Journal* of May 1914, remarks that "Dr Maassen's experiment tends to show that a *Nosema* infection is not necessarily very disastrous, since even the 24 colonies that were taken through the winter did not show an unusual number of dead bees. They wintered well, and developed normally in spring. Only 10 per cent. of the *Nosema*-infested colonies developed dysentery, and even these got over it, and became useful colonies."

In Australia, Canada, and the United States there is a disease of adult bees, known as "paralysis," with very much the same symptoms as Isle of Wight Disease. On the continent a similar disease is known as "*Maikrankheit*" or May Disease. In Australia the disease has long been studied by Mr F. R. Beuhne, B.Sc., who is quoted on page 51 of the report for 1912. He had stated that *Nosema* had been proved to occur all over Victoria, and that "many specimens of paralysis of the most pronounced type were entirely free from *Nosema*." In *Gleanings in Bee Culture* for December last, he writes again: "You can find hundreds of colonies with the *Nosema* parasite and no symptoms; and any number of others with all the symptoms of paralysis but no *Nosema* parasites in the bees." The reply of the Cambridge workers is that by "*Nosema*" Beuhne means "spores of *Nosema*" (page 52). They suggest that in all cases of disease in which he could not find spores, *Nosema* must have been present in the "young stage." In reply to the statement that "you can find hundreds of colonies with *Nosema*, and no symptoms," the Cambridge workers suggest that Victoria must contain a large percentage of stocks which consist of parasite carriers. But to assume that there are hundreds of stocks composed mainly of parasite carriers seems to be putting somewhat of a strain upon the term.

3. If *Nosema* be the cause of Isle of Wight Disease, it ought to be possible to produce the disease by a pure infection of *Nosema* spores. The Cambridge

experimenters made numerous attempts to infect healthy bees with *Nosema*, and these were usually very successful so far as transmitting *Nosema* and killing the bees were concerned. But the bees had never any real opportunity of displaying the characteristic symptoms of Isle of Wight Disease. The bees experimented on were either small lots confined in cages or bell-jars, or full stocks kept in confinement. Those kept in cages and fed on fresh spores died very rapidly indeed, usually in little more than a week after infection. A heavy spore infection was noted as early as the fifth day. When confined merely to an infected cage, or when fed on spores some months old, the bees lived longer (27 days), but were believed to have died of *Nosema* in the end. Controls were kept alive as long as 21 days! In two cases the bees died rapidly, but *Nosema* was not found. The fact is that it is not easy to understand the behaviour of bees confined in cages. I have kept a queen and her attendants for weeks at a time in my pocket without any signs of trouble. On other occasions when the conditions were apparently similar the bees died in a day or two, sometimes within a few hours. Queenless bees in a cage would probably worry themselves to death in quite a short time.

The first experiments on full stocks were carried out in 1910 in Scotland. A hut was divided with double partitions of muslin into four compartments, 9 feet by $3\frac{1}{2}$ feet, and a healthy stock placed in each compartment in July. The stocks in I., II. and III. each received an addition of diseased bees, while IV. was kept as a control. The bees in I. were all dead by 11th March, and the dead bees contained numerous spores of *Nosema*. But this stock had shown "no obvious signs of disease"! (p. 87). No. II. died off by the end of March after suffering from dysentery, and "spores of *Nosema apis* were found in moderate numbers." No. III. was a stock of hybrids, and the bees remained well and active, till they died of starvation about the end of March. No spores were found. The control stock in No. IV. remained "strong and well till the middle of March, after which they gradually died off." No spores were found in the bodies. Two things are noteworthy: (1) there is no proof that any of the stocks suffered from Isle of Wight Disease, and (2) the infected bees survived practically as long as the control bees.

Similar experiments were carried out at Cambridge in 1911 by Graham-Smith and Bullamore. Compartments $9\frac{1}{2}$ feet by $3\frac{1}{2}$ feet were used, and six stocks of bees were placed in these on 18th May. I. and VI. were control stocks. The former died out on 17th July, and the latter on 17th October, a difference of exactly three months. The fact that of two similar stocks, one survives just twice as long as the other under confinement, indicates how little reliance can be placed on these experiments. Neither stock gave spores of *Nosema*. No. II. was given sealed stores from a badly infected

stock, and died out early in October without yielding any stage of *Nosema*. No. III. got a frame of sealed brood from a badly infected stock, and survived till 30th October (longer than either of the controls). A small proportion of the bees gave "young stages" of *Nosema*. No. IV. was fed on syrup containing numerous old spores. The bees were doing well on 8th December, but were dead by the middle of February. The hive was much soiled with dysenteric material in which *Nosema* spores were plentiful. Bees from an infected hive were introduced into No. V., and this stock died out on 12th October, without any evidence of infection with *Nosema*. These experiments were quite inconclusive. We have no proof that any of the bees suffered from Isle of Wight Disease at all, and it is again apparent that the *Nosema* infection did not appreciably hasten the death of the bees. Indeed the stock shown to have the heaviest *Nosema* infection lived longest of all.

The difficulties of the observers are obvious. They were afraid to infect a stock living under natural conditions lest they should spread the disease, so they were compelled to experiment on bees in confinement. We get little glimpses of the behaviour of the bees, and these indicate the very unnatural condition to which they were reduced: "The bees roamed round the windows during the first day or two, and many died. . . . The queen gradually ceased to lay. . . . The bees became listless, and many failed to return to the hive at night. . . . The bees did not appear to be interested in anything." In 1912 further experiments on full stocks of confined bees were attempted, but with equally disappointing results, and the account concludes with the remark: "It was found that even in winter bees cannot be kept satisfactorily in such compartments" (Report of 1913, p. 25).

In view of this difficulty, it occurred to me that in Lewis we had a very convenient area for further experiments on bee disease. There were no hive bees on the Island when I brought in the first stock in May 1909, and the history of each stock subsequently introduced was known to me. Further, it would be easy to carry out experiments on full colonies of bees living under natural conditions, and yet so far apart that no cross-infection could occur. In the spring of 1914 a Government grant for the investigation of bee disease became available through the Natural History Department of the University of Aberdeen. From that time I have been associated with Dr Rennie of the Natural History Department in carrying out further observations and experiments in Lewis and elsewhere. The results of these joint researches, along with many observations previously made by me in Lewis, of which a careful journal was kept, are dealt with in the paper by Dr Rennie and myself in the present volume of the *Proceedings*.

IV—Observations and Experiments bearing on “Isle of Wight” Disease in Hive Bees.¹ By John Anderson, M.A., B.Sc., Lecturer in Bee-keeping, North of Scotland College of Agriculture, and John Rennie, D.Sc., F.R.S.E., Lecturer in Parasitology, University of Aberdeen.

(With Plate.)

(Read 24th January 1916. MS. received 11th February 1916.)

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I.—INTRODUCTION.

THESE observations were commenced in 1909 by one of us (J.A.), whose journal contains a detailed record of the history of each stock of bees in the Island of Lewis. In the autumn of 1913 J.R. paid two visits to the Nicolson Apiary at Stornoway, and subsequently arrangements were made, through Professor J. Arthur Thomson, for continuing the research in association with the Natural History Department of Aberdeen University.

The work here reported on was carried out with the aid of grants from the Development Fund and the University of Aberdeen through the Joint Committee on Research in Animal Nutrition of the University of Aberdeen and North of Scotland College of Agriculture. In the work we have been assisted by Mr John Innes, B.Sc., M.B., who has carried out most of the examinations of bees for the presence of *Nosema*, and

¹ This constitutes a preliminary report, indicating the trend of the results so far accomplished. Although the number of experiments is not large, stress is laid upon the fact that they are the only ones on record in this country which have been made upon full stocks of bees living under natural conditions. Further experiments are in progress, the results of which will be recorded in a subsequent report.

after his retirement on taking up military service, by Miss Beatrice Simpson, M.A., who continued this work. Mr Robert Ewen, M.A., Nicolson Institute, Stornoway, has acted as local supervisor of the hives in Lewis since May 1915. We have also had the valued co-operation, in connection with the Deeside epizootic, of Mr A. H. E. Wood, of Glassel House, and of Miss Nancy Robinson, both of whom are bee experts of the British Bee-Keepers' Association. The latter has provided a detailed record of the Deeside outbreak, which has proved of value as a basis for scientific study.

We are indebted also to various local observers in Lewis and elsewhere who have taken charge of experimental hives, forwarded diseased bees, and otherwise supplied helpful information regarding the disease.

II.—THE COURSE OF THE DISEASE, AS OBSERVED IN THREE DISTINCT LOCALITIES.

(a) LEWIS OBSERVATIONS.

Prior to the 20th May 1909, all hive bees in Lewis had become extinct, but on that date one stock was brought to Stornoway and placed in the grounds of the Nicolson Institute. These were black bees obtained from Wormit, Fife, and their previous history is unknown. In autumn of the same year a second stock of black bees was imported from Duirinish, and placed at Bayhead, Stornoway. Since 1909, other bees have been introduced at various dates, as stocks or swarms, and some queens have also been imported. At the present time there are bees in Stornoway, Lurebost, Sandwick, Bayble, Tong, Tolsta, Barvas, Shawbost, Carloway, Breasclete, Achmore, Marybank, Laxdale. The races include Blacks, Italians (Ligurians), Cyprians, Carniolans, and certain hybrids.

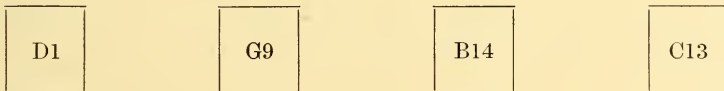
First Appearance of Isle of Wight Disease.—On the 20th September 1910, two lots of driven bees arrived in Stornoway from Sussex. They had come from cottagers' skeps, but had travelled to Lewis in swarm boxes on standard combs containing some honey. These standard combs probably came from the apiary of the bee-master who "drove" the bees, and it is possible that the disease was derived from these combs. One box was sent unopened to Bayble, $5\frac{1}{2}$ miles from Stornoway, and the other lot was retained in Stornoway. The bees in both cases were fed on syrup, settled down quietly, bred freely, and gathered pollen up to 4th November 1910.

On 31st January 1911, bees were observed crawling in front of this stock,

apiary number, A9. Next day a letter was received from Bayble stating that the other stock of driven bees had begun to crawl on the same day. The symptoms in both cases were those of Isle of Wight disease; bees emerged on the alighting board and did not fly, some eventually fell off the board on to the ground where they collected in little clusters, finally dying of cold and hunger. Bees of this stock continued to die in this way at Stornoway till 2nd March. On this date the survivors were killed and the hive and ground disinfected. Caustic soda was spread upon the soil, which was then turned over, and all the combs and quilts were burned. The Bayble stock was also killed off and the hive disinfected.

Second Attack. Two Stocks affected, B14, C13.—On the 6th October 1911, two other stocks in Stornoway Apiary began to crawl. On this occasion, samples of living bees were sent for diagnosis to Dr Graham-Smith, Cambridge, who reported “young stages of *Nosema apis* in both stocks.” Spores were apparently not observed, and it was not stated whether the examples seen included intracellular forms. One of these stocks (B14) consisted of American Golden Bees, and in their case crawling ceased after a few days; on 14th October they were busily engaged once more carrying in pollen. They wintered in excellent condition, built up rapidly in spring, and never showed any further sign of Isle of Wight disease. They were not again tested for *Nosema*. Unfortunately the queen died of old age, 15th June 1912, and the strain became extinct. The noteworthy feature in the case of this stock is that the symptoms, although associated with the presence of *Nosema*, disappeared in a few days.

The other stock (C13) which consisted of black bees, became rapidly worse, and, on 12th October 1911, it was destroyed. These two stocks stood side by side.



Arrangement of Stocks, October 1911.

Third Attack. One Stock, No. D1.—Crawling bees were first observed in front of this stock, the position of which is indicated above, on 20th January 1912. The bees were a black stock, numerous, and having abundance of natural stores. It had wintered in excellent condition. Samples were again sent to Cambridge, and Dr Graham-Smith reported the presence of all stages of *Nosema*.

This stock was allowed to die out naturally, but the hive had been removed to another site, and the original stance disinfected. A small remnant was found stiff and motionless on one comb, on 29th February 1912. Thorough disinfection of the site was effected by spraying crude carbolic acid, of such strength that the worms came up and died, and the grass also was killed. All inside fittings of the hive were burned, paraffin was also poured on the hive site, and burned off.

Fourth Attack. Stock D4.—This stock, a strong one, crowded with bees and brood, along with two others, came from Exeter on 21st May 1912, where as yet the disease was unknown. It was placed on the stance of D1, referred to above. Isle of Wight disease symptoms appeared on 28th May, exactly one week after the arrival of the stock upon the island, and large numbers of crawling bees were observed in front of this hive on every fine day. On 8th June, all the stores were exhausted and all the brood was dead. Syrup was supplied, and the queen laid more eggs. On the 13th June there were still numerous bees, eggs, a few grubs, and food. At this date samples were sent to Cambridge, and Dr Graham-Smith's report upon them is as follows:—

“The bees you sent all arrived dead. No spores were found by microscopic examination, and it was impossible to say for certain whether young stages of *Nosema* were present or not. I tried to infect some healthy bees, but this experiment has turned out negative. 2/7/12.”

On the 17th bees were lying about in large numbers on the alighting board and on the grass around, and dying off rapidly.

On the 11th July, the remaining bees, along with queen, were sent to Dr Graham-Smith, who kept them for some time. His report regarding them is:—

“The bees you sent have been doing moderately well, and nothing very special has yet been found in those which have died.”

This must mean that *Nosema* was not found, yet the behaviour of the bees, and the high mortality clearly indicated Isle of Wight disease.

In the case of this stock no disinfecting measures were adopted, nor in any subsequent instance in the Nicolson Apiary, Stornoway.

Fifth Attack. One Stock (K.M.).—This stock arrived in Stornoway from the South of England on 31st May 1912. Its ten combs were crowded on 11th June and a super was added. The super was quite full of bees on 22nd June, and some sections were ready for sealing on 13th July. Later a

second super was required, and some excellent sections were removed. Crawling began on 10th September, and was very typical when observed on the following day. On 12th October, all the bees were dead except the queen and a handful of workers. This stock was situated about 200 yards distant from the Nicolson Apiary.

Sixth Attack. Stock E14.—This stock consisted of Swiss pedigreed bees (blacks), and was imported from Exeter on 4th June 1913. When a super was added on 9th June the hive was crowded with bees and brood. When examined nine days later the super was crowded with bees, the foundation had been drawn out, and some honey stored in the cells. The stock had been placed in a garden which had not previously been used for bee-keeping, a short distance from the Nicolson Apiary.

On the 19th, bees were observed crawling in front of the hive, exactly a fortnight after their arrival in Lewis. Numerous bees were examined on the spot, their intestinal contents being searched microscopically. *Nosema* spores were not found. Sick bees were sent to Cambridge, and regarding these Dr Annie Porter reported: "A very few spores in one bee, young stages in some of the others, the rest negative." Notwithstanding the apparent paucity of *Nosema*-infected bees, the mortality amongst members of this stock continued, and at this period was exceedingly heavy. On 7th July, the Swiss queen was replaced by a Cyprian imported from Nicosia. The Swiss queen was caged with some Cyprian bees, and died of injuries received from them. She was sent to Dr Annie Porter, Cambridge, for examination, but no report was obtained regarding her condition. By this time, not many blacks were left alive; by September the stock was weak in numbers, but apparently healthy, and very few blacks were present. On 16th September, one of these was found to contain spores in abundance, but no spores were found in the young Cyprians. A few of these were observed to "crawl" on fine days, but the stock proved too weak to winter, and was allowed to die out.

Seventh Attack. Two Stocks affected, Gp. and Gs.—A stock of black English bees had been brought to Stornoway from the mainland of Ross (Duirinish) in the autumn of 1909. It prospered normally during 1910, 1911, and 1912, producing several swarms, and giving surplus honey. In 1913 it swarmed on 25th July. "Crawling" began in the swarm three days after it was hived, and was well marked and typical when observed on 16th August. On this date a few crawlers were observed in front of the parent stock. On 6th September, when the apiary was again visited no crawlers

were found in front of the swarm, but a large number was seen in front of the parent stock. Both hives were examined comb by comb on this occasion, and found to have queens and brood in all stages. The swarm was small in number, but lively, and apparently quite healthy. The parent stock was more numerous, but a considerable number of bees showed dislocation of the wings, an indication which, however, has little importance as a symptom of the disease. On the 12th September, sample bees were taken from the parent stock. These were picked off the combs, bees with dislocated wings being specially selected. Owing to unfavourable weather conditions there were no bees out of doors at this date. Microscopic examination showed no recognisable traces of *Nosema*.

The hives in which the bees were housed had no previous history of Isle of Wight disease. The bees were too few to keep warm in the hives during winter, and, on this account alone, survival was not possible.

Eighth Attack. One Stock, F14.—Without any disinfecting measures, Hive No. 14, which housed the previously mentioned infected stock (E14), was used for a lot of Welsh driven bees procured in the late autumn of 1913. The infected combs were also retained with contained honey. In early spring, 1914, heaps of dead were found on the floor; later, on fine days many "crawlers" were observed. At the beginning of April, the bees covered only a single comb, but they were carrying pollen freely, and there was a patch of brood. Crawling had now ceased, the stock built up during the summer of 1914, wintered on natural stores, and was quite strong in the spring of 1915. On 17th June 1915, J. R. examined six live bees, active after journey (posted 14th), all parts normal, no *Nosema* observed. Other samples of bees which were sent to Aberdeen for examination arrived dead, and were not satisfactory for Isle of Wight disease diagnosis. On the other hand, it can be stated positively that *Nosema* spores were not present in the bees examined. Bees were examined individually, and also pulped in groups. The colons contained masses of pollen, but *Nosema* was not found. A stained smear was also made of one bee, and this gave a negative result.

In August 1915, the stock was found weak and queenless. In October it was quite extinct, and the local observer (Mr Gibson) reported that crawling had been very marked.

In October the hive was restocked with a new lot of driven bees from Wales, the old combs and stores being retained. Efforts were made to put this stock in good condition for wintering, but the weather was rather cold while feeding was going on.

This is now the third stock housed in the same hive in which two previous

stocks had died of Isle of Wight disease. This new stock and hive is named G14.

No further cases of Isle of Wight disease have arisen in the Nicolson Apiary, although, as the records below show, *Nosema* could be obtained from bees there at almost any time.

Outbreaks of Isle of Wight Disease in Lewis.

Date of Introduction of Stock	Date of Outbreak	Stock	<i>Nosema</i> x, o, or y.s.	How terminated	If Site, etc., disinfected
29/9/10 from Sussex	31/1/11	Blacks A9 and Bayble	—	Destroyed 2/3/11	Yes
	6/10/11	American Goldens B14	y.s.	Recovered	—
	6/10/11	Blacks C13	y.s.	Destroyed 12/10/11	Yes
21/5/12 from Exeter	20/1/12	Blacks D1	x	Allowed to die out 29/2/12	Yes
	28/5/12	Blacks D4	?	Remainder sent to G-S., Cambridge	No
31/5/12 from S. Eng.	10/9/12	Blacks KM	—	Died out 12/10/12	Yes
4/6/13 from Exeter	18/6/13	Swiss pedigreed E14	Very few spores in 1; numerous in Sept.	Died out before Winter	No
Autumn 1909 from Duirinish	28/7/13	Blacks Gp	o	Died out Winter 1913-14	No
Autumn 1913 from Wales	Early Spring 1914	Welsh F14	o	Recovery in 1914 Relapse in 1915	No
11/7/14 from Exeter	12/7/14	Black (at Bayble)	o	Blacks died out in Autumn ; remnant of Yellows sur- vived Winter	—

The number of stocks in the apiary varied from 4 to 14 during this period.
x—spores present. o—spores absent. y.s.—young stages.

*Summary of Characteristics of Isle of Wight Disease as seen in
Lewis Outbreaks.*

(1) *In relation to area beyond the Island.*

(a) Simultaneous outbreak of two cases $5\frac{1}{2}$ miles apart of stocks introduced from same source (Sussex), 4 months previously. A9 and Bayble stock.

- (b) D4. Disease appeared 1 week after stock arrived from Exeter.
 E14. " 2 weeks " " "
 KM. " 3½ months " " S. England.
 F14. " 6 months after introduction from Wales.

See also under (2).

(2) *In relation to other affected stocks in Lewis.*

- B14. } More than 7 months after the termination of the previous
 C13. } outbreak.
 D1. Three months after B14 and C13.
 F14. Six months after introduction, upon which it had been placed
 in hive in which a stock, E14, had just died out from
 Isle of Wight disease.

(3) *Duration, where not interfered with.*

- B14. A few days, and recovered.
 D1. 40 days, and died out.
 KM. 32 days, and died out.
 E14. June to beginning of winter, and died out.
 Gp. July to winter, died out.
 F14. Few weeks—recovery—recurrence in the following year,
 lasting August to September 1915.

(4) *Relation to Nosema apis.*

1. Spores found in only two cases coincident with Isle of Wight disease symptoms.
2. Young stages were found in two other affected stocks, one of which completely recovered.
3. Healthy stocks known to have *Nosema* all the time in which no outbreak of Isle of Wight disease occurred.
4. A particular case, E14, in detail.

Placed on a new site when introduced.
Strong stock.
Mortality heavy.
Extreme paucity of <i>Nosema</i> in bees while this mortality in progress.
<i>Nosema</i> fluctuations at different stages.

(5) *Effect on Apiary as a whole.* No more than two stocks ever displayed symptoms at one time or in succession. During this period the apiary contained various races and strains of bees.

(b) EXAMPLE OF NATURALLY OCCURRING OUTBREAK OF ISLE OF WIGHT DISEASE, SHOWING SPONTANEOUS RECOVERY.

CRAIBSTONE APIARY.

On 4th June 1915, three strong stocks of bees imported from Devonshire were placed in this newly constituted apiary and housed in perfectly fresh hives. During the fine weather of June they were very prosperous, each stock swarming once and one of them twice. The swarms were hived separately. Three races were represented, viz. pure Italian, pure Carniolan (queen imported from Austria in 1914), and ordinary black bees.

Symptoms of Isle of Wight disease made their appearance on 30th June, and continued, with fluctuations, till near the end of August. All the stocks and swarms were affected more or less, but the heaviest mortality occurred in the blacks (D4). Three of the seven stocks died out owing to their failure to mate the virgin queens. In all three cases drone breeders were developed. On 22nd September four stocks survived and no symptoms of Isle of Wight disease were apparent, either in the behaviour of the bees, which was perfectly normal, or in the condition of their internal organs. At no stage of the disease were spores of *Nosema* found, although repeated examinations of the contents of the alimentary canal were made.

While the disease was at its height the number of affected bees was very great. Their behaviour was of the usual character, and the walk leading from the hives was littered with crawling bees to a distance of at least 25 yards. Heaps lay on the flower-beds, and a low box-hedge was full of bees incapable of flight.

The mortality was, in consequence, very considerable, and the weather conditions were exceedingly unfavourable to bee life. The recovery is therefore all the more notable.

On 22nd September one of the stocks (D4) was decidedly weak. It was headed by a young queen, had brood on two combs and plenty of store for the number of bees. This is the stock which had the heaviest mortality during the crawling period. Two other stocks (A1 and C3) were in excellent condition for wintering, headed by young queens, populous as to bees, and with plenty of stores. The fourth stock (B2) is the only one now that is not headed by a queen of this year. Possibly on this account, and also on account of heavy losses during the crawling period, this stock is also rather short of bees. The queens in D4 and B2 are black, C3 has a young Carniolan queen. A1, originally pure Italian, is now filled with dark bees, the offspring of a young queen.

On 23rd September, a small lot (3 lbs.) of driven bees was united to D4, and a new stock, E5, consisting of a small lot of Welsh driven bees with their own queen, was placed between C3 and B2. On 10th October, an Italian queen, supplied by Penna, was caged over D4, the original queen having been removed, and this Italian queen was duly accepted. On the same date it was observed that B2 (the weakest stock in the apiary) had been entirely robbed out. D4 and E5 were fed with sugar syrup and duly wintered down.

On 28th December, the four Craibstone stocks were examined. Except at A1 there were scarcely any dead bees to be seen, either on the ground, on the alighting boards, or on the floors of the hives. Even at A1 the number of dead bees was not remarkable.

D4 was opened, and the bees were found active and in good condition generally.

During the mild days in January 1916 the bees were moving freely and even carrying pollen. The behaviour of C3, E5 and D4 was normal, but A1 showed very definite "crawling" symptoms and a high death-rate.

(c) ISLE OF WIGHT DISEASE ON DEESIDE.

1.—HISTORY OF OUTBREAK.

By NANCY M. ROBINSON, First-Class Expert, B.B.K.A.

So far as can be ascertained, Isle of Wight disease was not recognised anywhere on Deeside until 1913, when it appears to have broken out in several distinct districts.

(1) On *Lower Deeside*, in *Culter* and the surrounding districts, the disease was at its worst in 1914.

A.—A's apiary was the first affected. He had bought bees from the South of England in 1912. These stocks did well early in 1913, but they had died out by 1914 after showing all the usual symptoms of Isle of Wight disease.

In 1913 these stocks had been taken to the heather, east of the Hill of Fare, in the Echt district, and several apiaries there, including two large ones, were badly affected by the same disease in 1914 and 1915.

During 1913 and 1914 all bee-keepers within a radius of two miles or more from A's apiary found their bees affected or dying off rapidly, and by the end of 1914 there were no bees left in that area.

Some apiaries were started again but with little or no success, owing to the recurrence of the disease.

In 1915 cases of the disease appeared still farther afield and embracing a far wider area.

Drumoak.—In the parish of Drumoak, on the north side of the Dee, a case of Isle of Wight disease occurred in 1913.

B.—B had sent to England for driven bees in 1912, and in the spring of 1913 the disease first began to show in his apiary.

During this year his six stocks gradually dwindled and died out. The hives were cleaned up and disinfected.

As far as is known no further cases occurred in this parish in 1913, unless it might be at H's, which is mentioned later. But in 1914 all the apiaries in B's vicinity became affected.

C.—C lived about a quarter of a mile north of B. In June 1914, C reported that his bees were not working, although the weather was good and there was plenty of nectar to be had. The apiary, consisting of two hives and a ruskie, was found to be in the final stages of the disease, and in July there were very few bees left and less honey than in June. The owner then destroyed his bees and disinfected his hives.

D.—D was another neighbour, living about three-eighths of a mile north-east of B. He had only one stock, which was found to be very weak in June 1914. The stock was left until August, when it was so much reduced that the owner destroyed the few bees that were left and disinfected his hive.

E.—E's apiary, situated three-quarters of a mile north-east of B, was attacked in August 1914. The bees may have been suffering earlier, but no record of this exists. E had sent samples of bees to the *British Bee Journal*, which reported them to be suffering from Isle of Wight disease. Incidentally, it may be mentioned that bees from the same source sent to Aberdeen University investigators were reported as free from *Nosema*. Only two stocks appeared to be infected, but in September 1914 the remainder showed marked signs of the same trouble. In October three out of four stocks were seriously affected, and between this time and April 1915 these three stocks had died off, and the remaining one was so weak that there was merely a handful of bees on the comb. These the owner treated with candy and quinine without success, and the stock died out before the end of the month.

F.—F lived about a mile north-east of B and owned four stocks. In August 1914 there were slight indications of Isle of Wight disease. In September one stock became badly affected, and the three others all showed symptoms. The worst of the affected stocks was removed to Aberdeen for experimental purposes (60 DD. of this report). The *British Bee Journal* reported

on samples of bees sent: "It is Isle of Wight disease." Dr Rennie reported: "*Nosema* can not be found in this stock."

The remaining stocks were not destroyed; but all died out except one, before April 1915. This stock was then very weak and was destroyed, and the hives and appliances were disinfected.

G.—G kept two stocks of bees, about three-eighths of a mile east of B. In June 1914 both were very strong; but at the end of June, drones were being thrown out in great numbers, and later in the year the bees were suffering from Isle of Wight disease. Before April 1915 both stocks were dead.

H.—H's house was quite close to G. In the spring of 1914 H had an empty hive in his garden; it was filled with old combs and had been left uncared for since the loss of a stock during the previous winter. (The symptoms accompanying the loss of this stock were unmistakably those of Isle of Wight disease. *J.R.*) In June a swarm came and took possession of this empty hive and flourished remarkably. 1914 proved a good season for honey, and this stock came through the winter, 1914-1915, very well. When visited in April 1915, the bees were found working vigorously and very strong for that time of year.

A swarm came off at 9.30 A.M. on 22nd May (the earliest swarm known on Deeside that year). H succeeded in skepping it, but unfortunately it rose later and was lost.

In due time a second swarm came off, which was skepped successfully, and stock and swarm both appeared to thrive.

Later, this swarm showed distinct signs of Isle of Wight disease during two or three days, and then it seemed to recover. At the end of the honey season, the two stocks were united. For further history of the united stock, see p. 59 of this report.

J.—J, three-quarters of a mile south-east of B, kept two stocks of bees, No. 1 and No. 2. When visited in June 1914 both stocks were found very strong, but No. 1 was especially good and was working well in the supers. In July large numbers of drones were being thrown out of the hive, in spite of fine weather and a good honey flow.

In August No. 1 showed marked signs of the disease, and J then destroyed the bees. This stock had given him 126 sections.

No. 2 swarmed, and the old queen having been killed the swarm was returned to the parent hive. A young queen mated successfully, and this stock did very well in 1914, but died out during the winter 1914-1915.

It may be mentioned here that J had earlier in the season assisted some of his neighbours in destroying their infected bees and cleaning and disinfecting their hives.

In 1915 J resumed bee-keeping. He obtained a swarm and placed it in one of his disinfected hives. This stock built up steadily at first, later it began to show some symptoms of the trouble, and then partially recovered.

K.—K lived a mile south-west of B. He had only one stock, which became seriously affected with Isle of Wight disease during the summer of 1914. It was destroyed in September 1914.

In 1915 numerous outbreaks occurred farther afield from B's apiary. There were several cases about $1\frac{1}{2}$ to 2 miles north of B. Many of the stocks had died out during the winter, and not from starvation as there was plenty of honey in the combs. Those stocks which survived soon began to show the ordinary symptoms of Isle of Wight disease, and all died out. B's stocks, it may be noted, were cleaned out and disinfection effected in 1913.

On the south side of the Dee, opposite Drumoak, two cases were noted in 1915.

L.—L lived rather over 2 miles south-east of B's apiary, and owned six hives and two ruskies. In June 1914, all were strong and apparently well, but owing to the prevalence of Isle of Wight disease in the district, L was warned to watch his bees carefully. No symptoms were recognised until June 1915; all the stocks were then strong, but later they became seriously affected and eventually died out before the end of the year. L dealt a good deal in so-called "remedies."

M.—M's apiary was 2 miles south of B. In May 1915, several of his stocks were found to be affected. M was inclined to think the disease was derived from some bees from Culter, which had been brought to the heather near by, in August 1914, and which had died out while there.

(2) *Banchory-Ternan District.*

In this district the distance between the outbreaks has been greater than in the others.

N.—A case occurred at Crathes in June 1914. N's apiary lies about three miles east of B. There were three stocks, Nos. 1, 2 and 3. The following observations were made:—

13th June.—A warm, bright day. There were numerous dead bees outside the hives, and a great many unable to fly and crawling on the ground all over the garden. No clustering was seen, and no old bees observed crawling. The wings and abdomens appeared to be normal, but the bees seemed weak. Stocks all seemed strong.

15th June.—A fine day. Only a few bees were seen crawling, and very few dead bees in front of the hives. Birds were seen to pick some up, and possibly numbers may have disappeared in this way.

16th June.—A fine day. Bees appeared normal. No. 2 looks like swarming. No crawling bees seen.

21st June.—A dull, rather cold day. Bees were clustering on the ground near all three hives in small groups. No. 2 appeared to be the only normal stock, and was strong. The bees from No. 1 and No. 3, both inside and outside the hives, appeared weak and dormant and unable to sting. There were very few dislocated wings. The abdomens and general appearance of the bees, with a few exceptions, seemed normal. It is doubtful whether any bees from No. 2 were clustering, although there were clusters under that hive.

22nd June.—A fine day. The symptoms just as previous day. No. 1 and No. 3 stocks were destroyed and the hives disinfected.

24th June.—No 2 was working well and looked like swarming. The ground was limed.

26th June.—No. 2 working well.

29th June.—Swarm came off, but got away and was lost.

9th July.—Bees working well, but some few drones observed crawling.

15th August.—No. 2 working well and seems strong. Supers nearly full. This stock died out during the winter 1914-1915. All stocks belonging to three bee-keepers, who were near neighbours of N, were lost also.

O.—O's apiary was 2 miles north of N. O had six stocks, and in July 1914 these were all found to be suffering from Isle of Wight disease. Only one stock survived till 1915, and that eventually died out.

Several cases were reported at Raemoir in 1914 which were not verified as the stocks had been destroyed before notice was received.

In 1915, there were two outbreaks, three-quarters of a mile distant from each other, at this place.

P.—P had five stocks in good hives, clean and well kept. The stocks were all strong. All appeared healthy in June 1915, but in July Isle of Wight disease was very marked. Numerous bees were crawling on the ground and clustering; others were climbing up grass and leaves; many had dislocated wings and distended abdomens. In those examined the colon was very much enlarged and clogged. There were many dead lying about.

Three of the hives contained parent stocks, while the other two held swarms. The parent stocks seemed to be more severely attacked. P destroyed all his bees at the end of July and cleaned and disinfected his hives and appliances.

Q.—Q's apiary was not so well kept, and his stocks were weak, consequently the outbreak did not appear so marked, and the disease lingered on for a long time. I have frequently noticed that when a really strong

(*i.e.* numerous) stock becomes affected, disease progresses much more rapidly than in the case of weaker stocks.

R.—A serious outbreak occurred in July 1915, in R's apiary, situated about a mile and a half south-east of N's apiary. R owned one hive and five ruskies, and by the end of 1915 nearly all his bees were dead.

S.—This brings us within a mile of Banchory village where a case broke out in July 1915 in S's apiary. This was on the east side of the village and within a mile of the last outbreak at R's.

S owned five hives and a ruskie. In May three stocks were very weak. Numerous dead bees lay near the hives, but this might have been the result of robbing.

In July, Isle of Wight disease was marked in a swarm in this apiary. In August all the other stocks but one began to show the same symptoms, and S destroyed them. The one left was strong and gave two crates of sections, which was good for a poor season.

At this date no cases farther west of Banchory and Raemoir have come under notice until Dinnet and Tarland are reached—15 miles away.

(3) *Dinnet Area.*

T.—In 1913, two bee-keepers at Dinnet, very near neighbours, found their bees suffering from some trouble they were unable to recognise. They consulted the North of Scotland College of Agriculture bee expert (Mr Manson), who found the bees to be suffering from Isle of Wight disease. His opinion was confirmed by the *British Bee Journal* expert, to whom samples of bees were sent. The owners were recommended to destroy their stocks in order to prevent the spread of infection. They not only did this, but burnt up bees, hives, and all appliances. One bee-keeper, T, owned fourteen stocks. Before the disease was recognised a swarm had come off and settled in the roof of a cottage close at hand. This swarm seemed to be strong and working well; and owing to the difficulty of removing the bees, it was left alone. T had brought bees from England not very long before the outbreak, and the disease was attributed locally to these imported bees.

In 1914, T started keeping bees again. He had made himself new hives and bought two stocks from a bee-keeper west of Ballater. In July 1914, he had six hives and three ruskies; all were very strong and doing well in the supers, and there was no appearance of disease.

In October 1914, the stocks seemed in splendid condition, and T was also feeding two stocks of driven bees. These had been obtained locally.

In the spring of 1915 he reported that several stocks had shown marked signs of dysentery, but there were no crawlers. T disinfected his hives after the attacks of dysentery.

In the spring of 1915 the swarm of bees already mentioned, which had settled in the roof of the cottage in 1913, showed marked symptoms of the disease. T, with the help of neighbours, promptly removed the bees, disinfected the place, and blocked up the entrance.

In June 1915, T's stocks were strong and working well.

In August 1915, one stock showed very slight signs; there were very few crawlers, and it is understood that T meant to destroy it.

U.—U's apiary is situated about half a mile due east from T.

In 1914, he owned seven hives and five ruskies.

In October 1914, there were no signs of Isle of Wight disease; but robbing was going on very vigorously. On this account some stocks were probably weak.

During the following winter, 1914-1915, five stocks died out, and all showed signs of dysentery in the early spring.

In June the remaining stocks were fairly strong, and all combs were badly marked with dysentery. When visited the weather was dull and no crawlers were seen.

The following day was bright at intervals, and a few crawlers were then observed. These were found to have the colon very much dilated and clogged.

In August 1915 only one stock remained, viz. the one which had appeared the weakest in June. It showed slight but distinct traces of the trouble, and U decided to destroy the bees and clean up and disinfect his hives. He did so in order to prevent the disease spreading among his neighbours.

No other cases in the immediate neighbourhood have been reported, although there are several apiaries near by.

V.—V's apiary is situated about five miles north-east of T. It consisted of ten hives and twenty-five ruskies.

In August 1915 all seemed very strong and well cared for, but examination showed the ground covered with bees unable to fly, with distended abdomens, dislocated wings, and all the usual appearances of Isle of Wight disease. I could not locate any special stocks as being the affected ones, for the bees were distributed all over the grass, and not in front of any particular hives. Samples of bees were sent to Aberdeen University investigators as usual, who reported that the appearances were those associated with the disease. The bees sent did not contain *Nosema*.

A week later, I found only three hives and one ruskie left. The rest had been destroyed on receipt of the above-mentioned report.

The surviving stocks were examined, but no symptoms of Isle of Wight disease were apparent. The owner, as a precaution, however, destroyed them.

X.—X, situated about one mile north of V, had originally come from Strathdon, and his bees had never flourished, but had been continually dying out. V had been down to work among them several times in 1915, and used his own gloves, smoker, and veil.

Drones had been thrown out of one of X's stocks abnormally early, and V had come in order to advise. Later, a first swarm came off this stock, and died out very shortly afterwards. A second swarm then came off, and these bees also died off.

When the stock was visited in August 1915, there was merely a handful of bees left. X then destroyed these, his last stock, and cleaned and disinfected his hives.

Y.—In 1914 X had sold an old hive to a neighbour Y, who lived about two miles south of his apiary. The stock which was placed in this hive died, and another stock beside it was reported dying out also.

No other cases within a radius of five miles are known.

2.—EXTRACTS FROM DIARY OF VISITS OF *J. R.* TO DEESIDE BEE-KEEPERS.

23rd August 1915. Visited Anguston Apiary.—Found twenty-one hives in small garden all affected with Isle of Wight disease. Ground littered with dead bees so that it was not possible to walk in garden without treading on them. Some had been treated with a syrup of sugar and jalap, and were reported to be improved, but this was not permanent. Sample taken; pulped. Negative result as regards *Nosema* spores.

Visited R's Bees at Drumoak.—Both stock and swarm active. Swarm had required an eke. There were a few crawling bees about, but not many. This is a case where intermittent crawling, moderate only, has occurred. Is this an aspect of the resistance of this stock where the infection has laid hold of a few, but has not overcome the majority of the stock?

D—, Durris.—When last seen, one stock had Isle of Wight disease; now, four or five have it. He has been spraying ground with Izal, and feeding an advertised preparation to the diseased stock, but apparently without effect. The disease has spread. Bees examined did not contain *Nosema* spores. When visited again in January 1916, all the stocks were extinct.

24th August. Visited Cullerlie, K's Apiary.—Isle of Wight disease prevalent in most stocks. No. 10 has got it. But the Italians, Nos. 25 and 18, are both going on well with no signs. Hybrids also are well, and these have swarmed lately. This swarm has settled in the top of a hive at Woodside which has got Isle of Wight disease very badly. I saw both stocks working (above and below) from the same hive. Took sample from No. 10. Result—failure to find *Nosema*.

H—, Finnercy.—Has Isle of Wight disease in most of his stocks. Took a sample from the worst, but did not find *Nosema* spores. Examined all K's sample, also H's. All had congested colons with pollen in a pasty condition. Most had chyle-stomachs, purplish; some were quite dark.

Main Features of Deeside Epizootic.

This report deals with twenty-three apiaries extending from Culter, near Aberdeen, to Dinnet, a stretch of about 30 miles along the Dee valley, and covering 3 or 4 miles on either side.

- I. The epizootic was observed first in 1913, in particular at Culter and Dinnet, and in stocks introduced from the South of England. In the Culter case one year at least elapsed between the time of arrival and the commencement of the outbreak. The disease is still prevalent in this district.
- II. Within the area there has been a very considerable amount of destruction of bees and appliances, of disinfecting generally, and also of experimenting by the bee-keepers with advertised remedies. All these efforts have failed to cure the disease or to affect recognisably its continuance.
- III. There are instances of stocks "passed over" within apiaries, though in close proximity to sick stocks. In this area at least one example is known of a stock prospering in a non-disinfected hive in which a stock had died out of the disease.
- IV. Bees, in a number of instances, were sent by bee-keepers to the editors of the *British Bee Journal*, and were reported to be suffering from Isle of Wight disease. We have been unable to find *Nosema* in the bees of Deeside generally.

III.—INVESTIGATIONS BEARING ON THE RELATION OF
NOSEMA APIS TO ISLE OF WIGHT DISEASE.METHODS OF EXAMINATION OF BEES FOR THE PRESENCE OF *NOSEMA APIS*.

As carried out by JOHN INNES, B.Sc., M.B., Captain R.A.M.C.

Each bee was examined in a routine manner, and the following notes were made:—

- (1) Activity, as determined by movements in the postal cage—usually a match-box.
- (2) Power of flight on exposure in open space.
- (3) Dislocation of wings; if present or absent.
- (4) Gait; whether co-ordinated or paretic.
- (5) Response to stimuli, such as handling, etc.

The chyle-stomach and colon of each bee were examined systematically, and the removal of these parts from the body was carried out in the following manner. The head of the bee was firmly crushed between fairly stout dissecting forceps, and while held thus, the last segment of the abdomen was grasped with straight fine-pointed forceps, and gentle traction applied. In this way the colon was carefully pulled out and the chyle-stomach also came away with it. These organs were placed on a slide, separated at their anatomical junction, and teased. Cover-glasses were then applied, and the preparation examined microscopically in the wet, unstained condition. If the spores of *Nosema apis* were present they were readily identified by their shape, size, and refractility. Young, intracellular stages and planonts were also observed in like manner.

Stained preparations from smears of the colon, and of the chyle-stomach, were made from every sample of bees examined, and the stain which was almost exclusively used was the iron-hæmatoxylin of Heideinhain. Although requiring longer time for staining, this was found to give the most reliable and most definite results. The fixative used was a hot alcoholic solution of corrosive sublimate.

Various other stains were tried, such as Giemsa, Romanowsky, Ehrlich's triacid, etc., but the varying results led to their abandonment in favour of the more stable hæmatoxylin preparation.

No stain, however, was found which would show up the spores clearly. Various experiments in this connection were tried, but with no success. Heat had very little effect in helping the stain to penetrate the resistant spore capsule. For its identification in stained preparations we could

rely only upon the surrounding structures being stained and the spore, left untouched, appearing as a clear structure.

The number of bees examined from each stock was, on an average, about eight. Where more than eight bees were available from a stock, then these were also examined.

The amount of infection was reported as slight, heavy, or very heavy, according to the number of spores found.

Where young stages were found, these were recorded as such, but it was rare to find a heavy *young stage* infection without the presence of a fairly heavy infection with spores.

The routine here described was that followed by Dr Innes in the laboratory, in all cases of bees which were sent for *Nosema* diagnosis from the Lewis stocks, from apiaries on Deeside, and several other districts. Examinations of bees for *Nosema* by the other workers was mostly, though not exclusively, confined to the searching for spores. These were obtained by examining bees in the fresh state and by the pulping method described later. Miss Simpson and Dr Rennie also prepared a number of sections of the alimentary canals of *Nosema*-infected bees (apparently normal in behaviour), of Isle of Wight diseased bees, and of healthy bees, some of which are utilised in illustration of the present work.

DIAGNOSIS OF NOSEMA INFECTION IN DEAD BEES.

Graham-Smith, Fantham and Porter, in their report upon *Nosema* as the cause of Isle of Wight disease, express the opinion that dead bees are unsuitable for *Nosema* diagnosis (p. 41). This opinion is reflected in the Board of Agriculture Leaflet, where it is stated that "it is not possible as a rule to express any opinion from an examination of dead bees." Leaving out of the question altogether the problem of Isle of Wight disease, and considering only that of *Nosema* infection, this statement has not been borne out by our experience. Undoubtedly, the most reliable means of diagnosis of *Nosema* infection is the recognition of the spores, and our experience has been that these are recoverable from bees at least as long as seven months after their death. We have in our possession at the present time (January 1916), a number of dead bees which were artificially infected with *Nosema* early in June 1915, in which we are still able to obtain spores, not only from numbers pulped together, but readily from individual bees.

Graham-Smith, Fantham and Porter are of opinion that spores are not often formed in the warmer months of the year. They state: "Undoubtedly

the most certain evidence of the presence of *Nosema apis* is afforded by finding the characteristic spores. Unfortunately these are not always present. . . . Our observations show that during the warmer months the parasites often do not reach the spore stage, but seem to kill the affected bees before this stage is reached" (p. 48 of 1913 report).

Our evidence is unfortunately rather contradictory, as we have been able to find abundance of spores in the months of May, June, July, August and September as readily as in other months. Our illustration of a section of a chyle-stomach in which every visible cell is heavily infected with spores (Pl. I. fig. 2) is from a summer bee. And we are a little doubtful of any heavy mortality resulting entirely from infection in the period of the bees' maximum vigour, at an early stage of the parasites' growth. This is especially so since we have found, throughout the summer, living bees without any obvious signs of disease, which proved to be very heavily infected with spores. Further it is claimed that the chyle-stomach of the bee is, even under normal conditions, constantly shedding and renewing its secreting epithelium.

PULPING EXPERIMENTS.

The routine of examining individual bees for *Nosema* diagnosis, although valuable and most reliable as regards the single bee in question, has several serious disadvantages. The first of these is due to the amount of time required to examine thoroughly even one bee, and the second, which depends upon this fact, is that one is led to base conclusions regarding a whole stock upon the results obtained from the examination of relatively insignificant numbers. A small sample of bees taken at random from a stock does not correspond, say, to a sample of a homogeneous fluid or solid substance.

This difficulty has been largely overcome in our later work by the introduction of the method of pulping collections of bees designed for examination for the presence of *Nosema* spores. Our method is simply to cut off the abdomens of the bees, letting them drop into an ordinary mortar. They are then gently pulped in sufficient water to render the contents fluid. Sometimes we have removed the alimentary canals from behind the honey sac and teased these collectively in a little water in a large watch-glass. Samples of the resulting fluid in either case are taken up with a pipette, and if *Nosema* spores are present in the pulped preparation, they are usually found in the first drop examined. Our first experiment of this nature was as follows.

Four samples of dead bees were taken. Two of these were from collections of bees which had been infected by feeding with *Nosema* spores nearly three months previously, and the remaining two consisted of bees from Isle of Wight diseased stocks.

- (a) Pulp of twenty-six *Nosema*-infected bees yielded, on examination, numerous spores in the first and every succeeding drop of fluid taken from the mass.
- (b) Pulp of a second (separate) lot of *Nosema*-infected bees—about a dozen bees. Result as in case of (a).
- (c) Pulp of bees, "crawlers," from two stocks—different apiaries on Deeside—same stocks as were used for infection in second Shawbost experiment (p. 54)—about twenty bees. Result: No *Nosema* spores observed after repeated examinations.
- (d) Pulp made of about two thousand bees from a stock which had died out from Isle of Wight disease at Banchory. The fluid, after draining off from the solid residue, was tested extensively (twenty separate examinations), and *Nosema* spores were not found.

Other similar tests are given below:

1. Thirty "crawlers" from DES1 stock (p. 57) were picked up on 10th September. They were allowed to die in a small cage, and on 14th were pulped in a little water in the usual way. In this stock there had been found previously an unidentified organism. The first field examined in the first small drop contained numerous spores of this organism. *Nosema* spores were not seen.

2. Sample from Anguston, consisting of nineteen "crawlers," had their abdomens pulped and examined for *Nosema* spores. Negative result.

3. On 11th September 1915, visited Anguston and found nineteen of the stocks had succumbed to Isle of Wight disease since last visit. Took a sample of dead bees from the site of one of the dead stocks.

On 20th September these bees, sixty in number, were pulped, and examined. Nineteen samples were dealt with and no *Nosema* found.

4. On 25th September 1915, seven bees which had died in transit from Glenhouse, Stornoway, were pulped. Negative result as regards *Nosema* spores. These were "crawlers" from the front of the hive, but we have no other record of Isle of Wight disease in connection with this stock. Seven live ones which survived the journey were similarly treated. Result: Negative as regards *Nosema*.

5. Six bees which remained of the lot of Carniolans (No. 7) from Stornoway were pulped on 25th September. No *Nosema* was found.

6. Pulped 27 chyle-stomachs of Welsh driven bees, which were hived to-day in Desswood apiary (29th September 1915), and examined twelve drops for *Nosema*. Result: Negative.

Numerous further tests of this nature have been made, and in every case where *Nosema* was known from previous experience to be present in the collection from which the bees were taken, *Nosema* spores were found.

As early as 1913 we had become doubtful of the conclusion that *Nosema apis* stood in direct causal relation to Isle of Wight disease. From February of that year we regularly examined bees for *Nosema* spores, especially any that crawled or seemed sickly. We found such spores very frequently, particularly in old bees and not necessarily in association with unusual mortality in a stock. We have found bees with a heavy spore infection able to fly perfectly and even to carry loads of pollen and nectar. We have had under observation for three years, 1913-1915, a stock of Ligurians, G9 (Nicolson Apiary), which has stood in proximity to several of the forementioned stocks throughout their periods of crawling. This stock has never displayed any noticeable crawling symptoms. Yet all the time *Nosema* has been present in it, sometimes in enormous quantities (see Pl. I. fig. 4—a microphotograph, taken in the present year, of the colon contents of an apparently healthy bee from this stock).

It is significant that, while G9 contained *Nosema* over a prolonged period, it failed in any marked way to infect the apiary generally. We have not found *Nosema* distributed in the bees of all the stocks, but only in a few stocks at any one time, and where it occurred, Isle of Wight disease was not present.

History of certain Stocks in Lewis—with special reference to the alleged connection between Nosema apis and Isle of Wight Disease.

We visited Bayble on 7th May 1914, and took samples of a stock of bees which had no history of crawling. Spores of *Nosema* were found in several of the bees, the infection being very heavy in a number of cases. On 4th September, when again visited and examined, this stock was in a highly prosperous condition; it filled the brood box of ten combs and crowded also a super of ten shallow frames filled with honey. On 14th August 1915, this stock was still prosperous and had never shown any crawling symptoms. Sample bees from this stock were taken in September, and these were found to be free from spores. Twenty bees were examined: these were lively, vigorous, and flew readily after two days in transit. The chyle-stomachs of

five examined individually were of a healthy appearance; the colons were not markedly congested, and contained watery material consisting almost entirely of indigestible pollen residues. The abdominal parts of the remaining bees were pulped, and drops of the fluid examined as offering the most reliable means of detecting the presence of *Nosema* spores. This stock remained healthy alongside the next-mentioned.

Meanwhile there had been in the same apiary, and in close proximity to this stock, an independent outbreak of Isle of Wight disease. A swarm of black bees arrived from the South of England on Saturday, 11th July 1914, and was duly hived. The bees began to crawl next day, and the symptoms were very marked when we visited the apiary on 13th July. Then, nearly half of the stock was to be seen crawling or dead upon the ground.¹

Bees taken on this occasion were examined in Stornoway by J. A. and J. R. with negative results, and stained preparations were afterwards made without young stages being found. This swarm was headed by an Italian queen, which had been supplied just before the stock was despatched to Lewis. A little patch of brood was hatched, and the yellow bees did not "crawl." The blacks were all dead in autumn and the yellows were not strong enough to winter.

Stock G9: Nicolson Apiary.—This stock has no history of Isle of Wight disease and no abnormal death-rate. A few "crawlers" have occasionally been observed, but nothing to indicate disease, yet this stock is known to have harboured *Nosema* for at least three years. The original queen was a pure Ligurian imported from Bologna (apiary of Enrico Penna), in the autumn of 1911. A black stock on each side of this hive (the stocks already referred to as C13 and D1) died of Isle of Wight disease during that autumn and winter, but the Ligurians showed no signs of trouble. These extinct stocks were replaced in 1912 by two other black stocks (D4 and H12) which died out—D4 certainly, and H12 probably, from Isle of Wight disease before the following winter. But still the Ligurians showed no signs of this disease.

1st September 1912 was very windy, and the hive of G9 was blown right over, the combs being scattered. The bees were gathered up and the queen found uninjured, but this accident handicapped the bees for getting into condition for wintering. The spring of 1913 found them very weak and hardly any of the young bees were able to fly.

Examination for *Nosema* spores gave negative results at this stage. The queen eventually ceased laying, and she was transferred to a queenless black stock. In due course brood appeared, and in this case most of the young bees

¹ Bees from this stock were used in Tolsta experiment (see p. 52).

could fly. A number of those which "crawled" were sent to Dr Annie Porter, together with a description of the symptoms, and she reported as follows:—"Every bee contained spores of *Nosema*." This was in July 1913. The crawling referred to here was not typical of Isle of Wight disease, and lasted for quite a short time. Also the number involved was very limited, and consisted entirely of young Italian bees. At intervals during June, weak and aged bees, both blacks and Italians, had been picked up in front of this hive and examined on the spot, by one of us (J.A.). These were full of spores of *Nosema*, but none were found in the young Italians examined at the same time.

A neighbouring queenless black stock was now united with this Ligurian stock, and soon there was a prosperous colony with plenty of brood, worker and drone. On 12th September 1913, bees taken at random off the frames were examined and no spores of *Nosema* were seen. During the winter of 1913-14 frequent samples were taken, and a large proportion of the bees examined were found heavily infected with spores. Yet those bees were quite active and healthy and could fly perfectly.

On 19th December 1913, the old queen died and stock G9 continued queenless and broodless for over three months. On 28th March 1914, we added a small lot of Italians which had been found starving in another hive. The queen was a Penna Italian imported in 1913. Bees of this stock were found to be heavily infected with *Nosema* on 2nd June.

When we examined the stock on 20th June 1914, it was quite prosperous with a good show of brood. The weather was wet and cold, and diligent search in front of the hive resulted in the finding of eight benumbed bees. Seven of these were full of spores of *Nosema*. Eight bees were also picked off the combs at random, and three of these contained spores of *Nosema*. Again, on 13th July, one bee out of six examined contained an abundance of spores. This stock is still alive at the present time.

NOSEMA INFECTION EXPERIMENTS.

(a) *Infection of a full Stock of Bees with Nosema apis.*

On 11th July 1914, a small lot of Cyprian bees which were known previously to harbour *Nosema* were placed in confinement. On 28th July most had died, and the remainder appeared weak. Four were examined, two live and two dead. All contained *Nosema* spores in quantity. The whole lot of bees, ninety-one in number, were mashed with honey, and fed to a full stock of bees at Achmore, Lewis. These were ordinary black bees imported

as a swarm from the South of England in June 1914. They had been examined on 30th June, and again on 13th July, and found negative as regards *Nosema* spores and young stages. There were no other hive bees within a radius of $5\frac{1}{4}$ miles.

On 19th of August, the stock was visited and examined. It covered nine combs, and clustered on the dummy. Not a "crawler" nor dead bee was to be seen in front of the hive, although the weather was very favourable for this. Ten bees, taken at random, were examined for *Nosema*, and spores were found in four, two of these showing a very heavy infection.

On 7th September, a second sample consisting of twelve bees was examined, again taken at random from within the hive, and five were found infected, three of them heavily. The day was fine, and there were no indications of Isle of Wight disease.

On 10th October, the bees were again visited and samples taken, from inside the hive as formerly. It was a fine October day, and the behaviour of the bees was normal.

On 13th October nine of the sample bees were examined. They were active, flying readily, and their intestines were normal in appearance. No spores of *Nosema* were found. On the 14th, eight more bees were examined, again with negative results. On the 22nd, three bees of another sample were taken. These arrived alive and active. On examination they were found to have the intestine normal, and to contain no spores of *Nosema*.

From the foregoing it appears certain that this stock of bees was definitely infected with *Nosema*, but this infection failed to produce Isle of Wight disease.

The following are illustrations of numerous artificial infections with *Nosema* carried out on small lots of bees confined in cages.

(b) *Laboratory Experiments.*

I. *On 14th June 1915.*—*Nosema* spores derived from bees of Stornoway, stock No. 7 (Carniolans), were used to infect some bees taken from an observation hive at Marischal College, Aberdeen.

On the 17th, *Nosema* spores were found in plenty in five bees taken at random from the infected lot. These spores were in alimentary canal; no intra-cellular forms were seen. Our view is that those seen were the spores ingested.

19th June 1915.—Numerous spores were found in the colon of one dying bee, and a few in the chyle-stomach. Young stages were observed in cells of chyle-stomach (J. A.).

21st June.—A dead bee from infected lot was examined; spores were found in colon, but not in chyle-stomach. Many cells of the chyle-stomach showed intra-cellular stages (J. A. and J. R.).

1st July 1915.—On 30th June, two bees were found dead. When examined on this date a few spores were found in both, and a great many young stages were seen, especially in one bee. A stained smear showed many meronts within the cells, there being frequently four parasites in one cell (J. R. and J. A.).

This infection experiment, through pressure of other duties, was allowed to come to an end about this time. But the dead bees were preserved, and in September they were found to contain *Nosema* spores in great abundance. At this latter date, however, several attempts to produce infection by means of these spores failed.

II. 20th September 1915.—On this date thirty bees from *Craibstone No. 41* (a stock originally Italian, but now consisting entirely of black bees) were confined in a small cage, and fed on spore-infected material mixed with honey. The spore material was obtained from the 14th June experiment. Five bees were killed and their chyle-stomachs pulped and examined, before infection, for *Nosema* spores. Result—negative (J. A. and J. R.).

On 21st, the bees were again fed with the spore-laden material. Up to 25th the behaviour of the bees was normal; they fed freely, and were quite active. There had been no mortality except in the case of three, which died on the 21st. In one of these ingested spores were found.

On 26th, one bee died and one was killed. No spores were found in either of these.

On 28th September, two died and two were in a weakly state. No spores were found in any of these.

On 29th, one died and no spores were found. The bees were fed on Scholtz candy.

The intestine in the last examined bee was whitish, and not unlike the appearance of a *Nosema* infection, but, as stated, spores were not observed.

On 7th October, fourteen bees which had died were pulped. These were black bees: no *Nosema* spores were found.

It is clear from the foregoing that the spores used in this experiment failed to infect.

III. On 30th September, a small lot of Welsh bees were caged and fed on *Nosema*-infected material of 15th June. Spores were present in the material fed. A similar number of bees were caged as a control, and fed on clean candy. Feeding with the infected material, in the case of the first lot, was continued on the 1st and 2nd October, after which clean candy was given.

On 7th October, it was found that sixteen bees of the infected lot had died. These were pulped (abdomens) and examined for *Nosema* spores. Free spores in moderate numbers were found; two or three in every field examined of the first drop taken. One live bee examined gave a negative result. In the control, two bees had died. These were pulped (abdomens only), but no spores were found.

16th October 1915.—Five bees dead. These were pulped on 18th, and *Nosema* spores were found. Other three were examined, and spores found in all. Other six were pulped, and spores were again found. All the control bees had died at this date.

From these results it seems probable that no infection had taken place.

IV. 4th January 1916.—On this date all the Desswood stocks were in flight. The opportunity was taken to procure a number for experiment, and samples were captured on the alighting board of the "Kelly" hive. These were fed with candy, which on the same day was well smeared with pulped matter from bees of the June experiments. This matter was found on preliminary tests to contain *Nosema* spores in plenty.

The bees were kept in a small wooden cage with glass cover. By the 6th several had died. Nine were removed at this date, but of these, two were dead shortly after caging, having probably been hurt.

6th January 1916.—Two were allowed out of the cage, and these flew quite strongly, and one of them defecated.

8th January 1916.—Other six bees were found dead. One released proved unable to fly, although it was quite active. When lifted it used its sting. This bee had chyle-stomach, pale in colour, and colon dilated with a pasty mass of pollen. Search in the dead bee and in the surviving one failed to find any trace of *Nosema* spores. Another live bee very active was taken, killed and examined. This bee had a pale chyle-stomach and inflated watery colon. Numerous free spores were found in the latter, but a very thorough search failed to discover any trace of infection in the chyle-stomach.

12th January 1916.—On the 12th all the bees had died. These (thirteen) were pulped, and examination showed free *Nosema* spores in moderate numbers.

V. 24th June.—Infected two boxes of "Kelly" bees with *Nosema* material from No. 7 Stornoway hive.

1st July.—Examined two bees which had died. Planonts seen in both bees and intra-cellular forms in stained film. No free spores seen.

8th July.—On this date the chyle-stomach of a bee of this experiment, taken alive, was found on examination to contain enormous numbers of spores and planonts. Spore clusters common.

VI. *20th June.*—Fresh spores of *Nosema* were, on this date, mixed with honey and fed to a number of bees in a small cage. On the 26th several of the bees were killed, and an examination was made of the alimentary canal. Planonts were seen in very large numbers. A further examination on the 30th revealed the presence of both planonts and meronts. Spores were not seen.

In connection with the foregoing experiments control lots of bees were in most cases kept. Further we have had a very considerable experience with caged bees under the same conditions as those of the experiments. We have not been able to detect significant differences in mortality amongst such caged bees. No conclusions are therefore drawn with reference to the cause of death. Our experience is that captivity in small cages without a queen is eventually fatal to the healthiest of bees.

With regard to the behaviour of the bees while under experiment, it was not possible to decide whether Isle of Wight was present. The condition of the intestine which we have learned to associate with Isle of Wight disease, and which we find has been described by Imms (*Jour. B. of A.*, xiv. pp. 133-4), has never been observed in those caged bees.

The experiments numbered II.-IV. were made in September and January with spores obtained from bees which died in June. These dead bees were kept in a laboratory cupboard under ordinary conditions, and the results would suggest that in some instances at least the vitality of the spore is brief.

CONCLUSIONS REGARDING RELATION BETWEEN NOSEMA APIS AND ISLE OF WIGHT DISEASE.

Our main conclusion regarding *Nosema apis* is that so far we have been unable to recognise any causal relation between the presence of this parasite and the disease. We have found it to be present over prolonged periods in healthy stocks, while we were unable to find it in other stocks in the apiary, nor did Isle of Wight disease spread under these conditions although various races of bees were present. Deliberate infection of a stock with *Nosema* did not produce the disease. It is well established also that the disease occurs where the parasite cannot be found. We have numerous instances of this on Deeside.

From known facts regarding *Nosema* in other countries, *e.g.* in Germany and in Victoria, Australia, it appears that *Nosema apis* is just as common in healthy bees as in diseased. They are practically all "parasite carriers."

We recognise that *Nosema* may be a contributing weakening factor favouring in certain cases the development of this disease. But we have not found that it is an essential factor.

IV.—OBSERVATIONS AND EXPERIMENTS BEARING ON THE INFECTIVITY OF ISLE OF WIGHT DISEASE. AS DISTINGUISHED FROM MICROSPORIDIOSIS.

(a) ATTEMPTS TO PRODUCE ISLE OF WIGHT DISEASE BY ARTIFICIAL INFECTION.

No. 1. Tolsta Experiment. July 1914.

The stock utilised in this experiment was a small swarm of unknown race, originally imported from the South of England. It was transferred for the purpose of this experiment from the Nicolson apiary to Tolsta which is six miles from the nearest hive of bees. A control examination gave a negative result as regards *Nosema*.

On 18th July 1914, three large lots of "crawling" bees, numbering hundreds, were taken from the stock at Bayble suffering from Isle of Wight disease (see p. 46). These were beaten into a compost with honey and spread over the tops of the combs of the Tolsta bees. When the hive was visited on the 27th July everything had been cleaned up by the bees. There was no trace of the honey nor of the mashed-up bodies. The bees were multiplying and required extra combs.

On 19th August, they covered fully eleven combs and had gathered considerable stores of honey. Not a "crawler" was visible, nor even a single dead bee to be seen in front of the hive. Samples at this date were examined by Innes who reported:—"Bees alive, active. No *Nosema* spores found."

On 12th September, the bees were found to fully occupy twelve combs, and not a dead bee was to be seen. There were no indications of any kind suggestive of Isle of Wight disease.

On 17th October, one fully sealed outside comb of honey was removed leaving eleven combs loaded with honey. The bees were in excellent order.

On 7th November, the Tolsta bees were again visited. It was a fine mild day and the bees were flying freely. Several drones were observed in flight, but these were being attacked by the workers. The presence of drones so late in the season probably indicated that the queen was

failing. There was no crawling or other symptoms of Isle of Wight disease.

On 2nd January 1915, the stock was visited and found normal.

On 13th March, the stock was found lively and vigorous.

On 28th April, the bees were found numerous and lively; there was a patch of drone brood in worker cells suggesting the presence of a drone-laying queen. Probably the aged queen had died during the winter leaving eggs and young brood, from which the bees were able to raise a young queen. This queen could not be mated, however, at this season. This drone breeder was actually found on 3rd May and removed. After some difficulty a fertile queen was again established in the hive and the stock continued its prosperous career, giving, in July 1915, a natural swarm, which was lost.

On 8th August, the swarmed stock was found queenless and broodless and much reduced in numbers, but lively and vigorous, and with much stored honey. The stock was re-queened on 10th August with a young American Golden queen bred in Stornoway.

This stock, in spite of a heavy contamination with fresh Isle of Wight material, remains free from the disease to this date, January 1916.

No. 2. Shawbost. First Experiment. October 1914.

The bees which were the subject of this experiment were Carniolans, and the stock had swarmed in July 1914. It was headed, therefore, by a young queen, and occupied seven combs.

On 1st October, two ordinary match boxes of "crawlers" from an infected stock (60 DD, see p. 56) were sent to Lewis from Aberdeen. The crawlers were taken from a lot which came out in great numbers on a sunny afternoon when the "Isle of Wight" signs were most typical. They were picked up after having been out over night, and despatched by post alive, with food. These crawlers were mashed up on arrival, mixed with honey, and fed to the stock at Shawbost, on 3rd October.

On the 10th October, the bees were reported to be in fine order with brood on two combs. All infected material had been cleaned up by the bees, and not a dead bee was to be seen.

On 24th October, the local observer reported: "No sign of any disease."

On 20th February 1915, the stock on examination was found to be in good condition, and no dead were visible.

On 27th April, the stock was reported to be in fine condition, the bees were lively and "vindictive," and there was a good deal of brood.

At the beginning of June 1915, the stock was reported to be rather

weak in numbers but it built up rapidly, and on 12th August the report was as follows: "The seven original combs are now quite inadequate, and the bees have passed behind a double dummy and have built a considerable mass of new comb which is filled with honey. This is a highly prosperous stock."

On 4th September, the stock was still in excellent condition. At this date eleven months had elapsed since the Isle of Wight disease material was served up to the bees, and throughout the whole of that period the bees had been perfectly healthy, and no infection had resulted from the experiment.

No. 3. Shawbost. Second Experiment. September 1915.

On 24th August 1915, the colons and chyle-stomachs of twenty-five crawling bees were taken from front of hives No. 10 of K and the worst stock of H, Finnercy. Both stocks were very bad with Isle of Wight disease. The day was warm and sunny, and there were many hundreds of "crawlers" about in both cases. The intestines of all the bees (twenty-five in number) were drawn out, and in every case the colon was congested with pollen in a pasty condition. Most of the chyle-stomachs were purplish. These were laid out in a row and allowed to dry—and on the following day heaped together.

The above-mentioned bee-material was mixed in a little water and twelve samples examined. It consisted chiefly of pollen grains, a good many of which were digested. A few epithelial cells of the chyle-stomach in various stages of disintegration, some still showing the zymogen granules present, were seen, also some which seemed intact. None of these showed any sign of *Nosema* infection, and no free spores were observed.

Bacilli, long and short, and also cocci were seen in the preparations. This material was mixed with candy and sent to Lewis the same day, viz. 30th August. The local observer (Ewen) reported that on 4th September he fed this to Shawbost bees, and describes the bees at this date thus:—"I placed the compost on the top of the frames. The day was fine and the bees were very active. The stock in the beginning of June was very weak in numbers, but has done very well during the summer." This stock is still under observation, January 1916, and apparently healthy.

No. 4. Back Bees, Stornoway. June 1915.

In this experiment old combs and hives were used. The bees originally occupied only one of two hives, the other being left open in the hope that

any swarm might hive itself. The nearest bees to Back are at Tong, about 2 miles away, and the Tong bees have always been quite healthy.

At June 1915, the Back bees were so prosperous that they were supered. On 28th June, the super was removed and the tops of the frames smeared with a paste made by mashing diseased bees with honey. These bees were crawlers picked off the ground in front of an infected Deeside stock. The bees were sent alive from Aberdeen and pulped in Stornoway.

On 8th August the stock was visited, and it was found that the bees and the two hives had been shifted from the original site to a less suitable one in a very unskilful manner, by one who was not a bee-keeper. The bees had previously swarmed, and the swarm had occupied the vacant hive as had been expected. The combs and quilts had been disarranged, so that the swarm got a very poor chance. The jar used in infection was still on the parent stock and some comb had been built in it, but there was no trace of the Isle of Wight material.

On 14th August, both lots of bees had to be hurriedly shifted to still another site at a distance of about 400 yards, and during the process a considerable number of bees was lost. There was no brood in either hive; presumably both were headed by virgin queens. This absence of fertile queens, the two disastrous removals, and the swarming constituted a combination of factors which could not fail to weaken and discourage the bees.

On 19th June, the bees had been examined microscopically; no spores of *Nosema* were found.

On 11th September, bees from Back arrived in Aberdeen. They were active, and some of them survived until 16th. On this date live bees were examined individually for *Nosema* with negative results. The dead bees were pulped, and samples examined were also found free from *Nosema* spores.

On 20th October, bees were received which had been dispatched on the 12th, with the following report:—"Symptoms same as No. E14 in Nicolson Apiary. The stock is almost exterminated. The bees sent represent 'crawlers' and remnants in the hive."

Of these fifteen dead bees were pulped, and drops examined for *Nosema* with negative results.

On 28th October, Back was visited and both stocks were found almost extinct. A small knot of bees remained in each hive on the combs. The queen of one was warmed into activity, and lived for a few hours. There was plenty of food. The local observer (Morrison) reported that both lots had displayed the typical "crawling" symptoms.

It is worth noting that while this experiment has culminated after four months in the bees apparently contracting Isle of Wight disease, which did

not occur in other two similar experiments, it is not clear that this was due to the artificial infection. There were specially adverse circumstances in the present case. In the other two instances of attempted infection, the bees were maintained in good general external conditions. It should be noted further that *Nosema* was not found at any time during the experiment.

The foregoing experiments in artificial infection were made in Lewis upon isolated stocks. The following were carried out in Aberdeen.

No. 5. 60 DD. May 1915.

This stock, which stood in an apiary in a district suffering badly from Isle of Wight disease, was found, on 24th September 1914, to have large numbers of bees on the alighting board, and groups of "crawlers" on the grass around. The weather conditions were fine and sunny. The same thing was observed on the following day, and the hive and bees were removed to an observation area in Aberdeen. For a few days after this the stock seemed to be doing well enough and a good deal of pollen was being taken in. On fine sunny days, however, "crawling" became very evident, and on some occasions it was very extensive. As recorded elsewhere a sample of the "crawling" bees was utilised in an infection experiment (p. 53).

On 7th October, which was a fairly good day with a little sunshine, "crawling" was again in evidence, but pollen was still being gathered. About this time it was reported that three other stocks from the same apiary were suffering from the disease. All these eventually perished (p. 34).

Up to 17th October, bees "crawled" every fine day, but the last of them perished in the early winter, leaving abundance of stores in the hive.

On 19th May 1915, a fresh stock arrived from the South of England, Italian hybrids, fully covering ten combs crowded with brood. The queen had apparently been recently lost, but there were numerous queen cells on the combs. The new stock was put in the hive in which the above-mentioned stock, 60 DD, had been housed. There was no disinfection of any kind, but the dead bees and the old combs were removed. The honey was drained from some of those old combs and fed to the new stock.

On 3rd June, a swarm came off and was duly hived in a perfectly new hive on frames with full sheets of foundation. This swarm was also fed on honey drained from the old combs left by stock 60 DD.

On the afternoon of the following day a second swarm came off and was hived in a straw skep. This second swarm received none of the honey from the old combs, but was fed on a little honey bought in the open market.

Eggs were found in the parent stock (DEP) on 14th June, and the queen of the first swarm (DES 1) began to lay on the 15th.

The queen in the second swarm was long in being mated, and was balled by the bees on 28th June. A black virgin queen was introduced on the 30th June, and she began to lay in due course. The other two queens were as yellow as pure Italians, and the young bees were also light coloured.

The population of the parent stock was much depleted by the double swarming, and further, on 23rd June, foul brood was found to be present. This was a variety which attacks the larvæ before sealing, and attempts were made to treat the infected cells with dilute formalin. This treatment was successful so far in that the disease appeared to be checked, but unfortunately the queen was lost either during the manipulation, or poisoned by the formalin vapour. Queen cells were made from the brood in the hive and a black queen was produced, which ultimately began to lay. The stock was now very weak in numbers but was active in raising brood, in defending the hive against robbers, and in carrying pollen.

Up to 4th September it could not be said that there were any symptoms in the apiary of Isle of Wight disease. From the nature of the experiment here being recorded, a specially close watch was kept for indications of its appearing. Only at one period were suspicions aroused. The month of July was very wet and must have been very trying to the bees. On the 25th, a few "crawling" bees were seen in front of the parent stock and also the first swarm, as well as in front of another stock of black bees not related to the bees of the present experiment. And again, on the 31st, it is recorded that there were a few "crawlers," most in front of the first swarm (DES 1). August was also a wet month, but nothing of a suspicious nature was noticed. In spite of the very adverse circumstances above narrated, all three stocks remained perfectly healthy, and up to this date (20th September) the parent stock, which is housed in the presumably infected hive, was fed with honey from this hive, and was later given some of the original combs, is healthy and, as far as the eye can judge, growing in prosperity.

On 30th September, a lot of driven bees from which the queen had been removed was imported from North Wales and added to the little stock (DEP). The bees were fed on sugar syrup boiled with vinegar and were packed down for winter.

On 14th October, the first fine day since the addition of the Welsh bees, large numbers of bees were seen out upon the alighting board. This was probably related to robbing, which was being actively attempted at several hives in the apiary.

On the 28th December, a mild day, with a few bees offering to fly, the hive

was opened, and the quilts were found in a sodden condition owing to a defective roof. The bees, however, were in good condition with plenty of stores.

It has already been mentioned that "crawlers" were observed on two occasions in July in front of the hive occupied by the first swarm. From that date until the beginning of September there were no definite symptoms. August, like July, was mostly wet, and the Italians with their usual improvidence had converted practically the whole of their stores into brood. From 4th September onward this stock, however, now showed undoubted signs of the disease. The first half of this month was uniformly fine, with a great deal of sunshine, and on every occasion the alighting board and the grass in front was covered with numbers of "crawling" bees. Some of these were fairly active and could perform short flights but not sustained ones. Those which left the board were, as far as we could see, unable to return to the hive and crawled about, sometimes as far as twelve yards at least from the hive, ultimately dying on the ground. Those near the hive tended to form small clusters as the day advanced. The alighting board was always cleared in the course of the afternoon. All this is of course typical of Isle of Wight disease. Further, the internal appearance was that characteristic of this disease, although all our microscopical examinations failed to reveal the presence of *Nosema*. The appearance within the hive during these days was practically normal, pollen was being carried in, and there were no indications that the disease was making rapid progress. From 4th September sugar syrup was supplied to all the stocks, and this was freely appropriated by the bees and stored.

The question naturally arises here, Had this outbreak any connection with the proximity of the infected hive or the fact that this swarm came from it? In view of the prosperity of the parent stock which had continuously occupied the hive for four months, and the length of time, viz. three months, since the swarm constituting this stock left the hive, it does not seem likely. But we must admit the possibility of infection having been transferred and remaining latent until conditions favourable for its development within the bees had arisen.

No further "crawling" symptoms have been observed since the beginning of October. On 20th October, a large lot of Welsh bees (driven, queenless) was added to this stock. It is probable that these killed the queen, for on 1st November several dead yellow queens were found on the floor of the hive, and there were queen cells on one of the combs. No free virgin queen was observed, and another queen was caged over the stock. This queen was found on the alighting board a few days later. This stock, therefore, has a virgin queen (grand-daughter of the original English queen).

The second swarm, standing alongside the first, has never displayed any symptoms of the disease.

(b) NATURAL OCCUPATION OF ISLE OF WIGHT AFFECTED SITE.

The Hive and its Contents as Possible Sources of Infection.

The following case is related to the foregoing experiment in respect that it is a naturally occurring instance in which the same factors, viz. hive and combs of an extinct Isle of Wight diseased stock, are involved.

Bees which occupied a frame hive began to exhibit "crawling" and other symptoms of Isle of Wight disease in the autumn of 1913, and the last survivors perished in the spring of 1914. The hive was not disinfected nor the honey and dead bees removed, but the door was closed. In June 1914, a vagrant swarm alighted beside the hive and was allowed to enter. No particular attention was paid to them, for it was not expected they would survive. But it was observed that the new-comers were very diligent in removing the dead bees and getting the hive in order. The bees wintered in good order, and in May 1915 they swarmed. This top swarm was unfortunately lost, though followed for some distance, but a second swarm on 7th June was duly hived in a skep and placed alongside the parent stock. Both stocks were visited and examined for eggs on 12th, 15th, and 21st June, but none was observed. Up till this time both stocks appeared perfectly healthy and were working normally, except that the parent stock had only a small number of bees, and drones were unusually numerous. Thus it will be seen that in the case of the parent stock a full year had elapsed since the bees took possession of a hive and combs with a recent history of Isle of Wight disease.

On the 26th of June "crawling" symptoms were developed in the bees of the swarm, and these were very marked when the stocks were visited on 28th June. The garden in front of the skep for a considerable distance was covered with crawling bees, with characteristic grouping very noticeable. The internal appearance of the crawling bees was quite characteristic of Isle of Wight disease, and we satisfied ourselves that this disease was present. It should be added here that both in 1914 and 1915 the whole surrounding district had been swept by the disease, and there were very few stocks surviving in it. Examination of the combs showed that both queens were laying, and there was a good deal of sealed brood in the skep.

The crawling symptoms above noted became less noticeable from day to day. There were, however, fluctuations, till on 23rd August both stock and

swarm appeared to be free of the disease and were working normally. The skep being overcrowded had been provided with an "eke." On the 11th September, both stocks were found apparently in perfect health. The bees in the skep had extended their combs down into the eke.

All this time there had been no symptoms of Isle of Wight disease in the parent stock.

On 6th October, the parent stock in the bar-frame hive was found rather weak in numbers, and the bees in the skep were driven and united with it. The queen of the skep was removed and introduced to a stock in Desswood apiary. The combs of the skep were cut out and piled over the frames in the wooden hive.

On 29th December, the bottom of the hive was found to be thickly covered with dead bees, but there were bees still alive amongst the piled combs just under the quilt.

It may be noted that to date bees have been living in this hive on the old "Isle of Wight" combs for over 18 months without any symptoms of the disease appearing, and the conclusion is legitimate that the appearance of Isle of Wight disease in the swarm is to be traced to a separate source.

There has also come under our observation the case of a bee-keeper near Perth, who had lost several stocks from the disease, but had several remaining which were apparently in excellent condition, although he had fed them on the stores left by the diseased stocks. One in particular, through an accident, had been soaked with water during last winter (1914-15), and by spring the bees had been reduced to a handful. We examined this stock in October 1915, and found it in fine condition. The bees were black, but the owner declared they were Italians because they had had an Italian queen three years previously. Some of the surviving stocks displayed yellow bands, and the bee-keeper attributed their resistance to the admixture of Italian blood.

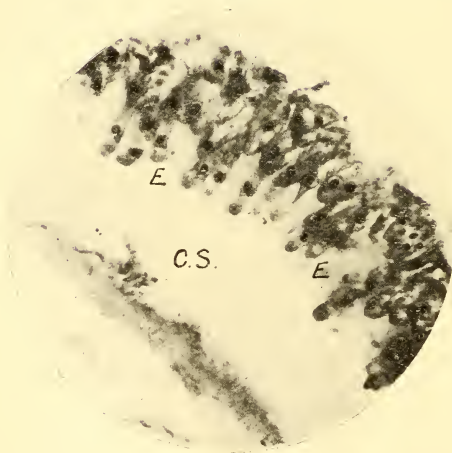
Of direct interest in connection with our failure to produce Isle of Wight disease by means of presumably infected hives and combs is the experience of Beuhne, of Victoria, as given in *The Australian Bee-keeper*, 15th August 1915. He says: "When a very heavy mortality occurred amongst the bees in the Grampians in 1909-10, and microscopic examination showed the parasite in the bees of the apiaries concerned, the question arose whether bee-keepers should follow the directions of the British Board of Agriculture, and destroy all the remaining bees as well as all the combs, or give the survivors a chance, and take a risk with the combs of the defunct colonies.

"My personal experience with this kind of mortality was in 1900-01, when

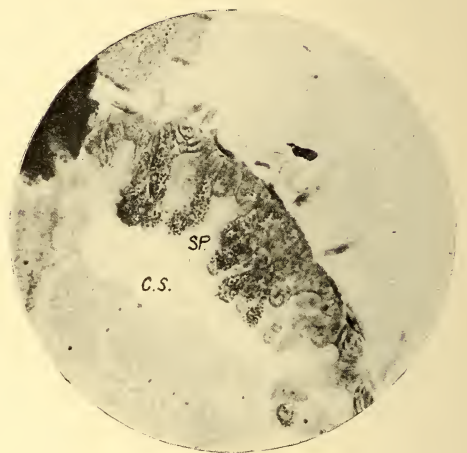


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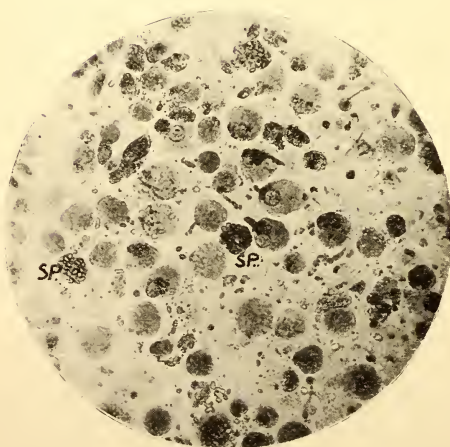
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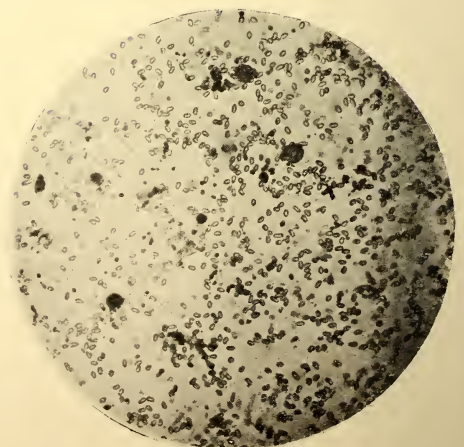
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3



4



nothing was known of *Nosema*, and therefore I was unaware of any risk, and used the combs from which the bees had disappeared, when restocking the apiary with purchased bees, and 'nothing happened.'

Beuhne is of opinion that "under ordinary conditions, that is, conditions favourable to bees, the parasite is merely a casual inhabitant of the intestine of the bee."

GENERAL CONCLUSION REGARDING INFECTIVITY.

The general conclusion to which the foregoing facts point is that Isle of Wight disease, although probably an infectious disease, is one which requires the coincidence of other and presently unknown external factors (besides a specific organism) before the disease develops. The disease is not necessarily conveyed by mere contact with contaminated hives or combs, or by feeding upon contaminated stores.

EXPLANATION OF PLATE.

- FIG. 1. Section of the chyle-stomach of a bee displaying symptoms of Isle of Wight disease. Spores of *Nosema* are not present, and no young forms were found in this outbreak. $\times 180$ (Iron-hæmatoxylin).
- FIG. 2. Section of the chyle-stomach of a bee infected with *Nosema*, but not suffering from Isle of Wight disease. The stained spore contents came out as black dots in the photograph. $\times 180$ (Iron-hæmatoxylin).
- FIG. 3. Portion of the teased chyle-stomach of a bee, showing detached cells, some containing spores of *Nosema*. Fresh preparation. $\times 180$.
- FIG. 4. Fresh unstained preparation, showing *Nosema* spores lying free in the gut. $\times 180$.
- FIG. 5. This shows the behaviour of a stock (E14) suffering from Isle of Wight disease. Note the bees, incapable of flight, clustering on the hive front. Large numbers on the grass cannot be seen, but some can be observed climbing up the leg of the hive.

- c.s.* Chyle-stomach of bee.
e. Epithelium lining chyle-stomach.
sp. Spores and epithelium of chyle-stomach.

(Issued separately, 14th September 1916.)

V.—Note on *Trypanophis grobbeni*, a Protozoan Parasite of Siphonophora. By J. F. M. Floyd, M.A., University of Glasgow.

(With Plate.)

(Read 27th March 1916. MS. received 27th March 1916.)

THE material for the following notes was collected during the summer of 1912, whilst the writer occupied the Oxford Table at the Zoological Station, Naples.

In June the colonies of the siphonophore *Halistemma tergestinum* were richly infected with *Trypanophis*, which, as Keysselitz records,¹ are found throughout the gastro-vascular system of the infected colony—the active parasites can easily be seen in situ with the aid of a dissecting lens ($\times 20$).

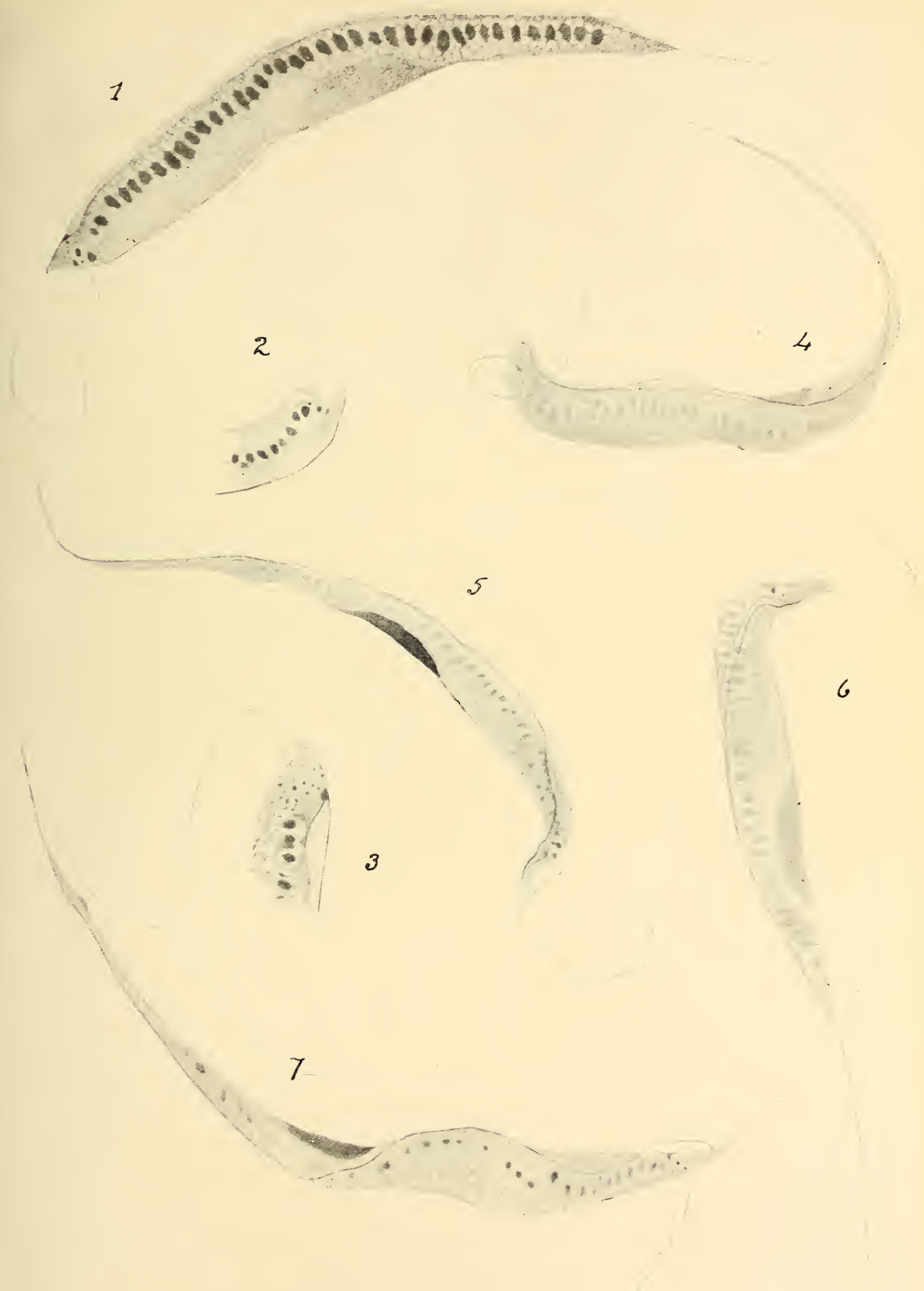
Examination of the contents of the coelentera of *Velella* gave negative results.

Film preparations of *Trypanophis* cannot readily be made because of the difficulty of ensuring that the animals adhere to the glass. Pieces of the Siphonophore were squeezed on to coverslips previously smeared with egg-albumen and these allowed almost to dry; by this means a certain number could be retained, but a large proportion were always washed off during fixation.

The smears were fixed in strong Flemming's Solution, bleached with hydrogen peroxide and stained in Mayer's hæmalum followed by a trace of eosin, or else in iron-hæmatoxylin. The process of partial drying causes the *Trypanophis* to appear broader and more flattened than is natural, and in their struggles individuals are liable to assume rather distorted shapes—but in life, although extremely active, they undergo little or no change of form, differing altogether in this respect from *Trypanoplasma*.

None of my preparations shows a differentiation within the nucleus ("trophonucleus") of a karyosome, like that figured by Keysselitz. In some there is a large clear space like a vacuole, and the nuclear substance is more deeply stained round its edges—possibly an artefact. A more finely alveolar structure than that of the surrounding cytoplasm is all that can be defined.

¹ *Arch. f. Protistenk.*, iii., 1904



J. F. M. del.

TRYPANOPHIS GROBBENI.

Figs. 1-6, \times approximately 1600; Fig. 7, \times 1800.

The nucleus stains bluish in hæmalum and eosin—grey in iron-hæmatoxylin. The position of the nucleus is constant, its shape more or less so. One side is always formed by the side of the body opposite to the undulating membrane. Its inner boundary is not very sharply defined from the coarser cytoplasm.

Keysselitz has figured a substantial kintonucleus from which the two flagella spring directly. No such body is visible in my preparations. The free flagellum springs from a more or less distinct basal granule, in the position shown in the figures. Close to this granule, in most of the figures, can be seen a deeply stained body, to which may perhaps be applied the name of kintonucleus. This body, when distinguishable, is surrounded by a halo of clear cytoplasm. It must be confessed that in many cases nothing so definite as the above can be made out owing to the confusion of a number of small darkly stained granules in this region—as *e.g.*, in Plate II. fig. 3.¹

The attached flagellum originates from the edge of the body at a point either on a level with the basal granule of the free flagellum or a little in advance of it.

The base of the narrow undulating membrane is sometimes marked, as in Keysselitz's figures, by a distinct line throughout its length (see Figs. 4 and 6). Especially may this be the case in hæmalum and eosin preparations in which the anterior end of this basal line may be quite intensely stained. Just before the basal line joins the flagellum there is a widening of the space between them, and, in consequence, the basal line dips inwards. The point of union may be marked, as in Figs. 1 and 3, by a darkly stained thickening or granule, but in Fig. 2 and in the hæmalum preparations this cannot be seen.

The "chromatic bodies" are embedded in a row; their arrangement and relation to the cytoplasm are best shown in Fig. 1. The foremost of them may be just behind the "kintonucleus," when visible, or there may be one or two in advance of it as in Figs. 1 and 2.

They take up eosin very readily and stain intensely in iron-hæmatoxylin.

Keysselitz figures a second partial row of smaller "chromatic bodies" in the anterior half of the body. The only trace of this I have been able to find is a tendency among the more anterior bodies of some specimens to duplicity—partial as in Fig. 4 or complete as in Fig. 5.

As to the clear zone about the kintonucleus, a similar condition of

¹ Figs. 1-6, \times approximately 1600; Fig. 7, \times 1800.

individual "chromatic bodies" may be seen in Figs. 2 and 3, and may be due to a shrinkage of the surrounding cytoplasm. The process of drying tends to stretch the walls of the cytoplasmic alveoli, giving an exaggerated appearance of coarseness.

In conclusion, I wish to express my indebtedness to the late Mr C. H. G. Martin who first directed my attention to *Halistemma*, and to Mr J. S. Dunkerly for advice and help during the progress of my work.

(Issued separately, 14th September 1916.)

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NATURAL HISTORY.
SESSIONS 1915-1916 AND 1916-1917.

PART 2.

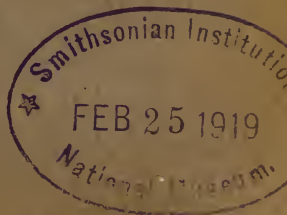
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MARCH 1917.

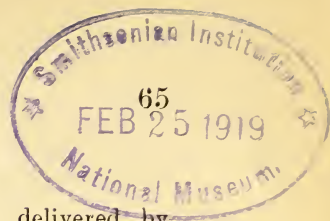


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The Utility of the Useless.



VI.—The Utility of the Useless. Presidential Address delivered by Principal O. Charnock Bradley, M.D., D.Sc., F.R.S.E., on 22nd November 1915.

FOR several reasons it is a profitable exercise to trace back a modern invention, or commercial appliance, to the fundamental discoveries from which it sprang. In the first place, the debt of commerce to pure science is thus demonstrated; for it is safe to say that none of the numerous inventions and devices which are of such immense commercial importance in the present day could have come into existence had it not been preceded by one, or possibly many, discoveries arising out of research pursued in a purely academic spirit. But, as being of far more importance from the point of view of the ardent beginner in scientific research, the tracing of the germinal discoveries upon which an invention is based is of value as showing how all academic research, remote though it may appear from the service of mankind, may contain within it the germ from which is to develop an influence capable of tincturing the whole fabric of a nation's existence. A moving pebble may start an avalanche. . . .

Moreover, the history of scientific discoveries serves to remind us of those complex factors underlying our daily life and the research, remote or recent, from which they have originated. The detailed processes of every day are so familiar that few spare the time to remember that upon scientific discovery depend all the contrivances and appliances which make modern life what it is. Indeed, one is tempted to pen the paradox that it is of the most familiar we have least knowledge. In contemplating the lordly oak, or in enjoying its shade, we forget its origin; and, assuredly, the timber-merchant wastes no thought on the acorn.

An interesting chapter in the history of science could be written on the opposition against which discoveries of fundamental importance and ultimate great commercial value have had to fight for general approval and acceptance. Galileo's telescope, the Darwinian hypothesis, the clinical thermometer, anæsthetics, and a host of other revolutionising introductions have been opposed with a greater or lesser degree of acerbity. In the light of its modern development, it is scarcely conceivable that the electric telegraph was neglected for years until its possibilities were foreshadowed in a dramatic fashion in connection with the arrest of a murderer. On the introduction of the electric telegraph, the "practical man" would have none of it, and yet in the short space of about half a century, the telegraph, and its younger relative the telephone, have completely revolutionised every-day, commercial and national life. However great their value may be in times of peace, in

time of war it is infinitely greater. Regard for a moment the influence exerted by the wireless form of telegraphy on

“This precious stone set in a silver sea,
Which serves it in the office of a wall,”

and something of the power of applied science, the offspring of pure science, becomes apparent. No text could better serve for a thesis on the small and neglected scientific beginnings of great things.

Search for the reason for resistance to new ideas and new speculations is not without interest to the biologist and sociologist. The first reason which suggests itself is that matter-of-fact, rule-of-thumb people are always in the majority, and, therefore, anything out of the ordinary is bound to meet with opposition in excess of approval. Or we might agree with George Eliot in saying that the practical mind and the narrow imagination go together, and with H. G. Wells in asserting that few have been accustomed to respond to the call of a creative imagination. There are few—and these not men of action—who are capable of looking forward into the future. We might also point to the fact that the pursuit of knowledge does not follow a straight line. It zig-zags hither and thither, frequently halts, and indeed often has to hark back. Such erratic progress cannot make a very urgent appeal to the practical mind.

But these explanations are probably not entirely just to that necessary member of the community, the “practical man.” It must always be remembered that only those of the future shall see the present—see it steadily and see it whole. The ultimate goal of a scientific discovery is hidden from those who were present at its birth. Moreover, a truth new-wrested from nature seldom carries with it an indication of future possibilities. In most cases, and especially if it is a germinal truth, it possesses few attractive features to the eye of him who seeks for signs of future utility. “Truth new-born looks a mis-shapen and untimely birth.”

In all probability what the sociologist has come to call the “Herd Instinct” is an important factor in producing resistance to the reception of the new and unusual. The “Herd Instinct” may be briefly explained as follows:—Man being a gregarious animal and leading the communal life, it is essential that his actions should be co-operative. The homogeneity necessary for co-operative action results from an inherent impulse on the part of each individual to think and act in conformity with the thought and action of his fellows. There seems good reason for concluding that homogeneity is the result of natural selection. There appears to have been an accumulation of experiences which, unconsciously so far as the individual is concerned,

have demonstrated the necessity for following custom if the safety of the community or herd is to be ensured.

Admitting the operation of the "Herd Instinct," it is not difficult to appreciate the reason of that opposition to innovation which is so well and so frequently illustrated in the history of scientific discovery. For our present purpose, however, it is not so much necessary to explain the cause of opposition as to recognise its reality. Realisation of its occurrence and effect in the past renders more easily borne its encounter in the present.

No department of science contains more mysteries for the layman than does electricity. And no department of physical science contains more striking examples of pure academic research paving the way for the introduction of enormously important instruments of applied science.

The discovery of the deflection of a magnet by the passage of an electric current along a wire in its vicinity—a discovery which, as Faraday expressed it, "burst open the gates of a domain in science, dark till now, and filled it with a flood of light"—could not have been made had not Volta devised the means whereby a constant and steady current could be produced. Nor, without the same means, could François Arago have discovered that a bar of iron becomes a magnet when surrounded by a coil of wire through which an electric current is flowing.

If Volta's investigations made possible research capable of revealing the industrial applicability of electricity, it may be claimed that Volta, in his turn, was indebted to the old frictional machine for a basis upon which to found his inquiries. Tracing the chain of research still further back, all the earlier discoveries depended upon an observation made by William Gilbert, of Colchester, one of the lesser sons of the Renaissance. If it is true to say that none of these inquiries was made in the utilitarian spirit, it is equally true to assert that Faraday's discovery of magneto-electric induction was the product of research undertaken from purely academic motives. When Faraday's sacrifices to science are remembered, it is not difficult to realise that his work was not stimulated by a desire for personal profit. That mankind in general has profited, and that the wealth of nations has been augmented, is abundantly evident.

When Sir Anthony Carlisle and Mr Nicholson made their extemporised Voltaic pile, and observed the decomposition of water by the current produced, they could not possibly have foreseen that by their speculative laboratory experiments they were laying the foundation of those enormous commercial industries which depend upon electrolysis. Much less is it conceivable that an enthusiastic youth of eighteen, endeavouring to make artificial quinine by the oxidation of aniline, could have foreseen that his accidental discovery

would lead to the utilisation of what was formerly a wholly disagreeable nuisance in the shape of coal-tar, and thereby form the germ of the now more than ever famous aniline dyes industry.

Fascinating though it is to follow the fortunes of small discoveries in the physical sciences and see how they ultimately develop into great instruments of human service, it is if anything even more fascinating to trace the history of small discoveries in the biological sciences. And this is so, no doubt, because the contact of biology with daily existence is not so obvious and self-assertive as is that of physics or chemistry; consequently the ramifications of influence of biological research are more subtle, but none the less real.

Modern medicine—using the term to include surgery—it is safe to say, is that phase of biological science which has the most obvious effect upon daily human existence. Examined closely, it is clear that modern medicine is based upon a multiplicity of scientific discoveries; some of them of outstanding magnitude, many of them of minor consequence.

Fed upon descriptions of marvellous operations served up by a sensational press, the layman is not slow to admit the wonders of modern surgery. Wonderful though the surgical stories of the lay-press may be, they are not really more marvellous than many of those stated in the cool, calculated and technical language of the medical and surgical periodicals. Regard for a moment an operation recently described by an Army surgeon. "Somewhere in France" a soldier was shot. The bullet was located in the cavity of the left ventricle of the heart, and removed therefrom by operation. This feat was rendered possible by a long series of discoveries leading away back into regions far from the utilitarian. The determination of the position of the bullet depended upon the studies of Sir William Crookes on high vacua—a thing of yesterday—combined with the discovery of cathode-rays about two hundred years ago. The operation was rendered free from danger of sepsis by the development of the "Germ Theory"—now so familiar that we have almost forgotten that it originally bore this name—which reposed upon a long line of arduous research including Pasteur's inquiries into fermentation and, still more remotely, the peculiarities of tartrate crystals. These and many more academic inquiries placed the surgeon in possession of the means to perform an operation which, not many years ago, would have been regarded as daring in the extreme.

Frankly, this particular operation was chosen as an example of the triumphs of modern surgery because it was both sensational and topical. But equally wonderful work is done daily and far distant from the grim romance of the battle-field.

Instances of the application of scientific discovery to every-day problems

and every-day needs might be multiplied almost without limit. But the foregoing must suffice to justify the contention that the fruits of academic research are not difficult to find in the appliances and contrivances which make the day's work what it is, and that the commercial wealth and prosperity of the world is in no small measure dependent upon discoveries of seemingly small and trifling moment and nearly always of little utilitarian complexion. He who wishes to demonstrate to the man of commerce that it is in his own interest to encourage and aid the man of science, need experience no difficulty in adducing facts in support of his argument. It is easily possible to prove the benefits that accrue to commercial undertakings out of the employment of a scientific staff. The proof is perhaps not so necessary now as it was not many years ago ; but the necessity still exists, though in a modified degree.

But, while science is of service to commerce, the entire subjection of science to commerce, or the requirements of the State, would not be productive of entirely good results. The bending of research to purely utilitarian ends would be fraught with grave danger in several directions, and not least in that it would discourage investigations instigated by a thirst for knowledge for its own sake—investigations which history has shown may develop into discoveries of surpassing moment.

After all, the business of the scientist is to discover truth regardless of possible monetary profit either to himself or to humanity at large. Let the inventor use the knowledge if he cares and can. "Your business, your especial business," said Pasteur once to his students, "must be, to have nothing in common with those narrow minds which despise everything in science which has no immediate application." And Pasteur, apart from the inestimable work he did leading to modern surgery, taught the vinegar makers of Orleans how to increase their output, instructed France how to prevent the souring of her wines, and helped the brewers of London by instructing them concerning the importance of the purity of their yeast.

VII.—Some Points in the Cytology of the later Spermatogonial and First Meiotic Nuclei of *Fasciola hepatica* (*Distomum hepaticum*). By Monica Taylor, S.N.D., B.Sc.

(Read 27th March 1916. MS. received 27th March 1916.)

(With Plates.)

It has been occasionally urged by cytologists that a pairing of chromosomes takes place in the latter half of the last spermatogonial division (Montgomery, Sutton, Stevens, Dublin) (3, 2), but literature dealing with the full history of the nuclear changes that take place in the interval that elapses between the last spermatogonial anaphase, and the spermatocyte I. prophase, is very scanty. In work, the completion of which has been interrupted by the war, Dr Agar found, that in *Lepidosiren*, the thirty-eight chromosomes of the last spermatogonial metaphase apparently pair into nineteen in the telophase. The spermatocyte I. resting nucleus in *Lepidosiren* is therefore constituted out of nineteen paired chromosomes which reappear as the nineteen pairs of leptotene threads in the beginning of the first meiotic prophase. As the seriation of the nuclei at this point is rather difficult in *Lepidosiren*, Dr Agar asked me to examine this stage of the premeiotic processes in *Fasciola hepatica*, since for any study of this sort it is necessary to have some very definite criterion for distinguishing the different generations of spermatogonia—Mäx Dingler, in a paper entitled “Über die Spermatogenese des *Dicrocoelium lanceatum* (*Distomum lanceolatum*)” (1), had demonstrated topographical relations which, if true for the genus, would make *Fasciola hepatica* very useful in this respect. In older specimens of *Dicrocoelium* (*Distomum lanceolatum*) the walls of the gonad, which is a much branched tubular organ, contain spermatogonial elements only. The cells containing “maturation” nuclei lie in the cavity of the gonad. This arrangement has been brought about as follows:—One spermatogonial nucleus gives rise by successive divisions to a group of eight nuclei. These eight nuclei then prepare for the first meiotic division and give rise to a group of sixteen nuclei. These sixteen in turn produce a group of thirty-two spermatid nuclei which eventually become the nuclei of the long thread-like spermatozoa. It is at the eight-nuclei stage that the group of cells loses its connection with the walls of the gonad and passes into the central cavity, there to undergo its subsequent conversion into thirty-two spermatozoa. Hence, by shaking out the contents of the gonad tubes, only cells undergoing the maturation divisions escape, and by examining the number of cells in the group the “spermatogenic position” of the nucleus can easily be determined. And on

account of their being grouped into masses of two, four and eight respectively, the two last spermatogonial divisions can be detected with a fair degree of certainty.

No account of the events between the last spermatogonial anaphase and the meiotic prophase is given for *Dicrocoelium*, nor is the earlier spermatogonial telophase described at length.

The oogenesis of *Fasciola hepatica* has been worked out by Adolf Schellenberg (4) who gives twelve and six as the somatic and reduced number of chromosomes respectively. Schubmann (5) gives eight as the somatic number.

MATERIAL AND METHODS.

The liver-flukes were obtained from infected sheep livers procured at a slaughter-house by Mr P. Jamieson. I should like to take this opportunity of thanking Professor Graham Kerr for the ever open hospitality offered in his laboratory to occasional visitors, and for the use of those requisites not possessed by the Notre Dame college laboratory.

To Dr Agar also, who, just before leaving for the battle-front, very kindly read through the first draught of this manuscript, my thanks are offered.

The eggs of the liver-flukes were incubated and then transferred to the fixative at regular intervals—the flukes were taken from the bile duct of the sheep, and placed either straight into the fixative or from warmed physiological salt solution into the fixative. Small portions containing gonad, as well as whole specimens, were then preserved. The fixatives employed were Flemming (strong solution), chloroform-acetic-sublimate, corrosive-acetic, corrosive alcohol, the fluids of Bouin, Zenker, Gilson-Petrunkewitsch and Hermann. The value of the various fixatives is discussed later.

Sections from 7μ to 10μ thick were examined first—this thickness facilitating the examination of all nuclei in an uncut condition. But in these preparations the whole “group” (Pl. IV. fig. 22) was not always included in one section, and in order to be absolutely certain of its content it was necessary to investigate either the succeeding or the preceding section or both. To obviate this difficulty and to insure absolute accuracy the thickness of the later preparations was increased so as to include the whole group, whether of eight, sixteen or thirty-two cells, in one single section. This was effected by making the sections about 15μ thick. The range was therefore from 7μ to 15μ .

The testis of *Fasciola hepatica* is too well known to require description. Examination of slides showed that the topographical relations of the cells and “groups” described for *Dicrocoelium lanceatum* are present also in this species. The spermatogonial nuclei are entirely confined to the periphery—the central lumen is filled with groups of eight, sixteen and thirty-two cells

and bundles of thread-like spermatozoa as well as the characteristic bodies (Restkörper) from which the spermatozoa have escaped. The "groups" are often rosette-like in appearance, five cells in one focus and three in another being a common arrangement of the eight-nuclei stage. Sometimes, however, the eight cells all lie in one plane (Pls. III. and IV. figs. 15, 22). The nuclei in a group are at about the same phase of development.

With three or four exceptions where a large number of sections was cut only a few slides from one specimen were prepared for examination.

The enormous number of gonad tubes, and their large size, combined with the smallness of the nuclear elements makes the inspection of one single section a somewhat lengthy process.

There is a very marked difference in the appearance of the nuclei in the different specimens which at first might be attributed to the different effects of the various fixatives, but which was eventually proved to be due to the fact that the nuclei were at different stages of development (Flemming fixation, however, does make the nuclear elements larger, while at the same time it does not preserve the morula-like arrangement as firmly as do the other fixatives). Thus in all the sections cut from one given specimen the majority of the nuclei were in the resting condition—there being comparatively few prophases. In others again, by far the greater number were in the early prophase condition. In others yet again, telophases were most plentiful, while in quite a large number of the sections a sort of intermediate condition between late telophase and resting nucleus was characteristic. Whether all the different stages could be obtained from one individual specimen by sectioning the whole gonad has not been determined—the large size of the gonad precluding such a lengthy operation.

This fact having been ascertained it became necessary to link up in sequence the different stages. By choosing unmistakable prophases or telophases and working backwards and forwards this was not a difficult matter—especially, as already stated, belated or precocious specimens could always be found interspersed among their more uniformly developing neighbours. This abundant supply of nuclei at about the same stage of development, while entailing the preparation and study of a very large amount of material, is advantageous for securing the finer gradations of change.

SPERMATOGONIAL DIVISIONS.

The spermatogonial cells differ very much in size, the larger younger ones being nearest the walls of the gonad, the smaller older ones being nearest the central lumen.

The resting nucleus (Pl. III. fig. 1) is a more or less uniformly pale staining

body, there being no crisp distinction between the chromatin and the rest of the nucleus. One or two plasmosomes may be present. As preparation for prophase begins the chromatin condenses out into a network of fine threads which anastomose in all directions, the nucleus meantime becoming larger (Pl. III. fig. 2).

N.B.—In a rapidly developing tissue such as is presented in the gonad of *Fasciola* there is, practically speaking, no true resting nucleus stage. In the present account the term resting nucleus is merely used to designate one of the many stages occurring between the more obvious telophases and prophases.

In *Fasciola* very early prophases can always be distinguished from late telophases by the purity of the colour assumed by the chromatin. The chromatin has a fresh-looking appearance which contrasts with the somewhat muddy colour it assumes in the older phases.

It is impossible to count the prophase threads at this stage (Fig. 2). Finally the threads thicken, shorten, and lie under the nuclear membrane, which, as is usual, is very much distended by the increasing volume of nuclear sap (Figs. 3-5). It is difficult to show twenty-four of these chromosomes in a drawing of a single prophase, but in most cases it is possible to count them. There is a difference in size, some being longer than others, but they are characteristically somatic-like, *i.e.* are simple, short, rod-like bodies—the rings, crosses, etc., of the meiotic prophases being absent. As prophase merges into metaphase (Pl. III. fig. 6) the chromosomes become aggregated towards the centre of the cell, finally becoming so massed together that it is quite impossible to count them. In this respect the spermatogonial metaphase is very different from that of the spermatocyte I. in which the twelve bivalent chromosomes stand out in diagrammatic clearness (Fig. 34).

As an instance of this tendency to dense massing in metaphase, in many studies of equatorial plates of the last two spermatogonial divisions, no more than from twelve to fifteen chromosomes could be counted, and this in sections where the Flemming fixation was exceptionally good. This fact may probably account for the discrepancy in the number assigned by different workers on *Fasciola* (*Distomum*) as the somatic number of chromosomes.

In metaphase the shape of the cell begins to change, and a longitudinal splitting of chromosomes can sometimes be witnessed. In anaphase the chromosomes separate off to either side, but the chromatin mass is again too dense for counting chromosomes (Pl. III. fig. 7). The spindle apparatus is exceedingly ill defined—the two daughter masses forming a cap for either end of the mother cell. When they separate, the newly-formed nuclei of the daughter cells, on account of this cap-like arrangement, might easily be

mistaken for synizetic nuclei (Fig. 8). Judging by the frequency of the occurrence of this stage, as well in the meiotic telophases as in the spermatogonial, it seems probable that the nuclei remain some time in this synizetic-like condition. Eventually from the black cap-like mass thick finger-like processes appear and grow out towards the opposite pole of the nucleus. It is significant to note that these finger-like processes are never more than twelve in number (Figs. 9, 10). Finally the chromatin is distributed throughout the nucleus (Figs. 11, 12) and loses its staining capacity; a plasmosome appears, and the resting nucleus results (Fig. 1). It is interesting to note, however, that optical sections of nuclei in this intervening stage between the synizetic telophase and the resting, frequently show twelve peripheral patches of chromatin—with varying capacity for stain (Fig. 12). Thus it would seem that even in the early spermatogonial generations there is a tendency for the twenty-four chromosomes to undergo some short pairing while they are in late telophase, since, as has been shown, never more than twelve radiating processes emerge from the telophasic mass. Later on it will be seen that this same tendency is also exhibited by the somatic nuclei.

The Telophase of the last Spermatogonial Division, because of its importance, and because the pairing of the chromosomes is more pronounced, is described in detail.

The last generation of spermatogonial cells can be recognised easily, because they are arranged in groups of eight. A black, dense cap of chromatin indicates an early stage of the telophase (Figs. 13–15).

As development proceeds this cap gradually enlarges and finger-like protrusions make their appearance (Fig. 16). Sometimes these protrusions are vacuolated, sometimes not. As the radiating processes lengthen out at the expense of the central mass the number of those which can be counted increases, but it is never more than twelve (Figs. 17–19). Finally these twelve masses are arranged very symmetrically around a gradually appearing plasmosome.

Frequently, too, while one pole of the nucleus shows twelve radiating masses the other pole already shows the characteristics of the resting nucleus.

The staining capacity of the chromosomic protrusions now begins to change—but locally—so that at this stage the nucleus has a coarsely dotted appearance due to those parts of the chromatin which have lost their capacity for stain (Fig. 20). Eventually even the local colouring disappears and the resting nucleus is the result (Figs. 21, 22).

From the foregoing account, therefore, it would seem that, since there are twenty-four chromosomes in prophase, and since never more than twelve chromosomes emerge from the telophasic masses of the



1



2



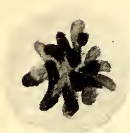
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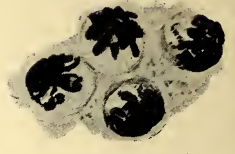
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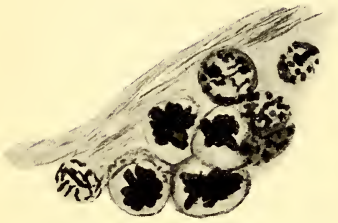
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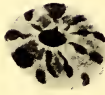
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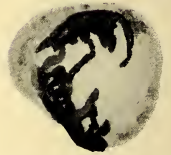
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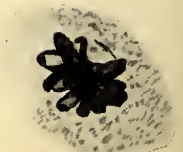
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16



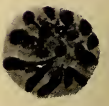
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19



20

last spermatogonial divisions, a conjugation of chromosomes takes place in the telophase, and that twelve fused pairs of chromosomes go to form the resting nucleus of the spermatocyte I. cells.

Before the resting nucleus stage is reached the mass of eight cells has lost its connection with the wall, and lies in the cavity of the gonad.

PREPARATION FOR FIRST MEIOTIC DIVISION.

Signs of approaching division are to be found in the gradually increasing size of the nucleus. The chromatin becomes more distinct and retentive of stain, and more abundant, round the plasmosome (Fig. 23). In the rest of the nucleus it is present in little beads which do not stain so deeply as the blocks round about the plasmosome.

The beads then form leptotene threads, but these are imperfect at this stage.

Almost simultaneously with their appearance a parallel conjugation of the earliest formed threads begins, so that it is difficult to obtain zygotene views which show twelve pairs of univalent chromosomes. It is possible in one nucleus to see a certain number of conjugating chromosomes, while at another focus the same nucleus has all the appearance of one that has just emerged from the resting condition. Hence while the cumulative evidence obtained from a study of many spermatocyte I. nuclei leaves little doubt that a parallel conjugation of the chromosomes takes place, the material is not productive of diagrammatic figures. The pachytene stage is very common (Fig. 24), twelve completely fused bivalents being of frequent occurrence (Fig. 25).

The chromosomes then seem to lose their staining capacity and to assume a beaded appearance (Figs. 26, 27), indications of their bivalent character being sometimes evident. Synizesis occurs at about this stage. The chromosomes escaping from the synizetic mass are sometimes pale staining and somewhat beaded in character (Fig. 29), sometimes, however, they have begun to thicken and shorten preparatory to the onset of late prophase (Fig. 30).

The strepsitene stage finishes simultaneously with the loosening of the definitive chromosomes from the synizetic mass (Fig. 30), the bivalent rings, crosses, loops, to the number of twelve, being the result (Figs. 31-33).

In the metaphase of the first maturation division a great contraction of the chromosomes takes place. A well-formed spindle with centrosomes is present—equatorial plates giving counts of twelve chromosomes (Figs. 34, 35). The univalents then separate off to the daughter cells, and two nuclei of spermatocyte II. value result. The remaining history of spermatogenesis of *Fasciola* resembles very closely that described for *Dicrocoelium*.

SOMATIC MITOSIS.

Dividing somatic nuclei, though rare, can be found in muscle and gland cells. An attempt to obtain an abundant supply of mitotic figures by cutting sections of developing eggs was not very successful. The small size of the nuclei and the large amount of yolk globules, coupled with the technical difficulties of sectioning eggs with thick chitinous coats, rendered the results unsafe as regards reliable cytological detail.

In the prophase (Fig. 36) it is possible to count twenty-four chromosomes, some of which are exceedingly small. The same massing of the chromosomes towards the centre of the cell, already described, succeeds the disappearance of the nuclear membrane. A perfectly typical spindle is organised (Fig. 37), the spindle fibres being best fixed in Gilson-Petrunkewitsch. The late telophase (Fig. 38) reveals the same tendency of the chromosomes to pair as was seen in the spermatogonial telophases, *i.e.* not more than twelve radiating processes emerge from the telophasic mass.

SUMMARY.

1. The number of chromosomes in *Fasciola hepatica* is twenty-four in the diploid and twelve in the haploid number.
2. Cells which have undergone the penultimate spermatogonial division are grouped in masses of four.
3. In late telophase of the penultimate spermatogonial division indications of a pairing of chromosomes can be detected.
4. Cells which have undergone the last spermatogonial division are grouped in masses of eight.
5. In telophase of the last spermatogonial division the twenty-four chromosomes pair into twelve.
6. In the late telophase of the somatic mitoses there is a tendency of the chromosomes to emerge in pairs from the telophasic chromatin mass.

EXPLANATION OF PLATES III. AND IV.

All figures, except 9, 10, 15, 22, were drawn with the Abbé camera under Leitz $\frac{1}{2}$ oil-immersion objective, and Zeiss compensating ocular 12, giving a magnification as reproduced of 2200 diameters.

Figs. 9, 10, 15, 22 are drawn to a magnification of 1270.

[CONTRACTIONS:—*F*= Flemming fixation : *S*=Spermatogonial.]

- Fig. 1. Resting nucleus. S. (Gil.-Pet.)
 „ 2. Very early prophase. S. (F.)
 Figs. 3-5. Prophases. S. (F.)
 Fig. 6. Metaphase. S. (F.)
 Figs. 7, 8. Telophases. S. (F.)

- Fig. 9. Group of four cells. Telophase of penultimate spermatogonial division. (Bouin.)
 „ 10. Portion of periphery of gonad tube showing group of four cells in late telophase and spermatogonial cells going into resting. (Corrosive alcohol.)
 „ 11. Spermatogonial nucleus between late telophase and resting. (Gil.-Pet.)
 „ 12. Spermatogonial nucleus between late telophase and resting. (F.)
 „ 13. From a group of four spermatogonial cells. (Corrosive alcohol.)
 „ 14. Telophase of last spermatogonial. (Gil.-Pet.)
 „ 15. Group of eight cells (telophase of last spermatogonial) lying in one plane. (Corrosive sublimate acetic.)
 „ 16. Telophase. S. (Corrosive sublimate acetic.)
 „ 17. Telophase—twelve paired chromosomes emerging from the telophasic mass. S. (Corrosive alcohol.)
 Figs. 18, 19. Late telophase—twelve paired chromosomes, appearance of plasmosome. S. (Corrosive alcohol.)
 Fig. 20. Very late telophase—gradual disappearance of the chromosomes. S. (Zenker.)
 „ 21. Resting nucleus of spermatocyte I. (F.)
 „ 22. Group of spermatocyte I, resting nuclei. (Gil.-Pet.)
 „ 23. Leptotene zygotene stage. (F.)
 Figs. 24, 25. Pachytene stage. (F.)
 „ 26, 27. Early strepsitene stage. (F.)
 Fig. 28. Synizetic nucleus. (F.)
 Figs. 29, 30. Early prophase—Fig. 29, from a group of eight cells in one of which there is a spindle.
 „ 31, 32. Prophase showing twelve bivalent chromosomes. (F.)
 Fig. 33. Chromosomes in nucleus represented in Fig. 32.
 „ 34. Equatorial plate of first meiotic division. (F.)
 „ 35. Spindle, chromosomes in metaphase. (Gil.-Pet.)
- SOMATIC NUCLEI.
- Fig. 36. Prophase. (F.)
 „ 37. Metaphase. (F.)
 „ 38. Late telophase—finger-like protrusions coming out of the telophasic mass. (Gil.-Pet.) Only one cell shown fully.

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3. MONTGOMERY, T. H., 1900. The Spermatogenesis of *Peripatus balfourii* up to the formation of the Spermatid, *Zool. Jahrb. Anat.*, Bd. xii.
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5. SCHUBMANN, W., 1905. Über die Eibildung und Embryonalentwicklung von *Fasciola hepatica*, L., *Zool. Jahrb. Anat.*, Bd. xxi.

(Issued separately, 6th December 1916.)

VIII.—**A Guide to the Literature of British Diptera.** Vice-Presidential Address by **Percy H. Grimshaw**, F.R.S.E., F.E.S., delivered 27th November 1916.

ONE of the main difficulties encountered by the student of British Diptera lies in the fact that there does not exist an up-to-date work dealing with the whole subject, and that therefore recourse must be had to articles which are scattered throughout our serial literature, whether periodical magazines or the proceedings of scientific societies. Such a procedure is in itself not an easy task, for many of the serials are not readily accessible to everyone, while it is no light undertaking to search their pages or indices on the chance (and such is a small one) of finding an odd paper which may be of use in the desired direction. It is true that, since the year 1864, the admirable "hardy annual" known as the "Zoological Record" has appeared regularly and is of the utmost service, but this publication is not found in every library, while the articles dealing with the British aspect of Dipterology have to be sought amid a bewildering mass of titles which include memoirs in the languages of all civilised nations.

In the following pages I have endeavoured to supply a guide to the literature of British Dipterology, going back about 150 years. I have used every reasonable means to make this bibliography sufficiently complete,¹ and I trust that there will be found, in one place or other, the titles of all books and papers in British literature which are of importance to, or which have any claim to be considered useful to, the student of our native Two-winged Flies. In some groups, especially those which comprise insects of economic importance, a fair amount of literature exists in our own country, but in others, on the other hand, no work appears to have been done by British authors since the early days of the science. For the study of these neglected groups it will be necessary to consult the literature of foreign countries, more particularly those of continental Europe, which possess a fauna similar to our own.

I. General Descriptive Works.

At the outset I propose to give a very brief account of some early works which attempted to cover the whole ground of British Entomology, and shall endeavour to indicate what special information they contain anent the particular Order in which we are concerned. It is somewhat difficult to

¹ In the present bibliography only "major articles" are included. The short notes which, in the main, are of a purely faunistic nature, are far too numerous for insertion in the list.

decide upon a starting-point, but I do not think it advisable to go further back than the following interesting volume :—

1. HARRIS, MOSES: An Exposition of English Insects. London, 1782.

This is a quarto publication, containing 51 copper plates, upon which are engraved and coloured nearly 500 figures of British Insects. No fewer than 25 of these plates are entirely devoted to Diptera, a surprisingly large proportion considering the date when this work was published. These 25 plates contain 299 figures, while the accompanying text is in parallel columns of English and French. A certain number of the species bear Linnean names and are quite recognisable when the description and figure are examined together, but unfortunately a large proportion of them are so badly drawn and described that their identity must ever remain a mystery. Verrall has, indeed, recognised an appreciable number of those which belong to the Families dealt with in the two important volumes of his "British Diptera" mentioned below, and since Harris's names predate those of Fallén and Meigen they have been resuscitated. Probably more of these early names will be restored by others who succeeded in recognising them when monographing other groups.

2. DONOVAN, E.: Natural History of British Insects. London, 16 vols., 1792-1813.

This work contains 576 plates, which are very superior to those of Harris, though unfortunately for the Dipterist only 39 are devoted to the Two-winged Flies, depicting in all some 60 species.

3. CURTIS, JOHN: British Entomology. London, 16 vols., 1824-1839.

This classical work was issued in monthly parts almost without interruption, the first appearing in January 1824 and the last in December 1839. The complete work contains no fewer than 770 plates, each being accompanied by a couple of pages of letterpress. The plates have never been surpassed for beauty, accuracy, and artistic merit. Curtis's plan was to figure and describe a typical representative of every native genus (*sensu lato*) differentiated in his time, while at the same time his letterpress contains a full description of the genus and an enumeration of the species known to him as occurring in Britain. In many cases exact localities are given for the rarer species, and the work is a decided advance on any of its predecessors. No fewer than 109 genera of Diptera are figured, while 817 species are recorded as members of the British fauna. At the time Curtis was publishing his monthly parts the great epoch-making work of Meigen (*Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten*) was also appearing on the Continent, and without a doubt our English author was

greatly assisted by the labours of his contemporary, and was enabled to identify and record a large number of species resting in British cabinets and hitherto unlabelled.

After the appearance of the above three works presumably the task of dealing with the whole of the British Insects became too heavy for one author to grapple with, so that special works began to appear dealing with a single Order. We accordingly find, after an interval of twelve years, the publication of the first separate work on British Diptera, viz. :—

4. WALKER, FRANCIS: *Insecta Britannica—Diptera*. London, 3 vols., 1851-1856.

This remains, unfortunately, the *only* work in the English language which attempts to describe the whole or greater part of the species of all the Families of British Two-winged Flies. Descriptions are given of 2074 species, while 363 additional species are mentioned as British but not described. Fortunately for the reputation of this work, its author (a notoriously careless worker) was materially assisted by A. H. Haliday, a Dublin entomologist whose descriptive writings were remarkable for their care and accuracy. Those Families which were taken in hand by Haliday were finished on his usual high standard, and such portions of the work still remain of considerable use to those students who have neither access to, nor the faculty of reading, the various modern monographs by continental authors. Much of Walker's share in these three volumes is, as usual, slipshod, and in some of the larger genera (*e.g. Chironomus*) his analytical tables are unworkable, not to say ludicrous. Most of the species described by Walker as new are unrecognisable without an examination of the type specimens, which were not marked as such and have apparently since been lost. Such species, therefore, as Verrall has remarked, are "only a burden to the list." A saving feature of this work lies in the thirty plates, from the hand of J. O. Westwood, and drawn with his usual skill and accuracy.

No general work of any importance appeared for nearly forty years after the date of Walker's last volume. In order to fill up this blank, the following projected work was commenced :—

5. THEOBALD, F. V.: *An Account of British Flies (Diptera)*. London, 1892.

Presumably owing to want of support this effort to produce a hand-book soon came to an end, only a single volume of 215 pages being published, dealing with half-a-dozen Families.

After devoting over thirty years to the study of Diptera, George Henry Verrall issued the long-expected pioneer volume of a great projected work on the Flies of Britain. The whole work was to occupy some fourteen

volumes, but, unfortunately for the science of Dipterology, Verrall only lived to publish two volumes. These are—

6. VERRALL, G. H.: British Flies. Vol. viii., Platypezidæ, Pipunculidæ, and Syrphidæ of Great Britain. London, Gurney & Jackson, 1st Jan. 1901.
7. VERRALL, G. H.: British Flies. Vol. v., Stratiomyidæ and succeeding Families of the Diptera Brachycera of Great Britain. London, Gurney & Jackson, 1st January 1909.

These two volumes stand out as exhaustive monographs of the Families concerned, and as such are by far the most important works of their kind in any European language. The only criticism that may be raised against them is that possibly the author, in his specific descriptions, has erred on the side of fulness. Thus, in his description of *Haematopota pluvialis*, the Common Cleg, diagnosed by Linnæus in 8 words, Verrall uses over 3600—without including general remarks on synonymy and distribution. Far be it from my intention to cast any slur on the work of the greatest British Dipterist of all time, but one *does* feel the working through of these descriptions tedious in the extreme.

In the years intervening between Verrall's two volumes, there appeared the following less ambitious but excellent guide for the student, under an unassuming and somewhat misleading title:—

8. WINGATE, W. J.: A Preliminary List of Durham Diptera, with Analytical Tables. *Trans. Nat. Hist. Soc. Northumberland, Durham, and Newcastle-upon-Tyne (N.S.)*, vol. ii., 1906.

This modestly announced volume is much more than a "List," for there is not only a concise and distinctly useful epitome of the external structure of flies, with an explanation of terms used in descriptions, but analytical tables of the whole of the British Diptera save the difficult Families Cecidomyiidæ and Mycetophilidæ.

The discovery of the intimate relationship that exists between Diptera and disease led to a vastly increased output of literature on flies in all parts of the civilised world, and a work which thus originated will be of much service as an atlas for the identification of certain British species. This is the following:—

9. AUSTEN, E. E.: Illustrations of British Blood-sucking Flies, with Notes. London, British Museum, 1906.

The plates in this work can hardly be surpassed for beauty and fidelity, but the accompanying text is very limited and does not aim at being more than of a general character.

A fuller work of this nature, and the latest general work published in this country, is—

10. PEARCE, E. K.: Typical Flies. A Photographic Atlas of Diptera, including Aphaniptera. Cambridge, 1915.

In this atlas over 150 photographs are reproduced of typical representatives of the various Families, and although the details of structure are not as a rule evident in the illustrations, yet the general appearance of the insects is fairly well brought out, and the book should prove a material aid to the beginner.

In the following general works on Entomology much useful information will be found on the special Order of Insects with which we are here concerned:—

11. WESTWOOD, J. O.: Introduction to the Modern Classification of Insects. 2 vols. London, 1839-40. *Diptera* in vol. ii. pp. 495-587, figs. 124-133.
12. SHARP, DAVID: The Cambridge Natural History. Vol. vi. London, 1899. Insects, Part ii. *Diptera* on pp. 438-522, figs. 212-249.

The following papers dealing with British Flies in general are arranged chronologically, and may be consulted with more or less advantage by the student:—

13. WAILES, GEO.: The Characters of the European Diptera from Meigen's *Systematische Beschreibung*. *London's Mag. Nat. Hist.*, vol. v. pp. 156-162 (1832).
14. WALKER, FRANCIS: Notes on Diptera. *Ent. Mag.*, vol. iii. pp. 178-182 (1836); vol. iv. pp. 113-117, 226-230 (1837).
15. HALIDAY, A. H.: Notes, etc., upon Diptera. *Ent. Mag.*, vol. iv. pp. 147-152 (1837).
16. DUNCAN, JAMES: Characters and Descriptions of the Dipterous Insects indigenous to Britain. *Mag. Zool. Bot.*, vol. i. pp. 145-167, 359-368, 453-459 (1837); vol. ii. pp. 205-222 (1838). In this paper only the Stratiomyidæ, Tabanidæ, Bombyliidæ and Conopidæ were dealt with, but in these Families most of the genera were illustrated by carefully drawn woodcuts, and many localities for the species given, all those recorded from Scotland being distinguished by a small *s* after the specific name.
17. VERRALL, G. H.: Notes on the Diptera in the Entomological Club Collection. *Entomologist*, vol. v. pp. 21-25 (1870-71).

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21. BRUNETTI, E.: Notes on Diptera in 1889. *Entomologist*, vol. xxiii. pp. 122-126 (1890).
22. VERRALL, G. H.: Critical Notes on Diptera. *Entomologist*, vol. xxiii. pp. 150-154 (1890).
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24. CARPENTER, G. H.: The Insects of the Sea [and Sea Shore]. *Knowledge*, vol. xxiv. (May 1901). *Diptera* on p. 194.
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26. SLADEN, F. W. L., BAGNALL, R. S., and COLLIN, J. E.: Some interesting British Insects. *Ent. Mo. Mag.*, xlix. pp. 171-174, pls. ii. and iii. (1913).—Several Diptera.
27. EDWARDS, F. W.: On the correct Names of some common British *Diptera*. *Ent. Mo. Mag*, lii. pp. 59-63 (1916).

II. Lists and Catalogues.

The following published "Lists" and "Additions to Lists" may be interesting as showing the progress of faunistic work in the country, while certain of them may serve useful also to the collector since they contain critical remarks and in some cases descriptions of species:—

28. CURTIS, JOHN: Guide to an Arrangement of British Insects. 1st Edition, 1829; 2nd Edition, 1837. Enumerates 293 genera and 2134 species of Diptera.
29. STEPHENS, JAMES FRANCIS: Systematic Catalogue of British Insects. In two Parts, 1829. The Diptera are contained in Part II., and comprise 219 genera and 1673 species.
30. MORRIS, F. O.: A Catalogue [of] British Insects in all the Orders. London, 1865, 8vo, 125 pp. (Diptera on pp. 56-77).
31. VERRALL, G. H.: A Hundred New British Species of Diptera. *Ent. Mo. Mag.*, xxii. pp. 179-182, 199-202, and 230-234 (1886).
32. VERRALL, G. H.: List of British Diptera. London, 1888, pp. 33, 4 and 12. This List is of considerable importance, and laid the foundation

for a more thorough study of our native species. It represents the results of more than 20 years' study on the part of the author, and indicates very clearly the state of our knowledge at the time. No fewer than 603 genera are recognised—a great advance on all previous works—while the names of 3527 species are printed, those requiring confirmation being either printed in italics or relegated to Parts II. and III., which give respectively those species which were “originally described from Britain; but probably unrecognisable unless from types” (195 species), and “reputed British Diptera” (843 species).

33. VERRALL, G. H.: A second Hundred new British species of Diptera. *Ent. Mo. Mag.*, xxx. pp. 76-79 and 140-146 (1894).
34. MEADE, R. H.: British Diptera unrecorded or undescribed by English Authors. *Ent. Mo. Mag.*, xxxv. pp. 30-33 and 100-103 (1899).
35. VERRALL, G. H.: List of British Diptera. 2nd Edition. Cambridge, 1901, 47 pp. This still remains the standard List, although since its publication some hundreds of additional species have been discovered, and a large number of doubtful ones confirmed, while much progress has been made in classification, subdivision of old and erection of new genera, and so on. Verrall's 2nd Edition is a great advance on the first, for, as the preface states, “about 300 species have been added to the old ‘List,’ and about 500 names have been altered in some way or other, such as being confirmed as British, placed under a different genus, changed in synonymy, etc.” The List as it stands contains in Part I. the names of 665 genera and 2881 species, and of the latter 303 are printed in italics as requiring confirmation.
36. VERRALL, G. H.: Another Hundred new British species of Diptera. *Ent. Mo. Mag.*, xlvii. p. 79 (1911). Completed by J. E. COLLIN, *op. cit.* xlviii. pp. 20-27, 56-59, 144-147, 190-197 (1912).
37. COLLIN, J. E.: Additions and Corrections to the British List of *Muscidae Acalyptrate*. *Ent. Mo. Mag.*, xlvi. pp. 47-48, 124-129, 169-178 (1910); xlvii. pp. 145-153, 182-187, 229-234, 253-256 (1911). This is an exceedingly valuable paper, correcting synonymy, adding species, and clearing up difficulties. It is only a foretaste, showing how much and yet how little we know of this section of the Diptera.
38. COLLIN, J. E.: Thirty Additions to the List of British Diptera. *Ent. Mo. Mag.*, xlix. pp. 104-106, 130-135 (1913).

III. Practical Hints.

The following papers are of a practical nature:—

39. SLACK,——: On examining Diptera under the Microscope. *Knowledge*, vol. vi. pp. 312, 313, figg. (1884).

40. AUSTEN, E. E.: How to collect Diptera (Two-winged Flies), with Notes on the Habits of the perfect Insects and Larvæ. London, British Museum (Natural History), 1900, 16 pp.
41. HOWLITT, F. M.: On the Collection and Preservation of Insects. *Parasitology*, Cambridge, vol. iii. pt. 4, pp. 485-489 (1910).
42. GRAHAM, W. M.: The Photography of Diptera. *Bulletin Ent. Research*, vol. ii. pp. 153-160 (1911).
- 42a. SCRIVEN, J. B.: The Preparation of Serial Sections of Insects, based upon Experiments with the Blow-fly. *Journ. Quekett Club* (2), viii. pp. 343-348 (1902).

IV. Structure and Classification.

The following papers may be useful as supplementary to the information given in general works:—

43. WALKER, F.: Notes on the Wing-bones of the Two-winged Flies. *Entomologist*, vol. vii. pp. 36-42, 100-102, 126-128, 147-149, 196-198, 219-221 (1874). The neuration of the wings of genera is illustrated by a series of 42 woodcuts, from drawings by A. H. Haliday.
44. OSTEN-SACKEN, C. R.: An Essay of Comparative Chætotaxy, or the arrangement of characteristic bristles of Diptera. *Trans. Ent. Soc. London*, 1884, pp. 497-517. An epoch-making paper of the first importance. In it are laid the foundations of a system of nomenclature for the bristle arrangement in Diptera, a subject which has since been studied in great detail, and which has proved invaluable in taxonomy.
- 44a. SHARP, D.: On the Use of the term Tegula in Diptera. *Ent. Mo. Mag.*, xxxii. p. 12 (1897).
- 44b. MEADE, R. H.: On the Terminology of the Scale-like Organs which lie between the roots of the wings and the scutellum of *Diptera*. *Ent. Mo. Mag.*, xxxiii. pp. 29-30 (1897).
45. OSTEN-SACKEN, C. R.: On a distinctive character of the Imagos of the Suborders of Diptera: Orthorrhapha Brachycera and Cyclorrhapha Athericera, introduced by Latreille (1825), but overlooked by later authors. *Ent. Mo. Mag.*, xxxviii. pp. 228-229 (1902).
46. WESCHÉ, W.: Modifications of the Legs in some Dipterous Flies. *Journ. Quekett Club* (2), viii. pp. 245-250, pls. xiii., xiv. (1902).
47. WESCHÉ, W.: Undescribed Palpi on the Proboscis of some Dipterous Flies, with remarks on the mouth-parts in several Families. *Journ. Roy. Micr. Soc.*, 1902, pp. 412-416, pls. ix., x.
48. HARRIS, W. H.: The Dentition of the Diptera. *Journ. Quekett Club* (2), viii. pp. 389-398, pl. xix. (1903).

49. WESCHÉ, W.: The Labial and Maxillary Palpi in Diptera. *Trans. Linn. Soc. Lond.*, ix. pp. 219-230, pls. viii.-x. (1904).
50. GRIMSHAW, PERCY H.: On the Terminology of the Leg-bristles of Diptera. *Ent. Mo. Mag.*, xli. pp. 173-176 (1905). A new nomenclature proposed.
51. WESCHÉ, W.: The Genitalia of both the Sexes in *Diptera*, and their Relation to the Armature of the Mouth. *Trans. Linn. Soc. Lond.*, ix. pp. 339-386, pls. xxiii.-xxx. (1906).
52. WESCHÉ, W.: The Structure of the Eye-surface and the Sexual Differences of the Eyes in Diptera. *Journ. Quekett Club* (2), x. pp. 367-384, pl. xxviii. (1909).
53. MACGREGOR, M. E.: The Posterior Stigmata of Dipterous Larvæ as a diagnostic character: with especial reference to the Larvæ incriminated in cases of Myiasis. *Parasitology*, Cambridge, vol. vii. pp. 176-188, pls. xv., xvi. (1914).

See also the general works in Section I. and Nos. 70, 92, 93, 103, 104, 111, 119, 123, 137, 142, 143, 191, 193, 202, 211, 226, 227, 296-309, 333, 343, 351, 352, 368, 376, 404, 416.

V. Physiology and Habits.

This section is far from complete. I have only included such papers as are of interest to the general student.

54. AUBIN, P. A.: The Buzzing of Diptera. *J. R. Microsc. Soc. Lond.*, 1914, pp. 329-334, pls. viii.-x.
55. WESCHÉ, W.: Some new Sense-organs in Diptera. *Journ. Quekett Club* (2), ix. pp. 91-104, pls. vi., vii. (1904).
56. HILL, A.: Sense of Smell in Flies. *Nature*, lxxx. p. 308 (1909).
57. EATON, A. E.: Flies riding on Beetle-back. *Ent. Mo. Mag.*, xxxii. p. 139 (1896); also J. J. WALKER, *id.* p. 161.
58. OSTEN-SACKEN, C. R.: Notes on Luminous Insects, especially Diptera. *Ent. Mo. Mag.*, xv. pp. 43-44 (1878).
59. PATTERSON, R.: Note on the appearance of Clouds of Diptera. *Ann. Nat. Hist.*, x. pp. 6-9 (1842).
60. STEWART, E. A.: Plague of Flies at Kilrea, Ireland. *Science Gossip*, xiv. pp. 140-141 (1878).
61. LETT, —: Swarms of Flies (?) at Lurgan in April 1881. *Science Gossip*, xvii. p. 262 (1881).
62. EVANS, W.: Lepidoptera (Moths) and other Insects at Scottish Lighthouses, chiefly in the Forth Area. *Scot. Nat.*, 1914, pp. 56-63, 129-135, 225-233, 253-256, 278-286.

63. HINDLE, E.: Note on the Colour-preference of Flies. *Journ. Hygiene*, Cambridge, xiv. pp. 46-47 (1914).
64. WILLIS, J. C., and BURKILL, I. H.: Flowers and Insects in Great Britain. Part I. *Ann. Botany*, xxxiv. pp. 227-273 (1895); Part II. *op. cit.* xvii. pp. 313-349 (1903); Part III. *tom. cit.* pp. 539-570 (1903); Part IV. *op. cit.* xxii. pp. 603-649 (1908).
65. WILLIS, J. C.; and BURKILL, I. H.: Notes on the Anthophilous Insect Fauna of the Clova Mountains. *Ann. Scot. Nat. Hist.*, 1903, pp. 29-37, 99-102; 1904, pp. 166-168.
66. AUSTEN, E. E.: Necrophagous Diptera attracted by the odour of Flowers. *Ann. Nat. Hist.* (6), xviii. pp. 237-240 (1896).
67. MACKENZIE, STAPLEY, and RANSOM: Various species of *Veronica* fertilised by Diptera. *Nature*, xxvii. pp. 127, 149, 150, 174 (1882).
68. SCOTT-ELLIOT, G. F.: Notes on Flower-haunting Diptera. *Trans. Ent. Soc. Lond.*, 1896, pp. 117-128.
69. ASHWORTH, J. H.: A Note on the Hibernation of Flies. *Scot. Nat.*, 1916, pp. 81-84.
- 69a. GASKELL, MAJOR T. K.: The Hibernation of Flies in a Fifeshire House. *Scot. Nat.*, 1916, p. 139.

See also works under Sections VII. to XI., and Nos. 3-7, 11, 12, 70, 106, 111-116, 119, 120, 123, 124, 128, 130, 134, 138, 139, 192, 195, 203-207, 212, 218, 226, 228, 229, 232, 237, 249-279, 282-285, 291, 292, 296-300, 310-344, 352, 397, 406.

VI. Life-History.

70. MIALL, L. C.: The Natural History of Aquatic Insects. London, Macmillan, 8vo, 395 pp. (1895). A charming book, which can be highly recommended to all students of Diptera. Chapter ii. gives an extremely lucid account of the life-histories of many Flies which have aquatic larvæ (*Culex*, *Corethra*, *Mochlonyx*, *Chironomus*, *Tanypus*, *Ceratopogon*, *Dixa*, *Dicranota*, *Ptychoptera*, *Simulium*, *Stratiomys* and *Eristalis*).
71. MACLEAY, W. S.: Notice on the larvæ of Diptera. *Philos. Mag.*, vol. ii. pp. 178-179 (1827).

See also works under Sections I., VII., VIII., IX., X., XI., and Nos. 111, 111a, 113-116, 118-121, 123-125, 130, 131, 134, 142, 143, 158-167, 168-185, 191-195, 200, 203, 212, 218, 226, 230, 233, 251-276, 283, 291-293, 296-300, 310, 314, 317, 318, 322, 334-344, 347-352, 355, 357-359, 374, 378-382, 384, 386, 388, 389, 397-399, 401, 403, 404, 409, 410, 412, 413, 415.

VII. Economic—Work of a General Nature.

Most of the general works (Annual Reports, etc.) on Injurious Insects contain important notes and observations on Diptera. A detailed bibliography under this heading is beyond the scope and purpose of the present paper. The student specially interested in Injurious Diptera will find it necessary to index for himself most of these works. A selection of the more important is given below:—

72. CURTIS, J.: *Farm Insects*. Edinburgh, 1860.
73. ORMEROD, E. A.: *Manual of Injurious Insects, with Methods of Prevention and Remedy*. London, 1881. This useful work has gone through several editions.
74. ORMEROD, E. A.: *Textbook of Agricultural Entomology*. London, 2nd Edition, 1892.
75. ORMEROD, E. A.: *Reports of Injurious Insects and Common Farm Pests*. London, 1878, and succeeding years.
76. THEOBALD, F. V.: *Reports on Economic Zoology*. London, British Museum, 1903, et seqq.
77. THEOBALD, F. V.: *Reports on Economic Zoology*. *Journ. S. Eastern Agric. Coll.*, 1900, et seqq.
78. CARPENTER, G. H.: *Injurious Insects and other Animals observed in Ireland*. *Econ. Proc. Roy. Dublin Soc.*, 1902, et seqq.
79. COLLINGE, W. E.: *Reports on the Injurious Insects and other Animals observed in the Midland Counties*. Birmingham, 1904, et seqq.
80. COLLINGE, W. E.: *Annual Reports of the Honorary Consulting Zoologist*. *Journ. Land Agents' Soc.*, 1907, et seqq.
81. WARBURTON, C.: *Reports of the Zoologist of the Royal Agricultural Society of England*, 1898, et seqq.
82. MACDOUGALL, R. STEWART: *Reports on Injurious Insects*. *Trans. Highl. and Agric. Soc. Scotland*.
83. *Journal of the Board of Agriculture*, vols. i. to xxii. (1894-1916).
84. *Review of Applied Entomology—Series A, Agricultural, and Series B, Medical and Veterinary*. Vols. i. to iv. (1913 to 1916).
85. *Bulletin of Tropical Diseases*. Vol. viii. now in course of publication. London, Tropical Diseases Bureau.
- 85a. EALAND, C. A.: *Insects and Man*. London, 8vo, 1915.
- 85b. EALAND, C. A.: *Insect Enemies*. London, 8vo, 1916.
- 85c. MIALI, L. C.: *Injurious and Useful Insects, an Introduction to the Study of Economic Entomology*. London, 1902, viii+256 pp., 103 cuts.

VIII. Flies and Man.

The subject of the transmission and causation of disease by flies to and in man has received considerable attention of recent years, and the literature in connection therewith is far too extensive to be cited in the present article. A full bibliography is given in C. Gordon Hewitt's work on the House-fly (see No. 298), to which I would refer the student. In the following list only such works are mentioned as possess some interest from the purely entomological point of view, excluding those of a more medical nature. The titles are arranged chronologically.

86. SPICER, W. W.: Flies parasitic on Man. *Science Gossip*, 1874, pp. 32-35, figs. 27-31.
87. BLOOMFIELD, E. N.: Undetermined Fly troublesome on hills of Yorkshire in the time of Ray. *Naturalist*, viii. pp. 93-94 (1883).
88. SMITH, W. G.: Larvæ beneath Human Skin. *Ann. Nat. Hist.* (5), xi. p. 213 (1883).
89. SENATOR, H.: Living Fly Larvæ in the Stomach and Mouth. *Journ. Roy. Micr. Soc.*, 1890, p. 717.
90. SHIPLEY, A. E.: The Danger of Flies. *Science Progress*, i. pp. 723-729 (1907).
91. DOANE, R. W.: Insects and Disease. London, 1910, 8vo, xiv+227 pp., and pls.
92. GRAHAM SMITH, G. S.: Flies in Relation to Disease: Non-bloodsucking Flies. Cambridge, 1913, 8vo, xiv+292 pp., 24 pls.
93. HINDLE, EDWARD: Flies in Relation to Disease: Bloodsucking Flies. Cambridge, 1914, 8vo, 398 pp. This and the preceding are works of paramount importance, and should be in the library of every Dipterist.

See also Nos. 53, 84, 85, 85a, 85b, 119, 122, 138, 227a, 298-300, 319-324, 329, 339-344, 347, 351.

IX. Flies and Domestic Animals.

For information under this heading a number of the general Economic Works should be consulted (Section VII.), and also those under the heading *Estridæ* (Nos. 251 to 271). See also Nos. 335-337 and 409.

94. ORMEROD, ELEANOR A.: Flies injurious to Stock, being life-histories and means of prevention of a few kinds commonly injurious, with special observations on Ox Warble or Bot-fly. London, 1900, 8vo, vi+80 pp.

X. Flies and Other Insects.

Much information on this subject will be found in the papers cited under the heading *Tachinidæ* (Nos. 277 to 293).

95. Dipterous parasites on Lepidoptera, etc., are discussed in *Nature*, vol. xxxi. pp. 29, 54, 82, and 103 (1884). The following paper, though not of much importance, may afford some points of interest:—
96. MEADE, R. H.: Notes on parasitic Diptera. *Entomologist*, vol. xv. p. 24, (1882).

XI. Flies Injurious to Vegetation.

Much information on this subject is given in the works cited under the headings *Economic—General* (Section VII.), *Cecidomyiidæ* (Nos. 145-185). See also Nos. 218, 230, 230a, 249, 250, 348-350, 355, 357-359, 378, 379-382, 384, 386, 388, 389, 389a, 397, 401, 403, 404.

The following works may be consulted in addition, though with the exception of the volume by Miss Ormerod none is of much importance:—

97. BOLD, T. J.: Larva in Turnips in Northumberland in 1864. *Nat. Hist. Trans. North. and Durham*, i. p. 124 (1865).
98. ORMEROD, ELEANOR A.: Handbook of Insects injurious to Orchard and Bush Fruits, with means of prevention and remedy. London, 1898, 8vo, pp. 10 and 286.
99. WESTWOOD, J. O.: Notæ Dipterologicæ. No. 6. On the Minute Species of Dipterous Insects, especially Muscidæ, which attack the different kinds of Cereal Crops. *Trans. Ent. Soc. Lond.*, 1881, pp. 605-626.
100. INCHBALD, P.: Observations upon our Plant-feeding and Gall-making Diptera and Hymenoptera in 1882. *Entomologist*, xv. pp. 217-222 (1882).
101. THEOBALD, F. V.: The Insect Pests of Fruit. *Rep. Mus. Assoc. Norwich*, vol. ii. pp. 38-41 (1908-9).
102. THEOBALD, F. V.: The Insect and other Allied Pests of Orchard, Bush and Hothouse Fruits; and their prevention and treatment. Wye, 1909, 8vo, xvi+550 pp.
- 102a. PETHERBRIDGE, F. R.: Fungoid and Insect Pests of the Farm. Cambridge, 8vo, 1916.

XII. Systematic.

ORTHORRHAPHA NEMATOCERA.

GENERAL.

103. WESCHÉ, W.: The Phylogeny of the Nemocera, with Notes on the Leg

Bristles, Hairs, and certain Mouth-glands of Diptera. *Biol. Bulletin*, xxiii. pp. 250-270, pl. i. (1912).

104. WESCHÉ, W.: The Mouth-parts of the Nemocera and their relation to the other Families of Diptera. *Journ. Roy. Micr. Soc.*, 1904, pp. 28-107, pls. iii.-viii. Corrections and Additions, *op. cit.* 1909, pp. 1-16, pls. i.-iv.
105. EDWARDS, F. W.: Ten new British Diptera (Nematocera). *Ent. Mo. Mag.*, li. pp. 164-167 (1915).

SCIARIDÆ.

There are no general papers on this Family. The general works of Walker (4) and Theobald (5) are here of very little use, and it is necessary to consult foreign literature. See also—

106. EDWARDS, F. W.: Sexual Dimorphism in a Species of *Sciara*. *Ent. Mo. Mag.*, xlix. pp. 209-211 (1913).
107. EDWARDS, F. W.: A Second British Species of *Plastosciara*. *Ent. Mo. Mag.* li. pp. 263-264 (1915).

MYCETOPHILIDÆ (Fungus-Gnats).

The most helpful memoir on the British species of this Family which has yet appeared is—

108. EDWARDS, F. W.: Notes on British Mycetophilidæ. *Trans. Ent. Soc. Lond.*, 1913, pp. 334-382, pls. xii.-xviii. A very thorough revision of the Family. 124 species are added to the list, and 50 names proved to be synonyms or wrongly identified. An analytical key is given to all the European genera, and in the case of several of the larger genera keys are also given for the identification of species.

Other papers are—

109. EDWARDS, F. W.: Some Mycetophilid Synonymy. *Ann. Mag. Nat. Hist.*, xii. pp. 55-56 (1913).
110. JENKINSON, F.: Notes on certain Mycetophilidæ, including several Species new to the British List. *Ent. Mo. Mag.*, xlv. pp. 129-133, 151-154 (1908).

BIBIONIDÆ.

There is no British paper on this Family.

The general works of Walker (4), Theobald (5), and Wingate (8) may be consulted.

CHIRONOMIDÆ (Midges).

Besides the general works above mentioned there is no British paper on

these difficult but interesting Diptera. The following volume is of importance as an introduction to the study of their anatomy and life-histories:—

111. MIALL, L. C., and HAMMOND, A. R.: The Structure and Life-history of the Harlequin Fly (*Chironomus*). Oxford, 1900, 8vo, vi+196 pp., illustrations.

Of accounts of habits, new British species, etc., we have the following:—

- 111a. CARPENTER, G. H.: *Clunio marinus*, Haliday: a Marine Chironomid. *Ent. Mo. Mag.*, xxx, pp. 129-130 (1894).
112. TAYLOR, T. H.: Note on the Habits of *Chironomus (Orthocladius) sordidellus*. *Trans. Ent. Soc. Lond.*, 1903, pp. 521-523.
113. MUNDY, A. T.: The Anatomy, Habits and Psychology of *Chironomus pusio*, Meigen (the early stages), with Notes on various other Invertebrates, chiefly Chironomidæ. Leicester, 1909, 4to, pp. 1-56, pls. i.-viii.
114. MUNDY, A. T.: A net-building *Chironomus* larva. *Naturalist*, 1907, pp. 389-391.
115. BARNARD, K. H.: Chironomid Larvæ and Watersnails. *Ent. Mo. Mag.*, xlvii, pp. 76-78 (1911).
116. IMMS, A. D.: *Clunio bicolor*, Kieff: a Marine Chironomid new to the Fauna of Great Britain. *Proc. Liverpool Biol. Soc.*, xvii, pp. 81-86 (1903).
117. GRIMSHAW, PERCY H.: *Tanytarsus signatus*, V. d. Wulp, a new British Fly. *Scot. Nat.*, 1914, pp. 257-258.

For life-histories of *Chironomus*, *Tanypus*, and *Ceratopogon*, see No. 70.

CULICIDÆ (Gnats or Mosquitoes).

The discovery of the dissemination of malaria and other diseases through the agency of mosquitoes has led to an increased study of the taxonomy, anatomy, and bionomics of our native species.

The following is probably the most useful paper for purposes of identification:—

118. EDWARDS, F. W.: Notes on the British Mosquitoes (*Culicinae*). *Entomologist*, xlv, pp. 191-195, 217-220, 260-264 (1912).

For more detailed accounts reference may be made to general monographs dealing with the species of the whole world. Such are—

119. THEOBALD, F. V.: A Monograph of the Culicidæ or Mosquitoes. London, 5 vols., 1901-1910.
120. GILES, G. M.: A Handbook of the Gnats or Mosquitoes, giving the Anatomy and Life-history of the Culicidæ. London, 1900. Second Edition, 1902.

121. GILES, G. M.: A Revision of the Anophelinæ, being a first Supplement to the second Edition of "A Handbook of the Gnats or Mosquitoes." London, 1904.

Of much interest are also the following:—

122. NUTTALL, G. H. F., COBBETT, L., and STRANGWAYS-PIGG, T.: Studies in relation to Malaria. I. The geographical distribution of *Anopheles* in relation to the former distribution of ague in England. *Journal of Hygiene*, i. pp. 1-44 (1901).
123. NUTTALL, G. H. F., and SHIPLEY, A. E.: Studies in relation to Malaria. II. The structure and biology of *Anopheles* (*Anopheles maculipennis*). *Journal of Hygiene*, i. pp. 45-77, 269-276, 451-484, pls. i., ii., viii.-x. (1901); ii. pp. 58-84 (1902); iii. pp. 166-215, pls. 6-9 (1903).

Other papers (arranged chronologically) are as follows:—

124. SWINTON, JOHN: Some Observations on Swarms of Gnats. *Philos. Trans.*, vol. lvii. pp. 111-113 (1767).
125. BRIGHTWELL, T.: On the Larva of *Corethra plumicornis*, Meig. *Zool. Journ.*, v. pp. 396-397 (1832-34).
126. ANON.: How to Collect Mosquitoes (Culicidæ). London, British Museum (Natural History), 1899, 14 pp.
127. AUSTEN, E. E.: Mode of Preservation of Mosquitoes. *Nature*, lix. p. 582 (1899).
128. ANNETT, H. E., and DUTTON, J. E.: The Hibernation of English Mosquitoes. Thompson Yates Lab. Rept. Liverpool, iv., pt. i., pp. 93-96 (1901).
129. WATERHOUSE, C. O.: Notes on some British Culicidæ. *Ann. Mag. Nat. Hist.* (7), xv. pp. 674-676 (1905).
130. IMMS, A. D.: Notes on the Structure and Behaviour of the Larva of *Anopheles maculipennis*, Mg. (preliminary note). *Proc. Phil. Soc. Cambridge*, xiv. pp. 292-295 (1907).
131. IMMS, A. D.: On the Larval and Pupal Stages of *Anopheles maculipennis*, Mg. *Journal of Hygiene*, vii. pp. 291-318, pls. iv., v. (1907); Part II., *Parasitology* (Cambridge), i. pp. 103-133, pls. ix., x. (1908).
132. IMMS, A. D.: On the Affinities of the Subfamily Corethrinæ of the Culicidæ. *Journ. Econ. Biol.*, vii. pp. 1-4 (1912).
133. EDWARDS, F. W.: The Identity of *Culex geniculatus*, Olivier. *Ent. Mo. Mag.*, xlix. pp. 107-108 (1913).
134. MACGREGOR, M. E.: Note on *Culex pipiens* breeding 66 feet below ground. *Journ. Trop. Med. and Hygiene*, xix. p. 142 (1916).

For life-histories of *Culex*, *Corethra*, and *Mochlonyx*, see No. 70.

PTYCHOPTERIDÆ and DIXIDÆ.

No special literature on these Families exists. The life-histories of *Ptychoptera* and *Dixa* are dealt with in No. 70.

SIMULIIDÆ (Sand-Flies).

The literature on this group is at present limited, but the supposition that Pellagra is conveyed by these flies will, no doubt, soon result in increased attention being paid to them.

The best memoirs on the British species are—

135. EDWARDS, F. W.: On the British species of *Simulium*. I. The Adults. *Bull. Ent. Research*, vi. pt. i., pp. 23-42 (1915).
 136. EDWARDS, F. W.: The British species of *Simulium* (Diptera). *Ent. Mo. Mag.*, li. pp. 305-309 (1915).

The following may also be consulted:—

137. TAYLOR, T. H.: On the Tracheal System of *Simulium*. *Trans. Ent. Soc. Lond.*, 1902, pp. 701-716.
 138. HEWITT, C. GORDON: *Simulium* Flies and Pellagra. *Nature*, lxxxv. p. 169 (1910).

For life-history see also No. 70.

ORPHNEPHILIDÆ.

No special literature.

PSYCHODIDÆ (Moth-Flies).

The best systematic account of the British species is—

139. EATON, A. E.: A Synopsis of British Psychodidæ. *Ent. Mo. Mag.*, vol. xxix. pp. 5-8, 31-34, 120-130 (1893); vol. xxx. pp. 22-28, pls. i.-iv. (1894); Supplement, vol. xxxi. pp. 208-213, 245-250 (1895); vol. xxxii. pp. 70-76, 127-131, 202-211 (1896); vol. xxxiii. pp. 114-125 (1897); vol. xxxiv. pp. 117-125, 154-158 (1898).

As a further Supplement to this valuable paper the author still further improved his classification in the following:—

140. EATON, A. E.: New Genera of European Psychodidæ. *Ent. Mo. Mag.*, vol. xl. pp. 55-59 (1904).
 141. EATON, A. E.: *Telmatoscopus rothschildi*, a new Species of Psychodid Diptera found in London. *Ent. Mo. Mag.*, vol. xlviii. pp. 7-9 (1912).

For structure and life-history the following are the most important:—

142. MIALL, L. C.: The Life-history of *Pericoma canescens* (Psychodidæ), with a bibliographical and critical appendix, by Baron Osten-Sacken. *Trans. Ent. Soc. Lond.*, 1895, pp. 141-153, pls. iii., iv.
 143. DELL, J. A.: The Structure and Life-history of *Psychoda sexpunctata*, Curtis. *Trans. Ent. Soc. Lond.*, 1905, pp. 293-311.

RHYPHIIDÆ.

No special papers.

CECIDOMYIIDÆ (Gall-Midges).

As might be expected from the economic importance of these flies there is an extensive literature. Space will only allow of a selection of the most important papers.

The student, at the outset, will find the following paper a useful guide to nomenclature:—

144. COLLIN, J. E.: A List of the British Cecidomyiidæ arranged according to the views of recent Authors. *Ent. Mo. Mag.*, xl. pp 93-99 (1904).

Additions to this List are given in the following:—

145. EDWARDS, F. W.: Two Diptera (Cecidomyiidæ) new to Britain. *Ent. Mo. Mag.*, xlviii. pp. 136-137 (1912).
146. BURKILL, HAROLD J.: Additions to the List of British Plant-Galls. *Entomologist*, xlix. pp. 4-8 (1916).

Of the volumes and papers dealing with Galls, including those made by insects of this Family, the most useful are—

147. CONNOLD, E. T.: British Vegetable Galls. An Instruction to their Study. London, 1901, 4to, xii + 312 pp., 130 pls.
148. CONNOLD, E. T.: Plant-Galls of Great Britain. A Nature-study Handbook. London, 1909, xii + 292 pp.
149. SWANTON, E. W.: British Plant-Galls; a Classified Text-book of Cecidology. London, 1912.
- 149a. MÜLLER, ALBERT: British Gall-Insects. *Entomologist's Annual*, 1872, pp. 1-22 (Diptera on pp. 12-17).
150. BINNIE, F. G.: On Dipterous Gall-makers and their Galls. *Trans. Nat. Hist. Soc. Glasgow*, i. pp. 154-164 (1876).
151. FITCH, EDWARD A.: British Gall-Gnats. *Entomologist*, xiii. pp. 146-154 (1880).
152. HARKER, A.: On the Gall-Midges (Cecidomyiidæ). An Introductory Paper. *Proc. Cotteswold Nat. F. Club*, ix. pp. 220-228 (1890).
- 152a. TRAIL, J. W. H.: Galls. *Ann. Scot. Nat. Hist.*, 1897, pp. 171-188.
153. BAGNALL, R. S., and HARRISON, J. W. H.: Records of some new British Plant-Galls. I. Diptera (Cecidomyiidæ). *Ent. Record*, xxviii. p. 51; II. Some more Cecidomyiid Galls, *t.c.* pp. 158-159. III. New Cecidomyiid Galls found during the Summer, *t.c.* pp. 197-203 (1916); IV. and V. More new Cecidomyiid Galls, *t.c.* pp. 247-252 (1916), and *op. cit.* xxix. pp. 12-15 (1917).
154. WALLACE, HENRY S.: A new British Cecidomyiid Gall on Meadow Grass. [*Mayetiola radicifera*, Rubs.] *Ent. Mo. Mag.*, lii. p. 230 (1916).

Scottish students should consult the following interesting series of papers:—

155. TRAIL, J. W. H.: Scottish Galls. *Scot. Nat.*, vol. i. pp. 123-125, 156-159, 192-197, 234, 235 (1871-72); vol. ii. pp. 30-32, 78-80, 170-173, 251-254, 301-305 (1873-74); vol. iv. pp. 13-18, 168-170 (1877-78); vol. v. pp. 213-217 (1879-80); vol. vi. pp. 15-20, 255-257 (1881-82); N.S. vol. i. pp. 206-216 (1883-84); vol. ii. p. 250 (1885-86); vol. iii. pp. 107-110 (1887-88); vol. iv. pp. 226-232 (1889-90).
156. TRAIL, J. W. H.: New Scottish Galls. *Ann. Scot. Nat. Hist.*, 1892, pp. 264-266.
157. TRAIL, J. W. H.: The Gall-making Diptera of Scotland. *Scot. Nat.*, N.S., vol. iii. pp. 281-288, 309-328, 373-382 (1887-88). (In this paper references are given to previous records of the occurrence of Galls in Scotland.)

HESSIAN FLY (*Mayetiola destructor*). For information concerning this, the most important member of the Family, the following may be consulted:—

158. KIRBY, WILLIAM: Some Account of the Hessian Fly (*Cecidomyia destructor*). *Loudon's Mag. Nat. Hist.*, vol. i. pp. 227-228, figs. (1829).
159. ORMEROD, ELEANOR A.: The recent Appearance of the Hessian Fly, *Cecidomyia destructor*, in Great Britain. *Journ. Roy. Agric. Soc.* (2), xxii. pp. 721-727 (1886).
160. WHITEHEAD, C.: Official Reports on the Hessian Fly. *Journ. Roy. Agric. Soc.* (2), xxii. pp. 727-729 (1886).
161. ORMEROD, ELEANOR A.; The Hessian Fly in Great Britain. London, 1886.
162. FREAM, W.: On the Hessian Fly, or American Wheat-midge, *Cecidomyia destructor*, and its Appearance in Britain. *Rept. British Assoc.*, 1887, pp. 767-768.
163. CAMPBELL, F. MAULE: The Hessian Fly. *Trans. Hertf. Soc.*, iv. pp. 180-192 (1887).
164. ORMEROD, ELEANOR A.: *Cecidomyia destructor*, Say, in Great Britain. *Trans. Ent. Soc. Lond.*, 1887, pp. 1-6, woodcuts.
165. ORMEROD, ELEANOR A.: The Hessian Fly and its Introduction into Britain. *Trans. Hertf. Soc.*, v. pp. 168-176 (1889).
166. ENOCK, F.: The Life-history of the Hessian Fly, *Cecidomyia destructor*, Say. *Trans. Ent. Soc. Lond.*, 1891, pp. 329-366, pl. xvi.
167. The Hessian Fly (*Cecidomyia destructor*). *Bd. of Agric. Leaflet*, No. 125 (Dec. 1904; revised Feb. 1907).

Other species are dealt with in the following:—

168. KIRBY, WILLIAM: History of *Tipula tritici* and *Ichneumon tipulæ*, with some Observations upon other Insects that attend the Wheat. *Trans. Linn. Soc. Lond.*, vol. iv. pp. 230-239 (1798); vol. v. pp. 96-111 (1800).
169. SHIRREFF, PATRICK: Some Account of the Wheat Fly (*Cecidomyia tritici*). *Loudon's Mag. Nat. Hist.*, vol. ii. pp. 448-451 (1829).
170. HENSLOW: On *Cecidomyia tritici*. *Report Brit. Assoc.*, 1841, pp. 72-73.
171. COUCH, JONATHAN: A few Remarks on the Midge Fly which infests the Wheat (*Cecidomyia tritici*). *24th Ann. Rept. Roy. Cornwall Polytech. Soc.*, 1856, pp. 25-26.
172. INCHBALD, P., and MEADE, R. H.: A new Cecid. *Entomologist*, xix. pp. 152-154 (1886). [*Cecidomyia muricata*, sp. n.]
173. TRAIL, J. W. H.: A new Gall-midge. *Scot. Nat.* (N.S.), vol. ii. p. 250 (1885-86). [*Hormomyia abrotani*, sp. n.]
174. MEADE, R. H.: Description of the Ash-cauliflower Gnat. *Ent. Mo. Mag.*, xxv. p. 77 (1888). [*Diplosis fraxinella*, sp. n.]
175. MEADE, R. H.: *Diplosis pyrivora*, Riley, the Pear-gnat. *Entomologist*, xxi. pp. 123-131 (1888).
176. INCHBALD, P.: *Lasioptera cerealis*, Lind. *Entomologist*, xxi. pp. 193-197 (1888).
177. MACDOUGALL, R. S.: Gall-gnats on Osiers and Willows. *Journ. Board Agric.*, xii. pp. 499-503 (1905).
178. COLLINGE, W. E.: The Life-history of the Pear-midge, *Diplosis pyrivora*, Riley. *Rept. Econ. Zool.*, No. 2, 8 pp. (1905).
179. The Pear-midge (*Diplosis pyrivora*). *Board of Agric. Leaflet*, No. 53 (Oct. 1898; revised July 1905).
180. Gall-gnats injurious to Willows and Osiers. *Board of Agric. Leaflet*, No. 165 (May 1906).
181. ALDERSON, E. MAUDE, and CONNOLD, E.: On the Occurrence of *Oligotrophus lemei*, Kieff., in England. *Ent. Mo. Mag.*, xlv. p. 202 (1909).
182. ENOCK, F.: *Clinodiplosis equestris* (Wagner); an Insect new to Britain. *Entomologist*, xlii. pp. 217-219 (1909).
183. CARPENTER, G. H.: Some Dipterous Larvæ from the Turnip. *Journ. Econ. Biol.*, vi. pp. 67-74 (1911). [Cecidomyiid not identified.]
184. TAYLOR, T. H.: Cabbage-Top in Swedes. No. 82, Univ. of Leeds and Yorks. Council for Agric. Education, 8vo., 21 pp. and figs. (1912). [*Contarinia nasturtii*, Kieff.]
185. GRIMSHAW, PERCY H.: *Oligotrophus ventricolus*, Rübs., a new Yorkshire Gall-midge. *Naturalist*, 1914, pp. 333-336, figs.

(See also works in Section XI.)

TIPULIDÆ—sens. lat. (Crane-flies).

The most useful general systematic account of the Family is the following:—

186. VERRALL, G. H.: List of British Tipulidæ, etc. ("Daddy Long-legs"), with notes. *Ent. Mo. Mag.*, xxiii. pp. 117-125, 156-160 (1886); 206-209, 263-267 (1887); xxiv. pp. 108-112 (1887); xxv. pp. 20-27, 97-99 (1888).

The general works of Walker (No. 4) and Wingate (No. 8) may also be consulted with advantage.

Additions to the List are supplied in the following papers:—

187. GRIMSHAW, PERCY H.: On the Occurrence of a new British Fly (*Trichocera maculipennis*, Mg.) in the Forth District. *Ann. Scot. Nat. Hist.*, 1906, pp. 210-211.
188. CARTER, A. E. J.: *Triogma trisulcata*, Schum., a Fly new to Britain. *Ent. Mo. Mag.*, xlviii. p. 84 (1912).
189. BERGROTH, E.: A new British Tipulid. *Ent. Mo. Mag.*, xlviii. pp. 133-136 (1912). [*Ephelia verralli*, sp. n.]
190. CARTER, A. E. J.: Two Diptera (Limnobiidæ) new to Britain. *Ent. Mo. Mag.*, xlix. pp. 180-181 (1913).

Structure and Bionomics.

191. BROWN, JAMES MEIKLE: Some Points in the Anatomy of the Larva of *Tipula maxima*. A contribution to our knowledge of the respiration and circulation in Insects. *Trans. Linn. Soc. Lond.*, xi. pp. 125-135, pls. xxiv.-xxvii. (1910).
192. MIALL, L. C.: *Dicranota*; a Carnivorous Tipulid Larva. *Trans. Ent. Soc. Lond.*, 1893, pp. 235-253, pls. x.-xiii. [See also No. 70.]
193. MIALL, L. C., and SHELFORD, R.: The Structure and Life-history of *Phalacroceras replicata*. With an appendix on the literature of the earliest stages of the *Cylindrotominæ*. *Trans. Ent. Soc. Lond.*, 1897, pp. 343-366, pls. viii.-xi.
194. The Daddy Long-legs or Crane Fly (*Tipula oleracea*, *Tipula paludosa*, etc.). *Board of Agric. Leaflet*, No. 11. (July 1894; revised July 1905). See also *Journ. Board Agric.*, i. p. 49 (1894).
195. RENNIE, JOHN: On the Biology and Economic Significance of *Tipula paludosa*. *Ann. Appl. Biol.*, ii., No. 4, pp. 235-240, pl. xxxvi. (1916).

ORTHORRHAPHA BRACHYCERA.

GENERAL.

For the Families Stratiomyidæ to Asilidæ our chief authority is Verrall's volume cited under "General Descriptive Works" (No. 7).

196. DUNCAN, JAMES: Characters and Descriptions of the Dipterous Insects indigenous to Britain. *Mag. Zool. Bot.*, vol. i. pp. 145-167, 359-368, 453-459 (1837); vol. ii. pp. 205-222 (1838). [See No. 16 for particulars.]

STRATIOMYIDÆ.

The following papers deal exclusively with this Family and may be consulted, as also the volume by Verrall (No. 7) and the general works of Walker (No. 4) and Wingate (No. 8).

197. BRUNETTI, E.: List of the British Stratiomyidæ, with analytical tables and notes. *Entomologist*, xxii. pp. 81-86, 130-134 (1889).
198. AUSTEN, E. E.: An Addition to the British Stratiomyidæ, with the description of a new genus. *Ent. Mo. Mag.*, xxxvii. pp. 241-246 (1901).
199. SHARP, D.: *Pachygaster minutissimus*, Zett., a Stratiomyid Fly new to Britain, with notes on *P. tarsalis*. *Ent. Mo. Mag.*, xxxix. pp. 221-222 (1903).
200. AUSTEN, E. E.: On the Preliminary Stages and Mode of Escape of the Imago in the Dipterous genus *Xylomyia*, Rond. (*Subula* Mg. et Auct.) with especial reference to *Xylomyia maculata*, F., and on the systematic position of the genus. *Ann. Nat. Hist.*, iii. pp. 181-190 (1899).

For life-history of *Stratiomyis* see No. 70.

LEPTIDÆ.

No special papers. Verrall's volume (No. 7) should be consulted, or, failing this, the general works by Walker (No. 4) and Wingate (No. 8).

TABANIDÆ (Breeze-flies, Gad-flies, etc.).

See Nos. 4, 7 and 8.

The following may also be consulted:—

201. AUSTEN, E. E.: On the British Species of the genus *Chrysops* (Family Tabanidæ). *Ent. Mo. Mag.*, xxxiii. pp. 224-228 (1897).
202. CRAGG, F. W.: The Structure of *Hæmatopota pluvialis* (Meigen). *Sci. Mem. Med. Ind. Calcutta*, No. 55, pp. 1-33, 7 pls. (1912).

CYRTIDÆ.

See Nos. 4, 7 and 8.

There is no special literature on this Family.

BOMBYLIIDÆ.

See Nos. 4, 7, 8 and 16.

No special literature.

THEREVIDÆ.

See Nos. 4, 7 and 8.

Also the following:—

203. COLLINGE, W. E.: Observations on the Life-history and Habits of *Thereva nobilitata*, Fabr., and other Species. *Journ. Econ. Biol.*, iv. pp. 14-18, pl. iv. (1909).

SCENOPINIDÆ.

See Nos. 4, 7 and 8.

No special literature.

ASILIDÆ (Robber-flies).

See Nos. 4, 7 and 8.

No special literature.

EMPIDIDÆ.

See Nos. 4 and 8.

The following papers will be found useful:—

204. VERRALL, G. H.: On the Species of *Empis* allied to *E. stercorea*, Linn. (including one new to Science). *Ent. Mo. Mag.*, viii. pp. 281-284 (1871-72).
205. HAMM, A. H.: Observations on *Empis livida*, L. *Ent. Mo. Mag.*, xlv. pp. 181-184 (1908).
206. HAMM, A. H.: Observations on *Empis opaca*, F. *Ent. Mo. Mag.*, xlv. pp. 132-134 (1909).
207. HAMM, A. H.: Further Observations on the Empinæ. *Ent. Mo. Mag.*, xlv. pp. 157-162 (1909).
208. CARTER, A. E. J.: *Hilara aëronetha*, Mik.: a Dipteron new to the British List. *Ent. Mo. Mag.*, xlvii. p. 83 (1911).
209. CARTER, A. E. J.: Two Flies of the genus *Tachydromia* new to the British List. *Scot. Nat.*, 1913, pp. 36-37.
210. WOOD, J. H.: *Hilara albocingulata*, sp. n. *Ent. Mo. Mag.*, xlix. p. 13 (1913).
211. EDWARDS, F. W.: A remarkable case of Venational Teratology in Diptera. [*Tachydromia articulata*, Mcq.] *Ent. Mo. Mag.*, l. p. 59 (1914).

In view of the absence of any recent British account of this Family, the following work will be found of much value, especially from the fact that it is written in English:—

212. LUNDBECK, WILLIAM: Diptera Danica. Part III. Empididæ. Copenhagen, 1910.

DOLICHOPODIDÆ.

An excellent general systematic account of this Family is the following:—

213. VERRALL, G. H.: List of British Dolichopodidæ, with tables and notes.

Ent. Mo. Mag., xl. pp. 164-173, 194-199, 223-228, 241-245 (1904); xli. pp. 51-57, 81-83, 108-112, 167-172, 189-196, 248-252 (1905). In this useful paper analytical keys are given for the determination of all the genera and species, also full details of distribution.

Other papers which may be consulted with advantage are—

214. HALIDAY, A. H.: The Characters of two new Dipterous genera (*Orphnephila* and *Machærium*), with indications of some generic subdivisions and several undescribed species of Dolichopidæ. *Zoolog. Journ.*, vol. v. pp. 350-368 (1830-31).
215. VERRALL, G. H.: List of British Dolichopidæ. *Ent. Mo. Mag.*, ix. pp. 71-74 (1872-73).
216. VERRALL, G. H.: Notes on some British Dolichopodidæ, with descriptions of new species. *Ent. Mo. Mag.*, xii. pp. 31-35, 142-148, 195-198, 245-248, 268-270 (1875-76).
217. WOOD, J. H.: *Thrypticus nigricauda*, a New Species; and notes on a few other Dolichopodidæ from Herefordshire. *Ent. Mo. Mag.*, xlix. pp. 268-270 (1913).

LONCHOPTERIDÆ.

See general works, Nos. 4 and 8.

CYCLORRHAPHA.

SYRPHIDÆ (Hover-flies).

The best general account of this Family is contained in the volume by Verrall (No. 6).

The following may also be consulted:—

218. HARDY, JAMES: Memoirs on Scottish Diptera. No. 1. The Sow Thistle Stem-boring Fly (*Cheilosia chalybeata*, Meig.). *Scot. Nat.*, i. pp. 177-180 (1871-72).
219. VERRALL, G. H.: Notes on some British Syrphi. *Ent. Mo. Mag.*, v. pp. 7-8 (1868).
220. VERRALL, G. H.: On the European Species of *Syrphus* allied to *S. ribesii*. *Ent. Mo. Mag.*, v. pp. 190-194 (1869).
221. VERRALL, G. H.: On the British Species of *Platycheirus*, including four species new to Britain. *Ent. Mo. Mag.*, vii. pp. 127-130 (1870).
222. VERRALL, G. H.: List of British Syrphidæ. *Ent. Mo. Mag.*, vi. pp. 173-176 (1870). Additions and Corrections, *op. cit.* vii. pp. 200-203 (1870-71); ix. pp. 251-256, 281-286 (1872-73).
223. VERRALL, G. H.: On the British Species of *Chilosia*. *Ent. Mo. Mag.*, vi. pp. 203-207 (1870).

224. SHARP, D. : *Chamæsyrrhus lusitanicus*, Mik., a new British *Syrphid* Fly. *Ent. Mo. Mag.*, xxxix. p. 197 (1903).
225. VERRALL, G. H. : *Callicera yerburyi*, n. sp. : a British *Syrphid* new to Science. *Ent. Mo. Mag.*, xl. p. 229 (1904).
226. BUCKTON, G. B. : The Natural History of *Eristalis tenax* or the Drone-fly. London, 8vo, pp. viii + 88, ix. pls. (1895). [See also No. 70.]
227. WILKINSON, J. J. : The Pharynx of the *Eristalis* Larva. 8vo, 9 pp. + 1 pl.
- 227a. THOMSON, J. ARTHUR : Note on the Occurrence of the Larva of the Drone-fly (*Eristalis tenax*, Linn.) as a temporary Endoparasite in Man. *Proc. Roy. Phys. Soc. Edin.*, xiii. pp. 160-161 (1894-97).
228. HARRIS, W. H. : Remarks on the Emission of Musical Notes and on the Hovering habit of *Eristalis tenax*. *Journ. Quekett Club* (2), viii. pp. 513-520 (1903).
229. SAUNDERS, E. : Mimetic resemblance between *Paragus bicolor*, Fab., a *Dipteron*, and *Prosopis variegata*, Fab., a *Hymenopteron*. *Ent. Mo. Mag.*, xxxvi. pp. 83-84 (1900).
230. The Narcissus Fly (*Merodon narcissi* [clavipes?]). *Journ. Bd. Agric.*, iii. p. 287 (1896).
- 230a. Narcissus Flies (*Merodon equestris* and *Eumerus strigatus*). *Bd. of Agric. Leaflet*, No. 286 (July 1914).

PIPUNCULIDÆ.

In addition to the general works of Walker (4) and Wingate (8) and the volume by Verrall (6), the following papers have been published on members of this Family :—

231. WALKER, FRANCIS : Observations on the British Species of Pipunculidæ. *Entomol. Mag.*, vol. ii. pp. 262-270 (1835).
232. JENKINSON, F. J. H. : *Verrallia aucta* and its Host. *Ent. Mo. Mag.*, xxxix. pp. 222-223 (1903).
233. SCOTT, HUGH : The Pupal and Adult Stages of a Fly new to Britain [*Pipunculus melanostolus*]. *Ent. Mo. Mag.*, xlv. pp. 9-11 (1908).

PLATYPEZIDÆ.

See Verrall's volume (6), also the general works of Walker (4) and Wingate (8).

The following may also be consulted :—

234. WOOD, J. H. : *Agathomyia viduella*, Zett. : A new British Fly. *Ent. Mo. Mag.*, xxxix. p. 271 (1903).
235. WOOD, J. H. : The Occurrence in Herefordshire of *Callimyya elegantula*,

- Fall, and *Agathomyia boreella*, Zett. *Ent. Mo. Mag.*, xli. pp. 5-7 (1905).
236. WOOD, J. H.: *Agathomyia elegantula*, Fall.,—a correction, and *A. zetterstedti*, Zett., a species new to Britain. *Ent. Mo. Mag.*, xlvi. pp. 45-46 (1910).

PHORIDÆ.

The most important account of these tiny flies yet published in this country is the following:—

237. WOOD, J. H.: On the British Species of *Phora*. *Ent. Mo. Mag.*, xlii. pp. 186-196, 262-266 (1906); xliv. pp. 164-174, 215-218, 253 (1908); xlv. pp. 24-29, 61-63, 113-120, 143-149, 191-195, 240-244 (1909); xlvi. pp. 149-154, 195-202, 243-249 (1910); xlviii. pp. 94-99, 166-181, pl. v. (1912); l. pp. 152-154 (1914).

Scottish species are dealt with in—

238. MALLOCH, J. R.: Phoridæ in Dumbartonshire; with description of a new species. *Ent. Mo. Mag.*, xliv. pp. 11-13 (1908).
239. MALLOCH, J. R.: Notes on Phoridæ in Dumbartonshire; with description of a new species. *Ent. Mo. Mag.*, xliv. pp. 203-205 (1908).
240. MALLOCH, J. R.: Some Phoridæ in Dumbartonshire in 1908; with description of a new species. *Ent. Mo. Mag.*, xlv. pp. 34-36 (1909).
241. MALLOCH, J. R.: Scottish Phoridæ, with tables of all the British species and notes of localities. *Ann. Scot. Nat. Hist.*, 1910, pp. 15-21, 87-92.

Other useful papers are—

242. OSTEN-SACKEN, C. R.: The position of *Phora* in the System of Diptera. *Ent. Mo. Mag.*, xxxviii. pp. 204-205 (1902).
243. WESCHÉ, W.: The Systematic Affinities of the Phoridæ and of several Brachycerous Families in Diptera. *Trans. Ent. Soc. Lond.*, 1908, pp. 283-296, pl. vii.
244. MALLOCH, J. R.: Some Observations on the Dipterous Family Phoridae. *Trans. Nat. Hist. Soc. Glasgow*, viii. pp. 153-156 (1911).
245. MALLOCH, J. R.: A Division of the Dipterous genus *Phora*, Latr., into Subgenera. *Glasgow Naturalist*, i. pp. 24-28 (1909).
246. WINGATE, W. J.: A new Species of *Phora*, and four others new to the British List. *Ent. Mo. Mag.*, xlii. pp. 110-111 (1906).
247. COLLIN, J. E.: *Phora opaca*, Mg., and *Phora perennis*, Mg. *Ent. Mo. Mag.*, xlii. pp. 177-179 (1906).
248. WOOD, J. A.: *Phora gracilis*, a new species belonging to Becker's Group I. *Ent. Mo. Mag.*, xliii. p. 228 (1907).

249. DONISTHORPE, H. : *Ænigmatias blattoides*, Meinert, captured in Scotland. *Ent. Record*, xxv. p. 277 (1913).
250. DONISTHORPE, H. : Some Notes on the genus *Platyphora*, Verrall, and *Ænigmatias*, Meinert, and a Species new to Britain. *Ent. Record*, xxvi. pp. 276-278 (1914).

CESTRIDÆ (Bot-Flies, Warble-Flies).

The most important memoirs dealing with the Flies of this Family are given below. There has been no recent general account of the group published in Britain, and the works of Walker (4) and Wingate (8) afford the principal means of identification.

The older papers are of considerable interest, and are as follows :—

251. CLARK, BRACY : Observations on the genus *Cestrus*. *Trans. Linn. Soc. Lond.*, iii. pp. 289-329 (1797).
252. LEACH, W. E. : On the Arrangement of Cestrideous Insects. *Mem. Wernerian Nat. Hist. Soc.*, ii. pp. 567-568 (1818).
253. MACLEAY, W. S. : On the Insect called *Oistros* by the ancient Greeks and *Asilus* by the Romans. *Trans. Linn. Soc. Lond.*, xiv. pp. 353-359 (1825). Abstract in *Philos. Mag.*, lxv. pp. 43-47 (1825).
254. CLARK, BRACY : Of the Insect called *Oistros* by the Ancients, and of the true species intended by them under this appellation. *Trans. Linn. Soc. Lond.*, xv. pp. 402-411 (1827). Abstract in *Philos. Mag.*, iii. pp. 283-289 (1828).
255. MACLEAY, W. S. : On the Cestrus of Mr Bracy Clark. *Zool. Journ.*, v. pp. 18-25 (1829).
256. MACLEAY, W. S. : Note on Oestrus. *Zool. Journ.*, v. p. 276 (1830).
257. HILL, — : Account of the Larva of a supposed *Oestrus hominis* or Gad-fly, which deposits its eggs in the bodies of the human species. *Edinb. New Philos. Journ.*, viii. pp. 284-288 (1830).
258. CLARK, BRACY : Supplement to a Treatise on the *Cestri* and *Cuterebræ* of various Animals. *Proc. Linn. Soc. Lond.*, i., No. xii., p. 100 (1841). Appendix to a Treatise, etc. *Trans. Linn. Soc. Lond.*, xix. pp. 81-94 (1845).
259. SELLS, W. : Observations on the Cestridæ. *Trans. Ent. Soc. Lond.*, iii., Part 2, pp. 72-78 (1842).
260. CLARK, BRACY : Note on *Cestrus equi*, the Bot of Horses. *Entomol. Mag.*, v. pp. 336-338 (1838).

Recent Memoirs on HYPODERMA.

261. ORMEROD, E. A. : Observations on Warble-fly or Ox-bot-fly. Appendix

to "Report of Observations of Injurious Insects and Common Farm Pests during the year 1894, with methods of prevention and remedy." London, 1894, 62 pp.

262. AUSTEN, E. E.: The Larval Stage of *Hypoderma bovis*. [Translation of article by P. Koorevaar.] *Ann. Nat. Hist.*, iv. pp. 69-73 (1899).
263. AUSTEN, E. E.: The Life-history of Warble-flies. *Ent. Mo. Mag.*, xxxvii. pp. 92-95 (1901).
264. Warble Flies (*Hypoderma lineata* and *H. bovis*). *Board of Agric. Leaflet*, No. 21 (Sept. 1894; revised July 1905).
265. IMMS, A. D.: On the Life-histories of the Ox Warble-flies *Hypoderma bovis* (De Geer) and *H. lineata* (Villers). *Journ. Econ. Biol.*, i. pp. 74-91 (1906).
266. CARPENTER, G. H., and STEEN, J. W.: The Warble-fly. Experiments on Cattle as to its Treatment and Life-history. *Journ. Dept. Agric. Ireland*, viii., No. 2 (22 pp. 2 pls.) (1907).
267. CARPENTER, G. H., and PRENDERGAST, W. F.: The Warble-flies. Further Experiments as to Life-history and Treatment. *Journ. Dept. Agric. Ireland*, ix., No. 3, pp. 1-13 (1909).
268. CARPENTER, G. H., and HEWITT, T. R.: Some new Observations on the Life-history of Warble-flies. *Irish Naturalist*, xxiii. pp. 214-221 (1914).
269. CARPENTER, G. H., and HEWITT, T. R.: The Reproductive Organs and the Newly-hatched Larva of the Warble-fly (*Hypoderma*). *Sci. Proc. R. Dublin Soc.*, xiv. pp. 268-289, pls. xxi.-xxvi. (1914).
(See also Nos. 94, 275, 276.)

Gastrophilus.

270. COLLINGE, W. E.: Some Observations on the Eggs of the Horse Bot-fly, *Gastrophilus equi* (Fabr.). *Journ. Econ. Biol.*, v. pp. 9-17 (1910).

Oestrus.

271. COLLINGE, W. E.: Note on the Deposition of the Eggs and Larvæ of *Oestrus ovis*, Linn. *Journ. Econ. Biol.*, i. pp. 72-73 (1906).
- 271a. The Sheep Nostril Fly (*Oestrus ovis*). *Board of Agric. Leaflet*, No. 118 (Aug. 1904; revised July 1906).

Cephenomyia and Pharyngomyia.

272. GRIMSHAW, PERCY H.: On the Occurrence in Ross-shire of *Cephenomyia rufibarbis*, a new British Bot-fly parasitic on the Red Deer. *Ann. Scot. Nat. Hist.*, 1895, pp. 155-158.

273. GRIMSHAW, PERCY H.: *Cephenomyia rufibarbis* in Britain. *Proc. Ent. Soc. Lond.*, 1896, p. xvi.
274. BLOOMFIELD, E. N.: *Cephenomyia auribarbis*, Mg.: Larvæ, etc. *Ent. Mo. Mag.*, xxxiv. pp. 7-8 (1898).
275. AUSTEN, E. E.: Notes on the Cestrine parasites of British Deer. *Ent. Mo. Mag.*, xxxiv. pp. 8-13 (1898).
276. YERBURY, J. W.: Habits of *Cephenomyia rufibarbis* and *Hypoderma diana*. *Proc. Ent. Soc. Lond.*, 1904, pp. lxxvii, lxxviii.

TACHINIDÆ.

The best general systematic account of the British Tachinidæ is—

277. MEADE, R. H.: Annotated List of British Tachiniidæ. *Ent. Mo. Mag.*, xxvii. pp. 85-94, 125-129, 153-157, 228-232, 263-267, 324-329, (1891); xxviii. pp. 17-20, 35-39, 75-79, 93-97, 126-130, 150-153, 177-182, 210-212, 233-237, 259-262 (1892); Supplement, *op. cit.* xxx. pp. 69-73, 107-110, 156-160 (1894).

Other general papers (arranged chronologically) are—

278. MEADE, R. H.: Parasitic Diptera. *Ent. Mo. Mag.*, xvi. pp. 121, 122 (1879). (See also No. 96.)
279. MEADE, R. H.: Notes on Diptera. *Entomologist*, xiv. pp. 285-289 (1881).
280. WAINWRIGHT, C. J.: Tachinidæ collected in 1900. *Ent. Mo. Mag.*, xxxvii. pp. 212-215 (1901).
281. WAINWRIGHT, C. J.: Notes on Tachinidæ. No. 1. *Ent. Mo. Mag.*, xli. pp. 199-207 (1905).
282. MORLEY, C.: On a few Tachinidæ and their Hosts. *Entomologist*, xxxix. pp. 270-274 (1906).
283. LEIGH, H. S.: Observations on the Life-histories and Bionomics of some Tachinidæ. *Entomologist*, xli. pp. 113-116 (1908).

On particular species (arranged chronologically)—

284. NEWMAN, EDW.: An Account of the parasitic *Musca larvarum* preyed on by parasitic *Pteromali*. *Loudon's Mag. Nat. Hist.*, v. pp. 252-255 (1832).
285. NEWPORT, GEO.: Notes on the Dipterous Parasites which attack the Common Earwig and the Emperor Moth (*Metopia Forficulæ* and *Exorista larvarum*). *Proc. Linn. Soc. Lond.*, ii., No. liii., pp. 247-249 (1853).
286. MEADE, R. H.: Description of a new Dipteron of the genus *Phorocera* inhabiting Britain. *Ent. Mo. Mag.*, xxxiii. pp. 223-224 (1897).

287. AUSTEN, E. E.: Two additional British Species of the Dipterous genus *Erigone*, Rob.-Desv. *Ent. Mo. Mag.*, xli. pp. 57-60 (1905).
288. HAMM, A. H.: *Setulia grisea*, Mg., and *Cerceris arenaria*, Linn., in the New Forest. *Ent. Mo. Mag.*, xlv. pp. 273-274 (1909).
289. WAINWRIGHT, COLBRAN J.: *Setulia grisea*, Mg., a Tachinid new to Britain and its Allies. *Ent. Mo. Mag.*, xlv. pp. 275-277 (1909).
290. COLLIN, JAMES E.: *Zenillia (Myxoxorista) roseanae*, B. and B., a new British Dipteron. *Entomologist*, xlii. pp. 1-2 (1909).
291. WESCHÉ, W.: Notes on the Life-history of the Tachinid Fly *Phorocera serriventris*, Rondani, and on the Viviparous Habit of other Diptera. *Journ. Quekett Club* (2), x. pp. 451-458, pl. xxxvi. (1909).
292. RENNIE, J.: Note upon a Tachinid parasite (*Bucentes geniculatus*, D. G.) of *Tipula* sp. *Proc. Roy. Phys. Soc. Edinb.*, xviii. pp. 231-234 (1912).
293. WARDLE, R. A.: Preliminary Observations upon the Life-histories of *Zenillia pexops*, B. and B., and *Hypamblys albopictus*, Grav. *Journ. Econ. Biol.*, ix. pp. 85-104, pls. iv.-vi. (1914).

SARCOPHAGIDÆ (Flesh-flies).

The following papers will be of considerable aid in the identification of British Flesh-flies:—

294. MEADE, R. H.: Monograph upon the British species of *Sarcophaga*, or Flesh-fly. *Ent. Mo. Mag.*, xii. pp. 216-220, 260-268 (1875-76).
295. MEADE, R. H.: On Two Additional British species of Sarcophagidæ, or Flesh-flies. *Ent. Mo. Mag.*, xxv. pp. 27-28 (1888).

MUSCIDÆ, *sensu stricto* (House-flies, Blue-bottles, etc.).

Of late years great attention has been paid to the structure and bionomics of certain members of this Family, especially in the case of *Musca domestica*, the Common House-fly. To give anything like a complete bibliography of the Muscidæ is entirely beyond the scope of this paper. The following list must therefore be regarded merely as a selection of those volumes and papers published in this country which are considered to be either of outstanding importance, easily accessible, or of special interest to the general student of British Diptera. Thus the great majority of memoirs whose interest is mainly a medical one have been excluded.

No general account of the Muscidæ from a systematic point of view exists in British literature beyond the general works of Walker (4) and Wingate (8). The keys given in the latter are the most useful for the purpose of identification.

Full details of the typical House-fly (*Musca domestica*) and Blue-bottles

or Blow-flies (*Calliphora vomitoria* and *erythrocephala*) from all points of view are given in the following important works:—

296. LOWNE, B. T.: The Anatomy and Physiology of the Blow-fly (*Musca vomitoria*). London, 1870, 121 pp., 10 pls.
297. LOWNE, B. T.: The Anatomy, Physiology, Morphology, and Development of the Blow-fly (*Calliphora erythrocephala*). London, 1890-1895, 2 vols., pp. 778, 52 pls. and 108 figs.
298. HEWITT, C. GORDON: The House-fly (*Musca domestica*, Linn.): its Structure, Habits, Development, Relation to Disease and Control. Cambridge University Press, 1914, 382 pp., 104 figs. In this work a very full bibliography is given, which includes papers in all languages and many of a purely medical interest.

The following memoirs may also be consulted:—

299. HEWITT, C. GORDON: The Structure, Development, and Bionomics of the House-fly, *Musca domestica*, Linn. Parts I, II., and III. *Quart. Journ. Micr. Sci. Lond.*, li. pp. 395-448, pls. xxii.-xxvi. (1907); lii. pp. 495-545, pls. xxx.-xxxiii. (1908); liv. pp. 347-414, pl. xxii. (1909).
300. SUMMERS, SOPHIA L. M.: Epitome of blood-sucking Muscidae, *Glossina* excepted. *Journ. School. Trop. Med. Lond.*, i. pp. 189-205 (1912).

Further papers dealing with anatomy are—

301. ANTHONY, —: The Suctorial Organs of the Blow-fly. *Monthly Microsc. Journ.*, vol. xi. p. 242 (1874).
302. STEPHENS, J. W. W., and NEWSTEAD, R.: The Anatomy of the Proboscis of Biting Flies. Part 2, *Stomoxys*. *Ann. Trop. Med. and Parasit.*, i. pp. 169-198, pls. xii.-xix. (1907).
303. HEWITT, C. G.: The Proboscis of the House-fly. *Brit. Med. Journ.*, 23rd November 1907, p. 1558.
304. WESCHÉ, W.: The Proboscis of the Blow-fly, *Calliphora erythrocephala*, Mg.—A Study in Evolution. *Journ. Quekett Club* (2), x. pp. 283-294, pls. xxii., xxiii. (1908).
305. NELSON, E. M.: Some Hairs upon the Proboscis of the Blow-fly. *Journ. Quekett Club* (2), x. pp. 227-228 (1908).
306. GRAHAM-SMITH, G. S.: Some Observations on the Anatomy and Function of the Oral Sucker of the Blow-fly (*Calliphora erythrocephala*). *Journ. Hygiene*, ii. pp. 390-408, 5 pls. (1911).
307. HAMMOND, A.: On the Thorax of the Blow-fly (*Musca vomitoria*). *Journ. Linn. Soc. (Zool.)*, xv. pp. 9-31, 2 pls. (1881).
308. HEPWORTH, J.: On the Structure of the Foot of the Fly. *Quart. Journ. Micr. Sci.*, ii. pp. 158-160 (1854).

309. MERLIN, A. A. C. E.: The Foot of the House-fly. *Journ. Quekett Club* (2), vi. p. 348 (1897). Supplementary Note, *op. cit.* ix. pp. 167-168 (1905).

Papers dealing mainly with the habits of House-flies—

310. NEWSTEAD, ROBERT: On the Habits, Life-cycle, and Breeding-places of the Common House-fly (*Musca domestica*, Linn.). *Ann. Trop. Med. Liverpool*, i. pp. 507-520, pls. xliv.-xlix. (1908).
311. GRAHAM-SMITH, G. S.: Observations on the Habits and Parasites of Common Flies. *Parasitology*, viii. pp. 440-544, pls. xxiii.-xxx. (1916).
312. HINDLE, E., and MERRIMAN, G.: The Range of Flight of *Musca domestica*. *Journ. Hygiene*, Cambridge, xiv. pp. 23-45 (1914).
313. HINDLE, E.: The Flight of the House-fly. *Proc. Phil. Soc. Cambridge*, xvii. pp. 310-313 (1914).
314. GRIFFITH, A.: The Life-history of House-flies. *Public Health*, 1908, pp. 122-127.
315. VARLEY, C.: Microscopical Observations on a Malady affecting the Common House-fly. *Trans. Micros. Soc. Lond.*, iii. pp. 55-57, 1 pl. (1852).
316. THEOBALD, F. V.: Swarms of Flies bred in House-refuse. *2nd Report on Economic Zool. Brit. Mus. Nat. Hist.*, pp. 125-126 (1904).
317. JEPSON, F. P.: The Breeding of the Common House-fly (*Musca domestica*) during the winter months. *Journ. Econ. Biol.*, iv. pp. 78-82 (1909).
318. SAUNDERS, WINIFRED H.; Fly Investigation Reports.—I. Some Observations on the Life-history of the Blow-fly and of the House-fly, made from August to September 1915, for the Zoological Society of London. *Proc. Zool. Soc. Lond.*, 1916, pp. 461-463.
319. SAUNDERS, WINIFRED H.: Fly Investigation Reports.—II. Trials for Catching, Repelling, and Exterminating Flies in Houses, made during the year 1915 for the Zoological Society of London. *Proc. Zool. Soc. Lond.*, 1916, pp. 465-468.
320. SAUNDERS, WINIFRED H.: Fly Investigation Reports.—III. Investigations into Stable Manure to check the Breeding of House-flies, made during the year 1915 for the Zoological Society of London. *Proc. Zool. Soc. Lond.*, 1916, pp. 469-479.
321. LODGE, OLIVE C.: Fly Investigation Reports.—IV. Some Enquiry into the Question of Baits and Poisons for Flies, being a Report on the Experimental Work carried out during 1915 for the Zoological Society of London. *Proc. Zool. Soc. Lond.*, 1916, pp. 481-518.

The following series of "Reports on Flies as Carriers of Infection" have been published by the Local Government Board (Reports on Public Health and Medical Subjects, New Series), and contain information of considerable interest:—

- 322.** JEPSON, F. P.: Some Observations on the Breeding of *Musca domestica* during the winter months. No. 3, Prelim. Repts., pp. 5-8 (1909).
- 323.** AUSTEN, E. E.: Notes on Flies examined during 1908. How to distinguish the more important species of Flies found in houses. No. 5, Prelim. Repts., pp. 3-4 (1909).
- 324.** NUTTALL, G. H. F., and JEPSON, F. P.: The part played by *Musca domestica* and Allied (non-biting) Flies in the Spread of Infective Diseases. A summary of our present knowledge. No. 16. Further Prelim. Repts., pp. 13-41 (1909).
- 325.** BERNSTEIN, J.: Summary of Literature relating to the Bionomics of the Parasitic Fungus of Flies; *Empusa muscae*, Cohn, with special reference to the economic aspect. No. 40. Further Repts. (No. 3), pp. 41-45 (1910).
- 326.** COPEMAN, S. M., HOWLETT, F. M., and MERRIMAN, G.: An Experimental Investigation on the Range of Flight of Flies. No. 53. Further Repts. (No. 4), pp. 1-10, 1 map, 1 table (1911).
- 327.** AUSTEN, E. E.: Memorandum on the Result of Examinations of Flies, etc., from Postwick Village and refuse deposit; with a Note on the Occurrence of the Lesser House-fly at Leeds. No. 53. Further Repts. (No. 4), pp. 11-12 (1911).
- 328.** HEWITT, C. G.: Observations on the Range of Flight of Flies. No. 60. Further Repts. (No. 5), pp. 1-5, with map (1912).
- 329.** AUSTEN, E. E.: British Flies which cause Myiasis in Man. No. 60. Further Repts. (No. 5), pp. 5-15 (1912).
- 330.** COPEMAN, S. M.: Hibernation of House-flies (Preliminary Note). No. 85. Further Repts. (No. 6), pp. 14-19 (1913).
- 331.** NUTTALL, G. H. F., HINDLE, E., and MERRIMAN, G.: The Range of Flight of *Musca domestica*. No. 85. Further Repts. (No. 6), pp. 20-41, 11 charts (1913).
- 332.** HINDLE, E.: Note on the Colour Preference of Flies. No. 85. Further Repts. (No. 6), pp. 41-43 (1913).

Stomoxys, Lucilia, etc.

- 332a.** MEADE, R. H.: On *Musca hortorum*, Fallén, and Allied Species. *Ent. Mo. Mag.*, xvii. pp. 22-28 (1880).

333. TULLOCH, F. : The Internal Anatomy of *Stomoxys*. *Proc. Roy. Soc. Lond.*, Series B, vol. 77, pp. 523-531 (1906).
334. NEWSTEAD, R. : On the Life-history of *Stomoxys calcitrans*, Linn. *Journ. Econ. Biol.*, i. pp. 157-166, pl. xii. (1906).
335. MACDOUGALL, R. S. : The Sheep Maggot-fly—Preliminary Report. *Trans. Highl. and Agric. Soc. Scot.*, 1904, 16 pp.
336. The Sheep Maggot-fly (*Lucilia sericata*). *Board of Agric. Leaflet*, No. 126 (Feb. 1905).
337. MACDOUGALL, R. S. : Sheep Maggot and Related Flies. Their classification, life-history, and habits. *Trans. Highl. and Agric. Soc. Scot.*, 1909, p. 42.
338. GUTHRIE, L. G. : On a Toad killed by the Larvæ of Blow-flies. *Ent. Mo. Mag.*, xxviii. pp. 9-12 (1892).

The agency of the flies of this Family in disseminating disease is fully dealt with in the works of Graham Smith (No. 92), Hewitt (No. 298), and others, but the following memoirs (arranged chronologically and selected from a much longer list) may be consulted with advantage :—

339. HEWITT, C. GORDON : On the Bionomics of certain Calyprate Muscidæ and their Economic Significance, with especial reference to Flies inhabiting houses. *Journ. Econ. Biol.*, ii. pp. 79-88 (1907).
340. AUSTEN, E. E. : Blood-sucking and other Flies known or likely to be concerned in the spread of Disease. In: Allbutt's and Rolleston's *System of Medicine*, vol. ii. pp. 169-186 (1907).
341. HEWITT, C. G. : The Biology of House-flies in relation to the public health. *Journ. R. Inst. Pub. Health*, xvi. pp. 596-608, 3 figs. (1908).
342. NASH, J. C. T. : House-flies as Carriers of Disease. *Journ. Hygiene*, ix. pp. 141-169 (1909).
343. HEWITT, C. G. : House-flies and how they spread Disease. Cambridge, 12 mo., xii + 122 pp. (1912).
344. AUSTEN, E. E. : The House-fly as a danger to Health, its Life-history and how to deal with it. *Brit. Mus. Econ. Series*, London, i. 12 pp., 2 pls. (1913).

ANTHOMYIIDÆ.

The most complete systematic account of the British species is the following :—

345. MEADE, R. H. : Descriptive List of the British Anthomyiidæ. London, Gurney & Jackson, 8vo, 79 pp. (1897). Analytical keys are given of all the genera and species, also short descriptions and indications

of distribution. This work is virtually a revision of the following paper, which should be simultaneously consulted:—

- 346.** MEADE, R. H.: Annotated List of British Anthomyiidae. *Ent. Mo. Mag.*, xviii. pp. 1-5, 27-28, 62-65, 101-104, 123-126, 172-176, 201-205, 221-224, 265-270 (1881-82); xix. pp. 29-33, 145-148, 213-220 (1882-83); xx. pp. 9-14, 59-61, 104-109 (1883-84). Supplements, *op. cit.* xxiii. pp. 179-181, 250-253 (1886-87); xxiv. pp. 54-58, 73-76 (1887-88); xxv. pp. 393-396, 424-426, 448-449 (1888-89).

The following papers are of interest from a bionomic or economic point of view:—

- 347.** JENYNS, L.: Notice of a Case in which the Larvæ of a Dipterous Insect supposed to be the *Anthomyia canicularis*, Meig., were expelled in large quantities from the human intestines. *Trans. Ent. Soc. Lond.*, ii. p. 153 (1839).
- 348.** HEWITT, C. GORDON: On the Life-history of the Root Maggot, *Anthomyia radicum*, Meigen. *Journ. Econ. Biol.*, ii. pp. 56-63, pl. vi. (1907).
- 349.** LUCAS, W. J.: Some Points in the Life-history of *Anthomyia spreta*, Meig. *Entomologist*, xlii. pp. 241-242, pl. vi. (1909).
- 350.** FRYER, H. F., and FRYER, J. C. F.: *Hylemyia coarctata*, Flin.: a destructive wheat pest. *Ent. Mo. Mag.*, xlv. pp. 134-135 (1909).
- 351.** HEWITT, C. G.: An Account of the Bionomics and the Larvæ of the Flies *Fannia (Homalomyia) canicularis*, L., and *F. scalaris*, Fab., and their relation to Myiasis of the Intestinal and Urinary Tracts. *Parasitology*, Cambridge, v. pp. 161-174, pl. vii. (1912); also Repts. Local Govt. Board on Publ. Health and Med. Subjects (N.S.), No. 60. Further Repts. (No. 5) on Flies as Carriers of Infection, pp. 15-22, 3 figs. (1912).
- 352.** HUIE (Miss), L. H.: The Habits and Life-History of *Hylemyia grisea*, Fall., an Anthomyiid Fly new to the Scottish Fauna. *Scot. Nat.*, 1916, pp. 13-20, 8 figs.
(See also No. 92.)

The two following papers are monographs of genera:—

- 353.** GRIMSHAW, PERCY H.: On the British species of *Hydrotæa*. *Ent. Mo. Mag.*, xli. pp. 239-247 (1905); xlii. pp. 8-11, 72-77 (1906).
- 354.** MALLOCH, J. R.: The British Species of the Dipterous genus *Fannia*, Rob. Dsv. *Scot. Nat.*, 1912, pp. 133-139, 154-162, 175-182, 201-209, 233-235.

Papers on particular species:—

- 355.** HARDY, JAMES: Memoirs on Scottish Diptera. No. II., *Anthomyia*

- sonchi*, sp. nov. (the Sow-Thistle Fly). *Scot. Nat.*, i. pp. 209-212 (1871-72); No. III. *Anthomyia Jacobææ*, sp. nov. (the Ragwort-seed Fly), *tom. cit.* pp. 254-256 (1871-72); No. VI. *Anthomyia mitis*, Meigen (the Dock-leaf Miner), *op. cit.* ii. pp. 63-68 (1873-74).
356. GRIMSHAW, PERCY H.: On a new British Fly (*Hydrotæa pilipes*, Stein) from the Forth District. *Ann. Scot. Nat. Hist.*, 1904, pp. 158-160.
357. Mangold Fly (*Pegomyia betæe*, Curtis). *Board of Agric. Leaflet*, No. 5 (Jan. 1898; revised Oct. 1905). See also *Journ. Bd. Agric.*, i. p. 47 (1894).
358. The Onion Fly (*Phorbia cepetorum*). *Board of Agric. Leaflet*, No. 31 (July 1896; revised Feb. 1905). See also *Journ. Bd. Agric.*, iii. p. 157 (1896).
359. The Cabbage Root Fly (*Phorbia brassicæ*). *Board of Agric. Leaflet*, No. 122 (Dec. 1904).
360. WATERSTON, JAMES: *Polietes hirticornis*, Meade, ♀. *Ent. Mo. Mag.*, xlii. pp. 269-270 (1906).
361. GRIMSHAW, PERCY H.: *Hydrotæa borussica*, Stein, a Fly new to the British List. *Ann. Scot. Nat. Hist.*, 1907, pp. 223-225.
362. CARTER, A. E. J.: Two new British Diptera: *Pegomyia esuriens*, Mg., and *P. univittata* v. Ros. *Ent. Mo. Mag.*, xliv. pp. 128-129 (1908).
363. MALLOCH, J. R.: Two new Species of *Anthomyiidae*, in the genus *Fannia*, R. D. (= *Homalomyia*, Bouché). *Ent. Mo. Mag.*, xlvi. pp. 67-68 (1910).
364. HARDY, J. RAY: A *Dipteron* new to the British Fauna. [*Fannia (Homalomyia) insignis*, Stein.] *Ent. Mo. Mag.*, xlvi. p. 188 (1910).
365. WOOD, J. H.: Four unrecorded British *Anthomyiidae*, two of them being at the same time new to Science. *Ent. Mo. Mag.*, xlix. pp. 84-87 (1913).
366. WORDSWORTH, J. T.: Note on an Anthomyid Fly, *Phaonia (Hyetodesia) trimaculata*, Bouché, new to the British List. *Ent. Mo. Mag.*, li. pp. 142-143 (1915).

ACALYPTRATÆ.

The most important recent paper on the Acalyptrate Muscidæ is that by Collin (No. 37).

SCATOMYZIDÆ.

367. MEADE, R. H.: A descriptive List of the British Cordyluridæ. *Ent. Mo. Mag.*, xxxv. pp. 169-177, 217-224 (1899).
368. WESCHÉ, W.: The Male Organs of the Flies *Scatophaga lutaria* and *S. stercoraria*. *Journ. Quekett Club* (2), viii. pp. 411-416, pl. xxii. (1903).

PHYCODROMIDÆ.

No special literature.

BORBORIDÆ.

369. HALIDAY, A. H. : British species of the Dipterous Tribe Sphæroceridæ. *Entomol. Mag.*, iii. pp. 315-336 (1836).
370. COLLIN, J. E. : Four new Species of Diptera (Fam. Borboridæ) found in Britain. *Ent. Mo. Mag.*, xxxviii. pp. 55-60 (1902).

DRYOMYZIDÆ.

No special literature.

HETERONEURIDÆ.

371. COLLIN, J. E. : Three new Species of the "albimana" group of the genus *Heteroneura* (Diptera). *Ent. Mo. Mag.*, xlvi. pp. 106-108 (1912).

HELOMYZIDÆ.

372. COLLIN, J. E. : The genus *Heteromyza*, Fallén (Helomyzidæ). *Ent. Mo. Mag.*, xxxvii. pp. 106-113 (1901).
373. MALLOCH, J. R. : *Eccoptomera microps*, Mg., and *Agromyza bicornis*, Kalt., two Diptera new to the British List. *Ent. Mo. Mag.*, xlv. pp. 180-181 (1908).

SCIOMYZIDÆ and SAPROMYZIDÆ.

No special literature.

LONCHÆIDÆ.

374. CAMERON, A. E. : On the Life-history of *Lonchæa chorea*, Fab. *Trans. Ent. Soc. Lond.*, 1913, pp. 314-322, pl. xi.

ORTALIDÆ.

375. WESCHÉ, W. : An Addition to the British List of Diptera. [*Ulidia nigripennis*, Lw., teste Austen, but only *erythrophthalma*, Mg., teste Collin, *Ent. Mo. Mag.*, xlvi. p. 174 (1910).] *Ent. Mo. Mag.*, xli. p. 227 (1905).
376. LAMB, C. G. : A Case of Antennal Teratology in the Diptera [*Ptilonota guttata*, Mg.]. *Ent. Mo. Mag.*, xlvii. p. 216 (1911).

TRYPETIDÆ.

377. WALKER, FRANCIS : Descriptions of the British Tephritites. *Entomol. Mag.*, iii. pp. 57-85 (1836).
378. HARDY, JAMES : Memoirs on Scottish Diptera. No. V. *Trypeta alternata*, Fallén (the Rose-hip Fly). *Scot. Nat.*, ii. pp. 21-23 (1873-74).
379. WADSWORTH, J. T. : Some Observations on the Life-history and Bionomics

of the Knapweed Gall-fly *Urophora solstitialis*, Linn. *Ann. Appl. Biol.* (Cambridge), i. pp. 142-169, pls. xi., xii. (1914).

380. The Celery Fly (*Acidia heraclei*). *Bd. of Agric. Leaflet*, No. 35 (March 1897; revised Aug. 1905).
381. The Asparagus Fly (*Platyparea pæciloptera*). *Bd. of Agric. Leaflet*, No. 124 (Dec. 1904).
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BRAULIDÆ.

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A considerable number of volumes and papers of a purely faunistic character have been published, and I hope to have an opportunity of preparing a list of these, arranged geographically, at an early date. It will be published as a Supplement to the foregoing.

(Issued separately, 12th March 1917.)

IX.—*Calliobdella nodulifera* (Malm 1863).¹ By W. Harold Leigh-Sharpe, B.Sc. (Lond.).

(*With Plates.*)

(Read 23rd October 1916. MS. received 8th December 1916.)

RECORD AND HABITAT.—The material upon which the following observations are based was sent to me, through the courtesy of Prof. L. A. L. King, by Mr Richard Elmhirst from the Scottish Marine Biological Association, Millport. It consisted of—(1) Two leeches taken in May 1915 off S.E. of Bute; (2) about three dozen leeches brought in at various times by fishermen; (3) two leeches caught by Mr Elmhirst, while trolling with “fly,” who noticed that the leeches were moving rapidly as though trying to leave the host fish as it was brought out of the water. These specimens were fixed in Schaudinn’s fluid, and from them most of the sections were cut.

All these leeches were taken on the saithe or coalfish, *Gadus carbonarius*, Linn., from the head and gill-covers. I have also a specimen sent by Dr Bowman of Aberdeen, taken from a megrim, *Lepidorhombus* (*Arnoglossus*) (*Zeugopterus*) *megastoma*, caught in the Minch on 15th March 1910. Leeches are uncommon on flat-fish (except *Hemibdella soleæ* on the sole), but, as the megrim was caught in a trawl, there is a chance that the leech was derived from other fish taken at the same time. Unlike most of the leeches that have come under my observation, *C. nodulifera* appears to be catholic in its choice of hosts. Thus Malm originally records it from *Gadus morrhua*. Johansson found it on *Gadus morrhua*, *G. aeglefinus*, *G. merlangus*, *Merluccius vulgaris*, *Molva vulgaris*, *Raia batis*, *Hippoglossus vulgaris*, *Anarrhichas lupus*, and *Trigla gurnardus*. Olsson found it on *Gadus morrhua*, *Molva vulgaris*, *Trigla gurnardus*, *Raia batis*, *Gadus virens*, *Sebastes norvegicus*, *Raia fullonica*, *Acanthias vulgaris* and *Chimæra monstrosa*. Nor does this exhaust the list. It is unnecessary, however, to continue since it is obvious that the host is here of but little physiological significance; I have quoted these at length only to show that, apart from isolated instances in which single specimens have been recorded, the bulk of the evidence points to the fact that the Gadidæ are preferred.

¹ References to previous papers :—

1914. *Calliobdella lophii*: *Parasitology*, vii, 204.

1916. *Platybdella anarrhiche*: *Parasitology*, viii, 274.

At the end of either of these papers will be found a full list of references to other authors hereinafter cited.

I have examined the two specimens in the British Museum which are labelled *Pontobdella littoralis*, Johnston, since it is possible that the latter is *Calliobdella* sp., and probable that it is either *Calliobdella nodulifera* or *Trachelobdella lubrica*, Grube. One of these specimens recorded from Sukkertoppen, Greenland, as living on *Laminaria* (Holboll's Coll.), does indeed resemble the species I am considering, but, as is only natural in a preserved specimen, no respiratory vesicles are visible. The pigment cells, however, under the low power of the microscope form a valuable clue. The other specimen, from 30 fathoms, off the coast of Greenland, is spoilt and unrecognisable as a leech.

SYNONYMY.—I do not know whether this preference for the *Gadidæ*, which I have mentioned, influenced Johansson when he remarked that he considered three species of Malm, viz. *Piscicola crassicaudata*, *P. subfasciata* and *P. gracilis* to be identical with *Calliobdella (Piscicola) nodulifera*. Let us consider what their claims are. In *C. nodulifera*, Malm saw the respiratory vesicles in series on both sides of the abdomen, and in his figure shows thirteen pairs. Unless he is mistaken on this point the animal he saw should, in my estimation, be placed in the genus *Trachelobdella*. But in the other three species he says there are no respiratory vesicles. I will pass over this point considering it natural that they collapsed after death and so were invisible. The remaining characters are :

P. crassicaudata.—Posterior sucker oval and almost double the anterior.

Anterior sucker sub-elliptical. Body with irregular yellowish-brown dots. Host: *Gadus morrhua*.

P. subfasciata.—Transverse bands across the body. Suckers circular, and the posterior broader than the abdomen and twice the size of the anterior. Host: *Gadus merlangus*.

P. gracilis.—Posterior sucker a quarter as broad again as the anterior, broader than the abdomen; body irregularly dotted; no bands. Host: *Trigla gurnardus*.

Now, when we come to consider that the most prominent *specific* character of *Calliobdella nodulifera* is that the posterior sucker is broader than the abdomen and twice the size of the anterior sucker (though Malm says it is not quite), and the next important that it is dotted irregularly with brownish-yellow, we can, I think, very easily read these characters to cover what is written about the three preceding species, such distinguishing marks as a sucker being "as quarter as large again" being of but little use in a spirit-preserved specimen, where only a unit multiple such as twice as large, or four times as large, is the least that can be appreciated. In none of these

species were any eyes observable. Assuming, therefore, that these three species had respiratory vesicles which Malm failed to see, we can safely say they are synonymous with *C. nodulifera*. In *P. crassicaudata*, however, a blood-red colour was observed, which is very lurid and arresting in his coloured plate. This, however, is only a variation, and would not constitute a specifically different feature.

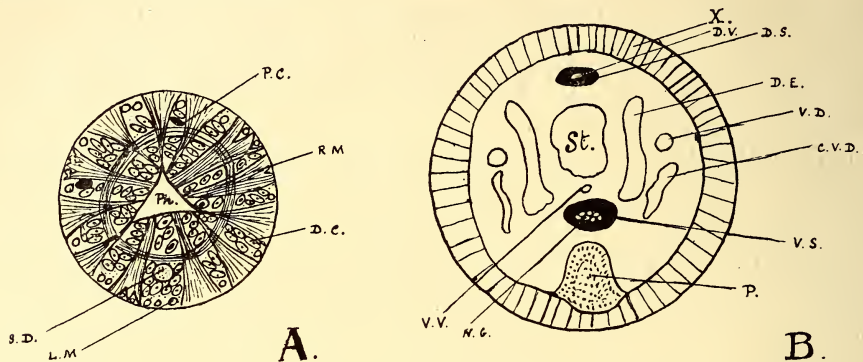


FIG. 1. TRANSVERSE SECTIONS THROUGH VARIOUS PORTIONS OF THE NECK OF *CALLIOBDELLA NODULIFERA*.

A. Through the pharyngeal region. B. Through the anterior portion of the clitellum. R.M. radial muscles; L.M. longitudinal muscles; Ph. pharynx; D.C. dermal cells; P.C. pigment cells; S.D. salivary duct; X. The body wall, containing the layers shown in Plate VI., but without the cocoon-gland cells; St. stomach; D.S. dorsal sinus; V.S. ventral sinus; D.V. dorsal blood-vessel; V.V. ventral blood-vessel; V.D. vas deferens; C.V.D. coiled portion of the vas deferens; D.E. ductus ejaculatorii; P. penis; N.G. nerve ganglion.

ORGANISATION.—The segmentation and the respiratory, digestive and reproductive systems are as I have described them for *Calliobdella lophii* (1914); the cocoon-gland cells as I have described them for *Platybdella anarrhichæ* (1916). The bursa and the penis do not in this species attain to so great a development in proportion to the size of the body as in *C. lophii*. A large proportion of the preserved leeches have the penis extruded.

BODY WALL.—The *epidermis* consists of a layer of columnar cells elongated in a direction at right angles to the long axis of the body, having their nuclei, which are large, away from the external border, and a cuticle secreted at the free edge. At frequent intervals among these epithelial cells are flask-shaped glands, usually known as epithelial glands, which are mucus-secreting. They are present in most leeches, e.g. *Branchellion*, *Piscicola*, *Cystibranchus*, etc., but notably absent in *Platybdella*. The *derma* is rich in large flattened cells 35–45 μ in length and half as thick, which do not appear to form a definite layer as in *Platybdella*, but are scattered as in *Branchellion*.

Their nuclei are large, and flattened in the same manner and direction as the cells. The large dermal cells are embedded in a matrix of connective tissue cells, among which are numerous fibre-forming cells more conspicuous than in other genera. The most striking feature of the derma is the occasional occurrence of large pigment cells, which are about 40μ in length, almost as large as the large dermal cells. The pigment is yellowish-brown, and the leech can be recognised by the pigment cells when viewed by transmitted light, after the whole specimen has been cleared in oil of cloves. The colour does not dissolve in alcohol, and is preserved in the sections. Below the derma lie the muscle layers, which consist, as in most leeches, of one row of circular muscles, one row or so of oblique muscles, and some three rows of longitudinal muscles, below which are the cocoon-gland cells, concerning which I have nothing further to add to the description of them which I have already given in the case of *Platybdella*. In *Calliobdella* they attain the same huge and remarkable size as in *Platybdella*, viz. $200-150\mu$ by $100-150\mu$. Amongst these cells run the cocoon-gland cell ducts interspersed with longitudinal muscle fibres in the proportion of three of the former to one of the latter.

CÆLOM.—The body cavity consists of the five following parts, which can be well seen in Plate V. :—a dorsal sinus, a ventral sinus, two lateral sinuses, and, in the cæcum region of the abdomen, an intestinal sinus. The dorsal blood-vessel is for the greater part of its length inside the dorsal sinus, but in the cæcum region it lies outside and dorsal to it, the intestinal sinus being between it and the dorsal sinus. The ventral blood-vessel is outside the ventral sinus, and dorsal to it. This is not so in *C. lophii*, and constitutes a specific difference. The ventral nerve cord is within the ventral sinus. The intercommunications of the sinuses can be best seen from Plate V.

GENERIC CHARACTERS.—See *Parasitology*, vii. pp. 215 and 217.

SPECIFIC CHARACTERS.—The body is not so flattened, nor is the neck marked off so distinctly from the abdomen as in *C. lophii*. The body is bestrewn with yellow dots due to the presence of characteristic pigment-cells, which are more numerous than, and are of a different colour and character from, those in *C. lophii*. The posterior sucker is twice the size of the anterior. According to Hesse the eggs are oval, while those of *C. lophii* are spherical. The ventral blood-vessel is outside the ventral sinus. Not confined to one host, but appears to show a preference for the Gadidæ.

EXPLANATION OF PLATES V. AND VI.

PLATE V. *Calliobdella nodulifera*.—Transverse sections through various portions of the abdomen. *A.* Through the anterior part of the testis region. *B.* Through the middle part of the testis region. *C.* Through the posterior part of the testis region. *D.* Through the anterior part of the caecum region. *E.* Through the middle part of the caecum region. *F.* Through the posterior part of the caecum region. *X.* The body wall, containing the whole of the layers shown in Plate VI. *St.* stomach; *C.* caecum; *R.V.* respiratory vesicles; *D.V.* dorsal blood-vessel; *V.V.* ventral blood-vessel; *D.S.* dorsal sinus; *V.S.* ventral sinus; *L.S.* lateral sinuses; *I.S.* intestinal sinus; *Int.* intestine; *N.G.* nerve ganglion; *N.C.* nerve cord.

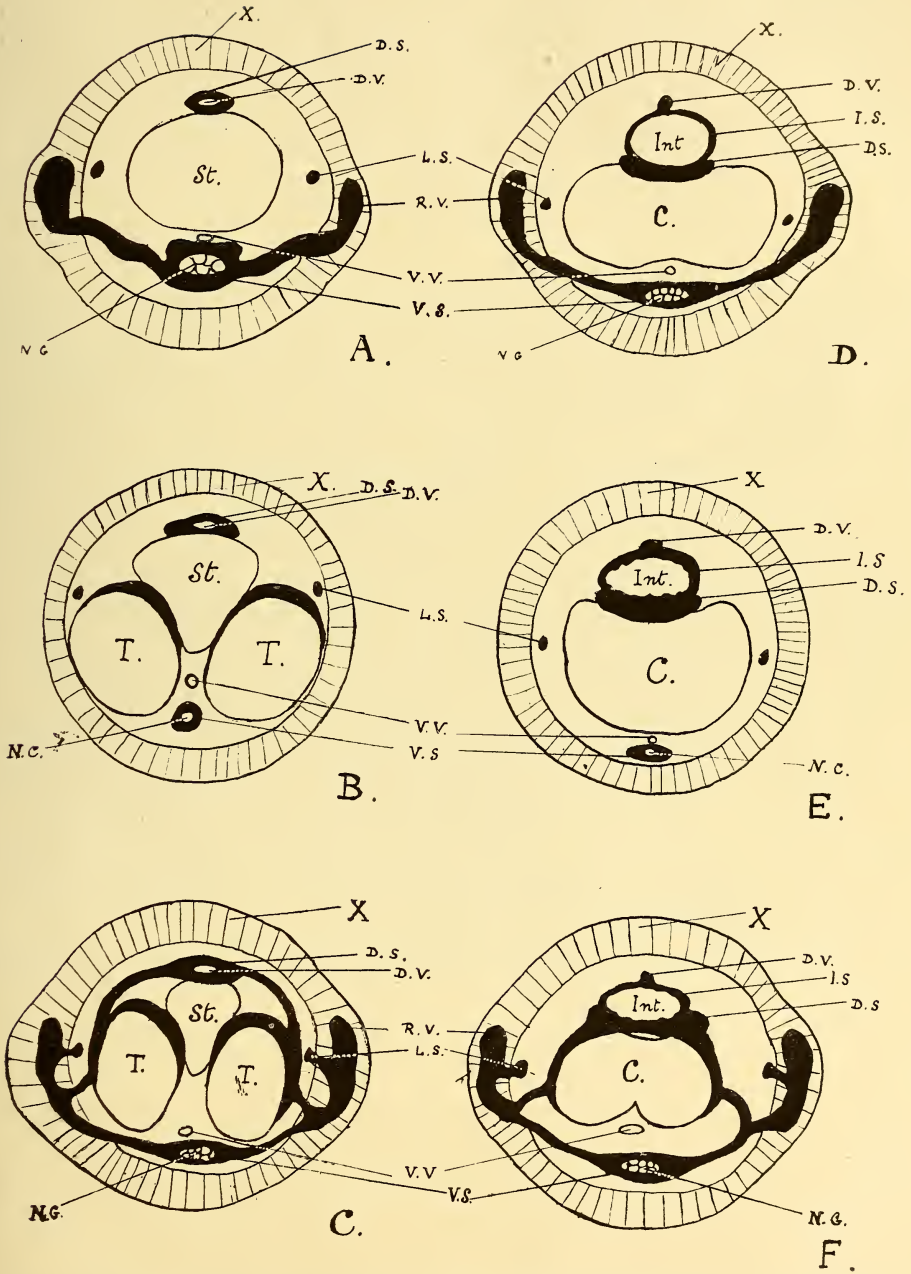
PLATE VI. *Calliobdella nodulifera*.—Longitudinal section through the body wall, viewed under a high magnification, from a preparation stained in Hæmalum, 5 min., Eosin, 5 min. *Cut.* cuticle; *Ep.* epidermis; *S.* epithelial mucus gland; *Fibr. L.* fibrous cell layer; *D.C.* large subdermal cells; *P.* yellowish-brown pigment cell; *M.L.* muscle layers (*C.* circular; *Ob.* oblique; *Long.* longitudinal); *c.g.c.* cocoon-gland cells; *c.g.c.d.* cocoon-gland cell ducts.

(Issued separately, 12th March 1917.)

PLATE V.

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Royal Physical Society, Edinburgh.

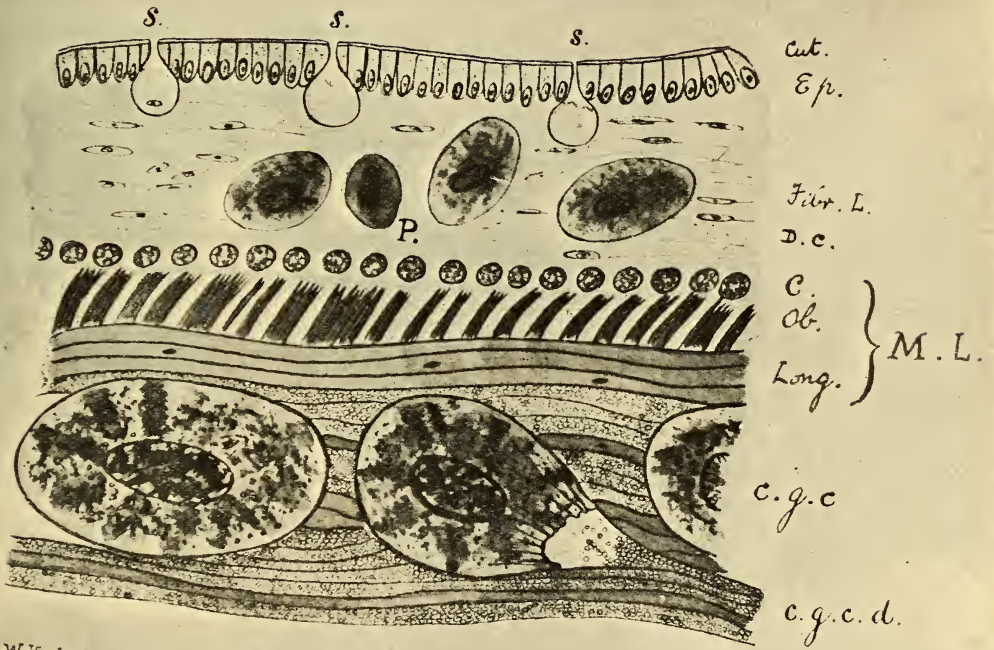


TRANSVERSE SECTIONS THROUGH THE ABDOMEN OF CALLIOBDELLA NODULIFERA.

PLATE VI.

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LONGITUDINAL SECTION THROUGH BODY WALL OF CALLIOBELLA NODULIFERA.

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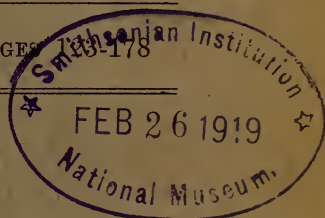
PROMOTION OF ZOOLOGY AND OTHER BRANCHES OF
NATURAL HISTORY.

SESSIONS 1915-1916 AND 1916-1917.

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EDINBURGH: M'FARLANE & ERSKINE,

DECEMBER 1917.

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X.—“The genus *Hylastes*, Er., and its Importance in Forestry—a Study in Scolytid Structure and Biology.” By James W. Munro, B.Sc. (Agr.), B.Sc. (For.). Communicated by William Evans, F.R.S.E.

(With Plates and Text-Figures.)

(Received 18th December 1916. Read 18th December 1916.)

IN the British literature on the Scolytidæ or Bark Beetles little attention has been paid to the genus *Hylastes*, and even from economic workers in the group the genus has received only scanty consideration.

The genus *Hylastes*, Er., comprises five British species, of which three are of considerable interest to the forester, namely, *Hylastes ater*, Pk., *H. palliatus*, Gyll., and *H. cunicularius*, Er. The remaining species, *H. opacus*, Er., and *H. angustatus*, Herbst, are sufficiently uncommon to be considered rare by collectors of the Coleoptera.

It is the object of this paper to describe the general structure, life-history, and habits of the various species of *Hylastes*, and especially to estimate their economic importance in our woodlands. The writer has practical experience of only three of the five species, and this paper is accordingly confined to these three, namely, *H. ater*, Pk., *H. cunicularius*, Er., and *H. palliatus*, Gyll. In the case of *H. ater* and *H. palliatus* systematic observations on the life-history and habits have been made both in the field and in the laboratory. In the case of *H. cunicularius* no laboratory observations were made, and the field observations were unfortunately made at somewhat irregular intervals. The latter, however, are of sufficient interest to justify some account of them being given here.

MATERIAL.

Three sets of material have been made use of in the study of *Hylastes*.

- (a) Material used for the comparison of the various species and the description of the structure of *H. ater*.
- (b) Material used in the laboratory observations and confined to the two species *H. ater* and *H. palliatus*.
- (c) Material studied in the field.

Material for Comparison of the Species.

Adults and larvæ of *H. ater* and *H. palliatus* were obtained from practically all the eastern counties of Scotland during 1914–16. *H. cunicularius* material,

however, was obtained only from two districts—a limited number of adults and larvæ from Skene, Aberdeenshire, in October 1914, and the greater part from Darnhall, Peeblesshire, during 1915–16.

Material used in Laboratory Observations.

(a) *H. ater* material.—Adults and larvæ from Kingswells, Aberdeenshire, were the subject of experiments during winter, 1914–15. In October 1915, adults and larvæ were obtained from Drumshoreland, West Lothian, and Balerno, Midlothian. These, together with adults obtained at Balerno in April 1916, formed the material for the chief experiments.

(b) *H. palliatus* material.—Adults obtained at Balerno, Midlothian, in May 1916, were used for laboratory experiments.

Material for Field Observations.

(a) *H. ater* material.—The majority of the field observations on this species were made in an open Scots pine wood, near Balerno, in which a few trees had been felled, from the roots of which the laboratory material was obtained. This area afforded excellent opportunities for comparison between the life-history in the field and in the laboratory. Other localities were also visited, the chief being a felled area at Drumshoreland, Midlothian, and a recently planted area on Darnhall Estate, Peeblesshire.

(b) *H. palliatus* material.—The chief centre for field observations on *H. palliatus* was a mixed wood of larch, spruce, and Scots pine near Balerno, Midlothian, which had suffered badly from snowbreak and windbreak. It also afforded a check for the laboratory observations, as the laboratory material was obtained from it. Observations on *H. palliatus* were also made in other localities, the chief being a large area of Scots pine on Earlyvale Estate, Peeblesshire.

(c) *H. cunicularius* material.—Field observations on *H. cunicularius* were restricted to two areas adjoining one another on Darnhall Estate, Peeblesshire. In October 1915, these consisted of a fairly extensive planted area and a smaller area in process of felling. In May and June 1916, this latter area was cleaned and planted, and on it all observations relating to the habits of *H. cunicularius* were made.

THE STRUCTURE OF *H. ATER* AND COMPARISON WITH *H. PALLIATUS*
AND *H. CUNICULARIUS*.

Methods.

In the study of the structure of *H. ater* and comparison of it with that of its congeners, the following methods were adopted :—

In the case of the adults, sketches were made from mounted specimens by means of a simple dissecting microscope and a camera lucida of the Abbé type adapted for use with low power magnification. This type of camera is not in common use in Britain. It was originally designed by the Leitz firm, but, at my suggestion, it has been copied and is now obtainable from Watson & Sons of London. It has proved extremely useful for obtaining sketches for the comparison of general characters in species, and in the study of *Hylastes* especially, as affording fairly accurate sketches indicating the relative proportions of the thorax and elytra in the various species.

For more detailed structure a binocular dissecting microscope and a Porro prism have proved most useful, as also for the preparation of slides for examination under the higher powers of the ordinary compound microscope.

For general structure, magnifying powers of 8, 16, 20 and 50 diameters have been used, and for detailed structure the $\frac{1}{8}$ -inch and $\frac{2}{3}$ -inch objectives, used in combination with a No. 4 eyepiece. Two pairs of fine-pointed forceps and a pair of dissecting-needles have proved all that was necessary for dissection purposes.

In examining detailed structures, such as the mouth-parts, the meso- and meta-terga, and tergites of the abdomen, boiling in 10 per cent. caustic potash was resorted to, and the parts when clear were washed in water and alcohol and, after clearing in clove oil, were mounted in Canada balsam in the ordinary way. The same methods were used in the examination of the gizzard and the chitinous parts of the genitalia.

Examination and preparation of the reproductive organs and alimentary canal required more care. These were dissected out in a 10 per cent. solution of salt and water, fixed in corrosive sublimate, stained with borax carmine, passed through the usual alcohols and mounted in Canada balsam.

Generic Characters.

According to Fowler¹ the members of the genus *Hylastes* show the following characters:—"Eyes not divided; funiculus of antennæ seven-jointed, the first joint large and shining, the second short; club of antennæ ovate; thorax not prolonged over the head, not bordered at the sides; anterior coxæ contiguous; third tarsal joint dilated and bilobed."

Of the three species of the genus under review, I have chosen *H. ater*, Pk., as the type for description and comparison. It is the largest species of the genus, and is nearly always to be found in numbers in most districts where pine woods occur.

¹ *Coleoptera of Great Britain and Ireland*, vol. v. p. 432.

Head and Mouth-parts. (Plate VII.)

Head (Figs. 1, 2).—The chief feature of the head is the absence of well-defined regions. Viewed from above, there is no division into *frons*, *epicranium*, or *vertex* as in the ground beetles such as *Harpalus*. Labrum and clypeus are absent. The anterior border of the head is therefore the epistome, which lies like a bridge over the mandibles. It is not sharply defined posteriorly, but it can be made out as a slightly raised ridge bearing rows of bristles. In the middle of this ridge a U-shaped depression surrounded by a slight elevation probably indicates the remains of the clypeus and labrum. From this depression a more or less distinct median line runs backwards to the line of the eyes, which are easily recognised. On either side of this line, lying anteriorly, is a well-marked depression. Viewed laterally, the absence of definite regions is again a feature of the head. The eye with its supra-orbital ridge, the pregena and the antenna with its triangular scrobe or pit, are the chief features. Viewed from beneath, the head shows a distinct gular suture running forward from the occipital foramen. This suture joins at right angles the precula, a narrow short plate lying between the pregenæ. Anterior to these plates is the hypostome, to which are attached the maxillæ and labium.

Mouth-parts (Figs. 3–6).—These consist of the *mandibles*, the *maxillæ*, and the *labium*. The *mandibles* are strongly chitinous, triangular in general shape. Their inner surfaces each bear three teeth, of which the first or apical is the most prominent. They are controlled by two muscles, one (*ad.* in figure) the adductor which closes them, the other (*ab.* in figure) the abductor which draws them apart. The adductor is the larger. Each of these muscles is strengthened by a chitinous tendon imbedded in it.

The *maxillæ* are of the typical Scolytid type. The cardo is distinct. The stipes is fused with the palpifer, galea, and lacinia, but the regions are recognisable by the variation of their bristles. A distinct fold serves to indicate the line of fusion of the palpifer; this bears a three-jointed *palp*. The galea is indistinct. The lacinia is easily recognised. In addition to bristles it bears a row of broader spines which probably serve to clean the mandibles of resin, as Blackman has observed in *Pityogenes hopkinsi*.¹

The *labium* consists of the *submentum*, *mentum*, *ligula*, and *labial palpi*. The *submentum* is peculiar and consists of a forked process adjoining the median portion of the hypostome. The labium bears on its dorsal or inner surface a well-defined tongue-shaped ligula (Fig. 5) armed with short

¹ Blackman, *Observations on the Life-history and Habits of P. hopkinsi*, Swaine, Syracuse University Techn. Pub., No. 2.

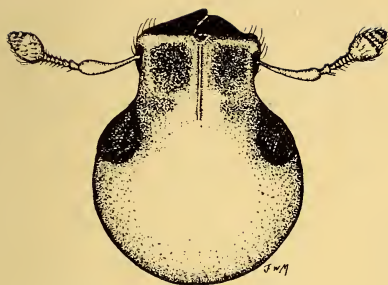


FIG. 1.—Head from above.

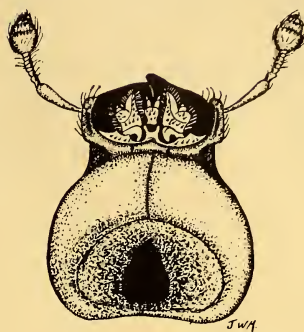


FIG. 2.—Head from below.

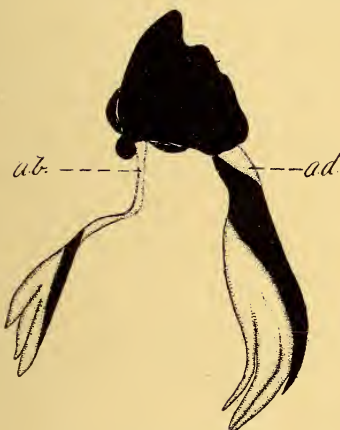


FIG. 3.—Left Mandible.

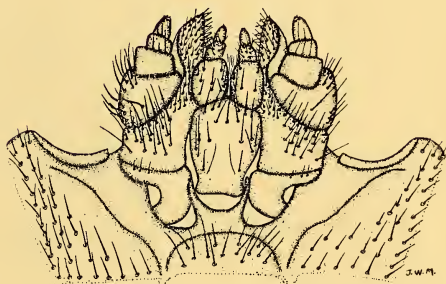


FIG. 4.—Maxillæ and Labium
(ventral aspect).

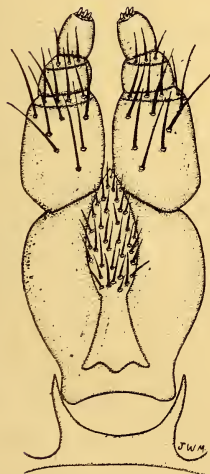


FIG. 5.—Labium.

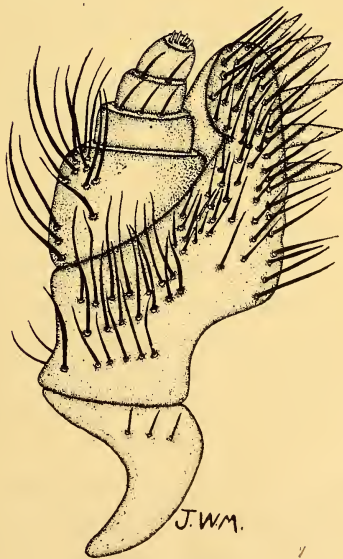


FIG. 6.—Maxilla.

stout spines. The palpi are three-jointed, the first joint being as long as the second and third joints together.

Antennæ (Fig. 7).—These, as is usual in the Scolytidæ, are geniculate and are divisible into three parts—the *scape* or shaft adjoining the head, the *funiculus* or whip forming the median portion, and the *club* or apical



FIG. 7.—The Antenna of *H. ater*.

portion. The whip is seven-jointed, the first joint being large and conspicuous, the second joint smaller, the third joint smallest, while the remaining four increase gradually to the seventh which adjoins the club. The club is oval, slightly acuminate, and shows three sutures.

Thorax. (Figs. 8-12.)

The *thorax* is divisible into three distinct segments, *prothorax*, *mesothorax* and *metathorax*.

Prothorax.—This is the most prominent of the three regions. Viewed dorsally, it is long and narrow with the sides sub-parallel and rounded in front. It is markedly longer than broad (Fig. 12). It is strongly punctured at the sides, less so at the disc, where there is a more or less distinct impuncturate median line. This line is very variable, being sometimes reduced to a mere patch. It is not raised. No division into separate regions is visible, and, except for the puncturation, the dorsal surface of the prothorax is featureless.

Viewed from the side, the prothorax is seen to taper ventrally towards the coxæ, which are large and prominent. Its puncturation is coarser than that of the dorsal surface, except for a small and slightly raised circular area above the coxæ.

Viewed ventrally, the prosternum is distinct, being defined by two ridges running from the anterior border to the coxæ. The coxæ are almost contiguous.

Mesothorax.—Viewed dorsally, this region is almost completely hidden by the prothorax anteriorly and by the elytra posteriorly, only the circular scutellum being visible. If the prothorax and elytra are removed the

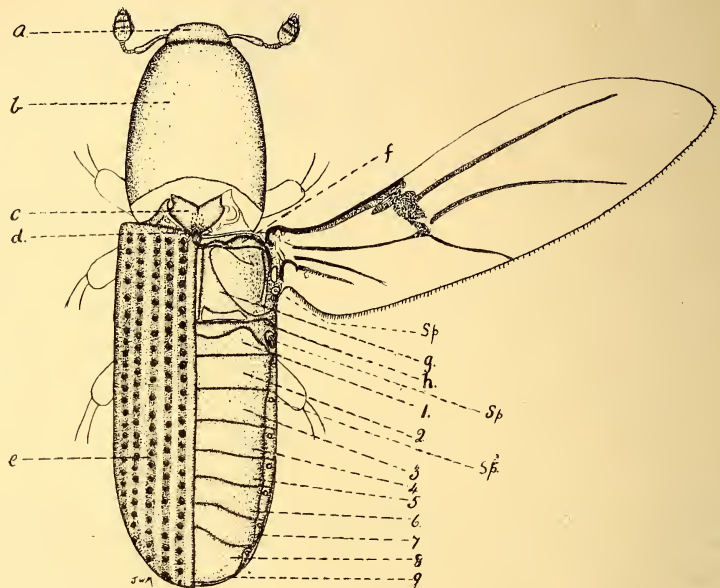


FIG. 8.—*H. ater* ♂, Pk. (dorsal aspect). (Right elytron and part of pronotum removed.)

- | | |
|----------------------------|-----------------------------------|
| a. Head. | f. Prescutum of metathorax. |
| b. Prothorax (pronotum). | g. Mesoscutum of metathorax. |
| c. Mesothorax (mesonotum). | h. Postscutum of metathorax. |
| d. Scutellum. | sp. Spiracles. |
| e. Elytron. | 1, 2, 3, etc. Abdominal tergites. |

following regions can be recognised—the *prescutum*, the *scutum*, and the *scutellum*. The prescutum and the circular scutellum are strongly chitinous. The scutum and the lateral extension of the scutellum are soft and flexible. The *prescutum* is peculiar in shape. Its anterior border is roughly V-shaped. Its lateral borders diverge about the middle to form a lobe and then taper posteriorly to meet the scutellum. The *scutum* is rudimentary and is divided from the lateral extensions of the scutellum by a mere line of folding. The *scutellum* is knob-like and extends laterally as a thin band of flexible chitin.

Viewed from the side, the mesothorax shows the episternum lying anteriorly, and the epimeron adjoining it posteriorly. Both are irregularly triangular in shape.

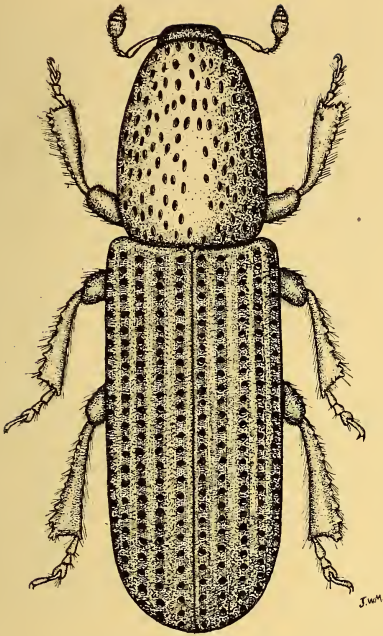


FIG. 9.—Dorsal Surface.

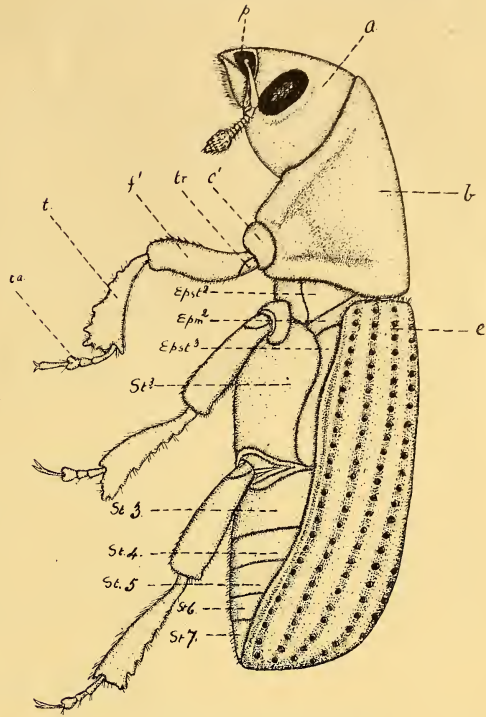


FIG. 10.—Side View.

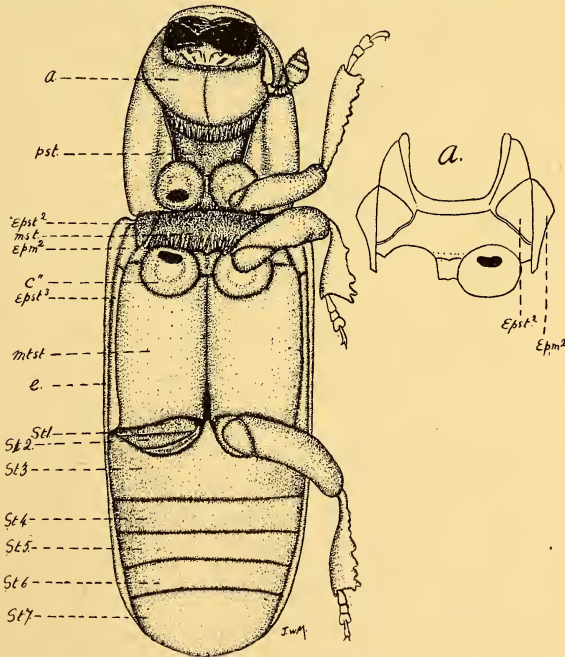


FIG. 11.—Ventral Aspect of ♀ (Mesosternum at side).

- | | | | |
|---|--------------------------------------|--|--------------------------|
| <i>a.</i> Head. | <i>b.</i> Prothorax. | <i>e.</i> Elytron. | <i>p.</i> Antennal pit. |
| <i>Epst².</i> Episternum of mesothorax. | <i>Epm².</i> Epimeron of mesothorax. | <i>St³.</i> Sternum of metathorax. | |
| <i>Epst³.</i> Episternum of metathorax. | <i>St³.</i> 3rd Abdominal sternite. | <i>St⁴.</i> 4th Abdominal sternite, etc. | |
| <i>c', c''.</i> Coxa. | <i>tr.</i> Trochanter. | <i>f¹.</i> Femur. | <i>t.</i> Tibia. |
| <i>Pst.</i> Prosternum. | <i>Mst.</i> Mesosternum. | <i>ta.</i> Tarsus. | <i>Mst.</i> Metasternum. |

From the ventral aspect the mesothorax is seen to be divided into *prosternum*, *mesosternum* and *poststernum*, while the episternum and epimeron are again visible. The *prosternum* is a narrow area divided from the mesosternum by a linear impression. The *mesosternum* occupies the remainder of the mesothorax, except for a small trapezoidal area lying between the coxæ. This represents the *poststernum*.

The Metathorax.—The regions of the metathorax are somewhat complicated and are best indicated by the figures. The three regions—*prescutum*, *mesoscutum*, and *postscutum*—are visible dorsally on the removal of the wings and the elytra.

Viewed ventrally, the epimeron and the various areas connected with the wing attachment are visible together with the long narrow episternum.

On the under surface, the sternum occupies nearly the whole of the area. It bears a well-marked, median line, running from its anterior to its posterior borders. A small irregular, triangular piece lying between the coxæ represents the poststernum.

Wings and Appendages.

The *elytra* or first pair of wings are attached to the prescutum. They are distinctly furrowed, the furrows being further deepened by rows of circular pits. The *strigæ* are roughly crenate. The wings are attached to the metascutum and are of the typical Scolytid type.

Legs.

All the usual joints are present in the legs of *Hylastes*. The three pairs of legs are all somewhat similar in structure. They vary in two respects—in the shape and position of the coxæ and in the tooth-like projections on the outer margin of the tibiæ.

In the first pair of legs the coxæ are almost contiguous. They are roughly circular and very prominent. The tibiæ are shorter and broader and bear six teeth on the outer margin.

In the second pair of legs the coxæ are more oval, less prominent than in the first pair and slightly wider apart. The tibiæ are slightly longer and narrower than in the first pair of legs and bear seven teeth on their outer margin.

The coxæ of the third pair of legs are only slightly prominent. They are almost contiguous and extend laterally to the wing covers. The tibiæ of the third pair of legs are longer and narrower than in the others. They bear on their outer margins a series of small teeth variable in number, followed by seven or eight more prominent teeth. It should be observed that by the articulation of the trochanters and coxæ the legs are capable of a pivot-like movement.

H. ater nearly always walks in the same plane as the surface on which it is moving, the tibiæ alone being vertical.

Spiracles.

I have been able to locate only one pair of *spiracles* on the thoracic region, namely, on the metathorax just beside the wing attachment.

Abdomen. (Figs. 8-11.)

Tergites and Pleurites.—These are visible dorsally. Eight segments are distinct. Except for the last four and for the spiracles of the first they call for no special mention. The spiracles of the first segment are very large, probably five times the size of the succeeding spiracles. On the tergites of segments 5, 6 and 7 paired membranous areas can be distinctly seen as semi-transparent oval patches. They are further distinguished by the nature of their bristles which are bifid and stouter than those of the general covering. Tergites 7 and 8 are of special interest, as they afford very definite secondary sexual characters. In the male beetle both of these segments are visible. In the female, tergite 7 covers tergite 8. The seventh tergite is further distinguished in the male as being the seat of a somewhat rudimentary stridulating organ. This is composed of two tiny processes on the posterior border of the tergite, and a stouter chitinous band extending across the tergite just anterior to these processes. In *Hylastes ater*, as will be seen later, another secondary sex character occurs on the seventh abdominal sternite, but, in *H. palliatus* and *H. cunicularius* it is wanting, or not sufficiently marked to justify any reliance being placed on it. Accordingly, the secondary sex characters exhibited by the seventh and eighth tergites are of considerable interest.

Sternites.—Seven of these can be distinguished. Sternites 1 and 2, however, are hidden by the coxæ of the third pair of legs. They lie in the coxal cavities, and are represented by two membranous bands of chitin separated by a narrow linear fold. The remaining sternites, 3 to 6, call for no special mention. They are densely covered with fine bristles or hairs. Sternite 7 affords a valuable secondary sex character. In the male there lies in the middle of the sternite a distinct hollow fringed by a pubescent fovea which, despite wear and tear, is wonderfully constant. In the female, the 7th sternite is broader and deeper than in the male, and both depression and fovea are absent. I have found these characters of the greatest value in determining sex. The character of the male is mentioned by Fowler in his description of *H. ater*. Sternites 8 and 9 are probably represented by certain plates to be described later with the genitalia.

Comparison of External Features of H. PALLIATUS and H. CUNICULARIUS with H. ATER.

The chief feature for comparison of these three species is the general conformation; *H. ater* is elongate and narrow, *H. cunicularius* elongate and broad, and *H. palliatus* short and broad. Throughout the structure of each the proportions of the various parts correspond with those of the whole insects. Thus, the metathorax shows those proportions as also does the metasternum. Certain parts of the external structure, however, afford additional comparative characters, notably the prothorax (Fig. 12). For the

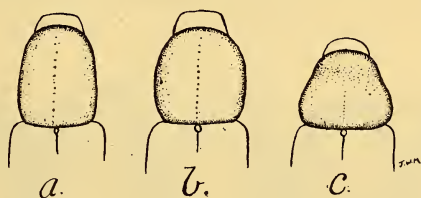


FIG. 12.—Prothorax.

a. *H. ater*. b. *H. palliatus*. c. *H. cunicularius*

sake of brevity, I have summarised the most important features in the following table. It should be observed that the mouth-parts of all three species are very similar and afford no comparative characters.

Character	<i>H. ater</i>	<i>H. cunicularius</i>	<i>H. palliatus</i>
Length	4.5 mm.	3.5-5 mm.	2.5-4 mm.
Breadth of Elytra at base	1.3-1.5 mm.	1.5-2 mm.	1.3-1.5 mm.
Head	Frontal ridge distinct, narrow.	Frontal ridge less distinct.	Frontal ridge more or less distinct, broad.
Prothorax	Longer than broad, elongate oval, sides sub-parallel. Impuncturate median line not raised, not extending to apex. Puncturation sparse on disc.	As broad as long but varying slightly, roundly oval. Impuncturate line raised, extending to apex. Puncturation uniform throughout.	Broader than long, blunt pear-shaped, sides tapering anteriorly. Impuncturate line raised, not extending to apex. Puncturation uniform throughout.
Metasternum	Slightly broader than long.	Markedly broader than long.	Twice as broad as long.
Sternite 7 of male	Fovea present.	Fovea absent.	Fovea absent.
Colour of mature adult	Black, shining.	Dark brown to black, dull.	Pale brown to dark brown.

Alimentary Canal of H. ater, adult. (Figs. 13 and 14.)

The alimentary canal of *H. ater* may be divided into three regions—the *foregut*, the *midgut*, and the *hindgut*. The *foregut* comprises the œsophagus or gullet, the crop and the gizzard or proventriculus. The *midgut* comprises the ventriculus and the stomach with its diverticula. The *hindgut* comprises the intestine with its malpighian tubules, the colon and the rectum. The *foregut* terminates at the junction of the gizzard with the ventriculus, the *midgut* at the malpighian tubules, and the *hindgut* with the rectum or anus.

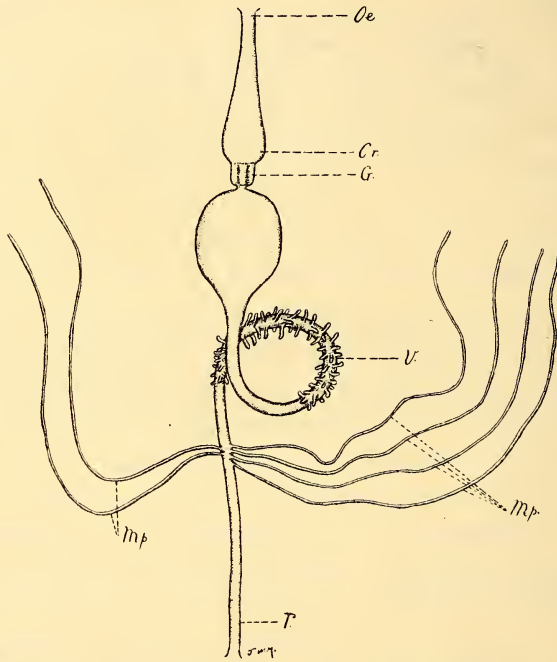


FIG. 13.—Alimentary Canal of *H. ater*, Pk.

Oe.	œsophagus.	V.	Villi.
Cr.	Crop.	Mp.	Malpighian tubules.
G.	Gizzard.	R.	Rectum.

Foregut.—The *foregut* opens at its junction with the hypopharynx and the epipharynx, which form the entry to the œsophagus. The œsophagus is a narrow tube which dilates gradually to form the crop. No glands open into the œsophagus. The crop narrows slightly at its junction with the gizzard, which is easily recognised by its brown, strongly chitinous appearance. In cross-section the gizzard is roughly octagonal in shape. It is composed of eight plates (Fig. 14), each bearing a complex arrangement of teeth and bristles which, doubtless, serve for the crushing and tearing of the bast and

bark on which *Hylastes* feeds. The junction of the gizzard and the ventriculus is very distinct, being marked by a sudden constriction of the canal. This is rendered more distinct by the large size of the ventriculus, which is fully twice the diameter of the gizzard. The ventriculus tapers posteriorly to its junction with the stomach. The stomach is a long tube, narrow at its extremities but slightly dilated in its middle portion, which is further distinguished by the numerous villi or diverticula arising from it; these are short and usually curved. The stomach terminates at its junction with the intestine which, for convenience sake, may be said to be further distinguished by the opening of the malpighian tubules into it. The intestine is a long, narrow, coiled tube varying in diameter according as it is filled with frass



FIG. 14.—Gizzard of *H. ater* cut open to show structure (only half the organ is shown).

or not. The malpighian tubules are six in number, and are arranged in two groups of two and four respectively. They are remarkably long, very narrow tubes, much coiled, and difficult to dissect out without mutilation. The *foregut* extends from the mouth to the prothorax; the *midgut* occupies the meso- and meta-thoracic regions; while the *hindgut*, together with the reproductive organs, fill the abdominal cavity.

Reproductive Organs of H. ater. (Plate IX. Figs. 15–18, and 19.)

The importance of an examination of the reproductive organs of the bark beetles, and, particularly, of a knowledge of those of the female, in studying the biology of a species has been insisted on by Nusslin. The state of these organs in the female is a valuable key to her sex maturity and even to her approximate age.

Male Reproductive Organs (Fig. 15).—These comprise the *testes*, the paired *vasa deferentia* with their *sperm sacs* and *diverticula*, the unpaired *vas deferens*, and the *penis*. The *testes* are two in number, lying on either side of the median line. Viewed ventrally, they appear as flat discs; laterally, they appear

doubly convex. Each disc presents the appearance of being made up of a number of segments. From the centre of each disc a short tube arises, the paired vasa deferentia, which unite to form the unpaired vas leading to the penis. Midway between the testes and the unpaired vas a short tube opens from the paired vasa and immediately branches into two long diverticula. Just below these short tubes the bulb-shaped sperm sacs lie. The unpaired vas deferens is formed by the junction of the paired vasa, and for about a third of its length is of the same diameter. It then tapers, and, enclosed in chitin and muscle, enters the penis. The penis comprises three chitinous plates—the ring, the sheath, and the fork. The ring is a thin circular band

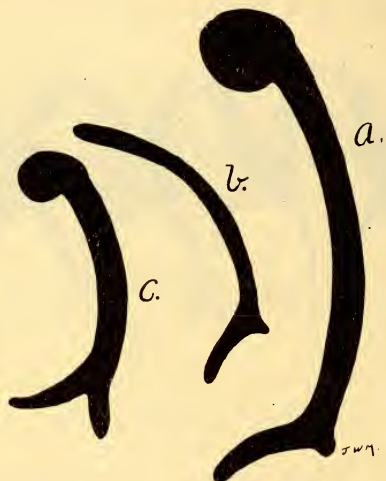


FIG. 19.—Male Genital Forks (all to same scale).
a. H. ater. *b. H. palliatus.* *c. H. cunicularius.*

of chitin encircling the sheath. It bears anteriorly a short projection, the anterior process. The sheath consists of a fine plate of chitin, the edges of which overlap and partly enclose the fleshy part of the penis. It extends anteriorly into two fine rods, the femora, which are attached to the ring and fork by muscle. Towards the base of the sheath two small plates arise from either side. The fork is a long chitinous rod diverging at its posterior end into two branches, a long and a short, not unlike the toe and heel of a boot, and terminating anteriorly in a flattened club (Fig. 19).

These chitinous parts of the genitalia in the male serve as valuable characters for the identification of species. The fork is the most convenient of these characters.

Female Reproductive Organs (Figs. 16, 17, 18).—These consist of the ovaries, the paired oviducts, the unpaired oviduct or uterus, the receptaculum seminis, the bursa copulatrix, the vagina, and a pair of slime glands. The ovaries are two

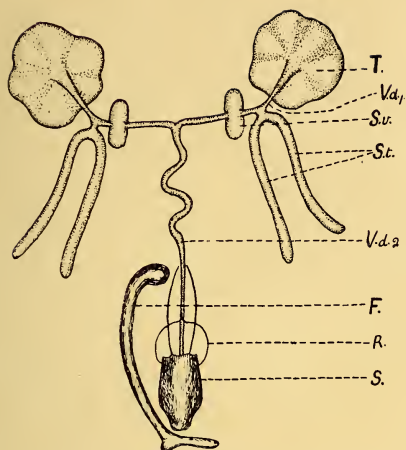


FIG. 15.—Male Reproductive Organs.

- | | | | |
|----------------------------|----------------------|-----------|---------|
| <i>V.d.</i> ₁ . | Paired vas deferens. | <i>T.</i> | Testes. |
| <i>S.v.</i> | Seminal vesicles. | <i>F.</i> | Fork. |
| <i>S.t.</i> | Seminal tubes. | <i>R.</i> | Ring. |
| <i>V.d.</i> ₂ . | Vas deferens. | <i>S.</i> | Sheath. |

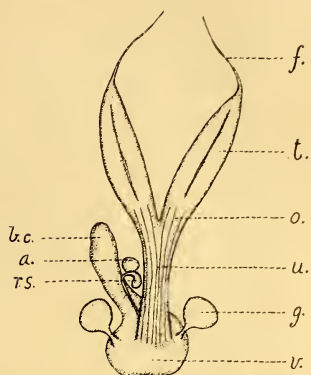


FIG. 16.—Female Reproductive Organs (immature).

- | | |
|-------------|-----------------------|
| <i>f.</i> | Terminal filament. |
| <i>t.</i> | Terminal chambers. |
| <i>o.</i> | Oviduct. |
| <i>u.</i> | Uterus. |
| <i>g.</i> | Slime gland. |
| <i>v.</i> | Vagina. |
| <i>bc.</i> | Bursa copulatrix. |
| <i>a.</i> | Accessory sac. |
| <i>T.s.</i> | Receptaculum seminis. |

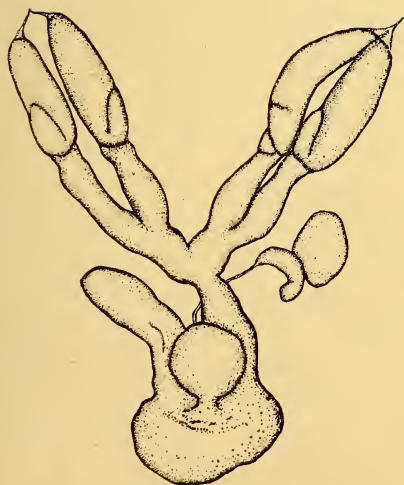


FIG. 17.—Female Reproductive Organs (developing).

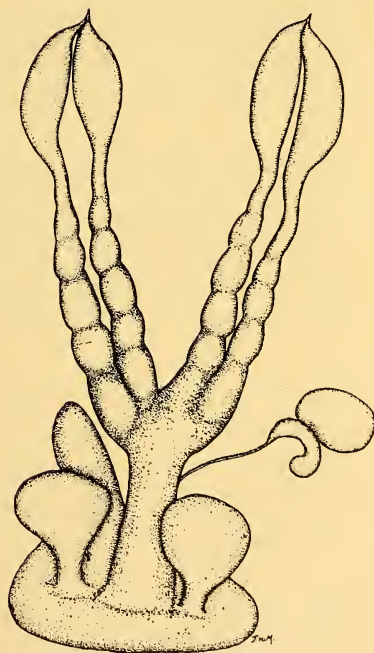


FIG. 18.—Female Reproductive Organs (mature)

MALE AND FEMALE REPRODUCTIVE ORGANS OF *HYLASTES ATER*.

in number, lying on either side of the median line. Each consists of two egg-tubes, each with a terminal chamber and opening into the paired oviducts. The paired oviducts are short, and unite to form the *uterus* which is strengthened by longitudinal chitinous ribs or strands. The bursa copulatrix opens from the uterus as a diverticulum almost as large as that organ itself. At the base of the bursa, the receptaculum seminis opens into the uterus by a long, narrow tube. The receptaculum is a hook-shaped vesicle closed with chitin, and appended to it is a globe-shaped diverticulum. Just below the bursa is the vagina into which the uterus opens, and also the slime glands which lie on either side of the uterus. These are somewhat flask-shaped, the neck of the flask opening into the vagina. The vagina is surrounded by a thin membranous band of chitin which binds the spiculum ventrale to it. This last is a thin, short, forked, chitinous plate.

Four stages of development of the female reproductive organs are worthy of description—the immature, the developing, the ripe or developed stage, and the condition after egg-laying.

In the immature reproductive organs of the female *Hylastes* (Fig. 16), the egg-tubes wholly lack the familiar pearl necklace appearance, and appear to consist entirely of terminal chambers. The uterus, bursa, and receptaculum are not dilated, and the slime glands are small.

In the developing organs (Fig. 17) the egg-tubes appear as if unfolding from the terminal chambers which are now more distinct. If pairing has taken place the bursa and receptaculum may be distended; the slime glands may also be large.

The ripe or mature organs (Fig. 18) show the terminal chambers distinctly marked off from the egg-tubes, which resemble a string of pearls graduated in size. The bursa and receptaculum are usually distended, and the corpus luteus is present at the junction of the egg-tubes with the paired oviducts. The slime glands are full and distended. Where oviposition is in progress, the *oviducts* and *uterus* may contain eggs.

After oviposition the reproductive organs present a shrivelled appearance. The bursa, uterus, and egg-tubes all appear wrinkled, as also in some cases the spermatheca and accessory sac. Some time after egg-laying the organs appear to recover, and, except that the egg-tubes are stretched and more or less distinct from the terminal chamber, and the uterus and bursa are wrinkled, they somewhat resemble the immature condition.

It should be noted that the shapes of the receptacula in *Hylastes*, like the chitinous parts of the male reproductive organs, afford characters for distinction of the species. They are much less trustworthy than the latter, however, and can be relied on only in the case of immature females.

Egg of H. ater.

The egg of *H. ater* calls for no special comment. It is oval in shape, shining white in colour, and shows neither sculpturing nor micropyle. It measures .9 mm. long and .54 mm. in diameter. The eggs of *H. palliatus* and *H. cunicularius* do not differ from that of *H. ater*.

Larva of H. ater. (Plate X. Figs. 20-25.)

In general appearance this larva is a curved, white, fleshy, legless grub, with wrinkled body and well-marked yellowish head. It is made up of fourteen segments including the head, which forms the first segment. The next three segments form the thorax, and the remaining ten the abdomen. All the body segments are somewhat similar in shape and size, except the ninth and tenth abdominal. The ninth is smaller than the others, while the tenth segment is reduced to form the anal lobes. The first thoracic and the first eight abdominal segments each bear a pair of spiracles. The thoracic segments each bear a pair of foot-calli or pads.

For the sake of brevity further description of the larva may be omitted; the accompanying figures of the *H. ater* larva, it is hoped, will serve to take its place. I have been unable to obtain any satisfactory characters for the identification of species in the larvæ of the genus *Hylastes*, although I have examined large numbers of the larvæ of the three species under consideration.

Pupa of H. ater.

The pupa of *H. ater* calls for no special comment. It is naked and free, and shows all the parts present in the adult beetle. The abdomen terminates in a pair of spiny processes. The three species, *H. ater*, *H. palliatus*, and *H. cunicularius*, can readily be distinguished in the pupal as in the adult stage by the configuration of the thorax.

HABITS AND LIFE-HISTORIES OF THE THREE SPECIES.

Habitat.

All the three species of *Hylastes* under consideration attack conifers.

H. ater breeds in the roots of the Scots pine, and feeds either on similar roots or on young conifers of various species below soil level. Its egg, larval, and pupal stages are spent in Scots pine roots of trees from twenty to seventy years of age.

H. cunicularius breeds in the roots of spruce, where its egg, larval, and pupal stages are spent, and feeds on similar roots or on the roots of other young conifers, like its congener *H. ater* (Fig. 28).

H. palliatus breeds on the stems and crowns of Scots pine, larch, and spruce; the first and the last mentioned being its more common hosts. It feeds in the same situations and, unlike its congeners, may proceed to feed without leaving its pupal chamber. *H. palliatus* feeds in the stumps of spruce and Scots pine above soil level (Fig. 26).

Mother-galleries.—The mother-galleries of the three species of *Hylastes* are similar in general character, but are nevertheless peculiar in each species (Plate XI. Fig 27).

The mother- or brood-gallery of *H. ater* (Fig. 27 a) is vertical (*i.e.* parallel to the axis of the root in which it is cut), and consists of a more or less straight tunnel beginning with a crutch-shaped brood chamber. The tunnel is narrow and usually shows one or two recesses near its base. One arm of the crutch is longer than the other.

The mother-gallery of *H. cunicularius* (Fig. 27 c) is also vertical, but broader and shorter than that of *H. ater*. The tunnel usually shows well-defined egg niches, and the arms of the crutch are short and equal. Recesses in the tunnel are absent.

The mother-gallery of *H. palliatus* (Fig. 27 b) is vertical, narrow, and comparatively short. It may or may not show egg niches, and the arms of the crutch are unequal in length. Recesses are absent.

It should be observed that typical galleries, as described above, are not always found in any of the species. The nature of the breeding-ground affects the cutting and shape of the galleries considerably. Too moist or too dry conditions, too thick or too thin bark, varying depth of soil-covering in the root-feeding species, all tend to produce irregularly-shaped galleries. In the root feeders two galleries often unite, presenting an apparently long gallery or an uncharacteristic branched or curved one. In the case of *H. palliatus* the galleries are often interfered with by those of the Common Pine Beetle, *Myelophilus piniperda*, L., or of the Two-toothed Pine Beetle, *Pityogenes bidentatus*, Hbst., and of the larva of the Lesser Pine Weevil, *Pissodes pini*, L. The galleries of *H. ater* are also interfered with by the last-mentioned larva, but more commonly by the larva of the Large Pine Weevil, *Hylobius abietis*, L. *Hylobius* larvæ occasionally obstruct the galleries of *H. cunicularius*.

The Larval Galleries.—In the root-feeding species, the larval galleries, which arise at right angles from the mother-galleries, are nearly always confused owing to the small diameter of the roots on which they occur. The pupating chambers in which they terminate are, however, usually very distinct. The larval galleries of *H. palliatus*, cut as they are in material 3 to 6 inches in diameter, are usually fairly distinct and form one or other of two patterns. They may radiate, as it were, from the mother-gallery as

distinct individual galleries, increasing in width as they diverge to terminate in a more or less distinct pupal chamber; or one or several of the larvæ may follow in the track of an earlier hatched member of the family to diverge later, causing the galleries to form a more or less branched pattern.

Galleries cut by the Adults while Feeding.—The galleries cut by the adults while feeding may be either collective or individual. Collective galleries occur when the beetles feed side by side and head in the same direction. Individual galleries occur when each beetle chooses its own direction and works alone. A combination of the two types, *i.e.* collective galleries followed by individual, is not uncommon.

LIFE-HISTORY OF *HYLASTES ATER*.

The life-histories of *H. ater* and *H. palliatus* have been studied both in the field and in the laboratory, as has been said. Observations on the life-history of *H. cunicularius* have been made in the field. The laboratory observations may be dealt with first, beginning with those on *H. ater*. Before describing my laboratory experiments, however, it may be well to refer to one important point in regard to them. All the beetles which I have used in these experiments were, I believe, virgin beetles proceeding to the production of their first brood. This was the case with the females at any rate. All of these were taken from groups of beetles which I had observed the previous autumn. I examined numbers of these then, and found that all the females were only recently emerged and sexually immature. In the spring when I began my experiments I again examined numbers of these beetles, and again found virgin females; but these were now fully mature, and in many cases showed the corpus luteus in their oviducts.

Laboratory Observations on H. ater.

During the winter of 1914–15 and the spring of 1915 I endeavoured to breed *Hylastes ater*. I collected the adults in the field and supplied them with Scots pine roots embedded in damp moss. I also tried to rear larvæ in the roots in which they occur. All the experiments with the adults failed as none of the beetles entered the roots, but, crawling about in the moss, sooner or later died. With the larvæ I was successful until the month of March 1915, when, owing to the damp condition of the moss, they were killed out by the growth of the fungus *Fomes annosus*.

In the autumn of 1915 I again collected adults and larvæ, and met with better success by keeping them in roots covered with soil. The larvæ pupated and the adults survived the winter. These adults were used in the 1916 experiments. The pupæ however failed to transform.



FIG. 26.—Scots Pine Bark, showing winter-feeding galleries of *Hylastes palliatus*, adult. The portions coloured black have been eaten away.



FIG. 27.—Galleries of *Hylastes*.

- a. *H. ater*. b. *H. palliatus*.
c. *H. cunicularius*.



FIG. 28.—Lower portion of young Scots Pine, showing "frass" of *H. cunicularius*. The unshaded areas indicate the gnawed portions. (From Nature.)

In April 1916, I began a number of experiments with adult beetles. These I collected from Scots pine stumps at Balerno and at Eddleston and from young conifers at Eddleston. They had been there to my knowledge since October 1915. Three others I collected at Eddleston on a young Scots pine in which they fed in the laboratory throughout the winter. During February, March, and April, I paid particular attention to *H. ater* in the field, in order that I might begin my laboratory experiments as soon as the beetles either swarmed or paired and commenced their brood-galleries. On 12th April, I found a pair *in copulo* in the soil. On the 20th, numbers were crawling on the Scots pine stems near their winter quarters. On that date I cut three roots, about $2\frac{1}{2}$ feet long, from different Scots pine root-stumps cut that day, which were free from *Myelophilus*, *Pissodes*, or other pine-dwelling insects. These I placed in a large box in about 18 inches of soil with an end of each root just visible. On the 26th of April, I introduced twelve adult *H. ater* into this box, but I did not place them on the roots. On the 27th, I added two more roots to this box and introduced eighteen more beetles. At the same time I placed a similar box, but of smaller size and containing three roots and twelve beetles, in the open. As this last experiment proved unsatisfactory owing to the soil becoming sodden with rain and soot, which evidently prevented the beetles from boring, I abandoned it. Accordingly my observations on the life-history under laboratory control were based on forty *H. ater* breeding on five roots. On 1st May, a pair had begun boring while seven others were crawling on the roots when exposed.

In examining the material to observe the progress of my experiments I chose three of the smaller roots, and every few days I carefully exposed the beetles' borings in them and noted the results. During the first week or two I supplemented these examinations with examinations of roots brought in from the field. This was necessary to determine the method of working, as I was in doubt which sex cut the brood-gallery. In the later weeks my laboratory material was adequate for all the examination required, and, except for comparison of field progress with laboratory progress, no further field material was required. After each examination and exposure of the galleries I took care to replace the roots without displacing the beetles at work in them. These methods have proved very satisfactory.

Pairing.—This may take place either in the soil or in the crutch of the gallery described below. Any pair of beetles may pair more than once, and pairing may take place before the beetles or, at any rate, the females of them, are fully mature.

The Cutting of the Brood-gallery and the Laying of the Eggs.—This gallery is termed the mother-gallery by the German entomologists, and the name is

probably more appropriate than was intended. The boring is begun by the female, which cuts out a crutch-like tunnel about $\frac{1}{2}$ inch to $\frac{3}{4}$ inch in length. The male is not always present at this operation, but, if he is, he clears away all the bore meal. Once the crutch is finished he joins his mate inside the crutch, and she now begins the brood- or mother-gallery proper. The male again acts as scavenger until $\frac{1}{2}$ inch to 1 inch of the mother-gallery is cut. At this stage he cuts a small niche at the side of the gallery. The female continues her boring a little farther. She then returns and nibbles the sides of her tunnel and, depositing her eggs, embeds them in the dust she has made in nibbling. She then returns to the end of her tunnel and begins boring afresh, the male removing the frass she passes back to him. The portion of the gallery occupied by the eggs is lined with bore meal, and the eggs are further protected by slimy threads which probably serve to consolidate the frass surrounding them.

The Hatching of the Egg.—The eggs of *H. ater* are comparatively long in hatching, the period varying from a fortnight to three weeks (11th May to 30th May). My observations indicate that the later laid eggs hatch in a little less time than the first laid.

The newly hatched larvæ at first crawl about the frass surrounding them. They then start boring at right angles to the mother-gallery; later hatched larvæ apparently take advantage of the tunnel cut by the earlier hatched ones. On the third day after hatching, the complex of larval tunnels extends to $\frac{1}{4}$ inch distance from the mother-gallery. This complex consists at first of two or three fine tunnels at right angles to the mother-gallery, then these lines become confused and a complex network or a large cut-out space only is to be seen. A fortnight later this network or space is extended, and from its distant margin distinct individual tunnels arise which later terminate in the pupal chambers.

Duration of Egg-laying and Cutting of the Mother-gallery.—The cutting of the mother-gallery and the laying of the eggs by *H. ater* is of long duration, extending over six to seven weeks (1st May to 27th June). It is interesting to note that egg-laying ceases approximately with the pupation of the larvæ hatched from the first laid eggs. The average number of eggs per gallery is 120.

Duration of the Larval Stage.—Eight to nine weeks (22nd May to 20th July) is the duration of the larval stage. Of these six or seven are devoted to feeding and the remainder to resting prior to pupation.

Duration of the Pupal Stage.—This is of short duration, varying from nine to eleven days (20th July to 31st July).

Total period from Egg to Adult.—The total period from egg to adult is from two to three months' duration (11th May to 31st July).

Emergence of the New Brood and subsequent Behaviour of the Parent Brood.—A word of explanation is necessary here. On 3rd August, I divided my material into two parts. The first part I examined, removing all the black, and therefore presumably parent, beetles from the roots, and from 3rd to 10th August I removed all the pale or young beetles as they became darker. The parent beetles I placed in a case by themselves (Cage 1). It contained fresh pine roots buried in soil and two young (four-year-old) Scots pine plants. I placed the young beetles or offspring in Cage 2, which was also supplied with roots and young pines. The second part of my material I removed without examination and buried it in Cage 3, which was supplied, like the others, with fresh roots and young pines. The object of doing this was to determine by observations on Cage 1 the behaviour of the parents, and on Cage 2 the behaviour of the offspring. Cage 3 served as a check on these, lest the removal of the beetles in Cages 1 and 2 from their old breeding-ground before they had left it of their own accord might affect their behaviour. In Cages 1 and 2 the colour of the beetles indicated whether they were parents or offspring. In the case of the Cage 3 specimens I resorted, later, to an examination of the reproductive organs for this information.

The young beetles both in Cage 2 and Cage 3 sought fresh feeding-ground. They showed a preference for young conifers, for in Cage 2 the pines were attacked first and the roots later. The parent beetles also sought a fresh host but did not show any preference, for in Cage 1 both pines and roots were attacked simultaneously. The young beetles remained feeding from 12th August until 31st October, when the experiment was closed. The parent beetles in both Cages 1 and 3 remained feeding for three to four weeks (10th August to 4th September) when they emerged again and, having paired, commenced egg-laying, thus giving rise to their second brood.

The Second Brood.—The period elapsing between the laying the eggs of the first brood and those of the second brood varied from fourteen to sixteen weeks (10th May to 4th September). The eggs of the second brood began to hatch on 18th September, and on 31st October, when the experiment was closed, the second brood was in the larval stage.

Field Observations on Hylastes ater.

Hylastes ater is essentially a root dweller, and it probably breeds only in Scots pine. It is, however, found feeding on Scots pine, larch?, spruce, and Douglas fir in newly-formed plantations, where it attacks these below soil level. Owing to the fact that *Hylastes ater* lives below the soil level it is less easily observed than its congener *H. palliatus*. A further difficulty is that

in order to make observations the breeding- or feeding-ground of the beetle must be disturbed by removing the bark from stumps or roots, and this, together with the removal of the soil from them, practically prevents continuous observation on any pair or group of beetles. This difficulty is common to the study of all the Scolytidæ, but it is increased in the case of *H. ater* (and also in the case of *H. cunicularius*) by the underground habitat. There are no means of getting over this difficulty, but where examination of a number of beetles out of the many infesting a given stump show these to be uniform as regards sex maturity, and where they are all engaged in making brood-galleries, it is permissible to assume that their individual behaviour and progress are alike. I believe I have satisfactory proof of this as the result of a comparison of the behaviour of three individuals in the laboratory with others in the field. On 7th October 1915, I obtained at Eddleston several *H. ater* adults feeding in a young plantation. I removed a young pine containing three of these, and kept it in the laboratory throughout the winter. The three beetles remained on the pine, where I observed them on 5th April. On 6th April, I again visited Eddleston, and again found *H. ater* adults feeding on the pines. It is perfectly safe then to assume that those in the field, like those in the laboratory, have fed on the pines all winter. Further evidence of this was supplied by the state of the female reproductive organs of the beetles. On 7th October, I examined five beetles taken at Eddleston, four were females and immature. On 6th April, I examined four beetles, of which two were females just arrived at maturity. My observations and notes, therefore, form a fairly reliable account of the life-history.

In view of the fact that my notes refer only to the stage in the metamorphosis and to the habitat of the beetles, which involves considerable repetition, I have summarised them as far as they relate to the life-history in the table given below. Immediately following is a summary of my notes on the habits of *H. ater*, the nature of its breeding- and feeding-grounds and of the insects commonly associated with it.

A word may be said here on distribution. *Hylastes ater* is widely distributed in Scotland, and it is probable that it is on the increase at present owing to the extension of felled areas caused by the drain on our timber resources.

Breeding-ground.—The favourite and usual breeding-ground of *H. ater* is the Scots pine clearing. It also occurs on the roots of standing dead and sickly pines in high forests. Unlike *H. palliatus*, *Myelophilus piniperda*, and others among the Scolytids, it restricts itself, except in rare instances, to the roots and stumps below the soil level. It was twice found on a larch stump

in Aberdeenshire. It shows a striking similarity in habits with the Pine Weevil, *Hylobius*, with which it is closely associated. Like *Hylobius* it breeds below soil level in the stumps and roots, and it also feeds on young newly planted conifers.

Hylastes ater has considerable powers of flight, and during the period April to July may be seen flying in the sunshine, alighting on the road or on palings or telephone poles on its way to its breeding- or feeding-grounds. Swarming is not limited to a definite period. Like *Myelophilus piniperda* and *Hylastes palliatus*, *H. ater* is attracted to the sawn butts of felled pines where it is trapped by the exuding resin.

Hylastes ater is a bast feeder. It bores in the bast and cambium layers, penetrating the bark in order to reach them. It may even enter from the sawn surface of the stump, boring vertically into the cambium until below soil level where it reaches the roots. It prefers the roots to the broader and more extensive areas of the stump, a fact which makes it the more difficult to find.

Feeding-ground.—The feeding-ground of *H. ater* is recently formed coniferous plantations, where it attacks the young trees below soil level. I have found it on young conifers all the year round.

Young plants attacked by *H. ater* show a distinctly faded foliage, and if the attack is severe they die. Several individuals attack one plant. I have taken eleven beetles from a single Scots pine plant, the root-stem of which was less than $\frac{1}{2}$ inch in diameter. The beetles feed in ranks, as many as four occurring side by side. In examining plants for injury by *H. ater*, it is important that they should be lifted by means of a trowel, otherwise the stem is bared of the bark which shelters the beetles and which remains behind with them in the soil. In such instances an attacked plant looks as if it had been stripped of its bark in the act of being pulled up. Sometimes, however, distinct grooves can be seen on the root-stem itself, and these are a sure indication of the presence of *H. ater*. The conifers I have observed to be attacked by *H. ater* when feeding are Scots pine, spruce, larch, and Douglas fir.

Insects associated with Hylastes ater.—These may be divided into three classes—insects harmful to the forester; insects useful to the forester, being predaceous or parasitic on the first class; and insects which are neither harmful nor beneficial.

In the first class four species are commonly to be found, *Hylobius abietis*, L., *Pissodes pini*, L., *Myelophilus piniperda*, L., and *Hylastes palliatus*. The three last mentioned are found on the upper portions of the stump, and only in rare instances penetrate to the roots. I have found, however, that on roots

which I laid bare of soil in my search for *H. ater*, and which I neglected to cover again, *H. palliatus* began its brood-galleries. In wind-blown stems, too, *H. palliatus* and *H. ater* and even *M. piniperda* are found side by side on the roots. In these instances *H. ater* had begun work prior to the throwing up of the roots, while *M. piniperda* and *H. palliatus* had come afterwards.

The second class of insects associated with *Hylastes ater* are more numerous than the first class, and are both Coleopterous and Hymenopterous. Of the Coleoptera five genera are conspicuous—*Clerus*, *Pityophagus*, *Rhizophagus*, and *Ips*. The species are *Clerus (Thanasimus) formicarius*, L., *Pityophagus ferrugineus*, F., *Rhizophagus dispar*, Pk., *R. ferrugineus*, Pk., and *R. depressus*, F., *Ips 4-pustulata*, L., and *Tachyporus chrysolinus*, L. Of the Hymenoptera the chief are two species of the Family Braconidæ and a species of *Chalcid*. Owing to difficulty in determining the species in this order I have not paid close attention to them.

The beetles predaceous on *H. ater* I have found only in two stages, as adults and larvæ. Where the larvæ only were present I have contented myself with a note of the genus.

Clerus or *Thanasimus formicarius* appears to be a northern insect, inasmuch as during all my observations from 1914 to date, I have never found it in the galleries of *H. ater* in this district. In Aberdeenshire and Perthshire, on the other hand, I have taken it on several occasions. According to Perris¹ and others it is one of the chief enemies of the Scolytidæ.

Pityophagus ferrugineus is also more common in the north, and, in fact, my specimens taken at Balerno in Midlothian are the first record of the species in the Forth area since 1843.² It appears that it is chiefly predaceous on *H. ater* or that it is a soil dweller. I have never found it above ground in the galleries of other Scolytids, although all the other beetles in this class are common in the galleries of *M. piniperda* and *H. palliatus*.

Of the genus *Rhizophagus*, *R. dispar* is the commonest. All three species, however, are to be found in nearly every district. In my own experience, *R. dispar* has proved extremely voracious; two of its larvæ on one occasion completely despoiled the eggs and larvæ in an *H. ater* gallery.

Ips 4-pustulata is also common throughout the areas in which my observations were made. I have not, however, obtained its larva. *Tachyporus chrysolinus* is only one of many small Staphylinids which infest the galleries of *H. ater*. I have singled it out for mention because I found it in enormous numbers in a clearing at Countesswells, Aberdeenshire. I am indebted to Major A. O. C. Watson for confirming my identification of it.

¹ Perris, *Larves des Coléoptères*.

² I am indebted to Mr Wm. Evans for this information.

Of the third class of insects inhabiting the galleries of *Hylastes ater* the chief belong to the Diptera, Families Sciaridæ and Mycetophilidæ. I have never reared these flies, and, as I have found them only in the larval state, I am unable to give the genera or species.

LIFE-HISTORY OF *H. PALLIATUS*.

Except for its habitat, *H. palliatus* does not differ in any remarkable way from *H. ater* as regards life-history. The mother-gallery is cut in the same manner, the eggs are laid in the same manner except that in some cases niches are cut for them, the hatching of the larvæ, etc., are all quite similar, so that to describe all these phenomena would involve tedious repetition. Accordingly, I propose to restrict myself to a short account of my laboratory experiments, followed by a summary of my field observations on *Hylastes palliatus*.

Laboratory Observations on H. palliatus.

These were begun on 2nd May 1916, when forty adult *H. palliatus*, the females of which were, I believe, proceeding to their first egg laying, were introduced into three breeding-cages, each containing two stems of Scots pine 2 feet long. From time to time these logs were examined, as in the experiment with *Hylastes ater*. Observations were made on the cutting of the gallery by *H. palliatus*, as in the case of *H. ater*, and, in view of the fact that no remarkable differences in the breeding habits of the two species were observed, it is hoped that the following summary of laboratory observations may suffice as a description of the life-history.

Egg laying and Cutting of the Brood-Gallery.

This period extends from three to four weeks (4th May-30th May) in spring, and six to seven weeks in early autumn (17th July-7th September).

Hatching of the Egg.—The duration of the egg stage is four to six days (8th May-12th May, 12th May-18th May).

Duration of the Larval Stage.—This extends from eighteen to twenty days in the summer or spring brood (12th May-17th June).

Duration of Pupal Stage.—This lasts from twelve to twenty days (1st June-29th June).

Total Period from Egg to Adult.—This extends for from four to six weeks (4th May-29th June).

Emergence of the New Brood and Behaviour of the Old.—These were removed from their breeding-ground on 1st July to fresh pine logs. The young adults fed till 18th September, when some began the brood-gallery. Eggs were observed on 18th September, and newly hatched and older larvæ on 6th October. The old adults fed till 17th July when they began egg laying, and continued till 7th September when some died and others began feeding again.

The Second Brood of the Old Adults and First Brood of the Young Adults.—The eggs of the second brood were laid on 17th July and subsequently. Larvæ hatched on 26th July and subsequently. On 31st October all the second brood were in the larval stage.

The young adults from the first brood laid eggs on 18th September and subsequently. Larvæ were observed on 6th October, and this new brood were in the larval stage on 31st October.

Field Observations on H. palliatus.

Breeding-ground.—*Hylastes palliatus* is found chiefly on Scots pine and spruce, but it also occurs on larch. In standing trees it attacks the stems and crowns, but is most easily observed on the stumps of felled pine and spruce where it occurs only above ground. It prefers thin bark trees, thirty to sixty years of age. Like its congeners it is a bast feeder, and when it occurs on stumps it bores from the cut surface directly into the cambium, thus avoiding the cutting of a passage through thick bark.

H. palliatus often occurs in enormous numbers in suitable localities. I have examined standing spruce stems at Woodlands, Kincardineshire, riddled from base to crown with its exit holes; and on Scots pine stumps at Eddleston, Peeblesshire, I have counted over twenty galleries in a piece of bark 2 feet long and about a foot broad.

The Feeding-ground of H. palliatus.—*H. palliatus* feeds and breeds in similar situations, and accordingly little further need be said in regard to the feeding-ground. The number of beetles which feed together is a feature of the species. On Portmore Estate, Eddleston, in October 1916, I obtained a piece of bark 2 inches square, from a Scots pine stump, on which no less than forty beetles were feeding. At Balerno, Midlothian, on 2nd May 1916, in a wood above Threipmuir reservoir, I obtained, on a Scots pine branch 3 inches in diameter and 1½ feet long, seventy adult *H. palliatus*.

Insects associated with H. palliatus.—These fall into the three groups described for *H. ater*, as follows:—

Injurious Insects.—Amongst these the bark beetles and the pine weevils again take first place. The following are the species most worthy of mention:—*Myelophilus piniperda*, L., *Pissodes pini*, L., *Pityogenes bidentatus*, Hbst., *P. quadridentatus*, Hart., *Dryocetes autographus*, Raty., *Trypodendron lineatum*, Ol., and *Hylobius abietis*, L. The first four occur with *H. palliatus* on the stems and crowns of Scots pine; the next two on the stems and crowns of spruce (*P. bidentatus* I have found once on spruce with *H. palliatus*), while *H. abietis* occurs with it on Scots pine stumps, as also does *P. pini*.

Useful Insects.—Of these the same beetles which associate with *H. ater* are also commonly found in the galleries of *H. palliatus*, with the exception of *Pityophagus ferrugineus*, F. Of the Hymenoptera in this group, I have found two Chalcids which are probably parasitic on *H. palliatus* larvæ, but which have not been identified.

Of the third group the larvæ of Sciarid flies are the chief inhabitants of the galleries of *H. palliatus*.

LIFE-HISTORY OF *H. CUNICULARIUS*.

The life-history and habits of *Hylastes cunicularius* have been studied by me only in one locality, namely, on Darnhall Estate, Eddleston, Peebles-shire. I first found the species breeding, in October 1914, in Aberdeenshire, when larvæ and adults were found on the roots of a spruce stump. On 7th October 1915, I found it feeding along with *H. ater* at Darnhall. I have already published¹ a short general account of *H. cunicularius*, to which I contribute additional observations in this paper.

Breeding-ground.—The breeding-ground of *H. cunicularius* is the spruce stump and roots. The species prefers the smaller roots, often a considerable distance away from the stump, and, in my experience, rarely breeds on the stump itself. Its breeding habits are very similar to those of *H. ater*, and where spruce and Scots pine stumps occur on the same felled area, the two species may be found on it—*H. cunicularius* occurring on the spruce roots and *H. ater* on the pine roots. In fact, these were the conditions at Darnhall.

Feeding-ground.—Except when *H. cunicularius* remains to feed in its breeding-ground, it feeds in exactly the same situations as *H. ater*, so that further description of the feeding-ground is unnecessary.

¹"*Hylastes cunicularius*, Er., and its Relations to the Forest," *Scottish Naturalist*, Nov. 1916.

SUMMARY OF LABORATORY OBSERVATIONS ON *H. ATER*.

7th October 1915	}	Adults and larvæ feeding; larvæ pupated 18th April.
to 24th April 1916		
26th to 27th April		<i>Hylastes</i> introduced into breeding-cage.
1st May	.	Boring begun by 1 pair.
3rd May	.	5 pairs boring.
8th May	.	Crutch of gallery completed, and gallery proper 1 inch long. In others only the crutch is completed.
11th May	.	Galleries proper $\frac{1}{2}$ inch to $1\frac{1}{2}$ inch long. First batch of 5 eggs laid.
22nd May	.	Galleries 2 inches to 3 inches long. 20 eggs laid and 5 hatched.
24th May	.	Larvæ and eggs in all galleries.
30th May	.	Galleries $3\frac{1}{4}$ inches to 5 inches long.
5th June	.	Some larvæ well grown.
13th June	.	Do. do.
19th June	.	Full-grown larvæ. Egg-laying still in progress.
3rd July	.	Larvæ resting prior to pupation; others feeding.
15th July	.	Do. do.
20th July	.	Pupæ, larvæ resting, larvæ feeding.
31st July	.	Adult but still pale beetles; pupæ and larvæ.
3rd August	.	Do. do.
10th August	.	New series of experiments started. Cage 1. Parent beetles only. Cage 2. Young brood only. Cage 3. Parents and young brood together.
16th August	.	Beetles in all 3 cages feeding.
21st August	.	Beetles in Cage 1 cutting typical crutch. Beetles in other cages feeding.
29th August	.	Beetles in Cage 1 egg laying. Young brood in Cages 2 and 3 feeding. Parents in Cage 3 cutting brood-galleries.
7th September	.	Cage 1. Roots showing eggs and larvæ. Cage 2. Beetles feeding. Cage 3. Eggs and larvæ and young brood feeding.
18th September	.	Do. do.
29th September	.	Do. do.
12th October	.	Cages 1 and 3 show larvæ. Cages 2 and 3 (young brood) beetles feeding.
20th October	.	Do. do.
31st October	.	Do. do.

Tabular Summary of Laboratory Observations on H. ater.

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1915										+++ ---	+++ --○	+++ --○
1916	+++ ○○○	+++ ○○○	+++ ○○○	+++ ○○●+	+++ ...-	+++ ...-	+++ ...○	+++ ...○	+++ ...○	+++ ---	+++ ---	

+ + = adult beetles. ○ ○ = larvæ resting to pupate.
 . . = eggs. ● ● = pupæ.
 - - = larvæ.

The above table shows that *H. ater* is to be found in the imago and larva stages throughout the year, and that eggs and pupæ are found in the warmer months only, from April to August.

SUMMARY OF FIELD OBSERVATIONS ON *H. ATER*.

Month	Locality	Stages	Remarks
October	Tully Methlick, Aberdeenshire + + - - . ○	The occurrence of eggs at this time is unusual. This is the more usual occurrence. The adults were recently emerged and the larvæ full grown. Adults feeding on young conifers and Scots pine stumps. Larvæ half and full grown.
	Peeblesshire	+ + + - - -	
November	Fifeshire Forfarshire Midlothian	+ + + - - . do. do.	Adults feeding (immature). Larvæ full grown and others resting to pupate.
December	do.	do.	
January	do.	do.	All larvæ lying to pupate. Some of the adults newly emerged (still pale in colour). Others feeding on larch plants. Adults pairing, some in galleries, some in soil. Brood galleries begun. Eggs laid; newly-hatched larvæ present in the brood-galleries. Some adults only begun boring; others still feeding. Some adults still feeding (probably late-hatched individuals of previous autumn brood). Some adults just begun boring. Larvæ full grown and ready to pupate. Pupæ becoming tinged with yellow. Adults newly emerged and feeding on recently felled stump. Larvæ of all sizes and pupæ. Young and old adults feeding. Some (probably old) adults begun egg laying again. In some galleries are newly-hatched larvæ.
February	do.	do.	
March	do.	+ + ○ . . .	
April	Peeblesshire	+ + ● ●	Some of the adults newly emerged (still pale in colour). Others feeding on larch plants. Adults pairing, some in galleries, some in soil. Brood galleries begun. Eggs laid; newly-hatched larvæ present in the brood-galleries. Some adults only begun boring; others still feeding. Some adults still feeding (probably late-hatched individuals of previous autumn brood). Some adults just begun boring. Larvæ full grown and ready to pupate. Pupæ becoming tinged with yellow. Adults newly emerged and feeding on recently felled stump. Larvæ of all sizes and pupæ. Young and old adults feeding. Some (probably old) adults begun egg laying again. In some galleries are newly-hatched larvæ.
	Midlothian	+ + ●	
May	do.	+ + ● . . - -	Some adults still feeding (probably late-hatched individuals of previous autumn brood). Some adults just begun boring. Larvæ full grown and ready to pupate. Pupæ becoming tinged with yellow. Adults newly emerged and feeding on recently felled stump. Larvæ of all sizes and pupæ. Young and old adults feeding. Some (probably old) adults begun egg laying again. In some galleries are newly-hatched larvæ.
June	do.	+ + . . . - - -	
July	do.	+ + . . . - - ○ ●	Some adults still feeding (probably late-hatched individuals of previous autumn brood). Some adults just begun boring. Larvæ full grown and ready to pupate. Pupæ becoming tinged with yellow. Adults newly emerged and feeding on recently felled stump. Larvæ of all sizes and pupæ. Young and old adults feeding. Some (probably old) adults begun egg laying again. In some galleries are newly-hatched larvæ.
August	do. Peeblesshire	+ + ● - - . do.	
September	do.	+ + . . . - - ●	

Tabular Summary of Field Observations on H. ater.

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1915										+++ --⊙	+++ -⊙⊙	+++ -⊙⊙
1916	+++ ⊙⊙⊙	+++ -- ⊙⊙⊙	+++ -- ⊙⊙⊙	+++ -⊙●	+++ ⊙●●	+++	+++	+++ -- ⊙●	+++ -- ⊙	+++ -- ⊙		

The above tables correspond fairly well with the laboratory results, and again show adults and larvæ all the year round with the egg and pupal stages occurring in summer.

SUMMARY OF LABORATORY OBSERVATIONS ON *H. PALLIATUS*.

- 2nd May . . . 40 adults placed on Scots pine stems 2 feet long.
- 4th May . . . Numerous borings in logs; many in close proximity.
- 8th May . . . First stem examined. Some beetles still feeding.
2 pairs cutting galleries. 1 gallery contains eggs.
- 12th May . . . 3 galleries containing eggs; 2 also contain newly-hatched larvæ.
- 18th May . . . Galleries contain eggs and larvæ.
- 22nd May . . . Do. do.
- 30th May . . . Eggs and larvæ. Some of the larvæ apparently full grown.
- 5th June . . . Larvæ and pupæ.
- 13th June . . . Larvæ, pupæ, and pale adults.
- 17th June . . . Brown and pale adults, larvæ, and pupæ.
- 19th June . . . Do. do.
- 23rd June . . . Young adults feeding; some crawling about on the surface of the stems.
- 1st July . . . All adults—old and young—removed to fresh stems. Larvæ and pupæ left to emerge.
- 3rd July . . . All adults feeding.
Larvæ pupating and pupæ emerging.
- 10th July . . . Adults feeding.
Larvæ pupated; pupæ emerged.
- 13th July . . . All young brood now in adult stage.
Late emerged adults transferred to fresh stems.
- 17th July . . . (a) Old adults cutting brood-galleries.
(b) Young adults feeding.
- 20th July . . . (a) Eggs and newly-hatched larvæ.
(b) Young adults still feeding.

- 26th July . (a) Eggs and larvæ.
 (b) Still feeding.
- 29th July . (a) Larval galleries on two stems interfered with by larval
 tunnels of *P. pini*.
 (b) Young adults feeding.
- 3rd August . (a) Larvæ—some well grown.
 (b) Young adults feeding.
- 10th August . (a) Do.
 (b) Do.
- 21st August . (a) Larvæ well grown.
 (b) Feeding.
- 29th August . (a) Larvæ well grown.
 (b) Young adults pairing
- 7th September (a) Adults have left roots; larvæ pupating.
 (b) Young adults cutting brood-galleries.
- 18th September (a) Some old adults feeding; others dead. No more larvæ
 pupated.
 (b) 3 eggs in gallery of young adults.
- 28th September (a) Old adults feeding. Larvæ and pupæ dried up by
 exposure of galleries.
 (b) Eggs in young adults' galleries.
- 6th October . (a) Old adults feeding; more dead.
 (b) Eggs and larvæ.
- 20th October . (a) Do.
 (b) Do.
- 31st October . (a) Do.
 (b) Larvæ.

Tabular Summary of Laboratory Observations on H. palliatus.

As will be observed, these observations extend only over the six months May to October 1916. Owing to the heating of the laboratory during the winter, difficulty was experienced in keeping pine stems or logs suitably moist for the breeding or rearing of *H. palliatus*, which prefers thin-barked material.

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1916				+++	+++	+++	+- -	+++	+++	+++		
				---	---	⊙	⊙ ● +	⊙ ● +	⊙	---		
						● ++		⊙ ● +	⊙ -	+++		

SUMMARY OF FIELD OBSERVATIONS ON *H. PALLIATUS*.

Month	Locality	Stages	Remarks
October	Aberdeenshire	+++---	Adults recently emerged, feeding in close proximity to their pupal chambers.
	Kincardineshire	+++	Adults feeding on Scots pine logs in company with larvæ of <i>Pissodes pini</i> .
	Fifeshire	+++---●	Feeding on 1-year felled Scots pine stumps.
	Midlothian	+++---●	On 1-year stumps, together with <i>M. piniperda</i> .
	Peeblesshire	++--	Feeding on Scots pine stumps in large numbers.
November	Fifeshire	do.	On half-fallen Scots pine and larch.
	Forfarshire	do.	On Scots pine stumps and on fallen spruce stems.
December	Midlothian	do.	On 1-year stumps.
January	do.	do.	do.
February	do.	do.	do.
March	do.	do.	Adults feeding on fallen spruce stems in company with <i>D. autographus</i> . <i>Hylastes</i> occurring on the drier portions, <i>Dryocetes</i> on the wetter.
April	do.	++--●	Adults feeding.
May	Peeblesshire	do.	do.
	Midlothian	++--	Adults swarming. Numbers crawling on half-fallen larch and Scots pine, and others with wing-covers projecting out of the bark, busy boring. No eggs.
	do.	++----	Some adults still feeding, others busy with their brood-galleries.
June	do.	++--...○	Young larvæ half and full grown.
July	do.	++...--○●	All stages present. Some adults feeding on Scots pine branches.
August	do.	do.	Many adults feeding; others cutting brood-galleries.
September	Peeblesshire	do.	
	do.	do.	Eggs few in number.

Tabular Summary of Field Observations on *H. palliatus*.

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1915										+++ ---●	+++ ---	+++ ---
1916	+++ ---	+++ ---	+++ ---	+++ ---●	+++ ...○	+++ ...○	+++ ...○	+++ ...○	+++ ---●			

COMPARISON OF THE LIFE-HISTORIES OF *H. ATER* AND *H. PALLIATUS*.

In comparing the life-histories of the two species, I have combined field and laboratory observations in the following tables. The reason for this

is obvious in that it is impossible to distinguish young and old broods in the field.

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>H. ater.</i>												
1915										+++ ---	+++ --○	+++ --○
1916	+++ ○○○	+++ ○○○	+++ ○○○	+++ ○○●	+++ +++	+++ +++	+++ +++	+++ +++	+++ +++	+++ +++		
				<i>a</i>	···	···	·-○ +++	○● +++	+++	+++ +++		
				<i>b</i>				···	···	·-○ ---		
<i>H. palliatus.</i>												
1915										+++ --●	+++ ---	+++ ---
1916	+++ ---	+++ ---	+++ ---	+++ --●	+++ +++	+++ +++	+++ +++	+++ +++	+++ +++	+++ +++		
				<i>a</i>	···	···-○ ●·	-○ ●+	●●+ +++	+++ +++	+++ +++		
				<i>b</i>				···	···-○	○●		
				<i>a</i> ¹					···	---		

In the above table, it will be seen that the most interesting period in the life-histories is that extending from May to September—the months May, August, and September being of special interest. Both species produce two broods in the year (marked as *a* and *b* in the table). In the case of *H. ater* only brood *a* matures. It does not give rise to a third brood, and brood *b* attains only the larval stage (it probably endures all winter). In *H. palliatus* brood *a* matures and gives rise to a third brood, *a*¹, which reaches the larval stage, while brood *b* also matures. In my laboratory experiments it reached the pupal stage, when untoward circumstances caused the pupæ to shrivel. I have no doubt that they would shortly have emerged.

ECONOMIC IMPORTANCE OF THE GENUS *HYLASTES*.

From the point of view of the forester, the three species of *Hylastes* under consideration may be divided into two groups—*H. ater* and *H. cunicularius* forming the first, *H. palliatus* constituting the second.

H. ater and *H. cunicularius*.

These two species are essentially enemies of the young newly-formed coniferous plantations, and more especially of such as are formed on

recent pine and spruce clearings. Unfortunately it is a prevalent custom in Scottish forestry to plant felled areas immediately after the removal of the timber. As a result of this custom *H. ater* and *H. cunicularius* are encouraged.

The methods of attack of *H. ater* and *H. cunicularius* are exactly similar, as are also the injuries they cause to the young plantations. The best example of an attack by the two species, which I have had an opportunity of observing, occurred on Darnhall Estate, Peeblesshire. It began in 1915 on a narrow strip planted that year, known as the Laidlaw strip, and spread to an adjoining area felled during 1915-16, and planted in spring 1916. This area is known as the Kaim Wood. Both areas contain spruce and Scots pine stumps. I first observed the presence of *Hylastes* in the Laidlaw strip in October 1915, where I found numbers of *H. ater* and *H. cunicularius* on the young plants. I made a rough estimate of the plants attacked during two subsequent visits in October and November, and concluded that about 30 per cent. of them had been killed. The Pine Weevil, *Hylobius*, however, was also present in the area.

The source of infection of this area by *Hylastes* lay, I believe, in the felled areas on Portmore Estate on the other side of the valley, where felling had been going on for some time. This much is certain, that neither of the species of *Hylastes* was breeding in the particular area under observation, as all the stumps which I examined in it were rotted with fungus and could afford no suitable habitation for *Hylastes*. At this time (October 1915), the Kaim Wood was only partly felled and harboured few *Hylastes*. Out of seven stumps examined only one yielded beetles. On it I found three adult *H. ater* and a few larvæ. In April 1916, I again visited the two areas, and again found *H. ater* and *H. cunicularius* on the young plants on the Laidlaw strip. The Kaim Wood, however, was covered with snow, and I made no attempt to examine the stumps in it. My next visit was delayed until August 1916, when I found the plants on the Laidlaw strip almost free of *Hylastes*. In the Kaim Wood, which was by this time felled and planted up, I found both *H. ater* and *H. cunicularius* attacking the newly-planted conifers, and also breeding in the stumps and roots in large numbers. All stages of both species were present on the roots—egg, larval, pupal and adult. The Pine Weevil, *Hylobius*, was also present in the adult stage in the plants, and in the larval stage in the stumps and roots. I now had an opportunity to make a careful and systematic examination of all the sickly and dead plants (which amounted to nearly 60 per cent. of the total number in the area), Mr Chalmers, Overseer of Darnhall Estate, having granted me permission to uproot such sickly plants as were unlikely to

recover. The following is a summary of my examination of a hundred of these plants, showing the cause or causes of injury :—

Killed solely by <i>Hylastes</i>	45
„ by <i>Hylastes</i> and <i>Hylobius</i> together	27
„ solely by <i>Hylobius</i>	15
„ by bad planting	13

It may be remarked that the above table shows a small percentage of deaths caused by *Hylobius*, which is commonly regarded as the source of all evil in young plantations. This at first sight appears a just observation, but in the area in question spruce stumps predominate, and these, although they afford breeding-ground for *Hylobius*, are not its favourite host, which is the Scots pine. Further, the number of Bark Beetles reared in a stump is very much greater than the number of Pine Weevils. I have no reason whatever to suspect that the hundred plants I selected throughout the area are not quite representative of the conditions in it. In fact, I am sure that if I had counted the stumps on which I found *Hylobius* larvæ and the numbers I found on each stump, and also counted the stumps which yielded *Hylastes* and the numbers yielded by each, that the figures would have been somewhat more in favour of *Hylastes* than the above summary shows. The Kaím Wood affords an excellent example of *Hylastes* attack, and it also affords a most interesting illustration of misapplied preventive measures. After the area was felled and the timber removed, the overseer, Mr Chalmers, caused all the brushwood to be burned on the top of the stumps, charring the stumps and roots considerably. Either such a precaution is wholly useless or it was taken at the wrong time. It was, I believe, taken primarily to prevent weevil attack. In this respect it may have been not wholly unsuccessful, but, as regards *Hylastes*, it completely failed. As I have observed, the swarm period of *Hylastes* is not limited to a short period, and while the act of charring may have repelled one invasion it has certainly not repelled them all. Apart from that difficulty there is this to be considered, that *H. ater* and *H. cunicularius* are soil dwellers, and while the fresh stumps probably serve to attract them to a felled area they are not the chief breeding-ground of the beetles, which is rather the root-system. Brushwood burning, therefore, unless it can be so arranged as to char the root-system as well as the stump (a very difficult matter), is practically useless as a preventive measure against *Hylastes*. Such a statement by no means condemns that excellent practice. *H. ater* and *H. cunicularius* are not our only forest enemies, and brushwood burning is always justified by the numbers of *M. piniperda*, *H. palliatus*, *P. bidentatus*, and other Scolytids it destroys or prevents from breeding.

Hylastes palliatus.

The damage done to the forest by *H. ater* and *H. cunicularius* is easily observed, and the financial loss is not difficult to estimate. This is not the case with *H. palliatus*. It occurs in older woods, and on the stems and crowns of the trees whose foliage is lost in the general canopy, so that sickly and even dead trees are easily overlooked. *H. palliatus*, moreover, is usually a follower of the Pine Beetle, *M. piniperda*, and where it is obvious that a tree has been killed by these two beetles, it is not always easy to determine what part either of them played in its destruction. This difficulty is of less common occurrence in spruce woods, but, on the other hand, the fungus, *Fomes annosus*, may cause a kindred difficulty.

I have, unfortunately, been unable to observe the development and termination of an attack by *H. palliatus* in our woodlands, and must content myself with giving a general account of my various observations made from time to time. Unlike its congeners, *H. palliatus* is harmful both in the larval and in the adult stages. Its galleries restrict the sap flow and reduce the vitality of the attacked tree, or, if numerous, stop the sap flow and kill the tree. *H. palliatus* rarely attacks vigorous healthy trees. It prefers trees weakened by squirrel attack, by smoke damage, or by suppression, by lack of light, by fungus, by the attacks of the Pine Beetle, *M. piniperda*, and by the lesser Pine Weevil, *P. pini*. It is a secondary pest. Owing, however, to its occurrence in large numbers, it is not improbable that in certain cases it ranks in point of destructiveness with *M. piniperda*. In plantations at Skene, Aberdeenshire, and on Earlyvale, Peeblesshire, I have found *H. palliatus* predominating over *M. piniperda* and proving decidedly more harmful.

As a rule, *H. palliatus* is of less importance as a forest pest than its congeners *ater* and *cunicularius*. It attacks trees at an age when they are better able to overcome attack, and, moreover, trees killed by *H. palliatus* are still useful as timber. The loss caused by *H. palliatus* is purely a loss of increment or interest, the loss caused by its congeners is a loss of interest and capital as well.

Preventive and Remedial Measures.—The question of preventive and remedial measures is too complex and debatable to be dealt with in this paper. It is intimately bound up with our Scottish system of forestry and even with our land legislation. In the writer's opinion, prevention of insect attack is as much the concern of the silviculturist as of the entomologist, and until forest protection is properly recognised in this country as a real and necessary branch of forestry, little can be done in that direction.

From the point of view of this paper, preventive and remedial measures may be divided into two classes—silvicultural and special. Silvicultural measures are those which are completely in the hands of the forester, and are chiefly preventive measures. Special measures are those which are somewhat without the province of the forester, and are both preventive and remedial. Special measures should be used only when silvicultural measures fail or are too late in application.

As regards *Hylastes* silvicultural measures consist of careful management of thinnings, arrangement of felling and planting, and barking of all timber and stumps immediately on felling.

Hylastes palliatus is, in the writer's opinion, best controlled by silvicultural measures. Regular thinning of growing woods, cutting out of sickly and suppressed stems, and the barking of all timber immediately on felling, together with the burning of the bark peeled off, will deprive *H. palliatus* of its breeding-ground and render it innocuous. Such measures involve no extra work for the forester if he is managing his woods properly.

With *Hylastes ater* and *H. cunicularius* such measures are of less value, as these beetles are enemies of the young plantation during the first few years of its existence. Silvicultural measures against these root-feeders consists of careful planting and planning of felling and planting. There is little doubt that if the system known as Natural Regeneration of woods were more fully employed *H. ater* and *H. cunicularius* would soon become negligible as forest pests. This system, however, is more costly and troublesome than planting. It implies careful management of all woods and precludes extra-ordinary fellings such as are occurring at present, owing to the scarcity of timber and the prevailing high prices. Further, it also implies the extinction of the rabbit.

The planning of felling and planting is also a difficult matter in present-day forestry. It involves a strict following of the working-plan, and, like Natural Regeneration, precludes extra-ordinary fellings. The aim in planning fellings is so to arrange them that areas about to be planted shall be as far removed as possible from areas about to be felled. The object in this is to prevent such pests as the Pine Weevil and the two *Hylastes* from finding breeding-ground and feeding-ground in close proximity. On large estates such an arrangement of fellings may be distinctly useful as a preventive measure against these pests, but on small estates it is impossible.

Careful planting is the best weapon the forester has against *Hylastes*. Strong, healthy, well-rooted plants undoubtedly are less liable to attack than poorly-rooted plants, and even when attacked are better able to resist. The system known as notching, whether it is mere dibbling or

the more elaborate L and T notching, is penny wise and pound foolish wherever there is reason to suspect the presence of *Hylastes* in the neighbourhood. Ball- or pit-planting in such conditions is true economy.

Special measures are more likely to be necessary against *H. ater* and *H. cunicularius* than against *H. palliatus*. Unfortunately they are difficult to devise and costly to carry out. Uprooting of stumps is undoubtedly the most effective special measure. I have repeatedly observed that the roots of wind-blown trees are never attacked by the root-feeding *Hylastes*, or if attacked before being blown are deserted after uprooting. Such a method is unfortunately costly, and leaves the felled area littered with stumps which have to be got rid of. They possess almost no market value and are heavy and awkward to remove. Burning them is as costly as removing them, and it is doubtful whether uprooting of stumps will ever be generally adopted for these reasons. Another method is the burning of brushwood and other litter on the tops of the stumps. I have already referred to it, and have doubts as to its value. It is also costly, ranging from 30s. to £2 per acre.

Creosoting of the stumps is yet another method. I have, unfortunately, no experience of it, but it appears to me that it is open to the same objections as brushwood burning. It is probably cheaper.

The real difficulty in fighting *Hylastes* lies in the unsatisfactory condition of forestry in Scotland. Each estate has its own methods, and when there is a possibility of the carefully managed forest becoming infested from a neighbouring badly managed one, it is not to be wondered at that both landowners and foresters are inclined to leave their insect enemies alone, so long as their depredations are not alarming. Unfortunately this *laissez-faire* attitude is involving considerable loss in our woodlands, a loss which, under the present circumstances, ought to be seriously considered.

XI.—Body Colour as affected by Blood Colour in Amphipods and Isopods, with some Remarks on a Bacterial Infection of *Gammarus*. By John Tait, M.D., D.Sc. (From the Laboratory of Physiology, Edinburgh University.)

(Read 26th February 1917. Received 26th February 1917.)

THE observations here recorded have been made at intervals in the course of an investigation chiefly on blood coagulation in Crustacea (see Tait, 1, 2, 3, and Tait and Gunn, 4).

BODY COLOUR AND BLOOD COLOUR.

The discovery that *Ligia oceanica* undergoes a marked change in shade in response to its surroundings (Tait, 5) led me to pay attention to the colours of other forms. P. Mayer (6), Matzdorff (7), and V. Bauer (8) had previously studied reflex colour change in *Idotea*. Since the observations on *Ligia* were made, I have found that *Sphaeroma serratum* undergoes a similar change of shade in response to its background, whereas *Oniscus* and *Conilera* do not (Tait, 2). Piéron (9) in a recent paper, to which I have failed to get access, has also studied colour change in isopods.

Chromatophores occur in the hypodermis of very many isopods, and naturally the colour of these animals is largely due to the chromatophores. On the other hand, the common shore amphipods (*Gammarus marinus*, *G. locusta*, *Orchestia littorea*, *Talitrus locusta*) have no chromatophores. Their colours are nevertheless very diverse. Among *Gammari*, which tend to be uniformly "self-coloured," dark greens, slate-greys, and browns are common, dark reds are not uncommon, while pale yellows and whites are occasionally met with. Individual specimens of *Orchestia* or of *Talitrus* are more variegated, the ventral surface being lighter than the dorsal, probably in relation to their dorsi-ventral posture, while the dorsum tends to be transversely banded. *Orchestia* is either brown (or blue and brown) above and bluish below, or of a bright yellow-brown with no sign of blue below. *Talitrus* is much paler, only the dorsum being marked with pigment. These colours, in contrast with those of some of the isopods mentioned above, are permanent (over considerable periods of time) in spite of change of surroundings or of lighting.

Examination shows that the colour of the blood of these amphipods closely corresponds with that of the animals themselves. A dark green *Gammarus* has greenish blood plasma, a slate-grey specimen bluish plasma, a brown has brown, while a brownish-red has violet plasma. The pale yellow and the white *Gammari* have plasma that is almost colourless, while the

blood of some of them, viewed in bulk, is actually milk-white (see next section). *Orchestia* in which a blue tint is visible have bright blue plasma; those in which no blue is to be seen, *i.e.* the yellow-brown specimens, have yellow plasma. *Talitrus*, so blanched in colour, has, as already noted by Bruntz (10), colourless blood. The external covering of these shore amphipods being devoid of chromatophores and being more transparent than that of most isopods, *the hue of the blood largely determines the colour of the animal*. It is for this reason that their colour is not subject to reflex alteration, but remains fixed in spite of change of eye illumination.

Even isopods that possess chromatophores may derive part of their colour from that of the blood. Thus, some specimens of *Idotea emarginata* are fundamentally darker than others, and no length of exposure on a white background can turn them into light-coloured individuals. While the blood of all individuals of this species is tinged with brown, that of the permanently dark specimens is deep brown. In such a case the underlying colour of the blood markedly limits the extent to which the animal can change its shade by retraction of chromatophores. Generally speaking, the residual colour of any isopod whose chromatophores have retracted to the utmost, is that of its blood plasma. It would be of interest to know whether these changes in blood colour are in any way dependent on the state of the isopod as regards moult (*cf.* Tait, 3).

The colour of the blood is best determined by allowing it to escape from the antennæ, and examining it against a white or a black background according to circumstances; though in many cases it is sufficiently pronounced to be seen with the low power of an ordinary microscope, as in making direct observations on arrest of hæmorrhage from the antennæ. To see the colour in its full depth a simple plan is to drop the animal, after its antennary flagella have been cut across, into a white porcelain dish containing sea- or preferably tap-water. Hæmorrhage is brisk, the blood pouring out and settling to the bottom of the dish in quantity. By heating the dish the colour changes produced with rise of temperature can be readily studied. Thus the bright blue blood of *Orchestia* turns at first violet and then reddish-brown with heat; yellow blood from the same species remains unchanged or becomes brownish.

It is generally agreed that the actual colour of the blood depends on the simultaneous presence, in different proportions, of two or three fundamental pigments—a blue, a yellow, and a red (see Newbigin, 11, also Winterstein, 12). Bauer (8) states that the prevailing greenish tint of *Idotea tricuspidata* is due to its vegetable food. Whether the blood is greenish he does not say, but in any case one would accept only after experimental evidence the conclusion

that the food pigments pass directly as such into the blood plasma. Heim (13) showed that an excess of yellow pigment is present in the blood of female crabs at the time of ripening of the ovaries; once the eggs are expelled the blood loses its yellow colour. G. Smith (14) and Robson (15) have amplified these results, and in particular have shown that the presence of the yellow pigment corresponds with an increased percentage of lipoid in the blood. In this connection it is important to note that the distinction between the blue and the yellow forms of *Orchestia* does not depend on sexual difference, for both varieties occur in the male sex.

In order to see whether one variety would pass into another, I kept four blue and four yellow examples of male *Orchestia* immersed in sea-water, without food, for a period of twenty-six days. At the end of that time the animals were removed alive and healthy, but all retained their original colour.

While the plasma of some amphipods is decidedly blue, I have hitherto come across no isopods with any trace of blue in their blood. The blood of the Oniscoidea seems to be devoid of colour.

WHITE GAMMARI.

Associated with ordinary specimens of *Gammarus marinus* on the beach one occasionally comes across a pale specimen, whose colour varies from light yellow almost to white. The first time I found these animals, on the seaward side of a storm-beach through which fresh water slowly percolated, they were quite numerous. A year later, at the same place, I found them equally numerous. As a rule, however, they are rare; but they do occur widely distributed round the coast. I have found them in the extreme north of Scotland and in the south of England.

When the antennæ of these animals are viewed with the microscope, the circulating fluid is seen to swarm with very fine particles much smaller than blood corpuscles, which, however, are also present though greatly reduced in number. The appearance presented by these particles escaping from a wound in the antenna reminds one of dry sand pouring from an orifice. They have none of that adhesive property which is such a marked feature in extravasated crustacean blood cells, and do not form a plug at the mouth of the wound (see Tait, 1). The blood corpuscles eventually arrest the hæmorrhage by agglutinating at the site of the wound, but these small particles do not get caught in the adhesive mass of cells thus formed.

The escaped fluid when viewed against a dark background is milk-white. The plasma itself is colourless, and the whiteness is due to dispersion of light from the surface of the multitudinous particles.

When examined with a high power these bodies are seen to have the shape of rice-grains, being short cylinders about three times as long as they are thick, with smooth contour and rounded ends. They are of uniform size. Though I have not actually measured them, I should say their length is about equal to the diameter of a human red blood corpuscle.

My first idea, judging from their occurrence in the blood and their smooth contour, was that they might be particles of fatty nature. They fail, however, to stain with osmic acid, with Scharlach R., or with Sudan III. They are readily fixed with corrosive sublimate or with formalin, and stain with basic aniline dyes. On subsequent differentiation with alcohol I have thought that I could see a nucleus in them. In addition to this their fixed shape and uniform size suggest that they are organised structures. The only feasible view with regard to them was that they were organisms of some kind, which, having gained access to the animal in some way, had multiplied in the blood. Against this view, however, was the apparent healthiness of the animals under such an overwhelming infection.

Quite recently I have found that Vejdovsky (16, 17) has described, in spirit specimens of *Gammarus zschokkei* (from Garschina Lake, Switzerland), the occurrence of a "gigantic" nucleate micro-organism, which he has named *Bacterium gammari*. The bacterium occurs in enormous numbers in cells of the body itself and also free in the blood, undergoing division by mitosis. Mencl (18), having re-stained Vejdovsky's specimens by the iron-alum method, has published a minute description of the microscopic appearances of the organism. Perusal of these accounts leaves little doubt in my mind that the particles which I have seen in *Gammarus marinus* are micro-organisms similar to, if not actually identical with, *Bacterium gammari*.

One interesting fact in connection with the infected animals is the disappearance of all pigment from the plasma in advanced stages of the disease. In brown-coloured *Gammari* with brownish plasma I have found these organisms present, yet few in number. When they are very abundant the plasma is colourless. Evidently the presence of the bacterium causes some change in metabolism, whereby already-formed blood pigment is destroyed or the manufacture of new pigment is inhibited. Heim (13) has directed attention to the occasional occurrence of white crayfish; it is possible that these animals suffer from an organismal infection similar to that of the *Gammari*.

SUMMARY.

1. Members of the Gammaridea owe their body colour in large degree to the colour of the blood; isopods in much less degree.

2. *Gammarus marinus* is occasionally attacked by a very large bacterium, which circulates in great numbers in the blood. The infected animals become white in colour, owing to their blood being deprived of pigment, and to reflection of light from the bacteria.

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XII.—*Eudemis nævana*, Hb., the Holly Tortrix Moth. By L. H. Huie, F.E.S., Department of Agricultural and Forest Entomology, Edinburgh University.

(With Plate.)

(Read 26th February 1917. Received 16th March 1917.)

[Also named *E. geminana*,¹ Stph.; *Steganoptycha* (*Grapholitha*) *nævana* and *Rhopobota nævana*, Hb.]

CLASSIFICATION.

Order LEPIDOPTERA.

Group TORTRICINA.

Family EPIBLEMIDÆ.

THIS moth is common in England, in the lowlands of Scotland, and in parts of Ireland. For many years holly trees in Edinburgh and neighbourhood have suffered from this pest. My own notes record it from public and private shrubberies, nurseries, hedges on the highways, etc.

The following observations were made in 1916 in a garden of 2¼ acres in extent, containing 110 holly trees of seven different varieties, every one of which was infested by the larvæ of *Eudemis nævana*. The garden contains also apple and hawthorn trees which are recorded as host plants for these caterpillars, but neither of these showed any signs of the pest, though the larvæ were reared artificially with perfect success on the leaves of both.

EPITOME OF LIFE-HISTORY.

The life-history of this insect is shortly as follows:—The moths emerge after pupation about the end of July and beginning of August. The eggs are laid in August on the under sides of holly leaves; the larvæ hatch out in late April or early May of the following year, and proceed at once to the apices of the shoots to feed on the young leaves of opening buds. Here they remain, at first feeding on the outer leaves, later working their way inwards. In the course of their life as caterpillars four moults take place. During the third and fourth instars the larvæ protect themselves when feeding by fastening the leaves together by a silken webbing, which prevents the buds from unfolding. Under the cover thus afforded the larva devours the youngest leaves, and often gnaws the growing point also. The caterpillar

¹ This name has been given to the form feeding on *Vaccinium*, but “there is no constant difference,” *Handbook of British Lepidoptera*, by Meyrick, p. 477.

is full fed about the end of June or beginning of July. About the same time the leaves of the bud, by reason of their growth, break the webbing that has spun them together, and the apex of the shoot becomes exposed. The caterpillar now seeks a retreat for pupation, often letting itself down by a thread to a lower branch. It may wander for a couple of days, and usually spins itself up finally between two contiguous leaves. Here it shrinks very considerably, and moulting for the fourth time passes into the pupal state about a week after it has ceased to feed. The moths emerge in from two to three weeks (seventeen days in some observed cases).

INJURY TO THE TREE.

The ultimate injury to the tree consists in the eating off of four or five of the youngest leaves, and usually in the destruction of the growing point, so that by the end of June infested shoots will only have supplied to the tree two, three, or four new leaves—the outer leaves of the bud, all more or less mutilated by gnawing—instead of the 9–12 leaves furnished by a healthy, normally elongated shoot. Further, the disfigurement during the infestation, owing to accumulations of frass and the distortion of the leaves produced by the webbings, gives to the trees a very unsightly appearance.

It is true that later in the season vigorous trees make up for the loss of new foliage by putting forth some younger leaves, either from the leading shoot, when the growing point has not been destroyed, or from lateral buds. The common holly, *Ilex aquifolium*, makes an especially good recovery in this way. But many trees recover only partially, the leaves of the new crop making but puny growth, while the damaged leaves below remain a permanent disfigurement to the year's shoots. Further, the trees which have been infested always present a more irregular, and less pleasing appearance than those which have suffered no check to the natural manner of their growth.

DETAILED ACCOUNT OF LIFE-HISTORY AND HABITS.

My observations began in February 1916. As already stated *E. nævana* is at this time of the year still hibernating as an embryo within the egg.

The *Egg* is scale-like, oval, scarcely 1 mm. in length, and about $\frac{3}{4}$ mm. in breadth, and adheres to the leaf by one surface (Fig. 5). It consists of a yellow or orange coloured yolk, enclosed in a double pellicle, which, viewed from the free surface, appears as a transparent membranous zone encircling the yolk. The inner pellicle is smooth, very thin and transparent; the outer is thicker, and, though it is also transparent, shows a honeycomb pattern.

Three or four micropyles indicate the cephalic end of the egg. A glandular secretion supplied at the time of ovi-position ensures adherence to the leaf. If the egg be detached the impression of the guard-cells of the stomata is plainly visible on its under surface. When the envelopes of the egg are removed under a dissecting microscope it is found that closely investing the yolk is still another coat, the serosa, consisting of a firm layer of epithelial-like cells with large nuclei. The orange-coloured appearance of the yolk is largely due to the tint of the serosa. The envelopes are so impervious that eggs which had been placed for six hours in 80 per cent. alcohol hatched out afterwards; and an egg a few hours old was seen to go through the usual early embryonic changes while lying in Bles's fixative.

The *Larva* emerges from the egg by gnawing an exit hole in the chorion, a process lasting from half an hour to one hour.¹ When first hatched the larva is under 2 mm. in length, of a yellow colour with a blackish head. The yellow colour is maintained through the first and second instars. The newly emerged caterpillars wander away at once in search of food, and soon reach the opening buds. The little larvæ are, however, quite able to eat leaves of the last year's growth, as was proved by depriving a small plant of all its buds. The larvæ which hatched from eggs on this tree made their way to the ends of the shoots, and finding no buds nourished themselves quite well upon the leaves of the previous year.

For the first few days the larvæ crawl about the outermost leaves of the buds, which at the time when the eggs of *E. næviana* are hatching out are still very small. A careful scrutiny of buds, with a hand lens, will reveal the presence of frass, and the fact that minute depredations are already being wrought on the outermost leaves. When the larvæ have reached a length of $2\frac{1}{2}$ mm., having gained also proportionately in girth (usually in about a week), they moult for the first time. Larvæ about to moult stop eating and encase themselves in a very delicate sheath of threads. At each subsequent moult the sheath woven for the occasion is thicker than that spun for the previous ecdysis. There are four instars of larval life; and after each moult, except the fourth, the larva devours its cast skin, leaving only the mask. I have a micro-preparation of a newly-moulted larva of the second instar, in the alimentary canal of which can be clearly seen the exuvia, with all six legs still attached.

In the second instar, the larva, except in the matter of size, has changed little in appearance. During this instar, which lasts about twelve days,

¹ The more intimate observations on the habits of the larvæ were made on specimens reared on pot plants, kept under observation in a cool greenhouse.

it becomes easy to recognise the infested buds, not only because the pellets of frass are more in evidence, but because the rolling of the leaves becomes apparent.

On dissecting the buds by removing one leaf after another, one finds that the outer leaves have been gnawed on their inner surface, apex, and edges, and there are accumulations of frass. As the bud opens the caterpillar shifts its feeding-ground inwards, so that the most severe damage and the heaviest accumulations of frass are not on the outermost leaves, which remain healthy enough to perform their normal service to the tree. Proceeding inwards in the examination of the bud one finds adhesions of a silky secretion that attach the inner surface of outer leaves to the outer surface and edges of inner leaves. Lastly, a very young leaf is reached enclosing the conical apex of the shoot. Within this young leaf the larva, about to moult for the second time, ensconces itself, spinning the edges of the leaf together so as to keep the leaf rolled. In the tube so formed the moult takes place. The larva at this stage is 5 mm. in length.

After the second moult there is a considerable change in the appearance of the caterpillar. The body, hitherto yellowish, has now assumed a dingy green colour. On the prothorax is a black horny plate, and the thoracic legs are black. The caterpillar henceforth does a great deal of spinning, and lives and eats in the rolled-up inner leaves of the bud, round which the more external leaves are webbed together to form a closed envelope. When disturbed, the caterpillar can move forwards or backwards with equal ease and rapidity, and if ousted from its dwelling will let itself down by a thread to a lower branch and spin up in another retreat. This it does very rapidly, moving its head from side to side, fastening the thread as it issues from the spinneret now to one leaf-edge, now to another. In this way tissues or sheets of the webbing are formed. I have several times watched a larva feeding and weaving simultaneously. This was the case when the field of operation was the inner (upper) face of a leaf, for the tissues of the inner leaf surface are greatly preferred to those of the back of the leaf. Each time the caterpillar brought its head to the leaf to fasten the thread, it took a bite from the surface. Obviously this habit tends to roll the leaf, for the young leaf thus becomes stripped of its upper surface, whereas the tissues of the under-surface continue to grow. However a leaf will roll under the influence of the caterpillar, whether it be gnawed or not. A larva about four weeks old was transferred from the bud which had hitherto sheltered it, to an uninfested bud. It stood on the lower surface of a fully expanded but still young and soft leaf, and began at once to weave from the edge of the leaf to the mid-rib. In three hours the half leaf had rolled backwards,

and formed a perfect tube in which the caterpillar was concealed, and where it moulted. This caterpillar being about to moult did not eat while spinning.

Another caterpillar was removed from its own bud to another, of which the oldest leaves were fairly large and had expanded. The caterpillar, standing on a leaf, of which the two halves were still somewhat folded together began spinning between this leaf and the one next below it. In $1\frac{1}{2}$ hour it had drawn the two leaves together to form a three-sided tube, the open side of the partially folded leaf being closed by the inner face of the other leaf.

The third moult takes place when the larva has grown to 9 mm.; this occurs about the middle of June in my experience. The coloration is the same in the fourth as in the third instar. It is now that the depredations become most conspicuous. Normally, in uninfested hollies, the season's buds have developed into shoots of 6 inches in length, by the third week of June, bearing 8-9 leaves, the oldest of which have attained full growth. The webbings spun by the caterpillars prevent the expansion of the infested shoots. The leaf-stalks and less damaged leaves nevertheless make some growth, which results in the shoots assuming the appearance of large, bulging, distorted buds disfigured by gnawed patches, with masses of frass mixed up in the meshes of larval webbings. Below these large, misshapen buds (Fig. 6) there may be as previously stated 2-4 less damaged leaves, saved by the elongation of their internodes from prolonged injury, and, through subsequent growth, possessing enough healthy tissue to enable them, in spite of their mutilations, to perform their functions.

In another 10-14 days the big buds just described are disappearing, because the outer leaves, distorted and largely gnawed though they are, have, by their growth, ruptured the webbings that bound them. It is then seen that the youngest leaves have been totally destroyed (Fig. 7). The apex of the shoot itself is often eaten off. The larva, now full fed, measures 12-13 mm. It moves to a lower position upon the branch, searching for a suitable place where it may spin up for pupation. After wandering for a day or two¹ it finally comes to rest, most often between two contiguous leaves, and encloses itself in a very dense silken sheath, or cocoon (Fig. 1), shrinks very considerably, and, after lying still for four or five days, moults for the fourth time, to become a pupa.

The *Pupa* measures $7-7\frac{1}{2}$ mm. in length. At first of a pale yellow colour, it soon changes to orange and later to brown. As it matures, the eyes, antennæ, and thoracic appendages of the imago become more and more

¹The larvæ are in a very unprotected state during this wandering, and I believe many of them fall a prey to birds. In the summer of 1916 the very wet weather that prevailed at the beginning of July proved fatal to a large number of them.

clearly seen. The segments of the abdomen are smooth on the ventral aspect, but the dorsal side of each of the first six bears a row of stiff, tooth-like, short bristles or points, parallel with the anterior edge, and a similar row of smaller but more numerous points slightly below the centre of the segment. The 7th, 8th, and 9th abdominal segments all bear one row of points, those on the 9th being larger in size and fewer in number than the rest. A cremaster is represented by a few rather long, hooked hairs situated at the posterior extremity of the pupa.

The cast-off skin shed at pupation lies at the posterior end of the cocoon; and when the moth is about to emerge the pupa protrudes itself from the other end to facilitate the free escape of the imago (Fig. 2). As already stated *E. nævana* remains in the pupal state between two and three weeks.

The *Imago* is described in great detail in Barrett's *Lepidoptera of the British Isles*. I offer the following shorter description (Figs. 1, 2, 3, 4):—

Wing expanse, $\frac{1}{2}$ – $\frac{5}{8}$ inch; body scarcely $\frac{1}{4}$ inch. Antennæ grey or brown, more than half the length of the body, very slender. Fore wings narrow, grey with brown markings, which vary exceedingly in intensity of tint, a broad basal blotch and an irregular oblique central band being the general pattern, which may vary from grey-brown to dark brown or black. Hind wings pale brownish-grey, deeply fringed.

The sexes do not differ in colouring or antennæ, but while the abdomen of the female is somewhat pear-shaped with the narrow end posterior, the abdomen of the male is cylindrical and more tufted at its extremity. Both sexes are furnished with a short proboscis, with which I have seen them suck up moisture.

The moths remain during daylight under the leaves and branches of the holly trees, where they are afforded protection from rain, wind and light. About sunset they emerge and flit about the branches, or keep up a swaying flight to and fro in front of a tree, coming to rest on a leaf, and after a time taking to wing again. The moths continue their activities after dark, as I often proved by means of a flash-light. Moths were bred out in a large cage supplied with two small holly plants, on which the females ovi-posit, but I was never fortunate enough to witness the actual laying of the eggs. Mating took place after sundown, and I once found a pair still coupled in the early morning. These captive moths lived from three to four weeks.

REMEDIES AGAINST THE PEST.

With a view to fighting this insect as a pest, a consideration of the life-history would suggest the following methods of attack:—

1. Treatment that might destroy the newly-hatched caterpillar on its way

from the egg to the shoot apex. With this object in view trees were sprayed with Paris green, lead arsenate, and lead chromate shortly before the hatching of the eggs was expected, and also after the first caterpillars had emerged. The results are given in the tables.

2. Treatment that might kill the young larvæ in the first or second instar, that is, while they are feeding on the outer leaves of the bud, and before they have begun to spin to any great extent. With this object in view a nicotine spray was used with very good results, as shown in the table. Based on the observation that a great number of such young larvæ had been drowned during a day of incessant rain, heavy syringing with water from a garden hose was also tried. This gives the best results if the day chosen for the treatment be one when the humidity of the atmosphere is sufficient to prevent the speedy drying of the leaves. On a bright day it is almost useless.

SUMMARY OF RESULTS OF INSECTICIDE SPRAYS.

The following is a general summary of the results of the various insecticides used, with regard to—

1. *The Mortality of the Larvæ due to the Spray.*

In control trees, on an average, about 85 per cent. of the buds become infested.

In trees treated, as described, with lead arsenate about 55 per cent. became infested.

In trees treated with lead chromate about 75 per cent.

Trees sprayed with Paris green showed no diminution of the percentage of buds infested. This must be ascribed partly to weather conditions unfavourable to the experiments.

In trees treated, as described, with nicotine an average of about 10 per cent. of the buds remained infested with living caterpillars.

2. *The Effect of the Spray on the Foliage.*

None of the insecticides used proved in the least detrimental to the health of the trees. The thin milky-white coating left by spraying with lead arsenate gave to the trees the bluish tint of a eucalyptus, and as this coating is not readily washed off by rain, the appearance of the trees was thus affected for several months.

The lead chromate spray is apt to make yellow patches on the leaves where a precipitate settles, giving them a "variegated" appearance, which is, however, not very noticeable.

Paris green, in the strength employed, did not alter the appearance of the foliage.

The nicotine spray cleansed the trees of other insects as well as the caterpillars. After spraying, these trees were freer from spiders and aphides than neighbouring control trees.

3. *The Ultimate Effect on the Tree.*

At the end of the season, trees successfully treated by the nicotine spray were distinguished by the marked superiority of the growth of their shoots, and by the absence of ragged and distorted leaves. Those trees which had been sprayed with lead arsenate and lead chromate showed comparatively little superiority over untreated trees, and in this respect were less distinguishable from controls except by the traces of the spray.

The insecticides used may therefore be arranged in order of their efficiency, as follows:—

- | | |
|--------------------|--------------------|
| (1) Nicotine. | (3) Lead chromate. |
| (2) Lead arsenate. | (4) Paris green. |

In order to test the effect of hydrocyanic acid gas on the eggs, three different fumigation experiments were made.

Experiment 1.—On 23rd February a young holly, 18 inches high (in a large pot of soil), with a number of eggs here and there on its leaves, was placed in a fumigation chamber, and exposed for an hour to hydrocyanic gas fumes. The proportions of cyanide of potassium, sulphuric acid, and water used in the experiments were—

Potassium cyanide	1 part by weight
Sulphuric acid	1 part „
Water	3 $\frac{3}{4}$ parts „

and the amount of space per unit of cyanide was at the rate of 1 oz. of cyanide 98 per cent. purity per 300 cubic feet of space. In Experiment 1, eggs removed after fumigation and examined microscopically were found to be uninjured, and the development of others left on the leaves of the plant progressed normally.

Experiment 2.—The same holly was—with the eggs in a more advanced stage of development—again exposed to an hour's fumigation with hydrocyanic acid gas. The gas was of the same strength as in Experiment 1, and the eggs held embryos that had reached a distinct caterpillar form, but the caterpillars were still surrounded by a thin layer of yolk. The plant after fumigation was placed out in the garden, and observations made. The eggs without exception hatched in due course.

Experiment 3.—On 18th May another young holly plant, in a pot of soil, and with many eggs on its leaves, was subjected to fumigation under severer conditions. The strength of the cyanide was greater, and the plant during fumigation was placed, not exposed in a large fumigation chamber, but covered by a box that just fitted the plant, and had a capacity of $12\frac{1}{2}$ cubic feet. The capsule in which the hydrocyanic acid gas fumes were generated was laid on the soil of the pot in which the holly was planted, and the fumes rose right up through the plant. The embryos in the eggs on this plant were well advanced; some of the eggs on the plant had already hatched before the experiment was done. After fumigation, twelve leaves bearing fourteen eggs were removed from the plant on 21st May and kept under observation. Nine of the eggs hatched in due course; in the other five the caterpillars had been killed. All the experiments were done at a temperature of 60° F. I am greatly obliged to Professor Gemmell for his courtesy in offering all the conveniences of his laboratory for these fumigation experiments.

My thanks are due to Dr Stewart MacDougall for suggesting this research on *Eudemis nevana*, and for his unfailing kindly counsel in its prosecution, and especially for his help in the fumigation experiments.

EXPLANATION OF PLATE.

- Fig. 1. Holly leaf bearing a cocoon of *Eudemis nevana*, with moth. Natural size.
 Fig. 2. Leaf with cocoon from which empty pupa case protrudes.
 Figs. 3 and 4. Male and female moth, both from life. $\times 4$.
 Fig. 5. Eggs on holly leaf. $\times 4$.
 Fig. 6. Holly shoot with leaves fastened together by larval webbing (see text).
 Fig. 7. Holly shoot at the end of larval life. The webbings have burst.

I am indebted to Mr Hugh Main for the photographs which form Figs. 3, 4, and 5, and to Mr Richard Muir for those forming Figs. 1 and 2.

TABLE I.—CONTROL TREES.

Variety of Holly.	Height of Tree.	Eggs per 100 Leaves.	Total Number of Buds counted on June 24.	Buds Infested out of total counted.	Buds Uninfested out of total counted.	Remarks.
Broad smooth-leaved variety.	10½ ft.	28	300	292	8	This is a companion tree to the holly of the same variety sprayed by nicotine on May 17th and again on May 29rd. It was left unsprayed, because at the time it contained a thrush's nest with nestlings.
Common Holly.	5½ ft.	10	125	119	6	This control was selected as bearing a small percentage of eggs in contrast to the tree cited above which possessed a rather large percentage. It is also comparable in height and build to a tree used for the nicotine experiment (see Nicotine report).
Common Holly.	11 ft.	12	300	261	39	This is an extremely full, well-grown tree—a companion tree to one of equal height and build, sprayed with nicotine after the larvæ had passed the first moult (see report on Nicotine spraying). Four other controls are mentioned in detail in the report on the row of trees treated with nicotine spray.

TABLE II.—RESULTS OF SPRAYING WITH LEAD ARSENATE.

The first five trees mentioned below were sprayed with Richard's Arsenate of Lead Paste, used in the proportion of 3 lbs. to 50 gallons of water. The two last-mentioned trees were sprayed with Corry's "Acme" Arsenate of Lead Paste, 1 lb. to 20 gallons of water.

Variety of Holly.	Height of Tree.	Eggs per 100 Leaves.	Date of Spraying	Condition of Pest at Time of Spraying.	Date of Hatching.	Number of Buds Examined on May 31.	Buds Uninfested	Buds Infested	Remarks.
Broad smooth-leaved variety.	9 ft.	24	April 29.	In the most advanced eggs the embryo had assumed the larval form, but much yolk remained to be consumed.	May 14-22 approx.	50	27	23	<p>These two are companion trees.</p> <p>The lead arsenate did not injure the leaves, though it remained on them as a thin white incrustation—imparting to them a milky or bluish look (one visitor, seeing them at a distance, asked if those were eucalyptus trees). This persisted in spite of heavy rains; but was less conspicuous with the Acme paste, than in the case of Richard's preparation.</p> <p>Six twigs bearing infested buds were plunged for thirty seconds in the solution used for spraying; the buds were allowed to dry, and were examined seven hours later. The larvae appeared unaffected.</p>
Broad smooth-leaved variety.	9 ft.	20	April 29.	Same as last.	May 14-22 approx.	50	15	35	
Golden Holly.	6 ft.	14	May 8.	Caterpillars in the eggs, but still undersized and surrounded by yolk.	May 17-25 approx.	50	31	19	
Silver Holly.	10 ft.	13	May 18.	Some eggs hatching out; others more backward.	May 17-25 approx.	50	31	19	
Narrow smooth-leaved variety.	15 ft.	18	May 18.	Eggs ripe; some may have hatched.	May 18-25 or 26 approx.	100	46	54	
Common Holly.	7 ft.	15	May 19.	Eggs hardly ripe, or very few.	May 19 or 20 to 27 or 28.	50	30	20	
Broad smooth-leaved variety.	6½ ft.	10	May 19.	Many eggs had hatched.	May 17-24 approx.	50	21	29	

TABLE III.—RESULTS OF SPRAYING WITH LEAD CHROMATE.

The formula for this spray was Lefroy's, viz.: Dissolve ½ oz. of lead acetate; dissolve separately ¼ oz. of powdered potassium bichromate; mix these in two gallons of water; and keep well stirred.

Variety of Holly.	Height of Tree.	Eggs per 100 Leaves.	Date of Spraying.	Condition of Pest at Time of Spraying.	Date of Hatching.	Number of Buds examined on May 29-30.	Buds Uninfested.	Buds Infested.	Remarks.
Broad smooth-leaved variety.	8½ ft.	16	April 29.	Embryo had assumed the larval form in most eggs; but much yolk remained to be consumed.	May 14-22 approx.	36	17 Mostly in the upper branches and upper middle.	19 Mostly in the lower branches and lower middle.	The lead chromate remained on the leaves as a yellow encrustation—more or less in patches—up to the time of counting the buds; but after May 17th the traces of the spray were very much diminished owing to a heavy fall of rain, lasting the whole of that day.
Broad smooth-leaved variety.	5½ ft.	31	April 29.	Same as above.	Same as last.	36	2	34	This is a small tree with few branches and consequently few buds, in proportion to the unusually heavy deposition of eggs.
Golden Holly.	5½ ft.	17	May 9.	Caterpillars in the eggs, but with their heads not yet darkened. Yolk almost used up.	May 15 or 16 to 23 approx.	50	19	31	...
Hedge-hog Holly.	10 ft.	60	May 10.	Owing to getting less sunshine the eggs on this tree were later of ripening than those above mentioned, and at this time the contained larvæ were still undersized and surrounded by some yolk.	May 18-26.	10	1	9	The buds of this variety remain very small for a long time. Many larvæ will certainly die of starvation.
Broad smooth-leaved variety.	9 ft.	20	May 16.	About 50 per cent. eggs already hatched; others about to hatch.	May 15-19.	50	2	48	Spraying with lead chromate did not kill the larvæ in the buds, and when branches bearing infested buds were plunged in the solution for 30-60 seconds the larvæ were uninjured.
Common Holly.	10 ft.	11	May 18.	Eggs hatching out.	May 16-24 approx.	36	20	16	...

TABLE IV.—REPORT OF SPRAYING WITH PARIS GREEN (BLUNDELL'S).

The spray was prepared and used in conformity with the directions on the jar — 1 lb. to 120 gallons of water, *i.e.* the "strong dose."

Variety of Holly.	Height of Tree.	Eggs per 100 Leaves.	Date of Spraying.	Condition of Pest at this Date.	Date of Hatching.	Number of Buds examined on May 28.	Buds Uninfested.	Buds Infested.	Remarks.
Broad smooth-leaved variety.	5½ ft.	10	May 1.	The embryo had assumed the larval form, but was still surrounded by yolk.	May 14-22.	50	5	45	This spraying was unnecessarily early, hatching being delayed by cold weather. A great deal of rain fell between the dates of spraying and hatching, a condition adverse to the success of the experiment, as Paris green is apt to be washed off.
Common Holly.	6 ft.	30	May 2.	Embryos in various stages, but none older than the above-mentioned stage.	Approx. from May 15-24.	24	2	22 holding in all 48 larvae.	The above remark applies to this tree. Leaves in all cases totally uninfested by the spray.
Broad smooth-leaved variety.	6½ ft.	12	May 10.	Eggs contained fully-formed larvae.	May 12-20.	50	6	44	Weather very unsettled. The spray had little chance of taking effect. Exceedingly heavy rain all day on 17th.
Broad smooth-leaved variety.	7 ft.	14	May 10.	About same as last.	May 12-20.	50	10	40	...
Yellow-Berried Holly.	13 ft.	22	May 18.	Ripe eggs.	May 18-26.	50	13	37	...
Broad smooth-leaved variety.	5½ ft.	10	May 18.	Some eggs already hatched; others ripe.	May 14-22 approx.	6	1	5	...
Broad smooth-leaved variety.	11 ft.	16	May 19.	Small larvae in buds; some eggs still unhatched.	May 15-23.	25	4	21	Larvae in the buds were not killed by this spray. Three buds opened on the day following the spray showed — (1) one quite healthy larva; (2) uninfested; (3) two healthy larvae. Foliage was in no case injured.

TABLE V.—RESULTS OF SPRAYING WITH NICOTINE.

The commercial nicotine insecticide "XL ALL" was used in the stronger proportion indicated on the bottle label, *i.e.* diluted with twelve times its bulk of water. This was strong enough to prove very irritating to the throat of the operator.

Variety of Holly.	Height of Tree.	Eggs per 100 Leaves.	Date of Spraying.	State of Infestation when Sprayed.	Number of Buds Examined after Spraying.	Buds Uninfested.	Buds Infested.	Remarks.
Broad smooth-leaved variety.	12 ft.	14	May 16.	Most of the caterpillars had hatched out, but not all.	300 (June 3).	288	12	An examination of buds shortly after spraying showed that the larvæ had been killed by the nicotine, but a subsequent examination on May 20th revealed the fact (as expected) that the remainder of the eggs had hatched, and a fresh infestation by newly-hatched larvæ had taken place. Thus many buds contained both living and dead larvæ. As these trees occupied a prominent situation it was desirable to rid them of the pest; they were therefore sprayed a second time on May 20th, resulting in the success indicated in the table.
Common Holly.	10 ft.	15	May 16.	"	100 (June 3).	100	0	
Broad smooth-leaved variety.	11 ft.	26	May 17.	"	100 (June 3).	99	1	
Broad smooth-leaved variety.	average 6 ft.	average 10	May 23.	Probably nearly all the eggs had hatched. Out of 18 buds sampled, 15 contained larvæ.	12 buds were examined 24 hours after spraying. 2 had not been infested. In the other buds 10 dead larvæ were found, and 2 not quite dead.	As these trees are desired to make as much growth as possible, it was inconvenient to deprive them of many buds, and so a final report of them was delayed until the buds had so far advanced that those infested could be detected without opening them at all. (See Table VI.)
Common Holly.	11½ ft.	10	June 3.	Larvæ about 2 mm. long. Some already in the second instar. Out of 100 buds examined before spraying, 85 contained larvæ.	Next day 15 buds were opened and all contained dead larvæ.	Twigs of trees with infested buds were immersed in the solution for 30 seconds, and examination showed that this was sufficient to kill the larvæ in every case.

TABLE VI.—LATER REPORT ON THE TWENTY-FOUR TREES PLANTED TO FORM A HEDGE,
SPRAYED WITH NICOTINE ON 23RD MAY 1916.

The entire row comprises twenty-eight trees; but four of them were left unsprayed to serve as controls. The first control tree occupies one end of the row; the other three are situated at intervals along the line. All the buds on the controls were counted on 21st June, and each control tree compared with a tree next to it, previously (23rd May) treated with nicotine spray. The injuries inflicted by the pest had reached their height at the date of this report.

Tree.	Total Number of Buds.	Buds Infested.	Buds Uninfested.	Remarks.
First control.	176	153	23	This row of trees were only sprayed once, and in a more "wholesale" manner than the three individual trees, reported upon in Table V.
Companion tree sprayed with nicotine in May.	234	35	199	
Second control.	214	143	71	
Companion tree sprayed with nicotine in May.	188	20	168	
Third control.	180	131	49	
Companion tree sprayed with nicotine in May.	142	20	122	
Fourth control.	224	154	70	
Companion tree sprayed with nicotine in May.	230	28	202	

TABLE VII.—FURTHER REPORT ON NICOTINE SPRAYING.

Variety of Holly.	Height of Tree.	Eggs per 100 Leaves.	Date of Spraying.	Condition of Pest at the Time of Spraying.	Contents of Dissected Buds soon after Spraying.	Ultimate Result shown when examined on June 24.	Remarks.
Common Holly.	5½ ft.	30	May 27.	12 buds opened before spraying yielded 24 small larvae.	12 buds opened on May 28th yielded 18 dead larvae—no living ones.	Out of 125 buds, only 5 were found infested.	This is a small tree with comparatively few buds, comparable to the common holly of similar height and build, used as a control.
Common Holly.	About 11 ft.	10	...	Some larvae in second instar.	All examined buds contained dead larvae.	Out of 300 buds, 26 were found infested.	...

By the last week of June both these trees exhibited normally elongated shoots, only the lower (oldest) leaves of which showed signs of slight gnawing by the very young larvae previous to the nicotine spray.



FIG. 1.



FIG. 2.

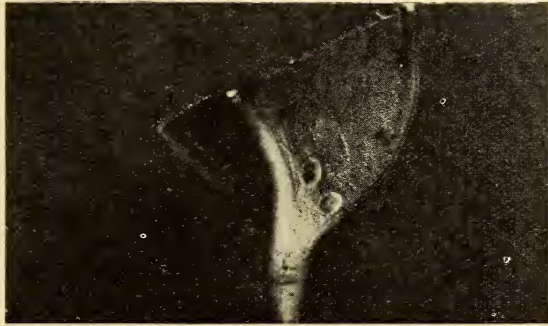


FIG. 5.



♂

FIG. 3.



♀

FIG. 4.



FIG. 6.



FIG. 7.

EUEMIS NÆVANA.

[For explanation of figures see p. 172.]



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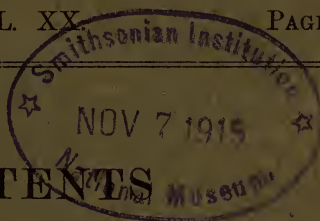
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XIII.—Note on the Collection and Culture of *Amœba proteus*¹ for Class Purposes. By Monica Taylor, S.N.D., D.Sc.

(Read 25th November 1918. MS. received 26th October 1918.)

SHORTLY after the commencement of the war, dealers' supplies of *Amœba proteus* began to fail. This shortage, coupled with the fact that the number of students of biology and medicine steadily increased, rendered an investigation of the sources of *Amœba* in the vicinity of Glasgow a problem of considerable usefulness. The unexpected discovery, in the autumn of 1915, of a rich culture of *Amœba* in one of the aquaria of the Notre Dame College Laboratory, the material for which had been collected near Glasgow, showed that it was possible of solution. The work, however, had to be undertaken as an "aside" to other pressing duties, hence the tardy completion of this note.

In 1916 rich cultures were unexpectedly found in an aquarium containing bladderwort gathered in a bog near Knockanes, Killarney. Quantities of the plant, packed tightly in a small tin box, had been sent for botanical purposes by Miss J. O'Donoghue to the College Laboratory, where the contents were emptied into a glass vessel containing Glasgow tap-water and exposed to good sunlight. Abundant assimilation was evident from the innumerable bubbles of gas in the aquarium, which fact incidently emphasised the importance of the oxygenation question in searching for natural sources of *Amœba*. Since the *amœbæ* in this case gradually "lost hold," eventually disappeared, and did not reappear (in spite of the fact that the trough was kept at a fairly uniform temperature), it seemed evident that the food-supply had been exhausted.

A search in the neighbourhood of Glasgow for a "site" similar to the one described for Knockanes was made during the succeeding months. Meanwhile, since the autumn of 1915, an examination of water from well-oxygenated ponds containing much water-weed, made in conjunction with Sr. Carmela, revealed the fact that although *Amœba proteus* can be discovered in almost every such pond, yet the labour of searching for and finding it in large numbers precludes such sources from being of practical value for class purposes. This search was useful, however, in that it brought out very strongly the almost universal occurrence of *Amœba proteus*, although no

¹ I am indebted to Miss L. Carter (Sr. Bernardine), B.Sc., for the identification of the species and for the information that she received supplies of *Amœba proteus* from the Auchter Water (Newmains, Wishaw) in 1910-1911, from Miss A. Gillespie.

place precisely similar to the Knockanes bog has yet been found in the neighbourhood.

Laboratory cultures were next tried—*Amœbæ*, with mud from the Knockanes bog to serve as food, were placed in a small aquarium fitted with a simple apparatus¹ for supplying well-aerated tap-water to the culture.

The aeration had a wonderfully refreshing effect on the *Amœbæ* which could easily be obtained from the culture in ever-increasing numbers. Before the end of the summer, however, they died down, presumably from insufficient food-supply.

These laboratory experiments cleared the ground for the discovery of a natural source. Towards the end of the same summer a tributary of the Allander Water, in one particular place, was noticed. This part of the stream seemed to repeat the conditions of the "Rowland" apparatus on a large scale, but with the additional advantage of a constant renewal of food material.

The tributary is an outlet from Loch Tannoch (Milngavie), a stagnant pond containing much decaying organic matter. In the particular place investigated the stream, which has a stony bed and is fairly rapid above this point, widens out into a sort of basin or pond with an almost level bottom, and in this pond much of the organic débris carried by the stream from the loch is deposited. There is no water-weed—the floor of this basin being of mud (sand and clay) overlaid with débris. The débris is, however, constantly washed, and constantly augmented by the water of the stream which, on leaving this pond-like expansion of its bed, tumbles over the stones banking it in at its distal end, and making thus a little waterfall, continues its course to the Allander. The mud in this part of the stream, containing as it does decaying organic matter and therefore microscopic plants and small flagellates in abundance, corresponded to the lower part of the "Rowland" apparatus. The ever-flowing water, which leaves the débris more or less undisturbed (*i.e.* the stream is not muddy), plays the same rôle in the oxygenation of the mud as was played by the tap-water of the said apparatus. The "site" seemed promising. An examination² of a specimen tube of this mud, made in August 1917, showed *Amœbæ* present in sufficiently large numbers to be of practical service for class purposes.

In the November of that year Libbie H. Hyman's method of *Amœba*

¹ This apparatus was devised by Fr. Rowland, S.J., B.Sc., at the suggestion of Sr. Bernardine, who very kindly placed it at my disposal.

² This examination is most quickly made over a dark background with the lowest power of a binocular microscope, when the whole *Amœbæ* content of a solid watch-glass can be easily surveyed. With a fine pipette the *Amœbæ* can easily be transferred singly from the solid watch-glass to the slide.

culture (*Journ. Exp. Zool.*, vol. xxiv., No. 1), by means of wheat, fell into my hands. By adding wheat grains to the mud containing *Amoebæ*, and by having sufficient water-weed, I was able to keep stocks alive throughout the winter of 1917-1918, the weed dispensing with the necessity of oxygenating the water by artificial means. In some cases the *Amoebæ* "lost hold" in the culture, ciliates or crustaceans or oligochæte worms, etc., making headway, to the almost total extinction of the first. In practice, therefore, it was found advisable to pick out the *Amoebæ* from the mud to a great extent, and thus give them a good start in the new culture. By dividing up into two lots a successful culture, and then adding water and new food-supplies to each sub-lot constantly during the warm sunny months of 1918, I have at the moment of finishing this note, 8th September 1918, millions of *Amoebæ* in laboratory cultures.

The tributary of the Allander was examined at intervals during the winter and spring of 1918. From December to May the *Amoebæ* were found to disappear, this disappearance coinciding roughly with the period of encystment described by Miss L. Carter.¹ In June they began to reappear, at first small in size and few in numbers, and up to the present the yield is not so abundant as in 1917. This may be due to the fact that the water has receded somewhat from the original shores of the "pond," the early summer having been a dry one. Laboratory cultures of this same material, possibly because kept at a uniform temperature with a constant food-supply, multiplied at a uniform rate.

Having thus determined the necessary conditions for the successful capture of *Amoebæ* in the open, and for their culture in large quantities under artificial conditions (*i.e.* a plentiful oxygenation with a liberal food-supply), it was found interesting, during the summer of 1918, to apply these principles to the detection of other sources of supply. The results of these investigations were satisfactory, and a list of the places so far investigated is given below. Further investigation of similar "sites" would reveal very many more sources. It must be remembered, however, that all natural "sites" are subject to fluctuations.

1. Tributary of the Allander draining Dougalston Loch, just before it enters the Dougalston Estate. This tributary is connected up with Bardowie Loch, the source of much organic material. The tributary itself brings down much débris which is mostly deposited at this place. The water of the tributary abundantly oxygenates the mud.

2. Overflow from the last loch on the east side of the old Strathblane

¹ 1915, Carter, L. A., "The Cyst of *Amoeba proteus*," *Proc. Roy. Phys. Soc., Edin.*, vol. xix., No. 8, p. 204.

Road. This overflow runs under the old Strathblane Road and widens out into a small pond. The best place in the overflow lies on the west side of the road.

Many similar "overflows" could be found at Milngavie, which abounds in lochs.

3. The Allander Water itself makes several basin-like expansions similar to the one already described for its tributary. These were not quite so good because of the great abundance of dipterous larvæ. The mud improved after it had been left for some time under a gently dripping tap. Hydra is of great use in keeping the cultures free from crustaceans, and it is significant to note that in all good habitats of *Amœba* it is invariably found.

4. On the south side of Glasgow, although only one place has been tested, the conditions are very favourable, especially in the neighbourhood south of Barrhead, where many overflows from lochs deposit in a more or less level part of their course quantities of débris, this débris being oxygenated by the constant flow of the water.

5. The districts around Gartcosh should similarly provide good "sites."

XIV.—The Brain and Cranial Nerves of *Acanthias vulgaris*, Risso; with some remarks on those of *Galeorhinus galeus* (Linn.), and of *Pristiurus melanostomus*, Günther. By G. L. Purser, M.A.(Cantab.).

(With Six Plates and Text-figure.)

(Read 27th January 1919. MS. received 28th December 1918.)

THE following is mainly a description of the brain and cranial nerves of *Acanthias*, in explanation of the drawings made from dissections.

The work, of which these figures are the outcome, was undertaken because at the present time a large body of students studying elementary zoology in this country use this species instead of *Scyllium*, and it was thought, therefore, that careful figures which include at least as much detail as is usually demonstrated to such students, should be published.

While doing the work on *Acanthias*, I took the opportunity given me by Mr Renouf of dissecting the nervous system in one specimen of *Galeorhinus* and in a few of *Pristiurus*, and so, although I shall not give a full account of, but only describe the chief points of interest in, their structure, I am publishing the drawings made of them.

My thanks are due to Professor J. Graham Kerr for his valuable suggestions with regard to the method of illustration to be used, and for his kindly criticism of the manuscript; and, finally, I must acknowledge my indebtedness to Mr L. P. W. Renouf, the Director, for giving me every facility for work at the Bute Laboratory and Museum, Rothesay, from which the material was obtained, and at which most of the dissection was carried out.

I.—THE BRAIN AND CRANIAL NERVES OF ACANTHIAS.

The **Rhombencephalon** (Figs. 2, 4 and 5).—The Medulla Oblongata appears, as in all other forms, as an anterior expansion of the spinal cord, so, as far as can be seen with the naked eye, there is no line of demarcation between them. The expansion, which is rather more gradual than in *Scyllium* and so forms a longer Medulla, is due to the enlargement of the central canal as well as to the thickening of the lateral and ventral walls. The cavity is here known as the IVth ventricle of the brain, and its dorsal wall, with the exception of the most anterior and posterior portions, is thin, non-nervous in character, and highly vascular. The thin portion of this dorsal wall, with its choroid plexus, was removed from the brains from which the drawings were made.

The ventral and lateral walls are not evenly thickened, but bulge into the cavity of the IVth ventricle to form a series of more or less longitudinal ridges, three in number on each side. (i.) The Median Longitudinal Bundles (*m.l.b.*), forming the floor of the ventricle, are well marked and easily seen when the choroid plexus has been removed (Fig. 2). They are directly continuous with the tracts in the corresponding position in the spinal cord. The grey matter of the ventral horn, however, comes to lie in the outer grooves which separate these bundles from the next pair which lie dorso-lateral to them. These, (ii.) the Visceral Sensory Columns (*v.s.c.*), are not in themselves evenly thickened but present a row of swellings, easily seen when the brain is divided into two by a median sagittal section (Fig. 5). The number of the swellings is five, and they have been considered as the nuclei of part of the Xth, the whole of the IXth, and part of the VIIth Cranial nerves: according to Johnston the column is the terminus of all the fibres from the visceral surfaces of the head. The last pair of ridges is that of (iii.) the Somatic Sensory Columns (*s.s.c.*), which form the rest of the lateral walls of the ventricle. Anteriorly they become double by the superposition of the Lobi Liniae Lateralis, one on each side. These lobes are so named because they are connected with the fibres of the Lateralis system found in the Vagus and Facial nerves. The posterior portions of these lobes, which are more conspicuous externally than in *Scyllium*, are best seen in the half-brain.

The anterior portions of the lateral walls project forward, on either side of the Cerebellum, as a pair of frilled appendages, the Restiform Bodies (Figs. 2 and 4, *r.b.*). The dorsal wall is thin, but the lateral ones are increased in area by a certain amount of foliation: the inner wall of each is in direct communication with that of the other by a thick transverse band which lies under the Cerebellum but arches over the cavity and forms the thickened anterior portion of the dorsal wall of the Medulla referred to above (Fig. 5).

The Cerebellum is not particularly well developed; perhaps not quite so much as in *Scyllium*. Its dorsal surface is marked by two grooves: a median longitudinal sulcus, which, however, does not extend to the anterior end; and a transverse one, a little in front of the middle. The walls are very thick so that the cavity is almost entirely obliterated. Johnston has figured the median sagittal section of the brain of *Squalus acanthias*, which shows a Cerebellum much more complicated, although, as the specimen should be of the same species as *A. vulgaris*, the figures should agree.

This completes the description of the Rhombencephalon, except for the nerves which emerge from it. Some of these differ markedly from those of *Scyllium*.

The Vagus, X, emerges laterally by one large bundle of roots and a small one, not shown in the figures, behind, the former being composed of a number of small roots with a large one in front (Fig. 4). Its branches are typical. The Lateral Line branch, after leaving the trunk, turns away from the surface and runs down between the muscles not far from the axial skeleton (Fig. 1). The Branchial branches are four in number and each forks over its gill-slit, the posterior branch being the larger. This post-trematic branch divides into two rami—an anterior to the upper angle of the cleft, and a posterior to its posterior wall; the pretrematic gives off a small branch to the pharyngeal wall and then continues its way to the anterior hemibranch of the cleft. The Visceral branch is that part of the main trunk which remains after the other branches have been given off; just before reaching the coelom it divides into four, all of which, however, run on to the œsophagus and thence to the viscera.

The Glossopharyngeal, IX, runs out from the Medulla at right angles to the surface for the first two or three millimetres, but then turns backward and traverses the Auditory capsule obliquely and parallel to the proximal portion of the vagus. As usual it swells out, at a considerable distance from its origin at the anterior end of the vagus root, to form a fusiform ganglion, beyond which it forks over the first gill-slit.

The VIIIth, VIIth, and Vth complex emerges by one dorsal and a bundle of ventro-lateral roots. The Auditory, VIII, is the hindmost of this latter set: it is short and dorso-ventrally compressed. For details of its distribution and for a description of the whole sense organ I cannot do better than refer to Retzius, but it should be noticed that the otocyst is of medium size, and instead of containing one or perhaps two large otoliths it possesses numberless small cuboid crystals, like very fine sand.

The rest of the complex consists of the dorsal root and three lateral ones just in front of the Auditory nerve, but bundles of fibres from the dorsal root come down and fuse with the lateral ones making the clear demonstration of the roots in relation to the VIIth and Vth nerves rather difficult. The result of these fusions, however, is that two trunks emerge from the cranium; one of which runs backwards and outwards, passing through the anterior portion of the Auditory capsule; and the other of which enters the orbit.

The hinder of these two is the Hyomandibular branch of VII (VII *hm.*). It is a mixed nerve: like IX, it supplies a cleft, in this case the Spiracular, but in addition it contains fibres of the Lateralis system and serves the sense organs on the skin of the hyoid arch. Its pretrematic branch, which should pass in front of the spiracle out of the mandibular arch, is very small (Fig. 1), and the branch of it which corresponds to the pharyngeal branches of the vagus

is the Palatine. This in *Scyllium* is well developed, but here, owing to the short distance from its origin to the roof of the mouth which it serves, it is reduced to a tuft of twigs given off a few millimetres from the nerve's source. The course of this Hyomandibular nerve is peculiar. It does not enter the orbit at all but runs through the anterior portion of the cartilage of the Auditory capsule.

The rest of this complex does enter the orbit, as I have said, and there divides into four trunks (Fig. 1). Beginning with the most dorsal we have the Superficial Ophthalmic (VII and V *oph.*). This is divisible into two bundles which in *Scyllium* enter the orbit separately—the individual branches of the Facial and Trigeminal—but here they are enclosed in one sheath. As in *Scyllium* and all other Selachians, they run dorsal to all other structures found in the orbit, and on leaving it spread over the dorsal surface of the snout. The VIIth fibres are part of the Lateralis system, and therefore go to the sensory canals of that region.

The second of the four trunks is the Deep Ophthalmic (V *prof.*). This is considered by some specialists as a separate cranial nerve, the Profundus, and not simply a branch of V. It is absent in *Scyllium*, at least as a separate trunk. In *Acanthias* it runs ventral to the Rectus and Obliquus Superiores muscles, and in contact with the eyeball. On leaving the orbit it also spreads over the dorsal surface of the snout.

The next trunk is the Mandibular branch of V (V *mn.*), which, while in the orbit, occupies very much the position the Hyomandibular has in other forms, *i.e.* it runs round the posterior wall, but instead of passing round the spiracle it, of course, continues to the corners of the mouth and innervates the lower jaw.

The last of these four trunks into which the anterior portion of the VIIth and Vth complex divides is a broad band of nerve fibres running postero-anteriorly along the floor of the orbit. This trunk, like its dorsal analogue the Superficial Ophthalmic, is composed of fibres from both V and VII, the Buccal branch of the latter and the Maxillary branch of the former. At the anterior end of the orbit, where they become embedded in the tissue of the head, they separate and the Buccal branch of the Facial (VII *b.*) runs up and supplies the sensory canals while the Maxillary branch of the Trigeminal (V *mx.*) spreads over the whole of the ventral part of the snout.

The only other cranial nerve connected with the Rhombencephalon is the Abducens, VI, which emerges about two millimetres from the mid-ventral line a little posterior to the root of VIII, and, as always, supplies the Rectus Externus muscle.

The **Mesencephalon** (Figs. 2–5). This division of the brain is shaped,

when viewed from the side, like a truncated wedge, the truncated apex being ventral. This ventral portion is very thick and directly continuous, without any line of demarcation, with that of the Rhombencephalon, but the dorsal wall is much thinner and expanded into a pair of lobes, the Optic Lobes, which are larger than in *Scyllium* in correlation with the relatively larger eye, and so project more in front of the Cerebellum.

Two nerves leave the Mesencephalon. The Patheticus, IV, which emerges behind the Optic Lobes from under the Cerebellum, is, owing to the more forward position of the Obliquus Superior muscle, rather longer than in *Scyllium*, but of just about the same diameter: it runs forward in contact with the Optic Lobe, and then, after passing through the cartilage of the cranium runs for a short distance with the Superficial Ophthalmic nerve before turning and entering the muscle. The Oculo-motor, III, arises from the ventral surface of the Mesencephalon near its anterior end, and enters the orbit in front of the anterior trunk of the VIIth and Vth complex. There it divides into three rami, two serving the Recti Superior and Internus muscles, and a third, running across the floor of the orbit and innervating the Rectus and Obliquus inferiores muscles (Fig. 1).

The **Fore-brain**. The posterior portion of the Fore-brain, the Diencephalon or Thalamencephalon, is, like the Mesencephalon, shaped like a truncated wedge, but in the reverse position. Its dorsal wall is quite thin, relatively very short, and at its posterior end gives rise to the Pineal Organ (Fig. 2). The stalk of this is a fine tube of considerable length: it is attached to the wall as far as the anterior end of the Diencephalon whence it projects freely forwards and ends in the roof of the cranium on a level with the anterior end of the Hemisphere region.

The thin dorsal wall of the Fore-brain has been removed from the brains which were drawn, except the half-brain used for Fig. 5, where the well-developed Velum Transversum can be seen hanging down from it into the cavity of the IIIrd ventricle. The Infundibulum is well developed too and its parts very well marked (Figs. 3, 4, and 5)—the paired Inferior Lobes in front, the Saccus Vasculosus behind, and the paired Corpora Mammillaria above. These latter rather obscure the roots of the IIIrd nerves. Attached to the ventral surface is the Pituitary Body: it is almost the same length as the Infundibulum, but much narrower, particularly in front where it lies between the Inferior Lobes. It has a median longitudinal groove, and decreases in thickness from before backwards.

The Optic Tracts, II, join the rest of the brain just in front of the Infundibulum, but neither the Chiasma nor the Thalami are at all conspicuous.

The last part of the brain to be described is the Hemisphere region, and it is of considerable interest because it differs strikingly from what obtains in *Scyllium*. The posterior part of the dorsal wall is thin, non-nervous and vascular, and from it folds hang down into the cavity forming a choroid plexus (Fig. 5). In front of this the walls are thick, and the anterior and ventral ones are expanded on either side of the middle line, so that when viewed from above the region exhibits a deep median notch in front, and from below a median longitudinal groove (Figs. 2 and 3). In spite of these expansions, however, this portion of the brain does not nearly fill the cavity of the cranium, but ends considerably behind the anterior wall (Fig. 1) and does not reach the membranous roof above.

On the dorsal surface there are a pair of swellings as in *Scyllium*, but they are not so conspicuous. On the other hand, the Olfactory tracts, which are given off laterally from the paired anterior lobes, are much longer and more slender than is the case in the majority of the sharks. This is correlated with the shape of the snout, which is long and pointed.

The cavity of the Hemisphere region is not complicated above the normal. It is single behind, and this unpaired portion opens in front into the first two ventricles of the brain, from which the canals of the Olfactory tracts pass directly.

From the centre of the anterior wall, *i.e.* at the bottom of the median notch, a pair of quite small ribbon-like nerves arise which follow the contour of the anterior wall of the brain and Olfactory tracts, and go to the Olfactory capsules. Owing to their being ganglionated and their fibres myelinated, both distinguishing features from ordinary Olfactory nerves, the morphology of these Pre-olfactory Nerves (Nervi Terminales) is of considerable interest. (The nerves are not shown in the figures.)

II.—THE BRAINS AND CRANIAL NERVES OF GALEORHINUS AND PRISTIURUS.

Turning now to *Galeorhinus* and *Pristiurus*, what chiefly strikes us with regard to the Cranial Nerves is their close agreement with one another and with those of *Scyllium*.

The nerve showing the greatest variation is the Profundus. This, of course, is absent altogether in *Scyllium* as a separate tract. In *Galeorhinus* it runs over the origin of the Rectus Superior but then curves down and passes under the Rectus Internus and Obliquus Superior muscles (Fig. 6). In *Pristiurus* it lies ventral to all these three muscles. So in each case—*Acanthias*, *Galeorhinus*, or *Pristiurus*—it takes a different course. That this is so, however, hardly affects the discussion as to its morphological standing,

because in every case it remains in close proximity to the muscles derived from the wall of the second head-cavity of the embryo.

With regard to the brains themselves, the relative proportions of their various parts can be seen by comparing the figures. That of *Pristiurus*, however, requires particular notice in connection with the chief sense organs. The sense organs of the skin are well developed: the otocyst is extraordinarily small; the eyes are of considerable size; and the olfactory organs are enormous, the pair taking up the whole width of the head where they are situated and projecting as well (Fig. 11). When we examine their respective brain-lobes we find that the Somatic Sensory Column is better developed than in the other forms (Fig. 15), and the Lobi Liniaë Lateralis are particularly large and conspicuous. Sagittal section through the Medulla brings out another point. In addition to the usual broad band connecting the two inner walls of the Restiform Bodies in the median plane just behind the Cerebellum, there is a smaller one (Fig. 15). That is, the Lobi Liniaë Lateralis as they go forward fuse together in the middle line before diverging to form the outer walls of the Restiform Bodies. The Auditory nerves are small, and the Optic Lobes are in proportion to the size of their sense organ, but the Olfactory Lobes are not enlarged at all above the normal and are therefore extraordinarily small relative to the organ they supply. This lack of correlation between the sizes of the sense organ and of its brain lobe reminds us of the eyes and Corpora Quadrigemina of Mammalia which show the same peculiarity (e.g. *Nycticebus*, *Nyctipithecus*, *Tarsius*).

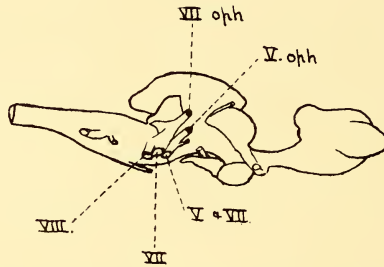
As a whole the Hemisphere region of these two forms is simpler than that of *Scyllium*: there are but slight indications of paired swellings. In *Galeorhinus* there are dorsal and antero-ventral swellings, the latter slightly lobed in front and the former a little behind, while in *Pristiurus* there is a very slight indentation anteriorly and a mid-ventral groove, but there is nothing even so well marked as the pair of prominences on the dorsal surface of *Acanthias*.

As seems to be general among the sharks, the Fore-brain in both these fish does not nearly fill its part of the cranial cavity. In *Galeorhinus* the unoccupied space, which is of very considerable size (Fig. 6), is filled with arachnoid fluid and fibres as is the case in *Echinorhinus* (Jackson and Clarke), and in *Lepidosiren* (Graham Kerr).

But the part of these brains which most attracts our attention is the Cerebellum. In *Pristiurus* it is rather wide and flattened, and has two sulci—a median longitudinal one along the posterior two-thirds, and a deep transverse one in front of the longitudinal one at about a quarter of the whole length of the Cerebellum from its anterior end. The depth of this

transverse groove becomes very apparent when the half-brain is examined (Fig. 15).

Galeorhinus possesses the most complex Cerebellum of any known fish, Amphibian or Reptile (Figs. 7, 9, and 10). It is rather prismatic in shape; tall with a longitudinal ridge, from which it gradually widens to its base. Its surface shows four unpaired transverse sulci and a pair of lateral ones between the second and third unpaired ones. There are no longitudinal grooves at all. The anterior sulcus is very long, and on nearing the base turns round and runs up parallel to its first part about half-way back towards the apex. In median sagittal section, internal folding of the walls of the sulci already mentioned increase the complication already found, while two other sulci at the posterior end which are hidden by the Restiform Bodies add to it still more. The wall, as compared with that of *Acanthias* or



Brain of *Scyllium*, seen from side. Nat. size.

Scyllium, is thin and shows that the sulci are produced by true folding rather than by the splitting up of a solid mass of tissue.

The careful dissection of the Medulla in these species has made me very doubtful as to the accuracy of the figures generally given for the brain of *Scyllium* with regard to the roots of the cranial nerves. What I have termed the VIIIth, VIIth, and Vth complex is in all the three species, with which we are concerned, on the same plan, and, except for the VIIIth, it is impossible to treat the branches, still less the trunks, as individuals or to identify their individual roots. The dissection of this region is very difficult, because the nerves are embedded in a compact mass of cartilage and because their sheathes, their toughest parts, are continuous with the perichondrium. Nevertheless, I am confident that my figures are true representations of the roots and of the trunks arising from them, and that the labelling is correct as far as it goes. Where I am not absolutely confident, as in *Pristiurus*, I have omitted detailed labelling, and have only put comprehensive names to the parts. So there has been neither straining of names to fit accurate drawing nor touching up of drawings to agree with names.

But the careful examination of the drawings brings out the fact that all these three species have a dorsal and a bundle of ventro-lateral roots (lateral in *Pristiurus*). The fibres of the dorsal root come down and combine with those of the other roots, and then the various branches of VII and V can be to some extent identified. So that the roots of these nerves which emerge from the Medulla are but factors of the various branches; they are few in number; their arrangement is the same in every case, but is quite different from what, according to the ordinary text-book figure, has been found in *Scyllium*.

Note.—Since the above paper was read, I have been able to dissect the VIIIth, VIIth, and Vth complex in *Scyllium*. It is just on the same plan as the others—one dorsal root emerging from underneath the Lobus Liniae Lateralis, and the others coming off laterally. These others are three in number, the middle one being rather dorsal to the hindmost, which is the root of VIII. Fibres from the dorsal root pass down to the lower branches and forward to the Ophthalmic branch of VII, while fibres from the lateral roots pass out to the lower branches or up to the Ophthalmic ones, so that the brain has the appearance shown in the text-figure (p. 190).

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LIST OF ABBREVIATIONS USED IN FIGURES.

PARTS OF BRAIN—

<i>cbl.</i>	Cerebellum.	<i>opt.ch.</i>	Optic Chiasma.
<i>cbr.</i>	Cerebrum.	<i>opt.l.</i>	Optic Lobes.
<i>c.m.</i>	Corpora Mammillaria.	<i>pit.b.</i>	Pituitary Body.
<i>dien.</i>	Diencephalon.	<i>p.s.</i>	Pineal Stalk, Base of.
<i>inf.l.</i>	Inferior Lobes.	<i>r.b.</i>	Restiform Body.
<i>inf.</i>	Infundibulum.	<i>s.s.c.</i>	Somatic Sensory Column.
<i>l.l.l.</i>	Lobus Linæ Lateralis.	<i>s.v.</i>	Saccus Vasculosus.
<i>med.</i>	Medulla.	<i>tel.</i>	Hemisphere Region.
<i>m.l.b.</i>	Median Longitudinal Bundle.	<i>vel.</i>	Velum.
<i>o.l.</i>	Olfactory Lobe.	<i>v.s.c.</i>	Visceral Sensory Column.

NERVES—

II	Optic Tract.	VII	Facial : Branches—
III	Motor Oculi.		VII <i>b.</i> Buccal.
IV	Patheticus.		VII <i>h.</i> Hyomandibular.
V	Trigeminal : Branches—		VII <i>oph.</i> Ophthalmic.
	V <i>mn.</i> Mandibular.		VII <i>p.</i> Palatine.
	V <i>mx.</i> Maxillary.	VIII	Auditory.
	V <i>oph.</i> Ophthalmic.	IX	Glossopharyngeal.
	V <i>prof.</i> Profundus.	X	Vagus : Branches—
VI	Abducens.		X <i>br.</i> Branchial.
			X <i>l.l.</i> Lateral Line.
			X <i>v.</i> Visceral.

OTHER STRUCTURES—

<i>ā.c.</i>	Auditory Capsule.	<i>r.e.</i>	Rectus Externus Muscle.
<i>c.c.</i>	Cranial Cavity.	<i>r.f.</i>	Rectus Inferior Muscle.
<i>g.s.</i>	Gill-slit.	<i>r.s.</i>	Rectus Superior Muscle.
<i>o.i.</i>	Obliquus Inferior Muscle.	<i>r.t.</i>	Rectus Internus Muscle.
<i>o.s.</i>	Obliquus Superior Muscle.	<i>sp.</i>	Spiracle.
<i>ol.o.</i>	Olfactory Organ.	<i>sp.c.</i>	Spinal Cord.

The author is indebted to the Carnegie Trust for a grant to cover the cost of reproducing the drawings which form Plates XIII.-XVIII.

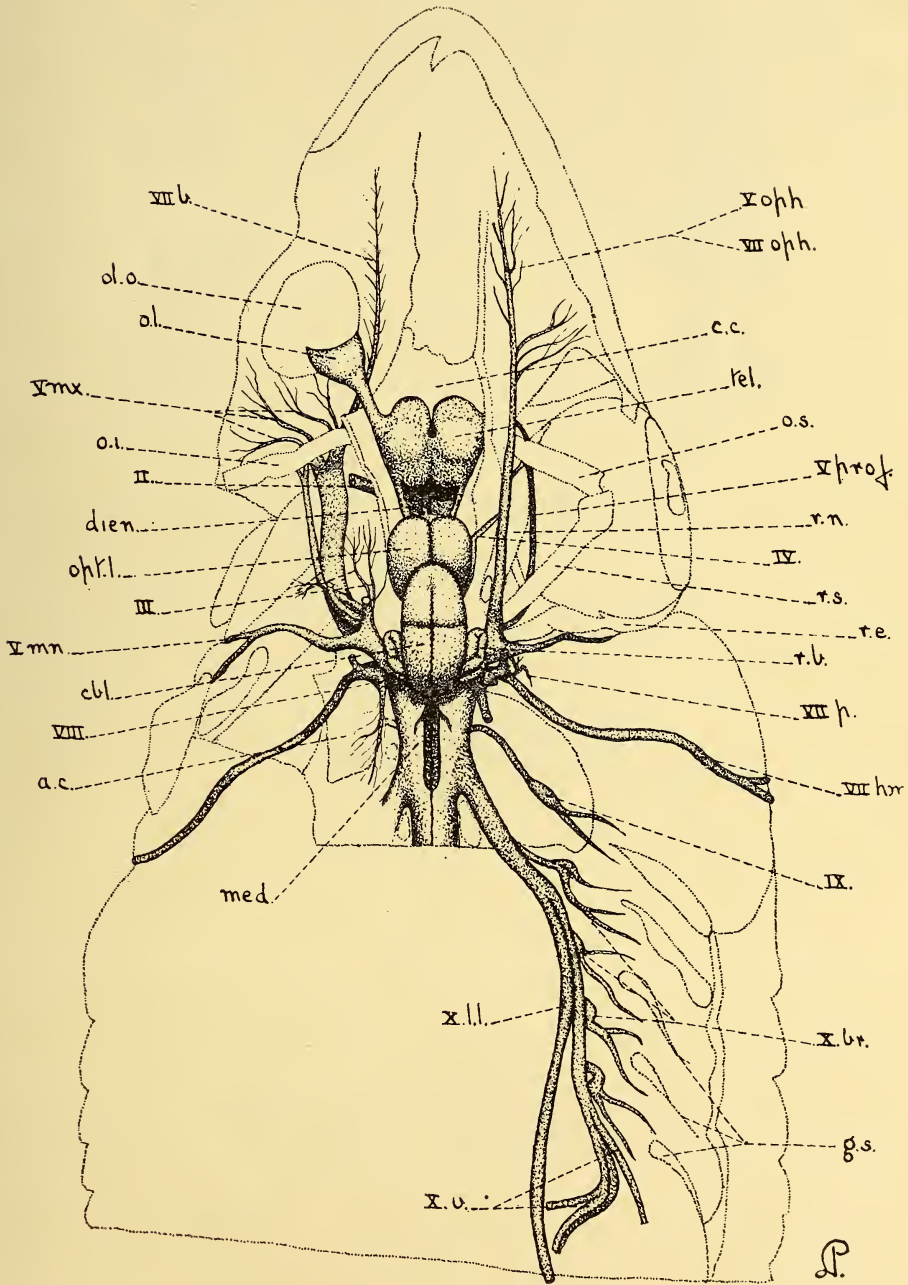


FIG. 1.

DISSECTION OF THE BRAIN AND CRANIAL NERVES OF ACANTHIAS,
 SEEN FROM THE DORSAL SURFACE. $\times \frac{6}{5}$.

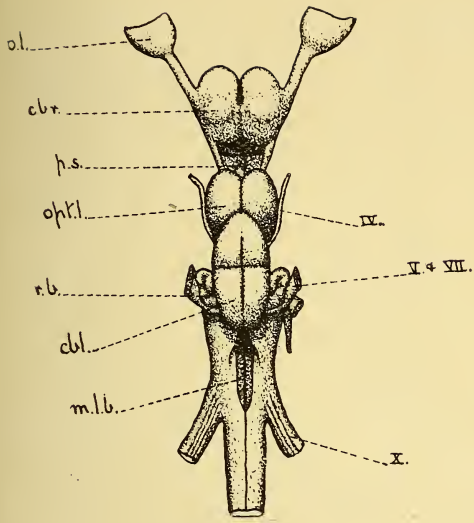


FIG. 2.—Seen from above. Nat. size.

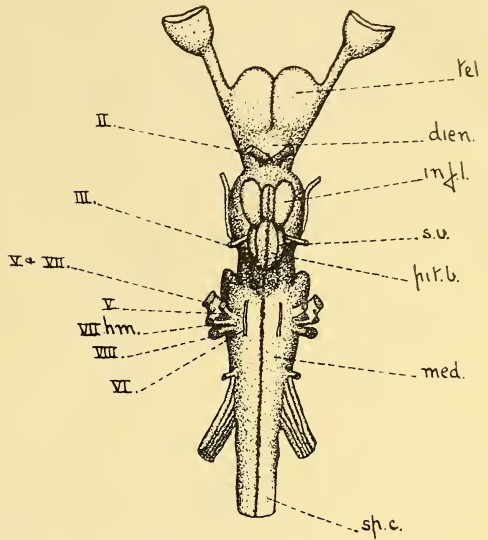


FIG. 3.—Seen from below. Nat. size.

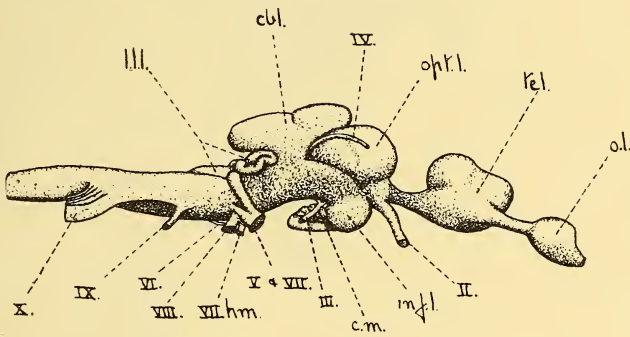


FIG. 4.—Seen from side. $\times \frac{2}{3}$.

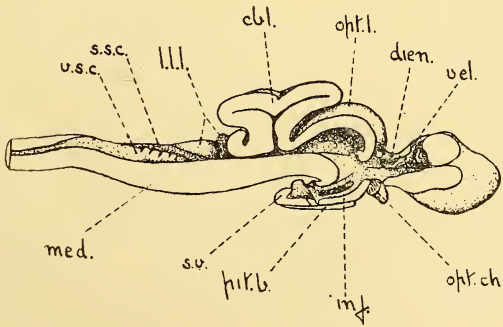


FIG. 5.—Seen in Median Sagittal Section (the Olfactory Lobe cut off). $\times \frac{2}{3}$.

THE BRAIN OF ACANTHIAS.

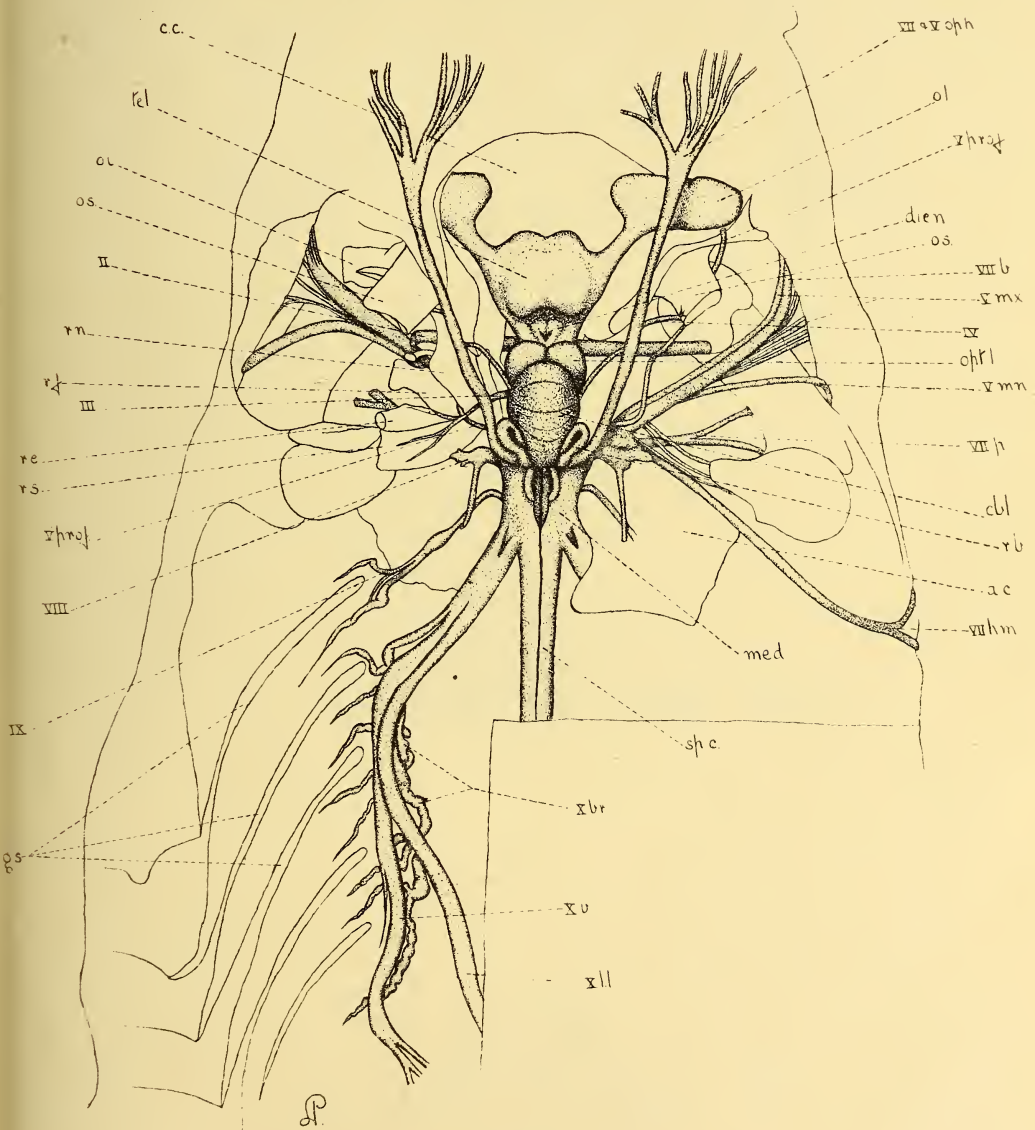


FIG. 6.

DISSECTION OF THE BRAIN AND CRANIAL NERVES OF GALEORHINUS,
 SEEN FROM THE DORSAL SURFACE. $\times \frac{25}{2}$.

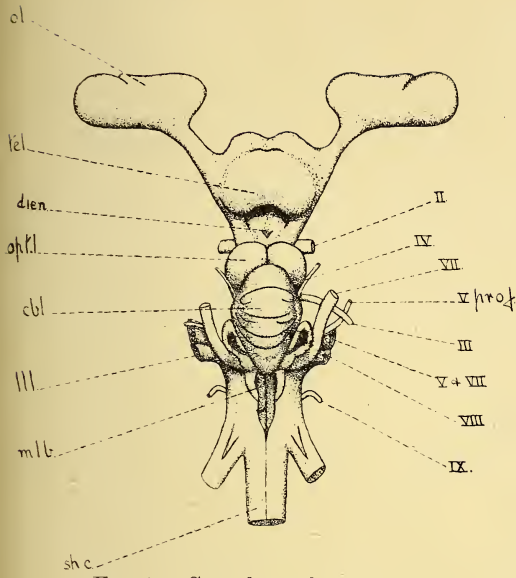


FIG. 7.—Seen from above. $\times \frac{3}{8}$.

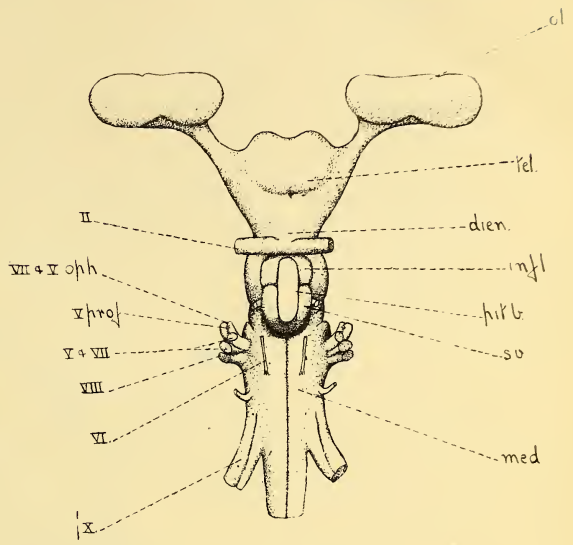


FIG. 8.—Seen from below. $\times \frac{5}{8}$.

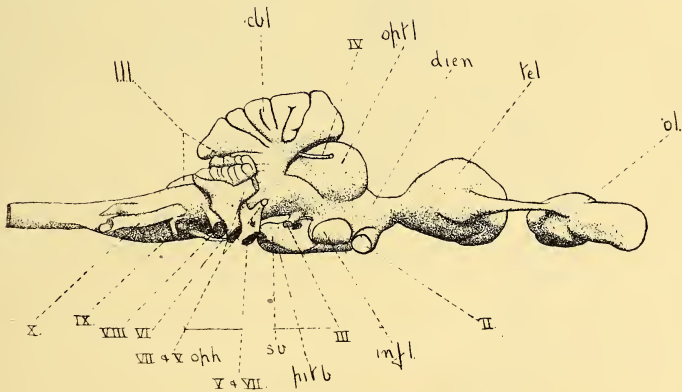


FIG. 9.—Seen from side. $\times \frac{6}{7}$.

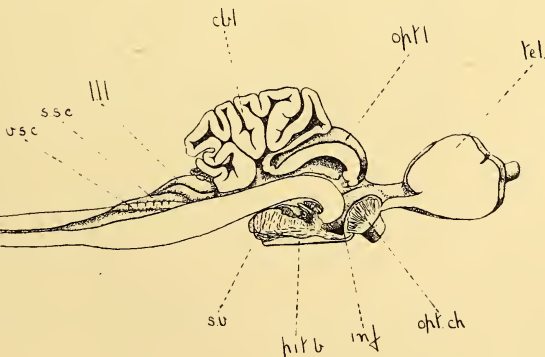


FIG. 10.—Seen in Median Sagittal Section (the Olfactory Lobe cut off). $\times \frac{6}{7}$.

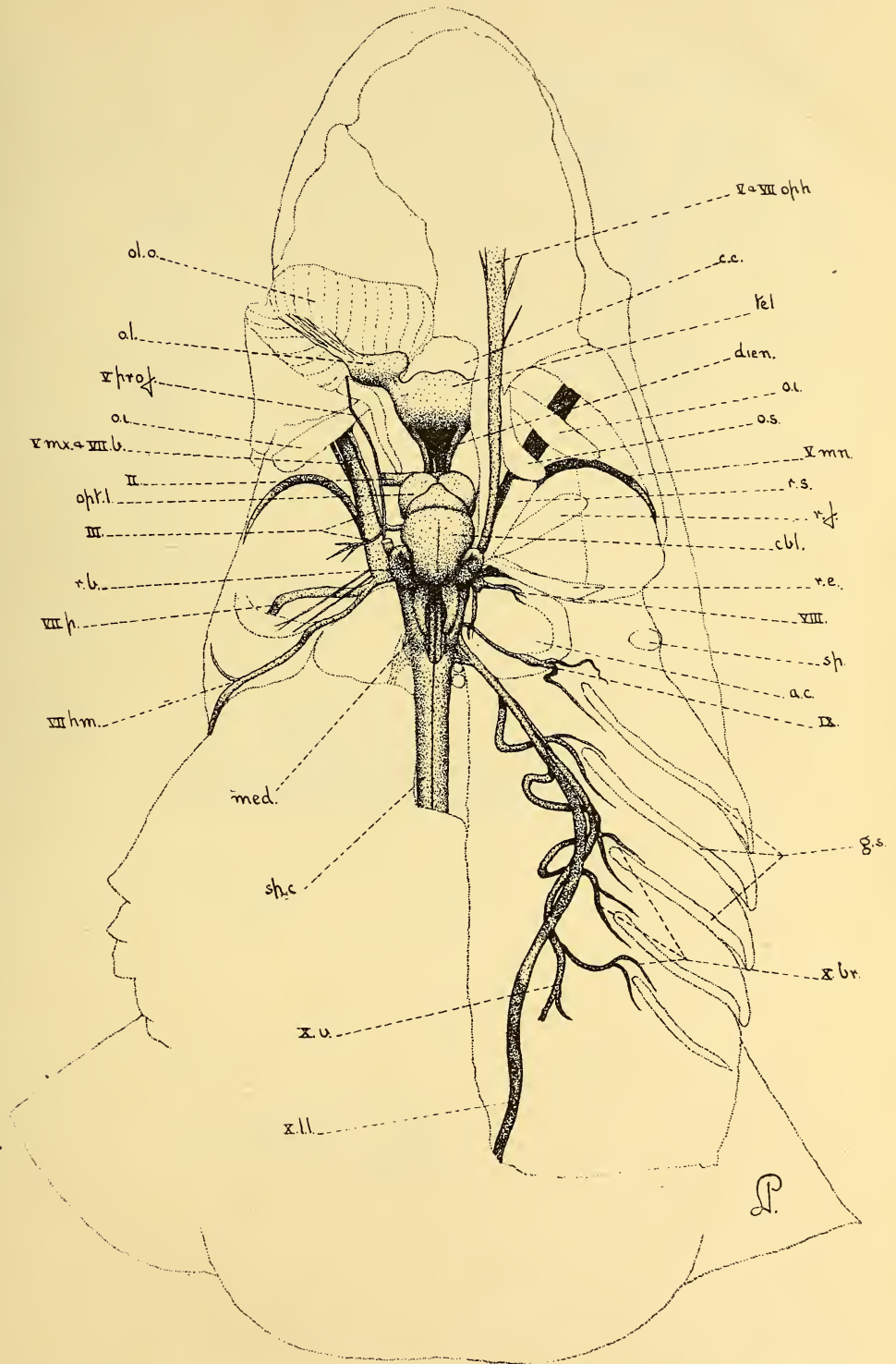


FIG. 11.

DISSECTION OF THE BRAIN AND CRANIAL NERVES OF PRISTIURUS,
 SEEN FROM THE DORSAL SURFACE. $\times \frac{1}{2}$.

PLATE XVIII.

Vol. XX.

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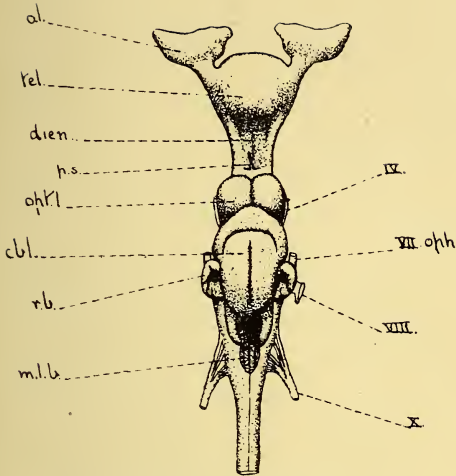


FIG. 12.—Seen from above. $\times \frac{7}{6}$.

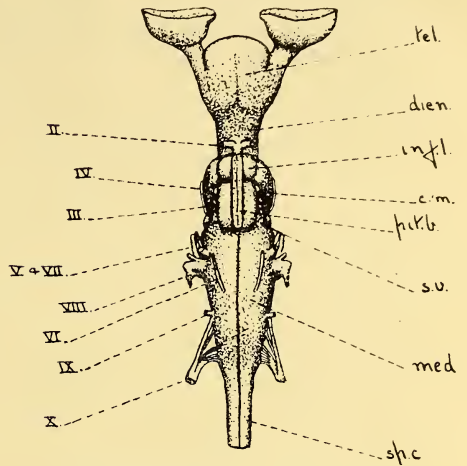


FIG. 13.—Seen from below. $\times \frac{7}{6}$.

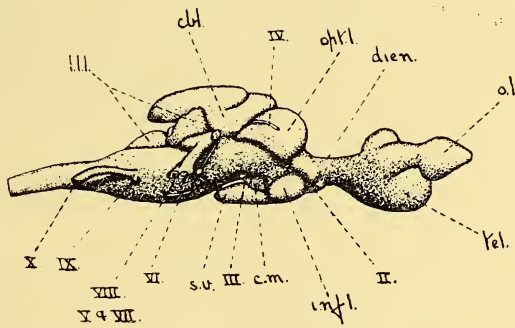


FIG. 14.—Seen from side. $\times \frac{7}{6}$.

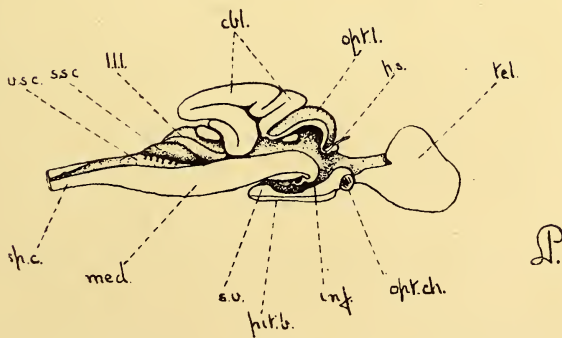


FIG. 15.—Seen in Median Sagittal Section (the Olfactory Lobe cut off). $\times \frac{7}{6}$.

THE BRAIN OF PRISTIURUS.

XV.—Some Observations on *Amœba proteus*. By Lucy A. Carter,
S.N.D., B.Sc., College of Notre Dame, Dowanhill, Glasgow.

(With Plate.¹)

(Read 16th December 1918. MS. received in final form 8th April 1919.)

INTRODUCTION.

PAPERS by Dr A. A. Schæffer² on the feeding habits and food reactions of ameba² have appeared in the *Journal of Experimental Science* with the following postscript: "After this paper was in manuscript the species reference of 'raptorial' and 'granular' amebas was investigated. The granular amebas were found to be of two species: *Amaeba*³ *proteus* Pallas emend. Leidy, and *A. discoïdes* Schæffer; the raptorial of one species *A. debia*⁴ Schæffer. See my paper in *Science*, September 1916, for description of these species." The September number of *Science* here alluded to gives a short but excellent note on the nuclear differences observed in uninucleate forms of the *proteus* type of amœba. It also recounts the loss of manuscript and illustrations in postal transmission. This is a loss greatly to be deplored by all workers on *A. proteus*.

There has been no intimation of the recovery of the MSS., after nearly three years, nor has any further expansion of the September note been forthcoming. Are these new specific names to stand without any further justification? As an answer to this question I wish to publish some observations by way of protest to this would-be addition to the already overburdened nomenclature list of *A. proteus*, together with what seem to be good reasons for such a protest. These observations extend over some eight years.

Until *Amœba proteus* in one or all of its so-called "species" can be raised in "pure" or at all events "persistent" cultures, and a complete life-history worked out, either uniting all the "species" or once for all separating them one from another by means of their individual life-cycles, the work must necessarily be tedious and difficult. As Metcalfe⁵ says

¹ For the use of the Abbé camera, by the aid of which the figures on Plate XIX. were drawn, and for a grant to cover the cost of reproducing the drawings, I am indebted to the Carnegie Trust.

² Schæffer, *Journ. Exp. Zool.*, vols. xx. and xxi., 1917; *Science*, 29th September 1916.

³ The spelling *ameba* and *Amaeba* is Schæffer's.

⁴ *A. debia* appears as *A. dubia* in the *Science* (1916) article—probably, therefore, a misprint—*A. dubia* being the earlier name.

⁵ Metcalfe, *Journal of Exp. Zool.*, vol. ix., 1910.

“It may be a case of years to work out the life-history, and I doubt if any one could keep up the necessary conditions, environmental and climatic, which would admit of *A. proteus* passing through its complicated history which, without doubt, it does in its own chosen habitat.”

While we are busy trying to achieve the possibly impossible, it seems to me that new names will only hinder where they are meant to help.

In 1910, while a Research Student in Glasgow University, I undertook, at the suggestion of Professor J. Graham Kerr, the study of *Amœba proteus*. The first point in this study was to be an attempt to raise pure laboratory cultures of this amœba, preparatory to some elucidation of its life-history.

For three years I worked assiduously on this one point, but regret to state that I was not successful to the extent I had planned. I worked with small numbers, and from the many cultures of small numbers which I did succeed in raising and keeping for a time, the longest pedigree actually traced was of six months' duration. This “existence” of the culture was uneventful but for the multiplication by division, watched in many cases, and carefully noted in all. No encystment took place, nor could it be induced artificially, although the period of successful culturing was from November to May, thus including the months during which the amœba naturally encysts. The three years were not wasted; a case of mitotic division¹ was obtained as also the natural encystment² of *A. proteus*, both facts helping considerably in the general summary here recorded.

It would seem that the greater part of the work on *A. proteus* has been carried out upon the large amœba described by Leidy³ under this name, without reference to the peculiarities in structure, etc., which present themselves only to the constant and careful observer. These differences are revealed by Leidy himself in his excellent illustrations and in his text, but he makes no reference to them as of any specific importance.

My own work was commenced under the same impression, that all the large amœbæ described as *A. proteus* by Leidy were alike in all respects, and my attention was not aroused to their dissimilarities until the food question forced itself upon me.

The excellent work of Allen and Nelson⁴ on the culture of diatoms, published about this time, seemed to open a door for an attempt at the pure culture of *A. proteus* from the well-known fact that *A. proteus* feeds on diatoms.

¹ Carter, *Roy. Phys. Soc. Edin.*, vol. xix., No. 4, 1913.

² *Ibid.* „ „ vol. xix., No. 8, 1915.

³ Leidy, *Freshwater Rhizopods of North America*, 1879.

⁴ Allen and Nelson, *Q.J.M.S.*, 1910, vol.

I watched, therefore, with great care the choice of diatom made by the amœbæ—the favourites were *Navicula*, *Nitzschia*, *Synedra*, *Pinnularia*, large and small. My next efforts were directed to the raising of “persistent” cultures of these diatoms (fresh water replacing sea water), and following the lines laid down by Allen and Nelson¹ I was successful.

The amœbæ of the general *proteus* type were picked out from the pond supply, washed thoroughly several times in a sterilised solution in which the diatoms and amœbæ flourished equally well. Each amœba was then placed in a sterilised watch-glass about half-full of the solution and supplied with a few diatoms from the “persistent” cultures.

At this juncture the first radical difference among the several amœbæ became evident—a difference casually remarked by many writers, but apparently only now beginning to attract attention. Certain amœbæ fed voraciously on the diatoms and increased in numbers—while the others would not ingest a single diatom; this food idiosyncrasy was so great that no other food being available this latter “type” or “species” of *A. proteus* died rather than feed on the diatoms present. Other varieties of diatoms were tried, but always with the same result. When, however, the amœba was placed in stream water in which many small organisms abounded it would live and feed well on small flagellates, green algal cells, bacteria, etc., but not on diatoms.

Upon the discovery of this differentiation in diet,² I revised my first opinion as to the unity of the members of the group and began to separate the amœbæ into two categories, viz. the diatom feeders and the non-diatom feeders. These characteristics coincided so strangely at the time with the localities from which the amœbæ were obtained that I classed the “types,” for my own convenience, “Lapworth” and “Sutton” types—the Lapworth amœbæ being the diatom feeders.

Other points of difference now became apparent in the nucleus and the crystals contained in the plasma. The Lapworth amœbæ contained a spherical nucleus, as a rule, the nuclear membrane being completely filled with regular evenly-distributed chromatin granules. In the Sutton amœbæ the nucleus was variable, oval in outline, with varying arrangement of chromatin granules. The crystals³ of the diatom-feeding amœbæ were large, of the octahedral series, truncated at both ends of the long axis, also

¹ *Loc. cit.*

² A non-diatom feeder may indirectly ingest a diatom by ingesting small organisms which have themselves already ingested diatoms, *e.g.* small amœbæ.

³ Leidy, *loc. cit.* There must be some mistake in the size of the crystals given on p. 47—0.075 mm. should surely be 0.0075 mm. A crystal of 75 μ would be larger than the nucleus of the amœba.

complete bipyramids of the same series. The non-diatom feeder contained medium and small crystals of this latter form.

Later in my study, the locality classification gave way completely—but I was in a position to differentiate between the two amœbæ formerly passing indiscriminately under one name. Whatever their locality, I had found that the diatom feeder reproduces by mitotic division of its nucleus with subsequent division of its protoplasm, as also by reproductive cysts; that the non-diatom feeder also multiplies by division, but I had not observed this in such a way as to be able to state whether the nucleus divided by mitosis or amitosis.

I wish to draw special attention to the amœba upon which I worked so persistently (the diatom feeder), because I have called it *A. proteus* Pallas, which name will be shown to be correct and should remain with this type if ever we can definitely prove that these amœbæ are not all one species.

During these years the multinucleate type of *A. proteus* had of course presented itself, but, with the non-diatom feeder, had been more or less discarded in the study of the diatom feeder.

At the end of this time I reverted to my original idea of one species, but now with strong reasons for preference for that which I had formerly taken for granted. It was, therefore, in July 1914, after a consultation with Mr C. H. Martin,¹ sometime Protozoologist at the University of Glasgow, and a great student of amœbæ, that I re-arranged the grouping of the amœbæ and designated the three types *A. proteus X*, *A. proteus Y*, and *A. proteus Z*, being with him practically convinced that the whole history is that of one amœba, complicated and involved no doubt, as recognised by all, but still one species only.

The suggested arrangement would, therefore, be:—

A. proteus X (Fig. 1). The amœba spoken of earlier as the "Lapworth" type; the diatom feeder; the amœba which I designate as *A. proteus* Pallas, in my preceding papers²; excellently figured by Leidy³ and by Grüber⁴ as *A. proteus*; by Cash and Hopkinson⁵ as *A. proteus* Pallas; the amœba renamed by Schæffer⁶ *A. debia* (or *dubia*) under the group of "raptorial

¹ The noble death of Lieut. Martin, in his country's cause, has left me without his further help and kind encouragement, but in writing up the notes embodied in this paper I am fulfilling his last wish expressed to me before going to the front, and at the same time recording my own thanks which are so justly due to him.

² Carter, *loc. cit.*

³ Leidy, *loc. cit.* (pl. 1 fig. 2, pl. 2 fig. 4).

⁴ Grüber, *Zeit. für wiss. Zool.*, Bd. xli., 1885, "Studien über Amöben."

⁵ Cash and Hopkinson, "British Freshwater Rhizopods," London, *Roy. Society*, vol. i., 1905.

⁶ Schæffer, *loc. cit.*

amebas." Its nucleus is shown in its typical condition by Grüber. The crystals contained in the plasma of this amœba are large.

A. proteus Y (Fig. 2). A series of amœbæ which show a gradation of characteristics from X to Z, so gradual that classification becomes at times almost impossible. It is a non-diatom feeder; the amœba spoken of as "Sutton" type in the beginning of this paper. Members of this series are most commonly figured as *A. proteus* in text-books and elsewhere, whatever form may be described in the text itself—e.g. Doflein in his *Lehrbuch der Protozoenkunde*, pp. 11 and 570, under the title of *A. proteus* Pallas; Cash and Hopkinson as *A. proteus* Pallas, var. *granulosa*; Schæffer breaks the series up into two species, *A. proteus* Pallas emend. Leidy, and *A. discoides* Schæffer. In the excellent figures by Leidy the individuals shown in plate ii. figs. 1 and 2 are apparently nearing the Z end of the series.

A. proteus Z. The multinucleate form of *A. proteus*, practically similar in all respects to *A. proteus* Y with the exception of the number of its nuclei. It also is a non-diatom feeder.

POINTS OF DIFFERENCE.

In 1879 Leidy summarised the history of this amœba and concluded, "I therefore suggest that the name *Amœba proteus* should be employed for the common large amœba,¹ recognisable as the *Proteus* of Rösel and the *Amœba princeps* of Ehrenberg; otherwise, according to the strict laws of scientific nomenclature it should be *Amœba chaos*."

From this it would seem that Leidy included in this species *proteus*—all the amœbæ of the *proteus* type as figured by him—thus including the multinucleate type.

I would certainly retain this name *Amœba proteus*, but with some such distinctions as those above mentioned to simplify matters as to the appearance, condition, or phase of life of the amœba at the time of observation, until the whole life-cycle, or life-cycles, if such there be, can be written.

The constitution of the individuals of the *proteus* group or series X, Y, Z is similar; a mobile mass of protoplasm, capable of pushing out pseudopodia from any portion of its mass; no pellicle, and apparently no differentiation of ectoplasm and endoplasm, which is to say that these latter are convertible

¹ It would be preferable to say large amœbæ—since Ehrenberg himself declared that *der kleine Proteus*, Rösel's amœba, was not like his *A. princeps* of Berlin, and he must have seen Rösel's illustrations.

one into the other, according as the protoplasm comes into contact with the external surroundings; nucleus, one or more; and contractile vacuole.

The differences, apparent or accidental, seasonal or pathological, are to be found in the granular condition of the plasma; the contained crystals; the appearance of the nucleus, together with the food-supply, habitat, and method of reproduction.

General appearance and granular condition of protoplasm, etc.—The granulation is shown in different degrees by the three types; *A. proteus X* showing the least, and *A. proteus Z* the greatest, degree.

In general appearance *A. proteus X* may be recognised not only by its freedom from an excess of granules, but also by the translucent limpidity which pervades it; by the easy mobility of the whole organism and by, what impresses one most, its glorious living when in a healthy condition and a happy environment. Its size is 200μ – 350μ . Its large crystals have already been alluded to, and these together with its clearness, suggestive of depth, purity, and freshness of habitat, combine to make it by far the most beautiful of the three forms of *A. proteus* under discussion, fully meriting the “*admirandæ simplicitas animal*” of Pallas.¹ Its food, as stated, consists very largely of diatoms, when these are obtainable, but not by any means only diatoms; hence a suggestion that change of diet combined with environment may produce *A. proteus Y*. This I have not yet proved to my own satisfaction.

Whether this be so or not, it is of interest to note that the supply of *A. proteus X*, from a pond which for two years had produced this type in abundance, with the rarest possible appearance of *Y* or *Z*, suddenly ceased, for no specific reason, and within a few months while no more *A. proteus X* could be obtained, both *A. proteus Y* and *A. proteus Z* were forthcoming in very respectable numbers. Now, however, it is impossible to obtain *Amœba proteus* of any “type” from this formerly plentiful source.

A. proteus Y is, as a rule, larger than *A. proteus X*, but not always so, 300μ – 500μ , and in exceptional cases more. Its protoplasm is usually very granular, as indicated by the names given to it by observers, but there is a gradation, the granular condition increasing while the whole amœba inclines to the dusky tinge as the individual amœbæ approach the *Z* end of the series (Fig. 3).

A. proteus Z is, generally speaking, very large; small members in the multinucleate condition may be found, but they are not common. The largest I have found measured some 1000μ , and when it lengthened out for division reached a measurement of 1500μ . The granulation is similar to

¹ Pallas, *Elenchus Zoophytorum*, 1766, p. 417.

but more concentrated than that found in *A. proteus Y*, from which it differs chiefly in the number of its nuclei.

With regard to the crystals contained by these amœbæ, two types may be recognised as predominating, both apparently based upon the octahedral form. Leidy,¹ Stolc,² and Vonwiller³ have shown these crystals well and, with Schubotz and others, have discussed their chemical or probable chemical composition.

The characteristic crystal of *A. proteus X* measures typically $6\ \mu \times 3\ \mu$ to $8\ \mu \times 4\ \mu$, is bipyramidal and usually doubly truncated. Occasionally crystal aggregates are met with similar to those figured by H. J. Carter,⁴ although not quite so perfect in form. Small crystals, if present at all, are few in number, sometimes regular octahedrons at other times resembling the larger crystals. In *A. proteus Y* there is a mixture in which the large crystal of *A. proteus X* predominates over complete, medium, and small crystals of apparently similar construction in inverse proportion as the condition of the amœba passes from the *X* to the *Z* end of the series; the number of large crystals in *A. proteus Z* being practically zero. The crystals found in *A. proteus Z* are figured by Vonwiller; always complete bipyramids. They vary in number; at one time very numerous, giving the well-known grey-black shade to the amœba, and at other times detected with difficulty, so few are they among the highly granular contents of this "type" of amœba.

The other inclusions—glistening bodies, staining or non-staining spherules, parasites, so-called embryos, etc.—are not constant.

The nucleus is a point open to discussion more than any other. Is the nucleus the same in all the amœbæ, to be classed as *A. proteus*? and when a difference in appearance is noted, is the amœba immediately to receive a new specific name? or, if it be admitted that there is a difference in the nucleus of the different members of the group, is it a radical difference or only a change brought about by environment, change of season, or by some phase in the life-history of the organism, a pathological condition or some physiological change in constitution? Any or all of these causes may be held accountable for much that is met with in the nucleus of *A. proteus*.

Without entering into the details of the nuclear constitution of the amœbæ under discussion, I wish simply to record observations, not deductions. Taking the nucleus of each "type"—*A. proteus X* is uninucleate—only twice

¹ Leidy, *loc. cit.*

² Stolc, *Kořenonožci*, 1899.

³ Vonwiller, *Arch. für Protist.*, vol. xxviii, 1913.

⁴ H. J. Carter, *A.N.H.*, vol. xii., 1863.

have I found a specimen in a binucleate condition, and on both occasions I was able to conclude from convincing evidence that it was a question of delayed division. The single nucleus is spherical, as a rule, the nuclear membrane being filled with coarse granules approximately equal in size, spherical in shape, and evenly distributed. Occasionally I have found an oval nucleus in this amœba, showing, when rolling over the well-known clear lens-like space between the chromatin and the nuclear membrane at the poles of the short axes, the discoid nucleus, so general in *A. proteus Y* but rare in *A. proteus X*.

In the *A. proteus Y* series a variety of nuclei may be met with, the members are, however, as a general rule, uninucleate, as *A. proteus X*, but individuals may often be found, seasonally it would seem, in the binucleate condition, which in this amœba is not necessarily a case of delayed division. However, if the nuclei present in a specimen of this series exceed two in number the amœba passes, according to my hypothesis, into the class of *A. proteus Z*. The single nucleus is oval in outline,¹ the granules varying in size according to their arrangement in the individual nucleus. If this arrangement is as in *A. proteus X*, then the granules are generally less coarse than is usual in the nucleus of this amœba; if submembrane blocks are present, and a large central mass of granules, then these latter are much larger and not equally spherical in form.

When the binucleate condition arises, either naturally or by inducement (Stolc),² both types of nuclei may be present in the same specimen, *i.e.* the nucleus of *A. proteus X* and *A. proteus Y*. I have found this in nature myself, and consider it significant. But in this series the variations of the nucleus are many and seem in some way graded with the other characteristics, and are at present under consideration.

In the multinucleate *A. proteus Z*, there is little doubt as to the similarity between the individual small nuclei and the single nucleus of *A. proteus Y* and frequently also of *A. proteus X*, an interesting fact if nothing more.

Vonwiller³ says that he has never found an amœba of the multinucleate type in the uninucleate condition. I can only say that each year I find it more difficult to reconcile myself to the idea, held by many, that the multinucleate form *A. proteus Z* does not arise from the uninucleate *A. proteus Y* or even *A. proteus X*. Dr Stolc has induced the multinucleate condition in *A. proteus Y*, and I have preparations of these amœbæ possessing

¹ I will not discuss the "ovoid" or "discoid" forms—Schæffer has done this in *Science*, *loc. cit.*

² Stolc, "Plasmodiogenie," *Arch. für Entw. der Organismen*, Bd. xxi., Heft 1, 1906.

³ Vonwiller, *loc. cit.*

one, two, four, six, eight, and so on up to about seventy nuclei. Odd numbers of genuine nuclei are rare, and when present two nuclei will be smaller than the rest.

REPRODUCTION.

Descriptions of the processes of reproduction vary, probably owing to the "type" of the original material.

To Awerinzew¹ is due the honour of being the first to describe mitotic division in the amœba he has called *A. proteus* Pallas. He gave no drawing of the amœba, simply the nucleus in its different phases of mitosis; the paper is written in Russian, an appended note in German gives no text description, but on my inquiry Awerinzew² assured me that he found division by mitosis common. As my description and drawings of the mitotic division in the nucleus of the amœba, which I have also styled *A. proteus* Pallas, differ from his own he questions the accuracy of these illustrations, considering the cases to be similar. My drawings are accurate. I should, therefore, prefer to conclude that we were working on different "types" of *A. proteus*. He on *A. proteus* *Y* and I on *A. proteus* *X*.

If this be so then the nucleus of *A. proteus* *Y* divides by mitosis and, from Stolc's³ account, by amitosis also. Here again, in this case, there is no distinction between the types, but Dr Stolc most courteously sent me all his papers on the subject and told me that he had worked on *A. proteus* as figured by Leidy. On reading his papers, I concluded that he had worked on *A. proteus* *Y* in these cases of direct division. His best paper with figures (1899) is written in his native language, the others in German. Unfortunately I have not been able to obtain a translation of the former since I received it, but the illustrations lead me to presume that he had observed both *X* and *Y*; the details are not clear.

With regard to *A. proteus* *Z*, the multinucleate form, it would appear to act as a plasmodium. Some authors mention having watched it nearly divide. I have been fortunate in obtaining division in three or four specimens. One particular case I watched during the whole night, and was finally rewarded by a division of this very large individual into two equal multinucleate daughter amœbæ. Do these multinucleate products divide, or fragment still more, or may it be as already suggested by some, that the amœba proceeds to encyst in this condition? Of either of these processes I have as yet no absolute proof of my own, although many observations point to both being probable.

¹ Awerinzew, *Zool. Anz.*, Bd. xxvii., "Über die Teilung bei *Amœba proteus*."

² Awerinzew, *loc. cit.*

³ Stolc, *loc. cit.*, also *Kořenonožci do Ottova slovníku naučného*.

The formation of reproductive cysts has only been observed by me, to my own satisfaction, in the case of *A. proteus X*, but I have watched strange isolated incidents in the behaviour of the other "types." The cyst described by Scheel¹ may be that of *A. proteus Y* or even *A. proteus Z*. No description of the free amœba is found in the text. So far then it would seem that—

A. proteus X multiplies by division (mitotic²) and by encystment.³

A. proteus Y multiplies by division (mitotic⁴ and amitotic⁵).

A. proteus Z divides as a plasmodium.

LOCALITY AND HABITAT.

Material was obtained from as many localities as possible, special note being taken of the type of *A. proteus* and the season of the year when found. In some localities all three types were to be met with, sometimes together at other times one type alone over a long period of time.

Mr Bolton of Birmingham was my main source of supply until 1916, sending material from Lapworth (pond), Sutton (ditch), Baddesley Clinton (pond), districts around Birmingham, England. Locally I obtained supplies from Wishaw, making my first find in the River Auchter there, also from Milngavie; and excellent specimens were received from Ireland, Killarney giving the best and most numerous.

The three types will live together in the same environment, but while *A. proteus X* will thrive upon a diet similar to that of the two other types it apparently prefers diatoms in addition when they are available. Occasionally *A. proteus X* may be found in few numbers with *Y* and *Z*, but as a rule when present it holds the field for numbers. *A. proteus Y* and *A. proteus Z* are often found together, in fact one may say always. *A. proteus Z* is found with *A. proteus X* in large numbers in certain seasons of the year. I have particularly noted autumn, about October.

At the outbreak of the war in 1914, other work prevented me from continuing an uninterrupted study of *A. proteus*, and also from collecting; thus my best thanks are due to my colleague Sister Monica Taylor, D.Sc., and her staff of the Zoology Department for their great help in finding sources nearer home and in keeping up the supplies of amœbæ for me. The results of the collecting and culturing of amœbæ have been embodied in a short paper by Sister Monica, to which I refer the reader.

¹ Scheel, *Kupffer's Festschrift*, 1899.

² Carter, *loc. cit.*

³ *Ibid.*, *loc. cit.*

⁴ Awerinzew, *loc. cit.*

⁵ Stole, *loc. cit.*

I owe to Mr Bolton an original method of bringing amœbæ to the surface of the mud in the collecting bottle; a method perfected for me in a small convenient apparatus by the Rev. James Rowland,¹ S.J., B.Sc., to whom I would here record my indebtedness.

There are a few points still calling for remark. The spherules often mentioned as present in *A. proteus*, particularly in *A. proteus Y*, are not all alike in composition; some stain well and may help in the identification of this uninucleate form in preparations, other spherules disappear if ammonia has been added to any of the reagents, and again others neither retain stain nor dissolve.

The crystals, too, which in the living amœbæ are a great help, disappear completely after treatment with the ordinary acid reagents. Thus it will be seen that should *A. proteus X* and *A. proteus Y* be in that phase in which the chromatin granules are evenly distributed in the nucleus and no diatoms present in the *X* specimen, it will be practically impossible to distinguish the one "type" from the other in a permanent preparation. This is important, because so many workers kill off at once and study their preparations, a method entirely unsuitable when working on *A. proteus*.

The foregoing observations are but a small percentage of those which have been made, but they are sufficient apology for the protest here raised against new specific names being given to *A. proteus* until a more conclusive life-history can be traced.

A short historical survey may add some weight also, showing as it does that there are names in plenty for this species of amœba whatever its ultimate fate may be. It may also convince others that if distinct species ever are formed from these amœbæ, the name *A. proteus* Pallas, should be retained by the form here designated provisionally *A. proteus X*, the type normally feeding on diatoms.

HISTORICAL SURVEY.

It would be superfluous to repeat the oft-told story of the discovery and naming of *A. proteus* but for the interest now being focussed upon the "variations" observed in the amœbæ passing under this name.

By all readers of *A. proteus* literature it must be evident that the earliest observers in this field were attracted by the size, general appearance and movements of these large amœbæ, and named them from some one or other of these characteristics. No nucleus has been included in descriptions before Auerbach,² 1856, exactly 100 years after the discovery made

¹ Professor of Physics and Chemistry, Mount St Mary's College, Chesterfield.

² Auerbach, *Zeit. für wiss. Zool.*, Bd. vii., 1856, p. 409.

by Rösel¹ in 1755, who gave the name of "*der kleine Proteus*" to the amœba he had found. Ten years later this amœba was described but not figured by Pallas² and renamed by him "*Volvox proteus*." This same amœba was placed by Ehrenberg,³ in 1838, with his *Amœba diffluens*, a type of amœba found by him in Siberia in 1829, and described in 1830.⁴ This *A. diffluens*, from Ehrenberg's description, is clear and limpid in general appearance and feeds voraciously on diatoms such as *Synedra ulna* and *Navicula gracilis*.

From the measurements given by this author for *A. diffluens*, it could not have been on account of its size that he considered it to be the same species as "*der kleine Proteus*," this latter being much larger than his Siberian discovery. On account of size and evidently general appearance, Ehrenberg did, however, separate a large amœba of this type, which he found near Berlin in 1831, and gave it a new specific name, *Amœba princeps*.

We may, therefore, presume that "*der kleine Proteus*," and also *Volvox proteus* Pallas, resembled in general appearance the clear, limpid diatom-feeding *A. diffluens*.

Thus it would seem that Ehrenberg himself divided the amœbæ into two classes, corresponding with the amœbæ here described as *A. proteus X* and *A. proteus Y*.

In 1841 Dujardin,⁵ giving no reason but the difference in size of the two amœbæ, removes Rösel's amœba, and consequently *Volvox proteus*, from the *A. diffluens* class and puts it in a class by itself. He gives it an average size of 200 μ , comparable with the *A. proteus X* of this paper.

It is obvious that later on the two larger amœbæ became confused by observers, and generally known under the name of *A. princeps*, with the result that these same observers doubted each other's descriptions.

The probability is that Ehrenberg's Berlin find was the amœba here designated as *A. proteus Y*, but that in his text he describes indifferently the diatom and non-diatom feeders under the title of *A. princeps* when the size of the amœba agrees with the limits he has set.

Thus Auerbach,⁶ in 1856, objects to Dujardin's description of *A. princeps* while sure of his own, yet in his illustrations he figures an amœba containing ingested diatoms and a nucleus circular in outline. It is only by a

¹ Rösel, *Insectenbelust*, iii. t. ci., p. 621.

² Pallas, *loc. cit.*

³ *Infusionthierchen als vollkommen Organismen*, 1838.

⁴ Ehrenberg, *Abh. der Akad.*, Berlin, 1830.

⁵ Dujardin, *Des Infusoires*, 1841.

⁶ Auerbach, *loc. cit.*

probability in his calculation that he brings the size of his specimen near to that of Ehrenberg's *A. princeps*.

In 1863 H. J. Carter¹ and Wallich² differed strongly over the amœba each had independently observed—the villous tuft being the chief cause of the dissention. From Carter's own description he certainly observed *A. princeps*, also the multinucleate form of *A. proteus*, and an infected specimen.

The amœba named *A. villosa* by Wallich feeds voraciously on diatoms and the villous tuft is not a constant feature, a fact recorded by Wallich himself, who thought the real difference between *A. princeps* and *A. villosa* might lie in the nucleus; which difference again might only be a phase in the life-history.

Leidy first groups these amœbæ under the name of *Amœba chaos*, but finally decides on *A. proteus* in his survey of 1879, placing *A. villosa* apart. The illustrations in this publication are the best produced, but no distinction of types is made, although peculiarities are recorded, with the obvious result that later workers think to make their description beyond reproach, by stating that the amœba they studied was *A. proteus* as figured by Leidy—but which?

Grüber³ broke away from this tentative grouping of Leidy's in 1884, but he retains the name *A. proteus* for one of the amœbæ, and the amœba chosen by him to perpetuate that name is the type I have here named provisionally *A. proteus X*, that is *A. proteus* Pallas, but in his figure the crystals are not well drawn.

Later Grüber calls into question Butschli's description of the nucleus of *A. proteus*, and concludes that if Butschli's description is accurate "then in one and the same species an entirely different arrangement of the chromatin in the nucleus is possible," and one would add very probable.

The well-known paper by Scheel⁴ (1899) on the cyst of *A. proteus* contains no description of the free amœba either in the text or in the illustrations.

In 1902 Penard's work on the "Faune Rhizopodique du Bassin du Lemán"⁵ appeared with excellent text descriptions and figures, though small, of each amœba met with. In his classification he also breaks up the *A. proteus* group, giving yet another set of specific names—thus

¹ H. J. Carter, *Annals and Mag. Nat. Hist.*, vol. xii., 1863.

² Wallich, *Ibid.*, vol. xi., 1863.

³ A. Grüber, *Zeitschrift für wiss. Zool.*, Bd. xli., 1885.

⁴ Scheel, *Festschrift f. Kupffer*, 1899.

⁵ Penard, *Faune Rhizopodique du Bassin du Lemán*, 1902.

A. proteus Pallas, *A. nitida*, and *A. nobilis*; the basis of differentiation being apparently size and nucleus. From his illustrations and text these three "species" would fall under the letters *X*, *Y* and *Z* of the suggestion here offered thus—*A. proteus* Pallas agrees with *A. proteus X*; *A. nitida* with *A. proteus Y*; *A. nobilis* with *A. proteus Z*. The fold in the nucleus of *A. nitida* Penard is not constant, and from what I have observed is only present in older cultures of *A. proteus Y*. The nucleus is not normal when this infolding is present to such an extent. I find that Schæffer has noted this also. *A. nobilis* is the multinucleate form.

In 1904 Awerinzew¹ described, as already mentioned, mitotic division in *A. proteus* Pallas. He did not otherwise describe the amœba; however, he told me that all the amœbæ upon which he had worked were *A. proteus* as described and figured by Leidy. The same answer was received from Dr Stole.² I have little doubt but that the amœba studied by Awerinzew was *A. proteus Y*, while Stole's drawings show that he observed both *X* and *Y*, and his descriptions reveal that he induced the *Z* condition in *Y*.

I have to thank both these eminent men for their courteous attention to any question I have put to them on this subject.

An excellent resumé of the nomenclature of *A. proteus*, by Cash and Hopkinson,³ was published in 1905. They give good illustrations of the amœba here called *A. proteus X* under the title of *A. proteus* Pallas, and with the following remark place *A. proteus Y* of my scheme as a variation:— "The nucleus and the contractile vesicle are normally as in *A. proteus*, but in general aspect and mobility this form is so distinct as to raise a doubt whether it really belongs to this species; Leidy, however, figures it as a form of *A. proteus* and it may for the present be distinguished as var. *granulosa*."

These authors neither figure nor mention the multinucleate form of *A. proteus* as such, but evidently put it into the *Pelomyxa* group under Cernyz's *A. princeps* and Brayley's *A. proteus*. One point, however, is to be noted, that they figure *A. villosa* with the nucleus of *A. proteus*. If there is a point of radical difference between *A. proteus* Pallas and *A. villosa* it is the nucleus; when, therefore, this difference ceases to exist, I should unhesitatingly place *A. villosa* with the diatom-feeding form of *A. proteus* as found in stagnant pools. The villous tuft is by no means special to *A. villosa* so called, nor is it always present in that organism itself; as a matter of fact when many amœbæ in a culture show this phenomenon,

¹ Awerinzew, *loc. cit.*

² Stole, *loc. cit.*

³ Cash and Hopkinson, "British Freshwater Rhizopods," London, *Roy. Society*, vol. i., 1905.

as I have seen *X*, *Y* and *Z* do at times, I suspect the culture, or some other environmental condition.

Calkins'¹ paper, giving a "probable" life-cycle of *A. proteus* introducing a sexual generation, appeared in 1904. However this life-cycle may be regarded, it is quite certain that Calkins worked with genuine *A. proteus*—*Y* and *Z* of my scheme. When, however, he comes to the large primary nucleus and small secondary nuclei in the cyst, I am seriously inclined to think with others that he is dealing with a parasite. At the same time I do not hold with Schubotz² who, writing in 1905, says that Calkins probably worked on *A. villosa*, and Awerinzew on a third variety, while he, Schubotz, claims to have worked on *A. proteus* Pallas. It depends upon which amœba is to be called *A. proteus* Pallas. My observations lead me to think that Schubotz certainly saw *A. proteus X* among others, but from his illustrations his research was mainly, if not wholly, carried out upon *A. proteus Y*. As for Calkins'³ amœbæ, they were by no means *A. villosa*, as usually described. His micro-photographs and text descriptions make it quite clear that the specimens he dealt with were *A. proteus Y* and *A. proteus Z*. His own remark is:—"While *A. proteus* has an average size of 300 μ , the individuals upon which I worked were somewhat larger than this, although in the same culture there were smaller and typical forms; in short, the general appearance was not different from that of *Amœba proteus* under ordinary circumstances of scarcity of food." What were the smaller and typical forms?

Schubotz' summary of the work done on *A. proteus*, especially the nucleus, is good, but, like myself, he finds it difficult to follow where no description accompanies the paper. He complains of Klemensicx, among others, who, he says, "omitted to give a description of the amœba form which he studied. He speaks of *A. proteus* without sketch or description of its characteristics. It remains uncertain whether I am studying the same form as he." This doubt accompanies almost every paper on *A. proteus* when time has been devoted to a study of the living material.

1906 brought Stolc's⁴ work of years on the inducement of the multi-nucleate condition in one of the uninucleate forms of *A. proteus*, with a suggested and most probable life-history, perhaps one of the clearest connected stories of all hitherto produced.

¹ Calkins, *Arch. für Protist.*, vol. v., 1904.

² Schubotz, *Arch. für Prot.*, vol. vi., 1905.

³ Calkins, *loc. cit.*

⁴ Stolc, *loc. cit.*

Metcalf¹ admits the difficulties arising from the "types," in a paper of his published in 1910. From his text he seems to have studied *A. proteus* Y, on which he makes the following note:—"Either the species *proteus* includes very diverse individuals, diversent as to food-habits, the condition of the crystals and plastids and plasma, or we should distinguish in the diverse types two or more species or sub-species if preferred. The species here studied feed almost wholly on bacteria, have numerous crystals . . . the species I had for study seems to be a form of *A. proteus*. The individuals are very large and quite typical *A. proteus*, except that their diet was almost exclusively bacteria, which is not ordinarily true of *A. proteus*."

Doflein's² text-book on Protozoa appeared in 1911 with a clear description and good figures of *A. proteus* Y, under the title of *A. proteus* Pallas.

Karl Gruber³ worked on the form *A. proteus* Y, under the name of *A. proteus*, in 1912.

In 1913 my own short paper⁴ on *A. proteus* Pallas, calls attention to the difference in diet of the two uninucleate forms, but I also refer the forms to Leidy's *A. proteus*.

In this same year Vonwiller⁵ published a note on the multinucleate form suggesting its withdrawal from the *proteus* group, at least the special multinucleate form upon which he worked, and as an alternative considered *A. nobilis* Penard to be a more suitable name. Dr Vonwiller sent me some beautiful preparations of his amœba for comparison with my own to which I found them similar, and, therefore, could not agree with his arrangement until we had further evidence. He had only studied the amœba two-and-a-half months, and admitted that it was hardly long enough under the circumstances. The war in 1914 stopped all further comparison of notes and work.

It is Schæffer's⁶ decision of 1916 and 1917 which has, however, called forth the protest which I have put forward in this paper. His grouping and specifications are given on the first page.

From his excellent text-descriptions it must be concluded that his *A. proteus* Pallas emend. Leidy, is the amœba already named *A. proteus* Pallas, var. *granulosa* by Cash and Hopkinson; that his raptorial *A. debia* (or *dubia*) Schæffer, the diatom feeder, corresponds to the *A. proteus* of

¹ Metcalfe, *Journ. Exper. Zool.*, vol. ix., 1910, pp. 301, 307.

² Doflein, *Lehrbuch der Protozoa*, 1911, pp.

³ Gruber, Karl, *Arch. für Protist.*, vol. xxv., 1912.

⁴ Carter, *loc. cit.*

⁵ Vonwiller, *loc. cit.*

⁶ Schæffer, *loc. cit.*

Grüber,¹ *A. proteus* Pallas of Cash and Hopkinson,² *A. proteus* Pallas of my own earlier papers and provisionally *A. proteus X* in this present paper. I hold it that if this amœba is to be finally separated from the others it should be the amœba to retain the name of *A. proteus* Pallas, for reasons already given.

There are at present recorded in Leidy's work of 1879 sixteen different names for the amœba described by him as *A. proteus*, while Cash and Hopkinson, in 1905, were able to produce at least twenty-three and to draw attention to the fact that this synonymy was not exhaustive; they did not include the multinucleate form. Can it be necessary to add to this list?

If the amœba is to keep the name *A. proteus* then some designation of its condition or "type" at the time of observation is absolutely necessary, hence the suggestion of *A. proteus X, Y* and *Z*. If, finally, the different "types" are proved to be also different species, evidenced by conclusive life-cycles, then the following names might be chosen from those already well known, e.g. *A. proteus* Pallas, *A. princeps* Ehrenberg, and *A. nobilis* Penard.

A remark made by Schæffer³ corresponds with my own sentiments in this work—"Whether these two types" (he does not seem to include the multinucleate form) "represent two or more species, or only different stages in the life-cycle of a single species has not yet been determined. . . . It is almost needless to say that it is of fundamental importance in physiological studies to know just what animals were used for observation and experiment. It is easy to see that the conclusions would be different from what they are if all the experiments in this paper had been performed on amebas of the granular type or on the raptorial type exclusively." The truth of this can only be appreciated by one who has studied *A. proteus* in all its forms in the living material.

Nothing but an intimate knowledge and careful microscopic study of the living amœbæ can give one an insight into the various conditions physiological, pathological or reproductive, as the case may be, in which these amœbæ may be found. Dr Schæffer is certainly carrying out this careful study, and his grouping of granular and raptorial is excellent, presuming that he places the multinucleate form with the granular amœbæ; but I do not think the position he gives to the old name *A. proteus* Pallas, nor the new names set forth as his own, are justifiable either now or in the future.

¹ A. Grüber, *loc. cit.*

² Cash and Hopkinson, *loc. cit.*

³ Schæffer, *Journ. Exper. Zool.*, vol. xx, p. 537.

Whether the hypothesis put forward in this paper—that all these amœbæ are of one species only—will prove to be a fact, or whether each type will eventually be shown to be a distinct species, is for the future to decide. In the meantime, this paper may help those interested in the study of *A. proteus* to work onwards *from* the differences, without having to rekind them for themselves, only then to discover that they have no longer time to proceed with such a problem.

SUMMARY.

1. The amœbæ passing under the name of *A. proteus* may be divided into three "types," herein designated as *A. proteus X*, *A. proteus Y*, *A. proteus Z*.
2. That these three "types" should not be given new specific names until there is more certain proof that they are distinct species, rather than phases in the life-history of one species of amœba.
3. That if, however, it be proved later that these amœbæ can be separated into distinct species, older names should be preferred to new ones—thus *A. proteus* Pallas (*X*), *A. princeps* Ehrenberg (*Y*), *A. nobilis* Penard (*Z*); or, *A. proteus* Pallas (*X*), *A. proteus* Pallas, var. *granulosa* (*Y*), *A. nobilis* Penard (*Z*).
4. Schæffer's classification into raptorial and granular amœbæ is very useful, but if used with the suggestion set forth in this paper, the so-called "species" would have to be rearranged.

Raptorial amœbæ *A. proteus* Pallas (*A. proteus X*).

Granular amœbæ { *A. proteus* Pallas, var. *granulosa* (*A. proteus Y*), or
A. princeps Ehrenberg (*A. proteus Y*), and
A. nobilis Penard (*A. proteus Z*).



FIG. 1.—*A. proteus* X.

FIG. 2.—*A. proteus* Y at X end of series.

FIG. 3.—*A. proteus* Y at Z end of series.

N, nucleus ; F, food vacuole ; C.V, contractile vacuole.

All the figures are drawn from living material, with the aid of an Abbé camera.

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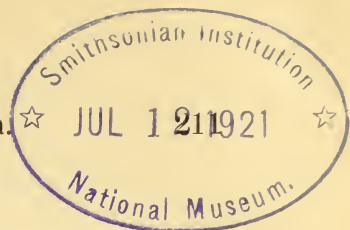
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The Prehistoric Find at Piltdown



XVI.—The Prehistoric Find at Piltdown. An Address delivered on 24th January 1921, by the retiring Vice-President, Prof. Waterston, M.A., M.D., St Andrews University.

I HAVE selected as the subject of my address the prehistoric find at Piltdown, which seemed to me to be a subject which would prove of interest to workers in a good many of the branches of Science represented here. Like all other evidence bearing upon the ancestry of man this find has appealed to a wide circle, and there has already grown up a large literature on the subject. One writer in 1915 gave sixty-eight references, and in 1918 no less than forty-three additional ones. The announcement of the discovery of prehistoric human remains has too often only been the prelude to an acrimonious discussion of the interpretation to be put upon them. The most recent discovery in England has been no exception to this rule, and a controversy has arisen of which the echoes have not yet died down. It will be a great misfortune if the conflict about interpretation should obscure the real value of what is, from almost every standpoint, one of the most valuable and instructive finds that has ever been made.

The place of the find was a flint-bearing stratum of gravel, overlying the Wealden beds at Piltdown in Sussex, in a portion of the basin of the Sussex Ouse. The gravel is found over a large plateau lying about 120 feet above sea-level, and 80 feet above the present level of the River Ouse.

[Prof. Waterston then gave an account of the finding at different places in the district of a large number of fossil fragments, which included portions of human skulls and of a mandible, of teeth and bones of a Tertiary elephant (stegodon), of mastodon, of a form of hippopotamus, etc.]

The authors' conclusions on the original find were, "A stratified Pleistocene gravel, containing in its lower layers the remains of a destroyed Pliocene deposit not far away, consisting of worn and broken fragments." All the bones were of considerable thickness, the left temporal bone being nearly complete and beautifully preserved. From the combined human cranial and mandibular fragments a skull was reconstructed, and the fragments were made the type specimens of a new genus of mankind, *Eoanthropus Dawsonii*. This form differed from other known species in the following characters:—

1. The skull bones were practically identical with those of modern man, and did not show the features of characteristic *Pithecanthropus*, or the Neanderthal man, such as the prominent supraciliary ridges.
2. The skull, as reconstructed, was of small capacity, and in this feature was unlike the majority of prehistoric crania.

3. The jaw was entirely different from any known specimen of the jaw of man, recent or prehistoric, the teeth were of the same size as those in the famous Heidleberg jaw, but the rest of the jaw was dissimilar.

The interior surface of the skull has been subjected to a very careful examination by Prof. Elliot Smith, and casts were made of this surface with a view to discovering the pattern of the convolutions and lobes of the brain which the skull contained. The conclusion has been drawn that the brain was of a simpler and more primitive type than any yet known in prehistoric man. The cranial fragments are undoubtedly of great antiquity, and one is not surprised to learn that the type of brain was simple, but I would remind you that few specimens of skulls are yet available for this purpose, and the reliability of the conclusions drawn from the endocranial casts of such crania, is not yet established.

At the first meeting, at which the remains were described, I expressed doubt of the propriety of assigning the mandible to the cranium, and in 1913 I expressed strongly the view that from a study of the mandible it seemed to me to be unjustifiable to assign both fragments to the same individual, on the principle that a correlation exists between cranium and mandible in the human and in the ape's skull, and that no such correlation was shown in the parts discovered.

The opinion which I expressed was met by the statement that the jaw was certainly very like a chimpanzee jaw, but that the teeth which it contained were entirely human, and the inference was made, but not expressed, that some undefined dental characters can override even the most striking structural features of the mandible.

Nor was the attitude of the upholders of the original view modified by the discovery of a canine tooth, which was most distinctly not human, but which they assigned to the same mandible, even though this involved the paradox of a characteristically human skull, whose jaw unmistakably resembled the jaw of a chimpanzee, which contained teeth of which a front one (canine) "differed fundamentally from that of any member of the genus *Homo*," while the back teeth were "essentially and characteristically human."

Some time after the publication of the original description, an important paper was published by Gerrit S. Miller¹ of the Smithsonian Institute at Washington. He made a careful examination of the casts of the fragments and of a large series of anthropoid material, and reached the definite con-

¹ *Smithsonian Miscellaneous Collections*, vol. 65, No. 12.

clusion that on the basis of the evidence furnished by the Piltdown Fossils and by the characters of all the Men, Apes, and Monkeys now known, a single individual cannot be supposed to have carried the jaw and the skull represented.

Within the last year Prof. Ramström¹ of Upsala has published figures and illustrations which give strong support to the same view. I would like to put before you, some of the reasons which led me at the first to doubt the conclusions drawn, and shall also give you some of the evidence which Mr Miller and Prof. Ramström have presented.

The crux of the matter lies, indeed, in the association together in one individual of the skull remains and of the jaw, for two features of the reconstruction hang upon this:—

1. The face, which is entirely hypothetical, except for the nasal bones, has been modelled so as to fit the jaw fragment.
2. The jaw conversely has been restored so as to fit the skull, *i.e.* the width between the condyles has been restored so as to fit the skull, *i.e.* the width between the condyles of the reconstructed jaw has been determined by the width between the glenoid surfaces of the skull, which is known from the actual fragments.

Characters of the Human Jaw.—The mandible of every human skull, prehistoric or recent, presents distinct and clear characters, by which it can be distinguished from the jaw of an anthropoid.

The ramus, and the coronoid process and condyle have considerable resemblance, though in details of structure differences may be present. The condyle, for example, is usually wide and narrow, the pit, on the anterior surface of its base, is less distinct than in man, the groove for the mylohyoid nerve lies behind the inferior dental foramen, and not in line with it, and the mylohyoid ridge is less distinct or even absent in the ape. All these characters have considerable value, but they do not possess the same degrees of constancy or definiteness that are shown in the front part of the mandible.

The human jaw presents in front a rounded arch, the opposite sides converge towards the symphysis in a curve whose character is influenced by the width between the rami. The lines of the molar teeth of the opposite sides, similarly converge to the median plane. The curve of the tooth row becomes more pronounced in the region of the premolar teeth. The area occupied by the teeth is less in man than in the chimpanzee, and the alveolar border is shorter, not only because the human teeth are on the whole smaller

¹ *Bull. Geol. Inst. Upsala*, vol. xvi.

but also because they are more closely packed together, especially towards the front.

In man the symphysis is short, and is not carried far back behind the incisor teeth, the curve of the front of the symphysis is concave except in the single case of the Heidleberg jaw. A vertical section, through the symphysis, shows an unmistakable difference between the jaw of every variety of human being and that of any ape. This difference in the symphysis is accompanied by a difference in the lower border of the body, in the human jaw it is rounded and in line generally with the upper part of the bone and the alveolar border. In the ape jaw, *e.g.* the chimpanzee, the lower border curves inwards towards the floor of the mouth, and forms a wide flange.

Correlation of Jaw and Skull.—The size and the form of the lower jaw stand in intimate correlation with the upper jaw, and through it with the whole skeleton of the face, and it in turn is correlated with the shape and form of the cranium. The length of the palate is, *e.g.*, correlated with the length of the skull. There is a further correlation, in that the width between the condyles of the mandible is that between the glenoid fossæ, which corresponds with the width of the skull. There is also a muscular correlation, since the muscles of mastication are attached at one end to the skull, and at the other to the jaw, and hence the strength or the weakness of such muscles will be shown at each attachment. A muscle with a large area of origin must have a correspondingly powerful insertion.

Comparison of the human jaw and skull with that of the ape shows that with the ape's long jaw there is of necessity a long palate. The implied maxillary protrusion causes an obliquity of the anterior opening of the nose, and thus the nasal bones do not project forwards, but lie comparatively flat.

The further correlations of jaw and skull in the associated changes in the basi cranial axis, in the position of the foramen magnum, the characters of the mastoid processes, and such like, are morphological features well established, but not demanding further elaboration here.

In the half mandible of the Piltdown find, we find a reproduction of all the features of the chimpanzee jaw which are usually considered distinctive; in its absolute measurements as well as in its proportions there is a similarity. The injury which the jaw has sustained has obliterated the more obvious features. To quote Mr Miller, "Deliberate malice could hardly have been more successful than the hazard of deposition in so breaking the fossils, as to give free scope to individual judgment in fitting the parts together," but the jaw fragment in its size, proportions, and in its structural characters displays features which render it indistinguishable from the jaw of a chimpanzee. One, therefore, believes that it must have articulated with a

cranium which showed a correlation in shape, in structure, and in its muscle markings, and such correlation is not shown by the human skull represented by the cranial fragments.

The Characters of the Teeth of Man and Apes.—The anterior teeth of the mandible of the apes show characters which distinguish them clearly from human teeth. The incisors are large and stout, the canine teeth are thick and so long as to project beyond the level of the crowns of the teeth. The premolar teeth show less difference, and the molar teeth generally resemble those of man, but are longer, narrower and have a thicker enamel.

The human characters, which were stated to be shown by the Piltdown molars, were the flattening of the crown, by wear, and the thinness of the enamel. They were stated to be "distinctly human, though of the most primitive type, and reminiscent of the ape's in their narrowness." I did not at first feel myself qualified to speak with certainty upon the differences which can be relied upon to distinguish human and anthropoid teeth, and I have not been able to examine a sufficiently large range of specimens to be able to speak from my own observations. I can, however, put before you the very striking facts which have recently been published by Mr Miller and by Prof. Ramström.

There is a wide range of variation in the teeth of the chimpanzee, and in spite of the projecting canines, the molar teeth of adult specimens often show a great amount of flattening from grinding down of the surface.

Mr Miller, dealing with certain specific characters in which the Piltdown specimens were stated to be human, has shown that in the ratio of crown height to maximum crown width (degree of "hypsodonty" in *Eoanthropus* represented by the figure 62·8), the teeth fall within the range for the chimpanzee, though there is an overlap, and this figure is distinctive of neither genus.

The tubercles are not larger than can be found in the chimpanzee, and the size of the pulp cavity is indistinguishable from that in man. In their obvious characters the teeth can be matched with those of a chimpanzee.

Prof. Ramström has devised some other tests for relationship, the most striking of which is the ratio between the proximo-distal length and transverse width. After examining a large series of teeth, he has been able to bring out that in human teeth the proximo-distal length is not usually greatly different from the width, the difference being not usually more than one millimetre, and the ratio of the two measurements does not fall below 90. In the chimpanzee, on the other hand, the difference between the two measurements is more considerable, 1, 2, or even 3 mm., and the ratio runs between 74·6 and 90. In the Piltdown teeth, the

difference between the figures is in each tooth 2 mm. and the index is 83.

So great a difference has not been found present in the case of any human molars, prehistoric or recent, and an index so low has not been obtained in any human case.

Lastly, I would mention briefly the question of the canine tooth which was found in the same layer. It was of conical form, laterally compressed so that the lingual surface was concave, the labial gently convex. The enamel on the inner face has been entirely removed by mastication, the surface forming a gently curved cavity evidently produced by a single tooth, and it extends to the basal edge of the crown. The tooth was stated to agree more closely with the milk canine of man and apes than with the corresponding permanent teeth, and was assigned to the left half of the mandible.

Subsequently, upon what appears to me to be conclusive evidence, it has been shown that the tooth is in reality the right upper canine, and Mr Miller found that it was almost identical with the right upper canine of a female chimpanzee from the French Congo in the collection at his disposal.

In conclusion, I would say, that at Piltdown a discovery of the first importance has been made. It has established the presence in England in the Pliocene or Pleistocene period of a form of anthropoid hitherto almost unknown in Europe, and also of a form of elephant hitherto unknown in Western Europe.

It has established the existence in England in the later Pleistocene time of a human species resembling closely in many details the Aurignacian race. It has added another to the evidences already known of the existence of man in a form similar to his present form at a very remote geological period.

On the question of the relation of the cranium and mandible, I am convinced that in dealing with separate fragments of uncertain origin, and of a mixed kind, each bearing indubitable evidence of its general affinities, it is not permissible to combine together such fragments in a single skeleton without clear evidence that such a combination actually existed. Especially is this the case in regard to two elements such as the mandible and the cranium, when, as in the present case, such association infringes the whole of the harmony of correlation which has hitherto been found to exist in authentic, complete specimens of similar prehistoric remains. The teeth, moreover, have now been shown not to possess the human characters at first attributed to them, and with this the only ground for assigning the mandible to the cranium has disappeared.

XVII.—Nuclear division in the Dinoflagellate, *Oxyrrhis marina*, Duj.

By J. S. Dunkerly, B.Sc., Lecturer in Zoology, University of Glasgow.

(With Text-figures.)

(Read 25th October 1920. Received 8th November 1920.)

THE following account of the nuclear division in *Oxyrrhis marina*, Duj., is based on some preparations made from laboratory cultures grown in sea water containing Allen and Nelson's modification of Miquel's nutritive solution. Coverslips were floated on the surface of the culture fluid and left for twenty-four hours, then fixed in Bouin's fluid and stained by Dobell's method with alcoholic iron hæmatoxylin. Many different stages of division in *Oxyrrhis marina* were seen, but the following stages have been selected as showing a probable sequence.

The resting nucleus is ovoid with a central body which may be called the karyosome, usually difficult to see on account of the deeply staining chromatin granules which mask it. The first appearance of division is shown by the appearance of two karyosomes (Fig. 1), the actual method of their formation not being seen. The chromatin now shows an indistinct fibrillar appearance, and the bulky equatorial plate is arranged at right angles to the long axis of the cell. Fig. 2 shows this at a slightly later stage when the chromatin is just dividing into the two daughter plates and two karyosomes are distinctly seen. At the two ends of the spindle can be seen the two faintly staining polar caps, comparable with those described by Ford (2) in *Amæba tachypodia* but larger, as would be expected from the larger volume of the chromatin mass in *Oxyrrhis marina*. In Fig. 3 the daughter plates have separated, the surfaces facing each other showing ragged threads of chromatin. Most important is the behaviour of the karyosomes at this stage. They appear to be connected by a distinct central strand or axis, in spite of the fact that two separate karyosomes are seen in earlier stages (compare Figs. 1 and 2). The expanded ends of the central axis are embedded partly in the concave sides of the daughter plates. The polar caps on the outer convex sides of the daughter plates are now more definitely conical in shape, and the whole figure shows a characteristic appearance of mitosis, except that the thick central axis takes the place of the numerous spindle fibres which would be seen in an ordinary mitotic figure.

The daughter plates on separating further have at first their concave

sides facing one another (Fig. 4), and their outer sides are convex, forming the basis of the polar caps. There are now two karyosomes present, presumably formed by the snapping across of the central axis, and they are embedded in the concave inner sides of the daughter plates. The daughter plates, no longer connected, draw apart and become inverted as regards their form. Their inner concave faces become convex and their outer convex faces become concave, still forming the bases of the pyramidal polar caps (compare Figs. 4 and 5). The daughter plates also rotate, forming an angle of about 45° with the longitudinal axis of the daughter cell (Fig. 5). Later the chromatin loses its thread-like appearance, the nucleus rounds itself off and is reconstructed. The karyosome is now in the centre of the granular chromatin of the nucleus, as shown in one of the nuclei in Fig. 6. At this point too the polar caps shorten and disappear finally.

Meanwhile the cytoplasm of *Oxyrrhis marina* has been dividing, as can be seen in the figures, until the form of a normal individual cell can be made out in each of the daughter cells. The division of the flagella was not followed, and no centrosome was seen.

The *Oxyrrhis marina* in this culture were infected by a parasite allied to the Haplosporidia, and four of these are shown in Fig. 7, one dividing.

The clearest figures of nuclear division in *Oxyrrhis marina* published hitherto were those of Keysselitz (4), drawn apparently from material left by Schaudinn. These figures are very small, do not indicate any polar cap, and show in the karyosomes very distinct centrioles, which I was unable to find in my preparations.

Most of the accounts of nuclear division in the Dinoflagellata (of which *Oxyrrhis marina* is a primitive or degenerate member), show massive chromatin plates similar to those described above for *Oxyrrhis marina*, but the presence or absence of a karyosome, and its function if present, are points that appear to be doubtful in some of the cases. Borgert (1) figures some "Nebenkörperchen" in the cytoplasm of *Ceratium* which, he thinks, probably divide independently of the nucleus. Jollos (3) decides that there is no centriole in *Ceratium*, and that the nuclear bodies described by him are plastin nucleoli, not centrosomes. Lauterborn (5) describes two to four nucleoli in *Ceratium* which on nuclear division taking place move to the poles of the spindle figure. A partial rotation of the daughter plates is described, resembling that above described for *Oxyrrhis marina*. One of his figures shows a faintly staining drawn-out body rather resembling the appearance of the karyosome in the daughter plate of *Oxyrrhis marina*.



EXPLANATION OF FIGURES.

All figures were drawn at table-level with camera lucida, using Zeiss 1/12" homog. immers. objective, N.A. 1.25, and $\times 12$ ocular, tube length 160 mm. Magnification of figures as reproduced is $\times 1900$ diam.

1. *Oxyrrhis marina*, nucleus showing two karyosomes.
2. Karyosomes separated, daughter plates with blunt polar caps shown, cell division commenced.
3. Central axis of mitotic figure shown between daughter plates of nucleus, elongation of polar caps.
4. Central axis disappeared, karyosomes embedded in daughter plates.
5. Alteration in form of daughter plates.
6. Karyosomes taking up central position in nucleus again, disappearance of one of the polar caps, advanced stage in cell division.
7. Parasitic spores in *Oxyrrhis marina*.

The only previous indication of the presence of the polar caps, which must be of some importance in the formation of the spindle figures, is to be found in two figures of Borgert (1).

LIST OF REFERENCES.

1. BORGERT. *Arch. f. Prot.*, xx., 1910.
2. FORD. *Arch. f. Prot.*, xxxiv., 1914.
3. JOLLOS. *Arch. f. Prot.*, xix., 1910.
4. KEYSSELITZ. *Arch. f. Prot.*, xi., 1908.
5. LAUTERBORN. *Zeitschr. f. wiss. Zool.*, lix., 1895.
6. SENN. *Zeitschr. f. wiss. Zool.*, xcvii., 1911.

XVIII.—*Rhabdamœba marina*, gen. n. et sp. n. By J. S. Dunkerly, B.Sc.,
Lecturer in Zoology, University of Glasgow.

(With Text-figures.)

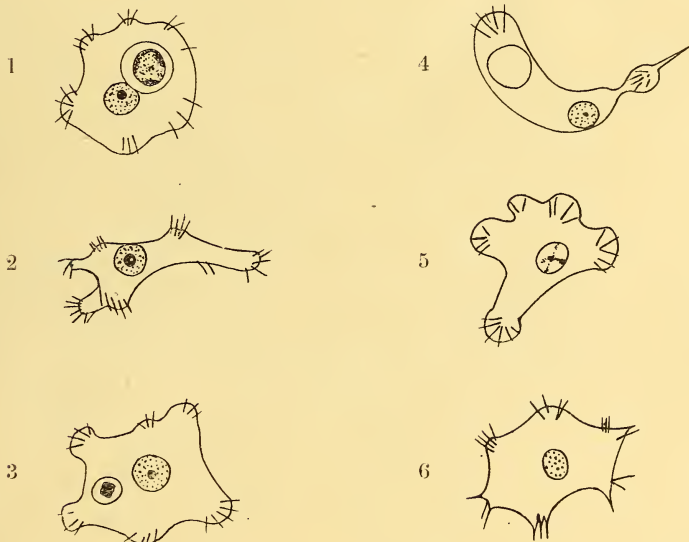
(Received 26th October 1920. Read 22nd November 1920.)

THE organism described in this note was found in some cultures of *Oxyrrhis marina* (division stages of which are described above). The culture medium was Allen and Nelson's modification of Miquel's solution in sea water, and the cultures had been started with some *Trichosphaerium* material from the Marine Laboratory, Plymouth. Coverslips were floated on the surface of these cultures for twenty-four hours, then fixed in Bouin's fluid and stained with iron hæmatoxylin by Dobell's method.

It was not until the mounted preparations were examined that the organism which is the subject of this note was discovered. The preparations had been made some months before being examined and the organism has not been seen again in the cultures, but, unfortunately, circumstances prevent at present a prolonged search of the cultures. It may be useful, therefore, to describe the appearance of this peculiar creature in the preparations, as it is so distinctive, and no published figures or description seem to fit it.

Rhabdamœba marina, gen. n. et sp. n., is a minute amœboid organism, the longest diameter being $10\ \mu$, and the diameter of an average rounded specimen (Fig. 1) only $7\cdot5\ \mu$. The protoplasm is extremely thin and transparent, the organism being visible only under the best lighting conditions. There is a central vesicular nucleus with a small karyosome and faint extra-karyosomatic granules (chromatin?) (Figs. 1-3). In some

specimens a food vacuole can be seen containing probably small vegetable cells (Figs. 1 and 3), showing that nutrition is holozoic, but the method of feeding was not observed. The most noticeable characteristic of the animal is that the pseudopodia, of which there are usually about six, are prominent knoblike structures which contain generally four or five pointed rod-like bodies, and these project slightly from the surface of the pseudopodia like tiny spines (Figs. 1-6). Their function, unfortunately, has not been ascertained, and no dividing forms or stages of nuclear division could be found. One individual only showed what may be a contractile vacuole as a clear spherical area (Fig. 4).



Rhabdamœba marina, gen. n. et sp. n.

Judging from the various forms found, some of which are shown in the six figures, the organism must be fairly motile, and this description taken in conjunction with the figures contains all that can be stated at present concerning this puzzling form. It may, of course, be a developmental form of some already described organism, but its extremely small size and its peculiar structure render it unlike anything known to me in the Rhizopoda, to which group, judging from its general structure and its vesicular nucleus, it obviously belongs.

All the figures were drawn with the camera lucida. The magnification of the figures as reproduced is $\times 2250$ diameters.

XIX.—Notes on Food-Capture and Ciliation in the Ephyrae of *Aurelia*.

By Prof. J. F. Gemmill, M.A., M.D., D.Sc.

(With Text-figures.)

(Read 22nd March 1920. Received 22nd March 1920.)

1. FOOD-CAPTURE.

If we examine a healthy young ephyra of *Aurelia* in clean sea-water under suitable magnification, we shall probably find the gastric cavity empty or nearly so. Turn the ephyra mouth-upwards and leave just enough water in the dish to allow it to pulsate without righting itself. Now introduce some drops of a culture rich in marine ciliates of good size, and allow mixing. In many cases you will hardly have time to get the ephyra under observation again before some of the ciliates have been taken into the gastric cavity. The number increases with surprising rapidity. As a rule the ingested ciliates are dead and disintegrating, but some species remain active after ingestion for a period which is longer or shorter according to the freshness and vigour of the ephyra. It is interesting to note how the ciliates are captured. The two lappets at the end of each ephyra arm are furnished, especially along their sides, with highly sensitive stinging cells capable of quickly extruding their long cnidotrichs. An infusorian touching a lappet is pierced and held by the stinging threads. Its movements usually get hampered by mucus or other colloid material produced, no doubt, chiefly by the lappet cells, but probably added to by the action of the poison on the prey. All the arms stop beating, or, more rarely, only the arm concerned ceases to beat. This arm now bends towards the manubrium and the manubrium bends towards the arm, while the lips stretch open widely in the same direction. The lappet is next slowly wiped across the lip and the infusorian thus detached. The latter now travels slowly down the manubrial canal to the stomach. I think it is carried by a central inhalant current which is compensatory to exhalant currents produced by ciliary action in the floor of the mouth angle grooves, but this may not be the whole explanation. It is curious to note how cleverly that part of the lappet which carries the infusorian is brought over the mouth. Thus if the prey is attached to the aboral surface, the arm and lappet curl completely round: if to the lateral surface, they are flexed in the necessary degree. Even the lips show fine adaptiveness, stretching and adjusting themselves to difficult captures. Their efforts, though persevering, are often fruitless, but they suggest appetite and desire as definitely as do the facial movements of ingenuous esurient higher

animals in the presence of food. Any arm may bring its contribution at any time, and the mouth seems sometimes puzzled which to attend to first. An ephyra swimming in a tank is occasionally seen to stop and flex one or more of its arms towards the mouth. It may be feeding in the manner just described, but in any case every pulsation is capable of wiping one or more of the lappets against the mouth.

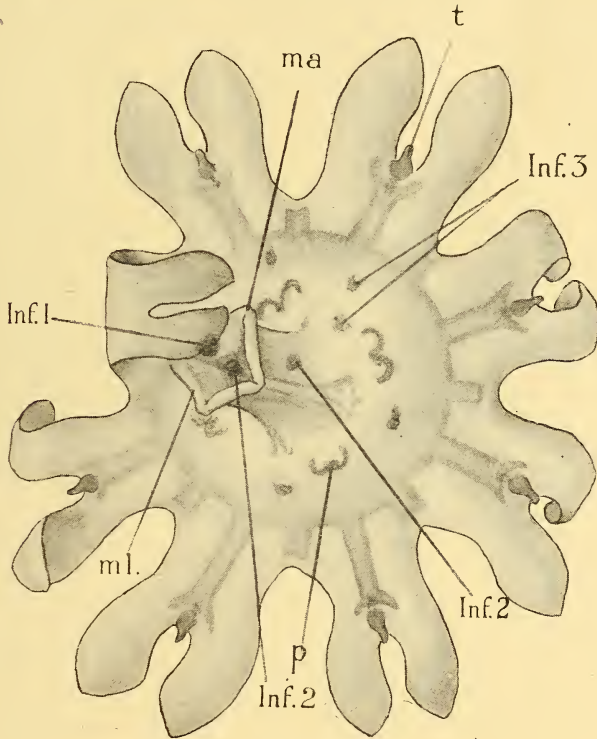


FIGURE 1.

To illustrate capture of infusoria by ephyræ ; see explanation in text.

Inf. 1. Infusorian paralysed and adherent to lappet but in course of being transferred to mouth.

Inf. 2. Infusorian within manubrial canal.

Inf. 3. Infusorian within gastric cavity.

m.a.—mouth angle ; *m.l.*—lip ; *p.*—gastric filaments ; *t.*—tentaculocyst.

Infusoria struck by the stinging threads are sometimes killed at once and begin to disintegrate before they are swallowed. Sometimes they are merely paralysed, and, resuming activity after a short time, manage to escape. Nauplius larvæ and minute Copepods may be attacked by young ephyræ with occasional success. However, out of over 2000 ephyræ 1 to 5 days' old from the Millport tanks, which I examined for abnormalities, not one showed

recognisable crustacean remains in the gastric cavity. On the other hand, I watched ephyrae in captivity capturing and swallowing infusoria for at least the first two weeks of their life.

The note on ciliation which follows will show that infusoria with other particles always tend to be swept towards the chief cnidoblast fire-zone (*i.e.* the lappets), from the whole exumbrellar surface, and from the subumbrellar surfaces of the arms and outer part of disc. The currents over the rest of the subumbrellar surface direct the prey to the lips, and observation shows that killing and paralysing can, though less readily, be done by the cnidoblasts of this surface. It is interesting to note that the scyphistoma captures infusoria in much the same way as the ephyra, the tentacles taking the place of the arm lappets, and twitching more quickly towards the mouth when the prey comes against them.

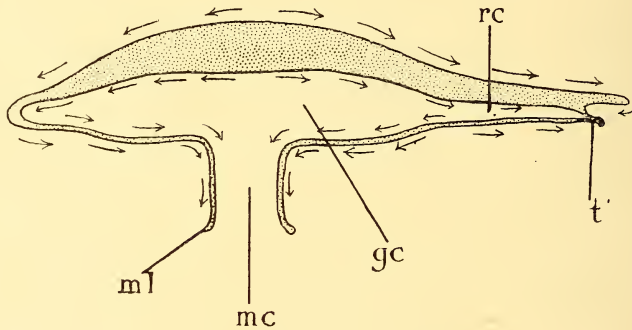


FIGURE 2.

Diagrammatic vertical section of an *Aurelia* ephyra passing through an arm on one side and an interspace on the other. See description in text.

g.c.—gastric cavity; *m.c.*—manubrial canal; *r.c.*—radiating canal; *t.*—tentaculocyst.

2. CILIATION.

It goes without saying that ciliary activity, though unobtrusive, is highly important for many marine animals, and deserves careful study by the morphologist as being a function to which the forms of particular animals or of their parts are closely related and in many cases subservient. Text-fig. 2 shows the general scheme of the ciliation in a young ephyra of *Aurelia*. The scheme may be summarised as follows:—

1. *Exumbrellar surface of disc, arms, and lappets*—currents centrifugally outwards. Many ephyrae show a torsion of these currents clockwise as seen from the aboral side, corresponding with the counter clockwise rotation which accompanies progression in the free swimming planula stage. Even 12-tentacled scyphistomas if

detached will move slowly aboralwards by ciliary action, and rotate counter clockwise as viewed from the aboral end.

2. *Subumbrellar surface of arms*—centrifugally outwards.

Subumbrellar surface of disc—centrifugally outwards on a marginal zone of about a quarter radius breadth; centripetally on remainder.

Subumbrellar surface of manubrium—towards the mouth opening.

3. *Internal surfaces*.—Roof of gastric cavity and of all radiating canals—centrifugally outwards.

Floor of gastric cavity and of all radiating canals—centripetally inwards.

Manubrial canal—ciliation absent or ill-defined, except in floor of radial grooves where it is weakly exhalant.

Gastric filaments—from base to tip of each filament.

The usefulness of the ciliation throughout the internal cavities is obvious. That of the external ciliation in relation to feeding is referred to on p. 224.

Widmark has described the ciliation in the *Aurelia* itself. Among characteristics he notes that there is well-marked centripetal movement of fluids along both the perradial and interradianal canals, and centrifugal movement along all the adradials, while the perradial grooves of the manubrial cavity exhibit strong ciliary action towards the mouth opening.

The medusa of *Melicertidium* exhibits much the same internal ciliary activities as the *Aurelia* ephyra, but externally ciliation is absent from the exumbrellar and considerable portions of the subumbrellar surfaces.

References to recent papers on ciliation in other marine invertebrates are given below.

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2. ORTON, J. H. *Journ. Mar. Biol. Ass. U.K.*, ix., 1912, pp. 144-178 (Ascidians, Molluscs): *ibid.*, x., 1913, pp. 19-49 (Amphioxus, Ascidians, Molluscs).
3. WIDMARK, E. M. P. *Zs. Allg. Phys. Jena*, xv., 1913, pp. 33-48 (*Aurelia*).
4. GEMMILL, J. F. *Proc. Zool. Soc. Lond.*, 1915, pp. 1-19 (Starfish); *ibid.*, 1919, pp. 263-265 (Ctenophore); *ibid.*, pp. 459-461 (Lepto-medusa).

XX.—Variation in Ephyrae of *Aurelia aurita*. By James W. Low, B.Sc., F.Z.S., Zoological Department, University College, Dundee.

(With Figures.)

(Read 22nd March 1920. Received 15th January 1921.)

It has long been known that considerable variation in the number of radial canals, tentaculocysts, and other structures, occurs in *Aurelia aurita*. There is an extensive literature on the subject, references to which may be found in the papers by Browne, M'Intosh and Hargitt, who have themselves done important work in describing, classifying and giving statistics of the various types of abnormalities found.

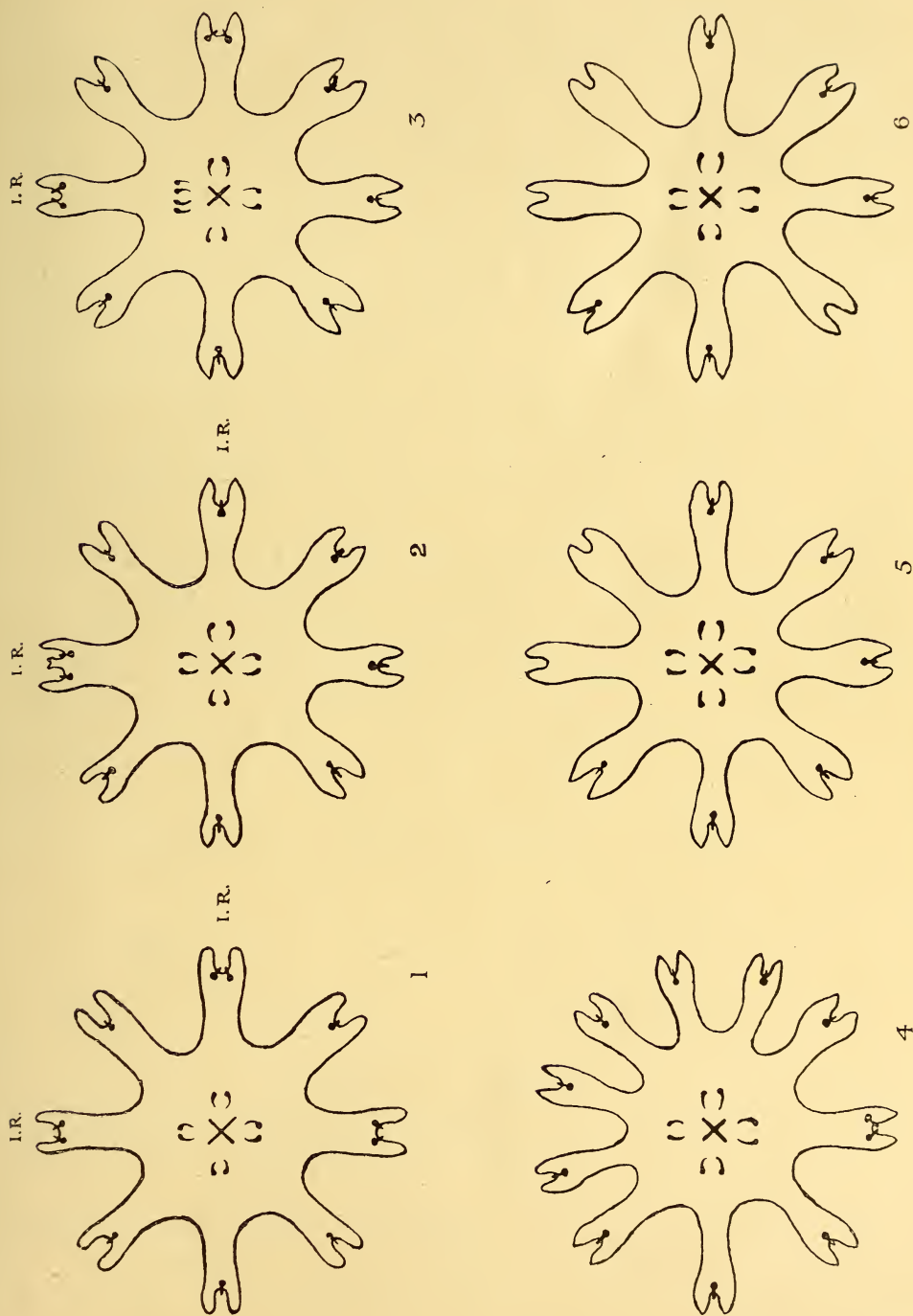
It was suggested to me by Professor J. F. Gemmill that an enquiry into the point whether individual strobilæ produced always normal ephyrae, or similarly abnormal ephyrae, might throw some light on the mode of origin of these variations.

The material on which the observations were made was obtained from the Dove Marine Laboratory, Cullercoats, Northumberland. The number of productive strobilæ examined was twenty-seven, out of a total of about forty, the remainder of which did not strobilate in the laboratory. Each strobila was kept in sea water and in a separate vessel, and the ephyrae given off were collected periodically so as to obtain them as far as possible in the order in which they were produced from the strobila.

My best thanks are due to Prof. Gemmill for many valuable suggestions and advice while carrying out the work. I am indebted to the Carnegie Trust for a grant towards expenses incurred in obtaining material.

It will be recalled that a normal ephyra of *Aurelia* shows eight arms (four perradial and four interradian), eight tentaculocysts, four pairs of gastric filaments, and four perradial mouth tentacles in the form of lappets, separated by four (interradian) mouth angle grooves.

Strobila No. 4 (see Table below) furnishes a case in which variation occurred, in different ephyrae, in both perradial and interradian arms. Among the first batch of ephyrae there occurred a ten-rayed form, which was due to doubling of two perradial arms. In the second batch from the same strobila, I found an eight-rayed form which showed "twin" tentaculocysts in one of the interradian arms, while in the third batch, besides normal forms, there occurred a nine-rayed form, due to doubling of one of the interradian arms. In strobila No. 6, all degrees of doubling of the interradian



FIGS. 1-6. Variations in Ephyrae of *Aurelia*.

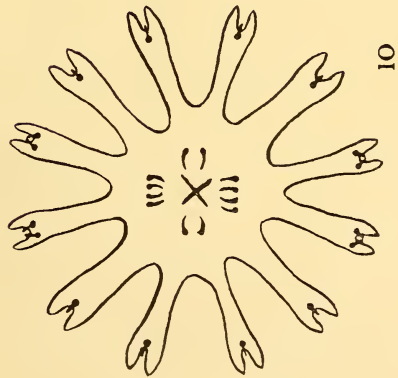
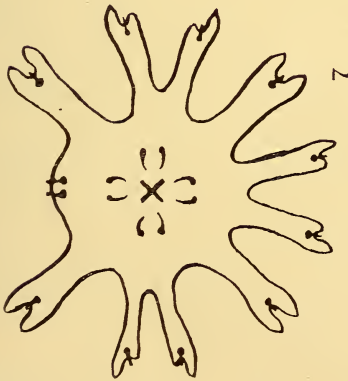
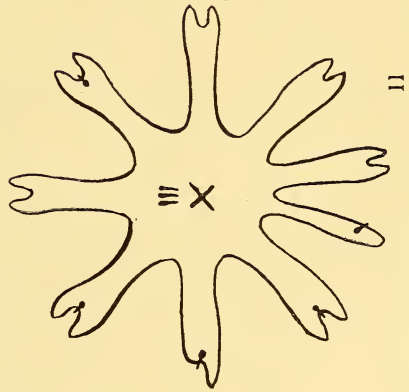
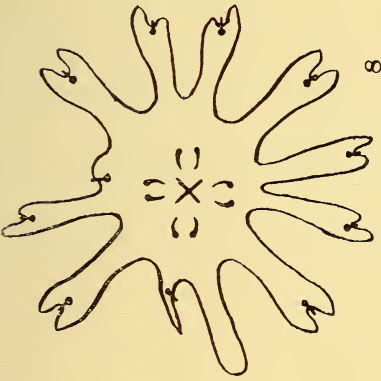
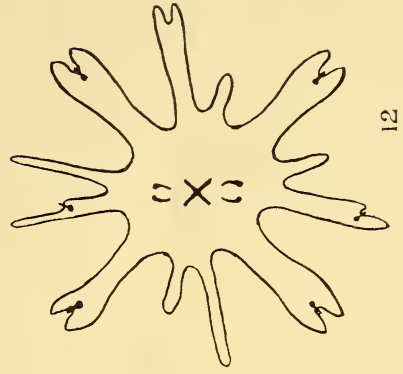
arms occurred, along with a tendency to reduction of tentaculocysts in the perradial arms. There was, however, one ten-rayed form due to doubling of two perradial arms, with "twin" tentaculocysts in another perradial arm. The ephyrae from strobila No. 8 showed variation in the interradial arms only. All degrees of doubling were found, from "twin" tentaculocysts in one interradial arm up to more or less complete doubling of the four interradial arms. Figs. 1-12 give a semi-diagrammatic representation of the chief variations found in this strobila. In strobila No. 10, reduction of the perradial arms occurred. Strobila No. 12 is of interest on account of the occurrence of a "twin" specimen. The attachment between two succeeding ephyrae had remained after their liberation from the strobila. The uppermost one was a twelve-rayed form, while the lower one was a normal eight-rayed type, showing that a large amount of variation occurs even between two succeeding ephyrae from the same strobila. From strobila No. 27 only ephyrae with four rays were liberated. The arms present were the interradials.

An analysis of the twenty-seven strobilæ examined shows that—

- (a) Twenty-two per cent. of the strobilæ produced only normal ephyrae.
- (b) Forty-four per cent. of the strobilæ produced ephyrae among which the variants varied in the perradial arms only.
- (c) Thirty per cent. of the strobilæ produced ephyrae among which the variants varied, some in the perradial and some in the interradial arms.
- (d) Four per cent. of the strobilæ produced ephyrae showing minor variation, *e.g.* in gastric filaments, only. (Arms normal.)

SUMMARY OF EPHYRÆ PRODUCED FROM THE VARIOUS STROBILÆ.

	Date	Number of Arms	Number of Ephyrae	Notes
STROBILA No. 1	14.2.20	8	6	Possibly due to doubling of 3 perradial arms and doubling of 2 interradial arms, or to doubling of 2 perradials and trebling of 2 perradials, with all the interradial arms single.
	"	14	1	
STROBILA No. 2	24.2.20	7	2	One perradial arm missing. One perradial arm missing, another without a tentaculocyst.
	"	7	1	
	"	8	1	
STROBILA No. 3	"	11	1	Three perradial arms doubled.
	14.2.20	8	8	
	"	11	1	



Figs. 7-12. Variations in Ephyrae of *Aurelia*.

	Date	Number of Arms	Number of Ephyrae	Notes
STROBILA No. 4	18.2.20	8	13	
	"	10	1	Two perradial arms doubled.
	24.2.20	8	1	"Twin" tentaculocysts on 1 interradial arm.
	"	8	6	
	27.2.20	8	1	Extra gastric filament.
"	8	1	One interradial arm doubled; no gastric filaments.	
"	"	9	1	
STROBILA No. 5	12.2.20	10	1	Two adjacent perradial arms doubled.
	14.2.20	8	9	
STROBILA No. 6	24.2.20	4	1	Probably 4 interradials, two of which were poorly developed; 2 mouth angles; no gastric filaments.
	"	8	6	
	"	8	1	"Twin" tentaculocysts on 1 interradial arm.
	"	9	1	One interradial arm imperfectly doubled.
	"	10	1	Two adjacent perradial arms doubled, with "twin" tentaculocysts on another perradial arm.
	27.2.20	8	1	
	"	8	1	Apparently 5 mouth angles; 1 pair of gastric filaments double.
	"	10	1	Two adjacent interradial arms doubled, another interradial with "twin" tentaculocysts, and 1 perradial with only one lobe, and without a tentaculocyst.
	"	12	1	Four interradial arms doubled, and 1 perradial without a tentaculocyst; mouth angles irregular.
	1.3.20	8	2	
"	4	1	Very irregular; 1 arm complete, 2 imperfect but with tentaculocyst each. Apparently gastric cavity opens by a single aperture.	
STROBILA No. 7	24.2.20	8	6	
	"	10	1	Two perradial arms doubled.
STROBILA No. 8	12.2.20	8	1	"Twin" tentaculocysts on 3 interradial arms.
	14.2.20	8	1	
	"	8	2	Tentaculocysts missing from 2 opposite perradials and also from 1 interradial.
	"	8	2	"Twin" tentaculocysts on 1 interradial arm, with hint of lappet between.
	"	8	1	Two tentaculocysts missing, on adjacent arms, 1 perradial and 1 interradial.
	"	10	1	Two adjacent interradial arms doubled, also "twin" tentaculocysts on another interradial arm.
	18.2.20	10	1	Three interradial arms imperfectly doubled, the fourth represented by "twin" tentaculocysts, the lobes being practically absent.
	"	11	2	Three interradial arms imperfectly doubled, and in one specimen one component of 1 interradial represented by tentaculocyst only, the lobe being absent; component of another without a tentaculocyst.
	"	12	4	Different degrees of doubling of the 4 interradial arms, but all imperfectly. In one specimen 2 opposite pairs of gastric filaments were doubled, and "twin" tentaculocysts in both components of corresponding arms.
	24.2.20	8	1	
"	8	1	All interradial arms with hints of imperfect doubling; 1 pair of gastric filaments and 3 single filaments in usual places.	

	Date	Number of Arms	Number of Ephyrae	Notes
STROBILA No. 8 (Continued)	24.2.20	9	1	One interradial arm imperfectly doubled; other interradials imperfect; only 3 single gastric filaments opposite 1 interradial arm.
	"	12	1	Four interradial arms imperfectly doubled; 2 opposite arms being represented by 1 lobe without tentaculocyst, and other lobe very small; 2 (opposite) pairs of gastric filaments only present.
STROBILA No. 9	12.2.20	8	4	
	14.2.20	8	5	
STROBILA No. 10	12.2.20	10	1	Two perradial arms doubled.
	14.2.20	4	3	Four perradial arms missing.
	"	5	1	Three perradial arms missing and another perradial without a tentaculocyst.
	"	6	1	Two perradial arms missing and another perradial arm without a tentaculocyst.
	"	6	1	Two opposite perradial arms missing.
	"	7	1	One perradial arm missing.
	"	8	2	
18.2.20	7	1	One perradial arm missing.	
STROBILA No. 11	14.2.20	12	1	Apparently due to doubling of 2 perradial arms and trebling of another perradial.
	"	8	3	
	18.2.20	8	11	
	24.2.20	8	3	
STROBILA No. 12	12.2.20	12	1	The most likely interpretation seemed to be that it was due to trebling of two perradial arms; if this interpretation is correct, the dextral component of one of the groups of three arms is as near to the adjacent interradial as to its neighbours, and the pair of gastric filaments is slightly adjusted so as to bring them almost opposite the interspace between the interradial and the component named.
	"	8	1	Normal. (Twin.)
	"	8	3	
	14.2.20	8	2	
STROBILA No. 13	12.2.20	8	3	
	14.2.20	8	1	
STROBILA No. 14	18.2.20	8	1	Extra gastric filament to one pair.
	"	8	6	
	24.2.20	8	7	
STROBILA No. 15	12.2.20	6	1	Two perradial arms missing and another without a tentaculocyst.
	"	6	2	Two perradial arms missing.
	"	8	4	
	"	9	1	One interradial arm doubled.
	14.2.20	6	1	Two opposite perradial arms missing.
	"	7	1	One perradial arm missing.
	"	8	1	
	"	8	1	"Twin" tentaculocysts on 1 interradial arm.
"	9	1	One interradial arm doubled.	
STROBILA No. 16	12.2.20	8	10	
	16.2.20	8	1	

	Date	Number of Arms	Number of Ephyrae	Notes
STROBILA No. 17	12.2.20	10	1	Two opposite perradials doubled and other two opposite perradials with "twin" tentaculocysts.
	"	6	1	One arm consisted of one lobe only and another had one lobe very small; apparently 3 mouth angles.
STROBILA No. 18	12.2.20	8	8	Apparently 3 interradial and 2 perradial arms present. Three perradial arms doubled. Four perradial and 1 interradial arm doubled.
	"	5	1	
	"	11	1	
	"	13	1	
	14.2.20	8	4	Extra gastric filament to one pair.
	18.2.20	8	4	
"	"	8	1	
STROBILA No. 19	12.2.20	8	9	Four perradial and 1 interradial arm doubled.
	"	13	1	
	14.2.20	8	3	
STROBILA No. 20	27.2.20	8	8	
STROBILA No. 21	27.2.20	3	1	Apparently 3 interradial arms in their normal positions, the fourth being missing. The gastric cavity appeared to be open on one side, with only one side of the mouth formed.
	28.2.20	4	1	Four interradial arms present.
STROBILA No. 22	27.2.20	3	4	All very imperfect; in one specimen the arms were all bilobed; in the others one arm was imperfect. No gastric filaments. The mouth appeared to consist of a single aperture without angles.
	"	5	4	Apparently 3 interradial and 2 perradial arms.
	"	6	1	Apparently 3 interradial and 3 perradial arms, one of the latter small. Apparently 3 mouth angles, and 3 pairs of gastric filaments.
	"	7	1	One perradial arm missing.
	"	8	11	
	"	8	1	One pair of gastric filaments missing.
	"	8	1	One perradial arm without a tentaculocyst.
	"	8	1	One perradial arm smaller than the others.
	"	8	3	Two interradial arms double at tips.
	"	12	1	Four interradial arms doubled.
STROBILA No. 23	27.2.20	8	2	Very difficult to interpret, but apparently 3 interradial and 2 perradial arms. One perradial arm missing.
	1.3.20	8	1	
	"	5	1	
	"	7	1	
STROBILA No. 24	27.2.20	8	4	
STROBILA No. 25	27.2.20	8	3	
STROBILA No. 26	27.2.20	8	3	Two perradial arms doubled.
	"	10	1	
STROBILA No. 27	27.2.20	4	2	Four interradial arms only.
	1.3.20	4	2	Four interradial arms only.

The relative frequencies of the different types of abnormality in the total number of ephyrae obtained are shown in Fig. 13.

As regards variation in the number of tentaculocysts, I found 29.9 per cent. to have fewer or more than the normal eight tentaculocysts. A

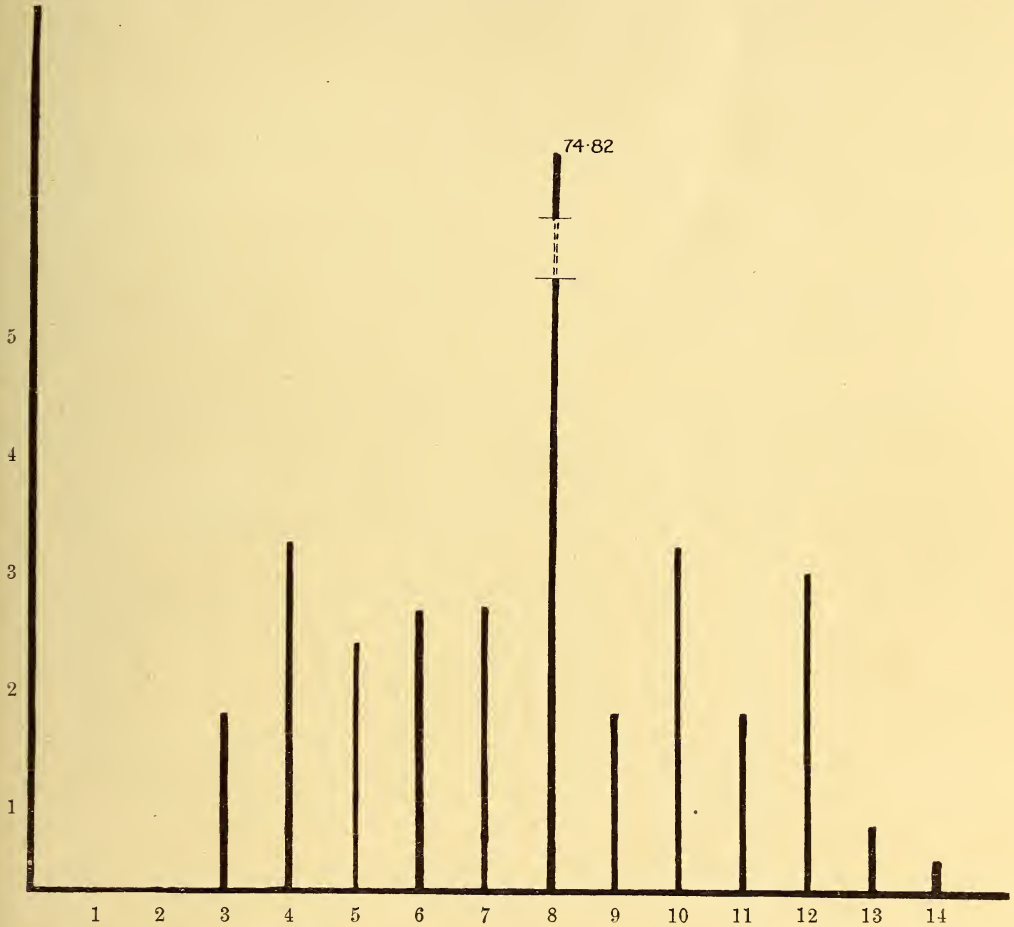


FIG. 13. Relative frequency of Abnormal Ephyrae of *Aurelia*.

(The vertical column shows frequency per hundred, and the horizontal the number of arms.)

comparison between this and the variation found in the number of tentaculocysts in adult forms is interesting. M'Intosh found the variation in question to be 16 per cent., Browne 20.2 per cent., while Hargitt, working with *Aurelia flavidula*, found 25 per cent. showing an abnormal number of tentaculocysts.

This points to the fact that there is a tendency during growth to elimination of the abnormal forms.

SUMMARY.

1. The same strobila may give rise to normal ephyrae and to ephyrae having more or less than the normal number of arms, and in particular cases there is abrupt discontinuity, for example, from a four-rayed form to a twelve-rayed form.
2. The total number of ephyrae produced from the twenty-seven productive strobilae was 278, of which ninety (*i.e.* approximately 32 per cent.) showed major or minor abnormalities. Of these 25.18 per cent. showed variation from the normal number of arms. Compared with the relative percentages for adult forms, this shows that there is a slight tendency during growth to elimination of abnormal forms. This is borne out by the figures given previously as regards tentaculocysts.
3. The largest number of ephyrae given off by one strobila was twenty-eight, the average production from an individual strobila being about ten; it is possible that some of the strobilae may have given off some ephyrae before being collected, and in this case the number would be slightly higher.
4. Seventy-eight per cent. of the strobilae produced ephyrae at least some of which varied in some respects from each other and from the normal eight-rayed type, as compared with 22 per cent. of the strobilae which produced only normal ephyrae.
5. The greatest variation in the number of arms in the ephyrae produced from one strobila was from a four-rayed form to a twelve-rayed form. Taking the ephyrae produced as a whole, the abnormalities which occurred varied from a form with three rays up to a form with fourteen rays.
6. The interradial arms appear to be more constant than the perradial arms, as instanced by the four-rayed forms, in which it is the interradial arms which are present.

The whole forms a striking example of variation in an asexual generation, a field which I hope to work at later, for studying the question whether variations produced in an asexual generation are transmitted to the succeeding sexually produced generation.

EXPLANATION OF FIGURES 1-12.

All the forms semi-diagrammatically represented were produced from strobila No. 8.

- Fig. 1. "Twin" tentaculocysts on three interradial arms.
 ,, 2. "Twin" tentaculocysts on one interradial arm, with hint of lappet between.
 ,, 3. "Twin" tentaculocysts on two interradial arms; one pair of gastric filaments doubled.
 ,, 4. Two adjacent interradial arms doubled, also "twin" tentaculocysts on another interradial.
 ,, 5. Two tentaculocysts missing (adjacent arms).
 ,, 6. Tentaculocysts missing from two opposite perradial and also from one interradial arm.
 ,, 7. Three interradial arms imperfectly doubled, the fourth represented by "twin" tentaculocysts, the lobes being practically absent.
 ,, 8. Three interradial arms imperfectly doubled; one component of one interradial represented by tentaculocyst only, the lobe being absent; component of another without a tentaculocyst.
 ,, 9. Four interradial arms imperfectly doubled.
 ,, 10. Four interradial arms imperfectly doubled; two opposite pairs of gastric filaments doubled and "twin" tentaculocysts in both components of corresponding arms.
 ,, 11. One interradial imperfectly doubled; other interradials imperfect; only three single gastric filaments opposite one interradial arm.
 ,, 12. Four interradial arms imperfectly doubled and without tentaculocysts except in components of two (opposite) arms. Only two (opposite) pairs of gastric filaments present.

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(Issued separately, 6th May 1921.)

XXI.—Variations in the Afferent Branchial Arteries of the Skate.

By **Augusta Lamont**, B.Sc., Assistant in the Department of Natural History, University of Edinburgh.

(With Text-figures.)

(Received 2nd December 1920. Read 20th December 1920.)

THE object of the following brief notes and sketches is merely to record the occurrence of certain abnormalities in the afferent branchial arteries of the skate.

Such abnormalities do not appear to have been described hitherto. Dr Gemmill, in his work on the *Teratology of Fishes* (1912), makes no mention of abnormal afferent arteries either in the skate or in any other

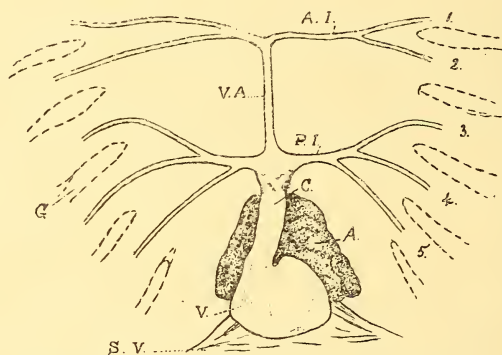


FIG. 1. *Raia circularis*, ♂. 1st June 1920.

genus of fishes; nor does Bateson in his *Materials for the Study of Variation* (1894) give any reference to previous records of variations in these blood-vessels. Having failed to find any other record of abnormalities of this kind, the present writer has thought it worth while to describe those special cases which have come under her notice.

The material described was obtained from among skate supplied for the class of Elementary Practical Zoology in the University of Edinburgh. Three of the specimens (Figs. 4, 5, and 6) came into the hands of the writer without any record of either species or sex, while another specimen (Fig. 3) has the species alone recorded. After becoming interested in the occurrence of these abnormalities, the writer collected the remaining three specimens during the summer and autumn terms of 1920 (Figs. 1, 2, and 7), and recorded both the species and the sex in each case. It will thus be seen that the abnormalities,

as far as recorded, are confined to the species *Raia circularis*, Couch, and occur in the male sex only.

The occurrence of the abnormalities in *Raia circularis* only, appears worthy of remark, because that species is not the one most frequently delivered for use in the class. Four species only, as far as the writer's experience goes, have occurred among the specimens delivered to the department of Zoology during a period of six years, and of the four, *Raia radiata*, Donovan, is by far the most common. *Raia circularis*, it is true, also occurs with considerable frequency, and on some occasions arrives at being the most numerous species in lots of from twenty to forty specimens delivered at one time. *Raia batis*, Linn., might be expected to be represented by from three to five individuals among such numbers, while *R. clavata*, Linn., occurs only very rarely. In order to give an exact record of the relative frequency of the four species, the numbers of each were counted on six days during the autumn term of 1920, and the result, out of a total of 184, was—*R. radiata*, 132; *R. circularis*, 36; *R. batis*, 15; and *R. clavata*, 1.

No very exact numbers can be given to indicate the frequency of the abnormalities in question, for the lots above enumerated were not dissected for afferent branchials. During the week before these enumerations were begun, two abnormal specimens (Figs. 2 and 7) were obtained, these two being the only variations of the kind observed among about 170 specimens dissected for afferent branchial vessels during the week. Among these 170 or so specimens *R. circularis* was well represented, and two or three specimens of *R. clavata* also occurred.

One other fact may deserve passing mention, and that is that the gills of the specimens represented by Figs. 1 and 4 were infested by the not uncommon Copepod parasite, *Charopinus dubius* (T. Scott). In Fig. 1 the gills on both sides were attacked.

Regarding the actual abnormalities a few words only are needed in explanation of the accompanying figures. In the majority of typical Elasmobranchs the normal condition presents five afferent branchial vessels on each side, running respectively on to the hyoid arch and the first four branchial arches. The method of origin of the afferent vessels from the ventral aorta—whether fused or independent—varies according to the genus. In *Raia* the first two afferent vessels (counting from the anterior end) arise normally as branches from the anterior innominate, while the last three are branches from the posterior innominate. Both anterior and posterior innominates are paired vessels arising directly from the ventral aorta. In none of the abnormal cases is the total number of five afferent vessels departed from, the exceptional conditions being usually occasioned by the

transference of the second afferent vessel from the anterior to the posterior innominate, or by the independent origin of the same second afferent vessel from the ventral aorta. In no case has a transference been observed of one of the three posterior afferents to the anterior innominate.

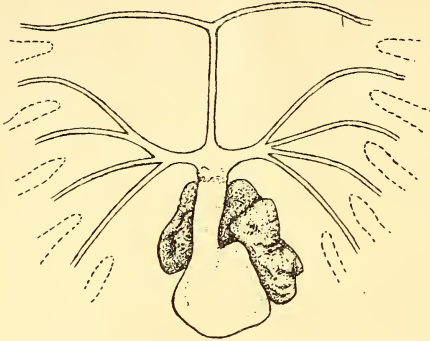


FIG. 2. *Raia circularis*, ♂.

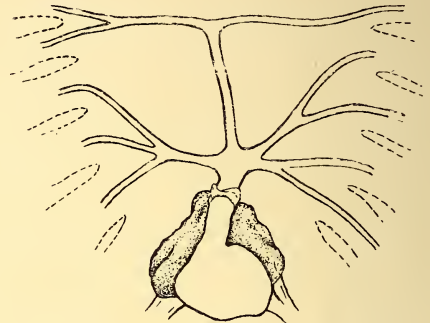


FIG. 3. *Raia circularis*.

Fig. 1 represents a condition which exhibits least departure from the normal. The right anterior innominate is very short and gives rise to two long afferent vessels, thus presenting a slight want of symmetry between the two sides.

In Fig. 2 a case is represented in which the abnormality affects both sides and is all but symmetrical. Each anterior innominate passes, without branching, into a single afferent branchial vessel, while each posterior innominate gives rise to four, that is, to one in excess of the normal number.

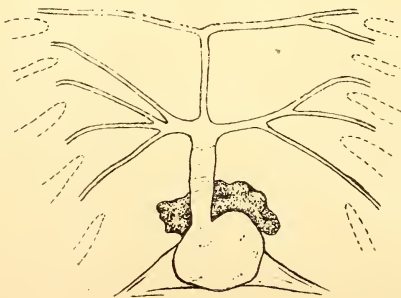


FIG. 4. *Raia*.
Species and sex not recorded.

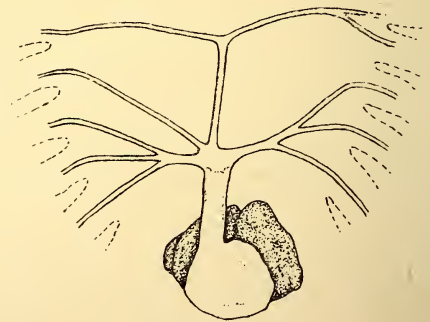


FIG. 5. *Raia*.
Species and sex not recorded.

Figs. 3, 4 and 5 are sketches of three closely similar cases in each of which the second afferent vessel has, so to speak, been transferred from the anterior to the posterior innominate, but on one side only.

Fig. 6 presents a new case. The second afferent branchial is again affected, but in this case it arises as a separate vessel from the ventral aorta.

Fig. 7 represents a second specimen in which the abnormality affects both sides, but in this case it is unsymmetrical, and in that respect presents a contrast to Fig. 2. It combines the two last conditions described, closely resembling Fig. 6 on the left side of the specimen and Fig. 5 on the right.

A comparison of these variations of the afferent branchial system in the skate with the usual condition displayed in some other Elasmobranchs, suggests that they should be regarded, not as actual malformations, but rather as indicating an unstable and fluctuating condition in the more specialised group of the sub-class. The origin of the first two afferent

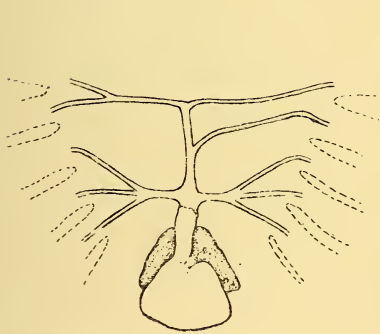


FIG. 6. *Raia*.
Species and sex not recorded.

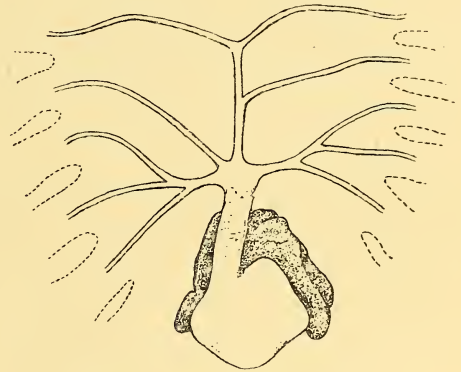


FIG. 7. *Raia circularis* ♂.

vessels as branches of an innominate artery, is a not unusual Elasmobranch condition which *Raia* shares, for example, with *Scyllium* and with *Chlamydoselachus*, which latter is considered by Ayers¹ as a primitive type in respect of its arterial system. When, however, as an abnormality in *Raia*, the second afferent branchial arises independently from the ventral aorta, the condition presented is the same as that exhibited by *Mustelus*. With regard to the three posterior afferents, the clumping together of these vessels in *Raia* as branches of a posterior innominate, may be regarded as a progressive departure from more usual Elasmobranch conditions. Finally, the tendency, as an abnormality in *Raia*, for as many as four afferent vessels to diverge from near the base of the ventral aorta, recalls in some degree the afferent system of the Dipnoan *Ceratodus*, in which the ventral aorta is so much shortened that all four afferent vessels arise close together immediately anterior to the conus arteriosus.

¹ H. Ayers, "The Morphology of the Carotids, based on a study of the Blood-vessels of *Chlamydoselachus anguineus* (Garman.)," *Bull. Mus. Comp. Zool*, Harvard, xvii., 1889.

If a record were kept of the occurrence or non-occurrence of similar variations in dog-fishes, by those who see large numbers of them dissected for teaching purposes, an interesting and suggestive comparison might be made as to the variability of, and the direction of variation in the afferent system of the two groups of Elasmobranch fishes.

The specimens described are preserved in the museum of the Natural History Department, Edinburgh University.

EXPLANATION OF FIGURES.

All the figures are $\times \frac{3}{4}$ and represent ventral dissections of the heart and afferent branchial system.

<i>S. V.</i>	Sinus venosus.	<i>C.</i>	Conus arteriosus.	<i>P. I.</i>	Posterior innominate.
<i>A.</i>	Auricle.	<i>V. A.</i>	Ventral aorta.	<i>G.</i>	Gill clefts.
<i>V.</i>	Ventricle.	<i>A. I.</i>	Anterior innominate.	1-5	Afferent branchial arteries.

(Issued separately, 6th June 1921.)

XXII. — A Description of certain Abnormalities of the Reproductive System found in Frogs, and a Suggestion as to their possible Significance. By F. A. E. Crew, M.B., Assistant in the Natural History Department of the University of Edinburgh.

(With Plates.)

(Read 23rd February 1920. Received 12th December 1920.)

DURING the last two years I have had the opportunity of examining four specimens of frogs (*Rana temporaria* and *R. esculenta*) in which well-marked abnormality of the reproductive system was present. Two of these were handed to me by Professor J. H. Ashworth, to whom I am greatly indebted both for the specimens and for much inspiring and kindly interest. All four were met with in the course of the ordinary work of the Practical Zoology Class within the University.

When the examination of these specimens was finished and their description completed, hearing that Mr Julian S. Huxley had met with a similar case, I wrote to him, briefly describing my own cases and asking if his confirmed certain conclusions at which I had arrived. In answer, came not only every sort of information, but also three frogs all showing well-marked abnormality. Mr Huxley had begun the examination of one of these, but on learning of my interest, he immediately, and with characteristic grace, handed the specimen and all his notes concerning it to me. A second frog, similarly met with during the ordinary class work at Oxford, had been preserved for future description, while the third was a specimen which had been incompletely described by A. F. S. Kent in the *Journal of Anatomy and Physiology*, vol. xix., July 1885, p. 347, and which had lain in the museum at Oxford since that date. The specimens and notes were given to me unconditionally, but it is convenient to ascribe two of the cases to Huxley and the other one to Kent, although I must be held responsible for the description of the histological findings and the interpretations based thereupon.

A grant from the Moray fund has enabled me to provide the illustrations without which the description would lose much of its point.

The cases are described in such order that the first most nearly approaches the typical female, and the last the typical male, in respect of both primary and secondary sexual characters.

CASE NO. I.

HUXLEY (1), (Fig. 1).—*Rana temporaria*. Adult, measuring 8 cm. from the *symphysis menti* to the *symphysis pubis*. Killed April.

Fore-limbs like those of a very well-developed female but no male characters were present. (Huxley was inclined to think that there were very slight traces of male characters about the finger-pads when the specimen was superficially examined at the time when its abnormalities were first noticed.) The *m. rectus abdominis* and its extension to form the *portio abdominalis* of the *m. pectoralis* were poorly developed. The *humeri* were of the female pattern and the skin of the flanks and back was warty.

The right gonad was an ovary of usual size. It appeared rather more deeply pigmented than the normal. The left gonad had been removed and sectioned before the specimen came into my possession. It was an ovo-testis. No particular note of the relative positions of ovary- and testis-portions was made before the gonad was sectioned, but it is thought that the smaller testis-portion lay upon the ventral surface and the external border of the gonad. The photograph certainly suggests that this was so, but as in no other case has the testis-portion been found in this position but always has been along the inner border of the gonad, it is perhaps reasonable to suggest that, as the photograph was taken while the specimen was under water, the testis-portion floated away from its natural position.

Vasa efferentia were absent on the right side; remnants of vessels other than blood-vessels were found in connection with the *hilus* of the left kidney, and two of these were regarded as efferent ducts. No distinct seminal vesicles were present upon the urino-genital ducts, but on each of these was a small but definite fusiform enlargement in the situation where normally the seminal vesicle of the male is to be found. The Müllerian ducts were well developed with well-defined, empty, and pigmented uterine segments. Ova were present in the upper portions of the ducts, and the glandular portions were active. The uterine segments and rudimentary seminal vesicles were bound together, and there were four openings into the cloaca (Fig. 1a).

On section, the right gonad was seen to be composed entirely of ovarian tissue. Ova were present in great numbers and in all stages of development. But the wall of the ovary was the seat of distinct overgrowth of connective tissue and of localised aggregations of polygonal masses of pigment (Fig. 2).

The left gonad consisted of two distinct portions—a smaller portion composed of spermatic tissue, and a much larger portion similar in structure to the ovary of the opposite side. The greater part of the spermatic tissue

was healthily normal, but at widely separated points two ova were found, one actually within a seminal tubule (Figs. 3 and 3a), and the other between the tubules. The ovum within the tubule lay among spermatozoa. The ovum appeared perfectly normal in structure, whereas the spermatozoa were deformed and breaking down. It is probable that the pressure exerted by the ovum, which very nearly filled the lumen of the tubule, was responsible for the degeneration of the spermatozoa within this and the neighbouring tubules. The second ovum lay between seminal tubules which were irregular in shape,—another pressure effect in all probability,—and showed signs of degeneration. *Vasa efferentia* were present in association with this testis-portion.

The ova within the Müllerian ducts were degenerate, and many consisted of nothing but granular material. No spermatozoa were found within the enlargements of the urino-genital ducts. There were ciliated cells upon the peritoneum. The pituitary was unexceptional.

CASE No. II.

Rana temporaria. Adult, measuring 7.7 cm. from the *symphysis menti* to the *symphysis pubis*. Killed April.

External characters.—On the base of the innermost digit of the left hand was an unpigmented but definite pad, in size smaller than that of the average male of the same size at this season. On the right hand there was no pad, but the digit was stouter than that of the typical female (Fig. 4). Fore-limbs moderately massive. Rut-muscle poorly developed. Skin of the back and flanks not warty.

On inspection, the right gonad was found to be an ovary, measuring $3.2 \times 1.7 \times .6$ cm., more deeply pigmented than usual, and more solid-looking. The left gonad had the appearance of an ovary, more deeply pigmented and firmer than the normal, which bore upon its inner border three nodules of tissue exactly resembling normal testis. The whole gonad measured $3.6 \times 1.8 \times .8$ cm., and of the three nodules of testis-substance, one, $6 \times 5 \times 4$ mm., was situated at the extreme anterior end of the inner border. Another, $7 \times 5 \times 4$ mm., lay at the extreme posterior end of the border, while the third, $3 \times 3 \times 3$ mm., was placed midway between the other two (Fig. 5).

Vasa efferentia connected each gonad to the adjacent kidney; they were few in number on the right—three only—but on the left were exactly like those of a normal male. Seminal vesicles were present, but were small and spindle-shaped. The Müllerian ducts were well developed and of the size

of the oviducts of the adult female, with uterine segments of moderate size. There were four openings into the cloaca.

The following hurried notes were made when the condition was first noticed, and were handed to me together with the specimen. "Terminal portions of oviducts distended with eggs ready to be laid. There were eggs also in the middle portions of the oviducts. These were extracted and among them was a considerable number of empty spheres of albumen, *i.e.* the albumen envelope was present but egg not contained therein. The proportion of these empty spheres was about one-fifth, at a rough estimate."

On section, the right gonad proved to be entirely ovarian in structure. It contained ova in all stages of development, but the connective tissue was everywhere hyperplastic, and a considerable number of the ova showed signs of degeneration. Polygonal masses of pigment were present apart from ova in great numbers, and the thickened wall of the ovary encroached upon its cavity.

The left gonad consisted mainly of tissues similar to those of the right, but the hyperplasia of the connective tissue, the presence of the pigment in excess, and the degeneration of the ova, were more pronounced. The three nodules upon the inner border had the structure of normal functional testis, and though in close and intimate contact with, yet were discrete from, the pathological ovarian tissues. The line of junction between the two tissues was very irregular, so that the ovarian pigment seemed to invade the spermiatic tissues along the lines of the intertubular connective tissue. Perfectly normal spermatozoa were seen to be aggregated at one point in a dilation of a *vas efferens* in connection with the middle lobule of testis-substance (Fig. 6). *Vasa efferentia* connected the right ovary to its kidney. The uterine segment contained only spurious ova with nuclei of granular debris. The peritoneum about the suspensory ligaments of the gonads bore ciliated epithelium upon the surface. There was nothing unusual about the pituitary or suprarenal bodies. Further dissection showed that the bones of the fore-limb were of the male pattern, though of but moderate development.

CASE NO. III.

KENT (Fig. 7).—*Rana temporaria*. Adult, measuring 6.5 cm. from the *symphysis menti* to the *symphysis pubis*. Killed January.

Non-pigmented finger-pads well defined; fore-limbs massive; rut-muscle well developed; *humeri* of the male pattern; skin of the back and flanks not warty.

Right gonad, measuring 15 × 7 × 7 mm., consisted of two distinct portions. The inner and larger portion had the appearance of normal testis, and its

surfaces were divided by a deep transverse groove into more or less equal anterior and posterior halves. Closely applied to the outer border and anterior pole of this testis-portion was a mass of ovarian tissue, abnormal in that it was firmer to the touch, more solid-looking, and more densely and uniformly pigmented, than is the normal ovary.

The left gonad was a testis of unusual shape, measuring $17 \times 5 \times 6$ mm.; its surfaces were uneven, and its anterior pole was irregularly flattened dorso-ventrally.

Vasa efferentia of the ordinary male arrangement were present in connection with the inner borders of both gonads. Seminal vesicles were present; the left one being well developed and the right one spindle-shaped, and non-pigmented. Such a difference in the degree of development of the vesicles of the two sides is not unusual in the male (Fig. 7a). The right Müllerian duct was well developed and much convoluted, but its uterine segment was small and non-pigmented. The left duct was rudimentary and straight but possessed a well-defined, though very small, non-pigmented uterine segment. No ova could be seen within these ducts. Uterine segments and seminal vesicles were intimately bound together in the more posterior portions, and there were four openings into the cloaca.

On section, the right gonad proved to be an ovo-testis. The testis-portion, discrete from the ovarian, consisted everywhere of normal spermatic tissue. The ovarian portion was applied to the outer border and to the anterior pole of the testis-portion and was pathological, showing degeneration of the ova, hyperplasia of the connective tissue, and a great relative increase in the amount of the pigment normally present in ovarian tissue (Fig. 8). Along the line of junction of testis and ovarian portions the actively growing spermatic tissues were seen to be enveloping ova and ovarian pigment (Fig. 8a). This undoubtedly illustrates the method by which ova and pigment become included amid spermatic tissues in such cases.

The left gonad (Fig. 9) had the structure of ordinary spermatic tissue save that throughout the gland, ova, some normal and others distinctly degenerate in appearance, were found within and between the seminal tubules. The presence of such an ovum within a seminal tubule was associated with obvious deformity and degeneration of the compressed spermatozoa.

The left Müllerian duct possessed a central lumen throughout its length and had a patent *ostium abdominale*. No ova were present in either duct, and no spermatozoa were found in the seminal vesicles. There were ciliated cells upon the peritoneum, and the pituitary, though distinctly smaller than usual, had the normal structure.

CASE No. IV.

Rana temporaria. Adult, measuring 7·8 cm. from *symphysis menti* to *symphysis pubis*. Killed June.

External characters.—Finger-pads as those of the typical male at other times than during the breeding-season. Fore-limbs massive. Skin of back and flanks not warty (Fig. 10).

On inspection, the right gonad had the appearance of a testis, irregularly shaped, and bearing along its outer border a broad raised crest of jet-black pigment. The gonad measured $11 \times 8 \times 6$ mm., and was scarred with deep grooves. The pigment at some points was flatly applied to the surface of the gonad, whilst at others it was piled up into rounded nodules resembling abnormal ovarian tissue. The left gonad, $13 \times 8 \times 7$ mm., and very similar in appearance to its fellow of the opposite side, was divided by deep constrictions upon its surfaces into three lobes, of which the anterior and middle had the appearance of testis with abnormal pigment along the outer border, while the posterior was entirely pigmented and looked like abnormal ovary (Fig. 11).

Vasa efferentia were present on either side. Pigmented seminal vesicles of average size were to be seen. The Müllerian ducts were well developed with empty but pigmented uterine segments. Four openings into the cloaca. The *m. rectus abdominis* and *humeri* were of the male type. On section, the right gonad consisted of ordinary spermatatic tissue, in all parts save these including the pigmented areas, which consisted of densely packed polygonal masses of pigment, hyperplastic connective tissue, and many ova, all of which showed signs of much degeneration (Fig. 12). This ovarian tissue was everywhere discrete from the testis portion of the gonad, but the line of junction between the two was very irregular so that the pigment of the ovary-portion seemed to invade the spermatatic tissues along the lines of the intertubular connective tissue.

The left gonad consisted of three lobes. The anterior and middle were similar in structure to the right gonad, but the posterior consisted entirely of ovarian tissues. In this there were but few ova, and all of them degenerate amid the dense masses of pigment. The substance of this lobe was continuous with the pigmented crest upon the outer border of the other two lobes of the gonad.

There was ciliated epithelium upon the peritoneum of the suspensory ligament of the gonads. The pituitary, though much smaller than usual, was normal in structure and the suprarenals were unremarkable.

CASE No. V.

Rana esculenta. Adult, measuring 8 cm. from the *symphysis menti* to the *symphysis pubis*. Killed November.

External characters.—External vocal sacs extruded in death. Forelimbs massive. Finger-pads well defined and lightly pigmented. Skin of the back and flanks not warty (Fig. 13).

On inspection, right gonad had the appearance of an unusually large, irregularly shaped testis which bore along its twisted outer border a discontinuous band of jet-black pigment which lay in deep uneven grooves. The gonad measured $16 \times 10 \times 8$ mm., and the pigment at some points was piled up into rounded nodules resembling pathological ovarian tissue. At the extreme posterior pole of the gonad was a small projecting spherical lobule of spermatic substance, separated from the main-body of the gonad by a deep constriction.

The left gonad, measuring $11 \times 6 \times 5$ mm., had the form of six rounded lobules. One of these, whitish in colour, stood out in vivid contrast to the others, and was placed upon the inner border of the gonad with the other five lobules arranged anteriorly, externally, and posteriorly in relation to it. The one was obviously normal testis-substance, while the others, irregularly rounded and intensely pigmented, closely resembled abnormal ovarian tissue.

Vasa efferentia on the right side were as those of the ordinary male. On the left side there were but four. Seminal vesicles, small and spindle-shaped. Müllerian ducts, well developed with uterine segments of moderate size. Four openings into the cloaca.

On section. In the right gonad, all parts save those including pigment had the structure of normal testis. The pigmented parts consisted of closely-packed polygonal masses of pigment and fibrous tissue only. No ova were found amid the pigment, but near to it were found, between the seminal tubules, two ova. The pigment was discrete from the seminal tubules but the line of junction between them was very irregular, and the inspection of single sections gave the impression that this typical ovarian tissue was invading the spermatic tissues along the lines of the intertubular connective tissue (Fig. 14). The seminal tubules in the neighbourhood of the pigment were imperfect in form. In the figure one of the ova is clearly seen to lie between and not within the seminal tubules.

Left gonad. The five black lobules had the structure of pathological ovarian tissue, consisting of polygonal masses of pigment, hyperplastic connective tissue, and amid these, a few very degenerate ova. The sixth

lobule had the structure of normal functional testis, and was quite discrete from the rest (Fig. 15).

Pigment similar to that of the ovarian tissues was found within the kidney of each side. Pituitary and suprarenals normal in size and structure. Ciliated epithelium upon the peritoneum. Rut-muscle and bones of the fore-limbs as those of a normal male.

CASE NO. VI.

HUXLEY (2), (Fig. 16).—*Rana temporaria*. Adult, measuring 7.6 cm. from the *symphysis menti* to the *symphysis pubis*. Killed October.

Non-pigmented finger-pads well defined; fore-limbs massive; rut-muscle developed as in the male; *humeri* of the male pattern; skin of the back and flanks not warty.

The right gonad was an irregularly shaped testis measuring $11 \times 9 \times 5$ mm., with uneven outlines and a scarred surface.

The left gonad, measuring $10 \times 5 \times 5$ mm., consisted of two sorts of tissue. The bulk of the gland was composed of testicular substance, the surface of which was divided into three unequal lobules by deep transverse grooves. The posterior lobule turned abruptly towards the dorsal body-wall. Along the outer border of this testis-portion of the gonad was a prominent crest of jet-black nodules of pathological ovarian tissue. The gonad was much deformed and twisted upon itself.

Vasa efferentia of the usual male arrangement were present on both sides in connection with the inner borders of the gonads. Seminal vesicles were present, being small, fusiform, and non-pigmented; the left one slightly better developed than the right. The right Müllerian duct was only weakly developed, but was convoluted and had a well-defined and pigmented uterine segment. The left duct was well developed. No ova could be seen within these ducts. The uterine segments and seminal vesicles were bound together, and there were four openings into the cloaca.

On section, the right gonad (Fig. 17) had the structure of ordinary spermatic tissue save that six ova were found, two actually within seminal tubules and the others between the tubules, at different points. At two other points localised masses of pigment, identical microscopically with that of the normal ovary, were found between seminal tubules. The ova differed in character, some being quite normal, others being distinctly degenerate in appearance. The presence of an ovum within a seminal tubule was associated with deformity and degeneration of the compressed spermatozoa.

The left gonad consisted of an inner normal testis-portion and an outer pathological ovarian portion. Ovary- and testis-portions were quite discrete; no ova or pigment were present amid the spermatic tissues; and the ovarian tissues contained exceedingly few ova and all these were degenerate. The greater part of the ovary-portion was composed of polygonal masses of pigment and hyperplastic connective tissue. The cavities of the lobulated ovary were obliterated by this pigment, but the divisions of the lobules were still distinct (Fig. 18).

The Müllerian ducts had a central lumen, but neither they nor their uterine segments contained any ova, and their glandular portions were inactive. No spermatozoa were present within the seminal tubules. There were ciliated cells upon the peritoneum, and there was nothing to note concerning the pituitary.

CASE NO. VII.

Rana temporaria. Adult, measuring 7.2 cm. from the *symphysis menti* to the *symphysis pubis*. Killed May.

External characters.—Fore-limbs massive. Finger-pads as those of the normal male at other times than during the breeding season—well defined but unpigmented. Skin of back and flanks not warty (Fig. 19).

On inspection, right gonad had the appearance of a normal testis save that at one point upon its outer border there was a pit with swollen lips and with a patch of jet black pigment at the bottom.

The left gonad was somewhat smaller in size, measuring $12 \times 5 \times 4$ mm., and had the appearance of an irregularly-shaped testis which bore a nodular crest of pigment along its outer border. This crest in its anterior half consisted of four rounded raised nodules, but in its posterior half the pigment was applied flatly to the surface of the testis. At the junction of the middle and posterior thirds of the gonad a deep constriction encircled its body.

Vasa efferentia as those of the ordinary male. Seminal vesicles well defined. Müllerian ducts moderately well developed with well-defined uterine segments heavily streaked with pigment (chromatophores). Four openings into the cloaca. Rut-muscle and bones of the fore-limb as those of the typical male.

On section. In the right gonad, all parts not involving pigment had the structure of normal functional testis. The pigmented area consisted of densely-packed polygonal masses of pigment, which included a circumscribed mass of granular debris. No ova and nothing resembling ova were found (Fig. 20). The pigment was everywhere without the seminal tubules, but

the line of junction between this typically ovarian pigment and the normal spermatic tissues was very irregular.

Left gonad. Structure as that of the gonad of the opposite side save that degenerate ova were found amid the pigment (Fig. 21).

Pituitary and suprarenals normal in size and structure. Ciliated epithelium upon the suspensory ligaments of the gonads.

GENERAL DISCUSSION.

It is convenient to discuss the abnormalities as they affect the primary and the secondary sexual characters.

I.—PRIMARY SEXUAL CHARACTERS.

A. *The primary sex-glands or gonads.*

In all seven cases both ovarian and spermatic tissue were present in the gonads. The relative amounts of the two varied. In Cases Nos. I. and II., ovarian tissue constituted the whole of one gonad and the greater part of the other: in Cases Nos. IV., V., VI. and VII., spermatic tissue preponderated in both gonads.

In every case without exception, the spermatic tissues were healthy and of normal appearance, whereas the ovarian tissues exhibited some degree of degenerative change.

With the possible exception of Case No. I., in which the exact position of the spermatic tissue is not definitely known, in every gonad in which both tissues were obviously present, the spermatic was situated upon the inner border of the gonad, or in these cases in which the spermatic tissues formed the greater part of the gonad, then the ovarian tissues were placed upon the outer border of what appeared to be an abnormal testis. This is the position in which the *vasa efferentia* could effect a connection between testis and kidney most readily.

Apparent increase in the amount of the normal pigment of the ovary was invariably associated with the presence of pathological changes in the ovarian tissues. In one gonad of Case No. VII. all that remained of the ovarian tissues was the pigment.

The proof that this abnormal pigment is ovarian can be supplied by microscopical examination. Upon the animal pole of a mature ovum, the essential product of the female, are polygonal masses of pigment, of constant shape and intrinsic origin (Fig. 21). Upon the peritoneal investment of a pigmented testis are branched chromatophores, pigment cells of characteristically elongated shape, which, lying in the superficial grooves, outline the

seminal tubules upon the surface of the testis. If this peritoneal coat of the testis is stripped off, all the pigment can be removed with it (Fig. 22).

In the case of the gonad of frog No. VII., as in all others, the abnormal pigment upon the outer border of the testis (or amid the spermatic tissues) consisted of polygonal masses of pigment exactly similar to those of the animal pole of the normal ovum (Fig. 23). This pigment is not found upon the peritoneal coat of the gonad but within it, and it is ovarian and not spermatic in origin. The presence of this alone is sufficient to indicate that other ovarian tissues are, or have been, present in the gonad. The increase in pigmentation is relative, and is due to the fact that when the ovarian tissues are undergoing degeneration and consequent absorption, or extrusion, the pigment, being one of the most resistant of the ovarian tissues, remains after the other more delicate tissues have disappeared. There is no reason to assume that degeneration is associated with an actual increase in the amount of pigment therefore, and if the pigment present in certain gonads of these cases were spread over an ovary of ordinary size, the colour of the gonad would not be remarkable.

Overgrowth of the connective tissue, on the other hand, is an actual feature of degeneration, and this was more or less pronounced in every case. There was no correlation between the amount of spermatic tissue present in the gonads and the degree of degeneration in the ovarian. Quite a small amount in Cases Nos. I. and II. was associated with appreciable degeneration in the ovarian tissues of both gonads. In these cases also it is to be noted that not only was the ovarian tissue of the gonad in which spermatic tissue was also present undergoing degenerative changes, but also that the ovary of the opposite side was similarly affected, though to a less extent.

The graded conditions found in these cases demonstrated that exceptionally both ovarian and spermatic tissues can become expressed in one and the same gonad of the frog, and suggest that the expression of the spermatic may not occur until the ovarian have attained functional maturity. Also it is seen that if the expression of the spermatic tissues is responsible for the coincident degeneration of the ovarian tissues, then the agent must be blood-borne as those of the gonad of the opposite side are equally affected. Such action could be explained in terms of the hormone theory, assuming, contrary to the conclusions of Lillie concerning the free-martin,¹ that there is a conflict of hormones in the case of the frog, that of the testis being far more powerful than that of the ovary.

The cases are so arranged as to suggest that the conditions found in the

¹ *Journal of Experimental Zoology*, vol. xxiii. p. 371.

gonads are grades of a single process. Synchronously, or in succession, upon the inner border of one or both gonads which previously had presented characters entirely ovarian and which, in some cases evidently, had attained functional maturity, one or more nodules of spermatic material made their appearance. Very shortly following the expression of the spermatic tissue, the ovarian tissues of both gonads began to degenerate and to become removed, whilst their further production became inhibited, whereas the spermatic progressively increased in amount and functional powers. Soon the gonads are as the right gonad in Fig. 7, and then as those in Fig. 11, irregular in shape, partly ovarian and partly spermatic, having the appearance of abnormal testes bearing pigment along the outer border. The irregularity of shape and the surface scarring result from the interference with the even growth of the active spermatic tissues which follows from the presence of what must be considered as foreign bodies, the pigment and fibrous tissues of the degenerating ovary. Then the gonad will become as the right one in Figs. 16 and 19, a normal testis, save that a small quantity of polygonal masses of pigment and slight scarring still remain upon the outer border. But scars heal and foreign matter is ultimately removed, and later the gonad will assume the form of a normal testis. A gonad which previously had every character of a perfect ovary, has thus become replaced by a perfect testis.

An ovum is seen lying amid the spermatic tissues between the seminal tubules, in Fig. 14, and within a tubule in Figs. 3 and 17. The tubules in the neighbourhood are contorted. In the case of the juvenile testis of the frog, the origin of the large cells closely resembling ova, which are sometimes found therein, may be a debatable question, but there is no doubt as to the origin of the ova as seen in this case. There is no reason to suggest that such cells have been produced by the spermatic tissues, for it is seen that the surface of the degenerating ovarian tissues are in intimate contact with the actively growing testis-portion of such a gonad, so that an ovum, a product of the ovary-portion, becoming extruded from the surface thereof, may readily become surrounded and included by enveloping spermatic tissue, and there remain among the connective tissue, between the seminal tubules, or actually within a seminal tubule, secure from the action of whatever is responsible for the rapid degeneration of the ovarian tissue generally (Figs. 6 and 8a). Such ova, therefore, may become the sole remains of ovarian tissues in a gonad which in every other respect is a perfect testis. Ultimately these ova must become resorbed, and the gonad thus becomes a perfectly normal testis. The pigment in Figs. 20 and 21 is a similar inclusion.

B. The Accessory Sexual Apparatus.

It is seen that wherever obvious spermatic tissue is present in a gonad *vasa efferentia* connect it with the adjacent kidney. In case No. 11, three of the efferent ducts of the gonad were traced into the ovary also. It would seem as though these had been developed in anticipation of the transformation of this into a testis. In these cases there is some evidence that the development of these ducts is consequent upon the expression of spermatic tissue in the gonad, and since the foundation material, out of which they are developed, is commonly possessed by both sexes, there is nothing remarkable in their adaptation in response to the demand which arises when spermatic tissue is developed later than is usual. Their number and complexity of pattern is normally subject to considerable variation, but roughly in these cases they are proportionate to the amount of spermatic tissue present in the gonad. Seminal vesicles were present in every case, smaller than those of the average male of the same species and at the same time of the year in the cases in which most of the genital tissue was ovarian, and equal in every way to those of the typical male, in the others, in which a considerable amount of spermatic tissue was present in the gonads of the individual. There is a suggestion, therefore, that the development of these male organs is proportionate to the amount and functional activity of the spermatic tissue in the gonads of the individual. The fact that the two vesicles are generally equally developed supports the conception that the blood-borne internal secretion of the testes may supply the stimulus which evokes their growth.

The degree of development of the Müllerian ducts varied. In those cases in which ovarian tissue constituted the bulk of the gonads, they were equal in every way to the functional oviducts of the mature female. In those cases in which considerable amounts of ovarian tissue still remained in both gonads, though it exhibited evidence of severe degenerative change, the ducts were well developed on both sides of the body. In two cases in which one gonad was almost entirely testicular (Figs. 7 and 16), the Müllerian duct of that side was but weakly developed.

The conditions found suggest that the degree of development of these ducts is decided by two conditions:—

- (1) The time during the development of the individual at which the spermatic tissue first makes its appearance; and
- (2) The extent of the expression of the spermatic tissue, whether it appears in both gonads synchronously, or first in one and later in the other.

It would seem that if the appearance of the spermatic tissue is relatively late then, in the presence of ovarian tissue of considerable amount and functional capacity, these ducts attain the condition characteristic of the oviducts of the adult female. If spermatic tissue then becomes expressed and the ovarian tissues removed in consequence, the Müllerian ducts, having overstepped the degree of development typical of the male, are not affected by the transformation of the gonads and do not atrophy though obviously useless. This is the case also with the ciliated epithelium found upon the peritoneum, for once developed it does not atrophy.

On the other hand, if the expression of the spermatic tissue is relatively early, it will occur before the Müllerian ducts have attained their full development in the presence of considerable amounts of functioning ovarian tissue, since the appearance of the spermatic tissue is associated with the cessation of the activities of the ovaries, for these degenerate almost at once, and the further development of the Müllerian ducts is thereby prohibited. The degree of development of these ducts is some indication, therefore, of the relative time when the transformation of the gonads began.

Further, the Müllerian ducts may be of unequal size. It would seem that the degree of development of a duct is determined, to some extent, by the degree of the functional activity of the ovary of the same side. For example, in Kent's case (Fig. 7), the conditions found suggest that the transformation first began in the left gonad and at a relatively early stage of sexual development. The left Müllerian duct is only feebly developed since the ovarian tissues were destroyed before they had attained any considerable degree of development. In the case of the right gonad, the appearance of the spermatic tissue was relatively later and did not occur in time to prevent the action of the ovarian internal secretion. The condition also suggests that in these cases in which the expression of the spermatic tissue is primarily unilateral, the destruction of the ovarian tissues of the opposite gonad is not so rapidly effected as that of those of the ovary-portion of an ovo-testis.

In Huxley's second case, the conditions are very similar (Fig. 16). In Cases Nos. I. and II., the expression of the spermatic tissue was primarily unilateral, and occurred at so late a stage in the development of the individual that the Müllerian ducts had already attained their full development. In Case No. IV., the expression of the spermatic tissue was very nearly synchronous in the two gonads, and occurred early; in Case No. VII., there was an interval between the appearance of the spermatic tissue in the two gonads, but in both it appeared before the Müllerian ducts had

attained their full development. In Case No. V., the interval was greater, but the expression of the spermatic tissue in both gonads was relatively late, for the Müllerian ducts are equal in every way to the oviducts of the adult female.

Since the Müllerian ducts do not atrophy after they have attained a considerable size, even when the ovarian tissues have become completely replaced by spermatic, the presence of these ducts, of a female pattern, in an otherwise perfectly normal male, is a certain indication that the gonads at one phase of their development contained functioning ovarian tissue, and that the individual is a male whose sexual development has been indirect, inasmuch as there has been a phase in its life-history during which, to all appearances, it was a female.

II.—SECONDARY SEXUAL CHARACTERS.

In the first case these were entirely female in type; in the second they were male but imperfectly developed; in the rest they were typically male, with one female character—the ciliated epithelium upon the peritoneum—in addition. In the first two cases, ovarian tissue constituted the bulk of the gonads, and this tissue, though degenerating, was sufficiently healthy to produce functional ova. In the rest spermatic tissue formed the greater part of the gonads, and such ovarian tissue as was present was pathological. In all cases, the spermatic tissue in the gonads was healthy and vigorously functional. The nature of the secondary sexual characters would seem to be determined, therefore, by the constitution of the gonads. Associated with functional ovarian tissue in the gonads are secondary sexual characters of the female pattern, and in conjunction with the presence of functional spermatic tissue in the gonads male secondary sexual characters are found. The expression of spermatic tissue in gonads which previously had the structure of ovary is associated with the assumption of male secondary sexual characters on the part of an individual which hitherto had shown secondary sexual characters of the female form. But as these characters of the female are mainly of a negative order, the imposition of the male characters cannot be regarded as difficult, for they are for the most part nothing more than the results of a greater degree of development locally of structures commonly possessed by both sexes.

The ciliated epithelium upon the peritoneum once developed remains; it does not interfere with the assumption of the male secondary sexual characters. The wartiness of the skin of the back and flanks is a seasonal development in the functioning female at the time of the breeding-season,

and is associated with the great activity of the ovaries at this time. In those cases in which the ovarian tissue was not actively functioning or capable of functioning, the wartiness was not developed. There is a suggestion here, therefore, that this peculiarly female secondary sexual character is expressed in response to the stimulus provided by the ovaries in a certain state of physiological activity.

Case No. I. could function and behave as a female; No. II. could function as a female possibly, but it is reasonable to wonder if a rutting male would have recognised this individual as a female, since the secondary sexual characters were of the male pattern. On the other hand, this individual could function as a male, yet it is questionable if it was sufficiently male to behave as one. The finger-pads are developed in anticipation of the nuptial embrace.

The others were equipped in such a way that they must have functioned and also have behaved as males, although in their gonads various amounts of pathological ovarian tissues still remained.

The question naturally arises as to whether these individuals are chromosomally females which become converted into males, or chromosomally males with an initial deficiency of the male-determining substance. The existence of sex-chromosomes has not yet been demonstrated in frogs, but it may be assumed that in these, as in other animals, sex-determination is effected by such a mechanism. Further, it is reasonable to assume, as Huxley points out,¹ that the frog is of the ♀ XX, ♂ XY type. This being the case, then these individuals, XX in composition, instead of developing into normal females, became transformed into "somatic" males by the action of some factor or combination of factors which over-rides the chromosome constitution. They have the chromosome constitution of the female sex, but the actual organisation of the male. The mating of such individuals, functioning as males, must disturb the sex-ratio of the next generation, and this fact may explain the unusual sex-ratios recorded by many authorities.

¹ *Journal of Genetics*, vol. x., No. 4, Dec. 1920.

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PLATE XX.

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FIG. 1.



FIG. 1a.

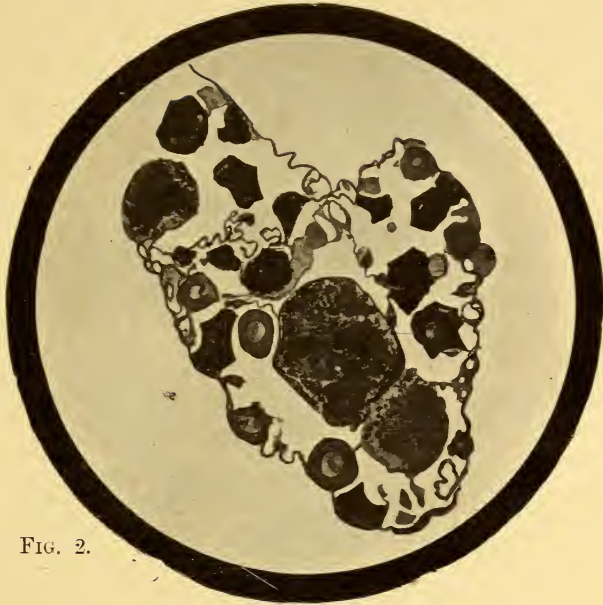


FIG. 2.

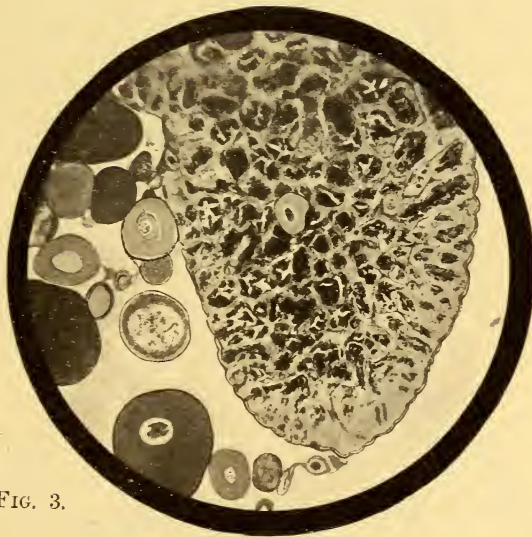


FIG. 3.



FIG. 3a.



FIG. 4.

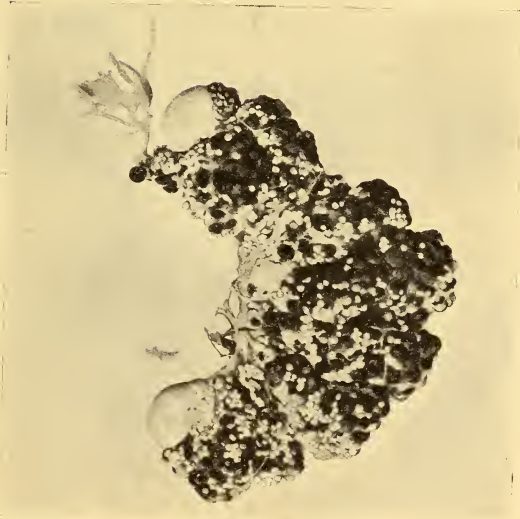


FIG. 5.



FIG. 6.

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FIG. 7.

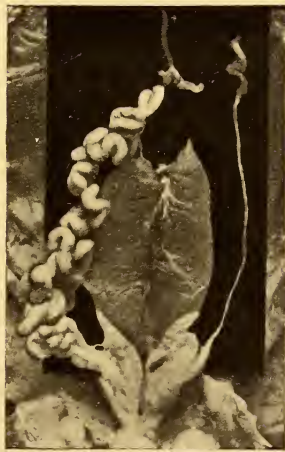


FIG. 7a.

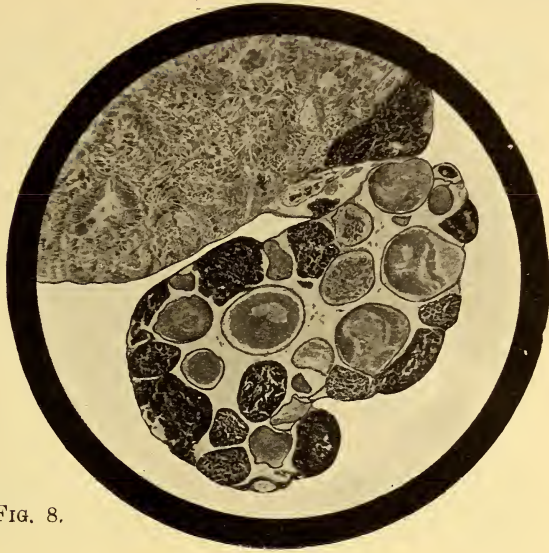


FIG. 8.



FIG. 8a.

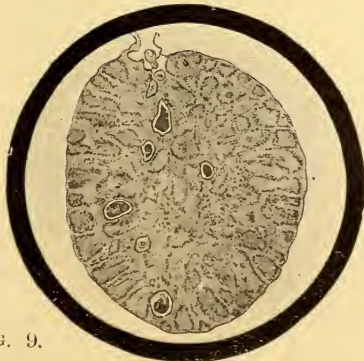


FIG. 9.



FIG. 10.

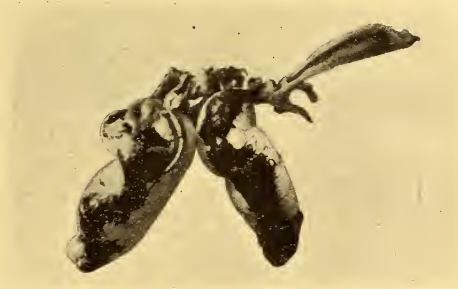


FIG. 11.



FIG. 12.

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FIG. 13.

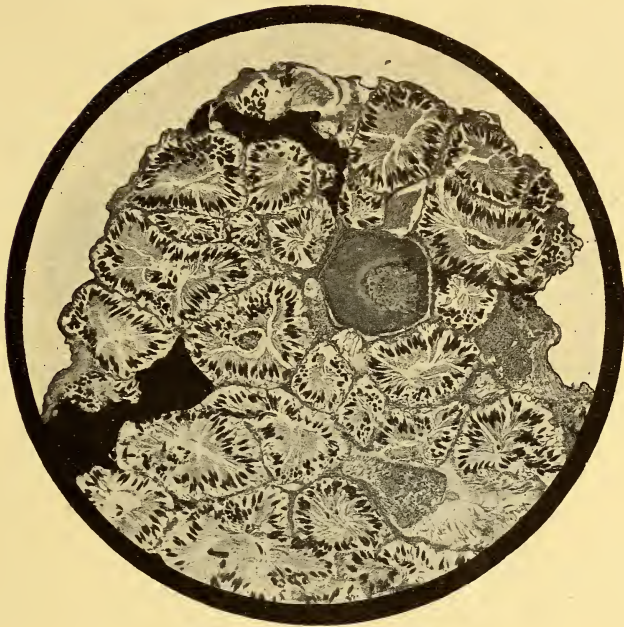


FIG. 14.



FIG. 15.

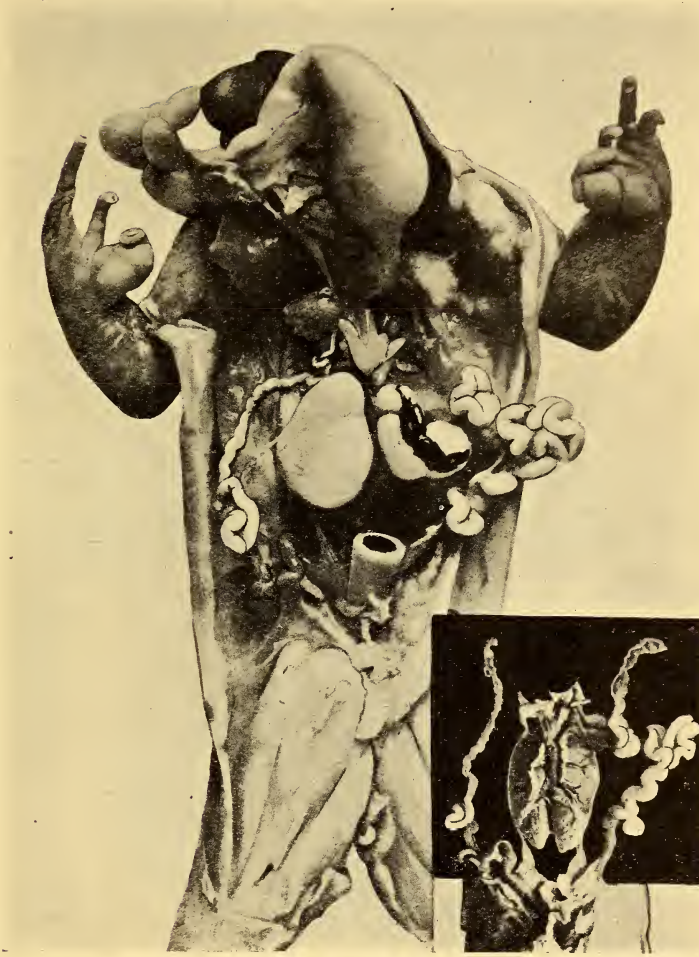


FIG. 16.

FIG. 16a.



FIG. 17.

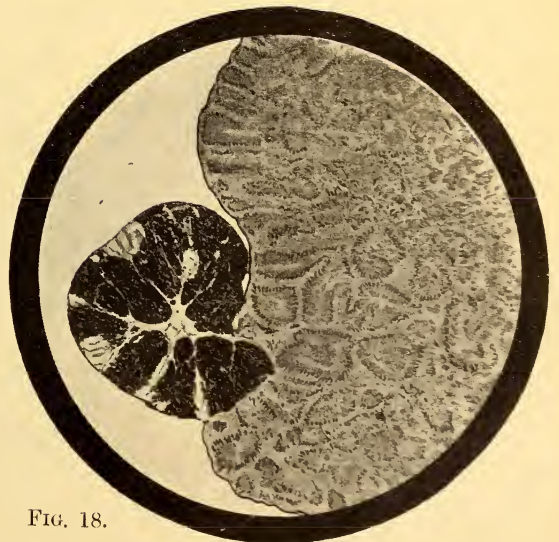


FIG. 18.



FIG. 19.

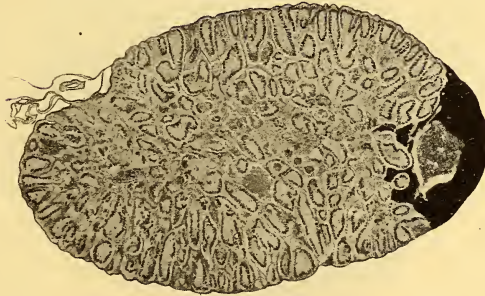


FIG. 20.



FIG. 21.

PLATE XXX.

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FIG. 22.

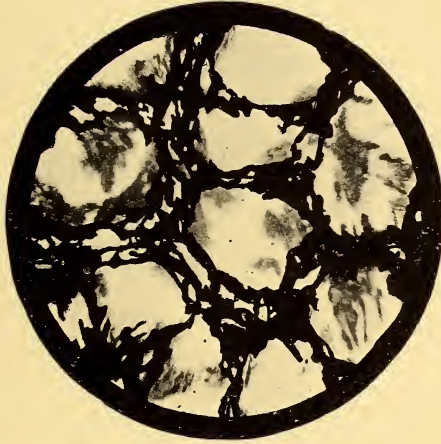


FIG. 23.



FIG. 24.

XXIII. An Early Embryo of *Myrmecophaga jubata*. By Sheina M. Marshall, B.Sc., Carnegie Scholar of the University of Glasgow. (Communicated by Prof. Graham Kerr.)

(With Plate and Text-figures.)

(Read 22nd November 1920. Received 27th November 1920.)

THE object of this communication is to publish, with short notes, a figure of an early embryo of *Myrmecophaga*, obtained by Professor W. E. Agar in the course of his expedition to the Gran Chaco in 1907-1908.

On the 16th November 1907, a male *M. jubata* was found by the Indians in the forest, and driven into the Mission Station in the Paraguayan Chaco about fifty miles due west of Villa Concepcion, and was shot in the station. Two days later a female, obviously the mate of the male, was found in the same way, and proved to be pregnant. It was accompanied by a young one, which is in accordance with the statements that the young accompanies the mother till she again becomes pregnant.

The foetus and placenta were preserved in corrosive acetic. This specimen was drawn by Mr Kirkpatrick Maxwell (Plate XXXI.), and was then cut into three parts, the middle portion of which contained the embryo. It was stained in bulk with borax carmine, and was sectioned in a plane approximately transverse to the head region.

We are practically ignorant of the embryology of that heterogeneous set of mammals known as the Edentata, except as regards the Armadilloes and the Manidæ. No published data regarding the early development of any of the Myrmecophagidæ have been found, consequently any details regarding an early embryo of *Myrmecophaga* are of special interest and importance, even when they happen to be such as we should expect from our knowledge of the development of other mammals.

G. Pouchet (*Mémoires sur le Grand Fourmilier*, Paris, 1874), publishes a description and figure of an embryo at a much later stage, when most of the adult features are already present. The internal organs, apart from the brain and salivary glands, are not described.

The general appearance of the present specimen (Plate XXXI.) may be said to be that of a typical eutherian embryo. It is very like a human embryo at the beginning of the second month. G. Phisalix (*Archives de Zoologie expérimentale et générale*, ser. 2, t. vi., 1888) dates at thirty-two days a human embryo 10 mm. long cut in the same plane, in which he describes structures

identical in many respects with those seen in this early embryo of *Myrmecophaga jubata*. There is, for instance, a well-marked asymmetry of the pharynx in both cases.

The placenta¹ is almost circular, and the false amnion² has been cut away so as to expose the true amnion containing the embryo. The head and neck bend is almost right-angled, and the hind part of the body slopes away at an obtuse angle to the back. The umbilical cord and tail extend up on the right side of the head. The limb rudiments are distinct, the fore limb rudiment being divided into a narrower proximal and a wider distal portion, whereas the hind limbs are undifferentiated.

Myotomes are visible from a point slightly tailwards of the fore limbs.

There is no trace of the cerebral hemispheres apart from a slight notching of the wall of the fore brain, but the mid brain is indicated and the thin roof of the medulla oblongata is clearly visible. The rudiment of the eye and three visceral arches can be made out.

The embryo is completely enclosed in the amnion. On the right hand side there is seen a whitish projection lying inside the amnion, close to the embryo. This bears a superficial resemblance to the yolk sac, but on examination of the sections it is seen to be only a proliferation of the cells of the amniotic wall. It springs from the point where the amnion leaves the umbilical cord, and is in the form of a large irregular sac which has no definite lining epithelium. The cavity does not extend into the amniotic wall and contains small masses of proliferating cells, as well as some coagulum.

The question as to whether this is a normal feature of the development of *M. jubata*, and, if so, what its morphological nature is, can only be decided when further material of the early stages become available.

The ventral wall of the alimentary canal is completely closed (except for the point of entrance of the allantois) and there is no trace of a yolk sac or yolk stalk.

The sections of the embryo are cut at $20\ \mu$ and most of the following work was done by means of reconstructions by the glass plate method.

The notochord is small in cross-section, and its anterior end is hook-shaped and lies just behind the pituitary diverticulum from the buccal

¹ I understand that the investigation of the minute structure of the placenta was entrusted by Professor Agar to another worker, but in any case the attempt to interpret minute details without access to the earlier stages of development involves so much risk of error that it seems advisable to postpone it for the present.

² I agree with those embryologists who think that the term "chorion," in spite of the archaeological interest that attaches to its having come down from the ancient Greeks, should be dropped from use owing to its having lost all precision of meaning.

cavity. It reaches almost to the tip of the tail, and is clearly marked off at its hind end from both the spinal cord and post-anal gut. The spinal cord ends blindly and has a wide cavity throughout its length. The spinal nerves have both dorsal and ventral roots, and can easily be traced in a ventral direction to the level of the dorsal aorta. The spinal ganglia are recognisable almost to the tip of the tail.

The medulla oblongata is large, with no trace of a cerebellum in front. Some of the cranial nerves are recognisable, namely, VII, VIII, IX and X with numerous roots.

The otocyst is narrow from side to side and is slightly concave towards the brain. It has a wide blunt projection ventrally, and a long slender tube—the ductus endolymphaticus—with a dilatation at its root, passes forwards and upwards. It has no connection with the skin.

The lentic vesicle is completely closed, and its walls are still equally thick all round. The retinal layer of the optic cup is much thicker than the other but there is no trace of retinal pigment. The choroid fissure is distinct, and the optic stalk has a wide cavity open to the brain.

The infundibular evagination is short and curved, and in the hollow between it and the brain lies the pituitary body, which is open to the buccal cavity by a narrow tube.

The olfactory organs are short pockets open to the exterior in the neighbourhood of the mouth. They have no connection with the buccal cavity at their inner end. A shallow groove on the inner side indicates the beginning of Jacobson's organ.

The pharynx in the region of the gill clefts is distinctly asymmetrical, the left side being further advanced in development. A slit extends backwards from the corner of the mouth on the left side for a considerable distance. It closely resembles a gill cleft at its lower end.

The first two gill clefts are open on each side and the third gill pouches are formed, though they do not yet reach the exterior. That on the right is very small. There is a slight invagination of the ectoderm in the position of the future cleft on the left side, which lies close to the opening of the second cleft. It is curious that Phisalix's human embryo also shows a slit from the mouth on the left and an asymmetry of the gill pouches in which the left side is further developed.

A small unbranched diverticulum near the mid ventral line at the level of the third gill pouch may represent the thyroid.

On the left, below the second gill cleft, the ectoderm comes into close relation with one of the ganglia of the vagus, forming an organ of Froriep.

The trachea bifurcates into right and left bronchi and each of these has several secondary pockets. The right lung is slightly larger than the left as is the case in the adult, according to Pouchet.

The oesophagus is continued into the stomach, a dilatation of the tube, and the gut then runs straight from stomach to anus, except for a loop into the umbilical coelome. It opens into the cloaca which is still separated from the exterior by a plug of tissue. The post-anal gut extends almost to the tip of the tail and there ends blindly.

The liver is very large and consists of a network of cells, the interspaces being filled with blood. Just before the bile duct enters the intestine, it gives off a long glandular pocket with one large duct and several small acini. In the adult, according to Pouchet, the gall bladder is embedded in the pancreas. The glandular mass round the main lumen is probably pancreatic. There is no sign of any other pancreatic rudiment.

There is a well-defined mesonephros present extending from about the level of the fore limbs to that of the hind limbs. The tubules have lost their segmental character and are crowded together, two approximately corresponding to each spinal ganglion. The tubules lie close to the posterior cardinal vein, have a typical S-shape, and open into the Wolffian duct. At the headward end the structure of the tubules is simpler and they are more crowded together. On the right hand side there is an isolated simple tubule in front of the end of the Wolffian duct. This perhaps indicates a shifting back of the kidney in accordance with its ultimate position. The beginning of the ureter on each side is just recognisable as a swelling on the Wolffian duct before it enters the widely expanded cloaca. From this there extends forward a mass of condensed tissue. There are no secondary tubules present.

The allantois is much expanded before its entrance into the cloaca but thins out before leaving the body wall. Its cavity, enclosed in a wall containing a network of small blood-vessels, extends for some distance down the umbilical cord but does not reach the placenta. The blood-vessels, apart from the main allantoic arteries which pass onwards to the placenta, die out at the same level.

The genital ridge is present as a slight thickening of the coelomic epithelium below the mesonephros. Farther tailwards this ridge is shifted in position, and comes to lie on the root of the mesentery.

The coelomic cavities are not yet completely separated off. The pleural cavities open widely into the peritoneal cavity. The left pleural cavity is connected with the pericardiac cavity by a narrow canal, while the right has a wide opening.

The apex of the heart (Fig. 1) is rotated ventrally, so that the longitudinal axis of the heart is almost at right angles to that of the body. The left duct of Cuvier is well formed and runs over the surface of the auricles. The right is a much shorter and wider vessel, receiving, as it enters the small sinus venosus, three large veins from the liver. These all enter the sinus venosus at the same level. Two of them form capillaries in the liver substance, while the third runs to the ventral side and receives the blood from a large vessel draining the gut and from the umbilical veins. The

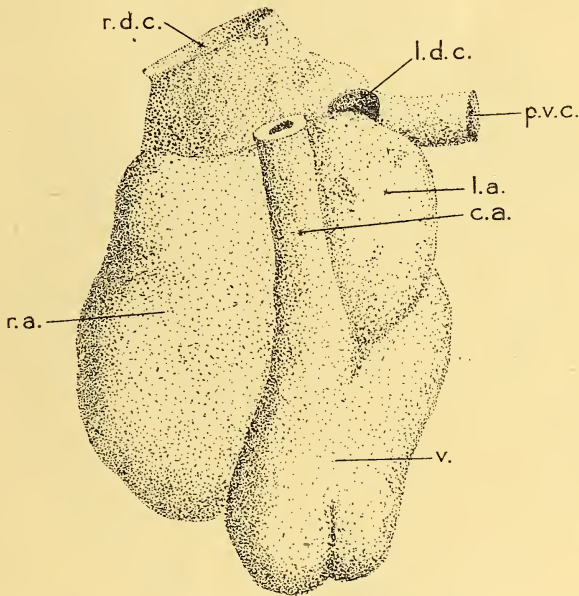


FIG. 1.—Heart of embryo of *M. jubata*, from the ventral side.

r.d.c., right duct of Cuvier ; *l.d.c.*, left duct of Cuvier ; *p.v.c.*, posterior vena cava ;
r.a., right auricle ; *l.a.*, left auricle ; *v.*, ventricle ; *c.a.*, conus arteriosus.

right umbilical vein is small and ends blindly in the body wall, while the left is large and is continued through the umbilical cord.

The right auricle, into which the sinus venosus opens, is much larger than the left and is separated from it by an incomplete septum. The right auriculo-ventricular valves are beginning to form. The auricles open freely into the ventricle whose cavity is as yet undivided. It has thick spongy walls. The future division is indicated by a longitudinal groove on the surface. The ventricle is twisted slightly so that the right half lies ventral to the left.

The conus arteriosus, with very thick walls, issues from the right side of the ventricle and runs forward into a short ventral aorta. It bends sharply

towards the head and gives off three aortic arches on each side (Fig. 2). These are the vessels supplying visceral arches II, III, and IV. There are traces of another vessel, that of the first arch in front of these. The vessels supplying the second visceral arch are slender, and are in process of disappearing. Those of the third visceral arch are larger. They, and those of the second arch, come out of the ventral aorta by a common stem. The right and left fourth aortic arches, the largest vessels, are united at their exit from the ventral aorta and run together for some distance in line with the proximal portion of the ventral aorta. The left vessel is larger than the right, foreshadowing its development into the definitive systemic aorta.

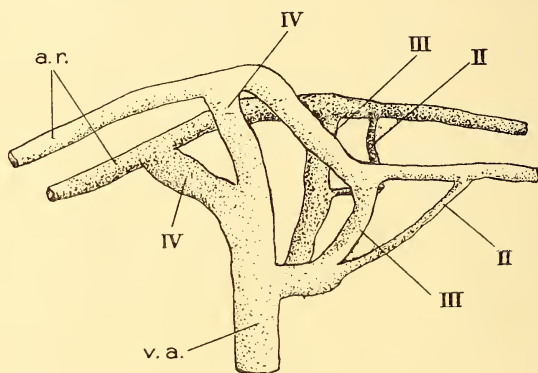


FIG. 2.—Aortic Arches: Diagrammatic drawing from reconstruction as seen from the right side.

a. r., aortic roots; *v. a.*, ventral aorta; *II, III, IV*, aortic arches.

The aortic roots unite about the level of the fore limbs and run back as the dorsal aorta, eventually dividing into two iliac arteries. Two umbilical arteries are present, one coming off the dorsal aorta on the left hand side, and the other off the right iliac. These run into the umbilical cord and unite in the placenta, eventually splitting up and joining a network of smaller vessels at the surface.

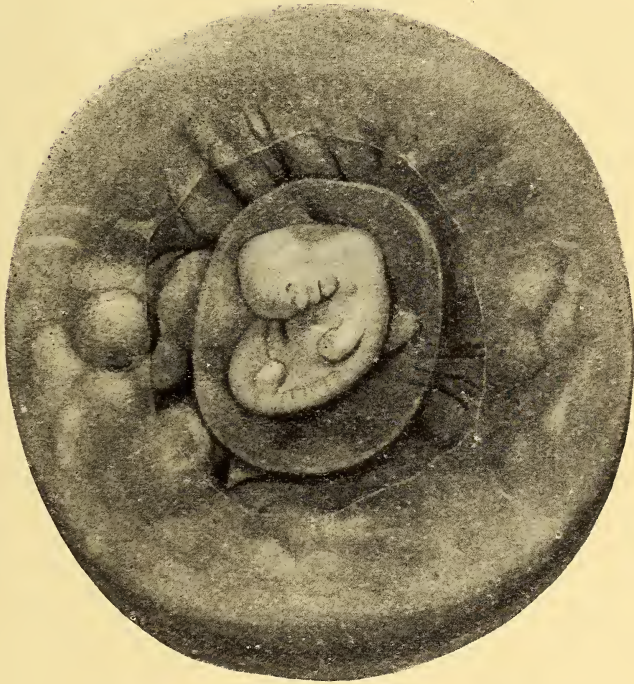
I am glad to take this opportunity of thanking Professor Agar for placing the material at my disposal, and for his help in working it out. To Professor Walmsley I am indebted for the use of his laboratory in Glasgow.

The work was carried out in the laboratory of Professor Graham Kerr, who very kindly assisted me and gave me every facility for work.

PLATE XXXI.

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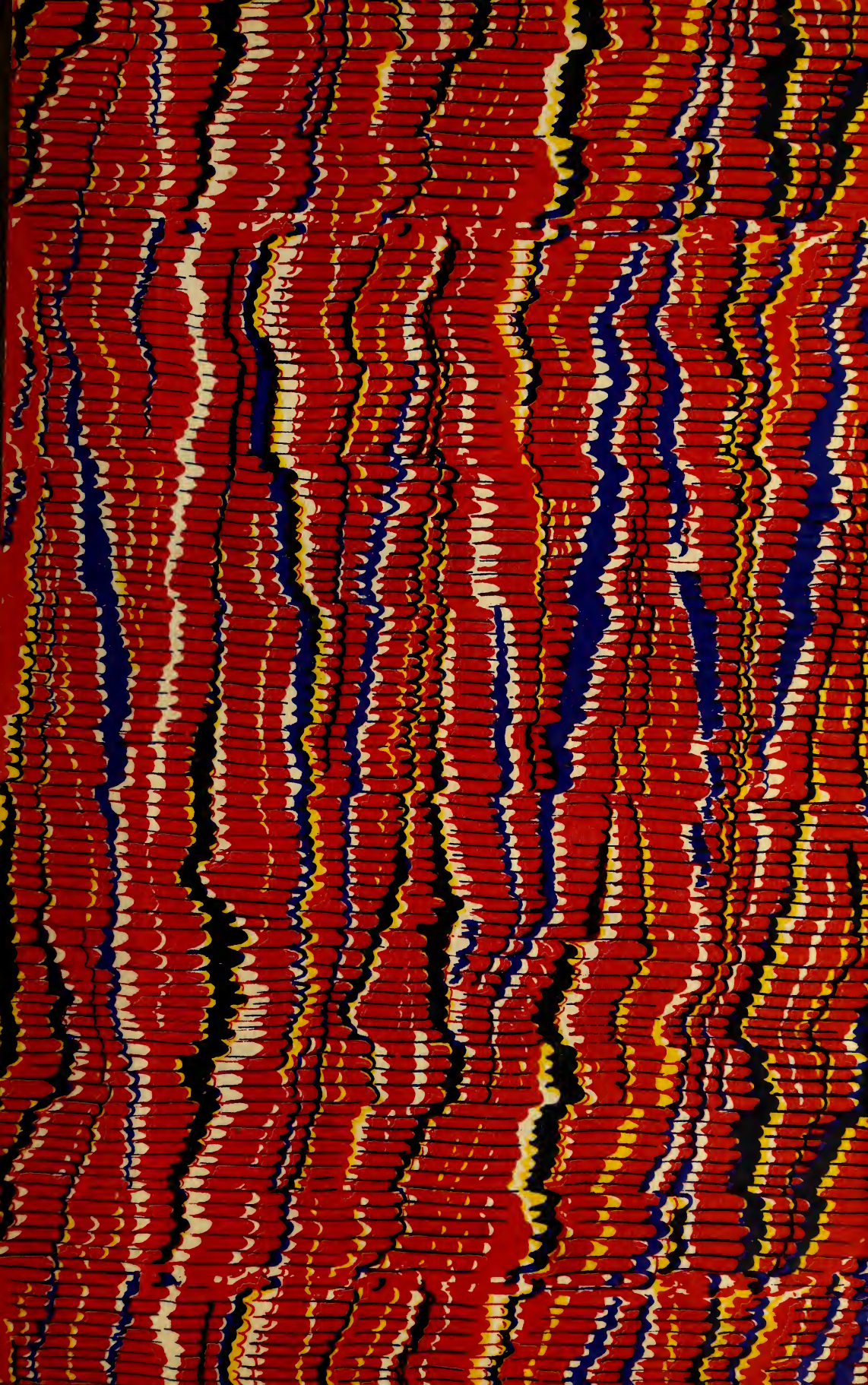
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EMBRYO OF MYRMECOPHAGA JUBATA $\times 2\frac{1}{2}$.

The embryo is seen lying on its right side, enclosed within the true amnion, and resting on the large disc-shaped placenta. A circular portion of the thin non-placental part of the blastocyst wall (false amnion) has been excised so as to display the embryo more clearly.





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