





Proceedings of the Linnean Society of New South Wales



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PART 1 (No. 410)

(Issued 3rd November, 1966)

(Presidential Address and Papers read March–April, 1966)

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(Papers read June-July, 1966)

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CORRIGENDUM

Page 110, line 37.—For *Vovotettix naracoortensis*, n.sp. read *Novotettix naracoortensis*, n.sp.

SYDNEY

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1967

ANNUAL GENERAL MEETING

30TH MARCH, 1966

The Ninety-first Annual General Meeting was held in the Society's Rooms, Science House, 157 Gloucester Street, Sydney, on Wednesday, 30th March, 1966, at 7.30 p.m.

Dr. D. T. Anderson, President, occupied the chair.

The minutes of the Ninetieth Annual General Meeting (31st March, 1965) were read and confirmed.

REPORT ON THE AFFAIRS OF THE SOCIETY FOR THE YEAR

The Society's Proceedings for 1965, Vol. 90, Parts 1 and 2, were published on 5th November, 1965, and 18th February, 1966, respectively. Part 3 has yet to be issued. The format of the Proceedings has been changed with Vol. 90 and there appears to be general agreement that the new, more modern style is a great improvement. All concerned with the alterations are to be congratulated on the result. The subscription price of the Proceedings is now \$11.40 per annum, including postage. A revision of prices for available Volumes and Parts of the Proceedings, postage included, has been made as follows:—1st Series (Vols. 1–10) (1875/6–1885), \$A16.40 per Volume; 2nd Series, Vol. 1 (Vol. 11) (1886) onwards, \$A11.40 per Volume; each Part, \$A5.15; \$A4.15 each for current numbers, and, for Volumes of five or six Parts, \$A1.15 each for the first and last Parts.

During the year 16 new members were admitted to the Society, three died, seven resigned and two were removed from the list of members. The numerical strength of the Society at 1st March, 1966, was: Ordinary Members, 270; Life Members, 32; Corresponding Member, 1; total, 303.

It is with regret that the deaths of the following members are recorded: Mr. G. H. H. Hardy, on 9th January, 1966; Miss Florence Sulman, M.B.E., on 15th June, 1965; and Dr. A. R. Woodhill, on 27th July, 1965. (See page 4 for obituary notices.)

Papers read at Ordinary Monthly Meetings totalled 26. Lecturettes were given at the following meetings: April, Some Aspects of Coastal Morphology in New South Wales, by Mr. J. R. Hails; June, Trace Fossils: their Classification and Palaeoecological Significance, by Dr. B. D. Webby; July, Ecology of *Ruppia* and *Zostera*, by Mr. R. Higginson; September, Opossums, by Dr. M. P. Marsh, and October, Some Problems of Evolutionary Theory, by Dr. Paul Ehrlich. Interesting discussions followed the lecturettes. We are grateful to these lecturers, who contributed greatly to the interest of the meetings. At other meetings notes and exhibits were presented. No meetings were held in May or August.

Dr. N. G. Stephenson, Mr. L. A. S. Johnson and Dr. Erik Shipp were elected members of Council in place of Professor B. J. Ralph, Professor W. L. Waterhouse and Professor I. A. Watson, who had resigned.

Two Special General Meetings were held to consider the recommendations from the Council that Rules V and VI be altered to read as follows:

Rule V.—No person declared elected under Rule IV shall be admitted to any of the privileges of membership until he has signed a written acceptance of membership and paid his first Annual Subscription.

Rule VI.—The Annual Subscription shall be three pounds ten shillings (seven dollars) and shall become due in advance on the first day of March in each year, or, in the case of New Members, immediately on election; provided that Ordinary Members elected after the first day of October in any year shall have the option of paying the Annual Subscription either for that year or in advance for the following year. Any Ordinary Member who has paid the Annual Subscription for forty years shall be exempt from payment of further subscriptions.

The recommendations were unanimously adopted on 29th September and confirmed on 27th October, 1965.

Library accessions from scientific institutions and societies on the exchange list amounted to 2,016 compared with 2,222 and 2,174 for the years 1964 and 1963 respectively. The total number of borrowings of books and periodicals from the library by members and institutions for the year was 253. Members and others continued to consult publications in the Society's rooms, and books and periodicals were made available for photographic copying. The following requests for exchange of publications were acceded to during the year: One copy of the Proceedings to the Institute of Botany and one to the Institute of Zoology, Academia Sinica, Nankang, Taipei, Taiwan, Republic of China, in return for their Botanical Bulletin and Zoological Bulletin respectively; Proceedings to the Central Library of the Academy of Science of Kazakh, Alma Ata, Kazakh, SSR., for the publications of the Botanical and Zoological Institutes; Reprints of geological papers to the All Union Geological Library, Leningrad, U.S.S.R.; Botanical reprints to the Academie des Sciences de Bulgarie, Sofia, Bulgaria, in return for its Bulletin of the Institute of Botany; and Botanical reprints, as a gift, to Estudos Gerais Universitarios de Mocambique, Laboratorio de Botanica, Lourenco Marques, Mocambique, as from 1965. The recently-formed Australian Society of Limnology sends its Newsletter to the Society's library. The Society now sends its Abstract of Proceedings and reprints of any papers required, instead of the Proceedings, to the Nasionale Museum, Bloemfontein, South Africa. The exchange of publications with the Universidad de Buenos Aires, Buenos Aires, Argentina, has been cancelled. The Lloyd Library and Museum, Cincinnati, U.S.A., was removed from the Society's exchange list owing to the publication "Lloydia" being no longer available by exchange as from 1966.

The total revenue accruing to the Society from its one-third ownership of Science House was \$2,244.18 for the year ending 31st August, 1965.

On 8th September, 1965, a lecture on Radio-carbon Dating in the Quaternary was delivered by Dr. Harry Godwin, Professor of Botany, University of Cambridge, under the joint auspices of this Society and the School of Biological Sciences, University of Sydney.

During the year the Society received as a gift from the Linnean Society of London a portrait of Linnaeus. This painting, copied from the Roslin portrait presented to the Linnean Society of London in 1814 by Joseph Sabine, one of the original Fellows of the Society, hung for many years in the meeting-room of the Society behind the President's chair. Further particulars of this portrait may be found in Proceedings Linnean Society, London, Session 118, 1905-1906: 68.

A conversazione, kindly arranged by Mr. Ronald Strahan, was held on the afternoon of Saturday, 18th September, 1965, in the Zoology Department, University of New South Wales, when material and apparatus were exhibited to an appreciative gathering by members of the Society and others engaged in scientific research.

A Conservation Photographic Exhibition arranged by the Society was put on show at the Australian Museum with the kind co-operation of the Director on 24th March, 1965. The photographs were subsequently shown in Tasmania and elsewhere and eventually presented to the Fauna Protection Panel.

The Council supported the nominations of Dr. R. C. Carolin and Professor J. LeGay Brereton of the University of New England, to fill two vacancies on the Fauna Protection Panel and these two gentlemen were appointed by the Chief Secretary.

During the year Council, finding an increasing number of matters involving Nature Conservation coming before it, appointed a Conservation Committee to consider and make recommendations concerning such matters. Already Council has made representations to the appropriate State Ministers regarding the

biological resources of the Clarence River valley in relation to flood-mitigation and water-conservation plans, the desirability of a Myall Lakes Reserve, and the appointment of an ecologist to fill a vacancy on the Kosciusko State Park Trust.

Linnean Macleay Fellowship

During the year Mr. A. J. T. Wright, B.Sc., the Linnean Macleay Fellow in Palaeontology, studied the Devonian sediments and faunas of the Mudgee district and the Capertee Valley area. A paper entitled "Ceriod Stringophyllidae (Tetracoralla) from Devonian strata in the Mudgee district, New South Wales" will appear in the Society's Proceedings, Vol. 90, 1965, Part 3. Owing to his appointment as Lecturer in Geology in Victoria University, Wellington, New Zealand, Mr. Wright did not seek reappointment. No appointment for 1966 was made.

Linnean Macleay Lectureship in Microbiology

Dr. Y. T. Tchan, Reader in Agricultural Microbiology and Linnean Macleay Lecturer in Microbiology, University of Sydney, reported on his work for the year ending 31st December, 1965, as follows: Progress has been made on the influence of higher concentration of acetate on the calcium requirement of *Azotobacter*. In collaboration with the Biochemical Department of the University of New South Wales the cytochemical studies of *Azotobacter* have been started, using strictly controlled cultural conditions. Advances have been made on the serological reaction of *Azotobacter*. It has been shown that antigenic properties of *Azotobacter* vary with ecological environment of the culture. On the study of herbicides, a new quick assay method has been designed and could be useful for field trials.

The Honorary Treasurer (Dr. A. B. Walkom) presented the balance sheets for the year ending 28th February, 1966, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A., and his motion that they be received and adopted was carried unanimously.

PRESIDENTIAL ADDRESS

The Comparative Early Embryology of the Oligochaeta, Hirudinea and Onychophora

On morphological and embryological grounds, the Onychophora (*Peripatus*) can be presumed to have evolved from a group of soft-bodied, metamericly segmented coelomates, usually referred to as lobopods. In terms of adult morphology, existing annelids do not fit the requirements of the hypothetical lobopod, and the possibility of including the ancestors of the Onychophora within the annelids has generally been rejected. A new comparison of onychophoran embryonic development with that of oligochaetes and leeches, however, reveals that onychophoran development can be interpreted as annelid development in a modified form. The extinct lobopods must therefore have had annelid-like embryos, which make it probable that they were paraphyletic with annelids. (For full text see pp. 10 *et seq.*)

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

President: R. C. Carolin, Ph.D., B.Sc., A.R.C.S.

Members of Council: D. T. Anderson, B.Sc., Ph.D.; R. C. Carolin, Ph.D., B.Sc., A.R.C.S.; L. A. S. Johnson, B.Sc.; E. Shipp, Ph.D.; N. G. Stephenson, M.Sc., Ph.D.; and A. B. Walkom, D.Sc.

Auditor: S. J. Rayment, F.C.A.

The President then installed Dr. R. C. Carolin as President.

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

OBITUARY NOTICES

GEORGE HUDDLESTON HURLSTONE HARDY

Mr. Hardy, who died on 9th January, 1966, had been a member of the Society since 1917. He was born in Twickenham, London on August 14th, 1882. He received an early training in the engineering profession, but soon developed an interest in entomology which remained with him all his life. He came to Perth, Western Australia, in 1911, remaining there for two years, and was then appointed to a position with the Tasmanian Museum, Hobart, which he held for five years. He arrived in Sydney in 1918 where he spent the following four years, and in 1922 was appointed Walter and Eliza Hall Fellow in Economic Biology at the University of Queensland. This position was held until 1932 and in 1949 he left Brisbane taking up residence at Katoomba, N.S.W. Due largely to his efforts the Entomological Society of Queensland was formed in 1924. He became its first Treasurer, holding this position for many years. Much of his scientific life time was devoted to the study of Diptera, and in all he published 144 papers on the biology and systematics of Australian Diptera. He contributed 40 papers to the Society's Proceedings between 1920 and 1959 and one (with T. H. Johnston) in 1923 entitled "A revision of the Australian Diptera belonging to the genus *Sarcophaga*". He also published papers in Papers and Proceedings of the Royal Society of Tasmania, Proceedings of the Royal Society of Queensland, Records of the Australian Museum, Australian Zoologist and Queensland Agricultural Journal, and in overseas journals including the Annals and Magazine of Natural History, Bulletin of Entomological Research, Stylops, Nature, Entomologist's Monthly Magazine and Proceedings of the Royal Entomological Society of London. Mr. Hardy took a keen interest in the Society during his stay in Sydney and Katoomba and attended meetings when possible. The sympathy of members of the Society is extended to his widow and married daughter. The following papers were published by him in addition to those given in the Bibliography of Australian Entomology, 1775-1930, by Anthony Musgrave:—

1931. Aphididae in Australia. *Proc. roy. Soc. Q'land*, 43: 31-36.
On genus *Damaromyia* Kertész. *Ann. Mag. nat. Hist.*, (10), 8: 120-128.
1932. Two new Australian species of *Pollenia*. *Proc. Linn. Soc. N.S.W.*, 57: 338-340.
Some new Australian Sarcophagid flies and notes on others. *Aust. Zool.*, 7: 275-281.
Australian flies of genus *Actina* (Stratiomyiidae). *Proc. roy. Soc. Q'land*, 43: 50-55.
Notes on Australian Stratiomyiidae. *ibid.* 44: 41-49.
Notes on *Sarcophaga peregrina*-group. *Bull. ent. Res.*, 23: 45-48.
Some Australian species of *Calliphora* (subgenera *Neopollenia* and *Proekon*). *ibid.* 23: 549-558.
1933. Miscellaneous notes on Australian Diptera. I. *Proc. Linn. Soc. N.S.W.*, 58: 408-420.
Notes on Australian Syrphinae. *Proc. roy. Soc. Q'land*, 45: 12-18.
1934. Miscellaneous notes on Australian Diptera. II. Empididae. *Proc. Linn. Soc. N.S.W.*, 59: 173-178.
Notes on Sarcophagid flies. *Aust. Zool.*, 8: 50-53.
Notes on Australian Muscoidea. *Proc. roy. Soc. Q'land*, 45: 30-37.
The Asilidae of Australia. Part 1. *Ann. Mag. nat. Hist.* (10), 13: 498-525.
The Asilidae of Australia. Part 2. *ibid.* (10), 14: 1-35.
The genus *Tabanus* in Tasmania. *Stylops*, 3: 43-48.
1935. Miscellaneous notes on Australian Diptera. III. Chrysosomatinae. *Proc. Linn. Soc. N.S.W.*, 60: 248-256.
The Asilidae of Australia. Part 3. *Ann. Mag. nat. Hist.* (10), 16: 161-187.
The Asilidae of Australia. Part 4. *ibid.* (10), 16: 405-426.
1936. Notes on Sarcophaginae in India and Australia. *Proc. Linn. Soc. N.S.W.*, 61: 89-97.
Notes on Australian Muscoidea. II. *Proc. roy. Soc. Q'land*, 48: 22-29.
1937. Notes on genus *Calliphora*: Classification, synonymy, distribution and phylogeny. *Proc. Linn. Soc. N.S.W.*, 62: 17-26.
1938. Miscellaneous notes on Australian Diptera. IV. Genus *Odontomyia* (Stratiomyiidae). *Proc. Linn. Soc. N.S.W.*, 63: 70-74.

1939. Miscellaneous notes on Australian Diptera. V. On eye-coloration and other notes. PROC. LINN. SOC. N.S.W., 64: 34-50.
Miscellaneous notes on Australian Diptera. VI. Dolichopodinae. *ibid.* 64: 345-352.
Notes on Australian Muscoidea. III. *Proc. roy. Soc. Q'land*, 49: 53-70.
Notes on Australian Muscoidea. IV. *ibid.* 50: 33-39.
1940. Miscellaneous notes on Australian Diptera. VII. On body-colour, and on species of Tabanidae, Cyrtidae and Asiloidea. PROC. LINN. SOC. N.S.W., 65: 484-493.
Notes on Australian Muscoidea. V. Calliphoridae. *Proc. roy. Soc. Q'land*, 51: 133-146.
1941. Miscellaneous notes on Australian Diptera. VIII. Subfamily Lomatiinae. PROC. LINN. SOC. N.S.W., 66: 223-233.
Aphididae in Australia. II. Subtribe Pentalonina. *Proc. roy. Soc. Q'land*, 52: 36-40.
1942. Miscellaneous notes on Australian Diptera. IX. Superfamily Asiloidea. PROC. LINN. SOC. N.S.W., 67: 197-204.
External terminalia of the Diptera. *Nature*, v. 149, No. 3781: 441-2.
1943. The Sarcophaginae of Australia and New Zealand. PROC. LINN. SOC. N.S.W., 68: 17-32.
Australian Stratiomyiidae. II. Tribe Myxosargini. *Proc. roy. Soc. Q'land*, 55: 11.
1944. Miscellaneous notes on Australian Diptera. X. Distribution, classification and the *Tabanus posticus*-group. PROC. LINN. SOC. N.S.W., 69: 76-86.
The copulation and terminal segments of Diptera. *Proc. roy. ent. Soc. London*, 19: 52-65.
1945. Miscellaneous notes on Australian Diptera. XI. Evolution of characters in the order; venation of the Nemestrinidae. PROC. LINN. SOC. N.S.W., 70: 135-146.
A new *Ceroides* with folding wings. *Proc. roy. Soc. Q'land*, 56: 81-84.
On flies that fold their wings. *Ent. mon. Mag.*, 81: 93-4.
1946. Miscellaneous notes on Australian Diptera. XII. Cyrtidae, Dolichopodidae and Phoridae. PROC. LINN. SOC. N.S.W., 71: 65-71.
1947. Miscellaneous notes on Australian Diptera. XIII. The origin of the *vena spuria*. PROC. LINN. SOC. N.S.W., 72: 229-232.
The wing venation of Syrphidae (Diptera). *Ent. mon. Mag.*, 83: 142-144.
Notes on Australian Muscoidea. VI. *Calliphora* in Australia and New Zealand. *Proc. roy. Soc. Q'land*, 57, 1945, 53-56.
1948. Miscellaneous notes on Australian Diptera. XIV. Venation and other notes. PROC. LINN. SOC. N.S.W., 73: 298-303.
On classifying Asilids. *Ent. mon. Mag.*, 84: 116-119.
The genus *Tabanus* in Australia. *Proc. roy. Soc. Q'land*, 59: 169-178.
1950. On the articulating scutellum in Diptera. *Ent. mon. Mag.*, 86: 230.
On the shortening of the radial vein in Diptera. *ibid.* 86: 231.
The twisting segments in Diptera. *ibid.* 86: 346-347.
1951. Miscellaneous notes on Australian Diptera. XV. *Tabanus*, *Heteropsilopus*. PROC. LINN. SOC. N.S.W., 76: 222-225.
Evolutionary trends in Diptera. *Ent. mon. Mag.*, 87: 56-59.
Theories of the world distribution of Diptera. *ibid.* 87: 99-102.
The phylogeny of Diptera. *ibid.* 87: 140-141.
The reticulation theory of wing venation in Diptera. *J. Soc. Brit. Ent.*, 4: 27-36.
1953. The phylogeny of Diptera. 2. Dolichopodidae. *Ent. mon. Mag.*, 89: 7-11.
The evolution of antennae in the Diptera. *ibid.* 89: 79-90.
1954. Reduction of the median field in the wing venation of Diptera. *Ent. mon. Mag.*, 90: 2-3.
The phylogeny of Diptera. 3. Empididae. *ibid.* 90: 78-80.
The evolution of antennae in the Diptera. 2. The genus *Microdon* (Syrphidae). *ibid.* 90: 97-98.
1955. The Diptera of Katoomba. Part I. Therevidae. PROC. LINN. SOC. N.S.W., 80: 177-179.
The phylogeny of Diptera. 4. Tabanoidea. *Ent. mon. Mag.*, 91: 193-196.
The first median vein in the wings of Diptera. *ibid.* 91: 197-198.
1956. The wing venation of Lomatiinae (Diptera-Bombyliidae). PROC. LINN. SOC. N.S.W., 81: 78-81.
The superfamily unit used in Diptera. *Ent. mon. Mag.*, 92: 213-215.
The median field in the wing-venation of Diptera. *Ent. mon. Mag.*, 93: 86-88.
1958. The Diptera of Katoomba. Part II. Leptidae and Dolichopodidae. PROC. LINN. SOC. N.S.W., 83: 291-302.
1959. The Diptera of Katoomba. Part III. Stratiomyiidae and Tachinidae. PROC. LINN. SOC. N.S.W., 84: 209-217.
1960. The time element in development of colour on adult Diptera and on that of a cicada (Homoptera). *Ent. mon. Mag.*, 96: 5-7.
1962. The anal field in the wing venation of Empididae and related families. *J. ent. Soc. Q'land*, 1: 25-29.

FLORENCE SULMAN

Miss Florence Sulman, M.B.E., who was born in Kent, England, died in Sydney on 15th June, 1965, at the age of 89 years. She had been a member of the Society since 1911 and had lived in retirement at Collaroy, New South Wales, for many years. She was a Vice-President of the Surry Hills Free Kindergarten and President of the Society of Arts and Crafts of New South Wales. She did not publish any articles in the Society's Proceedings but her "Popular Guide to the Wild Flowers of New South Wales", Vols 1 and 2 (1913, 1914) was a well-known text-book on the botany of New South Wales for many years. Miss Sulman was a daughter of the late Sir John Sulman, an eminent architect of Sydney.

ANTHONY REEVE WOODHILL

Dr. Anthony R. Woodhill, D.Sc.Agr., who died suddenly of a heart attack at his home at Hunter's Hill, New South Wales, on 27th July, 1965, at the age of 65 years, had been a member of the Society since 1932. He was elected to the Council on 23rd May, 1945, and was President for the year 1946/47. On account of ill-health he resigned from the Council on 19th June, 1963. After graduating in 1924 with distinction in entomology in the Agricultural Science course at the University of Sydney he was appointed to the N.S.W. Department of Agriculture, Entomology Branch. In 1930 he was appointed McCaughey Lecturer in Entomology, University of Sydney, and remained in that position, with subsequent promotion to a Readership, until his retirement on 21st February, 1965, except for a brief sojourn in England in 1939 to further his studies, which were terminated by the beginning of World War II, and three years (1942-1945) spent in the A.I.F. Dr. Woodhill published 12 papers in the Society's Proceedings between 1938 and 1959, including his Presidential Address, entitled "A brief review of progress in the control of some major agricultural insect pests in New South Wales during the period 1920-1945". A Memorial Notice for Dr. Woodhill is being prepared for subsequent inclusion in the Society's Proceedings.

BALANCE SHEETS

GENERAL ACCOUNT. Balance Sheet at 28th February, 1966.

LIABILITIES		ASSETS.	
Accumulated Funds—	\$	Fixed Assets—	\$
Amount received from Sir William Macleay during his lifetime	28,000.00	Commonwealth Loans, at Cost	30,097.00
Further sum bequeathed by his will	12,000.00	Debentures : Metropolitan Water, Sewerage and Drainage Board, at Cost	24,688.75
Contingencies Reserve	40,000.00	Sydney County Council	6,000.00
	46,924.13	Science House (one-third share), at Cost	29,670.43
Current Liabilities—			90,456.18
Bookbinding Account	1,824.66	Current Assets—	
Income Account	9,273.69	Cash in Hand	20.00
Suspense	16.43	Commercial Banking Company of Sydney, Ltd.	7,562.73
	11,114.78		7,582.73
	\$98,038.91		\$98,038.91

INCOME ACCOUNT. Year Ended 28th February, 1966.

INCOME ACCOUNT. Year Ended 28th February, 1966.		ASSETS.	
	\$		\$
To Salary	1,696.00	By Balance from 1964-65	7,717.82
Printing Proceedings	3,536.08	Subscriptions : 1965-66	999.60
Printing Reprints	468.25	Arrears	50.40
Illustrations (Blocks)	463.94	Advance	50.40
Insurance	26.96		
Postage	290.87	Entrance Fees	1,100.40
Petty Cash	39.35	Interest	33.60
	330.22	Science House	3,245.58
Audit	33.60	Rent	2,244.18
Printing and Stationery	345.62	Sales	67.50
Expenses	230.31	N.S.W. Government Grant	3,331.62
Freight	123.95	Fellowships Account (surplus income at 28th February, 1966, transferred)	800.00
Clearing	141.20	Sale of Reprints	2,562.60
Conversazione and Lecture	60.82	Donation towards Printing	845.02
	935.50		80.00
Library	297.68	Receipts for Year	14,310.50
Expenditure for Year	7,754.63		
Transfer to Contingencies Reserve	5,000.00		
Balance to 1966-67	9,273.69		
	\$22,028.32		\$22,028.32

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1966, and certify that the above Balance Sheet and accompanying Income Account are correct, and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1966, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, F.C.A., Chartered Accountant, Auditor.
Registered under the Public Accountants Registration Act, 1945,
as amended.

A. B. WALKOM,
Hon. Treasurer.

LINNEAN SOCIETY OF NEW SOUTH WALES.
LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

Balance Sheet at 28th February, 1966.

LIABILITIES.	\$	ASSETS.	\$
Accumulated Funds—		Fixed Assets—	
Amount bequeathed by Sir William Macleay	70,000.00	Commonwealth Loans, at Cost	60,885.50
Surplus Income Capitalized	48,272.98	Debtures:—	
		Metropolitan Water, Sewerage and Drainage Board, at Cost	35,296.98
		Rural Bank of N.S.W., at Cost	4,345.50
		State Electricity Commission	5,000.00
		Loan on Mortgage	12,070.00
		Current Assets—	117,597.98
		Commercial Banking Company of Sydney, Ltd.	675.00
	\$118,272.98		\$118,272.98

INCOME ACCOUNT. Year Ended 28th February, 1966.

To Salary of Linnean Macleay Fellow	\$ 2,666.67	By Interest	\$ 5,762.60
" Capital Account	533.33		
" Balance, being Surplus Income transferred to General Account	2,562.60		
	\$5,762.60		\$5,762.60

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1966, and certify that the above Balance Sheet and accompanying Income Account are correct, and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1966, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, F.C.A., Chartered Accountant, Auditor.

Registered under the Public Accountants Registration Act, 1945,
as amended.

Sydney, 9th March, 1966.

2nd March, 1966.

A. B. WALKOM,
Hon. Treasurer.

LINNEAN SOCIETY OF NEW SOUTH WALES.
BACTERIOLOGY ACCOUNT.

Balance Sheet at 28th February, 1966.

	\$	\$	\$	\$
LIABILITIES.			ASSETS.	
<u>Accumulated Funds—</u>			<u>Fixed Assets—</u>	
Amount bequeathed by Sir William Macleay	24,000.00		Commonwealth Loans, at Cost	30,636.25
Accumulated Income Capitalized	12,620.00		Metropolitan, Water, Sewerage and Drainage Board, at Cost	1,600.00
Research Fund	20.00		Loan on Mortgage	4,400.00
	36,640.00			36,636.25
<u>Current Liability—</u>			<u>Current Assets—</u>	
Income Account at 28th February, 1966		498.98	Commercial Banking Company of Sydney, Ltd.	502.73
		498.98		\$37,138.98

INCOME ACCOUNT. Year Ended 28th February, 1966.

	\$	\$	\$	\$
To University of Sydney (towards salary of Lecturer)	1,840.00		By Balance from 1964-65	457.63
" Balance to 1966-67	498.98		" Interest	1,881.35
	\$2,338.98			\$2,338.98

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1966, and certify that the above Balance Sheet and accompanying Income Account are correct, and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1966, as shown by the books. Certificates of the investments have been inspected.

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2nd March, 1966.

A. B. WALKOM,
Hon. Treasurer.

PRESIDENTIAL ADDRESS

THE COMPARATIVE EARLY EMBRYOLOGY OF THE OLIGOCHAETA, HIRUDINEA AND ONYCHOPHORA

D. T. ANDERSON

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[Delivered 30th March, 1966]

Synopsis

The primitive, large, yolky eggs of tubificid and lumbricid oligochaetes and glossiphoniid leeches undergo a modified spiral cleavage yielding a yolky blastula. The pattern of presumptive areas in the blastula wall is interpretable as a modification of the polychaete presumptive area pattern, in association with increased yolk. The same pattern of presumptive areas is retained in the secondarily microlecithal embryos of lumbricid oligochaetes, gnathobdellid and pharyngobdellid leeches and probably other clitellates, in spite of further cleavage modifications and of embryonic adaptations to albumenotrophy.

The primitive, large, yolky eggs of ovoviviparous Onychophora undergo centrolecithal cleavage, setting out a blastoderm around a central yolk mass. In viviparous non-placental species, although yolk is absent and cleavage is modified, a similar blastoderm is usually formed around a central cavity. In viviparous placental species, cleavage is highly specialized, yielding a small blastodermic vesicle at the end of a placental stalk and plate.

The blastodermal presumptive areas of Onychophora, like those of clitellates, retain a constant pattern in spite of secondary yolk loss and its attendant modifications. Taking into account the events of gastrulation, the blastodermal presumptive area pattern of Onychophora is interpretable as a modification of the primitive clitellate presumptive area pattern, in association with a further increase in yolk.

It is suggested that a clitellate-like mode of early embryonic development must have characterized the ancestors of the Onychophora, and that these ancestors were members of the spiral cleavage assemblage and were probably paraphyletic with the ancestors of annelids.

INTRODUCTION

Following a review of the embryology of polychaete annelids by Anderson (1966*a*), the embryonic development of clitellate annelids and the modifications which they show as compared with polychaetes now become a subject of renewed interest. While the development of yolky polychaete eggs always retains traces of a primitive mode of development from a small, microlecithal egg through a planktotrophic trochophore and metamorphosis, that of clitellates shows no such traces. As is well known, both oligochaetes and hirudineans deposit their eggs in a cocoon in which development proceeds directly to hatching as a miniature adult with numerous segments. Primitively, the embryo develops from a relatively large yolky egg, the cleavage, gastrulation and organogeny of which are adapted to the presence of voluminous yolk reserves. Secondarily, in the majority of clitellate families, the egg is small and microlecithal and the embryo is adapted to feeding on the albuminous contents of the cocoon. The nature of both types of modification has hitherto yielded no clue as to the possible marine antecedents of primitive clitellate development or the derivation of the secondary yolless from the primitive yolky condition. When the data of clitellate embryology are reexamined in the light of new understanding of polychaete development, however, solutions to both of these problems can be proposed, as will be shown below.

Primitive clitellate development exemplifies a particular modification of spiral cleavage development to voluminous yolk and the production of a metamERICALLY segmented annelid. The embryonic development of Onychophora is also primitively adapted to voluminous yolk, and to the formation of a metamERICALLY segmented animal with a number of annelid-like features. In the absence of "spiral cleavage" features in onychophoran development, the

derivation of Onychophora from a spiral cleavage ancestry has hitherto proved elusive of recognition (Manton, 1965) but, as will also be shown below, pursuance of the comparison in an appropriate way reveals the development of the Onychophora, not only as a modification of spiral cleavage development, but also as one with unmistakable clitellate-like antecedents.

It is true that certain difficulties attend this line of argument. The descriptive data on the embryology of the Oligochaeta, Hirudinea and Onychophora are incomplete in many critical ways and few of the available papers embody results obtained by modern histological techniques. Among the oligochaetes for example, *Tubifex rivulorum* and *Rhynchelmis limosella* are the only species with large, yolky eggs whose development has been adequately described (Schmidt, 1922; Penners, 1922, 1924; Swetloff, 1923*b*; Meyer, 1929), all other investigations being concerned with the specialized embryos of nauidids, *Bdellodrilus* and earthworms. The same situation obtains for the Hirudinea, where again only two forms with large yolky eggs, *Glossiphonia* and *Theromyzon*, have been investigated (Schliep, 1914; Schmidt, 1917, 1925*a*), the former descriptions being confined to specialized piscicolid, gnathobdellid and pharyngobdellid development. The Onychophora present a further difficulty in that nothing is known of the development of the large, yolky eggs of oviparous onychophorans and only a little of the yolky eggs of ovoviviparous species (Sheldon, 1888, 1889*a*; Evans, 1902). On the other hand, the specialized development of the viviparous Onychophora, especially as described for *Peripatopsis* by Manton (1949), provides many inferences which are of value for comparative purposes, and permits a picture to be drawn of clitellate and onychophoran development which holds much of interest for the phylogeneticist and epigeneticist.

CLEAVAGE

Primitive cleavage in the Oligochaeta

In *Tubifex* and *Rhynchelmis*, the spiral pattern of cleavage is retained, but is modified in ways related to the magnitude of the large, yolky egg and its development in a protective cocoon. The nature of these modifications has hitherto been obscured by employment of the Wilsonian system of enumeration of spiral cleavage (Wilson, 1892), which places emphasis on the integrity of quartettes and individuality of single blastomeres and their fate. If, as for polychaetes (Anderson, 1966*a*), attention is alternatively directed towards the formation and subsequent fate of presumptive areas in the wall of the blastula, the oligochaete response to yolk is much more clearly discerned.

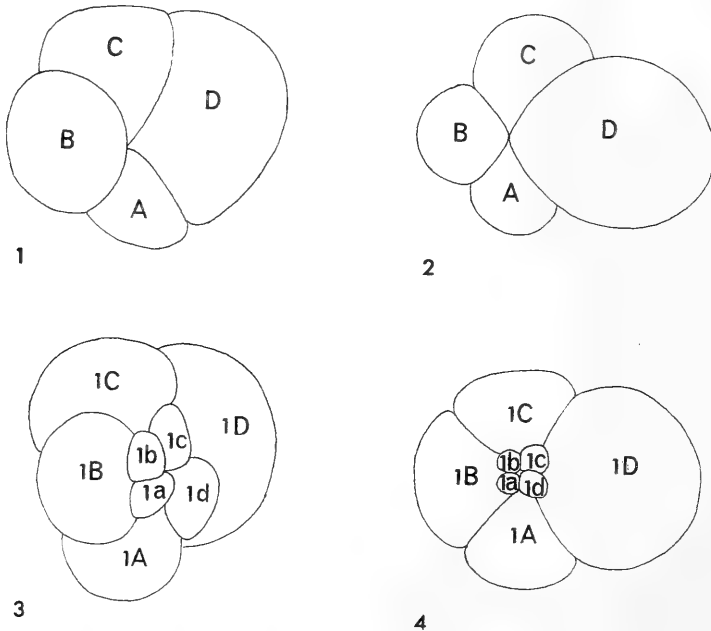
Both in *Tubifex* (Penners, 1922, 1924) and *Rhynchelmis* (Vedjovsky, 1886, 1888-92; Bergh, 1890; Penners, 1922; Swetloff, 1923*b*), the first two cleavage divisions are at right angles along the animal-vegetal axis of the egg, the next four perpendicular to this axis and, except for a precocious onset of bilateral cleavage in the D-quadrant, successively dextrotropic, laeotropic, dextrotropic and laeotropic in the classical spiral cleavage sequence. In association with the large size of the egg, 300-500 μ in diameter in *Tubifex*, 1000 μ in *Rhynchelmis*, the first division is very unequal, AB being much smaller than CD, and the second division maintains this inequality in the D-quadrant, D remaining large, while C is only a little larger than A and B (Figs 1, 2).

In polychaetes with yolky eggs, where the D cell is also disproportionately large, much of it is subsequently segregated into a ring of large ectoteloblasts and a pair of large M-cells within the ring, forming a growth zone which gives rise to several trunk segments before the yolk reserves of the embryo are exhausted (Anderson, 1966*a*). The large D cell in primitive oligochaetes is a developmental adaptation subserving a similar function. In *Tubifex*, for example, 34-38 segments are formed before the embryo hatches from the cocoon.

The orientation of the four quadrants in *Tubifex* at the 4-cell stage is as in polychaetes, D being dorsal, and A, B and C left-lateral, ventral and right-lateral respectively relative to the anteroposterior axis of the embryo, though there

is a change in quadrant orientation as development proceeds further. In *Rhynchelmis* at the 4-cell stage, on the other hand, the large D cell is posterior in position, with A on the left, B anterior and C on the right. Cleavage in *Tubifex* finally results in displacement of B-quadrant cells to an anterior and D-quadrant cells to a posterior position as described below. In *Rhynchelmis* quadrant reorientation, presumably through a redistribution of ooplasm, manifests itself in the egg.

Associated with the large size of the D cell, early cleavage after the 4-cell stage in *Tubifex* and *Rhynchelmis* differs from that of polychaetes in a marked tendency to precocious division of the D-quadrant cells, and to a lesser extent of the C-quadrant cells, so that the cells of each quartette cut off from the stem cells at the 3rd and subsequent divisions are formed in succession, the D-quadrant leading, the A and B quadrants lagging.

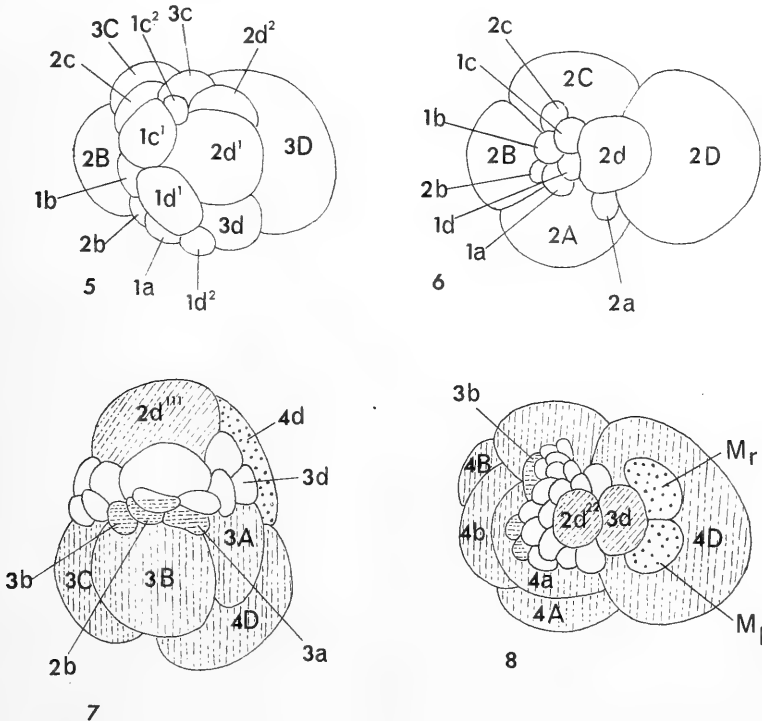


Figs 1-4.—1, *Tubifex*, 4-cell stage, anterior view with dorsal surface on the right. 2, *Rhynchelmis*, 4-cell stage, dorsal view with posterior end on the right. 3, *Tubifex*, 8-cell stage, anterior view, 4, *Rhynchelmis*, 8-cell stage, dorsal view. (After Penners, 1922; Swetloff, 1923b.) The key to the shading conventions employed in Figs 1-33 is provided by Fig. 13.

At the 3rd cleavage division (Figs 3, 4), dextrotropic and very unequal, a 1st quartette of very small cells 1a-1d is cut off from stem cells 1A-1D. In *Tubifex*, 1a-1d lie bilaterally on either side at the anterior pole, 1d and 1a to the left, 1b and 1c to the right. In *Rhynchelmis*, they are similarly bilateral, but dorsally placed.

The laeotropic 4th division begins with the division of 1D into 2d and 2D (Fig. 6). 2d is much larger than any cell of the 1st quartette, though in *Tubifex* it is only about one-quarter, and in *Rhynchelmis* less than one-quarter, of the size of 2D. In *Tubifex*, 2d pushes forward anterodorsally between 1d and 1c to lie in the dorsal midline, with the 1st quartette cells as an arc around its anterior face. In *Rhynchelmis*, 2d lies mid-dorsally behind the 1st quartette. 2a, 2b and 2c are now cut off laeotropically as small cells, so that 2a is added to the left, 2b to the front and 2c to the right of the micromere arc bordering 2d (Figs 5, 6).

At the same time, the 5th division begins in the D-quadrant. The products of this division as it affects 2D differ in the two embryos. In *Tubifex*, the d component of the 3rd quartette, 3d, is a small cell cut off dextiotropically and added to the left-hand end of the micromere arc (Fig. 5). In *Rhynchelmiss*, 3d is cut off in the dorsal midline as a cell directly behind and equal in size to 2d (Fig. 6). The latter cell, on the other hand, behaves similarly in both species at this stage, dividing unequally, with its smaller daughter pushing into the micromere arc while its larger daughter remains mid-dorsal. This is repeated at least twice in subsequent divisions, a cell being added on each occasion to the micromere arc, leaving the large cell in the mid-dorsal line. The final designation of the large cell as $2d^{111}$ in *Tubifex* and $2d^{22}$ in *Rhynchelmiss* (Figs 7, 8) does not alter the fundamental similarity of the process in the two species.



Figs 5-8.—5, *Tubifex*, 17-cell stage, dorsal view. 6, *Rhynchelmiss*, 12-cell stage, dorsal view. 7, *Tubifex*, 22-cell stage, anterolateral view. 8, *Rhynchelmiss*, 30-cell stage, dorsal view. (After Penners, 1922; Swetloff, 1923b.)

Meanwhile, the 5th cleavage division continues in the remaining quadrants, the stem cells 2A, 2B and 2C cutting off the small cells 3a, 3b and 3c to lie on the left, anteriorly and on the right respectively, at the outer rim of the micromere arc (Figs 5, 7). In *Tubifex*, the cells 1c and 1d, on the right and left in this arc, also divide equally, increasing the number of micromeres. In *Rhynchelmiss*, they are said not to divide again, but the evidence for this is not positive.

The later part of the 5th division is accompanied by precocious 6th division in the D-quadrant. The stem cell 3D divides into large 4d and 4D cells lying in midline (Figs 7, 8). In *Tubifex*, 4d is equal in size to 4D, although almost all of the yolk in the parent 3D stem cell is confined to 4D. In association with its relatively large size, 4d occupies the posterior midline, pushing 4D ventrally and 3A, 3B and 3C forwards. 3B thus comes to occupy an anterior position, while the micromere arc in front of 2d is lifted into a dorsal position. In

Rhynchelmis, 4d is much smaller than 4D, the two cells being posterodorsal and posteroventral respectively.

In the remaining yolky stem cells, 3A, 3B and 3C, further divisions are equal, simply increasing the number of yolky cells; and 4D now divides in the same way.

After the formation of 4d, the embryos of *Tubifex* and *Rhynchelmis* are remarkably similar in general construction. Each has (Figs 7, 8): (i) ventrally, a number of large yolky cells, the stem cells 3A-3C and 4D, forming a relatively greater proportion of the whole in *Rhynchelmis* than in *Tubifex*; (ii) posterodorsally, one (*Tubifex*) or two (*Rhynchelmis*) large cells in the midline, segregated via 2d in *Tubifex* and via 2d and 3d in *Rhynchelmis*, surrounded anteriorly and laterally by an arc of micromeres cut off from the stem cells as 1st, 2nd and 3rd quartette cells by a similar series of divisions in both species; (iii) posteriorly in the dorsal midline, a large 4d cell, relatively greater in size in *Tubifex* than in *Rhynchelmis*.

The orientation of these cells relative to the major axes is attained in *Tubifex* during cleavage. In polychaetes in which the D cell is disproportionately large, there is a tendency for A and C cells behind the prototroch to be pushed ventrally, and also for the posterior D cell, 4D, to be pushed ventrally as the large 2d and 4d cells are formed, but the anterior part of the embryo in front of the prototroch remains unaffected by this (Anderson, 1966a). In *Tubifex*, these tendencies are exaggerated and in the absence of a prototroch, associated with a large egg in a protective cocoon, they influence even the anterior end. After the formation of the 1st quartette, the axial relations of the eight cells are still as in polychaetes. Formation of a large 2d cell, however, displaces the posterodorsal stem cell 2D posteriorly and ventrally. Formation of a large 4d cell accentuates this, pushing 4D into a ventral position. The B quadrant stem cell is thereby displaced to the anterior end, so that 2b and 3b are cut off upwards at this end, in front of 2d. Similarly, the A and C quadrant stem cells are rotated forwards and upwards, and cut off 2a and 3a, and 2c and 3c, upwards on the left and right of 2d. In this way, the B quadrant becomes anterior, the D quadrant dorsal and posterior, and the A and C quadrants left and right vertical respectively.

It can be suggested that loss of the prototroch is prerequisite to this new pattern of modified spiral cleavage. While the prototroch persists (Polychaeta), modifications associated with an increased size of 2d and 4d posterior to the prototroch have little influence on cells anterior to it. With loss of the prototroch, a new quadrant configuration, established during cleavage in *Tubifex*, becomes possible. In *Rhynchelmis*, in association with a relatively greater yolk mass, the new configuration develops directly.

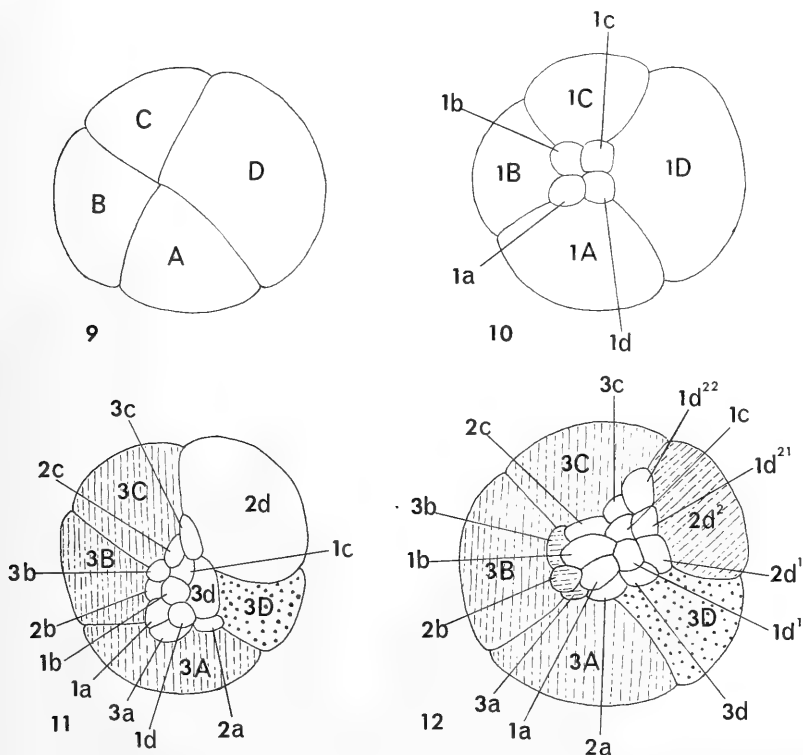
Primitive cleavage in the Hirudinea

From a comparative viewpoint, the important feature of cleavage in primitive leeches is its close similarity in every respect to cleavage in primitive oligochaetes. In *Glossiphonia* (Schliep, 1914) and *Theromyzon* (Schmidt, 1917, 1925a), as in the oligochaete *Rhynchelmis*, the quadrant orientation, B anterior, D posterior, is established after the first two cleavage divisions, and subsequent divisions proceed in a similar manner in the two species. In association with the large size of the egg, 500-1000 μ in diameter in *Glossiphonia complanata*, 600 μ in diameter in *Theromyzon*, the 1st cleavage division is unequal, although less markedly so than in primitive oligochaetes, AB being only a little smaller than CD. At the next division, AB divides equally into anterior B and left-lateral A, while CD divides into right-lateral C, equal in size to A and B, and posterior D, slightly the largest cell (Fig. 9). The parallel with *Rhynchelmis* is unmistakable and continues into subsequent divisions.

The 3rd division is very unequal, a 1st quartette of very small cells being cut off dextrotropically from the stem cells to lie in bilateral arrangement, dorsally

on either side of the midline, 1a and 1d to the left, 1b and 1c to the right (Fig. 10). As in oligochaetes, this division occurs first in the D quadrant, then in the C quadrant, with A and B lagging.

The laeotropic 4th division begins in the D quadrant. 1D divides into a large but yolky-free dorsal cell, 2d, displaced at this stage to the right, and an only slightly larger, but yolky, 2D cell lying posteroventrally and to the left. The three remaining cells of the 2nd quartette are then cut off as micromeres. 2a on the left, 2b anteriorly and 2c on the right, around the 1st quartette, making up a micromere cap (Fig. 11).



Figs 9-12.—9, *Glossiphonia*, 4-cell stage, dorsal view. 10, *Glossiphonia*, 8-cell stage, dorsal view. 11, *Glossiphonia*, 16-cell stage, dorsal view. 12, *Theromyzon*, 19-cell stage, dorsal view. (After Schliep, 1914; Schmidt, 1944.)

In the dextiotropic 5th division (Figs 11, 12), 2D, 2C, and 2A and 2B throw off, in sequence, small 3rd quartette cells 3d, 3c, 3a and 3b, which add to the edge of the micromere cap. 2d also divides unequally, throwing off a small cell 2d¹ on to the posterior edge of the micromere cap, the sister cell 2d² remaining large, posterodorsal and displaced to the right, with 3D lying posteroventrally below it and slightly displaced to the left. At the same time, the 4th division is completed in the 1st quartette, whose cells divide approximately equally into mid-dorsal 1a¹-1d¹ and adjacent 1a²-1d² in the centre of the micromere cap.

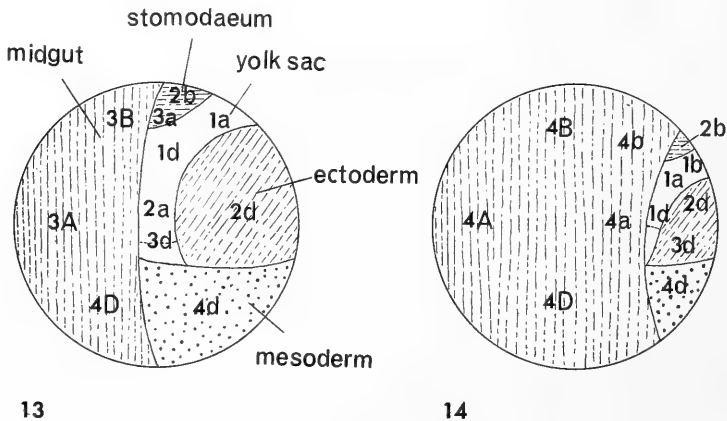
After the formation of 2d² at the 5th division, the embryos of *Glossiphonia* and *Theromyzon* have the same general configuration as those of primitive oligochaetes at a slightly later stage, namely (Fig. 12): (i) ventrally, a number of large yolky cells, 3A-3C; (ii) posterodorsally, a large cell 2d², slightly displaced to the right, with a cap of micromeres anterior to it, cut off from the stem cells as 1st, 2nd and 3rd quartette cells by a similar series of division in both species; (iii) posteroventrally, slightly displaced to the left, a large cell 3D.

The only difference between this pattern and that of oligochaetes summarized in the same way above is the lack of subdivision of 3D in leeches into posterior 4d and ventral 4D. The reason for this difference will be explained below in terms which minimize its significance.

Primitive fate of the cleavage blastomeres in the Clitellata

As in polychaetes (Anderson, 1966a), once the cell 4d has been cut off in oligochaetes from its stem cell, early in the 6th cleavage division, it becomes possible to assign all blastomeres to presumptive areas of specific subsequent fate. In primitive leeches, the cleavage blastomeres can similarly be assigned to presumptive areas by the end of the 5th cleavage division. In both groups, the pattern of presumptive areas is identical. Their most conspicuous feature in comparison with polychaetes is simplification, associated with the absence of presumptive larval organs. The areas comprise (Figs 13, 14, 18): (a) a dorsal area of presumptive ectoderm; (b) at the anterior edge of this area, in the dorsal midline, an area of presumptive stomodaeum; (c) a posterior area of presumptive mesoderm, incorporating presumptive germ cells; (d) a ventral area of presumptive midgut.

In the absence of presumptive prototroch, the separation of presumptive ectoderm into anterior and posterior parts seen in polychaetes is not found in clitellates. Presumptive ectomesoderm is also absent.



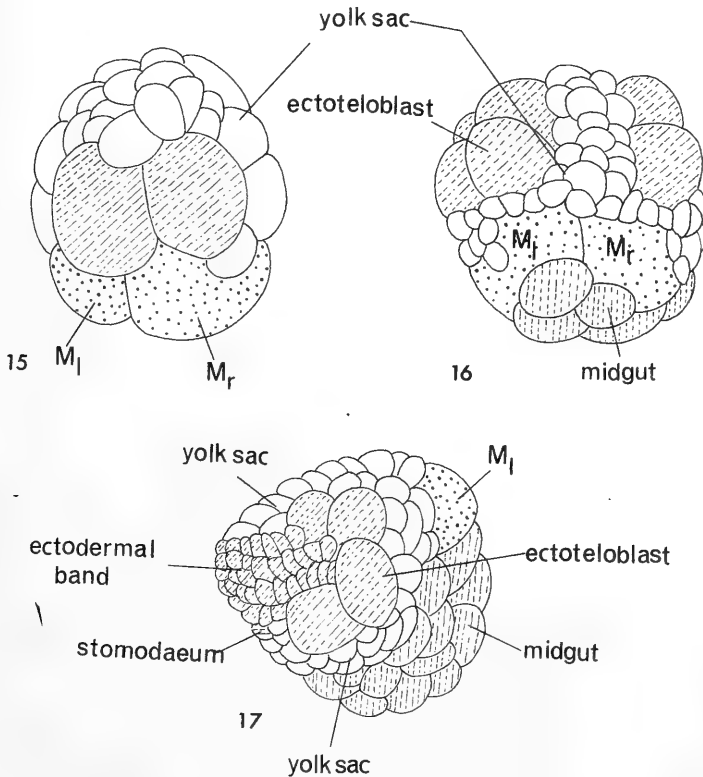
Figs 13-14.—13, presumptive areas of the blastula of *Tubifex*. 14, presumptive areas of the blastula of *Rhynchelmis*. Diagrams based on data from authors listed in the text.

For oligochaetes, the designation of the above areas is supported by the work of Penners (1922, 1924), Penners and Stablein (1930) and Meyer (1929, 1931) on *Tubifex*, Penners (1929) on *Peloscolex benedini*, and Vedjovsky (1888-92), Bergh (1890), Penners (1922), Swetloff (1923b) and Iwanoff (1928) on *Rhynchelmis*. *Peloscolex*, as far as it has been studied, develops in the same manner as *Tubifex*. Differences between *Tubifex* and *Rhynchelmis* occur only in the constitution of the presumptive ectoderm.

Of the four areas listed above, two in oligochaetes correspond in every respect to the homologous areas in polychaetes. The presumptive mesoderm is segregated posteriorly in the single cell 4d which, before it assumes its definitive mesodermal fate, throws off into the interior a pair of small cells, the primordial germ cells. 4d then divides bilaterally into M_1 and M_r , teloblasts which subsequently bud off paired ventrolateral mesodermal bands (Figs 15, 16). The presumptive midgut is segregated in the large, ventral, yolky cells 3A-3C and 4D. There also appears to be a close correspondence between the presumptive stomodaeal area of oligochaetes and that of polychaetes. Especially in *Tubifex*, and perhaps also

in *Rhynchelmis*, the anterodorsal micromeres which make up this area stem mainly from 2b and 3b, while 3a can also be implicated in *Tubifex* (Fig. 7). Although the area as a whole is displaced anteriorly, its similarity in relative position and mode of segregation to the stomodaeal presumptive area of polychaetes is conspicuous (compare Anderson, 1966a).

The presumptive ectoderm of oligochaetes is made up of one or, in *Rhynchelmis*, two large, central cells surrounded anteriorly and laterally by an arc of micromeres (Figs 7, 8). In *Tubifex* and *Pelosclex*, the single central cell, the main product of 2d, divides equally bilaterally into a pair of cells, each of which gives rise by further divisions to a transverse row of four ectoteloblasts (Figs 15–17). In *Rhynchelmis*, the anterior central cell, the main product of 2d,



Figs 15–17.—15, *Tubifex*, dorsal view of stage with paired M-cells. 16, *Tubifex*, posterior view of stage during ectoteloblast formation. 17, *Tubifex*, left lateral view of stage after onset of ectoteloblast activity. (After Penners, 1924.)

divides into a pair of cells which migrate laterally, while the adjacent, posterior, central cell, 3d, divides into a pair of cells each of which divides again into three cells in a transverse row with the large 2d cell at the end of it. The eventual product in each case, although resulting from a slightly different series of divisions, is a row of four ectoteloblasts on either side of the midline. Each ectoteloblast now begins to bud off a row of small cells forwards (Fig. 17).

While the ectoteloblasts are forming, the arc of micromeres multiplies and spreads (Figs 15–17): (i) back mid-dorsally, as a strip separating the two ectoteloblast groups; (ii) up towards the mid-dorsal line from its ends, behind the ectoteloblast groups.

The backgrowth mid-dorsally finally meets the upgrowth from the sides. When this stage is reached, the following sub-areas can be distinguished within the presumptive ectoderm: (1) the ectoteloblasts, incorporating presumptive material of the prostomium and cerebral ganglia and the major part of the ectoderm of the peristomium and trunk segments, and already beginning to bud off this material as ectodermal bands; (2) the presumptive temporary yolk sac ectoderm, mid-dorsally and laterally, later incorporated into the segmental epithelium; (3) the presumptive pygidial epithelium, incorporating presumptive proctodaeum, posterior to the teloblasts. This sub-area, as noted above, has a paired bilateral origin and is also of temporary yolk sac function at this stage.

In comparison with the presumptive ectoderm of the polychaetes (Anderson, 1966a, fig. 22), the presumptive mouth region ectoderm and telotroch are absent, the presumptive anterior (prostomial) ectoderm is incorporated into the ectoteloblasts and all extrateloblastic cells have a new presumptive fate as temporary yolk sac cells, although retaining a capacity for forming definitive trunk and pygidial epithelium. The adaptation of the majority of the ectoderm to a temporary yolk sac function is associated with the large volume of presumptive midgut soon to be accommodated within the interior of the embryo. Deletion of the telotroch, as of the prototroch, requires no explanation. Deletion of distinct mouth region ectoderm and incorporation of presumptive prostomium into the ectoteloblasts can be regarded as a simplification made possible by advanced lecithotrophy, based on the ectoteloblast pattern of polychaetes. The presumptive ectodermal pattern of oligochaetes is thus derivable from that of polychaetes, completing the correspondence of all presumptive areas and at the same time revealing a new presumptive area pattern of important comparative value.

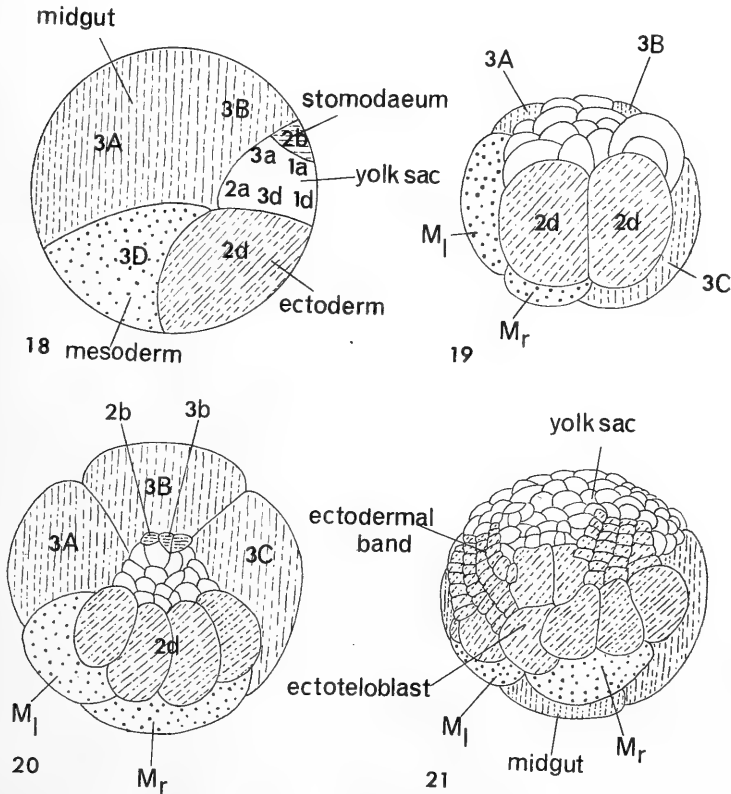
For leeches, while Schliep (1914) and Schmidt (1917, 1925a) provide the data which illustrate the way in which the presumptive area cells become segregated, their assignation to the fates listed above rests with the work of Whitman (1878, 1887), Nusbaum (1884, 1885, 1886), Bürger (1891, 1902), and Bychowsky (1921) on *Glossiphonia* and of Schmidt (1917) on *Theromyzon*, all of whom described aspects of later development. Presumptive mesoderm is segregated precociously in leeches into the cell 3D (Figs 12, 18), but the only significant difference between this and the polychaete-oligochaete condition is that presumptive midgut is eliminated from the D-quadrant. 3D divides equally bilaterally into M_L and M_R (Figs 19–21), teloblasts which, as in primitive oligochaetes, bud off paired ventrolateral mesodermal bands. The presumptive midgut is segregated, almost as in oligochaetes, into 3A, 3B and 3C (Figs 19, 20) of which the latter cuts off a small ectoderm cell 4c into the micromere cap before assuming its definitive fate. The position of the presumptive stomodaeum (Figs 18, 20) indicates that a major contribution is made to it by the anterior cells of the micromere cap, 2b and 3b, as in *Tubifex*. The presumptive embryonic ectoderm comprises a large dorsal posterior cell and the major part of the micromere cap in front of it. The large cell, as in *Tubifex*, is the main product of 2d and undergoes precocious division in the same sequence, equally bilaterally into four ectoteloblasts on each side (Figs 19–21) which together incorporate presumptive material of the prostomium, cerebral ganglion and the major part of the primordial epithelium of the trunk segments, and begin to bud off eight rows of small cells forwards, four on each side, as ectodermal bands. The micromeres multiply and spread back, between and around the ectoteloblasts and their products (Fig. 21), as in *Tubifex*, forming presumptive temporary yolk sac, later to transform into segmental and pygidial epithelium.

There is thus no doubt that cleavage and presumptive area formation in primitive oligochaetes and primitive leeches are fundamentally identical, supporting the classification of the two together as a single group, Clitellata. They can be interpreted as a particular modification of cleavage and presumptive area formation in polychaetes, associated with enhanced lecithotrophy and direct

embryonic development in a protective cocoon until numerous segments are formed and the adult organization is well established. It will be shown below that it is possible to argue in favour of the derivation of cleavage and presumptive area formation in Onychophora directly from a clitellate-like condition, assuming only further adaptation to increased lecithotrophy. Before pursuing this, however, the stability of presumptive area formation, in spite of secondary egg and cleavage specializations, will be displayed within the clitellates themselves by reference to the earthworms and to gnathobdellid and pharyngobdellid leeches.

Cleavage and presumptive areas in lumbricid oligochaetes

In earthworms, egg size is secondarily reduced, cleavage is modified and little trace of the spiral pattern remains. Attempts to draw comparisons with primitive oligochaetes and with polychaetes by means of the Wilsonian

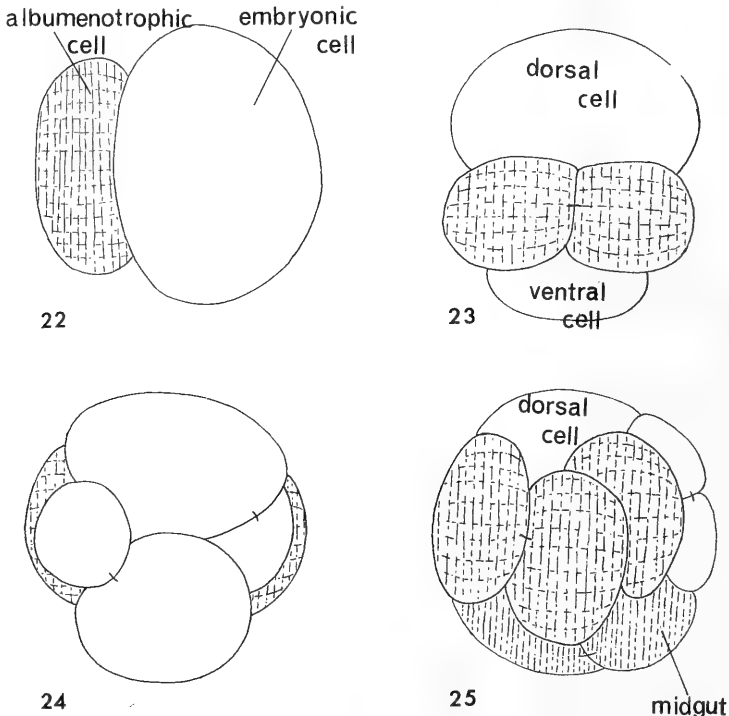


Figs 18-21.—18, presumptive areas of the blastula of *Glossiphonia* and *Theromyzon*. Diagram based on data from authors listed in the text. 19, *Glossiphonia*, postero-dorsal view of stage with paired M-cells. 20, *Theromyzon*, dorsal view of stage during ectoteloblast formation. 21, *Glossiphonia*, postero-dorsal view after onset of ectoteloblast activity. (After Schliep, 1914; Schmidt, 1917, 1925a, 1944.)

enumeration have therefore failed. The results obtained by Swetloff (1923a, 1928) on cleavage in *Bimastus* and *Eisenia*, using this notation, served at the time only to confirm the secondary specialization of earthworm cleavage, the bane of earlier workers (Wilson, 1889; Vedjovsky, 1888-92), without elucidating the mode of this specialization. The same results re-examined today, however, tell a different story, since they show that in earthworms the presumptive areas

of the blastula fall into a pattern identical with that of primitive oligochaetes, although the manner in which they are segregated is new and an additional paedogenetic structure has arisen.

Taking *Bimastus* as an example, cleavage of the microlecithal egg is modified from the very beginning. The 1st division is unequal, yielding a smaller anterior and larger posterior cell (Fig. 22). At the 2nd division, the anterior cell divides equally into right and left daughters, while the posterior cell divides into a larger dorsal and a smaller ventral daughter (Fig. 23). The right anterior cell now divides again, completing a group of three anterior cells which undergo no subsequent division (Fig. 25). These three cells, which are characteristic of earthworms (Hatschek, 1878; Vedjovsky, 1887, 1888-92; Wilson, 1889; Hoffmann, 1899; Swetloff, 1923*a*, 1928) and finally become internal at the



Figs 22-25.—*Bimastus*. 22, 2-cell stage, dorsal view with posterior end on the right. 23, 4-cell stage, anterior view. 24, 7-cell stage, posterior view. 25, 10-cell stage, anterior view. (After Swetloff, 1923*a*.)

anterior end of the embryo before being resorbed, are generally called provisional embryonic excretory cells. They become highly specialized, developing a complex series of intracellular canals, and show pulsatory activity. There is no experimental proof of their excretory function, however, and it is equally possible that they act as absorption and assimilation of albumen until the embryonic gut cells assume this function.

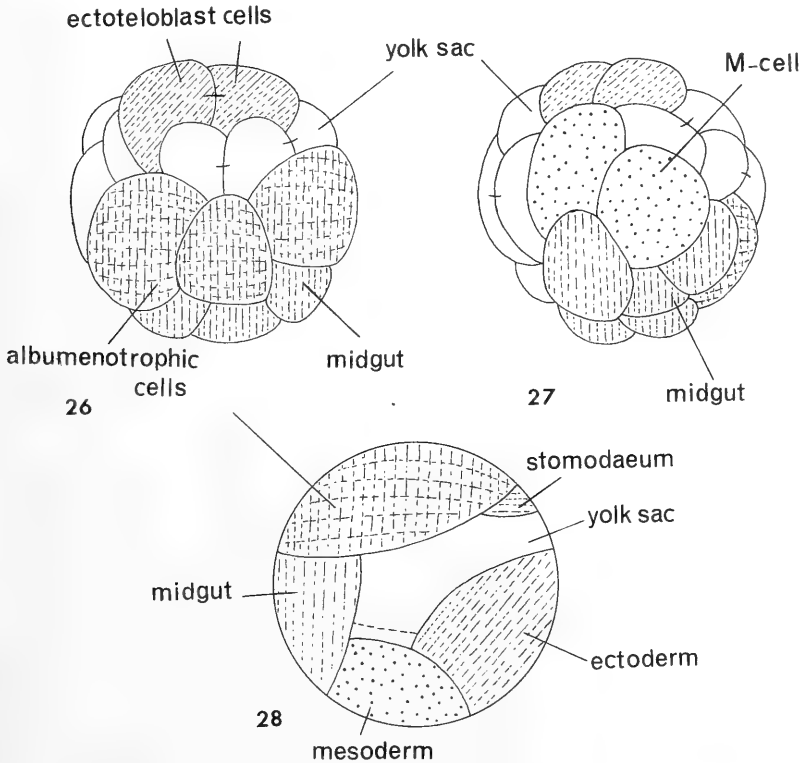
Meanwhile, continuing from the 4-cell stage, the posterior dorsal cell throws off a small cell downwards to the right, while the ventral cell cuts off a small cell upwards to the left (Fig. 24). The latter divides equally to form two small cells on the left, while the ventral cell cuts off a second small cell to the right (Fig. 25).

The large dorsal cell now divides transversely into a smaller anterodorsal and a larger posterior cell. The latter then throws off a small posteroventral cell, somewhat displaced to the right. At the same time, the ventral cell has

divided equally twice, and its products, together with the posteroventral cell, make up a group of five ventral cells containing most of the yolk of the original egg (Fig. 27). These are the presumptive midgut cells. In front of them lie the three excretory cells.

The large posterior cell divides equally bilaterally into two M-cells (Fig. 27), which subsequently bud off ventrolateral mesodermal bands. As in some polychaetes (Anderson, 1966a), the M-cells bud off one or two cells added to the presumptive midgut before assuming their definitive fate as mesodermal teloblasts.

The anterodorsal sister of the M-cell mother cell divides equally bilaterally into two cells (Figs 26, 27) which, by further division, give rise to four ectoteloblast cells on each side. The small cells on the right and left multiply and



Figs 26–28.—*Bimastus*. 26, early blastula, anterior view. 27, early blastula, posterior view. 28, presumptive areas of the blastula. (Based on data of Swetloff, 1923a.)

spread as a micromere arc in front of the anterodorsal cell (Fig. 26). In this arc, the anterior cells in the mid-line are presumptive stomodaeum, the remainder temporary yolk sac.

When cleavage in *Bimastus* is described in this way, it becomes obvious that the presumptive areas of the blastula (Fig. 28), although segregated by a new series of divisions consequent on secondary yolk loss, are identical in arrangement with those of primitive oligochaetes, the anterior cells having become paedogenetically specialized without disturbing the configuration of the basic pattern. Presumptive midgut is relatively less extensive, commensurate with a reduction in yolk, but is still segregated into a group of cells ventrally. Presumptive mesoderm is contained within a pair of M-cells posteriorly. Presumptive ectoderm dorsally has a large central ectoteloblast mother cell surrounded

anteriorly and laterally by an arc of small cells. Presumptive stomodaeum is confined to the anterior members of this arc, in the midline. The remainder develop as a temporary surface epithelium of the early embryo.

Judging from the position of the excretory cells, lying between presumptive stomodaeum and midgut, it seems likely that they are derived from ancestral presumptive midgut cells, in which case an albumen-absorbing function becomes even more probable.

Cleavage and presumptive areas in gnathobdellid and pharyngobdellid leeches

Like earthworms, the gnathobdellid and pharyngobdellid leeches lay small, microlecithal eggs and show developmental modifications associated with prolonged feeding from an early stage on cocoon albumen (Schmidt, 1944). Cleavage among these forms has been studied only in *Erpobdella atomaria* by Sukatschhoff (1903) and Dimpker (1917) and in *Hirudo medicinalis* by Schoumkiné (1953), but the results for the two species are sufficiently alike to suggest a basis of generalization for all gnathobdellids and pharyngobdellids. Not the least interesting aspect of cleavage and presumptive area formation in these animals is its similarity to that of earthworms, evolved in parallel from a fundamentally similar starting point.

In spite of great reduction in egg size, the first three cleavage divisions retain the primitive hirudinean pattern. The 1st division is unequal, giving a larger CD cell and smaller AB cell, the 2nd division unequal in the former, equal in the latter, with the result that a relatively large posterior D cell is flanked by equal A, B and C cells, on the left, anteriorly and on the right respectively. At the 3rd division, a 1st quartette of micromeres is cut off dextriotropically to occupy a dorsal position, bilaterally arranged on either side of the mid-line, 1d and 1a to the left, 1b and 1c to the right (Fig. 29).

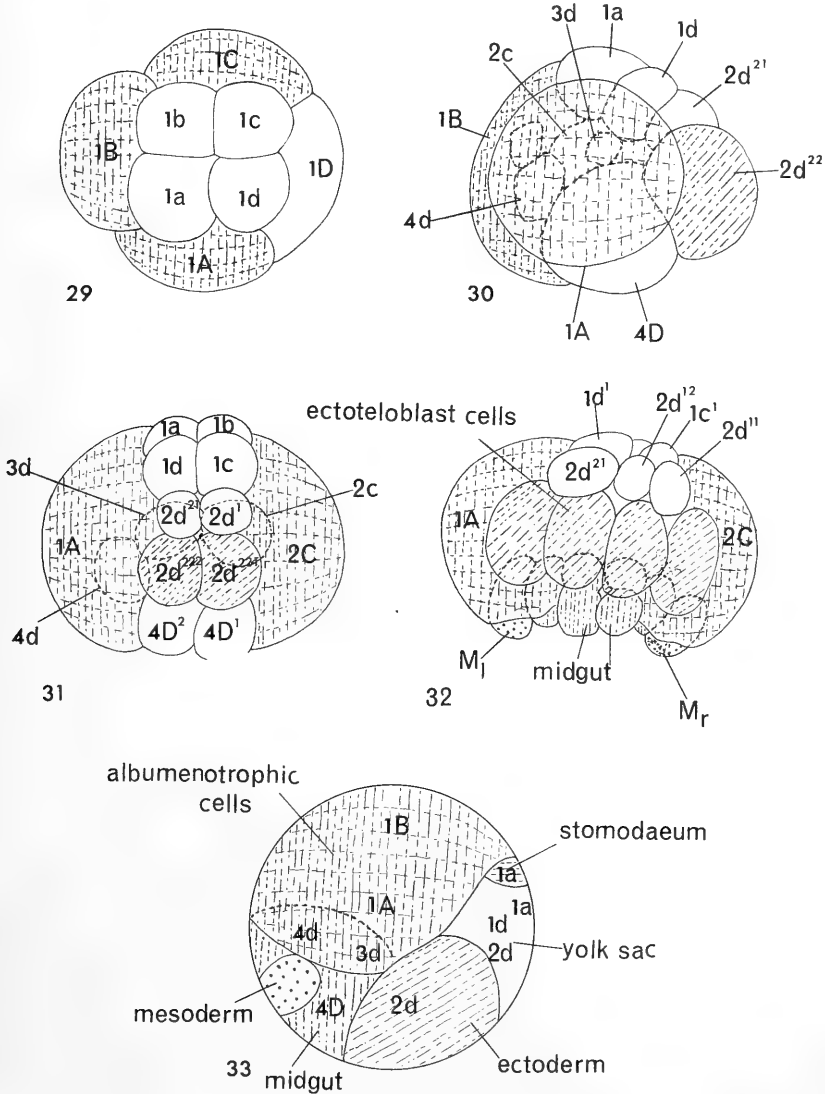
Further divisions are now specialized (Fig. 30). The large posterior 1D cell first divides transversely and equally into posterodorsal 2d and posteroventral 2D cells. The adjacent cell on the right, 1C, cuts off a small cell, 2c, upwards and inwards beneath the 1st quartette. 1A, 1B and 2C now do not divide again. Occupying the anterior and ventral surfaces of the embryo during cleavage, they eventually become overgrown during gastrulation and come to lie internally where they gradually degenerate. These cells clearly recall the three provisional excretory cells of earthworms. Although no mention is made in the work of Sukatschhoff, Dimpker or Schoumkiné of any pulsatory activity by the cells, or of the development of intracellular canals within them, it seems likely that their function is similar in leeches and oligochaetes, though whether excretory or absorptive is not yet clear. In leeches, as in earthworms, the relationship of the cells to the other presumptive areas suggests derivation from presumptive midgut, favouring a nutritive function.

From the posteroventral 2D stem cell, a second 3d, and third 4d, cell are cut off into the interior, leaving the large cell 4D still at the surface. Meanwhile, the posterodorsal 2d cell cuts off two small cells 2d¹ and 2d²¹ forwards at the surface behind the 1st quartette, leaving the large cell 2d²² still posterodorsal.

The dorsal micromere cap now begins to multiply and spread (Figs 31, 32). Behind it, the large 2d cell divides equally bilaterally into two, each of which further divides into a typical row of four ectoteloblasts on either side of the dorsal mid-line (Figs 31, 32). Posteroventrally, the large 4D cell also divides equally bilaterally into two, each of which then divides into a lateral cell and a group of three median cells (Fig. 32). The latter push forward into the interior beneath the ectoteloblasts and make contact with the cells previously cut off into the interior from 1C and 2D. The lateral products of the 2D cell are the M-cells, which now begin to bud off mesodermal bands in the usual manner. The internal products of 2D, together with 2c, constitute the presumptive midgut.

Taking into account the above series of divisions and what is known of gastrulation and subsequent development in *Erpobdella* and *Hirudo*, the

presumptive areas of these embryos (Fig. 33) can be seen to be identical with those of primitive leeches, if allowance is made for the paedogenetic specialization of the anteroventral and lateroventral stem cells and for a precocious movement of presumptive midgut cells into the interior during cleavage. The presumptive



Figs 29-33.—*Erpobdella*. 29, 8-cell stage, dorsal view with posterior end on the right. 30, 14-cell stage, left lateral view. 31, 16-cell stage, posterodorsal view. 32, 27-cell stage, posterior view. (After Sukatschoff, 1903; Dimpker, 1917.) 33, presumptive areas of *Erpobdella*, based on data of Sukatschoff (1903) and Dimpker (1917).

midgut, in association with secondary yolk reduction, is also much less voluminous than in primitive leeches, but is still segregated directly as a group of cells posteroventrally. Presumptive mesoderm lies as a pair of M-cells, one on either side posterolaterally, bordering the posteriorly displaced presumptive midgut. Presumptive ectoderm, dorsally, has a large ectoteloblast mother cell behind a

group of micromeres. Presumptive stomodaeum is made up by cells at the anterior margin of this group. Furthermore, the parallel with earthworms as a similar response to a similar nutritional situation is unmistakable, and is especially emphasized by the paedogenetic specialization of the "anterior" presumptive midgut cells as provisional embryonic, possibly albumenotrophic cells. In spite of great modification of the cleavage sequence, differently in earthworms and in gnathobdellid and pharyngobdellid leeches, and of changed embryonic nutritional relationships, the basic presumptive areas remain constant in composition, relative juxtaposition and fate.

Cleavage and presumptive areas in other clitellates

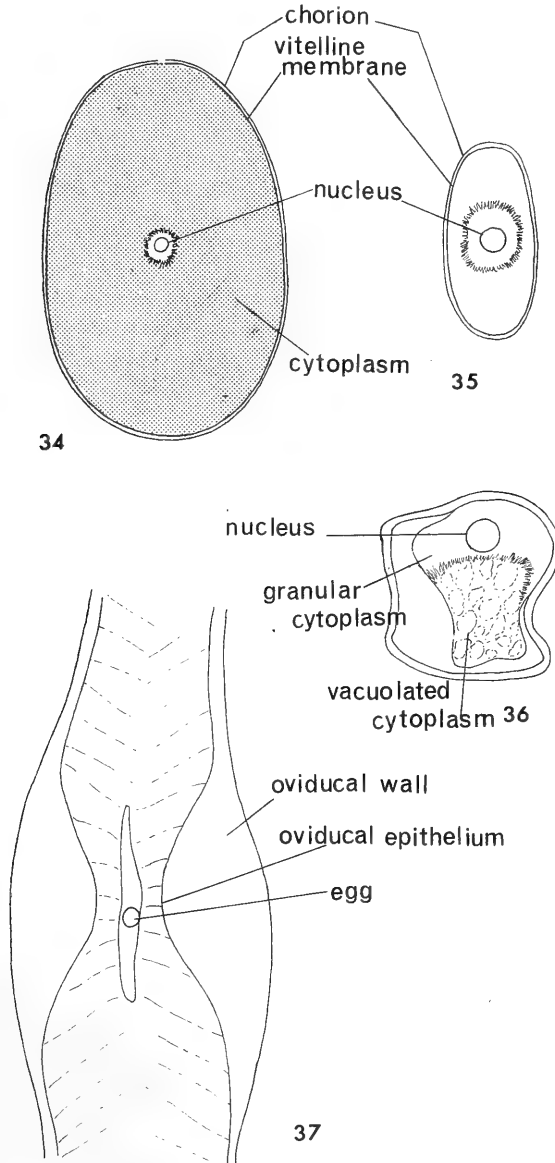
In other clitellates morphologically more primitive than the earthworms and gnathobdellid and pharyngobdellid leeches, namely, the naidid oligochaetes and piscicolid leeches, the eggs are also microlecithal. Here, however, in spite of the systematic position accorded to these families in their respective subclasses, cleavage and the trophic relationships of the embryo in the cocoon are yet more specialized. As the work of Swetloff (1926) and Dawydoff (1942) on naidids and of Schmidt (1921, 1924, 1925*b*, 1930, 1939, 1941, 1944) on piscicolids shows, one of the products of cleavage is a provisional cellular envelope within which ectoteloblasts, M-cells and presumptive midgut become established and express their fate in a normal clitellate manner, and it seems highly probable that the provisional envelope has an absorptive function, rapidly supplemented by further, precociously formed temporary organs subserving feeding on the ambient nutrient albumen of the cocoon. Although it is not intended at the present time to discuss the development of these embryos in detail, there is no doubt that they, too, can be interpreted as modifications of primitive clitellate development in which the basic pattern of presumptive areas is retained in combination with adaptations to albumenotrophy, and they are mentioned here for two reasons. Firstly, they illustrate how even the most aberrant modifications, seemingly totally unintelligible when described by the Wilsonian system of enumeration, can be understood relative to their primitive antecedents when the formation and fate of presumptive areas is recognized. Secondly, like the earthworms and the gnathobdellid and pharyngobdellid leeches, they exemplify the fact that parallel developmental modifications can originate from parallel, related antecedents and need not necessarily be assigned to a common ancestry.

Cleavage in the Onychophora

As has been shown above, cleavage and presumptive area formation in primitive clitellates are adapted to direct lecithotrophic development within a protective cocoon, all known cases of the development of clitellates with small eggs being interpretable as instances of secondary yolk loss, associated with specialized albumenotrophy. Furthermore, lecithotrophic clitellate development manifests a particular modification of the pattern of total spiral cleavage and presumptive area formation seen in yolky polychaete embryos. While it is not possible on this evidence to single out any living polychaete family as a clitellate ancestor, the general notion of a monophyletic relationship between clitellates and polychaetes is supported by the evidence of development. It is also clear that, as in polychaetes, the structure of the presumptive areas making up the wall of the blastula depends on the amount of reserve material incorporated into the egg and that cleavage is modified in ways commensurate with the establishment of these areas.

Now, just as the primitive eggs of clitellate annelids are relatively large and yolky, so too are those of Onychophora. As has been demonstrated especially by Manton (1949), all instances of the development of small eggs in Onychophora reveal evidence of secondary yolk loss. Yolky onychophoran eggs, however, are larger than those of clitellates and individually enclosed in adherent egg membranes, and secondary yolk loss is associated, not with cocoon life, but with viviparity. Concomitantly, the early development of yolky eggs in Onychophora

is more highly modified than that of clitellates, the specializations associated with onychophoran viviparity are different from those associated with clitellate albumenotrophy, and the early embryology of the two groups seems quite dissimilar.

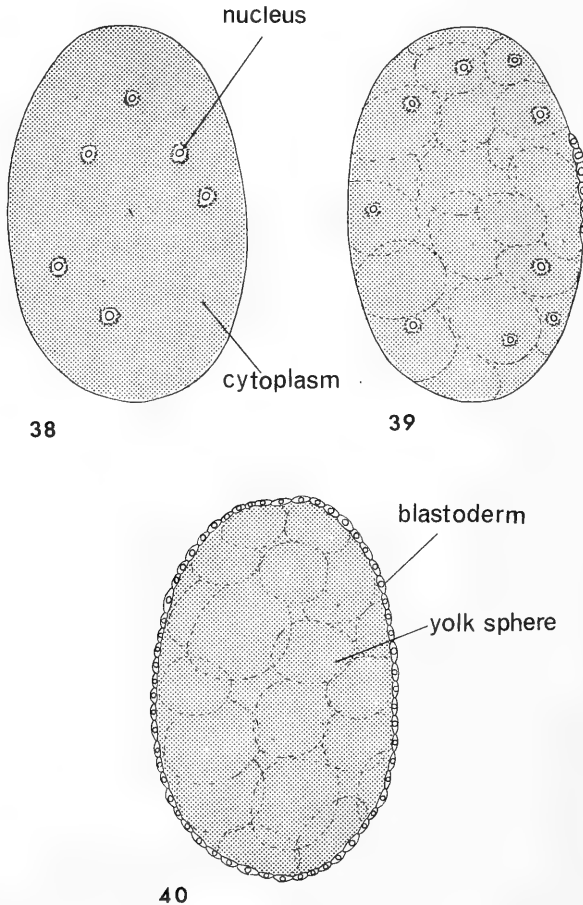


Figs 34–37.—34, diagrammatic longitudinal section through yolkly Onychophoran egg. 35, egg of *Peripatopsis balfourii* after dilatation. (After Manton, 1949.) 36, the same egg in transverse section. (After Manton, 1949.) 37, diagrammatic longitudinal section through upper oviduct of placental species, with zygote in lumen.

Only a little is known of the yolkly eggs of Onychophora, but it is clear that they combine dimensions of more than 1 mm. (*Ooperipatus*, 1.9 mm., Dendy, 1902; *Peripatoides novae zealandiae*, 1.5 mm., Sheldon, 1888; *Peripatoides orientalis*, 1.3 mm., Anderson, unpublished; *Eoperipatus weldoni*, 1.3 mm.,

Evans, 1902) with a primitive centrolecithal structure, dense with yolk, devoid of periplasm and containing the zygote nucleus in a more or less central cytoplasmic halo (Fig. 34). Two membranes enclose the egg, a thin vitelline membrane and an external chorion which is thick in the oviparous *Ooperipatus*, thin in the ovoviviparous *Peripatoides* and *Eoperipatus*.

The accounts of cleavage given by Sheldon (1888, 1889a) and Evans (1902), although incomplete, show that in yolky onychophoran eggs it follows the typical arthropod mode, with nuclei and associated cytoplasmic haloes dividing and



Figs 38-40.—Yolky onychophoran egg. 38, early cleavage, diagrammatic longitudinal section. 39, emergence of blastomeres at the surface, diagrammatic longitudinal section. 40, blastoderm stage, diagrammatic longitudinal section.

increasing in number in the yolk, then rising to the surface (Figs 38, 39). At the same time, the yolk divides into a number of irregular spheres. Grouped at first as a small disc of blastomeres, the superficial cells spread, with further divisions, to form a blastoderm enclosing the yolk spheres (Fig. 40). According to Sheldon, some of the nuclei and their cytoplasmic haloes in *Peripatoides novae zealandiae* remain within the yolk, but nothing is known of their fate, and Evans (1902) was unable to trace them in *Eoperipatus weldoni*. In general, it appears that cleavage in yolky onychophoran eggs is of a simple centrolecithal type, setting out a blastoderm around a yolk mass.

Development in the secondarily yolkless, viviparous Onychophora follows two modes, non-placental and placental. In the former, described with especial clarity for *Peripatopsis* by Manton (1949), the eggs released from the ovary are small and spherical (*P. sedgewicki*, 65–80 μ ; *P. moseleyi*, 150–172 μ ; *P. balfouri*, 380 μ ; *P. capensis*, 260 μ ; Sheldon, 1889*b*; Bouvier, 1904; Manton, 1949), but on entry into the oviduct, they swell rapidly and become ellipsoidal (*P. balfouri*, Fig. 35) or cylindrical with hemispherical ends. Their dimensions are then, *P. sedgewicki*, 260 \times 80 μ ; *P. moseleyi*, 520 \times 160 μ ; *P. balfouri*, 480 \times 220 μ ; and *P. capensis*, 600 \times 145 μ (Manton, 1949) and the swelling can be interpreted as a delayed partial recapitulation of the enlargement which occurs in a yolkly onychophoran egg during vitellogenesis. After swelling has taken place, the zygote nucleus lies in an irregular, granular cytoplasmic mass at one side of the egg (Fig. 36). The egg now becomes enclosed in two thin membranes which Manton (1949) suggests are vitelline membrane and chorion.

Early cleavage is similar in all four species (Figs 41–47). The cytoplasm of the egg breaks up into a number of spheres of different sizes, recalling the yolk spheres of *Peripatoides* and *Eoperipatus*, floating freely inside the egg membranes in a watery fluid. The zygote nucleus lies in one of the spheres, while the remainder are anucleate pseudoblastomeres. The onset of cleavage mitoses is thus somewhat delayed. When it occurs, the 1st blastomere divides to form a disc of blastomeres apposed to the inner surface of the egg membranes on one side of the egg, recalling the blastomere disc of the yolkly-egged species. As they form, the blastomeres of the disc gradually absorb the material of the disintegrating pseudoblastomeres. By the time 64 cells are present, the blastomere disc extends as a saddle around two-thirds of the egg circumference, leaving one side and both ends blastomere-free.

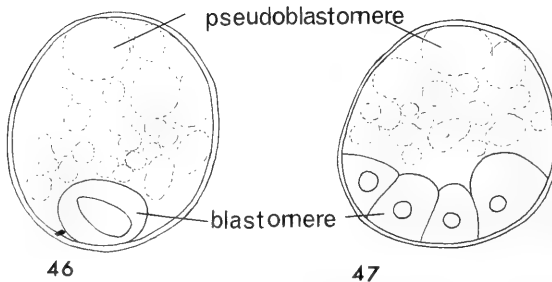
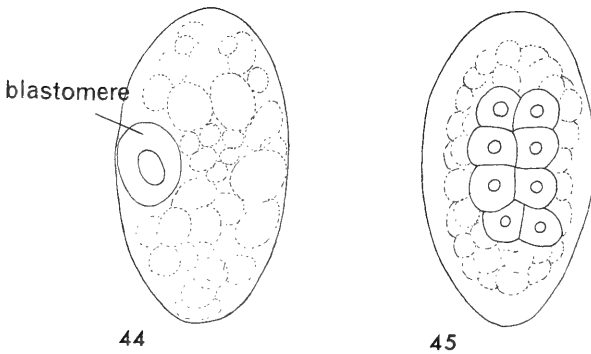
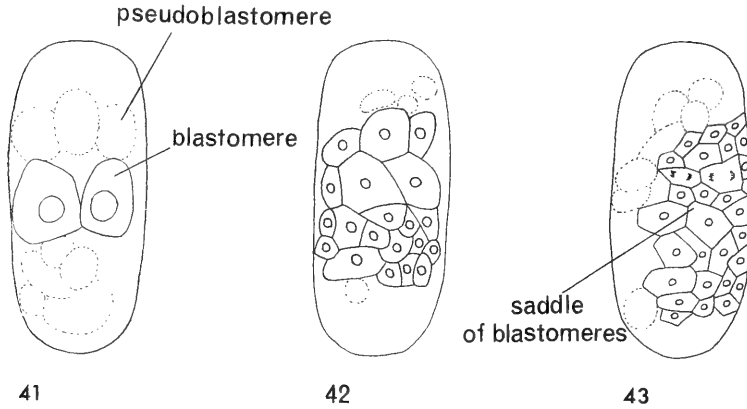
In *P. sedgewicki* and *P. moseleyi*, the saddle of blastomeres now gives rise by further cell division and marginal closure to a blastoderm of about 160 cells around a central fluid-filled space (Fig. 48). Cell division continues and at the same time the vitelline membrane is absorbed and the blastoderm swells by fluid uptake, stretching the outer membrane, until its diameter becomes, in *P. sedgewicki*, about 1000 \times 500 μ , in *P. moseleyi*, about 900 \times 500 μ . The only difference between these embryos and the more primitive yolkly onychophoran embryos at the same stage is replacement of yolk by fluid in the blastocoel.

In *P. capensis*, cleavage and blastoderm formation overlap a precocious onset of movement of cells into the interior (Figs 49, 50). At the edges of the saddle of blastomeres, cells enlarge and move into the concavity of the saddle. This process continues as the saddle cells divide further and spread as a blastoderm, so that the inner surface of the blastoderm becomes lined with large, vacuolated cells. The edges of the outer layer finally form a slit orientated along the anteroposterior axis of the embryo, and with closure of the slit the blastoderm becomes complete. No dilatation of the blastoderm occurs in *P. capensis*, although the surrounding egg membranes swell to the expected size as a result of fluid ingress.

In *P. balfouri* (Figs 51–54), the marginal cells of the saddle of blastomeres also enlarge and move into the interior as the saddle spreads to form a blastoderm, so that the blastocoel is temporarily filled with a mass of vacuolated cells; but these now disintegrate, while at the same time the blastoderm dilates, attaining a final condition like that of *P. sedgewicki* and *P. moseleyi*. The significance of the cleavage peculiarities of *P. capensis* and *P. balfouri* as compared with *P. sedgewicki* and *P. moseleyi* will be taken up below.

The placental viviparous Onychophora have eggs which are even smaller than those of the non-placental species and, furthermore, lack the recapitulatory swelling of the egg after release from the ovary (Fig. 37). Dimensions lie between 25 μ and 40 μ (Bouvier, 1904) and enclosing membranes are absent (Kennel, 1884, 1885; Sclater, 1888). Cleavage in these eggs is little understood. Kennel (1884, 1886) and Sclater (1888) showed, and further unpublished observations

by Manton and myself have confirmed, that it is total and equal, resulting in the formation of a morula lying in the lumen of the oviduct (Fig. 55). With further cell divisions, the morula becomes hollow, with a wall one cell thick, before attaching to the oviducal wall (Fig. 56). Rather than dilating to form a blastoderm, the hollow vesicle enters immediately into a further specialized phase, in which the cells in the region of attachment multiply to form a hollow stalk addressed terminally as a flat placental plate against the oviducal wall,



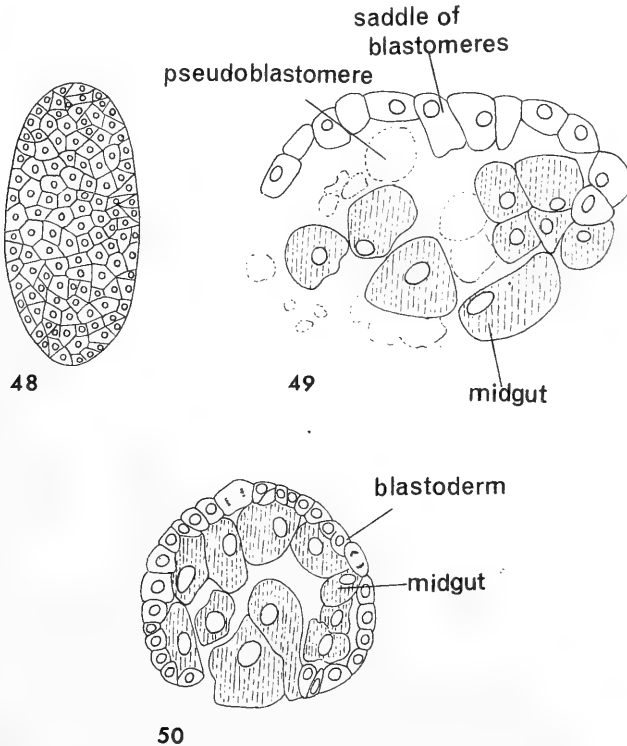
Figs 41-43.—*Peripatopsis moseleyi*. 41, 2-cell stage. 42, 21-cell stage. 43, saddle of blastomeres (After Manton, 1949.)

Figs 44-47.—*Peripatopsis balfouri*. 44, 1-cell stage. 45, 8-cell stage. 46, 1-cell stage, transverse section. 47, 16-cell stage, transverse section. (After Manton, 1949.)

while the remaining cells multiply to increase the size and cell number of the hollow vesicle at the free end of the stalk (Fig. 57). The further development and comparative significance of the stalk and vesicle will be examined below.

Developmental fate of the cleavage blastomeres in Onychophora

Just as in the Clitellata, the cells of the blastoderm or its equivalent immediate pre-gastrula stage in Onychophora can be assigned to presumptive areas of specific subsequent fate by taking account of the events of gastrulation and later development. The focal point in the elucidation of these presumptive areas is the composition of the blastoderm in yolky onychophoran embryos. Unfortunately, one of the weaknesses of Sheldon's work on *Peripatoides novae*

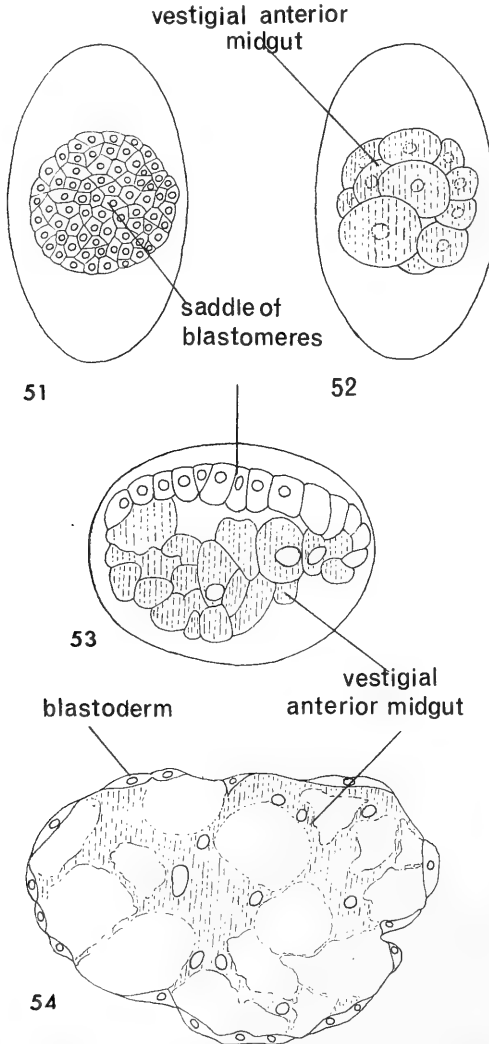


Figs 48-50.—48, *Peripatopsis moseleyi*, blastoderm stage before dilatation. 49, *P. capensis*, section through late cleavage stage. 50, *P. capensis*, section through almost completed blastoderm. (After Manton, 1949.)

zealandiae, and a matter calling urgently for reinvestigation, is a lack of accurate description of gastrulation and early segment formation. At the same time, Sheldon's results, together with those of Evans (1902) and some preliminary unpublished observations of my own on embryos of *Peripatoides orientalis* from New South Wales, permit the tentative construction of a presumptive area map for ovoviviparous species (Fig. 58). Anteroposterior and dorsoventral axes are fixed, the former corresponding to the long axis of the egg. Midventrally lies a long narrow band of presumptive midgut cells, soon to migrate into the interior, leaving an elongate slit at the surface. At the margin of the presumptive midgut lie, anteriorly, presumptive stomodaeum, laterally, paired ventrolateral bands of temporary yolk sac ectoderm and, posteriorly, presumptive proctodaeum. Midventrally behind the latter lie small areas of presumptive posterior midgut and presumptive mesoderm. Associated with the latter are presumptive germ

cells. Lateral to the ventral areas listed above, and converging posteriorly on the presumptive mesoderm, are two broad bands of presumptive ectoderm. Dorsally lies a further broad area of temporary yolk sac ectoderm.

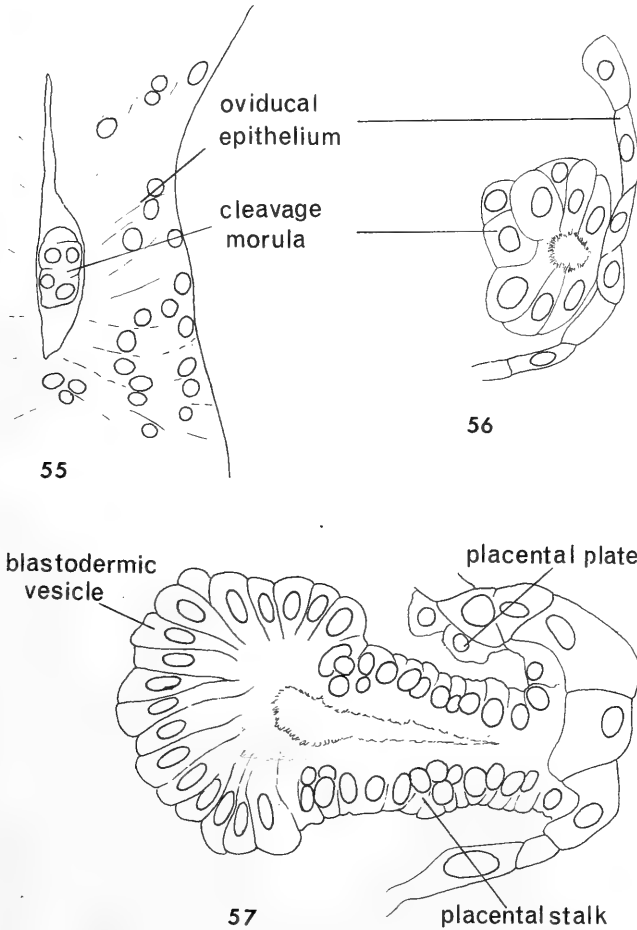
The data of Manton (1949) permit much more firmly substantiated presumptive area maps to be drawn for the viviparous non-placental *Peripatopsis*. In no case in this genus does the anteroposterior axis of the embryo correspond



Figs 51-54.—*Peripatopsis balfouri*. 51, saddle of blastomeres stage. 52, same embryo from opposite side, showing vacuolated cells. 53, transverse section through early saddle of blastomeres stage. 54, transverse section through blastoderm stage. (After Manton, 1949.)

to the long axis of the egg. It may fall in any direction, suggesting that the axial relations of the embryos are established late, after blastoderm formation, by processes which are at present obscure. This, however, does not confound the reality of the presumptive areas which can be discerned. In *P. sedgewicki* they centre on a terminal, and in *P. moseleyi* a lateral cell group which lie postero-ventrally relative to future development. The cells of the group (Fig. 59)

comprise presumptive mesoderm, presumptive posterior midgut anterior and internal to the mesoderm, presumptive ectoderm marginally, and a number of presumptive germ cells. The latter tend to lie between the presumptive midgut and presumptive mesoderm in *P. moseleyi* and at the posterior end of the presumptive mesoderm in *P. sedgewicki*, a minor discrepancy of localization with no special significance. Immediately anterior to the presumptive posterior midgut lie the presumptive proctodaeum and stomodaeum, conjoined. Lateral to them are ventrolateral bands of presumptive temporary yolk sac ectoderm, followed by

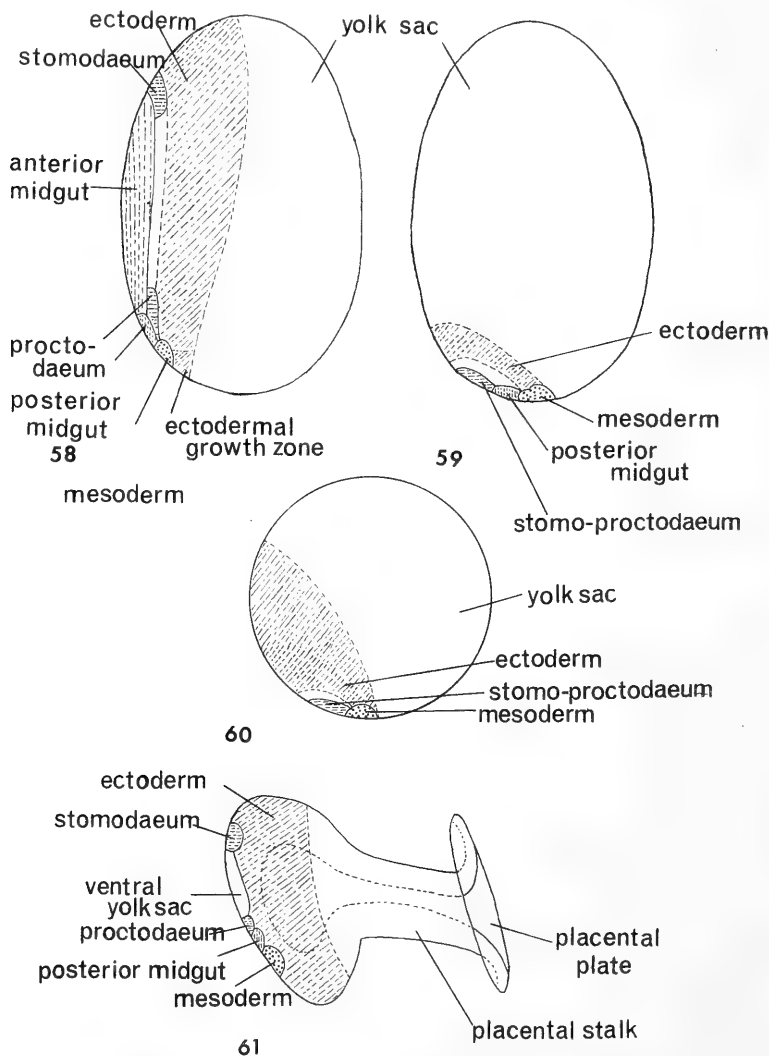


Figs 55-57.—Viviparous placental onychophoran. 55, early cleavage morula. 56, later morula attached to oviducal wall. 57, blastodermic vesicle and placental stalk.

broad bands of presumptive embryonic ectoderm, with the remainder of the blastoderm, laterally and dorsally, constituting further temporary yolk sac ectoderm.

The blastodermal presumptive areas of *P. balfourii* are identical with those described above, with the presumptive germ cells arising from the presumptive mesoderm as in *P. sedgewicki*. It is necessary to take into account, however, the temporary vacuolated cells budded off in *P. balfourii* from the edge of the saddle of blastomeres into the interior during blastoderm formation. Since the point towards which these proliferating edges converge and close subsequently forms the presumptive stomodaeum and proctodaeum, a place can be assigned

along the ventral midline of the latter as the site of origin of the temporary vacuolated cells, already budded off. By comparison with the presumptive area map for yolky species, the temporary vacuolated cells would appear to be modified midgut cells, as suggested by Manton (1949).



Figs 58–61.—58, presumptive areas of the blastoderm of yolky Onychophora, diagrammatic lateral view. 59, presumptive areas of the blastoderm of *Peripatopsis sedgewicki*, diagrammatic lateral view. 60, presumptive areas of the blastoderm of *P. capensis*, diagrammatic lateral view. 61, presumptive areas of the blastoderm of viviparous placental Onychophora, diagrammatic lateral view. (Figs 59 and 60 based on Manton, 1949.)

In *P. capensis*, where the blastoderm remains undilated, its presumptive areas show some differences from the preceding species (Fig. 60). Presumptive mesoderm, with which the presumptive germ cells are again associated, remains the same, as do the presumptive proctodaeum and stomodaeum in front of the mesoderm, ventrolateral temporary yolk sac on either side, embryonic ectoderm as paired lateral bands and further yolk sac ectoderm dorsally. The

yolk sac component, however, is not attenuated, and a presumptive posterior midgut area is absent. The midgut rudiment has already become internal, since it is formed by the cells which migrate into the interior from the edges of the saddle of blastomeres during cleavage and line the blastoderm internally. Midgut formation in this way, like the temporary midgut formation of *P. balfouri*, can be interpreted as a precocious budding from the future midline of the presumptive stomodaeum and proctodaeum, the point at which the blastodermal edges converge and fuse.

For the viviparous placental Onychophora, the work of Kennel (1884, 1885) and Sclater (1888) and a few unpublished personal observations lead to the following comments on presumptive areas (Fig. 61). By the time that these areas become discernible, the dorsal temporary yolk sac ectoderm has already grown out as placental stalk and plate, as well as occupying the dorsal surface of the blastodermic vesicle. The remaining areas show the expected orientation, but are small and compressed together. Presumptive mesoderm lies postero-ventrally, with presumptive posterior midgut in front of it, then presumptive proctodaeum. Presumptive ventral temporary yolk sac ectoderm occupies the ventral midline, with presumptive stomodaeum anterior to it. Laterally and anteriorly lie paired bands of presumptive ectoderm. The similarity of this presumptive area pattern to that of other Onychophora is clear, in spite of great differences in egg size and mode of cleavage, and is analogous to the similarities described above for the presumptive areas of yolky and secondarily yolkless clitellate embryos. In fact, throughout the Onychophora, in spite of great variations in mode of cleavage, the configuration of presumptive areas shows the same stability as in clitellates, only the presumptive midgut and temporary yolk sac ectoderm, the two areas intimately involved with the yolk, being much affected by secondary yolk loss.

GASTRULATION

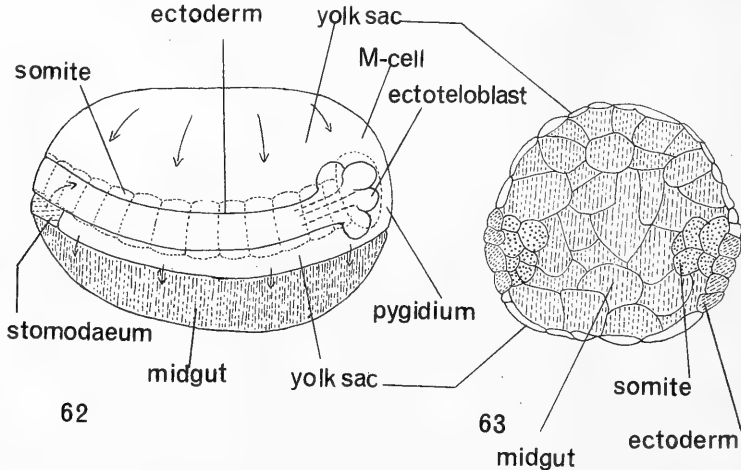
The considerations which have been presented so far permit the recognition of basic presumptive area patterns for the clitellate blastula and the onychophoran blastoderm. Comparison of the two patterns reveals, in the first instance, little in common between them. Presumptive areas, however, have not only a location but a fate, the expression of which begins with gastrulation. Indeed, gastrulation is most satisfactorily defined as the migration of the presumptive areas of the blastula or blastoderm into their organ-forming positions, consequent upon which the fate of the cells of each area is expressed in organ formation itself. This, of course, is not a new definition, being the one which has been employed by workers on vertebrate embryos for many years, but its applicability to invertebrate embryos has only recently been recognized (Anderson, 1962, 1966*a*, 1966*b*). When the parameters, not only of location and fate, but also of mode of expression of this fate, are brought into consideration, the seeming dissimilarity between primitive clitellate and primitive onychophoran embryos all but vanishes. The gastrulation phenomena of the albumenotrophic clitellate embryos, through which a microlecithal blastula becomes transformed into a precocious feeding stage with temporary functional organs, although they can be interpreted as secondary modifications of the gastrulation sequence of primitive lecithotrophic clitellate embryos, will not be discussed in the present context, since they are not pertinent to the comparison with Onychophora.

Primitive gastrulation in the Clitellata

Commensurate with the similarity of their presumptive areas, gastrulation takes an identical course in primitive oligochaetes and primitive leeches. Accounts of gastrulation have been given for *Tubifex* by Penners (1924) and Meyer (1929), for *Pelosclex* by Penners (1929) and for *Rhynchelmis* by Kowalevsky (1871), Vedjovskiy (1888-92) and Iwanoff (1928). The work of Whitman (1878, 1887) on *Glossiphonia* and Schmidt (1917) on *Theromyzon*, together with some fragments

in the papers of Nusbaum (1886) and Bürger (1902), provides corresponding information in the glossiphoniid leeches. Together, these studies yield a reasonably detailed picture, though further investigation is desirable.

As might be expected (Figs 62, 63), the large, yolk presumptive midgut rudiment becomes internal as a result of overgrowth by other cells. Cell divisions continue while the rudiment is still exposed at the surface, producing a solid mass of polygonal yolk cells. Presumptive ectoderm, as it continues to develop, spreads down on either side of this mass, eventually meeting in the midline ventrally to enclose it. Complete enclosure is not achieved until most of the segments formed in the embryo have been delineated.



Figs 62-63.—62, gastrulation in yolk clitellate embryo, diagrammatic lateral view. 63, transverse section through gastrula of *Tubifex*. (After Kowalevsky, 1871; Whitman, 1878; Penners, 1924; Meyer, 1929.)

The M-cells, as in yolk polychaetes (Anderson, 1966a), begin their teloblastic activity while still at the surface, so that budding overlaps the gastrulation movements of these cells into the interior. The latter comes about partly by an inward sinking of the M-cells on either side of the midgut posteriorly, but mainly by overgrowth by the posterior edge of the presumptive ectoderm, which spreads back over the M-cells as far as the edge of the exposed presumptive midgut.

The presumptive stomodaeum, formed as a flat plate of cells at the surface in front of the presumptive midgut, grows into the interior by cell division as a solid mass, formation of a lumen being much delayed.

The overgrowth and enclosure role of the presumptive ectoderm in primitive clitellate gastrulation is attained mainly through cell division and attenuation of the temporary yolk sac component of this area. The temporary assumption of this form by the majority of the presumptive ectoderm is, in fact, a primitive adaptation to rapid completion of an ectodermal surface layer around a large mass of yolk midgut. The ectoteloblasts, in contrast, proceed directly into processes underlying adult organogeny, while being moved from a dorsolateral to a lateral position as the temporary yolk sac ectoderm spreads. As already indicated, they begin their teloblastic activity as soon as they are formed, budding off four parallel rows of cuboidal cells on either side which push forwards towards the anterior end. The cell rows remain superficial, cleaving a path through the temporary yolk sac ectoderm, which at the same time pushes them ventrally as it spreads. The ectoblast rows of each side eventually meet in the midline, first anteriorly in front of the stomodaeal rudiment, then midventrally behind

the stomodaeum and progressively more posteriorly, completing enclosure of the midgut. Most of the temporary yolk sac ectoderm now lies dorsally between the two ectoblast bands, but a narrow strip also persists along the ventral edge of each band and, at the completion of gastrulation by midventral ectodermal fusion, comes to occupy the ventral midline as far forward as the stomodaeal rudiment. Posteriorly it remains contiguous with the pygidial temporary yolk sac ectoderm.

As the ectoblast bands grow in length, the mesodermal bands budded from the M-cells grow beneath them and are similarly carried, first to a lateral, then to a ventrolateral position. The development of these bands as paired segmental somites proceeds in anteroposterior succession and precedes corresponding segment delineation of the overlying ectoblast bands. Later in development, the temporary yolk sac ectoderm is incorporated segmentally into the segmental epithelium, save for the most posterior part, which transforms into the pygidial epithelium. A short intucking of the latter at the anus gives rise to a rudimentary proctodaeum.

Gastrulation in the Onychophora

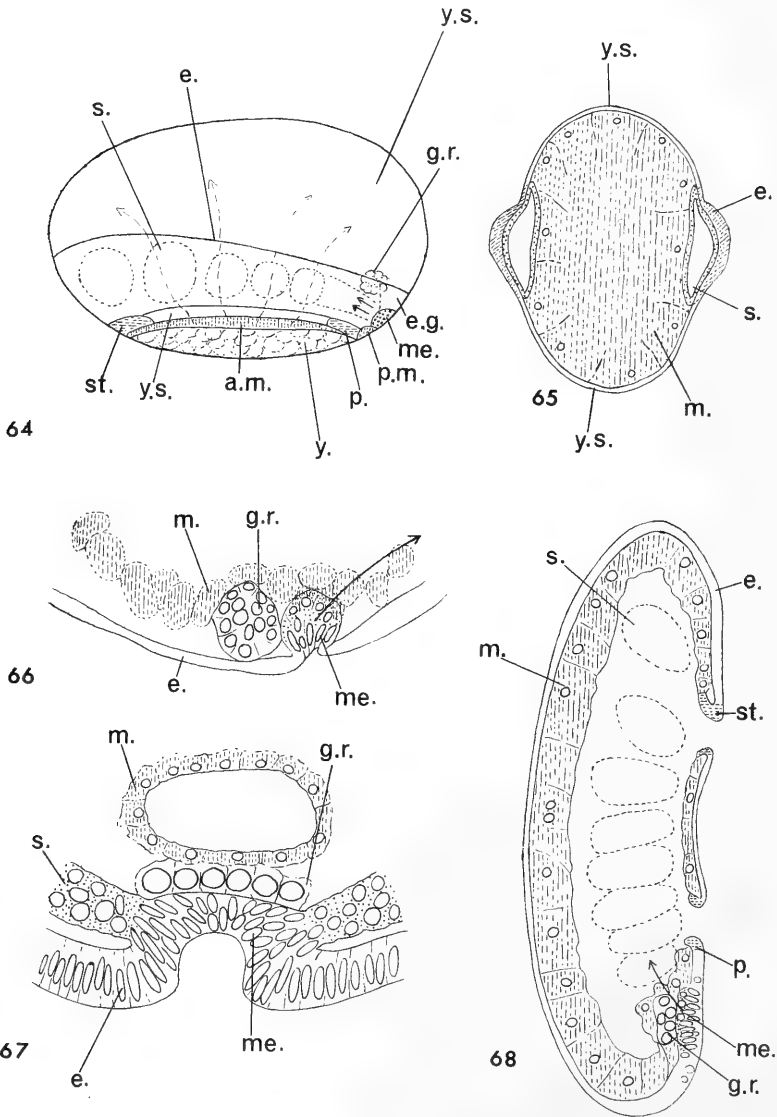
Unlike the clitellates, whose basic gastrulation sequence is adequately displayed by reference to lecithotrophic examples alone, the Onychophora call at the present time for consideration both of yolky and of secondarily yolkless species. As pointed out above, only the work of Manton (1949) on the secondarily yolkless *Peripatopsis* provides modern histological data on the early embryology of the group, so that to approach onychophoran gastrulation without reference to this work would be to ignore almost all of the pertinent evidence. Fortunately, as will be shown below, onychophoran gastrulation is little modified in consequence of secondary yolk loss, so that the events in *Peripatopsis* have an immediate bearing on primitive onychophoran gastrulation and its comparison with clitellates.

In yolky onychophoran embryos, where all presumptive areas are composed of small cells at the surface of a yolk mass, the direct entry of whole areas into the interior, conforming to the definition of gastrulation given above, is at a minimum. For the most part, cells which become internal are budded off from presumptive areas which retain a more or less superficial position and enter directly into organogeny. This condition is also retained in the secondarily yolkless species, the only exceptions being a precocious gastrulation activity of the presumptive midgut in *Peripatopsis capensis* and its vestigial equivalent in *Peripatopsis balfouri* (see below).

The presumptive midventral midgut in yolky embryos seems to retain a definite gastrulation movement (Fig. 64), sinking inwards at the onset of gastrulation, then separating to either side leaving a long midventral slit through which the yolk is exposed at the surface (Sheldon, 1888, 1889a; Evans, 1902; unpublished personal observations). The paired bands of sunken presumptive midgut cells become mitotically active, budding off further cells which migrate outwards and upwards through the peripheral yolk, acting temporarily as vitellophages and becoming enlarged and diffuse as they move, but eventually enclosing the yolk mass and forming the anterior part of the definitive midgut epithelium. At the same time, the presumptive posterior midgut area sinks slightly inwards and begins to proliferate cells which add to the midgut epithelium at the posterior end of the yolk (Fig. 64). It is likely that the latter activity is prolonged, resulting in progressive extension of the midgut as the trunk segments develop, but is completed before the full number of trunk segments is formed.

In *Peripatopsis sedgewicki*, *P. moseleyi* and *P. balfouri* (Manton, 1949), cells proliferated from the slightly invaginated presumptive posterior midgut form the entire midgut epithelium, spreading forwards and upwards beneath the

blastoderm to enclose a central fluid-filled space, and continuing to be proliferated until almost all of the trunk segments are formed (Fig. 68). The mid-ventral temporary vitellophage component of the midgut is lost in *P. sedgewicki* and *P. moseleyi* and only vestigially retained, with precocious proliferation during cleavage, in *P. balfouri*. In *Peripatopsis capensis*, in contrast, the mid-ventral component comes to line the inner surface of the blastoderm during cleavage,



Figs 64-68.—64, gastrulation in yolkly onychophoran embryo, diagrammatic lateral view. 65, transverse section through yolkly onychophoran gastrula. 66, sagittal section through proliferating presumptive mesoderm of *Peripatopsis moseleyi*. 67, transverse section through proliferating presumptive mesoderm of viviparous placental onychophoran. 68, sagittal section through embryo of *Peripatopsis balfouri*. (a.m., anterior midgut; e., ectoderm; e.g., ectodermal growth zone; g.r., genital rudiment; m., midgut; me., presumptive mesoderm; p., proctodaeum; p.m., posterior midgut; s., somite mesoderm; st., stomodaeum; y, yolk; y.s., temporary yolk sac ectoderm.) (Figs 66 and 68 after Manton, 1949.)

as described above, and develops directly as midgut epithelium, the posterior midgut area being lost.

The midgut in viviparous placental species again arises by prolonged proliferation from the presumptive posterior midgut area (Kennel, 1884, 1885; Selater, 1888; unpublished personal observations). After a slight insinking at the onset of gastrulation, the area proliferates cells which spread forwards and upwards to form an elongated epithelial sac. No trace of a midventral component is retained in these species.

In respect of onychophoran midgut development, then, gastrulation in the sense of movements of presumptive areas is slight and each one progresses quickly into proliferation as a precocious onset of organogeny. The significance of this as an adaptation to lecithotrophy will be discussed below.

The same feature characterizes entry of mesoderm into the interior in Onychophora and in the case is accompanied by consistent behaviour in all species (Sedgewick, 1885-1888; Sheldon, 1888; Kennel, 1884, 1885; Evans, 1902; Manton, 1949). The presumptive mesoderm invaginates a little and commences active proliferation, budding off two streams of cells which migrate forwards along bilaterally symmetrical ventrolateral paths (Figs 64-68). Proliferation continues until the mesoderm of all segments is established, by which time of course the anterior parts of the mesodermal bands are well advanced into organogeny. The unmodified persistence in secondarily yolckless embryos of a mode of mesoderm development obviously adapted to extreme lecithotrophy is in marked contrast to the variations in midgut development. Presumptive germ cells also show consistent gastrulation activity throughout the Onychophora, in spite of minor differences of localization in different species. Early in gastrulation they migrate inwards to lie immediately internal to the area of proliferating mesoderm (Figs 66, 67, 68), both in yolky and in secondarily yolckless species (Manton, 1949; unpublished personal observations). Once again, the basic adaptation to lecithotrophy persists with loss of yolk. In *Peripatopsis moseleyi*, where the cells are initially associated with presumptive posterior midgut, they become distinct before the midgut area begins to proliferate, moving into the interior and differentiating by nuclear enlargement, development of nucleoli and reduction to cytoplasmic basophilia, a characteristic germ cell pattern. In *P. sedgewicki*, *P. balfouri* and *P. capensis*, where the initial association is with presumptive mesoderm, differentiation of the germ cells follows migration into the interior as part of the first products of the mesodermal area, but subsequently proceeds in the same way.

Gastrulation activity in the stomodaeal and proctodaeal presumptive areas is closely linked with that of the presumptive midgut. In contrast to clitellate primitive gastrulation, in which the stomodaeal and proctodaeal areas remain superficial and penetrate into the interior by growth and cell division before developing lumina, these areas in yolky onychophoran embryos can be surmised, from the work of Sheldon (1888, 1889a) and Evans (1902), to invaginate shallowly at the ends of the midventral presumptive midgut invagination (Fig. 64). The lateral lips of this invagination separate from the edges of the midgut rudiment as these come together in the ventral midline below the yolk, and unite midventrally at the surface to establish the broad ventral band of temporary yolk sac ectoderm (Fig. 65). At each end, the stomodaeal and proctodaeal invaginations are thereby closed off as short tubes, each of which now proceeds to elongate and push inwards by cell division.

The results of Manton (1949) can be interpreted to show that in *Peripatopsis*, in spite of the absence of a midventral presumptive midgut component in the blastoderm, much of this sequence is retained. The confluent stomodaeal and proctodaeal presumptive areas invaginate together, producing a short midventral slit. The slit elongates (just how it does this is not clear, but ventral temporary yolk sac ectoderm cells appear to multiply to form its lateral lips) pushing the

stomodaeal and proctodaeal rudiments apart. At the same time, the midgut cells below the surface separate along the midventral line and establish contiguity with the edges of the slit so that the latter opens into the midgut cavity. The similarity of this to the corresponding stage described by Sheldon and Evans in yolky embryos is remarkable, although it is attained in a different way in association with presumptive midgut modifications related to secondary yolklessness. Further steps proceed as in yolky species. The midgut epithelium separates once again from the lateral lips of the ventral slit and closes midventrally. The lips themselves also close midventrally at the surface, establishing the narrow midventral band of temporary yolk sac ectoderm found in these species and completing the tubulation of the short stomodaeum and proctodaeum (Fig. 68). Elongation of the latter by cell division now proceeds.

In viviparous placental Onychophora, in association with extreme secondary reduction of the blastoderm, stomodaeal and proctodaeal gastrulation activity is greatly simplified, each area invaginating directly as a short tube (Kennel, 1884, 1885; unpublished personal observations).

Presumptive embryonic ectoderm in Onychophora, formed in situ in the blastoderm as paired ventrolateral ectodermal bands (Figs 64, 65), shows no gastrulation activity. The dorsal component of the temporary yolk sac ectoderm also lacks this activity. The paired ventral component in yolky and secondarily yolkless non-placental species comes together in the ventral midline during gastrulation as described above, to complete the ectodermal covering of the embryo. In placental species, this component is narrow and unpaired and forms directly in its definitive position. In general, the presumptive ectoderm in Onychophora proceeds directly into organogeny after formation, through blastoderm formation, as an almost complete covering epithelium. The spread of ectoderm in gastrulation following total spiral cleavage, as in clitellates, is obviated by this adaptation.

Comparison of gastrulation activities in the three main types of embryo in Onychophora only serves to emphasize, as in annelids (Anderson, 1966a and above), the remarkable stability of their presumptive areas irrespective of great differences in egg size, mode of embryonic nutrition and associated modifications of cleavage. The presumptive areas of all species are not only set out in the same relative juxtaposition but also proceed into the same lines of developmental activity; and where they do not, the differences are easily explained. Presumptive embryonic ectoderm, mesoderm and germ cells develop consistently in all species, irrespective of yolk loss. The dorsal component of the temporary yolk sac ectoderm may remain unexpanded following yolk loss (*Peripatopsis capensis*), but is always retained. The paired ventral component, in spite of yolk loss, maintains its role in assisting stomodaeal and proctodaeal invagination, except in the very small embryos of placental species, where it is greatly reduced. Stomodaeum and proctodaeum formation proceed in viviparous non-placental species in the same manner as in yolky species, and in a manner in placental species which is a direct simplification of this. The presumptive midgut is more affected by yolk loss, but only in simple ways. In most cases, the midventral area, which in yolky embryos produces the cells acting temporarily as vitellophages, is absent (retained vestigially in *Peripatopsis balfouri*) and midgut formation devolves wholly upon the posterior proliferative area. In *Peripatopsis capensis* the reverse has occurred, the posterior area being absent. Both types of modification are simplifications of the primitive condition of a dual development of midgut cells subserving temporary vitellophage function in a large yolk mass anteriorly and simultaneous elongation of the gut posteriorly, and both are equally advantageous in the absence of yolk.

In short, young onychophoran embryos are much less different from one another than they seem and the developmental peculiarities of the various types of yolkless embryo can be interpreted as simple derivations of a basic yolky type.

THE TRANSITION FROM SPIRAL TO CENTROLECITHAL CLEAVAGE AND
THE ORIGIN OF THE ONYCHOPHORA

Clitellate annelids such as *Tubifex*, *Rhynchelmis*, *Glossiphonia* and *Theromyzon* illustrate the adaptation of annelid development to extreme lecithotrophy without loss of total cleavage, the formation and structure of each presumptive area of the blastula being appropriately modified as compared with those of polychaetes. Yolky onychophoran embryos, with centrolecithal cleavage and a blastoderm, can reasonably be assumed to have a presumptive area pattern as outlined above. It can now be seen that each of the presumptive areas in Onychophora has its functional equivalent in the Clitellata, and the two can be compared as follows (Figs 13, 14, 18, 58).

The *presumptive midgut* is midventral to posterior in both. In clitellates it comprises a group of large yolky cells forming the ventral wall of the blastula. There is also reason to believe that it includes a number of small posterior midgut cells cut off from the M-cells. Although these cells have not been recorded in lecithotrophic clitellate embryos, they are known to be present in albumenotrophic clitellate embryos (Tannreuther, 1915; Swetloff, 1923b). They also occur in certain lecithotrophic polychaete embryos in which the large, yolky, ventral midgut cells show vitellophage adaptation and the small posterior midgut cells behind them give rise to the posterior part of the midgut in the growing trunk (see Anderson, 1966a). Since the posterior midgut cells have the same fate in secondarily specialized albumenotrophic clitellate embryos, it seems likely that they are also present in primitive lecithotrophic clitellate embryos, in which the further development of the yolky midgut cells shows extreme vitellophage specialization (Whitman, 1878, 1887; Bürger, 1902; Vedjovsky, 1888-92; Schmidt, 1917, 1922; Penners, 1924, 1934; Iwanoff, 1928) and the development of the posterior part of the midgut in the growing trunk has not been carefully studied.

In the Onychophora, the presumptive midgut comprises a ventral sheet of blastoderm cells and a separate small group of cells posteriorly in the midline, just in front of the presumptive mesoderm.

The large, yolky cells in clitellates undergo divisions as they become internal and show vitellophage specialization, usually by segregation of small cells within a yolk syncytium, before giving rise to the major part of the midgut. Posterior midgut cells probably sink in and multiply to form the posterior part of the midgut in the growing trunk. In Onychophora, the ventral presumptive midgut cells sink slightly into the yolk and bud at the surface, producing small cells which migrate through the yolk acting as vitellophages, then accumulate at the yolk surface as the main anterior part of the midgut. The presumptive posterior midgut cells sink in slightly, then bud off a stream of cells which form the posterior part of the midgut in the growing trunk. The midgut presumptive areas in both are thus, so far as can be discerned, similar in relative position and fate, and differ only in the greater adaptation of the onychophoran areas to yolk, through (i) early segregation of cells from yolk, ventrally and posteriorly; (ii) budding of ventral cells at the surface and migration through the yolk mass; (iii) early temporary vitellophage function of the migrating cells; (iv) budding of posterior cells at the surface; (v) greater contribution by posterior cells to midgut formation, associated with greater vitellophage specialization of the ventral component in the large yolk mass anteriorly.

For the experimentalist, the critical problem of this transition is how the epigenetic system producing a large yolky cell determined as midgut and regionalized ventrally can transform into the epigenetic system producing a small yolkless cell, identically determined and regionalized, at the surface of an acellular internal yolk mass. Although several embryos in which this transition takes place during cleavage are known among arthropods, the epigenetics of such processes are still obscure.

The *presumptive mesoderm* in clitellates and Onychophora is posterior in both. In the former it comprises a pair of large M-cells which become active as teloblasts while still at the surface, budding off two lateral streams of cells, potentially metameric, which push forward on either side of the yolky developing midgut. As they bud, the teloblasts gradually sink below the surface. In Onychophora, the presumptive mesoderm comprises a group of small cells cut off at the yolk surface, which sink in slightly and bud off two lateral streams of cells, again potentially metameric, pushing anteriorly on either side of the yolk in a similar way. As with the presumptive midgut, the only essential difference is adaptation to rapid budding in spite of increased yolk, substituting segregation of budding cells from yolk reserves in place of increased teloblast size.

The *presumptive germ cells* in both clitellates and Onychophora are small cells closely associated with the presumptive mesoderm and posterior midgut, and are thus similar in location and fate.

The *presumptive stomodaeum* is also basically similar in both, comprising a group of small superficial cells at the anterior margin of the presumptive midgut. Commensurate with the slight invagination of presumptive midgut in Onychophora, the initial penetration of adjacent stomodaeum into the interior is by invagination rather than by growth and cell division, but this minor discrepancy does not belie the correspondence of the two areas.

In respect of their *presumptive proctodaeum*, clitellate and onychophoran embryos appear superficially to be different. In the former, the presumptive proctodaeum can be interpreted as a paired bilateral rudiment on either side of the presumptive mesoderm, later coming together to lie above and behind the M-cells superficially. In the Onychophora, it is a midventral rudiment between the ventral and posterior components of the presumptive midgut. Given the precocious expansion of presumptive ectoderm in Onychophora, however (see below), together with the superficial position retained by the midgut and mesodermal rudiments, the shift of presumptive proctodaeum from a paired bilateral to a median ventral position in front of the mesoderm and posterior midgut must follow. Once in this position, its initial penetration by invagination rather than by the independent ingrowth that occurs in clitellates is, like that of the stomodaeum, a corollary of its new relationship with the modified ventral presumptive midgut.

The *presumptive ectoderm* in the onychophoran blastoderm takes on directly the pattern of ectodermal bands and temporary yolk sac ectoderm found in clitellates towards the end of gastrulation. By this time, in clitellates, the ectoteloblasts have budded off ectodermal bands which run forwards ventrolaterally to meet in the anterior midline in front of the stomodaeum, retaining teloblastic activity at their posterior ends. The temporary yolk sac ectoderm has spread to cover the surface of the embryo dorsally and laterally and has also been cut off as two marginal ventrolateral strips, extending on either side from the stomodaeum to the proctodaeum between the edges of the ectodermal bands and the still-exposed surface of the midgut rudiment. In Onychophora, where the stomodaeal, midgut, proctodaeal and mesodermal areas are small and lie in line along the ventral surface of the blastoderm, a direct formation of expanded ectoderm as blastoderm takes place, omitting the gastrulation spread and early teloblastic activity of clitellate ectoderm, but arriving at an identical condition of (a) paired broad lateral ectodermal bands meeting anteriorly in front of the stomodaeum and retaining the potentiality for proliferative activity at their posterior ends. These ends lie on either side of the midventral presumptive mesoderm and presumptive posterior midgut, and just behind the now midventral presumptive proctodaeum; (b) a broad dorsal and lateral area of presumptive temporary yolk sac ectoderm; (c) paired ventrolateral bands of presumptive temporary yolk sac ectoderm, running from stomodaeum to posterior midgut between the ectodermal bands and the ventral presumptive midgut and

proctodaeum. In association with the new position of the proctodaeum, presumptive pygidium is lost.

It is manifest that in spite of great superficial dissimilarity, the basic organization of the primitive clitellate blastula and the primitive onychophoran blastoderm are similar, all the detailed differences between them being functional adaptations in Onychophora to increased yolk. Large cells containing large amounts of reserve material are replaced by small cells at the surface of a central mass of reserve material. Cells previously adapted to temporary intracellular digestion of yolk have become adapted to temporary extracellular digestion of yolk. Presumptive ectoderm, in association with a relative reduction in size of other areas, develops directly in expanded post-gastrular form. Since the Onychophora retain a basic developmental pattern so easily derivable from that of clitellate annelids, in the same way that that of clitellates is derivable from the developmental pattern of polychaetes, a "spiral cleavage" origin for the Onychophora can hardly be denied. There are also strong grounds for believing that the soft-bodied coelomates which were the ancestors of the Onychophora, Myriapods and Hexapoda (Manton, 1964, 1965) must have had a clitellate-like pattern of embryonic development. The evidence of comparative morphology, of course, argues strongly against a clitellate origin of Onychophora, and we must assume that this ancestral clitellate-like pattern of development existed in some other, now extinct, group of metameric coelomates of the spiral cleavage assemblage. By analogy with the Clitellata (see above, p. 27) it may be further assumed that the more distant ancestors of the Onychophora combined the metameric coelomate condition with a mode of development resembling that of polychaete annelids. It is important to stress, however, that no more than a paraphyletic relationship between Annelida and Onychophora can be inferred from this. Thus, while the evidence of embryology tends to link the Annelida and Onychophora in paraphyly rather than to segregate them in polyphyly, it also supports the view of Manton (1965) that "the ancestral soft-bodied coelomates from which the Arthropoda probably descended may have been quite unlike any known annelid".

References

- ANDERSON, D. T., 1959.—The embryology of the polychaete *Scoloplos armiger*. *Q. Jl. microsc. Sci.*, 100: 89–166.
- , 1962.—The embryology of *Dacus tryoni* (Frogg.) (Diptera, Trypetidae (=Tephritidae)), the Queensland fruit-fly. *J. Embryol. exp. Morph.*, 10: 248–292.
- , 1966a.—The comparative embryology of the Polychaeta. *Acta Zool.*, Stockh., 47: 1–42.
- , 1966b.—The comparative embryology of the Diptera. *A. Rev. Ent.*, 11: 23–46.
- BERGH, R. S., 1890.—Neue Beiträge zur Embryologie der Anneliden. I. Zur Entwicklung und Differenzierung des Keimstreifens von *Lumbricus*. *Z. wiss. Zool.*, 50: 469–526.
- BOUVIER, E. L., 1904.—Les oeufs des Onychophores. *Nouv. Arch. Mus. Hist. nat.*, Paris, ser. 4, 6: 1–50.
- BÜRGER, O., 1891.—Beiträge zur Entwicklungsgeschichte der Hirudineen. Zur Embryologie von *Nepheleis*. *Zool. Jb.* (2), 4: 697–783.
- , 1902.—Weitere Beiträge zur Entwicklungsgeschichte der Hirudineen. Zur Embryologie von *Clepsine*. *Z. wiss. Zool.*, 72: 525–544.
- BYCHOWSKY, A., 1921.—Ueber die Entwicklung der Nephridien von *Clepsine sexoculata* Bergmann (*complanata* Savigny). *Revue suisse Zool.*, 29: 41–131.
- DAWYDOFF, G., 1942.—Étude sur l'embryologie des Naididae indo-chinois. *Arch. Zool. exp. gén., Notes et Revue*, 81: 173–194.
- DENDY, A., 1902.—On the oviparous species of Onychophora. *Q. Jl. microsc. Sci.*, 45: 363–416.
- DIMPKER, A. M., 1917.—Die Eifurchung von *Herpobdella atomaria* Carena. (*Nepheleis vulgare* Moq. Tand.) *Zool. Jb.* (2), 40: 245–290.
- EVANS, R., 1902.—On the Malayan species of Onychophora. Part II. The development of *Eoperipatus weldoni*. *Q. Jl. microsc. Sci.*, 45: 41–86.
- HATSCHKE, B., 1878.—Studien über Entwicklungsgeschichte der Anneliden. *Arb. zool. Inst. Univ. Wien.*, 3: 277–404.
- HOFFMANN, R. W., 1899.—Beiträge zur Entwicklungsgeschichte der Oligochäten. *Z. wiss. Zool.*, 66: 335–57.
- IWANOFF, P. P., 1928.—Die Entwicklung der Larvalsegmente bei den Anneliden. *Z. Morph. Ökol. Tiere*, 10: 62–161.

- KENNEL, J., 1884.—Entwicklungsgeschichte von *Peripatus Edwardsi* Blanch und *Peripatus torquatus* n. sp. *Arb. zool. zootom. Inst. Würzburg*, 7: 95–229.
- , 1885.—Entwicklungsgeschichte von *Peripatus Edwardsi* Blanch und *Peripatus torquatus* n. sp. *Arb. zool. zootom. Inst. Würzburg*, 8: 1–93.
- KOWALEVSKY, A., 1871.—Embryologische Studien an Würmern und Arthropoden. *Zap. imp. Akad. Nauk.*, 16, No. 12: 70 pp.
- MANTON, S. M., 1949.—Studies on the Onychophora. VII. The early embryonic stages of *Peripatopsis*, and some general considerations concerning the morphology and phylogeny of the Arthropoda. *Phil. Trans. R. Soc.*, B, 233: 483–580.
- , 1964.—Mandibular mechanisms and the evolution of the arthropods. *Phil. Trans. Roy. Soc. B*, 247: 1–183.
- , 1965.—The evolution of arthropodan locomotory mechanisms, Part 8. Functional requirements and body design in Chilopoda, together with a comparative account of their skeleto-muscular systems and an Appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodan haemocoel. *J. Linn. Soc. Zool.*, 46: 251–484.
- MEYER, A., 1929.—Die Entwicklung der Nephridien und Gonoblasten bei *Tubifex rivulorum* Lam. nebst Bemerkungen zum natürlich system der Oligochäten. *Z. wiss. Zool.*, 133: 517–562.
- , 1931.—Cytologische Studien über die Gonoblasten in der Entwicklung von *Tubifex*. *Z. Morph. Ökol. Tiere*, 22: 269–286.
- NUSBAUM, J., 1884.—Zur Entwicklungsgeschichte der Hirudineen. (*Clepsine*.) *Zool. Anz.*, 7: 609–615.
- , 1885.—Zur Entwicklungsgeschichte der Geschlechtsorgane der Hirudineen (*Clepsine complanata* Sav.). *Zool. Anz.*, 8: 181–184.
- , 1886.—Recherches sur l'organogenèse des Hirudinées (*Clepsine complanata* Sav.). *Arch. Slav. Biol.*, 1: 320–340 and 539–556.
- PENNERS, A., 1922.—Die Furchung von *Tubifex rivulorum* Lam. *Zool. Jb.* (2), 43: 323–368.
- , 1924.—Die Entwicklung des Keimstreifs und die Organbildung bei *Tubifex rivulorum* Lam. *Zool. Jb.* (2), 45: 251–308.
- , 1929.—Entwicklungsgeschichte Untersuchungen an marinen Oligochäten. I. Furchung, Keimstreif, Vorderdarm und Urkeimzellen von *Pelosclex benedeni* Udekem. *Z. wiss. Zool.*, 134: 307–344.
- , 1934.—Die Ontogenese des entodermalen Darmepithels bei limicolon Oligochäten. *Z. wiss. Zool.*, 145: 497–507.
- , and STABLEIN, A., 1930.—Über die Urkeimzellen bei Tubificiden (*Tubifex rivulorum* Lam. und *Limnodrilus udekemianus* Clarapède). *Z. wiss. Zool.*, 137: 606–626.
- SCHLIEP, W., 1914.—Die Furchung des Eies der Rüsselegel. *Zool. Jb.* (2), 37: 313–368.
- SCHMIDT, G. A., 1917.—Zur Entwicklung des Entoderms bei *Protoclepsia tessellata*. *Ann. zool. Abt. Ges. Freunde N.A. & E.*, 4 (N.S.) Mosc., 1: 22.
- , 1921.—Die Embryonalentwicklung von *Piscicola geometra* Blainv. *Zool. Anz.*, 53: 123–127.
- , 1922.—Zur Frage über die Entwicklung des Entoderms bei der *Rhynchelmis limosella* Hoffm. *Russk. zool. Zh.*, 3: 74–93.
- , 1924.—Untersuchungen über die Embryologie der Anneliden. 2. Die Besonderheiten der Embryonalentwicklung der Ichthyobdellidae und ihre Entstehung. *Zool. Jb.* (2), 46: 199–244.
- , 1925a.—Die polaren plasmatischen Massen Ei von *Protoclepsia tessellata*. *Russk. zool. Zh.*, 5: 138–164.
- , 1925b.—Untersuchungen über die Embryologie der Anneliden. I. Die Embryonalentwicklung von *Piscicola geometra* Blainv. *Zool. Jb.* (2), 47: 319–428.
- , 1930.—Der Keimentwicklungstypus der *Crangonobdella murmicanica* W. D. Selenck. *Russk. zool. Zh.*, 10: 5–15.
- , 1939.—Dégénérescence phylogénétique des modes de développement des organes. *Arch. Zool. exp. gén.*, 81: 317–370.
- , 1941.—Researches on the comparative embryology of leeches. 10. Early stages of development of the embryo in Ichthyobdellidae. À la memoire A. L. Sewertzoff, Moscow, 2: 357–489.
- , 1944.—Adaptive significance of the peculiarities of the cleavage process in leeches. *Sh. obshch. Biol.*, 5: 284–303.
- SCHOUMKINE, O. B., 1953.—Embryonic development of *Hirudo*. *Trudy Inst. Morf. Zhivot.*, 8: 216–279.
- SCLATER, W. L., 1888.—On the early stages of the development of a South American species of *Peripatus*. *Q. Jl. microsc. Sci.*, 28: 343–363.
- SEDGWICK, A., 1885.—The development of *Peripatus capensis*. Part I. *Q. Jl. microsc. Sci.*, 25: 449–468.
- , 1886.—The development of the Cape species of *Peripatus*. Part 2. *Q. Jl. microsc. Sci.*, 26: 175–212.
- , 1887.—The development of the Cape species of *Peripatus*. Part 3. *Q. Jl. microsc. Sci.*, 27: 467–550.
- , 1888.—The development of the Cape species of *Peripatus*. Part 4. *Q. Jl. microsc. Sci.*, 28: 373–398.

- SHELDON, L., 1888.—On the development of *Peripatus Novae-Zelandiae*. *Q. Jl. microsc. Sci.*, 28: 205-237.
- , 1889a.—On the development of *Peripatus Novae-Zelandiae*. *Q. Jl. microsc. Sci.*, 29: 283-294.
- , 1889b.—The maturation of the ovum in the Cape and New Zealand species of *Peripatus*. *Q. Jl. microsc. Sci.*, 30: 1-29.
- SUKATSCHOFF, B., 1903.—Beiträge zur Entwicklungsgeschichte der Hirudineen. II. Über die Furchung und Bildung der embryonalen Anlagen bei *Nephtis vulgaris* Moq.-Tand. (*Herpobdella atomaria*). *Z. wiss. Zool.*, 73: 321-367.
- SWETLOFF, P., 1923a.—Sur la segmentation de l'oeuf chez le *Bimastus constrictus* R. (fam. Lumbricidae). *Izv. biol. nauchno-issled. Inst. biol. Sta. perm. gosud. Univ.*, 1: 101-110.
- , 1923b.—Sur la segmentation de l'oeuf de *Rhynchelmis limosella* Hoffmstr. *Izv. biol. nauchno-issled. Inst. biol. Sta. perm. gosud. Univ.*, 1: 141-152.
- , 1926.—Über die Embryonalentwicklung bei den Naididen. *Izv. biol. nauchno-issled. Inst. biol. Sta. perm. gosud. Univ.*, 4: 359-372.
- , 1928.—Untersuchungen über die Entwicklungsgeschichte der Regenwürmer. *Trudy osob. zool. Lab. Sebastop. biol. Sta.*, 13: 95-329.
- TANNREUTHER, G. W., 1915.—The early embryology of *Bdellodrilus philadelphicus*. *J. Morph.*, 26: 143-216.
- VEDJOVSKY, F., 1886.—Die Embryonalentwicklung von *Rhynchelmis*. *Sber. K. boh. Ges. Wiss.*, 2: 227-239.
- , 1888-1892.—Entwicklungsgeschichtliche Untersuchungen. Prag.
- WHITMAN, C. O., 1878.—The embryology of *Clepsine*. *Q. Jl. microsc. Sci.*, 18: 215-315.
- , 1887.—A contribution to the history of the germ layers of *Clepsine*. *J. Morph.*, 1: 105-182.
- WILSON, E. B., 1889.—The embryology of the earthworm. *J. Morph.*, 3: 387-462.
- , 1892.—The cell lineage of *Nereis*. *J. Morph.*, 6: 361-480.

THE COMPOSITION, OCCURRENCE AND ORIGIN OF LERP, THE SUGARY SECRETION OF *EURYMELA DISTINCTA* (SIGNORET)

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[Read 30th March, 1966]

Synopsis

The sap-sucking insect *Eurymela distincta* extracts the phloem-sap from its host plant *Eucalyptus* or *Angophora* and secretes a white, waxy, saccharine material known as lerp. This paper discusses the occurrence of lerp; its composition is given and compared with that of the sap of the host. A suggestion is advanced and evidence given to support the suggestion that the saliva of the insect contains an enzyme which decomposes pectin of the cell-wall and the galactose so formed condenses with the sugars of the sap to form the more complex sugars of lerp.

The Sugar Lerp insect, *Eurymela distincta* (Signoret), secretes a sugary substance which collects on the leaves, twigs, and often in considerable amount on the ground beneath a tree infested with these insects. This substance, lerp, has often been confused with manna but it differs from manna both in its composition and mode of formation. Manna is a naturally occurring or physiologically induced secretion from certain trees, but which has not passed through the alimentary tract of an insect. Lerp and honey-dew, on the other hand, are the secretions of an insect which has ingested the phloem-sap, extracted the elements it needs, and excreted the remainder either with or without change in composition.

Eurymela appears to attack only certain species of *Eucalyptus* and *Angophora*. The writer has collected it from *E. punctata* and from *Angophora floribunda*.

Lerp occurs in nodules and masses varying in weight from 0.05 to more than 4 grammes. These nodules are composed of colourless interlaced acicular crystals 1 mm. to 2 mm. long, the nodule itself being white and waxy. It is almost completely soluble in water, the insoluble amounting to only a fraction of 1%. The composition of lerp varies slightly from sample to sample, apparently depending on the composition of the phloem-sap which forms the food of the insect. The compounds present in the phloem-sap of eucalypts vary in quantity and in composition with the season of the year, a character which they share with several other plants (Peel and Weatherley, 1959).

The sugars in the phloem-sap of several eucalypts consist of 70% to 85% sucrose, 10% to 20% glucose and 5% to 10% raffinose (Badsen, 1965). In lerp the sugars occur in a different form and proportion. The analysis of a sample of lerp is given in Table 1.

The following sugars have been identified in lerp:—stachyose, raffinose, planteose, melibiose, planteobiose, sucrose, glucose and fructose. It contains nearly 70% raffinose and in decreasing order, melibiose, stachyose and sucrose, with only minor amounts of the others. It is noteworthy that it contains no free galactose although 0.031% of galactose-1-phosphate was found. The significance of this will be referred to later in the paper.

Lerp is entirely free from amino-acids although the sap on which the insect feeds contains a considerable amount and of several kinds. In this character lerp differs from the honey-dew secreted by aphids (von Dehn, 1961; Mittler, 1953) and by *Eriococcus coriaceus* (Badsen, unpublished) in which the kinds of

amino-acids occurring in the phloem-sap of the host plant are unchanged but the proportions are reduced to about one quarter. This reduction of the amount of amino-acids occurring in the secretion may have some relation to the protein needs of the insect. It has been suggested (Gray, 1952) that, in order to obtain sufficient nitrogenous matter for its metabolism, the insect must take in an amount of carbohydrate much in excess of its needs. This excess carbohydrate is secreted, generally with considerable modification, as lerp or honey-dew. In the case of *Eurymela*, apparently all the amino-acid is absorbed and only the excess carbohydrate secreted, and in a markedly changed form.

It is noteworthy that all the new sugars occurring in lerp (and in honey-dew) are made by the addition of a molecule of galactose to a molecule of one of the pre-existing sugars: stachyose from raffinose, raffinose from sucrose, planteose from sucrose, melibiose from glucose, and planteobiose from fructose. It is also important to observe that no galactose exists normally in phloem-sap.

TABLE 1
Analysis of Lerp

Moisture	3.2
Ash	0.64
Reducing sugars (as melibiose)	9.7
Non-reducing sugars (as raffinose)	69.3
Methanol insoluble (pectin, uronic acids etc.)	9.4
Amino-acids, protein etc. . .	nil.
The ash contains	P_2O_5 representing 0.01% of the original lerp
	Na_2O } trace of each
	K_2O }
	CaO }

The processes by which the sugars of lerp are formed are probably as follows: The pectins of the cell-wall are hydrolysed by a pectin-splitting enzyme in the saliva of the insect and are broken down to galactose, uronic acids, etc. The galactose is converted to galactose-1-phosphate which in turn and with the aid of another enzyme condenses with the sugars existing in the sap to form new sugars in the lerp. There is considerable evidence to support this theory. It has been shown (Adams and McAllan, 1958) that the saliva of many sap-sucking insects contains pectinase which breaks down the pectin to galactose and uronic acids. No free galactose occurs in the lerp but, as mentioned above, a small amount of galactose-1-phosphate has been detected. There is thus no doubt that galactose-1-phosphate is present in the system. The small amount occurring in the lerp is probably that caught up in the stream of alimentary fluids and secreted before it could react with the other sugars.

It is very significant that in all the sugars formed by the condensation of the pre-existing sugars with galactose, the condensation takes place in the 1-6 position. It should also be observed that the sugars of the phloem-sap are almost completely involved in this change. The approximately 70% of sucrose of the sap yields about 70% raffinose in the lerp. The 10% glucose in the sap yields about 10% melibiose and so on.

Experimental

The various components of the phloem-sap and of the lerp were identified by descending paper chromatography using Whatman's no. 1 paper and butanol : acetone : water 3 : 4 : 2 as solvent. After 18 to 24 hours action the

paper was dried at 110° and sprayed with diphenylamine-aniline phosphate (Bailey and Bourne, 1960). The sugars were identified by comparison of their R_f and colour of the spots given by the reagent with those of authentic sugars. The identity of the less common sugars planteose, planteobiose and melibiose was further confirmed by submitting them to hydrolysis and recognition of the fragments.

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References

- ADAMS, J. B., and McALLAN, J. W., 1958.—Pectinase in certain insects. *Canad. Jour. Zoo.*, 36 : 305.
- BAILEY, R. W., and BOURNE, E. J., 1960.—Colour reactions given by sugars and diphenylamine-aniline sprays on paper chromatograms. *J. Chrom.*, 4 : 206.
- BASDEN, R., 1965.—The occurrence and composition of manna in *Eucalyptus* and *Angophora*. *PROC. LINN. SOC. N.S.W.*, 90 : 152.
- GRAY, R. A., 1952.—Honeydew secreted by Pineapple Mealy Bugs. *Science*, 115 : 129.
- MITTLER, T. E., 1953.—Amino-acids in phloem-sap and their extraction by aphids. *Nature*, 172 : 207.
- PEEL, A. J., and WEATHERLEY, P. E., 1959.—Composition of sieve-tube sap. *Nature*, 194 : 1955.
- PENFOLD, A. R., and WILLIS, J. L.—“The Eucalypts” : 325.
- VON DEHN, M., 1961.—Untersuchungen zur Ernährungsphysiologie der Aphiden. *Zeitsch. vergleich. Physiologie*, 45 : 101.

THE BREEDING BIOLOGY AND LARVAL DEVELOPMENT OF *HYLA JERVISIENSIS* (ANURA: HYLIDAE)

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(Plate I)

[Read 30th March, 1966]

Synopsis

The *Hyla ewingi* complex has had a confused taxonomic history. The present account provides a clear diagnosis of one member of the complex, *H. jervisiensis*, on the basis of morphology, mating call, breeding habits and a detailed study of larval development. The geographic distribution and relationships of *H. jervisiensis* are discussed and it is pointed out that the taxonomic situation is still not completely resolved.

INTRODUCTION

Hyla jervisiensis Dumeril and Bibron (*sensu* Moore, 1961) was, until recently, known only from a restricted area of coastal New South Wales (see Moore, 1961, p. 283, Fig. 56). In 1963, however, the presence of this species at two localities in eastern Victoria was discovered (Littlejohn, Martin and Rawlinson, 1963), and it has since been found at a third nearby location (15 miles N. of Orbost, Vic.). The previous southernmost record was a questionable specimen from Lawler's Creek, near Bodalla, N.S.W. (Moore, 1961). Apart from this record the species had not been found south of Jervis Bay, N.S.W. Thus the Victorian specimens represent a range extension of at least 100, and possibly, 200 miles. The geographic distribution as known at present is indicated in Figure 1. Reference to earlier accounts of *H. jervisiensis* (Fletcher, 1889; Copland, 1957; Moore, 1961) revealed that virtually nothing was known of its biology. Since a considerable amount of information on the breeding biology has been gathered concomitantly with general distributional studies, the additional data are presented here.

Moore (1961) compared individuals of this species from the Sydney area (its known northern limit) with sympatric *H. verreauxi* Dumeril (as *H. ewingi* Dumeril and Bibron; see Littlejohn, 1963, 1965) with which it has often been confused. Our material was collected near the south-western limit of the known range of *H. jervisiensis*, where it is sympatric with *H. ewingi* (*sensu stricto*) as well as *H. verreauxi* (Littlejohn, 1965). Since *H. jervisiensis* shows a closer resemblance to *H. ewingi* than to *H. verreauxi*, comparison will be made with the former species.

While there is little doubt that the specimens considered in this paper are conspecific with *H. jervisiensis* of Moore (1961), we nevertheless have some reservations regarding the use of the name. Firstly, we have not been able to find *H. jervisiensis* (*sensu* Moore) at its supposed type locality (Jervis Bay, N.S.W.), nor, as far as we are aware, have any specimens apart from the type ever been collected there. Secondly, we have collected two specimens of another *Hyla* there, which we are unable to refer to any presently recognized form, but which show morphological evidence of relationship with the *H. ewingi* complex. We heard, but did not record, the mating call of one of these specimens, and again were unable to refer it to any described member of the *H. ewingi* complex, nor indeed to any other described *Hyla* inhabiting the area. Subsequent visits to the area have not resulted in the collection of further data

on this form. The situation requires detailed analysis; possibly it will necessitate the re-erection of *Hyla kreffti* Günther (whose type locality is Sydney, N.S.W.) to accommodate the taxon treated in this paper; the true *H. jervisiensis* perhaps being represented by our unidentified Jervis Bay specimens. It should be noted, however, that Moore (1961) examined the types of both *H. jervisiensis* and *H. kreffti*, and considered them to be identical. Hence, at this stage, no decision is warranted.

MATERIALS AND METHODS

Mating calls were recorded in the field using an EMI L2B tape recorder and an AKG D19 dynamic microphone. The recordings were subsequently analysed on a Kay 6061-A sound spectrograph and/or a Cossor 1049 double beam oscilloscope. These two methods provided reasonably complete information on acoustic characteristics. Wet bulb air temperatures were taken at the calling sites.

Various developmental stages were collected in the field and, in some cases, further reared in the laboratory at room temperature (15.0–25.0°C), in enamel trays (approximately 33 × 21 × 4 cm.) containing pond water. Boiled lettuce was provided as food. In one instance fertilized eggs were collected and allowed to develop to an early larval stage, with a few being fixed every second day. On another occasion field collected larvae were taken through to metamorphosis to confirm their identity.

The descriptions, measurements and drawings are of preserved material. Adults were preserved in 70% alcohol, and larvae in 4% formalin or Tyler's (1962) fixative. Measurements were taken from mature adults and all available developmental stages, using vernier callipers reading to 0.05 mm. Drawings were made with the aid of a *camera lucida* attached to a stereoscopic microscope.

The staging system used in describing embryos and larvae is that of Gosner (1960).

ADULT MORPHOLOGY

As indicated in the introduction, the species most likely to be confused with *Hyla jervisiensis* is *H. ewingi* (*sensu stricto*). Moore (1961) included a table of differences between *H. verreauxi* (as *H. ewingi*) and *H. jervisiensis*, but

TABLE 1
Principal differences between Hyla jervisiensis and H. ewingi (sensu stricto) from East Gippsland, Vic.

	<i>H. jervisiensis</i>	<i>H. ewingi</i>
Body length	♀ 58.2 mm.*	37.5 mm. (range 34.5–40.8)†
	♂ 49.9 mm. (range 46.6–51.6)‡	35.0 mm. (range 33.2–37.0)‡
Tibia length/Body length ratio	♀ 0.53*	0.48 (range 0.43–0.52)†
	♂ 0.53 (range 0.50–0.54)‡	0.50 (range 0.47–0.52)‡
Light stripe below eye	Inconspicuous	Conspicuous
Texture of back	Usually warty	Smooth
Odour in life	Distinctive, curry-like	Not distinctive

* Based on 1 specimen.

† Based on 4 specimens.

‡ Based on 10 specimens.

most of the features listed will not distinguish *H. ewingi* proper from *H. jervisiensis*. Table 1 shows those of Moore's characters which are useful in diagnosis of *H. ewingi* as well as *H. verreauxi*, and also some other characters which we have found to be reliable. An adult male *H. jervisiensis* is shown in Plate 1, Figure 2 (see Littlejohn, 1963, for a figure of an adult *H. ewingi*).

The following key may be used to distinguish the three species in coastal south-eastern Australia :

1. Finger pads wider than fingers. Back patch not divided between the eyes. No spots on the groin 2
Finger pads same width as fingers. Back patch divided between the eyes. Spots on the groin. Body length of mature males less than 40 mm. *H. verreauxi*
2. Conspicuous white stripe below the eye. No distinctive odour in life. Body length of mature males less than 40 mm. *H. ewingi*
No conspicuous white stripe below the eye. Odour in life curry-like. Body length of mature males more than 40 mm. *H. jervisiensis*

BREEDING SITES AND BREEDING SEASON

Four breeding sites were examined: Royal National Park, N.S.W.; Bell Bird, Vic.; 12 miles W. of Cann River, Vic.; and 15 miles N. of Orbost, Vic. (Table 2). Only one of these sites (12 miles W. of Cann River) has been visited repeatedly, and the majority of the observations and collections were made

TABLE 2
Breeding sites of Hyla jervisiensis

Locality	Description	Date of Visit	Stages Present
Royal National Park, N.S.W.	Permanent stream in dense dry sclerophyll forest	May 24, 1960	Calling ♂♂
		August 20, 1962	Calling ♂♂
Bell Bird, Vic.	Permanent sluggish stream in open meadow	August 24, 1963	Calling ♂♂
12 miles W. of Cann River, Vic.	Series of small, temporary pools on road margin	August 24, 1963	Calling ♂♂, gravid ♀, eggs, larvae at stages 25-30
		November 3, 1964	Larvae in three size- classes, the largest being beyond stage 30
		January 14, 1965	Eggs
		March 6, 1965	———— (ponds dry)
15 miles N. of Orbost, Vic.	Large, permanent dam in dry sclerophyll forest	March 6, 1965	Newly meta- morphosed juveniles

there. At Royal National Park, N.S.W., Moore (1961) heard males calling in February, and we heard them at this location in May and August. Fletcher (1889) collected gravid females at Burrawang, N.S.W., in July. It thus seems likely that *H. jervisiensis* is able to breed throughout the year, possibly being triggered by rainfall.

MATING CALL STRUCTURE AND CALLING BEHAVIOUR

Recordings of three individuals and a chorus were obtained at the locality 12 miles W. of Cann River, Vic., on 24th August, 1963, together with those of one *H. ewingi*. Calls of only one *H. jervisiensis* were sufficiently clear of

those of other individuals to allow an accurate determination of all call characteristics; the one *H. ewingi* could be similarly treated (Table 3). It was possible to determine only pulse repetition rate and dominant frequency in the calls of the other two *H. jervisiensis*, and the following values were obtained (at a wet bulb air temperature of 8°C): Pulse repetition rate: 38.5 and 42.6 pulses/sec.; Dominant frequency: 1650 and 1550 cycles/sec.

Audiospectrograms of part of a call of each species are presented in Plate 1, Figure 1.

The mating call of *H. jervisiensis* is basically like that of *H. ewingi* and consists of a series of similar, repeated notes, each of which is broken up into a number of clearly separated pulses, that is, fully modulated. The entire call of *H. jervisiensis* is longer, as is the note duration, and the note repetition rate is much lower. The pulse repetition rates are similar, but the dominant frequency of the call of *H. jervisiensis* is lower. The apparent similarity of pulse repetition rates is rather interesting, for calls of sympatric hylids are

TABLE 3

Physical characteristics of mating calls of a Hyla jervisiensis and a H. ewingi recorded 12 miles W. of Cann River, Vic., on 24th August, 1963, at a wet bulb air temperature of 8.0°C.

Data are based on three calls of one individual of each species and call note values are for the middle note of a call. Mean values are given with ranges in parentheses.

Call characteristic	<i>H. jervisiensis</i>	<i>H. ewingi</i>
Call duration (seconds)	9.1 (6.0-12.3)	3.9 (3.4-4.4)
Notes per call	10.7 (7-14)	15.0 (13-17)
Note repetition rate (notes per minute)	70.5 (68.3-73.3)	232.6 (229.2-237.0)
Note duration (seconds)	0.67 (0.64-0.70)	0.15 (0.14-0.15)
Pulses per note	25.7 (24-27)	6.0 (6)
Pulse repetition rate (pulses per second)	38.5 (37.5-39.4)	41.0 (40.0-42.9)
Dominant frequency (cycles per second)	1683 (1600-1750)	2390*

* Calculated from one call only.

usually well differentiated in this component (Littlejohn, 1965). Presumably the differing dominant frequencies minimize acoustic interference and allow for efficient auditory discrimination.

In Royal National Park, males were calling along a stream, from marginal vegetation 1-2 m. above the ground. At 12 miles W. of Cann River the frogs were calling from the shallow water at the edge of the ponds, from the ground near the ponds, and from a height of up to 1 m. in the vegetation 7-8 m. from the ponds.

Wet bulb air temperatures taken at the sites of calling males were 8.0 and 11.0°C.

DEVELOPMENT

Oviposition and eggs.—The actual process of oviposition was not observed. The eggs, which are laid in small clusters attached to twigs or blades of grass, have dark brown animal hemispheres, creamy-white vegetal hemispheres, and individual jelly capsules. Within a cluster the eggs adhere to each other, and not all of them are attached directly to the supporting vegetation. Those that are attached appear to have short "stalks", possibly due to the weight of the egg cluster stretching the jelly at the point of adhesion (Figure 2). The

number of eggs per cluster varies from 1–31, with a mean of 6.8 in the 18 clusters counted. The total egg complement of a single female is unknown.

A series of 10 early gastrulae (stage 10) had the following dimensions: embryo diameter, 2.33 ± 0.02 mm. (mean and standard deviation); capsule diameter, 7.58 ± 0.64 mm.

Pre-hatching embryos.—Cleavage and gastrulation appeared normal and were not closely studied. The first set of embryos examined in detail have a total length of about 4 mm., and are in stage 18 (Figure 3). They are dark grey to black, with the yolk sac slightly paler. The tail bud is bent sharply to the left, and separated from the yolk sac by a ventral notch. There is a slight stomodaeal depression between the arms of the U-shaped ventral sucker. The gill plate, auditory vesicle and pronephros are recognizable.

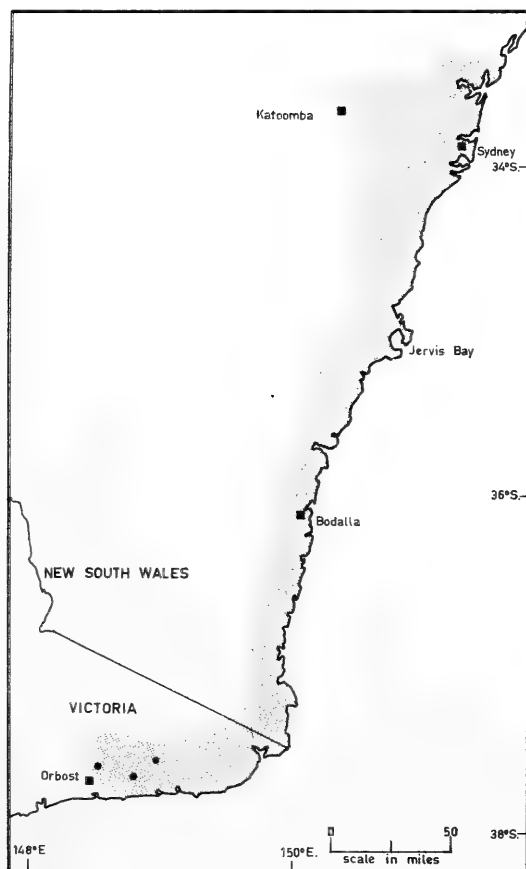


Fig. 1. The known geographic distribution (stippled) of *H. jervisiensis*. Only collecting localities additional to those of Moore (1961) are shown, and the positions of the type locality and some towns are indicated for reference.

Two days later the embryos are in stage 20, and have a total length of about 6 mm. (Figure 3). The overall colour is dark grey, but the tail fin is starting to become transparent. The stomodaeal depression is well-marked, and the ventral sucker has become separated into two portions, one at each side of the stomodaeum. Olfactory pits and optic bulges are visible. Two pairs of external gills are present, the anterior pair each having 4–5 branches, and the posterior pair 1–2.

Post-hatching embryos.—Hatching occurs at about stage 23 (Figure 3). Three individuals in this stage have total lengths of 8.8, 9.0 and 9.2 mm. There is little change in pigmentation, except that the tail fin is virtually transparent, and the cornea beginning to clear (the cornea is clear by stage 21 in Gosner's series, which is thus not precisely applicable to stages 21–23 of *H. jervisiensis*). The external gills are further developed, the anterior pair each having 4–5 branches, and the posterior pair 2–4. The mouth is open and the ventral suckers are still present. Embryos fixed 50 hours later are still in stage 23. The total length is about 10 mm. The operculum has almost completely covered the external gills on both sides, and the cornea is transparent. Ridges can be distinguished at the lateral and posterior margins of the mouth, foreshadowing the labial teeth and papillae.

Stage 24, in which the operculum closes on the right, was not observed. The next group of embryos fixed are in stage 25, when the operculum is fully closed and the spiracle visible. The horny jaws, labial papillae and labial

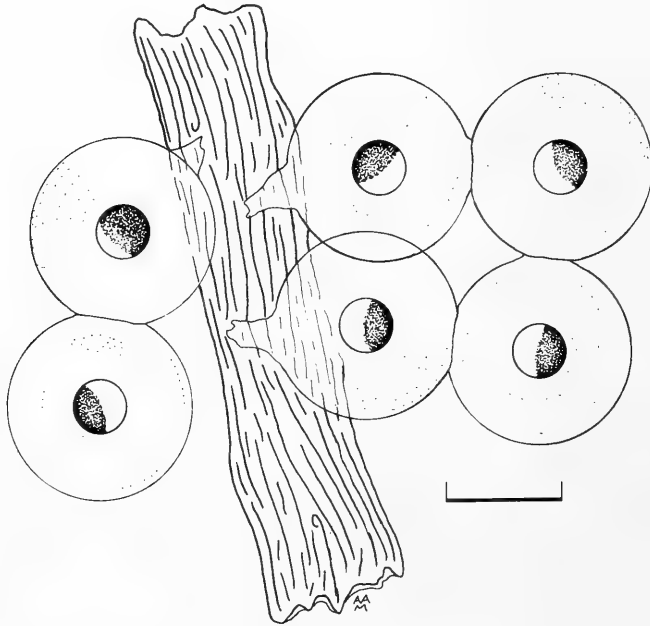


Fig. 2. Egg cluster of *H. jervisiensis*, 12 miles W. of Cann River, Vic. The bar represents 5 mm.

teeth, comprising the mouth disc, have also developed. During this stage the anus opens and the ventral suckers are lost. The mean dimensions of six embryos in this stage are: total length, 15.75 mm.; body length, 6.24 mm.; maximum body width, 3.80 mm.

Larvae.—The beginning of larval development is marked by the appearance of the hind limb buds in stage 26 (Limbaugh and Volpe, 1957). Apart from increase in size and progressive hind limb development, stages 26–40 are somewhat similar, and a description of a larva at stage 30 will suffice (Figure 3).

The overall body colour is dark brown, almost black. In ventral view the anterior half of the body is slightly lighter in colour. The myotomal area of the tail is darkly pigmented only along the dorsal edge, and is light brownish elsewhere. The tail fins are dusky, and blood vessels are clearly visible in the dorsal fin and posterior half of the ventral fin. The cornea is peculiar in having a somewhat greater diameter than the eyeball; the eye thus appearing to be

surrounded by a light-coloured ring. The spiracle is sinistral and ventrolateral in position, and is not visible in a dorsal view of the larva. The anus is dextral. The external nares are raised on small papillae, and open in an anterior direction. Both dorsal and ventral tail fins are arched and moderately deep.

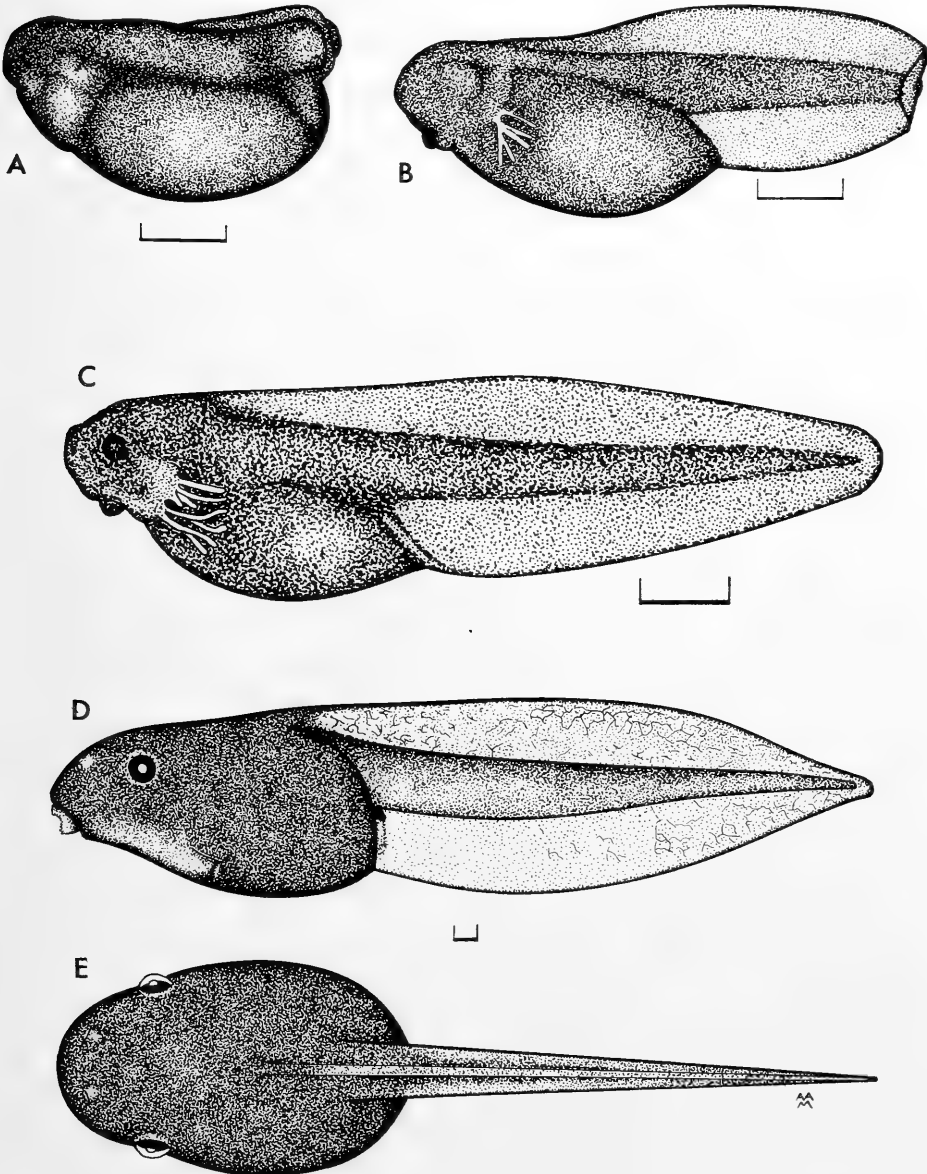


Fig. 3. Larval development of *H. jervisiensis*, 12 miles W. of Cann River, Vic. A: stage 18; B: stage 20; C: stage 23 (hatching); D and E: stage 30. The bar in each case represents 1 mm.

The mouth (Figure 4) is sub-terminal in position. The mouthparts appear to be fully developed by stage 27. Of the 14 larvae examined in stages 27–40, 12 have mouth discs virtually identical with that in Figure 4. The other two differ only in having a somewhat wider break in the second upper labial tooth row. The mouth is typically bordered by two to three rows of papillae, but at the corners of the mouth the papillae extend medially towards the jaws.

TABLE 4
Body dimensions (in mm.) and proportions of Hyla jervisiensis larvae. (Means are given with ranges in parentheses.)

Stage No.	Total length	Body length	Tail length	Maximum body width	Maximum mouth disc width	Body length		Body width		Mouth disc width
						Total length	Body length	Total length	Body width	
27	33.00	13.25	19.75	7.70	3.45	0.40	0.58	0.45		
28	32.85 (29.60-37.30)	13.25 (12.00-15.30)	19.60 (17.60-22.00)	7.97 (7.05-9.35)	3.73 (3.65-3.85)	0.40 (0.39-0.41)	0.60 (0.59-0.61)	0.47 (0.41-0.52)		
29	34.60	12.60	22.00	7.40	3.90	0.36	0.59	0.53		
30	40.16 (38.00-44.00)	16.20 (15.10-17.80)	24.00 (22.80-26.20)	9.62 (8.20-10.85)	4.28 (4.20-4.40)	0.40 (0.40-0.41)	0.59 (0.54-0.62)	0.45 (0.41-0.51)		
31	42.00	16.00	26.00	9.30	4.45	0.38	0.58	0.48		
32	41.60 (40.00-43.20)	15.92 (15.20-16.65)	25.68 (24.80-26.55)	9.13 (8.45-9.80)	4.58 (4.50-4.65)	0.39 (0.38-0.39)	0.57 (0.56-0.58)	0.50 (0.47-0.53)		
37	44.60	17.15	27.45	10.40	4.65	0.38	0.61	0.45		
39	49.20	18.60	30.60	11.80	5.45	0.38	0.63	0.46		
40	50.25	19.40	30.85	11.10	5.75	0.39	0.57	0.52		

The mouth formula is $\frac{1 \quad 1}{1 \quad 1}$, all the tooth rows being of subequal length.

The horny jaws are stout and have their inner margins serrated.

Body dimensions and proportions of larvae at stages 27–40 are presented in Table 4. Proportions remain relatively constant through this part of development, as noted by Limbaugh and Volpe (1957) for *Bufo valliceps*. The mean body proportions for all individuals in these stages are: body length/total length, 0.391 ± 0.015 ; body width/body length, 0.591 ± 0.025 ; mouth disc width/body width, 0.475 ± 0.042 .

Metamorphosis.—Three juveniles which metamorphosed in the laboratory have body lengths of 15.6, 16.2, and 18.3 mm. Two field-collected juveniles (15 miles N. of Orbost, Vic.) have body lengths of 18.2 and 19.7 mm. The juveniles are dark brown dorsally; the characteristic back patch of the adult is recognizable in only two individuals. The throat is dusky brown and the belly off-white; the thighs have a white ventral surface and an orange posterior surface. The dorsal surface is finely warty, and the ventral surface is granular from the level of the pectoral girdle backwards.

In the laboratory metamorphosis occurred in December. Juveniles were collected in the field on 6th March.

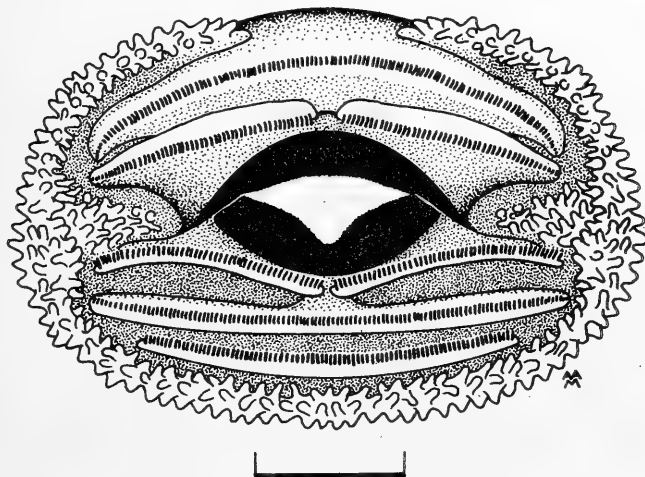


Fig. 4. Mouth disc of larva at stage 30 of *H. jervisiensis*. The bar represents 1 mm.

Larval life span.—No single individual has been reared from egg to metamorphosis, thus an exact figure for the duration of the larval life span is not available. A series of embryos took 14 days from egg to stage 25, while a group of larvae took 80 days from stage 30 to metamorphosis (at 15–25°C); thus the total span is probably in excess of 100 days. However, culture conditions in the laboratory may have been inadequate, so that under field conditions the development time could be shorter.

DISCUSSION

Oviposition and eggs.—The habit of depositing eggs in small clusters seems to be fairly widespread among hyliids. Examples of other species with this oviposition are: *H. caerulea*, 2000–3000 eggs in clusters of 100–200 each (Harrison, 1922); *Pseudacris streckeri*, 306–376 eggs in clusters of 2–14 each

(Fouquette and Littlejohn, 1960); and *Hyla regilla*, 500–1250 eggs in clusters of 5–60 each (Stebbins, 1962). However, there are also hylids which lay their eggs in a single mass, e.g. *H. phyllochroa* (Harrison, 1922) and *H. latopalmata* (Martin, ms.). The adaptive significance of these two types of oviposition pattern is not clear. Moore (1961, p. 173) suggests that scattering of eggs, i.e. depositing a few in each of several pools, is an adaptation to breeding in small, temporary bodies of water. Firstly, it provides for the contingency that some of the pools may dry out; and secondly, it prevents the possibility of the larvae being overcrowded. Another plausible hypothesis is that if the eggs are scattered in several masses there is less chance of a predator destroying the total egg complement. This point is discussed by Pyburn (1963).

The eggs of *H. jervisiensis* are unusually large (ovidiameter 2.33 mm.) among Australian hylids. For comparison, ovidiameters of some other Australian hylids are: *H. phyllochroa*, 1.2 mm.; *H. caerulea*, 1.44 mm. (Harrison, 1922); *H. ewingi*, 1.65 mm. (range 1.60–1.70); *H. aurea raniformis*, 1.30 mm. (range 1.25–1.35) (Martin, unpublished).

Larval morphology and adaptation.—*H. jervisiensis* tadpoles do not differ markedly in morphology from those of other Australian hylids which breed in still water. The ventrolateral, sinistral spiracle, dextral anus, fairly deep fins, and 2 | 3 mouth formula are all typical of Australian hylid larvae (Martin, ms. and unpublished). The pattern of life history is also typically hylid in character (Martin, ms.), and is shared by *H. ewingi*. However, the life histories of *H. jervisiensis* and *H. ewingi* differ considerably in detail, and provide further aid in diagnosing the species. *H. ewingi* lays smaller eggs (ovidiameter 1.65 mm.), without clearly defined separate capsules, in larger clusters (see Waite, 1929, p. 261, figure 188). *H. ewingi* hatchlings are smaller and have less well developed external gills (Martin, unpublished), and the larvae have relatively wider, lighter coloured bodies. The mouth discs of the two species also differ in proportions and in the arrangement of the labial papillae (Martin, 1965). Newly metamorphosed *H. ewingi* juveniles are smaller (body length 11.1–13.6 mm.; Martin, 1965).

The manner of oviposition suggests that the life cycle of *H. jervisiensis* may be adapted to ephemeral aquatic situations, such as the site 12 miles W. of Cann River, Vic. Water temperatures in the pools at this locality ranged from 9.5°C (about 2100 hours, 24th August, 1963) to 30.5°C (1430 hours, 14th January, 1965). Tolerance by the larvae of such thermal fluctuation is further evidence of adaptation to life in small, shallow bodies of water. However, anurans breeding in temporary water, even in mesic environments, are usually characterized by rapid larval development. Examples are *Pyxicephalus adspersus* and *Lechriodus fletcheri*, each having a larval life span of about 31 days (Balinsky, 1957; Moore, 1961). There is no suggestion that the larval life span is abbreviated to this extent in *H. jervisiensis*, a species which is not limited to temporary water situations for breeding (Table 1). Further studies are necessary to establish the normal duration of the larval phase of this species in the field.

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Literature cited

- BAILINSKY, B. I., 1957.—South African Amphibia as material for biological research. *S. Afr. J. Sci.*, 53: 383–391.
 COPLAND, S. J., 1957.—Australian Tree Frogs of the genus *Hyla*. *PROC. LINN. SOC. N.S.W.*, 82: 9–108.

- FLETCHER, J. J., 1889.—Observations on the oviposition and habits of certain Australian Batrachians. *PROC. LINN. SOC. N.S.W.*, 4: 357-387.
- FOUQUETTE, M. J., and LITTLEJOHN, M. J., 1960.—Patterns of oviposition in two species of hylid frogs. *Southwestern Nat.*, 5: 92-96.
- GOSNER, K. L., 1960.—A simplified table for staging Anuran embryos and larvae with notes on identification. *Herpetologica*, 16: 183-190.
- HARRISON, L., 1922.—On the breeding habits of some Australian frogs. *Aust. Zool.*, 3: 17-34.
- LIMBAUGH, B. A., and VOLPE, E. P., 1957.—Early development of the Gulf Coast Toad, *Bufo valliceps* Wiegmann. *Amer. Mus. Novitates*, 1842: 1-32.
- LITTLEJOHN, M. J., 1963.—Frogs of the Melbourne area. *Vict. Nat.*, 79: 296-304.
- , 1965.—Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution*, 19: 234-243.
- , MARTIN, A. A., and RAWLINSON, P. A., 1963.—New records of frogs in East Gippsland. *Vict. Nat.*, 80: 225-226.
- MARTIN, A. A., 1965.—Tadpoles of the Melbourne area. *Vict. Nat.*, 82: 139-149.
- , ms.—Some evolutionary and ecological aspects of Australian Anuran life histories.
- MOORE, J. A., 1961.—The frogs of eastern New South Wales. *Bull. Amer. Mus. Nat. Hist.*, 121: 149-386.
- PYBURN, W. F., 1963.—Observations on the life history of the Treefrog, *Phyllomedusa callidryas* (Cope). *Texas J. Sci.*, 15: 155-170.
- STEBBINS, R. C., 1962.—“Amphibians of Western North America”. University of California Press, Berkeley and Los Angeles.
- TYLER, M. J., 1962.—On the preservation of anuran tadpoles. *Aust. J. Sci.*, 25: 222.
- WAITE, E. R., 1929.—“The reptiles and amphibians of South Australia.” Harrison Weir Adelaide.

EXPLANATION OF PLATE I

Fig. 1. Audiospectrograms of part of a call of A, *H. jervisiensis*; and B, *H. ewingi*; recorded 12 miles W. of Cann River, Vic.

Fig. 2. Adult male *H. jervisiensis* from 12 miles W. of Cann River, Vic.

SEEDS AND FRUIT OF THE GOODENIACEAE

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[Read 30th March, 1966]

Synopsis

The microscopic structure of the seeds and fruits of the Goodeniaceae is examined. In general, the results are found to correlate with those in previous papers by Carolin and Peacock. Changes in the classifications proposed by previous authors are suggested. A new interpretation of the ovary of *Scaevola* is suggested. Seven seed types are recognized in *Goodenia* and its satellite genera, characterized by the relative position, size, and shape of the thickened (cells) and the mucilage cells of the epidermis of the testa. Eight pseudo-fruit types of *Scaevola* are recognized, based on the constitution of the three "layers" in the wall.

INTRODUCTION

Seeds and fruits play a prominent role in the classification of the Angiosperms and it is frequently instructive to re-evaluate their characters within a group.

The form of the fruits together with ovule number of the Goodeniaceae have been used to characterize the genera (Krause, 1912) and even to divide it into new families (Lindley, 1836). Their structure has also been used to distinguish between the species of *Goodenia* and *Velleia*, notably with regard to the presence or absence of a wing. No-one, however, has examined the seed structure at the microscopic level. Neither has anyone made any comparison of the seed types of this family and its supposed relations.

MATERIALS AND METHODS

In general, the seeds were collected from herbarium specimens, either made especially for the purpose or collected by other workers. Freshly collected seeds were sometimes used. Observations on the fruits were also made largely from herbarium specimens and sometimes in the field. All voucher specimens are cited separately. Herbarium abbreviations are those given in "Index Herbariorum", ed. 5.

Transverse sections of individual seeds were cut, although generally sections of the endocarp were also included in the case of drupaceous fruits. The testa or endocarp was usually so tough that it had to be softened in 20% nitric acid for periods of up to two months. Sections were cut on a sledge microtome at 20 μ without embedding or after embedding in collodion using amyl acetate as the solvent and the "dry" method (Steedman, 1960).

The vasculature of the seeds was observed in whole mounts of (usually) slightly immature seeds. Those embedded in an endocarp were extracted and those which required it were bleached in a commercial chlorine bleaching agent. They were then cleared and examined in Chloral-hydrate-lactophenol (CLP, Bersier and Bocquet, 1960).

The ratio a : b (radicle width : cotyledon width) was measured by a graticule in a binocular stereoscopic-microscope with a $\times 40$ magnification.

OBSERVATIONS

The food-store of the Goodeniaceae was not examined in such detail as the characteristics outlined below. Starch was not detected in any of the seeds examined below, through using polarized light. The following species

(all those examined) failed to show any blue coloration with iodine: *Goodenia bellidifolia*, *G. stelligera*, *G. ovata*, *G. mitchellii*, *Dampiera stricta*, *Scaevola albida*, *S. calendulacea*, *Velleia paradoxa*, *Brunonia australis*. None of these species gave a reaction to Hotchkiss' test for polysaccharides (Glick, 1949) except in the relatively thin cell walls. All showed the presence of oil using the Sudan III test. All of them also contained large numbers of aleurone grains which gave a weak reaction to Millons test (Glick, 1949). It seems, then, that food-store in the seed consists almost exclusively of oils and proteins.

BRUNONIA

This genus differs from all the others in the family in having a very reduced endosperm. The seed storage-tissue is contained in the two massive cotyledons, at the base of which is the minute embryo.

The single seed is uncompressed and contained in a membranous pericarp, itself surrounded by the broken, membranous remains of the corolla and the thickened calyx. The latter is the main dispersal unit as the tube and spreading lobes are conspicuously hairy.

The seed has a single vascular strand which extends partly down the micopylar side of the organ. The seed coat is thin and most of the internal walls of the testa are broken; there is apparently no thickening of the epidermis, although the highly refractive cuticle is fairly conspicuous. The brownish colour of the seed is due to the discoloured broken down inner regions of the integument which occupies a very narrow band immediately inside the testa. Just inside from this is a single layer of cells, apparently alive, but probably not functional, which represent the remains of the endosperm (Fig. 2, E, F). The bulk of the seed is taken up by the cotyledons.

There appears to be no differentiation of the epidermal cells as found in *Goodenia*, etc., and the epidermis does not seem to be mucilagenous in any way.

LESCHENAULTIA

The fruits of this genus are described as capsules dehiscing through four valves. This is partly incorrect. $a : b = 1$, embryo terete in all species.

In *L. biloba* the four sepaline ribs (two sepals are connate in this region) separate from the inner parts followed, almost immediately, by the four semi-free corolla parts (see Carolin, 1959) thus giving eight valves in all, four large ones and four small ones. The inner parts of the fruit are hard and woody. Moreover, during the development of the fruit, the outer walls of the loculi, particularly where these are free from the outer whorls, i.e., opposite four petal radius traces (Carolin, 1959), have grown inwards and partially fused, with smaller outgrowths from the axile placenta. The result is that the seeds are entirely surrounded by tissue derived from the loculus wall. As development proceeds the tissue between each seed separates horizontally (Fig. 1, A-D) thus forming an "article" containing the seed. Further growth causes the individual articles to separate from each other (Fig. 1, A). It is these units which, in the past, have been referred to as seeds: the so-called "testa." (Bentham, 1869, etc.) is really the inner layers of the pseudo-fruit, the cells of which have very greatly thickened walls (Fig. 1, F, G). The testa itself is a very inconspicuous, thin-walled layer, in some species showing narrow bands of thickening in the epidermis (Fig. 1, E). It seems probable that the thickened layers are homologous with the true fruit, since all the cells inside the closed "spurs" (Carolin, 1959) have thickened walls. It is implied, then, that the outer floral parts separate from the fruit and then the fruit breaks, like a lomentum, into a double series of articles (Fig. 1, A). The thickened layers of the fruit, whilst being fairly well-defined from the outer thin-walled cells,

are not bounded by a definite differentiated layer as in *Dampiera*. The shape of these articles is frequently a specific characteristic; *L. linarioides*, *L. longiloba*, and *L. filiformis* share the same significant features.

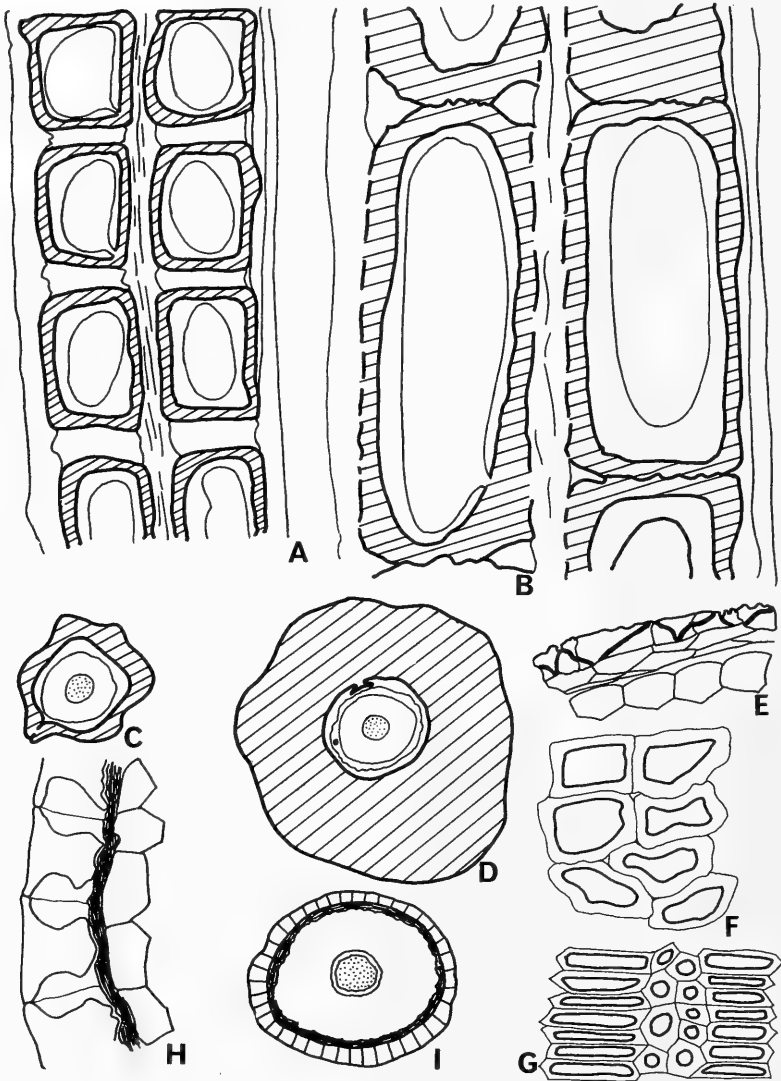


Fig. 1. A. longitudinal section of part of fruit of *Leschenaultia biloba* $\times 8$; B. same of *L. linarioides* $\times 8$; C. transverse section of pyrene, *L. filiformis* $\times 20$; D. transverse section of pyrene, *L. divaricata* $\times 12$ large stippling = dry soft tissue; hatching = hard tissue; E. epidermis of seed, *L. biloba* $\times 320$; F. cells from pyrene wall, *L. biloba* $\times 160$; G. cells from pyrene wall, *L. divaricata* $\times 160$.

L. divaricata shows some differences from the other species examined. No material was available for observation of the development of the fruit. The mature fruit, however, shows only a single seed developed at any one level and a cross-section shows that the article is derived from both loculi. The swelling of the seed has ruptured the septum (Fig. 1, D) and there is no

division along the placenta when the fruit breaks up, as there is in the other species. Moreover, the thickened cells of the article are more regularly arranged than in the other species (Fig. 1, G).

The seed itself seems to be fairly uniform in the genus. The vasculature is quite reduced, consisting of a single strand which scarcely reaches the top of the somewhat elongated, more or less terete seed (Fig. 3, D). The epidermis

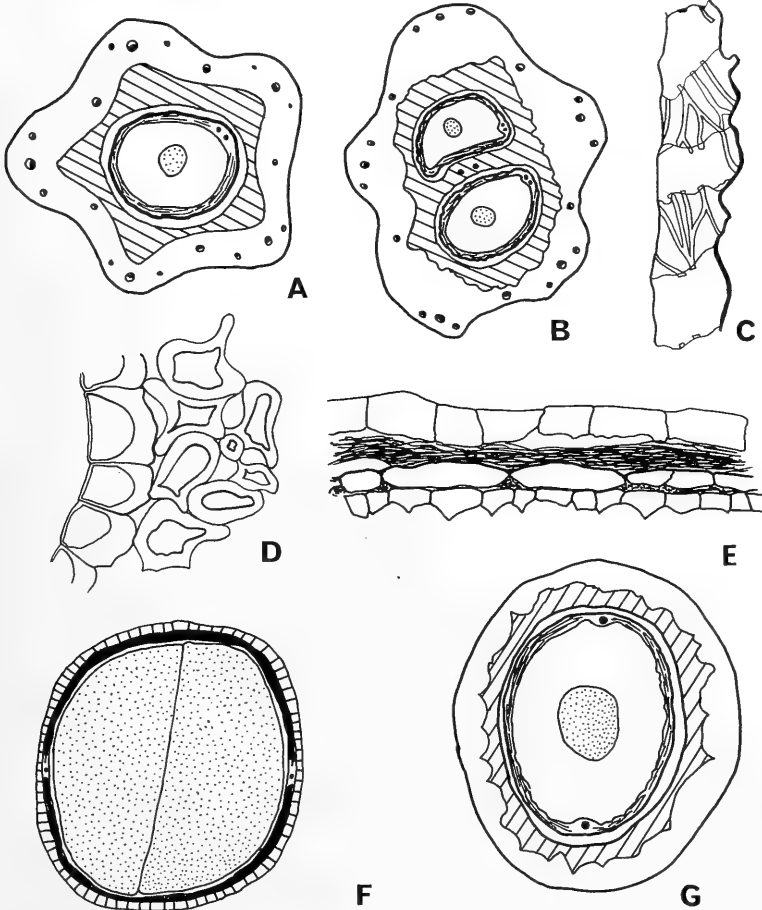


Fig. 2. A. transverse section of fruit, *Dampiera stricta* $\times 20$; B. transverse section of fruit *D. trigona* $\times 20$; C. epidermis of seed, *D. stricta* $\times 320$; D. cells of pyrene wall, *D. stricta* $\times 320$; E. seed epidermis, etc., *Brunonia australis* $\times 320$; F. transverse section of seed, *B. australis* $\times 20$; G. transverse section of fruit of *Diaspasis filiformis* $\times 20$, e=epidermis, en=endodermis, c=cotyledon: stipple=embryo, diagonal hatching=hard tissue.

of the testa is very narrow and is only thickened, if at all, by lignin bands similar to those of *Dampiera*. Indeed the seed resembles that of *Dampiera* sect.(eu)-*Dampiera* quite closely, although it is smaller, smooth, and has a reduced vascular system.

DAMPIERA

Embryo terete, a:b=1:1 in all species. The two forms of ovary (2-locular and 1-locular) are reflected in the fruit form (Fig. 2, A, B). But apart from the number of loculi there is no significant difference between seed and fruit of *D. trigona* in sect. *Dicoelia* and *D. stricta* and the rest of the

"*eu-Dampiera*". The fruit is divisible into a hard, woody inner layer with thickened cell-walls and a relatively soft but scarcely fleshy and never very thick outer layer. There seems, in general, to be little change in this latter layer as the ovary matures into a fruit; there is no visible increase in fleshiness. One cannot, strictly, equate these layers with endo- and meso-carp of a drupe as the "fruit" is a pseudo-fruit and not strictly equivalent to a drupe, a true fruit. Indeed, it seems probable that the hard inner layer is ovary and the soft outer layer the adnate outer whorls, although evidence for this would be hard to gather. The hard inner layer may be rugose or wrinkled as in *D. trigona* and *D. stricta*, or almost smooth as in *D. coronata*. The outer surface of the endocarp is delimited by a specialized group of often somewhat enlarged

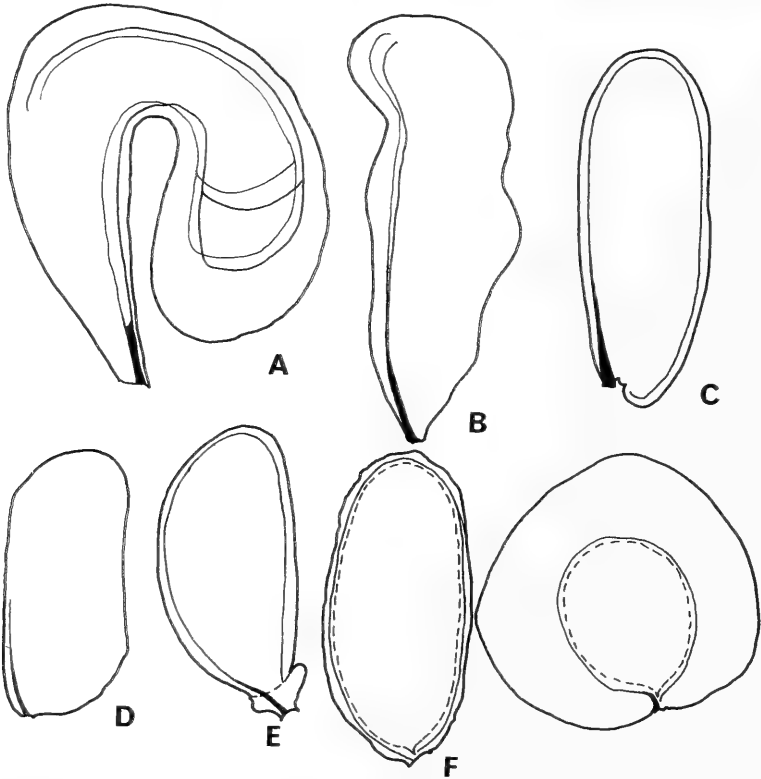


Fig. 3. Diagrams of cleared seeds showing vascular patterns; broken lines=edge of wing. A. *Dampiera coronata*; B. *D. purpurea*; C. *Scaevola calendulacea*; D. *Leschenaultia biloba*; E. *Goodenia barbata*; F. *G. heterophylla*; G. *Velleia connata*.

cells. These are more or less regularly arranged inside a zone of loosely arranged aerenchyma. The inner tangential and radial walls of this layer become thickened with a refractive substance which does not stain with normal lignin stains (safranin, gentian violet). Thus the limit of the pseudo-endocarp is quite clear. Inside this layer the parenchyma is heavily thickened with lignin (Fig. 2, B).

The seeds themselves usually follow the outline of the pseudo-endocarp; thus, those with corrugated "endocarp" have corrugated seeds and those with smooth "endocarp" a smooth seed. The testa is thin and delicate and is probably always slightly thickened with reticulate bands of lignin when quite mature. These, however, were only actually observed on *D. stricta*. The inner integument zones are, likewise, very thin-walled and consequently quite crushed in the mature condition.

All the seeds examined show a double vascular supply almost to the base, two strands diverging from the funicle, e.g. *D. stricta*, *D. trigona*, although both strands remain on the same side of the seed. In *D. purpurea* they remain very close together and appear to be single for almost half the length of the seed. These vascular strands normally end at the top of the seed (Fig. 3, B).

The sect. *Camptospora* is distinguished by the peculiar bent seed. The general structure is the same but the vascular supply, whilst recognizably based on the same pattern, is more developed. The main strands are longer, reaching almost to the base, and there are distinct and constant secondary, connecting strands (Fig. 3, A).

ANTHOTIUM

Embryo terete, $a : b = 1 : 1$. *A. rubriflorum* only examined. The seeds are small (c. 1 mm. long) and black. The vascular strand is single and very short indeed. The transverse section shows the small \pm terete embryo embedded in endosperm, the crushed brownish inner parts of the integuments, and the outer epidermis of the integument (Fig. 1, I). This latter has much thickened radial walls, which are black, but both tangential walls are thin and, indeed, the uppermost is usually collapsed inwards until the seed is placed in water. Thus the dry seed is alveolate on the surface but, when placed in water, the dry cell contents swell up, force the upper epidermis outwards, occasionally even rupturing it. This does not seem to be "mucilage" in the same sense as applied to the epidermis of *Goodenia*. There is none of the characteristic disc-like stratification within the cells; it takes much longer to swell up and there is no reaction with iodine (Fig. 1, H).

The cells of the epidermis appear to be all of the same type. There is no differentiation between thickened and mucilage cells.

DIASPASIS

D. filiformis is the only species. The false-fruit is differentiated into an inner, rugose, layer of cells with much thickened walls and an outer layer which is not particularly fleshy but consists largely of parenchymatous cells. The boundary of the two layers is quite clearly marked but the outermost thickened cells are not significantly different from the others (unlike *Dampiera*).

The seed is \pm ovoid in shape. There appears to be generally only one developed, the other ovule aborting, its loculus compressed and the septum frequently ruptured with the growth of the seed. The seed has a single vascular strand which continues almost to the micropyle (cf. *Scaevola*). The epidermis cells are only thickened with lignin bands (as in *Dampiera*); in no case is the thickening general. Moreover, there seems to be no differentiation of the epidermis above the vascular strand (as in *Goodenia*), except that these cells are more isolateral than the horizontally elongated cells elsewhere in the epidermis. The inner layers of the integument are crushed against the epidermis by the massive endosperm (Fig. 2, G). The central embryo is terete to very slightly spatulate.

GOODENIA (see Fig. 10)

Of all the genera in the family, *Goodenia* shows the greatest variation in seed morphology. In transverse section, seven different forms can be distinguished. The first one, as described below, is quite distinct and shows little relationship with the others. The next six, on the other hand, intergrade with one another. In all the species included to date within this genus, the fruit is capsular. The seed in all cases shows a single, unbranched vascular strand which extends from the funicle around to the micropyle (Fig. 3, E, F).

Type 1

Embryo terete, $a:b=1:1$. The seed here is ovoid and, in transverse section, is more or less circular in outline. The epidermis of the testa is palisade-like, i.e., elongated radially, and the cell-walls are much thickened with prominent pits but more or less straight sides (Fig. 4, B), not convoluted as in other types. The outer tangential wall is usually somewhat less thickened than the radial. All the epidermal cells have more or less the same form; there are no mucilage cells. The inner parts of the integument are crushed

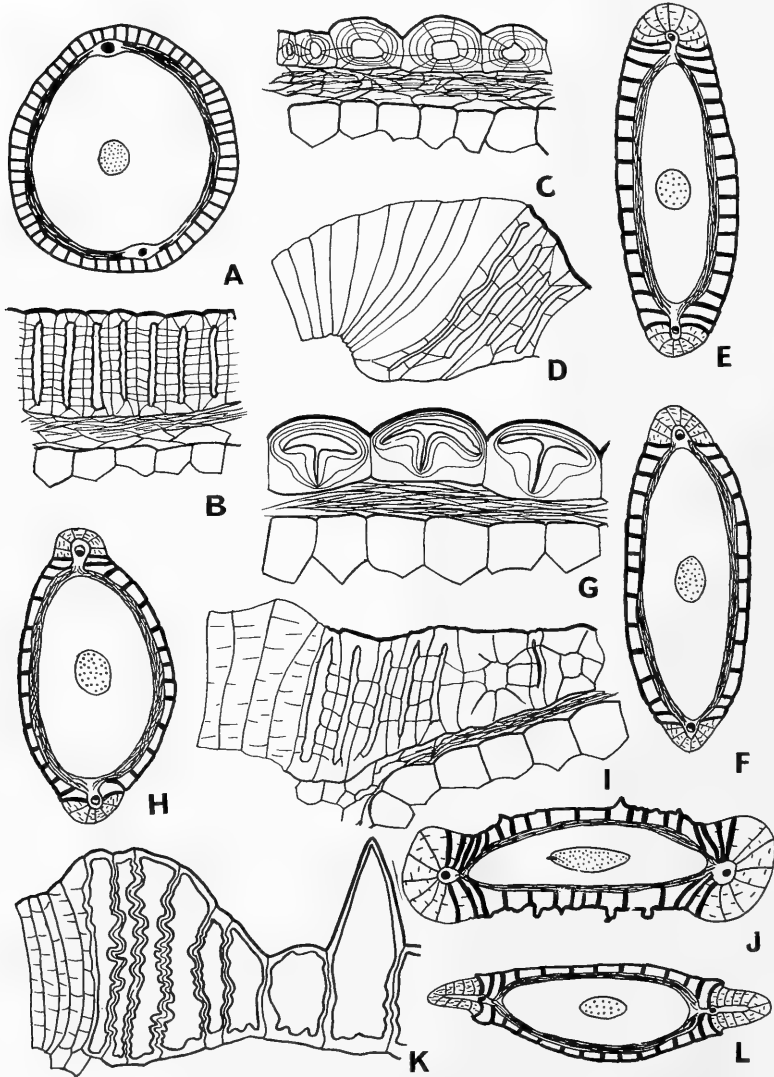


Fig. 4. Transverse sections of seeds. A. *Goodenia barbata* $\times 20$; B. *G. barbata*, epidermis $\times 160$; C. *G. ovata*, epidermis from middle of seed face $\times 160$; D. *G. ovata*, epidermis from margin $\times 160$; E. *G. ovata* $\times 20$; F. *G. azurea* $\times 20$; G. *G. azurea*, epidermis $\times 160$; H. *G. paniculata* $\times 20$; I. *G. paniculata*, marginal epidermis $\times 160$; J. *G. glabra* $\times 20$; K. *G. glabra*, marginal epidermis $\times 160$; L. *G. stelligera* $\times 20$.

against the epidermis by the massive endosperm, in the centre of which is the terete embryo (Fig. 4, A). The upper part of the funicle is swollen into a small strophiole, e.g. *G. barbata*, *G. strophiolata*, *G. chisholmii*.

In all the other types there is differentiation within the epidermis of the more or less compressed seed. The epidermal cells on the surface have much thickened walls, whilst those towards the margin have very thin walls and are generally filled with a mucilage which swells up and bursts through the outer-tangential wall on wetting and stains a deep blue with iodine. The vascular strand runs in a canal of uncrushed integument tissue just below these mucilaginous cells.

Type 2. (a)

Embryo slightly spathulate, $a : b = 2 : 3$ (*G. ovata*, etc.), $1 : 1$ (*G. paniculata*). The thickened cell walls in the epidermis are hardly convoluted, except those close to the mucilage cells and then not very much so; mostly the cells are \pm isolateral. The mucilage cells do not overlap the thickened cells a great deal, if at all, neither do the thickened cells arch over the mucilage cells. The margin is thus quite rounded without any secondary rims (Fig. 4, C-I), e.g., *G. ovata*, *G. paniculata*.

Type 2. (b)

Embryo slightly spathulate, $a : b = 2 : 3$ or $2 : 2\frac{1}{2}$. Intergrades with sub-type (a). The basic difference is that those thickened cells close to the mucilage cells are much more radially elongated than the other; the result is a distinct secondary rim on either side of the seed (Fig. 4, K-L; 5, B). Moreover, the walls of most of the thickened cells are convoluted. In some cases the mucilage cells only form a swollen rim, e.g., *G. amplexans*, whilst in others they form a more or less distinct wing, and the mucilage cells tend to overlie the thickened cells, e.g., *G. stelligera*, *G. calcarata*.

In still others the mucilage-cells appear to be non-functional and collapse before maturity, e.g., *G. macmillanii* (Fig. 5, A).

Type 3. (a)

Embryo slightly spathulate, $a : b = 2 : 2\frac{1}{2}$ or $2 : 3$. Intergrades with both types 2 and 4. They tend to be more rectangular in cross-section and the result is that the thickened cells towards the margin are much more radially elongated than the other thickened cells and they tend to overlie the mucilage cells somewhat. Moreover, the mucilage-cells are usually collapsed in the mature condition, giving a 3-rimmed structure to the margin, e.g., *G. heterophylla*, *G. hispida*, *G. disperma*, *G. auriculata* and *G. koningsbergeri* (Fig. 5, D-I). The mucilage cells appear to be non-functional. In all of these except *G. heterophylla* the integument cells between the vascular bundle and the endosperm have heavily thickened walls (cf. *Calogyne*). In *G. koningsbergeri* the mucilage cells are very reduced in number and the epidermis consists almost entirely of thickened cells (Fig. 5, F).

Type 3. (b)

Embryo slightly spathulate, $a : b = 2 : 3$ to $2 : 2\frac{1}{2}$. The marginal thickened cells here are very curved and appear crescent shaped in section, giving a secondary rim to the margin of mucilage cells, e.g., *G. hederacea*, *G. boormanii*, *G. sepalosa*. In *G. sepalosa* the marginal integument cells are heavily thickened (Fig. 5, C, J).

Type 4

Embryo spathulate, $a : b = 2 : 3$ to $2 : 4$. Intergrades to some extent with type 2b. The thickened cells have much-convoluted walls and those towards the margin are very elongated, far from overarched the mucilage-cells;

however, these latter overlie the thickened cells to a considerable degree. The mucilage cells are numerous and in all cases form a fairly distinct wing. Mucilage appears to be present in all the wings of type 4 seeds. The embryo tends to be spatulate and the cotyledons are generally slightly displaced laterally and do not directly overlay each other, e.g., *G. heteromera*, *G. glauca*, *G. subintegra*, *G. pinnatifida* (Fig. 6, A).

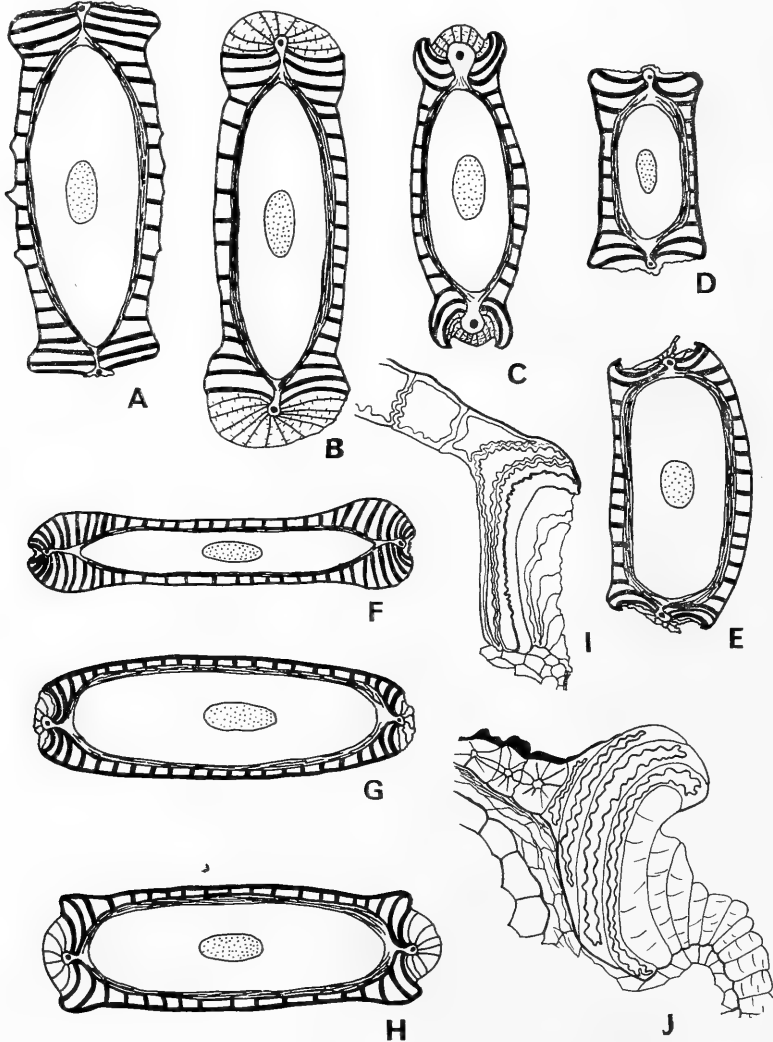


Fig. 5. Transverse sections of seeds. A. *G. macmillanii* $\times 20$; B. *G. amplexans* $\times 20$; C. *G. hederacea* $\times 20$; E. *G. heterophylla* $\times 20$; F. *G. koningsbergeri* $\times 20$; G. *G. hispida* $\times 20$; H. *G. lanata* $\times 20$; I. *G. heterophylla*, marginal epidermis $\times 160$; J. *G. boormannii*, marginal epidermis $\times 160$.

Type 5

Embryo spatulate, $a : b = 2 : 3$. This type shows distinct similarities with the previous one. The mucilage cells overlie the marginal thickened cells but those not overlying are not elongated radially. Moreover, the wing is a massive structure, as thick as the body of the seed throughout its width, because the internal parenchyma is very well developed, e.g., *G. mitchellii* (Fig. 6, B).

Type 6

The extreme form of this, type *b*, is represented by *G. havilandii* var. *pauperata* and *G. concinna*. The mucilage cells overlie the thickened cells as a separate, free flap; the cell lying immediately upon the thickened epidermis

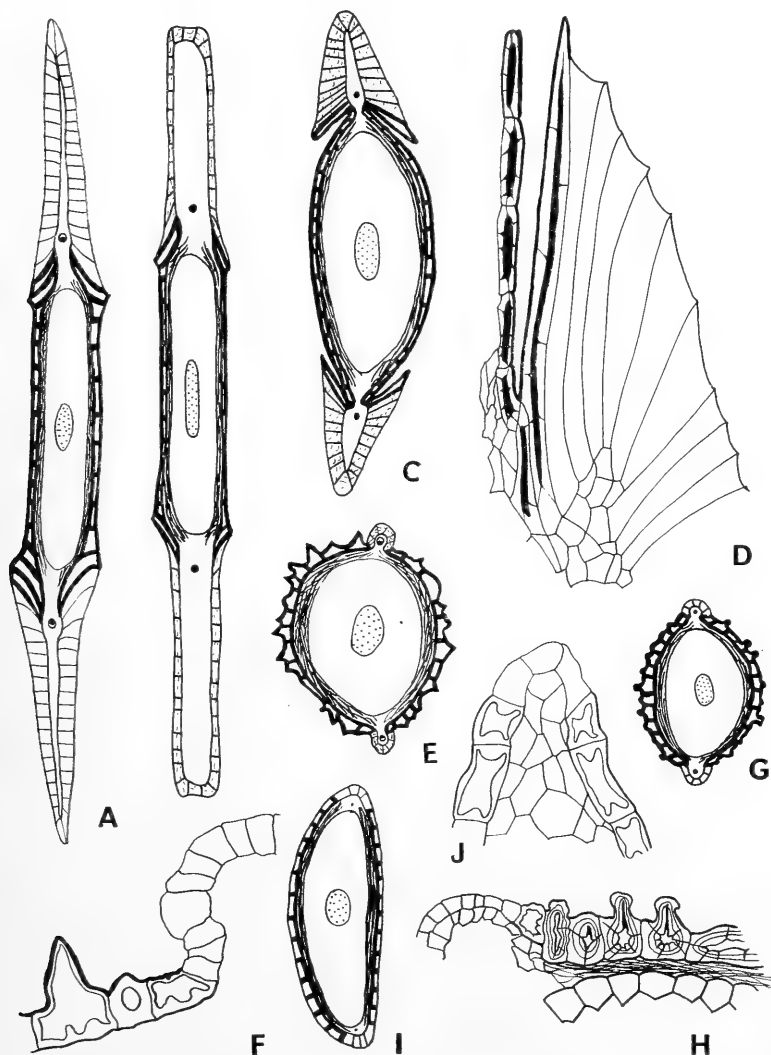


Fig. 6. Transverse sections of seeds. A. *G. linifolia* $\times 20$; B. *G. mitchellii* $\times 40$; C. *G. havilandii* var. *pauperata* $\times 20$; D. *G. havilandii* var. *pauperata*, marginal epidermal cells $\times 160$; E. *Pentaptilon careyi* $\times 20$; F. *P. careyi*, marginal epidermal cells $\times 160$; G. *Catosperma goodeniacearum* $\times 20$; H. *C. goodeniacearum* marginal epidermal cells $\times 160$; I. *G. pumilio* $\times 20$; J. *G. pumilio* marginal epidermal cells $\times 160$.

(but free from it) is thickened and spicule-like, but apparently not mucilaginous. The thickened cells of the testa are rather narrower and thinner-walled than in the previous types and the walls are less convoluted (Fig. 6, C, D).

G. caerulea and *G. pterygosperma* represent type 6a, a form closer to that found in type 2 in that the overlapping is much less pronounced (Fig. 7, J, K).

Type 7

Embryo \pm terete, a : b = 1 : 1. In this type the cell walls of the epidermis, even of the "thickened" cells, remain quite thin; the form of the marginal "mucilage" cells is no different from the thickened cells except in the thinner cell walls; this paler rim is almost invisible as there are so few mucilage cells. Indeed, it is even doubtful whether these latter actually contain mucilage, e.g., *G. pumilio* (Fig. 6, I, J).

CALOGYNE

Two types of seed are found in this genus, which are directly comparable with types also found in *Goodenia*. These types are numbered below as in the latter genus.

Type 4

All *Calogyne*s with a 3-fid style have this seed type with mucilage cells \pm collapsed at maturity, e.g., *C. pilosa*, *C. purpurea* (Fig. 8, A, B). They resemble the *G. hispida* group of *Goodenia* spp. in that the integument cells between the vascular bundle and the endosperm have thickened cell-walls. Embryo slightly spatulate, a : b = 2 : 3.

Type 6

Calogyne berardiana, with a 2-fid style, has this seed type which is quite distinct from type 4 (Fig. 7, A). Embryo spatulate; a : b = 2 : 4.

TABLE 1

Seed types in Goodenia and related genera (see Fig. 10)
(Sections and Series according to Krause, 1912)

	Section	Series
TYPE 1		
<i>G. barbata</i> R. Br.	Eu-goodenia	Suffruticosae
<i>G. strophiolata</i> F. Muell.	Eu-goodenia	Suffruticosae
<i>G. chisholmii</i> Maiden		
<i>G. phyllicoides</i> F. Muell.	Monochila	
TYPE 2. a		
<i>G. ovata</i> Sm.	Eu-goodenia	Suffruticosae
<i>G. varia</i> R. Br.	Eu-goodenia	Suffruticosae
<i>G. laevis</i> Benth.	Eu-goodenia	Suffruticosae
<i>G. viscida</i> R. Br.	Monochila	
<i>G. eatoniana</i> F. Muell.	Eu-goodenia	Caeruleae
<i>G. azurea</i> F. Muell.	Eu-goodenia	Caeruleae
<i>G. ramellii</i> F. Muell.	Eu-goodenia	Racemosae
<i>G. stapfiana</i> Krause	Eu-goodenia	Racemosae
<i>G. scaevolina</i> F. Muell.	Eu-goodenia	Caeruleae
<i>G. paniculata</i> R. Br.	Amphichila	
b		
<i>Neogoodenia minutiflora</i> Gard. et George		
<i>G. scapigera</i> R. Br.	Monochila	
<i>G. quadrilocularis</i> R. Br.	Eu-goodenia	Racemosae
<i>G. stelligera</i> R. Br.	Eu-goodenia	Racemosae
<i>G. dimorpha</i> Maiden et Betche		
<i>G. decurrens</i> R. Br.	Eu-goodenia	Racemosae
<i>G. bellidifolia</i> R. Br.	Eu-goodenia	Racemosae
<i>G. amplexans</i> F. Muell.	Eu-goodenia	Suffruticosae
<i>G. glabra</i> R. Br.	Eu-goodenia	Rosulatae
<i>G. grandiflora</i> Sims	Eu-goodenia	Foliosae
<i>G. macmillanii</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. calcarata</i> F. Muell.	Eu-goodenia	Foliosae

TABLE 1.—Continued.
Seed types in *Goodenia* and related genera (see Fig. 10)
(Sections and Series according to Krause, 1912)

	Section	Series
TYPE 3		
<i>G. disperma</i> F. Muell.	Eu-goodenia	Suffruticosae
<i>G. rotundifolia</i> R. Br.	Eu-goodenia	Rosulatae
<i>G. affinis</i> De Vr.	Eu-goodenia	Rosulatae
<i>G. hederacea</i> Sm.	Eu-goodenia	Rosulatae
<i>G. boormanii</i> Krause	Eu-goodenia	Rosulatae
<i>G. heterophylla</i> Sm.	Eu-goodenia	Rosulatae
<i>G. sepalosa</i> F. Muell. ex Benth.	Eu-goodenia	Foliosae
<i>G. hispida</i> R. Br.	Eu-goodenia	Foliosae
<i>G. auriculata</i> Benth.	Eu-goodenia	Foliosae
<i>G. armstrongiana</i> De Vr.	Eu-goodenia	Foliosae
<i>G. koningsbergeri</i> (Back.) Back. ex Bold.		
<i>Calogyne pilosa</i> R. Br.		
TYPE 4		
<i>G. glauca</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. heteromera</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. microptera</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. forestii</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. pusilliflora</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. heterochyla</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. vilmoriniae</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. tenuiloba</i> F. Muell.		<i>Incertae sedis</i>
<i>G. corynocarpa</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. armittiana</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. pinnatifida</i> Schlecht.	Eu-goodenia	Pedicellosae
<i>Calogyne berardiana</i> (Gaudich.) F. Muell.		
TYPE 5		
<i>G. mitchellii</i> Benth.	Eu-goodenia	Foliosae
TYPE 6. a		
<i>G. havilandii</i> var <i>pauperata</i> Black		
<i>G. micrantha</i> Helms ex Christ. et Ost.		
<i>G. concinna</i> Benth.	Eu-goodenia	Pedicellosae
b		
<i>G. trichophylla</i> De Vr.	Eu-goodenia	Caeruleae
<i>G. pterygosperma</i> De Vr.	Eu-goodenia	Caeruleae
<i>G. incana</i> R. Br.	Eu-goodenia	Caeruleae
<i>G. caerulea</i> R. Br.	Eu-goodenia	Caeruleae
<i>Symphobasis macropectra</i> (F. Muell.) Krause		
TYPE 7		
<i>G. pumila</i> R. Br.	Amphichila	
TYPE 8 = Type 7 of <i>Scaevola</i> (which see)		
<i>Verreauxia reindwardtii</i>		

SELLIERA

The fruit of this genus is berry-like but the seed is equatable with type 3 in *Goodenia*. Embryo slightly spatulate; $a:b=2:3$.

Indeed, it shows a striking resemblance to that of *G. koningsbergeri* although somewhat smaller. The mucilage is extremely sticky and probably is important in distribution as the "berry" appears to be eaten by sea-birds which thereby pick up these seeds on parts of their body, e.g., *Selliera radicans*.

It has only been possible to examine immature seeds of *S. exigua*, but it seems highly improbable that they are at all similar to those of *S. radicans*.

VELLEIA

Embryo spathulate; $a:b=2:4$ to $2:5$. Here again the basic form of the seed is very similar to a type within *Goodenia*, i.e., type 4, with a fairly conspicuous wing. The mucilaginous cells, however, pass on directly from the thickened ones; these are not curved as in the *Goodenia* type although

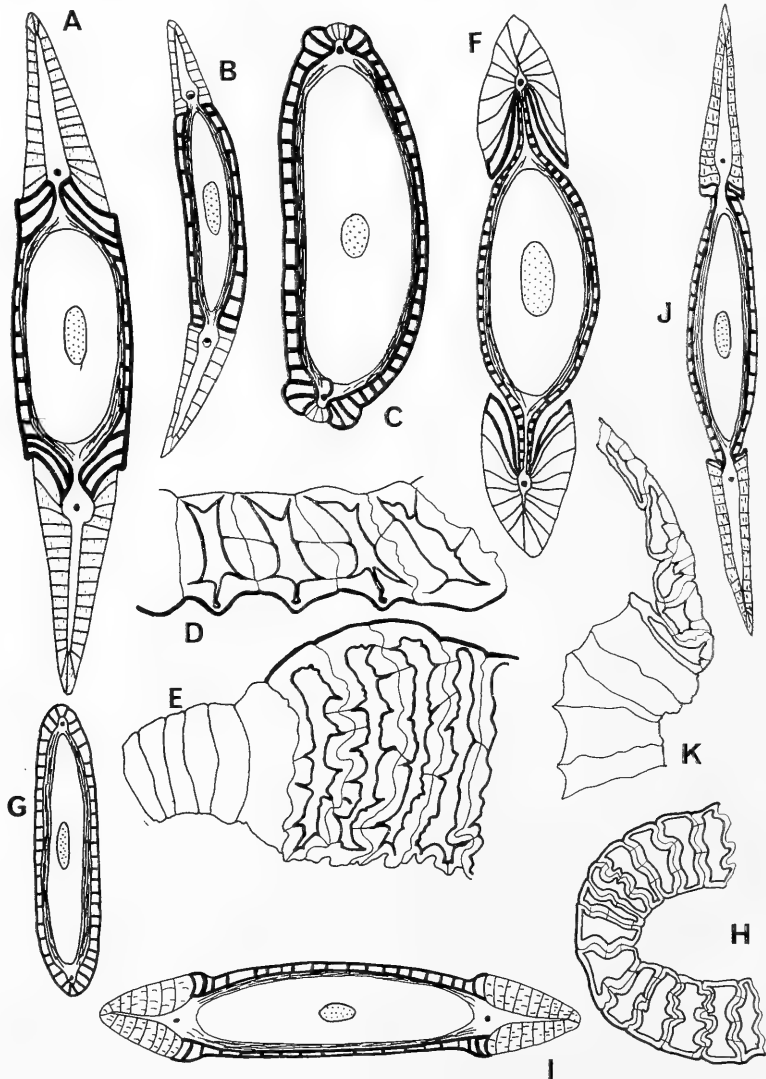


Fig. 7. Transverse sections of seeds. A. *Calogyne berardiana* $\times 50$; B. *Velleia spathulata* $\times 10$; C. *V. montana* $\times 20$; D. *V. montana*, epidermal cells $\times 160$; E. *V. montana*, marginal epidermal cells $\times 160$; F. *Goodenia concinna* $\times 12$; G. *Verreauxia reinwardtii* $\times 20$; H. *V. reinwardtii* marginal epidermal cells; I. *Neogoodenia minutiflora* $\times 20$; J. *Goodenia pterygosperma* $\times 20$; K. *G. pterygosperma*, marginal epidermal cells $\times 160$.

the walls are very convoluted. In only one of the species examined, *V. montana*, is there any conspicuous departure from this type. In *V. montana* the mucilage cells are very much reduced in number and form a minute rim enclosed by the overarching marginal thickened cells, e.g., *V. spathulata*, *V. paradoxa*, *V. discophora*, *V. cynopotamica* (Fig. 7, B-E).

CATOSPERMA

Embryo almost terete. In this genus the fruit is hard and indehiscent and contains up to four seeds. Each seed shows clearly the differentiation into thickened cells and "mucilage" cells, although the walls of the former are not convoluted as in *Goodenia*, etc., and the mucilage-cells, although very thin-walled, do not apparently contain mucilage. The marginal thickened cells are no different from their fellows and the mucilage cells form a rounded rim. The embryo appears to be \pm terete e.g. *C. goodeniacearum* (Fig. 6, C-H).

PENTAPTILON

This genus again shows an indehiscent dry fruit. The 4-6 seeds are pendulous and otherwise are remarkably similar to those of *Catosperma* (Fig. 6, E, F). Embryo not observed.

VERREAUXIA

Embryo almost terete. Another genus with indehiscent fruits, this time, however, containing only one seed. The fruit has an outer layer of thin-walled, collapsed cells, whilst the inner layer, probably corresponding to the true ovary wall, has interlocking cells with thickened walls. The seed does not correspond to any of the *Goodenia* types listed above. In *V. reinwardtii* the epidermis is undifferentiated, all the cells have thickened walls and there are no mucilage cells, but the seed is compressed and has no strophiole (cf. *Goodenia* type 1) (Fig. 7, E, H). There is only a single vascular strand which passes from the funicle around the periphery of the seed and reaches almost to the micropyle; the embryo was not observed.

In *V. paniculata* the situation is very slightly different in that the marginal cells do show some difference from the immediately adjacent cells. The walls are quite straight and not thickened so much, whereas the adjacent cells on the seed face are convoluted. Moreover, the walls of the marginal cells tend to stain more deeply with Chlorazol Black. These marginal cells do not, however, appear to contain mucilage, e.g., *V. reinwardtii*, *V. paniculata*.

SYMPHIOBASIS

No mature seed of this genus was available for study.

NEOGOODENIA

Embryo spatulate; $a:b=2:3$. This genus is distinguished from *Goodenia* primarily upon the single seed borne in a thin-walled, indehiscent, unilocular fruit (Gardner and George, 1963). The fruit wall appears to be quite unthickened (cf. *Verreauxia*, *Dampiera* and *Scaevola*) and the seed closely resembles that of some *Goodenia* spp. The epidermal cells on the body of the fruit have somewhat thickened walls and those of the prominent rim contain considerable quantities of mucilage. The marginal thickened cells do not project so extensively into the interior of the seed and the vascular bundle is consequently not "pinched off" from the rest of the integument (Fig. 7, I). Otherwise the seed falls close to *Goodenia* type 2b. The cotyledons are narrow. The fruit is actually similar to *Verreauxia* in that the seed is inserted on a basal abortive septum.

SCAEVOLA (see Fig. 11)

The seed of all *Scaevola* species show a single vascular bundle, unbranched, which extends from the funicle right around the seed almost to the micropyle. The seed is frequently slightly compressed and the vascular bundle runs just beneath the more or less prominent, marginal ridge (Fig. 3, C).

The fruit of *Scaevola* is indehiscent with a varying development of hard 'endocarp' towards the locules. This 'endocarp' grades into the unthickened cells towards the outside; there is no clear demarcation line as in *Dampiera stricta*. The testa of the seed consists of thin-walled cells which, at maturity, show bands of thickening; the cells are all of the same type; there are no

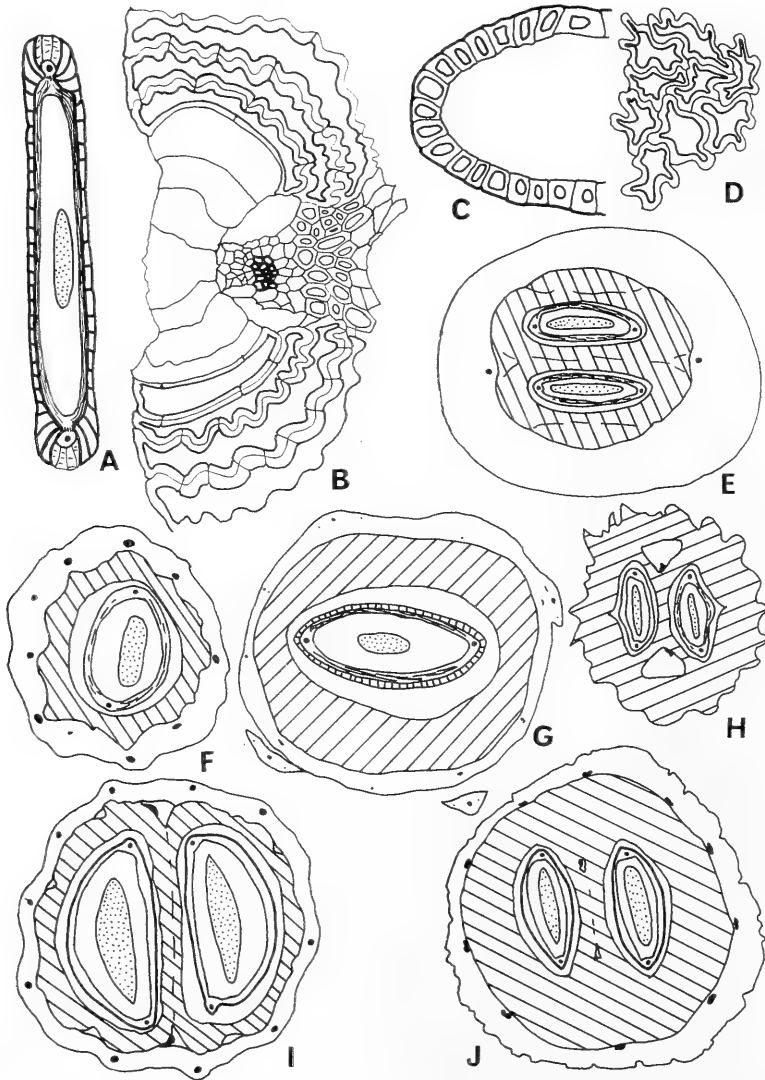


Fig. 8. Transverse sections of seed. A. *Calogyne pilosa* $\times 12$; B. *C. pilosa*, marginal epidermal cells $\times 160$; C. *Scaevola stenophylla*, marginal epidermal cells; D. surface view of epidermal cells, *S. stenophylla*. Transverse sections of fruits. E. *Scaevola spinescens* $\times 4$; F. *Scaevola humifusa* $\times 8$; G. *S. helmsii* $\times 20$; H. *S. calendulacea* (pyrene only); I. *S. ramosissima* $\times 8$; J. *S. chamissoniana* $\times 4$.

mucilage cells as in *Goodenia*. This applies to all the species except *Scaevola stenophylla*, *S. helmsii* and *S. fasciculata*: here, although there is no differentiation into mucilage cells towards the margin, the epidermal cells are all distinctly and more or less uniformly thickened. Moreover, they show the sinuate outline, in surface view, found in *Goodenia*, not the more regular shape as in other

Scaevola sp. Three zones are distinguished in pseudo-fruit walls and they will be referred to as epicarp, mesocarp and endocarp, although they do not correspond exactly to the zones so named in the true drupe. The epicarp here, in fact, is probably derived from the outer floral whorls (in the phylogenetic sense) whilst both the mesocarp and endocarp develop from tissue which is probably derived from the ovary itself. All three zones consist of more than one layer of cells and, as defined here, either the epicarp or the mesocarp may contribute towards the succulent part of the false-fruit where such occurs. The seven types of fruit described below are based upon differences in the constitution of these three layers and the number of loculi. Since much of the work was conducted upon herbarium material, it was not always possible to determine the relative succulence of the various layers. In the lists “*” indicates where fresh material has been examined.

Type 1.—Four loculi present; mesocarp and endocarp not differentiated from each other, epicarp dry.

S. porocarya. The fruit of this species contains four seeds which each occupy a separate loculus; two of these loculi arise at a lower level than the other two. In addition to these fertile loculi there are a large number of irregular cavities which apparently arise through the disintegration of vascular bundles. Bentham (1863) states that only two seeds are present but, although this may be the case when only two ovules are fertilized, the general rule is that four seeds are formed. There is no distinct separation of the pseudo-fruit wall into a fleshy external layer and a hard “endocarp”; the external tissues are only slightly softer than the internal ones (Fig. 9, H).

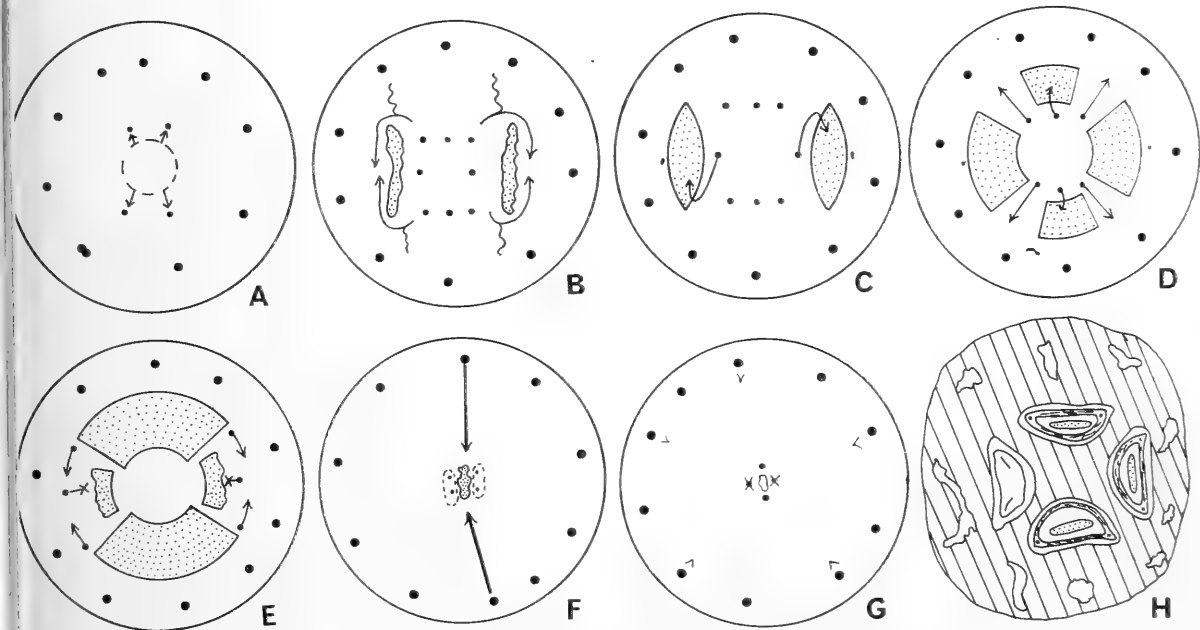


Fig. 9. *Scaevola porocarya*. A-G. Diagrams to show the vascular pattern at different levels in the pseudo-ovary. A. near base; B. two lowermost loculi appearing, movement of stands to form carpel dorsal shown; C. strands entering lower ovules; D. strands entering upper ovules; E. dorsals of lateral carpels disappear (x) replaced by laterals (shown by arrows); F. dorsals of anterior and posterior carpels pass to base of style; G. laterals of lateral carpels disappear (x) and staminal strands begin to separate from sepal-radius bundles (Δ); H. Transverse section of fruit showing spaces in “endocarp”.

This is the only case, so far reported in the family, in which a 4-locular ovary has been seen (cf. Carolin, 1958). It therefore calls for a rather more detailed consideration of the vascular network of the flower. This is shown in the series of diagrams which have been compounded from serial sections prepared in the manner indicated in the previous paper (Carolin, 1959). At the base of the flower the stele resolves into 7-10 peripheral bundles, mostly on petal or sepal radii (eventually 10 are formed) with a ring of indeterminate bundles in the centre. These very soon give rise to four bundles which pass outwards and around the back of the two lower loculi which are just forming; there they fuse and form a single bundle which eventually ends blindly at the base of the style. Meanwhile the central ring has resolved into light bundles; four of these pass into the ovules, the other four pass outwards (carpel laterals) and eventually appear to end blindly at the base of the style. Two large bundles are formed anteriorly and posteriorly, both from bundles on petal radii, which pass inwards and up into the style unchanged. The derivation of the other bundles to the floral parts is the same as in other *Scaevola* spp. (Carolin, 1959), and the full interpretation of the positioning of the different organ bundles is shown in Fig. 9, A-G.

Type 2.—2-loculi, sometimes with sterile loculi, mesocarp and endocarp not differentiated from each other, epicarp various.

This type would seem to be a straightforward derivation from type 1 by abortion of the lateral loculi. The pseudo-carpel lateral bundles (Carolin, 1959) are included within the hard endocarp and the epicarp shows varying degrees of succulence. Some species have no sterile lateral loculi, e.g., *S. oppositifolia*, *S. nitida*.

However, although *S. porocarya* is the only species which is known to have a truly 4-locular ovary, a number of others have false, sterile loculi in addition to those containing the ovules. In *S. calendulacea* (Fig. 8, H) and *S. globulifera*, for example, the cells surrounding the pseudo-carpel lateral bundles remain parenchymatous as the endocarp is formed by the thickening of the walls of the other innerzone cells. At maturity these parenchymatous cells have broken down, probably due to their failure to grow at the same rate as the others, and a large cavity remains. These two lateral cavities are connected at the base of the septum by a single cavity formed by the disintegration of the axile vascular strands and the parenchymatous tissue surrounding them (cf. *S. porocarya*). In *S. attenuata* the single basal cavity is extremely well marked, whilst the pseudo-carpel laterals extend only for a very short distance up the ovary so that no lateral cavities are formed.

The situation appears to be directly comparable to that in the Hawaiian *S. cerasifolia* (Skottsberg, 1923). Moreover, despite Skottsberg's illustrations to the contrary, *S. chamissoniana* also has very minute sterile loculi alternating with the two fertile loculi (Fig. 8, J). The former represent the ruptured pseudo-carpel lateral bundles; none of the adjacent tissues remain unthickened.

The epicarp may be dry as in *S. globulifera* or very well developed and succulent as in *S. calendulacea*.

The endocarp may be differentiated in colour and thickness of the cell walls from those of the inner endocarp as in *S. nitida*, *S. saligna*. In this species the inner endocarp is brown and the outer zone is colourless; moreover, the pseudo-carpel lateral bundles occur very close to the outer margin of the mesocarp. In this particular species no false loculi occur. The thickness of the mesocarp is often not uniform giving a gibbous appearance to the fruit of some species, e.g., *S. dielsii*.

Type 3.—2-loculi usually with 2 sterile loculi in a non-succulent mesocarp differentiated from the endocarp; epicarp various.

In this type the inner zone is not uniform, but two layers which intergrade into each other are formed. In *S. taccada* this inner endocarp consists of cells with thickened walls whilst the outer mesocarp has suberized cell walls.

TABLE 2
Fruit types in Scaevola (see Fig. 11)
(Sections according to Krause, 1912)

	Section
TYPE 1	
<i>S. porocarya</i> F. Muell.*	Xerocarpacea
TYPE 2 (without sterile lateral loculi)	
<i>S. oppositifolia</i> Roxb.	Enantiophyllum
<i>S. saligna</i> Forst. f.*	Xerocarpacea
<i>S. nitida</i> R. Br.*	Xerocarpacea
<i>S. dielsii</i> E. Pritzel*	Xerocarpacea
<i>S. attenuata</i> R. Br.	Xerocarpacea
(with sterile lateral loculi)	
<i>S. calendulacea</i> (Kennedy) Druce*	Xerocarpacea
<i>S. globulifera</i> Labill.*	Xerocarpacea
<i>S. chamissoniana</i> Gaudich.	Sarcocarpacea
<i>S. micrantha</i> Presl.	Sarcocarpacea
<i>S. indigofera</i> Schlechter	Sarcocarpacea
<i>S. glandulifera</i> DC.	Xerocarpacea
TYPE 3 (with a distinct mesocarp containing the lateral bundles.)	
<i>S. taccada</i> Roxb.	Sarcocarpacea
<i>S. mollis</i> Hook. et Arn.	Sarcocarpacea
TYPE 4	
<i>S. spinescens</i> R. Br.*	Crossotoma
<i>S. tomentosa</i> Gaudich.*	Crossotoma
TYPE 5	
<i>S. ovalifolia</i> R. Br.*	Xerocarpacea
<i>S. hookeri</i> F. Muell.*	Pogonanthera
<i>S. crassifolia</i> Labill.*	Xerocarpacea
<i>S. ramosissima</i> (Sm.) Krause	Xerocarpacea
TYPE 6	
<i>S. humifusa</i> De Vries	Xerocarpacea
<i>S. albida</i> (Sm.) Druce	Xerocarpacea
TYPE 7 (8 of <i>Goodenia</i>)	
<i>S. stenophylla</i> (F. Muell.) Benth.	Xerocarpacea
<i>S. fasciculata</i> Benth.	Xerocarpacea
<i>S. helmsii</i> E. Pritzel	Xerocarpacea

Embedded in the mesocarp are the two, narrow false-loculi formed in the same way as those of type 3. *S. mollis* has much the same construction, but the false-loculi are considerably larger in size (Skottsberg, 1923).

Type 4.—2-loculi, no sterile loculi; mesocarp succulent.

This represents the condition where only the innermost zone is thickened and the pseudo-carpel lateral bundles are embedded in a succulent mesocarp-epicarp, e.g., *S. tomentosa* (Fig. 8, E).

Type 5.—2-loculi; usually with 2 (small) sterile loculi; epicarp and mesocarp dry.

This seems to be the commonest form of fruit found in the sect. *Xerocarpea*. It can, in fact, be interpreted in two ways: either as the change of the mesocarp surrounding the pseudo-carpel laterals into the collapsed, thin-walled condition of the epicarp, or as the movement, outwards, of the pseudo-carpel laterals into the epicarp. The tissues surrounding these bundles tend to disintegrate to form small false-loculi just on the innermost boundary of the epicarp, e.g., *S. ramosissima* (Fig. 8, I), *S. crassula*.

Type 6.—1-loculus; \pm small sterile loculi; epicarp and mesocarp dry.

This differs from the previous type only in that the septum between the two ovules is present only at the base of the ovary (cf. Carolin, 1959), e.g., *S. albida*, *S. humifusa* (Fig. 8, F).

Type 7 (8 of *Goodenia*).

The pseudo-lateral carpel bundles in this case are included within the endocarp. There is no tendency to form sterile "loculi" and, due to the septum being extremely short, the fruit appears to be unilocular. The epicarp is very thin and, unlike most of the representatives of type 7, the endocarp surface is smooth, not rugose. The seeds are quite different from all the other *Scaevola* species in the very much thickened testa cell-walls and the irregular surface outline of these same cells (Fig. 8, G, C, D). In this respect they resemble the seeds of *Verreauxia* and, somewhat, those of *Goodenia scapigera*.

DISCUSSION

The genera of the Goodeniaceae can be divided into two groups on the basis of the seed vascular supply, corresponding precisely with that grouping suggested previously by Carolin (1959) and Peacock (1961). In the *Dampiera* group, i.e. *Dampiera*, *Anthotium*, *Leschenaultia* and *Brunonia*, the seeds have either a double vascular supply or a single strand; neither system, however, reaches right around to the micropylar side, they gradually get smaller and usually disappear towards the top of the seed. *Dampiera* spp. are fairly consistent in showing a double supply, in sect. *Camptospora* much elaborated to supply the large, peculiarly shaped seed. In *Brunonia* a single strand is found reaching around the top of the seed, whilst in *Leschenaultia* and *Anthotium* the single strand is very short indeed. The short, single strand can probably be interpreted as due to the fusion of the double supply of *Dampiera*.

So far as the fruits are concerned, *Anthotium* has the only dehiscent fruit in the group and the seeds are the only ones in the group with a conspicuously thickened testa epidermis. In *Dampiera* and *Leschenaultia* the seeds are contained in "endocarps", which function as the protective covering, the thickening of the seed coat epidermis is reduced to a few lignin bands per cell in *Dampiera* and is virtually non-existent in *Leschenaultia*. In *Brunonia* the protection is supplied by the tough calyx-tube whilst both the fruit wall and the seed-coat are very thin. The "endocarp" of *Dampiera* and *Leschenaultia* appears to correspond to the true fruit wall whilst the outer, unthickened parts correspond to the united, outer floral whorls (cf. Carolin, 1959). Whilst the general structure of the pseudo-fruit of *Dampiera* sect. *Dicoelia* does not differ greatly from that of *Scaevola* sect. *Xerocarpea*, the seed vasculature is totally different. There would appear to be no phylogenetic connection.

Thus it appears that, although this group is a fairly well-defined unit, one cannot detect any consistent and correlated trends within it. If we accept that the multiple nature of the strand is more primitive than a single strand, we are left with *Anthotium* with a primitive, capsular fruit and an advanced,

reduced seed vasculature, *Dampiera* with a primitive seed vasculature and an advanced indehiscent fruit, and *Leschenaultia* with an advanced seed vasculature and formation of an "endocarp" but a primitive (numerous) number of seeds. *Brunonia* shows so many other differences that it is impossible to fit it into any series at all. It seems, then, that this group represents the ends of a number of diverging evolutionary lines, each branch of which has had an effectively separate history, not basically uniform as in the other group.

The other group consists of *Goodenia*, *Calogyne*, *Selliera*, *Pentaptilon*, *Catosperma*, *Neogoodenia*, *Verreauxia Velleia*, *Scaevola*, *Diaspasis*.

If we accept as a general, although not binding rule, that the capsule is more primitive than an indehiscent fruit and a seed with a uniform testa is more primitive than one in which the seed coat is differentiated into several cell-types, the group of species centred around *Goodenia barbata* appear to carry the most primitive features in this group. It is interesting to note that the seeds are also strophiolate. It appears improbable that they are particularly close to the ancestral form, since the basic chromosome number is different from the rest of the group (Peacock, 1961). The latter author has listed other differences from the rest of the genus *Goodenia* and it seems they may merit separate generic rank. All other species of *Goodenia*, *Calogyne*, *Selliera*, *Pentaptilon*, *Catosperma*, *Neogoodenia* and *Velleia* have more or less flattened seeds with at least some of the cells on the margin differentiated into thin-walled "mucilage" cells. From this point of view, the last seven may be considered as "satellite" genera around the large, somewhat, polymorphic genus *Goodenia* (Fig. 10). Of the various seed-types (except type 1) described under *Goodenia* it is rather difficult to decide which, if any, is the most primitive. Type 2 would seem to be the least differentiated, particularly the form found in *G. ovata* where the marginal thickened cells are scarcely differentiated from the outer thickened cells. But, as will be suggested later, it is possible that there has been a reversal in that some forms have reverted to an entirely undifferentiated testa epidermis. It is difficult to say for certain whether the form of *G. ovata* seeds is due to primitiveness or more or less advanced reduction. However, the shrubby habit, the anatomy and the inflorescence (cf. Krause, 1912) indicate that the species associated with *G. ovata* have a combination of what are generally considered to be primitive characters and it seems reasonable to accept the *G. ovata* form as a starting point. Further evolution has progressed mainly through the elaboration of the marginal thickened cells and changes in the number and arrangement of the "mucilage" cells. Type 2 (b) represents a line in which the marginal thickened cells have become much enlarged, but the arrangement of them and their relationships with the "mucilage" cells remains much the same as in the *G. ovata* group.

Type 3 represents the line in which the marginal thickened cells are enlarged and overarching the mucilage cells which are often very reduced in number and, frequently, apparently non-functional. In *G. koningsbergeri*, in particular, the number of mucilage cells is very small. It is usual, in these cases in particular, to find that the integument cells immediately in from the vascular bundle become thickened, presumably to seal off the inner parts of the seed more effectively than the thin-walled "mucilage" cells, in this case probably containing little if any mucilage. In addition to this trend of reduction in the mucilage cell number, another trend seems to be operating in those species assigned to type 3 (b). In this case the marginal thickened cells become curved above, thus giving a ridge marking off the mucilage-cells from the body of the seed. The superficial appearance is not unlike that found in type 2 (b) but is due to an entirely different configuration of the cells involved (Fig. 10).

Another line is represented by those species assigned to type 4. In this case the marginal thickened cells are elongated, but their long axis is placed so that they underlie many of the "mucilage" cells.

Type 5 represents a derivative of this line in which the horizontal axis of the "mucilage" cells is shortened and the parenchymatous part of the wing is fairly massive.

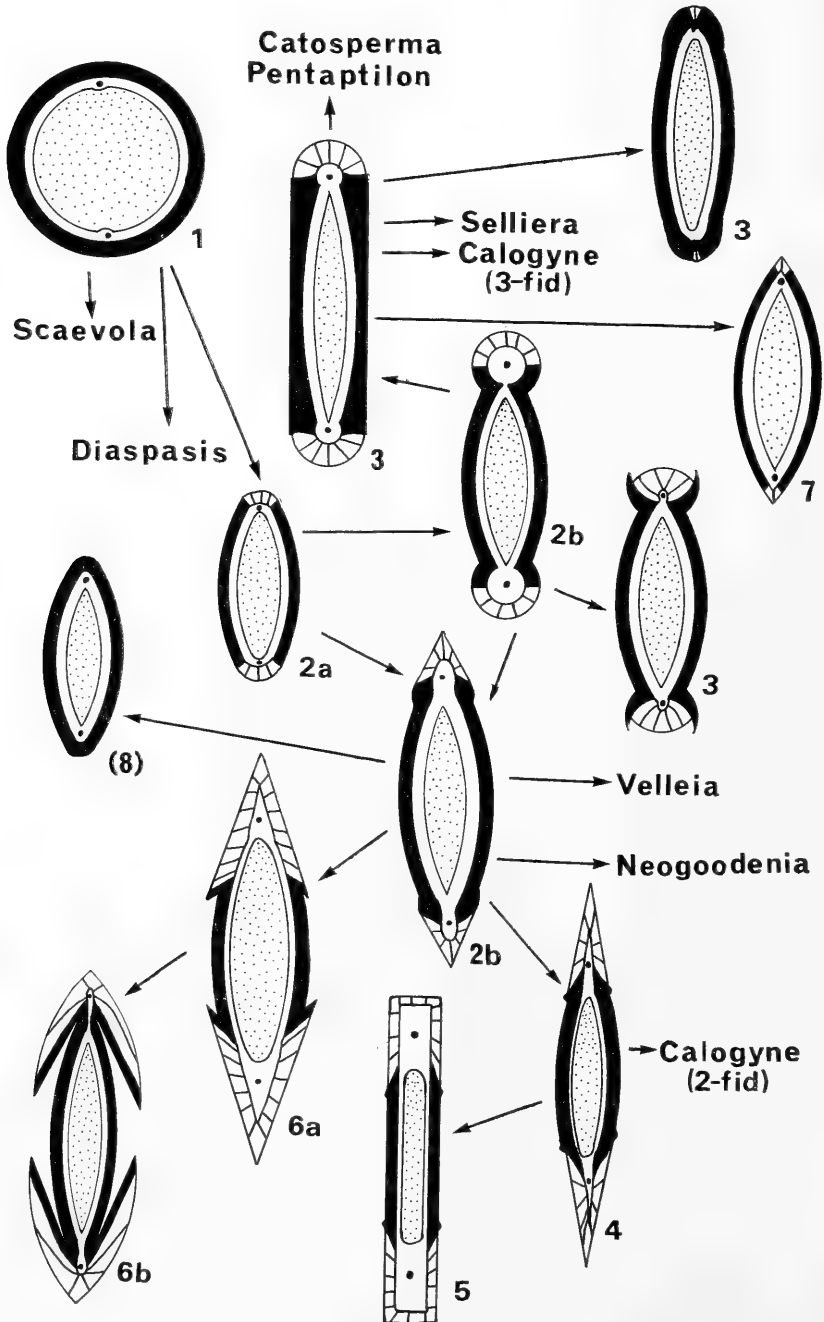


Fig. 10. Diagram to show the suggested relationships of the types of seed found in *Goodenia* and its satellite genera. Hatched areas=mucilage cells; solid black areas=thickened epidermal cells; stippled areas=endosperm and embryo.

Yet another line is shown by type 6, in which one of the marginal thickened cells becomes much elongated and supports the large "mucilage" cells overlying the outer parts of the body of the seed. These peculiarities are relatively undeveloped in *G. pterygosperma* and *G. trichophylla* but extremely well developed in *G. micrantha*.

Type 7 is a very reduced form and it is difficult to fit it into any of these lines; it could be the end product of reduction of any of them. Without evidence from other characters, which is being accumulated, it is impossible to place this species in any series.

These lines all seem to converge on that of type 2 (*a*) and, to some extent, intergrade with it. This is further evidence for considering it to be the basic, primitive type. Despite these intergrades the types are fairly distinct and close-knit and, for this reason, represent real biological units. Evidence is being accumulated that other distinctive characters are correlated with them. This being so it would appear that Krause's sections and series (1912) require a drastic overhaul. Of his sections, *Monochila* is particularly unsatisfactory, since it contains some species having type 2 and one species with type 1 seeds. *G. barbata*, *G. strophiolata* (and *G. chisholmii*), from section *Eugoodenia* should be linked with *G. phylloides*. Ser. *Suffruticosae* seems to be a rather heterogeneous group and needs breaking up. Ser. *Caeruleae* divides quite neatly into two groups with type 2 and type 6 seeds respectively. Ser. *Racemosae* is fairly uniformly type 3. Ser. *Foliosae*, on the other hand, splits into three fairly well defined groups: those centred around *G. grandiflora* with type 2 (*b*), those around *G. hispida* with type 3, and those around *G. heterochila* with types 4 and 5. There seems little doubt that this is a heterogeneous taxon when such widely differing seed types are found within it. It is interesting to find that *G. grandiflora* frequently has bracteoles despite Krause's placing them in the *Ebracteolatae*. Indeed, the presence or absence of bracteoles seems to be of little value in itself.

To turn to the "satellite" genera. *Calogyne* again has shown its heterogeneous nature (see Carolin, 1959). *C. berardiana* belongs to the evolutionary line represented by *G. glauca* and *G. heterochila*. All the other species belong to the line represented by *G. hispida* and *G. koningsbergeri*. *Calogyne*, as constituted, is an unsatisfactory genus and the 2-fid-styled species should be separated from those having 3-fid styles. *Selliera* belongs to the evolutionary line of type 3 similar to *G. koningsbergeri* which, indeed, has been referred to *Selliera* in the past.

Neogoodenia has a rather more basic seed-type, and it is consequently rather more difficult to assign it to any particular line of development. Although there is only a single seed in an indehiscent fruit, there is no doubt of its close affinity with *Goodenia* on account of its seed type. All the "satellite" genera so far discussed are so close to *Goodenia* that a case could be made for their inclusion in that genus.

The seeds of *Velleia* are very similar to types 3(*b*) and 2(*b*) of *Goodenia*. Thus, although they possess the "mucilage" cells, and thus a differentiated seed coat, the type shown is a fairly basic one. It seems probable, then, that *Velleia* has separated from the bulk of *Goodenia* subsequent to the differentiation of the mucilage cells in phylogenetic history, and thus after both had diverged from the *G. barbata* group: a further argument for accepting the latter as a separate genus. *Velleia*, however, must remain a generic entity by virtue of its other characters.

Both *Catosperma* and *Pentaptilon* show a seed structure undoubtedly derived from a *Goodenia* type, but the reduction which has apparently accompanied the closure of the fruit has made it impossible to decide to which line they belong on this evidence.

Verreauxia differs from all the other genera examined in this group so far by its lack of mucilage cells. All the epidermal cells of the compressed seed, even those on the margins, are uniformly thickened. They are distinctly thickened and the vasculature is quite definitely of the *Goodenia* type—there is no doubt about the position of the genus in this group. Thus *Verreauxia* is either a case of extreme reduction, the possibility of which is shown by *Goodenia koningsbergeri*, or has retained the primitive condition also shown by the *G. barbata* group. Evidence from other directions is needed before this problem can be resolved.

The discovery of the 4-locular nature of the ovary of *Scaevola porocarya* is of some significance in that it forces a new interpretation of the ovary structure, at least of *Scaevola*. Figures 9, A–G, show that the loculi must be considered as carpels; they have a vasculature in fair agreement with this hypothesis, although those of the opposing pairs of carpels have reacted in different ways to the adnation of the outer whorls to the ovary. The lateral pair of carpels have a dorsal strand each, produced from the union of two strands, themselves derived separately from the central stele. This is a very unusual condition; although the double nature of the dorsal bundle has been established in some primitive groups it is unexpected here. The posterior-anterior pair have a dorsal vasculature exactly similar to that found in other *Scaevola* spp. (Carolin, 1959). The adjacent lateral bundles of the carpels are united and the laterally opposite pairs eventually unite. Neither these nor the dorsal bundles of the lateral carpels extend into the style, rather unusual, as in other species the former do so and in *S. ramosissima* all four lateral bundles separate and are persistent through the style (Carolin, 1959). It appears that the evolution of the vascular system of the flower is just as uneven as the larger differences found in the *Dampiera* group (see above), advanced and primitive conditions occurring in the same species, indeed, at different levels within the same flower. It seems, then, that *Scaevola* has had a rather different history from that of the rest of the *Goodenia* group. The behaviour of the “pseudo-carpellary dorsal” bundles at the top of the ovary of *Goodenia*, etc., implies that the loculus is derived from two carpels (Carolin, 1959). The bundles similarly positioned in *Scaevola* remain single always; this fact, together with the discovery of the structure of *S. porocarya*, implies that the loculus in the case of *Scaevola* represents a single carpel. Furthermore, if this reasoning is accepted, *Goodenia* has “true” carpels placed diagonally in the flower whilst *Scaevola* has them placed anterior-posteriorly and (sometimes) laterally. This is not necessarily a particularly far-reaching difference since these two conditions may occur elsewhere in the plant kingdom within the same species (e.g., *Campanula*). It does, however, imply that the evolutionary histories of *Scaevola* and *Goodenia* are separate, and similarities in the ovary structure are the result of convergence rather than common origin.

The seeds of *Scaevola* are usually more or less compressed, although the structure of the testa is rather similar to that of *Dampiera*. However, there is little doubt that it is not closely allied to *Dampiera* since the seed has a single strand, the floral structure is different (Carolin, 1959) and the chromosome number is different (Peacock, 1961).

Within the genus the fruit types (see Fig. 11), once again, show only incomplete correlation with the Sections proposed by Krause. After the type exhibited by *S. porocarya*, it seems reasonable to suppose that type 2 is the most primitive since, in this case, the tissues which are most probably gynoeical in origin behave as a unit, i.e., form the “endocarp”. The false-loculi really represent a case of “regressive convergence” towards the condition in type 1 subsequent to the loss of the lateral carpel (loculi). These taxa belong mostly to the Sarcocarpaea and all of them have a highly developed “mesocarp”, be it fleshy or corky. The trend in the Sections *Crossotoma*, *Xerocarpaea* and *Pogonanthera* is towards the exclusion of part of the tissue of gynoeical origin

from "endocarp" formation, this part being around the false-loculi caused by the disruption of the "lateral" bundles. In sect. *Crossotoma* no false-loculi are formed and these tissues are included in the fleshy "mesocarp"; in sects *Xerocarpacea* and *Pogonanthera* the false-loculi are frequently present and the "mesocarp" is thin. *S. crassifolia* and *S. nitida* resemble *S. porocarya*

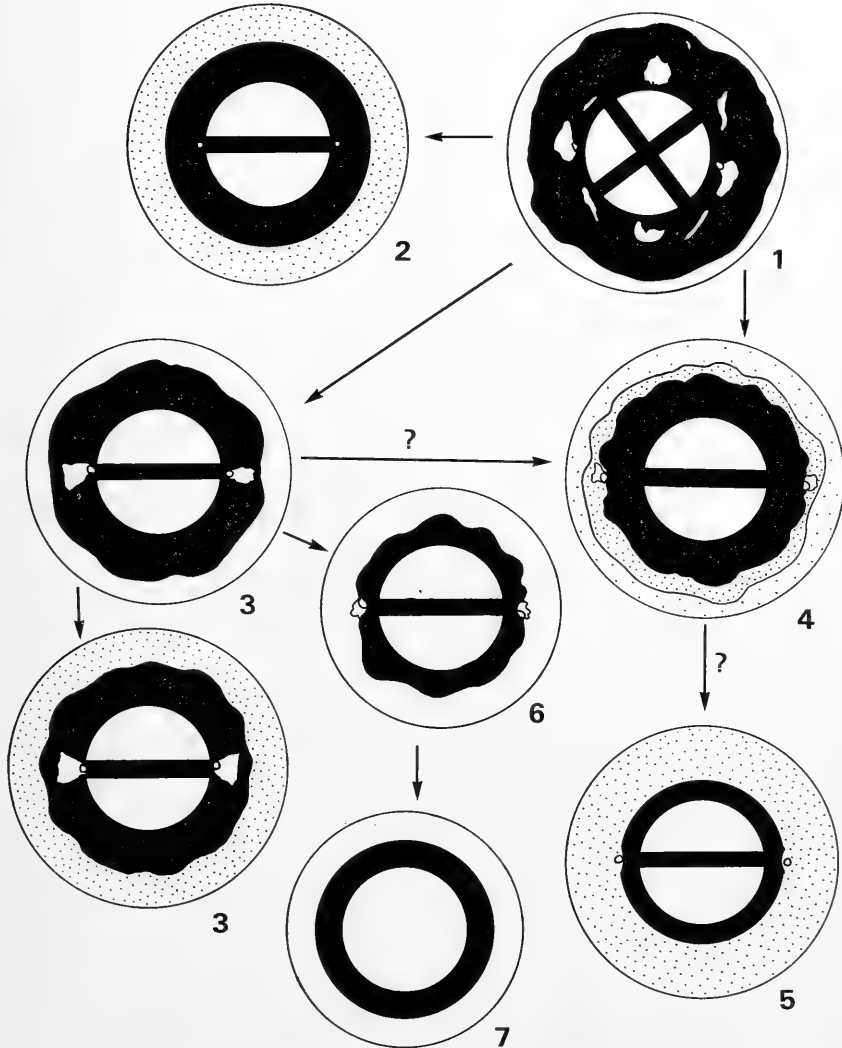


Fig. 11. Diagram to show the suggested relationships of the pseudo-fruit types of *Scaevola*. Open areas=dry, soft tissue; solid black areas=dry, hard tissue; stippled areas=fleshy (or corky) tissue.

so closely in many respects there seems little doubt that they are related despite the first two species having type 2 fruits. It appears, then, that the *Sarcocarpacea* have originated from the 4-locular type separately from the *Xerocarpacea* group and possibly earlier. Sect. *Pogonanthera* shows very few differences from *Xerocarpacea* in fruit structure and sect. *Crossotoma* appears to be a fleshy-"mesocarp" derivative of the *Xerocarpacea*.

The three species, *S. stenophylla*, *S. helmsii*, *S. fasciculata*, show very real differences in the seed form from the rest of genus; they also had a significantly different floral construction (Carolin, 1959). In fact, the seeds have very definitely thickened epidermal cells, quite unlike the lignin banding seen in the rest of *Scaevola* spp. Indeed, they resemble those of *Verreauxia* or *Goodenia* without the marginal mucilage cells. It was previously suggested that these species were closer to *Verreauxia* than *Scaevola* (Carolin, 1959) but other characters would seem to link them with a group of *Goodenia* spp., centred around *G. scapigera*. This would, in fact, imply not only an evolutionary trend towards reduction in ovule number and closure of the fruit, but also a loss of the mucilage cells and a reversal, in the evolutionary sense, to something more closely resembling the *G. barbata* type. The seed of *S. helmsii*, however, is compressed and not \pm circular in transection.

The rest of *Scaevola* ser. *Uniloculatae* shows a straightforward unilocular drupaceous fruit with a thin "mesocarp" and no false-loculi. Although there is no indication from the fruit or seed that there have been several origins of the unilocular condition from the (apparently) bilocular condition (cf. Carolin, 1959), other characters indicate that this may be so.

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References

- BENTHAM, G., 1869.—*Flora Australiensis*, vol 4. London.
- BERSLER, J. D., and BOCQUET, G., 1960.—Les méthodes d'éclaircissements en vascularisation et en morphogénie végétales comparées. *Arch. Sci. Phys. et Nat. (Gen.)*, 13: 555.
- CAROLIN, R. C., 1959.—Floral Structure and Anatomy in the Family Goodeniaceae. *PROC. LINN. SOC. N.S.W.*, 84: 242.
- , 1960.—The structures involved in the presentation of pollen to visiting insects in the Order Campanales. *PROC. LINN. SOC. N.S.W.*, 85: 197.
- , 1960b.—Floral structure and anatomy in the Family Stylidiaceae. *PROC. LINN. SOC. N.S.W.*, 85: 189.
- GARDNER, C., and GEORGE, A., 1963.—Eight new plants from Western Australia. *Jour. roy. Soc. W.A.*, 46: 129.
- GLICK, D., 1949.—"Techniques of histo- and cytochemistry". New York.
- KRAUSE, K., 1912.—"Das Pflanzenreich", 54—Goodeniaceae und Brunoniaceae. Berlin.
- LINDLEY, J., 1836.—"Natural System of Botany". London.
- MARTIN, A. C., 1946.—The comparative internal morphology of seeds. *Am. Midl. Nat.*, 36: 513.
- PEACOCK, W. J., 1963.—Chromosome numbers and cytoevolution in the Goodeniaceae. *PROC. LINN. SOC. N.S.W.*, 88: 8.
- SKOTTSBERG, C., 1923.—*Artemisia*, *Scaevola*, *Santalum* and *Vaccinium* of Hawaii. *Bull. Bish. Mus.*, 43: 1.
- STEEDMAN, H. F., 1960.—"Section cutting in microscopy". Oxford.

Voucher Specimens

Leschenaultia biloba Carolin 3428 (Syd.). *L. divaricata* Carolin 43 (Syd.). *L. filiformis* Perry 1710 (Canb.). *L. linarioides* Carolin 3324 (Syd.). *L. longiloba* no voucher. *Anthotium rubriflorum* no voucher. *Dampiera coronata* Carolin 3243 (Syd.). *D. purpurea* Carolin 4439 (Syd.). *D. stricta* Peacock 6011.26.6 (Syd.). *D. trigona* Carolin 3055 (Syd.). *Diaspasis filiformis* no voucher.

Goodenia affinis Carolin 3340 (Syd.). *G. amplexans* Black, Burnside Road 2.1904 (N.S.W.). *G. armstrongiana* Chippendale 18.5.59 (N.S.W. ex N.T. 6199). *G. armitiana* Perry 1904 (Canb.). *G. auriculata* Perry 1772 (Canb.). *G. azurea* Chippendale 12.4.59 (N.S.W. ex N.T. 5659). *G. barbata* Peacock 6012.5.1 (Syd.). *G. bellidifolia* Carolin 565 (Syd.). *G. caerulea* Sargent 4069 (N.S.W.). *G. boormanii* Peacock 6111.26.1 (Syd.). *G. calcarata* Beadle 8.1941 (Syd.). *G. chisholmii* Peacock 6012.4.1 (Syd.). *G. concinna* Benn 4.10.1963 (Syd.). *G. corynocarpa* no voucher. *G. decurrens* Peacock 6011.26.3 (Syd.). *G. dimorpha* Carolin Oct. 1963 (Syd.). *G. disperma* Mueller, Burnett River (K). *G. eatoniana* Koch, 2032 (N.S.W.). *G. glabra* Peacock

6111.31.1 (Syd.). *G. glauca* Wharton 9.2.1952 (Syd.). *G. grandiflora* Cambage 3978 (Syd.). *G. havilandii* var. *pauperata* Specht and Carrodus 34 (Syd.). *G. hederacea* Carolin 2044 (Syd.). *G. heterochila* Perry 2405 (Canb.). *G. heterophylla* Carolin 2032 (Syd.). *G. hispida* Eddy, 23.3.58 (N.S.W. ex N.T. 5220). *G. incana* Cleland, Nargin, 11.08 (N.S.W.). *G. koningsbergi* no voucher. *G. laevis* Carolin 3583 (Syd.). *G. macmillanii* Lucas, Macalister River, 12.10 (N.S.W.). *G. micrantha* Peacock 60856.5 (Syd.). *G. microptera* Chippendale 2.5.58 (N.S.W. ex N.T. 4232). *G. mitchellii* Carolin 4055 (Syd.). *G. ovata* Carolin 1936 (Syd.). *G. paniculata* Peacock 6012.2.2 (Syd.). *G. phyllicoides* Carolin 3575 (Syd.). *G. pinnatifida* Peacock 6111.9.1 (Syd.). *G. pterygosperma* Benn 8.10.1963 (Syd.). *G. pumilio* McKee 9471 (N.S.W.). *G. pusilliflora* Whaite 2491 (N.S.W.). *G. quadrilocularis* no voucher. *G. ramellii* Perry 1918 (Canb.). *G. rotundifolia* Peacock 6012.6.3 (Syd.). *G. scaevolina* Perry and Lizarides 2296 (Canb.). *G. scapigera* Carolin 3556 (Syd.). *G. sepalosa* Perry 1708 (Canb.). *G. stelligera* Peacock 6012.12.1 Syd.) *G. strophiolata* Doodlakine, Fitzgerald Nov. 1903 (N.S.W.). *G. tenuiloba* Peacock 60865.1 (Syd.). *G. trichophylla* Pritzel 827 (N.S.W.). *G. varia* Maiden Kangarcalaw 1902 (N.S.W.). *G. viscida* no voucher. *G. vilmorinae* Perry and Lazarides 2225 (N.S.W.)

Selliera radicans Peacock Jan. 1958 (Syd.). *Calogyne pilosa* Specht 218 (Canb.). *C. berardiana* Carolin 4224 (Syd.). *Neogoodenia minutiflora* George 910 (Perth). *Symphobasis macropletra* Speck 1368 (N.S.W.). *Pentaptilon careyi* Carolin 3325 (Syd.). *Verreauxia reinwardtii* Peacock 60845.1 (Syd.). *V. paniculata* no voucher. *Catosperma goodenicearum* Chippendale 14.7.1956 (N.S.W. ex N.T. 2331). *Scaevola albida* Carolin 2082 (Syd.). *S. calendulacea* Carolin 0785 (Syd.). *S. chamissoniana* Smith-White, Aug. 1961 (Syd.). *S. crassifolia* Carolin 3373 (Syd.). *S. dielsii* Briggs (N.S.W. 52429). *S. fasciculata* Briggs (N.S.W. 52427). *S. glandulifera* Peacock 60876.1 (Syd.). *S. globulifera* Briggs 3.10.1960 (Syd.). *S. helmsii* Carolin 3134 (Syd.). *S. hookeri* Carolin Jan. 1957 (Syd.). *S. humifusa* Carolin 3538 (Syd.). *S. indigofera* McKee 4714 (Syd.). *S. micrantha* McKee 4279 (Syd.). *S. mollis* Smith-White, Aug. 1961 (Syd.). *S. nitida* Carolin 3190 (Syd.). *S. ovalifolia* Carolin 4270 (Syd.). *S. oppositifolia* no voucher. *S. porocarya* Carolin 3358 (Syd.). *S. ramosissima* Carolin 3653 (Syd.). *S. spinescens* Carolin 3074 (Syd.). *S. taccada* S.U. Biol. Soc. Jan. 1948 (Syd.). *S. tomentosa* Carolin 3323 (Syd.).

FUNGI ATTACKING SEEDS IN DRY SEED-BEDS

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[Read 27th April, 1966]

Synopsis

Soil samples were brought to approximate equilibrium with atmospheres of 100, 95, 90, 85 and 80% R.H. The pattern of fungal colonization of wheat seeds buried in the soil samples was then compared with that occurring in seeds stored at similar humidities, and was found to be similar. The breakdown of buried seeds was due to such seed-borne fungi as members of the *Aspergillus glaucus* group and the *Penicillium chrysogenum* and the *P. citrinum* series and to various soil-borne aspergilli and penicillia, of which *P. expansum* was the most important. Only in the 80% R.H. series did most of the buried seeds survive for more than three weeks and the period was less than one week for those in the 100% and 95% R.H. series. Shaking the seeds with "New Improved Ceresan" fungicidal dust prior to planting did not enhance longevity.

INTRODUCTION

The subject of deterioration of stored grain due to fungal activity has been reviewed by Christensen (1957) who concluded that fungal invasion was the main cause of damage to the embryos of cereals. Species of *Aspergillus* and *Penicillium* are able to cause seed decay on an economically-important scale in atmospheres with a relative humidity as low as 70% (Snow, Crichton and Wright, 1944; Snow, 1945). Although fungi are active in soil at similar low relative humidities (Dommergues, 1962; Griffin, 1963b; Kouyeas, 1964), there has been no study of germination reduction in seeds sown in soil with a moisture content below that of the permanent wilting point. In Australia and similar regions, however, this is a matter of some importance, for germination of seed is often retarded by low soil moisture at, or immediately after, sowing.

MATERIALS AND METHODS

To control relative humidity in the experiment using soil, thin layers of air-dry sieved soil were placed in small containers in each of six vacuum desiccators, the basal portions of which contained one of the six sodium chloride solutions listed in Table 1. The desiccators were then evacuated for one week to allow the soils to attain the required relative humidity. The water contents of soil samples (Table 1) indicate that the 100% R.H. sample was at approximately permanent wilting point and that those from other humidities were considerably drier.

Sixty seeds were placed in perforated plastic containers hanging above c. 170 ml. solutions of sodium chloride in closed jars of 500 ml. capacity. In the experiments using soil, about 100 g. of soil, after equilibration, were also placed in the containers. After 10 weeks, a test using Clark's and Severinghaus' electrodes showed an oxygen concentration in the jars not below 19% and a carbon dioxide concentration not above 2%. Any change in the atmosphere of the jars was therefore negligible. In a small pilot experiment, variation between replicates in both the pattern of colonization and the rate of seed degeneration was also found to be negligible and the main experiments were therefore not replicated.

TABLE I
Moisture data for soil samples

	Relative humidity					Saturated soil	Field capacity	Permanent wilting point
	100	95	90	85	80			
Controlling salt solution (g. NaCl/100 ml. H ₂ O)	0	8.6	16.5	23.6	30.0	—	—	—
Suction (pF)*	—†	4.86	5.17	5.36	5.50	0	2.0	4.2
Moisture content (g. H ₂ O/100 g. dry soil)	21	10	9	8	7.3	63	39	18
Moisture content (% saturated)	.. 33	16	14	13	11.6	100	62	29

* Relationship between soil water suction and R.H. has been given by myself (Griffin, 1963a, b) with an error in the formula. M=molecular weight of water, not density.

† Not in true equilibrium.

The soil was a black earth (Stephens, 1962) of very heavy texture (pH 8.6) from Narrabri in the north-west wheat areas of New South Wales.

The wheat seeds were of the variety Mengavi and were harvested approximately one year before the start of the experiments.

At each sampling, five seeds were taken from each relative humidity and were sterilized by successive immersions in (1) 95% alcohol (momentarily), (2) 1% silver nitrate (0.5 min.) and (3) saturated sodium chloride (3 min.). Each seed was then cut aseptically into four portions, three seeds being placed on Petri dishes containing Czapek-Dox agar (3% sucrose) and two on dishes containing Czapek-Dox Sucrose agar (20% sucrose). Seeds from the same containers were also tested for ability to germinate when placed on wet filter-paper in a Petri dish.

All experiments were conducted at 25°C ($\pm 0.5^\circ$) in a dark room and no water was deposited on the surfaces of the containers.

TABLE 2
Number of seeds germinating, out of ten, after various periods in controlled humidity jars

Week	Relative Humidity				
	100	95	90	85	80
1	10	10	10	10	10
2	3	6	8	9	10
3	2	2	5	7	10
4	1	3	2	7	8
5	2	0	4	3	10
7	0	2	1	2	9
9	0	0	3	2	6
13	—	0	1	0	1
17	—	—	—	—	2

EXPERIMENTAL

Internal microflora of seeds

The experiment was made to study the pattern of colonization of the interior of the seed by the seed-borne flora. Wheat seeds alone were therefore placed in the experimental containers.

Data on seed germination are given in Table 2. The fungi isolated from surface-sterilized seed were, with very few exceptions, species of *Aspergillus* and *Penicillium*. Owing to the presence of many intermediary forms, these fungi have not been identified at the species level but have been referred in Table 3 to the appropriate group or series (Thom and Raper, 1945; Raper and Thom, 1949). Within the important *A. glaucus* complex, *A. amstelodami* (Mang.) Thom and Raper, *A. chevalieri* (Mang.) Thom and Raper, *A. repens* (Cda.) De Bary and *A. ruber* (Spiek. and Brem.) Thom and Church were isolated. Other fungi occasionally isolated but not included in Table 3 were *Alternaria* sp., *Aspergillus ochraceus* Wilhelm, *A. ustus* (Bain.) Thom and Church, *Mucor* sp., *Penicillium lilacinum* Thom and *P. purpurogenum* Stoll.

TABLE 3
Aspergilli and Penicillia isolated from surface-sterilized seeds

Week	Relative Humidity				
	100	95	90	85	80
1	<i>P. chrysogenum</i>	<i>P. chrysogenum</i>			<i>P. chrysogenum</i>
2	<i>A. candidus</i> <i>P. chrysogenum</i>	<i>A. glaucus</i> <i>P. chrysogenum</i>			<i>P. chrysogenum</i>
3	<i>A. glaucus</i> <i>P. citrinum</i>	<i>P. chrysogenum</i>	<i>A. glaucus</i>		
4	<i>P. chrysogenum</i>	<i>A. candidus</i> <i>A. glaucus</i> <i>P. chrysogenum</i> <i>P. citrinum</i>	<i>A. glaucus</i> <i>P. chrysogenum</i>	<i>A. glaucus</i>	
5	<i>A. candidus</i> <i>A. glaucus</i> <i>A. versicolor</i> <i>P. citrinum</i>	<i>A. versicolor</i> <i>P. citrinum</i>	<i>A. candidus</i> <i>A. glaucus</i> <i>P. citrinum</i>		
7	<i>A. versicolor</i>	<i>A. glaucus</i> <i>A. versicolor</i> <i>P. chrysogenum</i>	<i>A. glaucus</i>	<i>A. flavus-oryzae</i> <i>A. glaucus</i>	<i>A. glaucus</i> <i>P. citrinum</i>
9	<i>A. flavus-oryzae</i> <i>P. chrysogenum</i> <i>P. citrinum</i>	<i>A. candidus</i> <i>A. flavus-oryzae</i> <i>A. versicolor</i> <i>P. citrinum</i>	<i>A. flavus-oryzae</i> <i>A. glaucus</i> <i>P. citrinum</i>	<i>A. glaucus</i> <i>P. citrinum</i>	<i>A. glaucus</i> <i>P. citrinum</i>
13	—	<i>A. glaucus</i> <i>A. versicolor</i>	<i>A. glaucus</i> <i>A. versicolor</i> <i>P. chrysogenum</i> <i>P. citrinum</i>	<i>A. glaucus</i> <i>P. chrysogenum</i> <i>P. citrinum</i>	<i>A. glaucus</i> <i>P. citrinum</i>
17	—	—	—	—	<i>A. glaucus</i> <i>P. chrysogenum</i>

Internal microflora of seeds in contact with soil

Wheat seeds were buried in small quantities of soil in the experimental containers and the pattern of colonization of the interior of the seeds was again studied.

Data on germination are given in Table 4 and on the commonest fungi isolated (identified to group or series only) in Table 5. Other fungi sometimes isolated were *Aspergillus avenaceus* G. Smith, *A. flavipes* (Bain. and Sart.) Thom and Church, *A. ochraceus* Wilh., *Cephalosporium* sp., *Fusarium* spp., *Penicillium brevi-compactum* Dierckx, *P. canescens* Sopp, *P. frequentans* Westling, *P. funiculosum* Thom, *P. oxalicum* Currie and Thom, *P. purpurogenum* Stoll, and *Rhizopus stolonifer* Fr.

An attempt to improve longevity by coating seeds with a fungicidal dust before burying was unsuccessful. The seeds were shaken-up with an excess of "New Improved Ceresan" dust (ethyl mercuric phosphate—1.3% Hg) and then buried, but the decrease in viability was very similar to that in the previous experiments and the fungicide had clearly been ineffective. The only fungus to be isolated from any of the seeds was *Penicillium expansum* Link and this species was shown in a subsidiary experiment to be unusually tolerant of the fungicide when it was added to agar media. On an agar medium containing *c.* 1 p.p.m. of the fungicide, only *P. expansum* and *P. citrinum*, of the fungi tested, suffered no check to growth whereas the growth rates of *P. chrysogenum*, *P. urticae*, *Aspergillus versicolor* and *A. ruber* were, at most, half of the normal. *P. expansum* was the only fungus little affected by a concentration of *c.* 100 p.p.m.

TABLE 4
Number of seeds germinating, out of ten, after various periods in soil in controlled humidity jars

Week	Relative Humidity				
	100	95	90	85	80
1	1	4	10	10	10
2	2	1	4	10	10
3	0	0	2	7	8
4	0	3	0	2	10
5	2	0	0	0	10
7	—	1	0	0	7
9	—	0	2	3	4
13	—	0	0	3	0

DISCUSSION

The pattern of fungal colonization of the unburied seeds is similar to that described by many previous workers studying the deterioration of stored seed, with members of the *Aspergillus glaucus* group and the *Penicillium citrinum* and *P. chrysogenum* series being especially prominent. The rate of colonization increased with increasing humidity and there was little fungal invasion at 80% R.H. until five weeks had elapsed.

With the seed buried in soil, a greater variety of fungi was recorded, but the rate of deterioration was approximately the same as in stored seed. From a comparison of the fungi listed in Tables 3 and 5 it can be seen that seed destruction in soil was due to both seed-borne and soil-borne fungi, and of the latter, *Penicillium expansum* was particularly important.

In both experiments, early records of a fungus at the lower humidities presumably indicate its presence as spores or a few hyphae in the more superficial layers of the seed but still in a position shielded from the effects of surface sterilization (Hyde, 1950, 1951), so that the presence of the fungus could not be detected visually until after incubation on agar. Dead seeds, however, usually bore an external mass of conidiophores and were also heavily colonized internally. It seems reasonable to suppose that this fungal invasion was the cause of death, for cereal seeds seem to offer no resistance to fungal attack when held at moisture levels sufficient for fungal growth but insufficient for seed germination. Such a contention is also supported by the fact that the rise in respiration rates of ungerminated seeds with increase in moisture content is almost entirely due to increased respiration of fungi within, or on the surface of, the seed (Crocker and Barton, 1957).

The failure of the fungicidal dust is in accord with similar experiments with stored grain (Christensen, 1957) and should probably be attributed to the inactivity of the fungicide in the absence of free water. The isolation of *P. expansum* alone from dusted seeds cannot be interpreted as indicating that this species was the only one active in the seeds. Christensen has shown that although 'Ceresan-M' is not toxic to fungi inside seeds, the residual fungicide on the seed coat, diffusing into the agar, is able to suppress fungal growth from the seed on to agar. In the present instance, it is therefore likely that a mixed microflora caused the seed decay but that only *P. expansum* was able to grow out on to agar.

TABLE 5

Aspergilli and Penicillia isolated from surface-sterilized seeds which had been buried in soil

Week	Relative Humidity				
	100	95	90	85	80
1	<i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. urticae</i>	<i>P. chrysogenum</i> <i>P. citrinum</i>	<i>A. glaucus</i> <i>P. chrysogenum</i>	<i>P. citrinum</i>	<i>P. chrysogenum</i>
2	<i>P. chrysogenum</i> <i>P. urticae</i>	<i>P. chrysogenum</i> <i>P. urticae</i>	<i>P. chrysogenum</i> <i>P. urticae</i>	<i>P. chrysogenum</i>	<i>P. chrysogenum</i>
3	<i>P. expansum</i> <i>P. javanicum</i> <i>P. urticae</i>	<i>P. chrysogenum</i> <i>P. expansum</i>	<i>A. glaucus</i> <i>A. versicolor</i> <i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. expansum</i> <i>P. nigricans</i>	<i>A. glaucus</i> <i>P. chrysogenum</i> <i>P. citrinum</i>	<i>A. glaucus</i> <i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. rugulosum</i>
4	<i>P. expansum</i> <i>P. janthinellum</i> <i>P. rugulosum</i>	<i>P. brevi-</i> <i>compactum</i> <i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. nigricans</i>	<i>A. glaucus</i> <i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. expansum</i> <i>P. nigricans</i>	<i>A. glaucus</i> <i>P. chrysogenum</i> <i>P. expansum</i> <i>P. rugulosum</i> <i>P. urticae</i>	<i>A. flavus-oryzae</i> <i>P. chrysogenum</i> <i>P. expansum</i> <i>P. janthinellum</i> <i>P. rugulosum</i> <i>P. urticae</i>
5	—	<i>A. glaucus</i> <i>P. chrysogenum</i> <i>P. expansum</i> <i>P. javanicum</i>	<i>A. glaucus</i> <i>A. versicolor</i> <i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. expansum</i> <i>P. javanicum</i> <i>P. nigricans</i>	<i>A. glaucus</i> <i>P. brevi-</i> <i>compactum</i> <i>P. chrysogenum</i> <i>P. expansum</i> <i>P. nigricans</i>	<i>A. versicolor</i> <i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. expansum</i> <i>P. janthinellum</i> <i>P. rugulosum</i>
7	—	<i>P. chrysogenum</i> <i>P. expansum</i> <i>P. rugulosum</i> <i>P. urticae</i>	<i>P. brevi-</i> <i>compactum</i> <i>P. chrysogenum</i> <i>P. citrinum</i> <i>P. janthinellum</i>	<i>A. glaucus</i> <i>P. brevi-</i> <i>compactum</i> <i>P. expansum</i>	
9	—	<i>A. versicolor</i> <i>P. brevi-</i> <i>compactum</i> <i>P. chrysogenum</i> <i>P. expansum</i>	<i>A. versicolor</i> <i>P. chrysogenum</i> <i>P. expansum</i>	<i>A. glaucus</i> <i>A. versicolor</i> <i>P. expansum</i> <i>P. javanicum</i>	<i>A. versicolor</i>
13	—	<i>P. chrysogenum</i> <i>P. expansum</i> <i>P. rugulosum</i> <i>P. urticae</i>	<i>A. glaucus</i> <i>P. expansum</i>	<i>A. glaucus</i> <i>P. expansum</i> <i>P. javanicum</i>	<i>A. glaucus</i> <i>P. brevi-</i> <i>compactum</i> <i>P. chrysogenum</i> <i>P. janthinellum</i>

Seed decay was rapid in soils at about permanent wilting point or somewhat drier and only in the driest soils did seeds survive for more than three weeks. It seems unlikely that any seed treatment will improve longevity under these conditions, for much of the decay is due to fungi carried inside the testa and at least some of the soil-borne fungi are likely to be tolerant of fungicidal dusts, especially under dry conditions where the compounds are relatively inactive.

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References

- CHRISTENSEN, C. M., 1957.—Deterioration of stored grains by fungi. *Bot. Rev.*, 23: 108–134.
- CROCKER, W., and BARTON, L. V., 1957.—“Physiology of seeds”. *Chronica Botanica*, Waltham.
- DOMMERGUES, Y., 1962.—Contribution a l'étude de la dynamique microbienne des sols en zone semi-aride et en zone tropicale sèche. *Ann. Agron. Paris*, 13: 265–324, 379–469.
- GRIFFIN, D. M., 1963*a*.—Soil moisture and the ecology of soil fungi. *Biol. Rev.*, 38: 141–166.
- , 1963*b*.—Soil physical factors and the ecology of fungi. III. Activity of fungi in relatively dry soil. *Trans. Brit. mycol. Soc.*, 46: 373–377.
- HYDE, M. B., 1950.—The subepidermal fungi of cereal grains. I. A survey of the world distribution of fungal mycelium in wheat. *Ann. appl. Biol.*, 37: 179–186.
- HYDE, M. B., and GALLEYMORE, H. B., 1951.—The subepidermal fungi of cereal grains. II. The nature, identity and origin of the mycelium in wheat. *Ann. appl. Biol.*, 38: 348–356.
- KOUYEAS, V., 1964.—An approach to the study of moisture relations of soil fungi. *Plant and Soil*, 20: 351–363.
- RAPER, K. B., and THOM, C., 1949.—“A manual of the Penicillia”. Williams and Wilkins, Baltimore.
- SNOW, D., 1945.—Mould deterioration of feeding stuffs in relation to humidity of storage. III. The isolation of a mould species from feeding stuffs stored at different humidities. *Ann. appl. Biol.*, 32: 40–44.
- SNOW, D., CRICHTON, M. H. G., and WRIGHT, N. C., 1944.—Mould deterioration of feeding stuffs in relation to humidity of storage. I. The growth of moulds at low humidities. *Ann. appl. Biol.*, 31: 102–110.
- STEPHENS, C. G., 1962.—“A manual of Australian soils”. C.S.I.R.O., Melbourne.
- THOM, C., and RAPER, K. B., 1945.—“A manual of the Aspergilli”. Williams and Wilkins, Baltimore.

ON THE SPECIES *FENESTELLA HOROLOGIA* BRETNALL
AND *MINILYA DUPLARIS* CROCKFORD

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(Plate II)

[Read 27th April, 1966]

Synopsis

Taxonomic work has established the identity of *Fenestella horologia* and *Minilya duplaris*. This identity is discussed and the valid species *Fenestella horologia* is described.

INTRODUCTION

During the writer's work on the Permian Polyzoa of the Bowen Basin, similarities between the species *Fenestella horologia* and *Minilya duplaris* became increasingly evident. Both species were described first from the Permian of Western Australia.

Fenestella horologia Bretnall, 1926, is characterized by a single row of nodes placed on a carina, hour-glass shaped fenestrules and three zoecia per fenestrule, placed so that there is an aperture at the proximal and distal ends of the fenestrule on the dissepiment and one aperture at mid-length of the fenestrule.

Minilya duplaris Crockford, 1944c, the type species of *Minilya*, is characterized by the same features save for the presence of a double row of nodes on the branch. The nodes arise from a carina which zig-zags its way along the branch.

Crockford (1944c, p. 174) notes the difference in carinal appearance, for she states "This species (i.e. *Minilya duplaris*) is probably the same form described by Miss Hosking (1931) from the Wooramel River District as *Fenestella horologia* Bretnall, but it differs from *F. horologia* in having a double, instead of a single, row of nodes".

The importance of the double row of nodes as a feature of generic significance has been queried by Elias and Condra (1957, p. 66). They produce a very thorough criticism of Crockford's diagnosis of *Minilya* and reduce the differences between her genus and *Fenestella* to one, the double or single row of nodes.

Shulga-Nesterenko (1941, pp. 49-51) described *Fenestella virgosa* Eichwald and its varieties. On *F. virgosa* var. *sparsituberculata* only one row of nodes is developed whereas on *F. virgosa* a double row of nodes is developed. This variation made the possibility of a single and double row of nodes being developed on the one zoarium appear very real. Recently, Campbell and Engel (1963, p. 67) described *Fenestella* sp. 1, from the Tournaisian Tulcumba Sandstone, New South Wales, which has both a single and double row of nodes developed. With this in mind and because Hosking (1931) had mistaken *Minilya duplaris* for *Fenestella horologia*, measurements of both species were tabulated and plates, as well as primary type material, were studied.

The measurements for both species appear below (Table 1). The figures used by Crockford (1944e, p. 181, Pl. 1, figs 6, 7) are reproduced (Pl. II, figs 1, 2) as they appear in the original plate. From Crockford's measurements and the figures the similarity between the two species can be observed.

Additional measurements have been made by the writer on primary types of both species and these are presented in brackets.

To determine the base shape of the zoecial chamber, serial sections were cut through *Fenestella horologia* and *Minilya duplaris* and camera lucida drawings made. Superposition of the drawings enabled the median plate in the centre of the branch to be related to the nodes on the obverse surface and the change in shape of the zoecial chamber could be studied (see Pl. II, figs 3-5). The relation of the nodes to the median plate on *Minilya duplaris* changes from branch to branch.

Because of the similarity between the species, a thorough study was made of all Western Australian material labelled *Fenestella horologia* or *Minilya duplaris*. The result was that two specimens were located having the measurements tabled and showing both the single and double row of nodes on the one branch.

TABLE 1

	<i>Fenestella horologia</i> Bretnall (Crockford, 1944a, 1944c)	<i>Minilya duplaris</i> Crockford (Crockford, 1944c)
Bw	0.29-0.38 mm.	(0.26) 0.33-0.41 mm.
B/10	18-22	16-19 (21)
F/10	16-18	14-17 (18)
Fl	0.29-0.52 mm.	0.4-0.51 mm.
Fw	0.17-0.4 mm.	0.14-0.25 (0.32) mm.
Z/10	37 (35-39)	33 (37)
Zd	0.08-0.13 mm.	0.13 mm.
Z/F	2-3	2-3
Z-Z	0.21-0.34 mm.	0.27-0.35 mm.
N-N	0.23-0.31 mm.	0.13-0.17 mm.
N/5	(16-21)	(30-38)
Dw	0.1-0.29 mm.	0.1-0.3 mm.
Zb	(T)	(T)

Bw=branch width, B/10=branches per 10 mm., F/10=fenestrules per 10 mm., Fl=fenestrule length, Fw=fenestrule width, Z/10=zooecia per 10 mm., Zd=zoecial diameter, Z/F=zooecia per fenestrule, Z-Z=separation of centres of successive zoecial apertures, N-N=separation of centres of successive nodes, N/5=nodes per 5 mm., Dw=dissepiment width, Zb=zoecial base shape, T=trapezoidal.

One specimen, F.17538 Australian Museum Collection, is labelled *Fenestella horologia* but for the most part it shows the double row of nodes of *Minilya duplaris*. Measurements made on the zoarium showing the double row of nodes agree with the measurements tabled previously (see Pl. II, fig. 6).

Of interest was the spacing of the nodes. On the portion of the zoarium where a double row of nodes is a constant feature, the spacing varied from 0.12 mm. to 0.17 mm. The spacing in the first appearance of a single row varied from 0.14 mm. to 0.17 mm. This was not into the spacing of *Fenestella horologia* but unfortunately the single row condition does not persist for more than three nodes before reverting to a double row condition and then to a single row condition of similar length with the nodes separated by 0.14 mm. to 0.2 mm.

Another observation which can be made is that the two cases of the single row have the same orientation with respect to a straight line, even though they are separated by an area showing the double row condition.

A second specimen, labelled C.P.C. 1287c, was assigned to *Minilya duplaris* by Crockford (1957, p. 67). This specimen likewise has both a single and double row of nodes developed (see Pl. II, fig. 7).

Clearly the two species are conspecific and therefore, because of priority, *Minilya duplaris* is invalid. As this is the type species of the genus *Minilya*, the genus is also invalid.

There are not many specimens of *Minilya amplia* Crockford, 1944*b*, available for study but it is felt that when additional specimens are found this species will be identical with a species of *Fenestella* having both a single and double row of nodes developed.

SYSTEMATIC DESCRIPTION

Order CRYPTOSTOMATA Shrubsole and Vine, 1882
 Family FENESTELLIDAE King, 1850
 Genus FENESTELLA Lonsdale, 1839

Type Species.—(by subsequent designation of Riley, 1962, p. 76) *Fenestella subantiqua* d'Orbigny, 1850, p. 180, from the Silurian, Wenlockian, Wenlock Limestone, at Wren's Nest, Dudley, Worcestershire, England.

Diagnosis.—Zoarium fan or funnel shaped; zooecia in two rows on the branches, commonly increasing to three, proximal to bifurcation; rows of zooecia separated by a nodose carina on the obverse surface; reverse surface of varying ornamentation.

FENESTELLA HOROLOGIA Bretnall, 1926

- 1926, *Fenestella horologia* Bretnall, p. 15, Pl. 1, fig. 6.
 1929, *Fenestella parviuscula* Bassler, p. 76, Pl. cexli, figs 8–13.
 1931, ? *Fenestella parviuscula* Bassler; Martin, p. 391.
 1931, *Fenestella horologia* Bretnall; Hosking, p. 13, Pl. 4, fig. 3.
 1932, *Fenestella parviuscula* Bassler; Fritz, p. 99.
 1936, *Fenestella pectinis* Moore (partim); Chapman; in Raggatt, p. 128 (fide Crockford, 1944*c*, p. 158).
 1937, *Fenestrellina parviuscula* (Bassler); Elias, p. 314.
 1943, *Fenestrellina horologia* (Bretnall); Crockford, p. 266.
 1944*a*, *Fenestrellina horologia* (Bretnall); Crockford, p. 189, Pl. 1, fig. 1; Pl. 2, fig. A.
 1944*b*, *Fenestrellina horologia* (Bretnall); Crockford, p. 158.
 1944*c*, *Fenestrellina horologia* (Bretnall); Crockford, p. 167, Pl. 1, figs 3, 6.
 1944*c*, *Minilya duplaris* Crockford, p. 173, Pl. 1, figs 5, 7; text-figs 1C, D.
 1946, *Minilya duplaris* Crockford; Crockford, p. 132.
 1951, cf. *Fenestella ivanovi* Shulga-Nesterenko, p. 100, Pl. 19, fig. 1; text-fig. 38.
 1953, *Fenestrellina nodograciousa* Chronic; Chronic, in Newell, Chronic and Roberts, p. 111, Pl. 21, figs 4*a*, *b*.
 1955, cf. *Fenestella donensis* Morozova, p. 27, Pl. 4, figs 2, 3; text-figs 5, 6.
 1957, *Fenestella horologia* Bretnall; Crockford, p. 57.
 1957, *Minilya duplaris* Crockford; Crockford, p. 67.
 1957, *Minilia duplaris* [sic] Crockford; Elias and Condra, p. 65.
 1957, *Fenestella parviuscula* Bassler; Elias and Condra, p. 108.
 1961, *Fenestella nomatae* Sakagami, p. 34, Pl. 15, fig. 3; text-fig. 5.

Holotype.—Specimen 16, Western Australian Geological Survey Collection from the Gascoyne River District, Western Australia.

The label was lost; there are a number of specimens of the species on the block figured by Bretnall (1926, Pl. 3) (Crockford, 1944*a*, p. 190).

Neotype.—(chosen Crockford, 1944*a*, p. 190) No. 2/2405*c*, Western Australian Geological Survey Collection from the Permian, Sakmarian, Callytharra Formation, east of the Gascoyne-Wyndham River Junction, Western Australia.

Lat. 25°03', Long. 115°33', Glenburgh 1 : 250,000 Geological Series Sheet SG 50-6, at Fossil Hill, Fossil Hill Station, Western Australia (Crockford, 1944a, p. 190, Pl. 1, fig. 1). This specimen is presently housed at the Department of Geology and Geophysics, University of Sydney.

Diagnosis.—Species of *Fenestella* with hour-glass fenestrules, two or three zoecia per fenestrule; the relationship between zoecia and dissepiments is stabilized; nodes may be uniserial or biserial; zoecial base shape trapezoidal.

Discussion.—Crockford (1944a, p. 190) states that the specimen chosen as neotype is part of a block from the Gascoyne River District which was used by Bretnall for his original description. The specimen is designated "neotype" because there is doubt whether it was a syntype.

The specimen chosen and figured by Crockford as neotype can be seen on one of Bretnall's plates (1926, Pl. 3). In the lower half of this plate, there is a figure "1" on its side and the neotype is half an inch from the lower right-hand corner of this figure.

As recently as 1964, Crespín (1964) quotes the type locality of the neotype as being between the top of the Lyons Series and the top of the Byro Series, Gascoyne River District, Carnarvon Basin, Western Australia. The stratigraphic thickness represented is of the order of 3,500 feet. Because of the uncertainty, an effort was made to obtain more information concerning the type locality and to quote it as accurately as possible. The locality given for the neotype is the result.

With reference to the Glenburgh 1 : 250,000 Sheet, some mention must be made regarding the type locality and the stratigraphic horizon. Although the Callytharra Formation is not shown as outcrop at Fossil Hill, M. A. Condon (pers. comm.) has assured the writer that the Formation is present at this locality.

Description.

Micrometric Formula

B/10	D/10	Z/5	N/5	Bw	Zd	Zb
18-22	15-18	17-20	17-21	0.3-0.38	0.08-0.13	T

The branches are not parallel and show a tendency to diverge. They are capped by a nodose carina. Proximal to bifurcation, the branch width may increase to 0.48 mm.; distal to bifurcation, the branch assumes the usual proportions. The branches are of similar width to the fenestrules.

The fenestrules have a width of 0.17 mm. to 0.40 mm. and a length of 0.29 mm. to 0.52 mm. The fenestrules are hour-glass in shape because of the projection of the peristomes of the apertures into them.

The dissepiments vary in width from 0.10 mm. to 0.30 mm. Their width increases near the branch because an aperture is situated on the dissepiment. The dissepiments are perpendicular to the branches.

The zoecial apertures are in two rows, with the zoecia of one row alternating with those of the other. There are three zoecial apertures per fenestrule and in many cases two of them are partly or wholly situated on a dissepiment. The centres of the zoecial apertures are separated by 0.21 mm. to 0.34 mm. Well developed peristomes are evident on the apertures, more so on the side adjacent to the fenestrule than on the side adjacent to the carina.

Proximal to bifurcation, a third row of apertures is inserted but no case has been found of four rows of apertures. The third row of apertures is located distal to the bifurcation of the carina.

The carina is nodose and has one row of nodes developed which exhibit varying tendencies. They may be bifid or even trifid at their topmost extremity or they may not bifurcate. The centres of successive nodes are 0.23 mm. to 0.31 mm. apart.

The zoecial base shape in the upper portions of the chamber is triangular but at the base it is trapezoidal.

On the reverse surface both branches and dissepiments are rounded. Ornamentation of the outer layer consists of minute, randomly oriented nodes. The removal of this layer reveals longitudinal striations.

Remarks.—Species with similar meshwork formulae to *F. horologia* are *F. subquadratopora* Shulga-Nesterenko, 1952, and *F. subvischerensis* Shulga-Nesterenko, 1951. The former species has a different arrangement and spacing of the nodes, while the latter species has narrower branches and dissepiments and the hour-glass fenestrules are not well developed.

Fenestella girtyi (Elias), 1937, has similar dimensions to *F. horologia* but there is a difference in the base shape of the zoecial chamber and the relation between the apertures and the dissepiments is not well stabilized in *F. girtyi* whereas it is in *F. horologia*.

Fenestella vischerensis Nikiforova, 1938 (fide Shulga-Nesterenko, 1941), and *F. vischerensis* var. *baschkirica* Shulga-Nesterenko, 1941, have narrower dissepiments and branches, the latter feature being characteristic also of *F. microaperturata* Shulga-Nesterenko, 1941, and *F. microaperturata* var. *polaris* Shulga-Nesterenko, 1941. *F. microaperturata* also has a smaller zoecial diameter.

Range and Distribution.—*Fenestella horologia* Bretnall has been recorded previously from Western Australia (Bretnall, 1926; Crockford, 1951; Crockford, 1957). It ranges from the Callytharra Formation of Sakmarian age to the Liveringa Formation of Kungurian age.

As *F. parviuscula*, it has been recorded from the Bitaoeni and Basleo Beds of Timor. These are Artinskian-Kazanian in age; as *F. nodograciousa* (Chronic), it has been recorded from the Upper Pennsylvanian of Peru, and as *F. nomatae* Sakagami, it occurs in the Upper Permian of Japan. From the Artinskian of Vancouver Island, Canada, it is listed as *F. parviuscula* Bassler by Fritz.

In Eastern Australia, Crockford (1943, 1946) has recorded the species from the Lake's Creek Quarry, east of Rockhampton, and from Consuelo Creek, south-west of Rolleston. During work by the writer on the Permian Polyzoa of the Bowen Basin, it has been recorded from the Artinskian Buffel Formation, south of Cracow, from the Yatton Limestone, north-west of Marlborough, and from the Artinskian Cattle Creek Formation in the Reid's Dome area, south-west of Rolleston.

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References

- BASSLER, R. S., 1929.—The Permian Bryozoa of Timor. *Paläont. Timor*, 16: 37–90.
- BRETNALL, R. W., 1926.—Palaeontological contributions to the Geology of Western Australia, 7 (13): Descriptions of some Western Australian Fossil Polyzoa. *Bull. geol. Surv. West. Aust.*, 88: 7–33.
- CAMPBELL, K. S. W., and ENGEL, B. A., 1963.—The faunas of the Tournaisian Tuleumba Sandstone and its members in the Werrie and Belvue Synclines, New South Wales. *J. geol. Soc. Aust.*, 10: 55–122.
- CRESPIN, I., 1964.—Catalogue of type and figured specimens in Western Australia. Rep. Bur. Miner. Resour. Geol. Geophys. Aust., 71.
- CROCKFORD, J. M., 1943.—Permian Bryozoa from Eastern Australia, Part III: Batostomellidae and Fenestrellinae from Queensland, New South Wales and Tasmania. *J. Proc. r. Soc. N.S.W.*, 76: 258–267.
- , 1944a.—A revision of some previously described species of Bryozoa from the Upper Palaeozoic of Western Australia. *J. Proc. R. Soc. West. Aust.*, 28: 187–199.

- CROCKFORD, J. M., 1944b.—Bryozoa from the Permian of Western Australia, Part I: Cyclostomata and Cryptostomata from the North-West Basin and Kimberley District. *Proc. Linn. Soc. N.S.W.*, 69: 139-175.
- , 1944c.—Bryozoa from the Wandagee and Noonkanbah Series (Permian) of Western Australia. *J. Proc. R. Soc. West. Aust.*, 28: 165-185.
- , 1946.—A bryozoan fauna from the Lake's Creek Quarry, Rockhampton, Queensland. *Proc. Linn. Soc. N.S.W.*, 70: 125-134.
- , 1951.—The development of bryozoan faunas in the Upper Palaeozoic of Australia. *Ibid.*, 76: 105-122.
- , 1957.—Permian Bryozoa from the Fitzroy Basin, Western Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, 34.
- ELIAS, M. K., 1937.—Stratigraphic significance of some Late Palaeozoic Fenestrate Bryozoans. *J. Paleont.*, 11: 306-334.
- , and CONDRA, G. E., 1957.—*Fenestella* in the Permian of West Texas. *Mem. geol. Soc. Am.*, 70.
- FRITZ, M. A., 1932.—Permian Bryozoa from Vancouver Island. *Trans. r. Soc. Can.*, Ser. 3, 26: 93-110.
- HOSKING, L. F. V., 1931.—Fossils from the Wooramel District, Western Australia. *J. Proc. r. Soc. West. Aust.*, 27: 7-52.
- MARTIN, R., 1931.—De Palaeontologie en Stratigraphie van Nederlandsch Oost-Indie: Bryozoa. *Leid. geol. Meded.*, 5: 390-395.
- MOROZOVA, I. P., 1955.—Carboniferous Bryozoa of the Middle Don Basin. *Trudy paleont. Inst.*, 58.
- NEWELL, N. D., CHRONIC, J., and ROBERTS, T., 1953.—Upper Palaeozoic of Peru. *Mem. geol. Soc. Am.*, 58.
- RAGGATT, H. G., 1936.—Geology of the North-West Basin, Western Australia, with particular reference to the stratigraphy of the Permo-Carboniferous. *J. Proc. r. Soc. N.S.W.*, 70: 100-174.
- RILEY, N. D., 1962.—Opinion 622: *Fenestella* Lonsdale, 1839 (Class Bryozoa); Validation under the Plenary Powers in accordance with the accustomed usage. *Bull. zool. Nom.*, 19: 76-79.
- SAKAGAMI, S., 1961.—Japanese Permian Bryozoa. *Spec. Pap. Palaeont. Soc. Japan*, 7.
- SHULGA-NESTERENKO, M. I., 1941.—Lower Permian Bryozoa of the Urals. *Paleontologiya SSSR*, 5 (5): 1.
- , 1951.—Carboniferous Fenestellids from the Russian Platform. *Trudy paleont. Inst.*, 32.
- , 1952.—New Permian Bryozoa from the Uralian Region. *Ibid.*, 37.
- , 1955.—Carboniferous Bryozoa of the Russian Platform. *Ibid.*, 57.

EXPLANATION OF PLATE II

- Fig. 1. *Fenestella horologia* Bretnall; reproduced from Crockford, 1944c, Pl. 1, fig. 6. (nodes retouched). $\times 20$.
- Fig. 2. *Minilya duplaris* Crockford; holotype, reproduced from Crockford, 1944c, Pl. 1, fig. 7. (nodes retouched). $\times 20$.
- Fig. 3. Camera lucida drawing of *Fenestella horologia* Bretnall to show relation of nodes, median plate and apertures. $\times 25$.
- Fig. 4. *Fenestella horologia* Bretnall; camera lucida drawing to show the shape of the zoecial base chamber and relation to apertures. $\times 25$.
- Fig. 5. Camera lucida drawing of *Minilya duplaris* Crockford to show the relation of nodes, median plate and apertures. $\times 25$.
- Fig. 6. *Fenestella horologia* Bretnall; specimen F.17538, Aust. Mus. Collection, showing uniserial and biserial arrangement of nodes (retouched). $\times 25$.
- Fig. 7. *Minilya duplaris* Crockford; specimen C.P.C. 1287c showing uniserial and biserial arrangement of nodes (nodes retouched). $\times 20$.

TWO NEW SPECIES OF PERMIAN BRACHIOPODS FROM QUEENSLAND

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(Plate III)

[Read 27th April, 1966]

Synopsis

Cancrinella gyrandensis, sp. nov., and *Grantonia cracovensis*, sp. nov., are described from Permian strata at Cracow, Queensland.

INTRODUCTION

During a study of Permian sediments and faunas in the Cracow District in the south-eastern part of the Bowen Basin, Queensland, *Cancrinella gyrandensis* and *Grantonia cracovensis* were identified from the Barfield and Buffel Formations respectively. The species of *Cancrinella*, *C. gyrandensis*, is regarded as being identical with the form figured by Campbell (1953) as *Cancrinella* cf. *magniplica* sp. nov. from a locality north of Cracow.

This work is based on portion of a thesis submitted as partial fulfilment for the degree of B.Sc. with Honours in Geology of the University of Queensland.

All fossil specimen numbers prefixed by "F" and locality numbers prefixed by "L" belong to the University of Queensland, Department of Geology Catalogues. Map references refer to the Mundubbera 1:253,440 Military Map.

SYSTEMATIC DESCRIPTIONS

Phylum	BRACHIOPODA
Class	ARTICULATA
Suborder	PRODUCTOIDEA Mailleux, 1940
Superfamily	PRODUCTACEA Waagen, 1883
Family	LINOPRODUCTIDAE Stehli, 1954
Subfamily	LINOPRODUCTINAE Stehli, 1954
Genus	CANCRINELLA Fredericks, 1928

1928, *Cancrinella* Fredericks, pp. 784, 791. 1932, *Cancrinella* Dunbar and Condra, p. 257. 1937, *Cancrinella* Sarytcheva, pp. 78, 110. 1950, *Cancrinella* Hill, p. 12.

Type Species.—(By original designation) *Productus cancrini* de Koninck, 1842, p. 179, Pl. 9, figs 3a, b, from the Zechstein strata on the banks of the River Kidash, near Bielibei, Orenburg, Russia.

Diagnosis.—"Small, thin shelled productids with ventral valve convex and without sinus, and dorsal valve concave or slightly geniculated. Ornament of thin, radial striae and concentric wrinkles, and spines, scattered on the ventral area and always along the hinge line and on the ears. Hinge line without area or teeth, with cardinal process in the form of two loops on an elevated ridge in the dorsal valve. Median septum well defined." (After Sarytcheva, 1937).

Discussion.—For discussion of the type species, the reader is referred to Hill (1950), Bryant (1955) and Waterhouse (1964).

CANCRINELLA GYRANDENSIS, sp. nov.

(Pl. III, figs 1-5)

1953, *Cancrinella* cf. *magniplica* Campbell, p. 29.

Holotype.—F.43422 from the Barfield Formation, north-west of Cracow, Queensland; L.2573, 31628589, Par. Coteeda, Co. Dawson, 0.7 mile along the road to "Gyranda" from the Theodore Road, north of Cracow.

Paratypes.—F.43423, F.43424 from the above locality.

Diagnosis.—Very large *Cancrinella* with large visceral cavity and strong transverse wrinkling on the trail.

Description.—The shell is concavo-convex, of large size and elongate. The visceral cavity is large. Hinge line is straight and in length is generally a little less than the maximum width of the shell. The trail is long.

The ventral valve is very convex, the greatest convexity being at the umbo. The valve is more convex in transverse than in longitudinal profile. The umbo is incurved over the hinge line and the umbonal slopes are steep. The ears are small, slightly produced and flat. The venter is non-sinuate and gently rounded or flattened.

The ornament consists of fine radial capillae which increase by intercalation. They number from 28 to 33 in 10 mm. on the trail. The entire ventral surface is covered by transverse wrinkles, which are more strongly developed on the trail. Here they are up to 1.5 mm. high and extend across the valve. Spines are developed by an increase in the anterior end of a short raised portion of the capillae. Because of the nature of the surface, the arrangement of the spines cannot be determined.

The dorsal valve is concave, the region of greatest concavity being at the anterior end of the visceral disc. The curvature is approximately the same as in the ventral valve. The valve is sharply geniculate. The ears are flattened and differentiated from the visceral disc by a slight change in slope at 30° to the hinge line.

The ornament of the dorsal valve is similar to that of the ventral valve except that the transverse wrinkling is not as strongly developed.

The internals of both valves are poorly known. The visceral disc is two-thirds as wide as it is long. It does not vary greatly in proportion. A low median septum is developed in the dorsal valve.

Remarks.—This species has affinities with *C. magniplica* and is the same as those specimens figured by Campbell (1953, p. 29, Pl. 1, figs 6-8) as *C. cf. magniplica* from an erosional gully, halfway between Oxtrack and Delusion Creeks on the Cracow-Theodore Road.

C. magniplica has a much smaller visceral cavity and weaker wrinkles on the trail. It is more finely costate.

C. farleyensis (Etheridge and Dun), 1909, is more coarsely costate, with a smaller visceral cavity. It is less strongly wrinkled. Both the previously mentioned species are smaller in size than *C. gyrandensis*.

Campbell (1953) stated that a trend to coarser wrinkling was initiated in the Cattle Creek Formation and carried into the Ingelara Formation with accompanying decrease in the size of the costae. This is not the case as *C. gyrandensis* is more strongly wrinkled and has coarser costae than *C. magniplica*, even though it is found at a higher stratigraphic horizon than *C. magniplica*. However, a trend towards coarser transverse wrinkling may be associated with a tendency to increase the size of the visceral cavity as higher stratigraphic horizons are reached.

Of the overseas species, *C. rugosa* Cloud, 1944, from the Mid Guadalupian of U.S.A., shows some resemblance to this species. It is of slightly smaller size and does not have the strong transverse wrinkling. It is more coarsely costate.

Range and Distribution.—The writer has found the species only in the Barfield Formation in the Theodore-Cracow District. J. M. Dickins (pers. comm.) has advised the writer that he has not found the species elsewhere in the Bowen Basin.

Localities.—In addition to the previously mentioned localities, *C. gyrandensis* is recorded from the Barfield Formation at L.2572, 31698408, Par. Cracow, Co. Dawson, approximately 4.0 miles south-west of "Cracow". Specimens from this locality are F.43577-43581.

Dimensions.—(Ventral valve)

	F.43424	F.43423	F.43422
Length	67 +	68 +	75 mm.
Width (Maximum)	38	40	37 mm.

Suborder	SPIRIFEROIDEA Allen, 1940
Superfamily	SPIRIFERACEA Waagen, 1883
Family	SPIRIFERIDAE King, 1846
Subfamily	TRIGONOTRETIINAE Schuchert, 1898
Genus	GRANTONIA Brown, 1953

1953, *Grantonia* Brown, p. 60, Pl. vi, figs 1-8.

Type Species.—(By original designation) *Grantonia hobartensis* Brown, 1953, Pl. vi, figs 1-8, from the Permian, Artinskian, Berriedale Limestone, in Rathbone's Quarry, New Norfolk Road, near Granton, about 12 miles north-north-west of Hobart, Tasmania.

Diagnosis.—See Brown, 1953, p. 60.

Discussion.—The genus *Grantonia* was erected by Brown for specimens of *Trigonotreta stokesi* auctt. (non Koenig, 1825). Specimens referred to *Spirifer tasmaniensis* Morris, 1845 are synonyms of *Trigonotreta stokesi* Koenig, 1825.

Differences between *Grantonia*, *Neospirifer* Fredericks, 1924, *Trigonotreta* Koenig, 1825, and *Spirifer* Sowerby, 1818, may be seen in ornamentation and gross form. The writer (Wass, 1965) has discussed the differences between the first three genera.

Range and Distribution.—In Tasmania, the genus is found in the Quamby, Golden Valley and Cascades Groups and the Malbina Formation of Lower Permian age. In Queensland, the writer has found the genus only in sediments of similar age which are equivalent to the Cattle Creek Formation.

GRANTONIA CRACOVENSIS, sp. nov.

(Pl. III, figs 6-11)

Holotype.—F.43392, from the Buffel Formation, Cracow, Queensland; L.2575, 32128451, Par. Cracow, Co. Dawson, at the base of the ridge, half a mile north-west of "Cracow", six miles south of Cracow, Queensland.

Paratypes.—F.43393, F.43396-43398 from the above locality.

Diagnosis.—Species of *Grantonia* with four plicae developed on each side of the sulcus and nine costae in the sulcus; crural lamellae divergent.

Description.—The valves are biconvex and semi-circular in outline; the maximum width is at the hinge line.

In the ventral valve, the greatest convexity is at the umbo where it overhangs the hinge line. The ventral sulcus is evident at the umbo and widens greatly anteriorly with an associated increase in depth anterior to the muscle platform. The cardinal extremities are almost rounded; the cardinal areas are broad, triangular and striated both longitudinally and transversely, with the former being more pronounced. The areas are convex to the anterior margin.

The fine costae are spread over four plicae on each side of the sulcus. The ventral sulcus has a median costa with four costae of similar size developed on each side. Each side of the sulcus is bordered by a raised costa of larger size.

On the plicae adjacent to the sulcus, bifurcation begins to take place 8 mm. from the umbo, but on the more lateral plicae bifurcation is absent until 13 mm. from the umbo.

The entire surface is ornamented by concentric growth lines.

The high dorsal fold is bounded on both sides by four plicae and the surface is multicostate; on each side of the fold there are four costae but this may be increased to five anteriorly. Due to the slightly distorted nature of the external ornament, it is difficult to state accurately the number of costae on each side of a plication. In the anterior region there may be three.

The external ornamentation is reproduced on an internal mould.

In the ventral valve there is a wide, open delthyrium bounded on each side by dental lamellae which converge towards the centre of the valve and do not reach the floor. At their extremities they produce small, pyramidal projections which fit into sockets in the dorsal valve; the projections taper off very sharply anteriorly.

Heavy callus is present in the delthyrium and in the umbonal region; this callus is differentiated from the cardinal area by two prominent ridges that diverge at an angle of 45° from the umbo.

The long, narrow adductor scars are raised above the heart-shaped diductors which border them. The adductors are striated longitudinally; on the diductors, the striations are mainly concave posteriorly but in the anterior portion of the scar they tend to become convex posteriorly.

In the dorsal valve, the cardinal process is composed of numerous fine, parallel plates which parallel the median plane of the valve. Flanking the cardinal process are dental sockets which taper posteriorly and make an angle of 90° with one another. The dental sockets border two thin lamellae which diverge towards one another anteriorly and give rise to the crural plates. They do not seem to reach the floor of the valve.

A median septum extends half the length of the dorsal valve.

Remarks.—*Grantonia cracovensis* is easily distinguished from the type species by the diverging crural lamellae, the ornament and a wider muscle field in the former species.

Specimens from Beds 8 and 9 at Homevale (Mt. Britton) have been examined and they are considered to be identical with *G. cracovensis*. Preservation of the forms described by Maxwell (1964) as *Grantonia* cf. *hobartensis* is too poor to allow definite comparisons to be made with the Cracow material.

Range and Distribution.—The species has been found only in Queensland at Cracow and Mt. Britton in strata of Artinskian age.

Localities.—In addition to the previously mentioned locality, *G. cracovensis* is found in the Buffel Formation at L.2483, 3175 8603, 0.8 mile north-west of Rose's Pride Mine. The specimens from this locality are F.43595–43597.

Dimensions.—(Ventral valve).

	F.43392	F.43393	F.43398
Length	36	39	36 mm.
Width	52	59	54 mm.
Height	13	16	14 mm.

Acknowledgements

The writer wishes to thank Professor Dorothy Hill, F.R.S., of the University of Queensland, who supervised the project, and Dr. T. B. H. Jenkins of the University of Sydney for his critical reading of the manuscript. Photographic work is by the Photography Department, University of Queensland.

References

- BROWN, I. A., 1953.—Permian Spirifers from Tasmania. *J. Proc. r. Soc. N.S.W.*, 86 : 55-63.
- BRYANT, D. L., 1955.—Index, type species and bibliography of Productid genera. *J. Paleont.*, 29 : 283-294.
- CAMPBELL, K. S. W., 1953.—The fauna of the Permo-Carboniferous Ingelara Beds of Queensland. Pap. Dep. Geol. Univ. Q'land., 4 (3).
- CLOUD, P. E., in KING, R. E., DUNBAR, C. O., CLOUD, P. E., and MILLER, A. K., 1944.—Geology and Palaeontology of the Permian area, north-west of Las Delicias, South-Western Coahuila, Mexico. Spec. Pap. geol. Soc. Am., 52 : 49-69.
- DUNBAR, C. O., and CONDRA, G. E., 1932.—Brachiopoda of the Pennsylvanian System in Nebraska. *Bull. Neb. geol. Surv.*, 2.
- ETHERIDGE, R., and DUN, W. S., 1909.—Notes on the Permo-Carboniferous Producti of Eastern Australia. *Rec. geol. Surv. N.S.W.*, 8 : 293-304.
- FREDERICKS, G., 1928.—Contribution to the classification of the genus *Productus*. *Bull. geol. Com.*, 46 : 773-792.
- HILL, D., 1950.—The Productinae of the Artinskian Cracow fauna of Queensland. Pap. Dep. Geol. Univ. Q'land., 3 (2).
- DE KONINCK, L. G., 1842.—*Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique*. Liège.
- MAXWELL, W. G. H., 1964.—The geology of the Yarrol region. Part 1: Biostratigraphy. Pap. Dep. Geol. Univ. Q'land., 5 (9).
- SARYTCHEVA, T. G., 1937.—Lower Carboniferous Producti of the Moscow Basin. *Trav. Inst. paleozool. Acad. Sci. U.R.S.S.*, 6.
- STEHLI, F. G., 1954.—Lower Leonardian Brachiopoda of the Sierra Diablo. *Bull. Am. Mus. nat. Hist.*, 105 : 365-385.
- WASS, R. E., 1966.—The marine Permian Formations of the Cracow District, Queensland. *J. Proc. r. Soc. N.S.W.*, 98, Part 3 : 159-167.
- WATERHOUSE, J. B., 1964.—Permian Brachiopods of New Zealand. *Palaeont. Bull., Wellington*, 35.

EXPLANATION OF PLATE III

Figs 1-5. *Cancrinella gyrandensis* sp. nov. 1, F. 43422 from L. 2573. $\times 1$; 2, F. 43422 from L. 2573. $\times 1$; 3, F. 43422 from L. 2573. $\times 1$; 4, longitudinal section of F. 43424 from L. 2573. $\times 1$; 5, transverse section of F. 43423 from L. 2573. $\times 1$.

Figs 6-11. *Grantonia cracovenssis* sp. nov. 6, F. 43398 from L. 2575. $\times 1$; 7, F. 43392 from L. 2575. $\times 1$; 8, internal of ventral valve of F. 43393 from L. 2575. $\times 1$; 9, ornament of ventral valve of F. 43396 from L. 2575. $\times 1$; 10, internal of dorsal valve of F. 43397 from L. 2575. $\times 1$; 11, internal of dorsal valve of F. 43397 from L. 2575. $\times 1$.

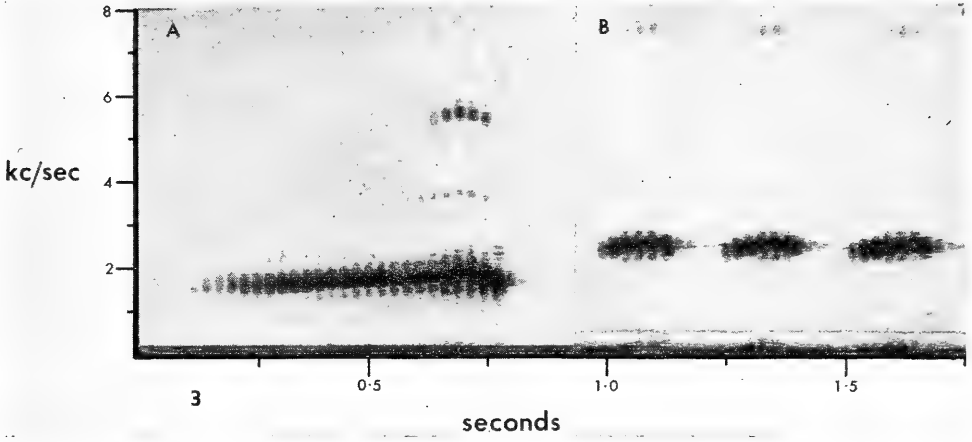


Fig. 1. Audiospectrograms of part of call of A, *Hyla jervisiensis*; and B, *H. ewingi*.

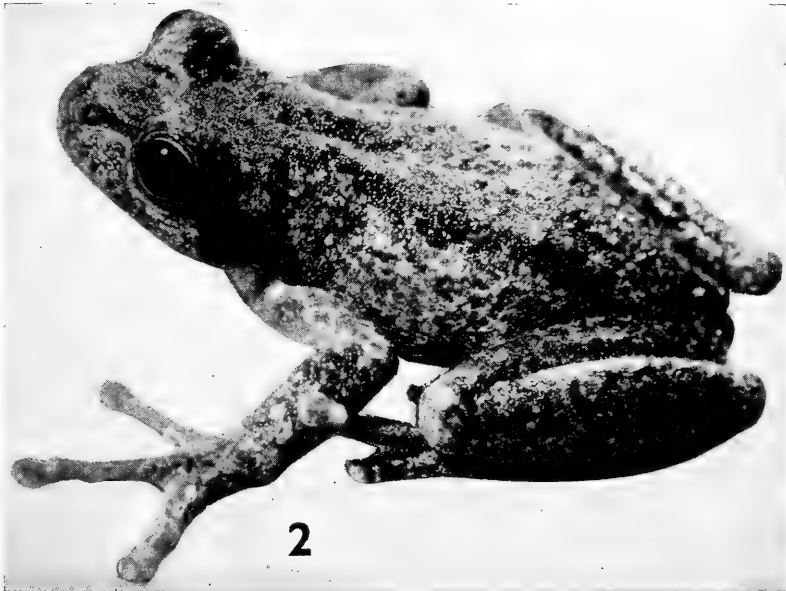
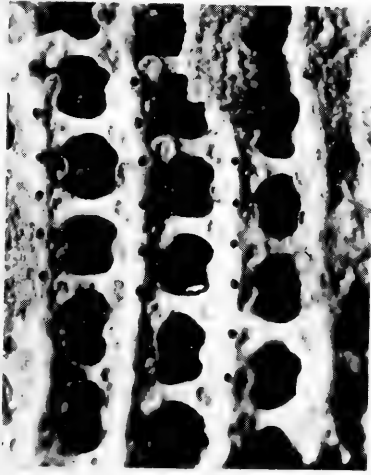
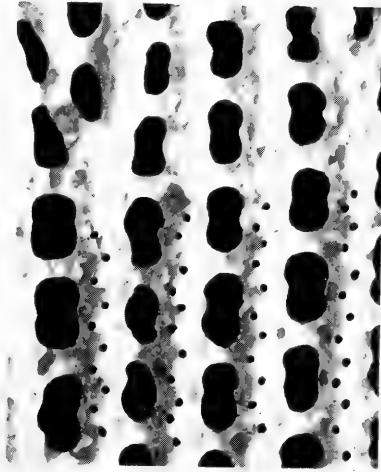


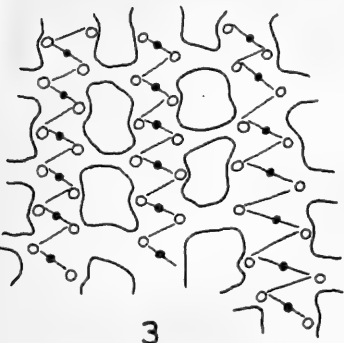
Fig. 2 Adult male *Hyla jervisiensis*.



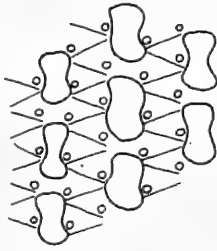
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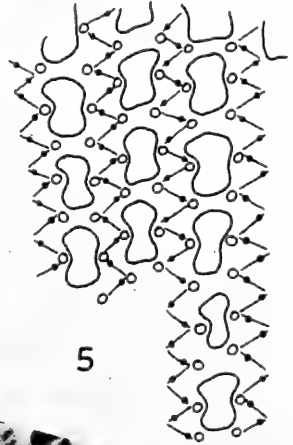
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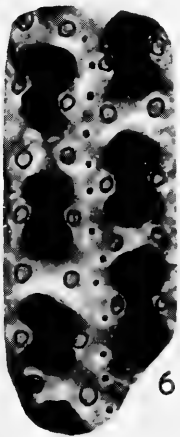
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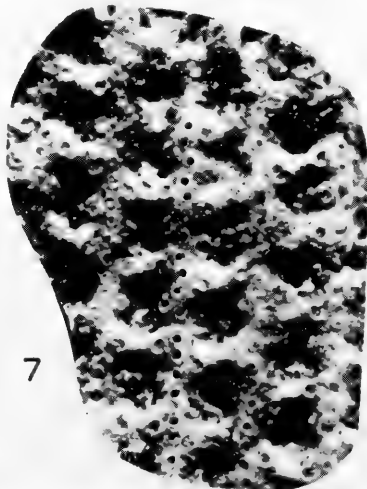
4



5



6



7

Fenestella horologia and *Minilya duplaris*.



Cancrinella gyrandensis and *Grantonia cracovens*.

SIR WILLIAM MACLEAY MEMORIAL LECTURE, 1966

THE CENTENARY OF MENDEL

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[Delivered 15th July, 1966]

Mendel, the centenary of whose work is the subject of this Sir William Macleay Memorial Lecture, had the unusual distinction of originating a new branch of science. Generally, in the development of science, a new advance depends on many predecessors whose work provides a basis for it. Genetics is an exception, owing its origin to one man, Gregor Johann Mendel, who expounded its principles at Brno in two lectures on 8th February and 8th March, 1865. His work made scarcely a ripple in the tumultuous sea of biological study, so stirred by the tidal waves of Darwinism in 1859. It was forgotten for the next 35 years, barely even noticed and certainly not understood. Mendel had no authority as a biologist and the very merits of his work, as we see it, must have made it suspect at the time and seemingly the work of an eccentric. Even the very simplest mathematical practices, beyond mere measurement, had found no place in biology.

A predecessor is a man who, at an earlier date, makes a discovery which his successor is able to enlarge into a general principle of universal validity. In this sense Mendel had no predecessors. There were many breeders who hybridised different species and varieties of plants and domesticated animals. However, the objectives they were studying do not really constitute basic genetics and claims that any of them had anticipated Mendel do not bear inspection. They were studying hybridism, whether sterility in a hybrid was due to the pollen parent or to the seed parent, whether either parent could be held responsible for the characters of different parts of the plant, which parent had prepotency in determining the characters of the hybrid, whether the parents were different species or merely varieties. Thus Colladon in 1822 was led to conclude that grey and white mice were different species! Generally, the parents used by the early hybridisers in their experiments were either different species or else varieties differing in many characters. The results obtained were chaotic and often inconstant or contradictory. They led to no general principles. This was the difference between previous attempts to study heredity and the revolution effected by Mendel.

The failure of his contemporaries to recognise the significance of Mendel's work confirms that there were no minds already prepared to see that the problem of heredity had been laid bare to complete solution. None saw that Mendel's researches supplied what he, rightly, considered to be missing from Darwin's theories, namely a mechanism of heredity and of the conservation of heritable variation. Indeed, the influence of Nägeli, interested in the same trivialities as the early hybridisers, led Mendel to fruitless and exacting work in hybridising hawkweeds, now known to lack sexual reproduction.

No earlier work anticipates Mendel's reduction of the problem of heredity to the study of single character differences which result, after crossing, in hybrid offspring in certain specified proportions. Goss, indeed, working also with garden peas, had observed dominance, recessiveness and segregation, going so far as to count the numbers of the different kinds in the F_2 . Likewise, Darwin observed these features in snapdragons. Neither arrived at any general principles as a consequence.

Mendel, in writing about previous work, clearly stated his new scientific procedures as follows: ". . . among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations".

The constancy of characters of hybrids, as Mendel explained, was the starting point of his work. It enabled him to postulate an explanation of his results by supposing that the characters were each determined by particulate factors, that the factors from each parent segregated completely at the formation of the germ cells and in equal numbers, and that there were equal chances of fertilisation of germ cells bearing either one of the two different factors, which thereby became recombined. In fact, Mendel made scarcely any distinction between the unit characters visible in the adult organisms and the unit factors borne in their germ cells, using the word *Merkmal* for both and treating them as a virtual identity. He left out everything that comes between them, how one determines the other, the whole of development. Knowledge of the connections is immaterial to an understanding of heredity.

Statistical analysis of Mendel's data led Fisher, in 1930, to conclude that Mendel knew what proportions to expect when he made his experiments. This means that he had thought out his scheme of particulate inheritance beforehand, as an abstract and simple combinatorial exercise, before putting it to the test. It was not an empirical discovery subsequently processed by induction into a scheme. Curiously, in reporting his work to the Natural History Society in Brno, Mendel presented the data at the first lecture and the mathematical explanation at the second one.

The statistical evidence is that Mendel's data agree much better with expectation than can reasonably be expected. Taken together, the figures published by Mendel would be expected to be equalled or improved upon, in their agreement with expectation, only once in 8,000 trials. There is no question of attributing deliberate falsification to Mendel or to his assistants, to whom Mendel's expectations would have been known. But enthusiastic amateurs are prone to give an experiment the benefit of a doubt, and to bias results unintentionally by discarding poor specimens and doubtful cases, to count a portion of a sample, stopping when the proportions are "good", thus making honest mistakes. Perhaps, indeed, Mendel did observe just this unusually consistent set of data. The conclusion that Mendel's work stemmed from an idea, worked out theoretically as a mathematical exercise, is supported by the very thorough manner in which Mendel expressed his system in mathematical terms and in a general form for universal application.

All of the main features of Mendel's theory would follow from the simplest possible assumptions of particulate inheritance. To conceive this simple hypothesis is exactly what Mendel, failed twice in an examination to qualify as a high school teacher, appears to have done. Moreover, the experiments to test the theory were performed with the most meagre facilities, a garden 35 × 7 metres, a few varieties of the garden pea (*Pisum sativum*), some forceps and bags to exclude insects from the flowers.

Mendel's theory could hardly have been formulated without some knowledge of the facts of fertilisation, that one egg and one sperm unite to form the zygote. This became known only a few years before his work and was not generally accepted even then. Thus Darwin thought more than one sperm was needed for each egg, both in animals and plants.

Direct observations of fertilisation were dependent upon the development of compound microscopes. Amongst lower plants fertilisation was observed in *Fucus* by Thuret in 1853, in *Oedogonium* by Pringsheim in 1856 and in fungi by De Bary in 1861. The role of the nucleus in fertilisation and cell division

was established by the work of Hertwig in 1875 on the fertilisation of the egg of the sea urchin. In seed plants, Amici in 1823 observed the production of the pollen tube, which he traced in 1830 to the ovary and even to the micropyle. In 1846 he showed, in orchids, that a cell, already present in the ovule and inactive until the pollen tube arrives, then develops into the embryo. This was confirmed and extended by Hofmeister. Hence Mendel could state "In the opinion of renowned physiologists, for the purpose of propagation one pollen cell and one egg cell unite in Phanerogams into a single cell, which is capable by assimilation and formation of new cells, of becoming an independent organism". However, this opinion was not generally accepted. Naudin (1863) repeated experiments of Kölreuter and Gärtner, placing counted numbers of pollen grains on stigmas and concluding that a fully viable seed required more than one grain. Mendel himself repeated this experiment, using *Mirabilis* as had Naudin, and found, as he wrote in a letter to Nägeli, that a single grain was sufficient.

The foundations of our knowledge of chromosomes, mitosis and meiosis were laid between 1882 and 1885; Mendel died in 1884. Roux published a remarkable essay in 1883 in which he argued that the linear structure of the chromosomes and their precise longitudinal division were such striking and universal phenomena as to indicate selective value. He suggested that this lay in their effectiveness in assuring that each daughter cell received the same complement of chromosomal material. Further he regarded this as a strong argument for identifying the chromosomes as the bearers of the units of heredity. These units were here for the first time specified as being arranged in a linear series. We have no information as to whether Mendel himself considered his different pairs of factors as being other than independent from one another.

In discussing the centenary of Mendel's work, it has been proper to consider what Mendel did discover, how he did it and how he proved his theory. But my main purpose is to give some account of where genetics has now reached and the paths by which it has advanced. However, the advance has been so fast and so far that it is impossible to do justice to all of it. Particular attention will be paid to the nature of the hereditary factors and how they act, with a glance at possible future advances.

The rediscovery in 1900 of Mendel's work, independently by Correns, Tschermak and de Vries, was rapidly followed by evidence of its universal applicability to all organisms as a strong probability. About a quarter of a century or so later this evidence was extended to microorganisms, first to fungi and algae and later to bacteria and viruses. These extensions have resulted in remarkable advances in knowledge at an unprecedented rate.

Early this century sex linkage, linkage and gene interaction were found as exceptions to the simple Mendelian rules. Polysomic inheritance, the effect of structural changes (such as interchanges, inversions and deletions) led to proofs that the chromosomes, visible microscopically, were the bearers of heredity. Probably the most fundamental of these discoveries was linkage. Many factors were found to be correlated in their segregation, rather than independent as Mendel's Second Law states, with recombinants being in a minority. All experiments have agreed with the hypothesis that the factors belong to a number of distinct linkage groups and that those in a linkage group are arranged in a linear array. The hereditary material, which carries the factors or is composed of them, is filamentous.

The name 'gene' was introduced and used in the sense of Mendel's factors in the germ cells. Genes were defined physiologically, namely that there is a heritable factor capable, under suitable circumstances, of being expressed as a recognisably distinct character. However, a gene responsible for a given character is detectable, in general, only if some other individual organism has

a different, alternative gene responsible for a difference in the character. These two genes are allelic genes. Alleles form a set of genes all affecting one function in various ways.

Whether two gene changes (mutations) are allelic or not is generally settled by the coupling and repulsion test, now often called the *cis-trans* test. Such changes in nomenclature, and there are many, as often reflect an ignorance of earlier knowledge as a radically changed point of view. Almost all mutational changes from the normal involve loss or partial loss of some characteristic. When combined with the normal, as a diploid in an animal or higher plant or in a yeast or as a heterocaryon in *Neurospora* or as a mixed population of bacteriophages growing in a bacterium, the mutant type is hidden by the normal. The normal is commonly dominant to the mutant which is recessive: it is as though the presence of a function in one covers up its absence in the other.

Thus the problem of defining a gene as a unit of function is essentially that of deciding whether any two mutants are different changes of the same normal gene or changes of two different genes. If the same function were lost in both mutants, there would be no gain of function by their combination in a diploid or a heterocaryon. However, if different functions were lost in each mutant, the two would be able to complement each other's loss, so restoring function. Thus with mutational changes in nonallelic genes, the coupling and repulsion phase heterozygotes both possess the normal function. However, with mutational changes in allelic genes, the repulsion phase heterozygote appears mutant whereas the coupling phase appears normal.

In various microorganisms, it has been shown that, if a large number of mutants are tested in pairs, they are divisible into a number of groups, such that complementation always occurs between members of different groups. Within groups, either no complementation occurs between any pair or no complementation occurs between some of the individuals and all other members of the group, some pairs of which complement. In the latter case, the class of noncomplementing members holds the group together. The genes responsible for differences within a group are allelic while those responsible for differences between groups are nonallelic. The significance of complementation between alleles will be mentioned later.

The differences between alleles, defined physiologically, are usually capable of genetic recombination. This has been demonstrated in *Drosophila*, maize, various fungi, bacteria and bacteriophages. Different pairs of alleles show different frequencies of recombination and these frequencies have been used to construct fine structure maps on the principle that the sites of mutation should be linearly arranged, with the frequency of recombination a function of the distance between them.

The clearest and most extensive evidence is drawn from studies of the *rII* genes of the bacteriophage T4. Here proof of the linearity is based on topological criteria rather than the statistics of recombination. Some *rII* mutants show no recombination with others, which themselves are able to recombine. The former can be regarded as more extensive abnormalities than the latter and may be deficiencies of various parts of the *rII* genes. If a series of them are analysed, some pairs showing recombination and others not, the results can be arranged in a matrix which can be represented as a linear map with the defects of the mutants extending over segments of various length. The overlaps define a unique order and none of the information requires the map to have more than one dimension. The total number of sites at which mutation has been shown to occur in *rII* exceeds 300, a value which probably represents little more than a third of the possible sites.

Thus, the heritable material is filamentous and is segmented into genes, distinguished by their functions. What are their functions? How do they

act? Of what are they made? What separates them? These are not independent matters, but certain functions were discovered first. Garrod, then Regius Professor of Medicine at Oxford University, suggested in 1909 that the function lost in a mutant was the ability to make a simple chemical transformation and that this was because of the loss of a specific enzyme. Hence, the proposition that each normal gene determined a specific enzyme. Garrod's theory was based upon the study of inborn errors of metabolism in man such as the failure in alcaptonuria to break down homogentisic acid and the failure in phenylketonuria to oxidise phenylpyruvic acid. Each of these metabolic defects is inherited as a simple recessive.

This gene-enzyme theory was ignored for more than 30 years. In the meantime, Beadle and Tatum had made the same proposal in 1941 and were able to obtain a large series of biochemical mutants in the fungus *Neurospora*. Some of these mutants provided the first evidence of definitive changes in the properties of specific enzymes accompanying alterations in specific genes. Later it was shown that gene mutation was associated with changes in the composition of the protein of which enzymes are composed. Gradually, through the application of analytical procedures suitable for small amounts of complex materials, mainly due to advances in chromatographic separation of amino acids and peptides, it was shown that a given protein is made up of a particular number of amino acids arranged in a precise sequence. It was shown also that the corresponding proteins, determined by heritable differences, may differ merely in the substitution of one amino acid for another at a definite place in the sequence. This was first shown for haemoglobin in man by Ingram in 1957, and has been extended to other systems, especially in bacteria and bacteriophages, by many workers. Among them, Yanofsky has shown, for the A protein of tryptophan synthetase in *Escherichia coli*, that the order of sites of allelic difference in the gene map parallels the order of positions of amino acid substitution in the protein specified by the normal gene at the locus. Another demonstration of this parallelism, or congruence, due to Brenner and his associates, is dependent upon the fact that some kinds of mutation result in the formation merely of fragments of the normal protein. In bacteriophage T4, they were able to show a strict correlation between the position of the mutant site in the gene map and the length of the peptide formed and so the position of discontinuity with reference to the normal polypeptide.

Questions left to answer at this stage include how the gene determines the protein, how the gene duplicates and what is the chemical and physical nature of the gene. It was a major achievement of the combined use of genetical and cytological methods to demonstrate that the chromosomes were the site of the genes. Further it was possible to demonstrate that there is a congruence in order of the genes in a linkage map and of the order of parts of a particular chromosome. Here it is reasonable to assume a collinearity in the sense that genes are parts of chromosomes, or of a constituent. The chromosomes were found to be composed of deoxyribonucleic acid (DNA), ribonucleic acid (RNA) and proteins, mostly basic ones. Amongst these materials, only the DNA was in constant quantity from cell to cell of an organism, doubling before each mitosis. This was circumstantial evidence for DNA being the heritable material, but there was some reluctance to accept that it could show enough variety to be genetic, especially as it was thought to be merely a repeating sequence of the four nucleotides. At the same time most of the protein of the chromosomes appeared equally monotonous, but some hope was centred in the small amounts of acidic protein present.

Clear evidence for DNA being the genetic material of bacteria and of bacteriophages came first from the demonstrations that it was the material of transformation in *Pneumococcus* and virtually the only material injected by phages into host bacteria. In the meantime, DNA and RNA were subjected to thorough chemical study, so that by 1951 Todd and Brown had established

in detail the structure of nucleosides and nucleotides and how they were linked together in nucleic acids to form linear molecules in which nucleotides are joined together by phosphate links to the 3 and 5 positions of their sugar residues. X-ray diffraction studies of DNA fibres enabled Wilkins to establish the constancy of pattern and approximate dimensions. Improvements in analysis of DNA from many sources resulted in the discovery of variations in the amounts of the four nucleotides, but with certain regularities, especially equivalence in the amounts of adenine and thymine and of guanine and cytosine, respectively, among the bases.

To account for these data, Watson and Crick in 1953 proposed that DNA consists of two spiral polynucleotide chains, relationally coiled about one another and joined by hydrogen bonds between their bases. This structure is now generally accepted as correct in principle, subject to refinements in details of bond angles and atom spacing. Besides suggesting how the molecule might replicate and preserve the same genetic information in the daughters, it provided a mechanism of mutation and suggested how the information in the DNA might be related to that in the polypeptide of a protein.

The double spiral structure predicts a semi-conservative mode of replication. Meselson and Stahl showed this to occur in the replication of DNA in *Escherichia coli* by following the distribution of heavy isotopes of nitrogen and carbon in the DNA of progeny developing in the presence of normal isotopes. Similar observations have been made with an alga and with mammalian cells. Labelling experiments to study the replication of chromosomes, in higher plants showed a similar semi-conservative process, but further work has disclosed complexities. Labelling experiments with the chromosomes of bacteria have also shown a semi-conservative process and, in addition, that the chromosomes are circular and are replicated sequentially starting from a particular site.

How is DNA related to protein? These are two filamentous materials, one composed of four different members (the nucleotide pairs), the other of about 20 (the amino acids). It appeared possible that the relation was analogous to two different codes, one with four and the other with 20 symbols, for the same information. Obviously a one to one or a two to one relation gives insufficient scope. The least proportionality likely is a three nucleotide pair to one amino acid relation. It is unlikely that the code could be mixed, since it would require commas between the elements of the code as well as stops at the ends of the section of DNA specifying one protein. Also, it is unlikely that the code is overlapping, since then several adjacent amino acids would generally be affected by one mutation. The triplet code provides 64 symbols, some of which represent signals other than amino acids. Moreover, it has been found that some amino acids are represented by more than one triplet, a degeneracy of the code.

The three to one relation was established for bacteriophage by ingenious experiments of Crick, Brenner and their associates. It was thought that certain mutants, induced by acridines, were due to the addition or subtraction of base pairs. Some reversions of these might have compensatory subtractions or additions near, but not at, the original mutant site. These suppressor mutations were separated and found themselves to be mutant. Whether base pairs were added or subtracted could be defined in terms of a standard. When three additive mutants, or three subtractive mutants, were put together the strain was approximately normal, rather than mutant, provided the sites of the mutants were fairly close together with specified parts of the gene.

The significance of a third important constituent of living matter, RNA, became clear through a different sequence of events, particularly through the efforts of biochemists to determine the mechanism of protein synthesis. It is not necessary to go into details. In essence, it is now fairly well established that an RNA polymerase catalyses the synthesis of specific RNAs by transcription from segments of the DNA, so that the sequence in a given RNA is

the complement of the sequence in the strand of DNA copied. There are three classes of RNA molecules: (1) two species of ribosomal RNA (rRNA), one about 1,500 and the other 3,000 nucleotides long, that form parts of the structure of the ribosomes concerned in protein synthesis; (2) several dozen species of transfer RNA (tRNA), each about 100 nucleotides long, that provides adapters for the amino acids joined in protein synthesis; (3) hundreds of thousands of species of messenger RNA (mRNA), of diverse lengths, perhaps ranging up to tens of thousands of nucleotides, that provide the templates for orderly polymerisation of amino acids into specific polypeptides. Thus some genes determine only RNA (rRNA and tRNA) but most are expressed as protein. Each species of transfer RNA becomes coupled to a specific amino acid and the latter is led to its proper position in the amino acid order by a specific triplet in the tRNA complementary to a triplet in the messenger RNA.

The discovery that polyribonucleotides stimulate the incorporation of amino acids in cell free systems able to synthesise proteins, led very quickly to solutions of which nucleotide triplets correspond to each amino acid. This was achieved by using synthetic polynucleotides composed either of single nucleotides or of random mixtures of two or more in various proportions. Of course, the information is incomplete and it is not yet known exactly how many of the 64 triplets do code for amino acids. Some triplets do not code for any amino acid and these have been referred to as nonsense triplets. In fact this is an unsuitable name, since at least some of them serve a special function in information transfer. In bacteria and bacteriophages, it has been shown that some mutations result in the termination of synthesis of a polypeptide so that only a fragment of the normal one is formed. Termination occurs because the mutation has resulted in triplet which signals that this very event should occur. The evidence is strictly genetical, dependent upon the demonstration that a distinct suppressor mutation may allow an amino acid to be inserted despite that the signal normally leads to the cessation of amino acid polymerisation.

Thus we have a strictly mechanistic theory of gene structure, function and replication. The gene is a sequence of nucleotide pairs, presumably a multiple of three in number. The gene replicates by enzymic processes and is transcribed into RNA by another enzymic process. Most species of RNA provide templates, when wound on a number of ribosomes, for ordering specific transfer RNAs, to which are coupled acylated amino acids, which can then be bound together in an order, specified by the messenger RNA. The polypeptides so formed fold to form proteins, generally enzymes. Many enzymes are composed of several similar protein units and in these cases some defective allelic mutants may complement in a hybrid enzyme by allosteric correction of folding errors in the mutant proteins.

The theory is further that there is a gene or a complex of genes for each and every function in an organism. This is substantiated by the discovery of genes for each enzyme of intermediary metabolism, of genes for some parts of the machinery of protein synthesis, of genes for a wide variety of morphological, physiological and behavioural characters, of genes for behaviour of constituents of cells, especially the chromosomes and mitochondria, and of genes controlling the action of other genes.

Genetics is a powerful method of biological analysis, discovering principles and mechanisms by analysis of numerical data of the distribution of heritable differences amongst progeny. In essence its principles extend from bacteriophage to man; it unifies biology. It may be expected soon to make decisive contributions to some of the outstanding fundamental problems in biology, such as the mechanisms of genetic recombination, differentiation and behaviour.

Mendel did indeed give us a legacy, one I am sure Sir William Macleay would appreciate were he alive today to see how genetics has made such good intellectual use of the bacteria, whose general study he fostered. I am grateful for the opportunity afforded of paying respectful tribute to both these benefactors.

Bibliography

GENERAL REFERENCES

The following deal with broad aspects of the subject and contain references to nineteenth century work—

- ILTIS, H., 1924.—“Gregor Johann Mendel, Leben, Werk und Wirkung”. (Springer, Berlin). English translation, E. and C. Paul, 1932, “Life of Mendel”. (W. W. Norton and Company, New York).
- ROBERTS, H. F., 1929.—“Plant Hybridization before Mendel”. (Princeton University Press, Princeton, N. J.).
- SACHS, J., 1875.—“History of Botany”. Translated by H. E. F. Garnsey, 1890. (Oxford University Press, Oxford).
- STURTEVANT, A. H., 1965.—“A History of Genetics”. (Harper and Row, New York).
- WILSON, E. B., 1896.—“The Cell in Development and Heredity”. (Macmillan Co., New York). Second edition, 1900; Third edition, 1925.
- ZIRKLE, C., 1935.—“The Beginnings of Plant Hybridization”. (University of Pennsylvania Press, Philadelphia).

SPECIAL REFERENCES

- BEADLE, G. W., and TATUM, E. L., 1941.—Genetic control of biochemical reactions in *Neurospora*. *Proc. nat. Acad. Sci.*, 27: 499–506.
- BENZER, S., 1961.—On the topography of the genetic fine structure. *Proc. nat. Acad. Sci.*, 47: 403–415.
- BRENNER, S., 1966.—Collinearity and the genetic code. *Proc. roy. Soc.*, B164: 170–180.
- BROWN, D. M., and LYTHGOE, B., 1950.—Deoxyribonucleosides and related compounds. Part II. A proof of the furanose structure of the natural 2-deoxyribonucleosides. *J. chem. Soc.*, 1990–1991.
- CRICK, F. H. C., BARNETT, LESLIE, BRENNER, S., and WATTS-TOBIN, R. J., 1961.—General nature of the genetic code for proteins. *Nature*, 192: 1227–1232.
- CORRENS, C., 1900.—G. Mendel's Regel über das Verhalten der Nachkommenschaft der Rassenbastarde. *Ber. deutsch. bot. Gesells.*, 18: 158–168. English translation 1950, in *The birth of genetics*. *Suppl. Genetics*, 35: 33–41.
- , 1905.—Gregor Mendel's Briefe on Carl Nägeli, 1866–1873. *Abh. math.-phys. Kl. Kön. Sächs. Gesellsch. Wiss.*, 29: 189–265. English translation, 1950, in *The birth of genetics*. *Suppl. Genetics*, 35: 1–29.
- DE VRIES, H., 1900.—Sur la loi de disjonction des hybrides. *C. R. Acad. Sci. (Paris)*, 130: 845–847. English translation 1950, in *The birth of genetics*. *Suppl. Genetics*, 30–32.
- FISHER, R. A., 1936.—Has Mendel's work been rediscovered? *Ann. Sci.*, 1: 115–137.
- GARROD, A. E., 1908.—Inborn errors of metabolism. *Lancet*, 2: 1–7, 73–79, 142–148, 214–220. Published separately as a book, 1909. (Oxford University Press, London).
- INGRAM, V. M., 1963.—“The Hemoglobins in Genetics and Evolution”. (Columbia University Press, New York).
- LYTHGOE, B., and TODD, A. R., 1947.—Structure and synthesis of nucleotides. *Symp. Soc. exp. Biol.*, 1: 15–37.
- MENDEL, G., 1866.—Versuche über Pflanzenhybriden. *Verh. naturforsch. Ver. Brunn*, 4: 3–47. English translations, 1901. *J. roy. hort. Soc.*, 26: Bateson, W., 1909, 1913. “Mendel's principles of Heredity”.
- MESELSON, M., and STAHL, F. W., 1958.—The replication of DNA. Cold Spring Harbor Symp. quant. Biol., 23: 9–12.
- TSCHERMAK, E., 1900.—Über künstliche Kreuzung bei *Pisum sativum*. *Ber. deutsch. bot. Gesells.*, 18: 232–239. English translation 1950, in *The birth of genetics*. *Suppl. Genetics*, 35: 42–47.
- WATSON, J. D., and CRICK, F. H. C., 1953.—The structure of DNA. Cold Spring Harbor Symp. quant. Biol., 18: 123–131.
- YANOFSKY, C., CARLTON, B. C., GUEST, J. R., HELINSKI, D. R., and HENNING, U., 1964.—On the colinearity of gene structure and protein structure. *Proc. nat. Acad. Sci. U.S.*, 51: 266–272.

THE RHAPHIDOPHORIDAE (ORTHOPTERA) OF AUSTRALIA

4. A NEW GENUS FROM SOUTH AUSTRALIA

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[Read 29th June, 1966]

Synopsis

A new genus *Novotettix* n.g. is erected, and the new species *Novotettix naracoortensis* n.sp. is described from limestone caves in south-eastern South Australia.

INTRODUCTION

A new monotypic genus *Novotettix* n.g., belonging to the family Rhaphidophoridae, is recorded here from Naracoorte in south-eastern South Australia. The new species, *Novotettix naracoortensis* n.sp., is placed in this genus.

The caves at Naracoorte are formed in Oligocene Gambier marine limestone, and occur at an altitude of about 200 feet above sea level. Twenty-eight caves are known, covering an area of 15 miles (Sexton, 1965). *N. naracoortensis* has been collected from Alexandra Cave and Victoria Cave on the South Australian Tourist Bureau Reserve. Specimens have also been taken in Haystall Cave, Corner Fence Cave, and Smoke Cave at Joanna, a district 9–10 miles south-south-east of the town of Naracoorte, and about four miles from the Tourist Reserve.

In both Alexandra and Victoria Caves temperatures range from 62°–64°F and relative humidity from 89–94%. Similar temperatures have been recorded from caves containing Rhaphidophorids in western Victoria and on the Nullarbor Plain. These temperatures are considerably higher than those recorded from caves in south-eastern Australia, where the range is from 49°–58°F, and the average temperature 54°–56°F (Richards, 1966). At Waitomo Caves in New Zealand, the highest temperature at which Rhaphidophorids could carry out their normal activities was found to be 60°F (Richards, 1965). Average cave temperatures there ranged from 53°–58°F. The southern Australian caves are the warmest habitats so far recorded in Australasia which support colonies of Rhaphidophoridae. The higher temperatures may be attributed to the low altitudes at which the caves occur.

Alexandra Cave contains a colony of over 1500 *N. naracoortensis*, in contrast to the rather sparsely populated caves in south-eastern Australia. About two-thirds of the insects occur on the walls 100 feet inside the entrance, and the remainder extend another 70 feet or more into the cave. The Rhaphidophorids share the cave with a fauna of carabids, pterostichids, isopods, two species of blattids, and two species of spiders. The very large number of Rhaphidophorids present may be accounted for by the absence of predators such as bats and rats. The Bat Cave, a short distance from Alexandra Cave, has a large colony of the bent-winged bat, *Miniopterus schreibersii* (Kuhl), but no *N. naracoortensis* have been observed in this cave. In Tasmanian caves, where no bats occur, large colonies of Rhaphidophoridae are also present. This dissociation of cave crickets and bats is quite the exception to the rule in caves throughout Australia.

N. naracoortensis is one of the larger of the Australian Rhaphidophoridae. Sexual dimorphism is strongly developed, males being larger than females. An adult male may reach a length of up to 18 cm. from the tip of its antennae to its hind tarsi.

The life history follows a similar pattern to that observed in other Rhaphidophorids, both in Australia and New Zealand (Richards, 1961, 1966). In late December and January adults appear. Mating and oviposition continue throughout the autumn.

The locomotor activity rhythm of *N. naracoortensis* has recently been discussed, and the similarity of its behaviour to that of New Zealand species noted (Richards, 1965).

This new genus *Novotettix* does not show any close affinities with other Australian Rhaphidophorid genera so far studied.

Genus NOVOTETTIX, n.g.

Body sparsely clothed with short setae. Legs long and slender. Antennae very long and tapering, almost touching at their bases; scape about three times as large as pedicel, which is narrower than scape, but broader than other segments; from segment four onwards segments subequal in length, but steadily decreasing in size; all segments thickly clothed with short setae. A single median ocellus present. Fastigium rising abruptly, grooved medianly and longitudinally. Maxillary palps with third and fourth segments subequal in length. Fore coxa unarmed. All femora sulcate ventrally. Apical spines on femora, tibiae, proximal segments one and two of hind tarsi constant in number. Fore femur bears two apical spines beneath, one prolateral and one retrolateral; fore tibia bears four apical spines, one above and one beneath both prolaterally and retrolaterally; fore tarsus unarmed. Mid femur bears two apical spines beneath, one prolateral and the other retrolateral; mid tibia bears four apical spines, one above and one beneath both prolaterally and retrolaterally; mid tarsus unarmed. Hind femur bears one prolateral apical spine beneath; hind tibia bears a pair of long apical spurs above, a pair of subapical spines above, a pair of short apical spurs beneath and a pair of subapical spines beneath, one from each pair being prolateral and the other retrolateral; two proximal segments of hind tarsus each bear two apical spines above, one prolateral and one retrolateral; other two segments unarmed. Subgenital plate of female trilobed, each lobe rounded apically. Subgenital plate of male triangulate.

Type species for the genus: Novotettix naracoortensis n.sp.

NOVOTETTIX NARACOORTENSIS, n.sp.

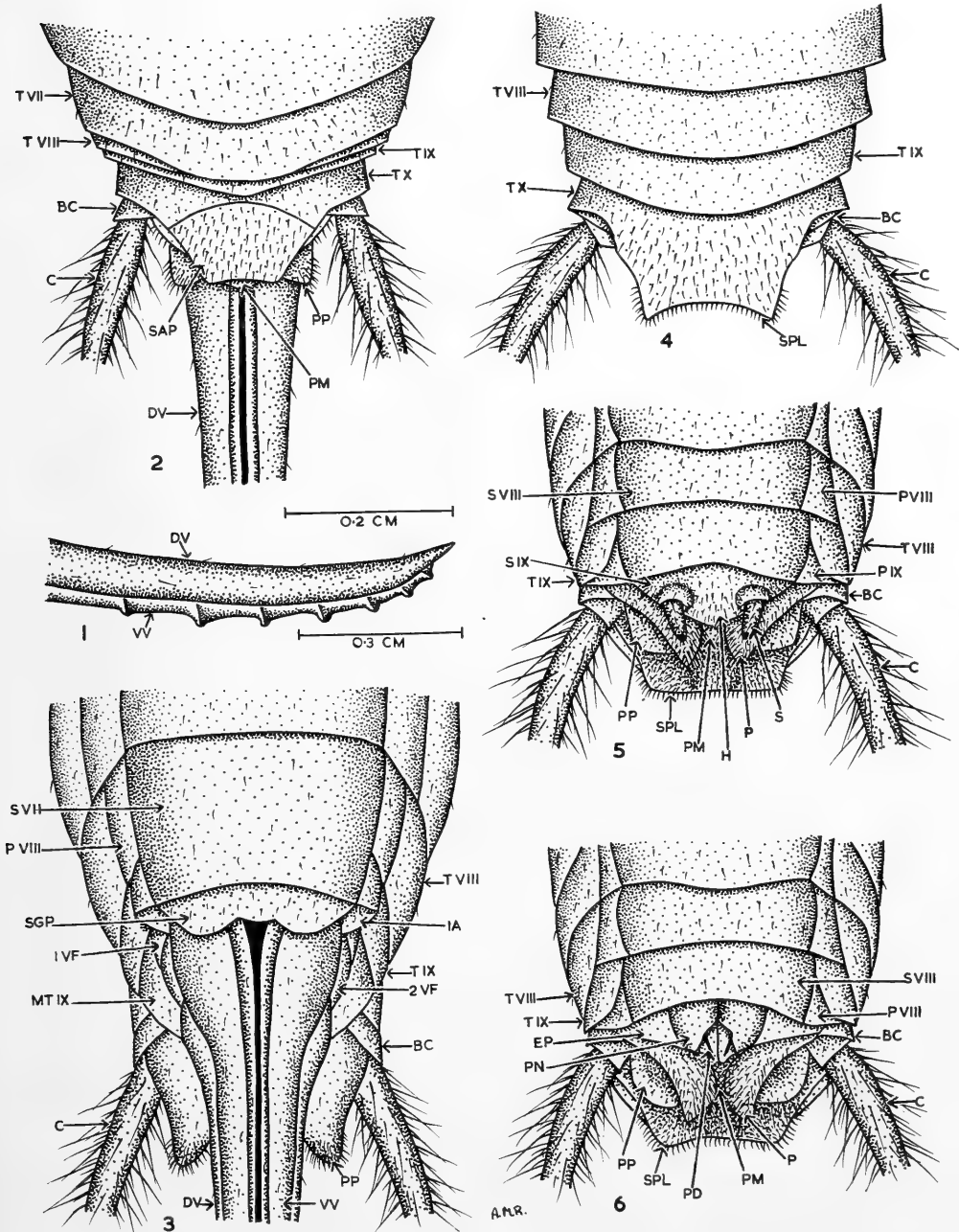
(Text-fig. 1. Figures 1-6)

Colour.—Basic colour ochreous with pronotum, mesonotum, metanotum and abdominal terga irregularly mottled with light brown; femora and tibiae banded or mottled with light brown and ochreous; all tarsi ochreous; antennae light brown; ovipositor light reddish brown.

Body.—Length up to 16 mm. in male, and 17 mm. in female. Surface of body sparsely clothed with setae. Antennae broken. Fastigium longer than high. Ovipositor 0.9 length of body; ventral valves armed distally 0.3 of total length to apex with seven well developed teeth (Fig. 1).

Antennae.—As in generic description. Third segment in male on dorsal aspect 2.6 as long as pedicel, and on ventral aspect 2.1 as long; in female on dorsal aspect 1.6 as long as pedicel, and on ventral aspect 1.3 as long. Sexual dimorphism present, male possessing longer, stouter antennae than female. No spines present on flagellum of either male or female.

Legs.—Fore and mid legs subequal in length, with hind leg 1.7 length of fore and mid legs. Sexual dimorphism is shown by fore, mid and hind legs of female being 0.8 as long as male. Hind femora, all tibiae and proximal two segments of hind tarsi armed with variable numbers of linear spines



Text-fig. 1.—*Novotettix naracoortensis* n.sp. 1, Distal portion of ovipositor showing teeth on ventral valve; 2, Female genitalia, dorsal view; 3, Female genitalia, ventral view; 4, Male genitalia, dorsal view; 5, Male genitalia, ventral view; 6, Male genitalia, ventral view, subgenital plate removed to expose structures beneath.

(Table 1). No spines on fore or mid femora and tarsi. Spines on hind femur of female fewer in number than those on hind femora of male. Apical spines constant in number as in generic description. Length of proximal segment of hind tarsus subequal with other three segments together. Ratio of length of legs to length of body: Fore leg, male 2.6:1; female 2:1. Mid leg, male 2.6:1; female 2:1. Hind leg, male 4.6:1; female 3.3:1.

TABLE 1

Variability in Number of Linear Spines on the Legs of 25 Specimens of Novotettix naracoortensis n.sp.

		Arith. Mean		No. of Specimens		Std. Dev.		Range (or Distribution)	
		L.	R.	L.	R.	L.	R.	L.	R.
Fore Femur	Pro.	0	0	25	25	0	0	0	0
	Inf.	0	0	25	25	0	0	0	0
Fore Tibia	Pro.	3.2	3.2	25	25	0.6	0.6	2-4	2-4
	Inf.	4.0	4.0	25	25	-	-	3(2), 4(23)	3(2), 4(23)
Fore Tarsus	Pro.	0	0	25	25	0	0	0	0
	Retro.	0	0	25	25	0	0	0	0
Mid Femur	Pro.	0	0	25	25	0	0	0	0
	Inf.	0	0	25	25	0	0	0	0
Mid Tibia	Pro.	0	0	25	25	0	0	0	0
	Sup.	0	0	25	25	0	0	0	0
Mid Tibia	Pro.	3.7	3.7	25	25	0.5	0.5	3(7), 4(18)	2-4
	Inf.	4.0	3.8	25	25	0.3	0.5	3-5	3-5
Mid Tarsus	Pro.	0	0	25	25	0	0	0	0
	Retro.	0	0	25	25	0	0	0	0
Hind Femur	Pro.	13.0	14.1	14	14	2.4	3.1	9-17	8-21
	Inf. ♂	16.1	17.9	14	14	4.0	3.6	9-25	13-28
Hind Femur	Pro.	7.7	8.1	11	10	2.7	2.0	5-13	4-12
	Inf. ♀	7.2	7.8	11	10	2.4	2.3	3-11	4-11
Hind Tibia	Pro.	63.6	62.6	25	24	4.1	6.6	57-72	48-75
	Sup.	68.9	67.7	25	24	8.1	6.6	55-81	59-83
Hind Tarsus	Pro.	8.8	8.4	25	24	1.2	1.3	6-11	6-11
	1 Sup.	8.8	8.5	25	24	1.9	1.6	6-15	6-11
Hind Tarsus	Pro.	3.1	3.0	25	24	0.7	0.7	2-5	2-4
	2 Sup.	2.8	3.0	25	24	0.6	0.8	2-4	2-5

Arith. Mean, Arithmetic Mean; Inf., Inferior; L., Left leg; Mid., Middle; Pro., Proximal; R., Right leg; Retro., Retrolateral; Std. Dev., Standard Deviation; Sup., Superior.

(Figures in parentheses represent number of specimens)

Genitalia.—FEMALE: Suranal plate, Fig. 2 (SAP), concave laterally, distal margin slightly emarginate; whole plate thickly clothed with setae. Subgenital plate, Fig. 3 (SGP), distal margin trilobed, each lobe rounded apically, two lateral lobes 0.25 longer than median lobe; whole plate sparsely clothed with setae. MALE: Suranal plate, Fig. 4 (SPL), convex laterally, distal margin emarginate and clothed with setae; rest of plate thickly clothed with setae on dorsal and ventral surfaces; on ventral surface disto-lateral regions slightly raised into two lobes. Subgenital plate, Fig. 5 (H), triangulate, 2.5 wider than long, sparsely clothed with setae. Two styli, Fig. 5 (S), short, broad, conical, thickly clothed with setae, length of styli being 0.7 length of sternite IX (S IX). Parameres, Figs 5, 6 (P), elongate, tapering to a point, retrolateral

margin concave, pro lateral margin convex, whole plate 2·7 longer than wide, distal portion of paramere thickly clothed with long and short setae. Pseudosternite, Fig. 6 (PD), 1·5 wider than long, convex laterally, tapering distally to a truncated apex. Penis, Fig. 6 (PN), two-lobed, each lobe subequal in width to length. Paraprocts, Figs 5, 6 (PP), crescent-shaped, twice as long as wide, sparsely clothed with setae.

Locality.—In limestone caves, Naracoorte, South Australia. Alexandra Cave (S4) (type locality), coll. A. M. Richards, 1964; G. F. Gross, 1958; E. Hamilton-Smith, 1956, 1958, 1961, 1962; Haystack Cave (S34), coll. P. F. Aitken, 1962; Smoke Cave (S71), coll. P. F. Aitken, 1962; Corner Fence Cave (S35), coll. P. F. Aitken, 1962; Victoria Cave (S2), coll. W. Hill, 1957; Cave two miles east of Naracoorte, coll. unknown, 1957.

Types.—Holotype male, allotype female, and two paratypes (male and female) in National Insect Collection, C.S.I.R.O., Canberra. Four paratypes (two males and two females) in South Australian Museum Collection, Adelaide. Two paratypes (male and female) in Australian Museum Collection, Sydney.

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I am indebted to Dr. P. Crowcroft, Director of the South Australian Museum, Adelaide, for the loan of material. I should also like to thank Mr. E. Hamilton-Smith, Sub-Aqua Speleological Society, Melbourne; and Mr. P. F. Aitken, South Australian Museum, for collecting and sending me specimens. I am grateful to the South Australian Government Tourist Bureau for permission to collect and study insects in the caves on their Reserve at Naracoorte.

References

- RICHARDS, AOLA M., 1961.—The life history of some species of Rhabdophoridae (Orthoptera). *Trans. roy. Soc. N.Z. Zoology*, 1 (9): 121–137.
 ———, 1965.—The effect of weather on Rhabdophoridae (Orthoptera) in New Zealand and Australia. *Ann. de Spéléologie*, XX (3): 391–400.
 ———, 1966.—The Rhabdophoridae (Orthoptera) of Australia. Part 3. A new genus from south-eastern Australia. *Pacific Insects*, 8 (3): 613–624.
 SEXTON, R. T., 1965.—Caves of the coastal areas of South Australia. *Helicite*, 3 (3): 45–59.

Index to Text-figure

BC, basal segment of cercus; C, cercus; DV, dorsal valve; EP, endoparamere; H, subgenital plate, male; IA, intersegmental apodeme; MT IX, membrane of tergite IX; P, paramere (ectoparamere); P VIII, P IX, pleurite VIII, IX; PD, pseudosternite; PM, perianal membrane; PN, penis; S, stylus; S VII, S VIII, S IX, sternite VII, VIII, IX; SAP, suranal plate, female; SGP, subgenital plate, female; SPL, suranal plate, male; T VII, T VIII, T IX, T X, tergite VII, VIII, IX, X; 1 VF, first valvifer; 2 VF, second valvifer; VV, ventral valve.

NOTES ON THREE RECENTLY PROPOSED AUSTRALIAN TERTIARY ECHINOID GENERA

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[Read 29th June, 1966]

Synopsis

The Eocene brissid genus *Gillechinus* Fell, 1964 (type species: *Gillechinus cudmorei* Fell, 1964=*Eupatagus coranguinium* Tate MS.) is considered to be a synonym of *Brissopatagus* Cotteau, 1886.

The Miocene temnopleurid genus *Irenechinus* Fell, 1964 (type species: *Irenechinus hentyi* Fell, 1964=*Coptechinus pulchellus* Bittner, 1892) is considered to be a synonym of *Ortholophus* Duncan, 1887. *Brochopleurus australiae* Fell, 1949 (= *Psammechinus woodsi* Laube, 1869) should also be referred to *Ortholophus*.

The Eocene fibulariid *Lenicyamidia* Brunnschweiler, 1962 (type species: *Lenicyamidia compta* Brunnschweiler, 1962) is considered to possess a typical clypeasteroid monobasal apical system.

In this note three recently proposed Australian Tertiary echinoid genera are discussed. Although the Tertiary echinoid faunas of Australia are at present being revised, it will be several years before relevant sections dealing with all these genera appear. In the interim it is desirable that some comments be given before these genera become established in the literature.

Genus GILLECHINUS Fell, 1964

This genus was proposed for a species of spatangoid from the "Lower beds, Aldinga, South Australia" which was named *Gillechinus cudmorei* by Fell. The species is in fact Ralph Tate's MS. form *Eupatagus coranguinium* and has been cited as such in literature on the Australian Tertiary (e.g. Pritchard, 1891, p. 183). In the collections available to me (including Tate's original syntypes from the Tate Collection, University of Adelaide) it appears that the species is confined to the Upper Eocene Tortachilla Limestone of the St. Vincent Basin, South Australia.

According to Fell, *Gillechinus* is similar to *Eupatagus* but differs "in the arrangement of the primary tubercles" and the "indistinct closure of the petals". He goes on to observe that *Gillechinus* is unknown outside Australia.

However, in the comparison of the genus with previously described forms, no mention is made of *Brissopatagus* Cotteau, 1863 (type species: *Brissopatagus caumonti* Cotteau). This brissid is world-wide in its distribution (Europe, Egypt, Madagascar, India, N. America) and is confined to Eocene strata. It differs from *Eupatagus* solely in the tuberculated, somewhat depressed areas anterior to each petaloid ambulacrum of the adapical surface. In some species these depressions may be present only in front of the anterior petals, whereas in others the depressions are not well defined. Indeed, Cooke (1942, 1959) has employed *Brissopatagus* as a subgenus of *Eupatagus*, for the differences from *Eupatagus* hardly warrant its generic separation.

Gillechinus cudmorei Fell is a typical species of *Brissopatagus*. Among previously described forms embraced by this genus it resembles most closely *Euspatangus* (*Brissospatangus*) *beyrichi* Dames (1877, p. 82-83, Pl. 11, Fig. 2)

from the Eocene of Verona. It differs from this form in its smaller size, and wider, more rounded outline. *Gillechinus* Fell, 1964, therefore, is here considered to be a synonym of *Brissopatagus* Cotteau, 1886.

Genus IRENECHINUS Fell, 1964

Fell (1964) has proposed the name *Irenechinus hentyi* gen. et sp. nov. for a specimen of a temnopleurid from the Middle Miocene Bochara Limestone, Hamilton district, Western Victoria. The elucidation of this genus requires discussion of some other Tertiary temnopleurids, in particular, *Brochopleurus australiae* Fell and other species which should be embraced by the genus *Ortholophus* Duncan.

Fell (1949) described the temnopleurid *Brochopleurus australiae* sp. nov. from early Miocene strata exposed along the Murray River Cliffs, South Australia. Examination of many hundreds of specimens from these strata indicates that the holotype (National Museum Victoria P4687) of this species is a juvenile specimen of the common temnopleurid "*Psammechinus*" *woodsii* Laube, 1869. The species exhibits a progressive loss of sculpture during growth so that in large specimens the ridges tend to meet and the sculpture is correspondingly obliterated. A similar loss of sculpture during growth has been reported in living temnopleurids such as *Desmechinus* and *Pseudechinus*. It follows, therefore, that *Brochopleurus australiae* Fell, 1949 is a junior subjective synonym of "*Psammechinus*" *woodsii* Laube, 1869.

A second, poorly preserved specimen which Fell included in his species (National Museum Victoria P4688), is here interpreted as the male form of *Paradoxechinus novus* Laube. Such small specimens differ from "*P.*" *woodsii* principally in the character of the coarser sculpture.

Fell's generic assignment of the species to the Indian Miocene genus *Brochopleurus* also cannot be accepted. In 1887 Duncan proposed the genus *Ortholophus* for his species *Temnechinus lineatus* Duncan 1877 (*non* Bittner, 1892) from Upper Miocene strata at Beaumaris, Victoria. In the past there has been much uncertainty as to the application of this genus (e.g. Mortensen, 1943, pp. 350-1) due to discrepancies in Duncan's descriptions. He gave his species as "sculptured by a network of ridge-like costae" but his figure of *O. lineatus* shows no trace of sculpture. Examination of the type specimen (British Museum (Nat. Hist.) G.S.L. 14078), together with topotype material, shows that Duncan's figure correctly portrays the ornament of mature specimens. In fact *Ortholophus* is a well founded genus and should embrace a group of Australian (and perhaps New Zealand) Tertiary temnopleurid species.

The genus thus employed includes moderate sized temnopleurids with crenulate tubercles, uniserial ambulacra and obscure gill slits. The apical system is regularly dicyclic. Juveniles are strongly sculptured, the sculptural ridges being lost with growth to varying degrees in different species. The girdle consists of rather low auricles united above the ambulacra. *Psammechinus woodsii* Laube is a typical representative of *Ortholophus*.

Ortholophus differs from *Brochopleurus* principally in possessing crenulate tubercles, and hence *Brochopleurus* is not considered to be a junior synonym of *Ortholophus*. Fell (1949), however, described and illustrated his *Brochopleurus australiae* (a small specimen of *Ortholophus woodsii*) as possessing smooth tubercles. The holotype is not well preserved in this respect but distinct crenulation of the tubercles is readily discernible. In this respect it may also be noted that Bittner, Duncan and Laube have all erroneously described (and illustrated) the tubercles as smooth in various species of *Ortholophus*.

To return to the genus *Irenechinus* Fell, this is distinguished by Fell from *Brochopleurus* by the crenulation of the tubercles. It is in fact a typical species of *Ortholophus* in which Fell has recognized the crenulation of the tubercles. The species *I. hentyi* is also identical with that which occurs in the Middle

Miocene horizons along the Murray River Cliffs (the Morgan Limestone) and which was named by Bittner in 1892 (p. 342-4, Pl. 1, Fig. 5) as *Coptechinus pulchellus*.

It is concluded that :

Brochopleurus australiae Fell=*Ortholophus woodsi* (Laube)

Irenechinus hentyi Fell=*Ortholophus pulchellus* (Bittner)

The genus *Brochopleurus* is accordingly unknown from the Australian Tertiary.

Illustrations of these and related temnopleurids will be given elsewhere (Philip, 1966).

Genus LENICYAMIDIA Brunnschweiler, 1962

This clypeasteroid genus, based on *L. compta* Brunnschweiler, 1962, from the Eocene Merlinleigh Sandstone, Western Australia, was proposed for a coarsely tuberculated fibulariid with an elongate periproct. Particular interest attaches to the apical system of the type species, for it is described as consisting of "Four large genital, one central madreporic, and five small ocular plates . . ." (Brunnschweiler, 1962, p. 167). Such an arrangement of plates is shown in Text-fig. 2A accompanying the original description.

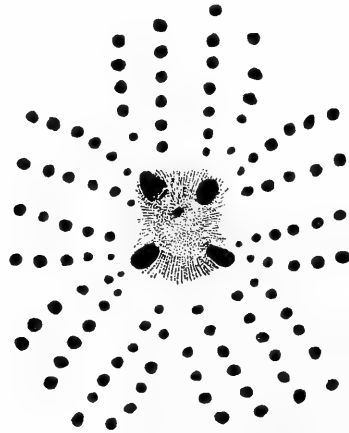


Fig. 1.—*Lenicyamidia compta* Brunnschweiler. Adapical portion of petals and apical system showing the fibrils of the stereome of the madreporite. Paratype, Bureau of Mineral Resources CPC 4812, $\times 20$ approx.

All known representatives of the order Clypeasteroidea possess a monobasal apical system, i.e., a fused genital disc (the madreporite), with five oculars which usually can be distinguished from the madreporite. The nature of the madreporite is known in *Echinarachnius* where genitals 1 and 3 are lost at metamorphosis and genital 5 does not develop (Gordon, 1929). Genitals 2 and 4 alone fuse to give the madreporite. The apical system of *Lenicyamidia compta* would therefore seem to represent a remarkable departure from that of other clypeasteroids.

Not only is the apical system of *Lenicyamidia*, as portrayed, unique among clypeasteroids, but with its "central madreporic plate" (which would therefore be genital 2) it is without parallel in the class Echinoidea.

Examination of type material of *L. compta*, however, indicates that the species possesses a monobasal system. All material of the species is silicified, and it was found impossible to develop sutures in the adapical region of any

specimen. However, the silification has not obliterated the original fibrils of the stereome. These radiate from the central portion of the apical system to outside the genital pores without marked discontinuities (text-fig. 1). Where alignment of the fibrils of plates of an echinoid test is discernible, the fibrils are generally normal to sutures. It is therefore concluded that *Lenicyamidia compta* lacks discrete genital plates in the apical system which, in its nature, corresponds closely with that of other clypeasteroid echinoids.

A comparison of *Lenicyamidia* with the closely related genera *Fibularia*, *Fibulariella* and *Cyamidia* will be given elsewhere.

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References

- BITTNER, A., 1892.—Über Echiniden des Tertiärs von Australien. *Sitz. k. Adad. Wissen. Wien. (Math. Natur. Cl.)*, 101: 331–373.
- BRUNNSCHWEILER, R. O., 1962.—On echinoids in the Tertiary of Western Australia with a description of two new Eocene Fibulariidae. *J. geol. Soc. Aust.*, 8: 159–169.
- COOKE, C. W., 1942.—Cenozoic irregular echinoids of eastern United States. *J. Paleont.*, 16: 1–62.
- , 1959.—Cenozoic echinoids of eastern United States. *U.S. geol. Surv. prof. Pap.*, 321: 1–106.
- DAMES, W., 1877.—Die Echiniden der vincentinischen und beronesischen Tertiaerabteilungen. *Paläontograph.*, 25: 1–100.
- DUNCAN, P. M., 1877.—On the Echinodermata of the Australian (Tertiary) deposits. *Quart. J. geol. Soc. Lond.*, 33: 42–71.
- , 1888.—A revision of the Echinoidea from the Australian Tertiaries. *Ibid.*, 43: 411–430.
- FELL, H. B., 1949.—An echinoid from the Tertiary (Janjukian) of South Australia, *Brochopleurus australiae* sp. nov. *Mem. nat. Mus. Vict.*, 16: 17–19, fig. 1.
- , 1953.—The origins and migrations of the Australasian echinoderm faunas since the Mesozoic. *Trans. roy. Soc. N.Z.*, 81: 245–255.
- , 1964.—New genera of Tertiary echinoids from Victoria, Australia. *Mem. nat. Mus. Vict.*, 26: 211–215.
- GORDON, Isabella, 1929.—Skeletal development in *Abracia*, *Echinarachnius* and *Leptasterias*. *Phil. Trans. roy. Soc. Lond., Ser. B.*, 215: 255–313.
- LAUBE, G. C., 1869.—Über einige fossile Echiniden von den Murray Cliffs in Süd-Australien. *Sitz. k. Akad. Wissen. Wien. (Math. Natur. Cl.)*, 59: 183–198.
- MORTENSEN, Th., 1943.—“A monograph of the Echinoidea” III (2), Camarodonta I. 533 pp. (C. A. Reitzel, Copenhagen).
- PHILIP, G. M., 1966.—The Tertiary echinoids of south-eastern Australia. Part IV—Camarodonta (2). *Proc. roy. Soc. Vict.* (in preparation).
- PRITCHARD, G. B., 1891.—Catalogue of Australian Older Tertiary Mollusca and Pliocene species in South Australian School of Mines Museum. *Ann. Rept. S.A. School of Mines and Industries*, 176–206.

CHROMOSOME NUMBERS IN *LAMPROTHAMNIUM*¹

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Synopsis

A comparison is made of the chromosome numbers of four species of *Lamprothamnium*, *L. papulosum*, *L. succinctum*, *L. macropogon* and *Lamprothamnium* sp., all polyploid, with the range of polyploid numbers in the related genus *Chara*. The possible use of chromosome number in the clarification of relationships and geographical distribution in *Lamprothamnium* is discussed.

Lamprothamnium J. Groves (1916) is a small genus of the family Characeae distributed in the Eastern Hemisphere from Europe through Africa and southern Asia to the Australasian region. It occurs in brackish water, usually quite close to the sea. Despite a widespread distribution and abundant records, the genus remains obscure in its relationships, and the limits of some species are uncertain (Ophel, 1947; Wood and Imahori, 1965). As stated by Wood (Wood and Imahori, 1965):

The status of genus *Lamprothamnium* is not clear. The species form a natural group and as such are accepted as a genus. On the other hand, *Lamp. succinctum* exhibits certain *Chara*-like features, especially the occurrence of oogonia above the antheridia, and the bract-cells and stipulodes are not huge as is so common in many forms of *Lamprothamnium*. It seems that this series of species is more similar to *Chara* subgen. *Charopsis* than subgen. *Charopsis* is to subgenus *Chara*. *Lamprothamnium* could well be construed to be a third subgenus of genus *Chara*, and be considered as derived recently from subgen. *Charopsis*.

Broadly based systematic studies are required for an evaluation of the position of *Lamprothamnium* in the Characeae. In the present paper, reports of cytological investigations (Hotchkiss, 1963, 1965) are continued with collections of *Lamprothamnium* from Europe and Australia. *Lamprothamnium papulosum* (Wallr.) J. Groves was collected in Denmark on September 5, 1965 and kindly sent by T. Christensen. Specimens of *Lamprothamnium* from the extensive

TABLE 1
Chromosome Numbers Reported in the Genus Lamprothamnium

Species with conjoined gametangia

<i>Lamprothamnium papulosum</i> (Wallr.) J. Gr.	ca. 50	Europe (Lindenbein, 1927)
<i>Lamprothamnium papulosum</i> (Wallr.) J. Gr.	56	Denmark (present report)
<i>Lamprothamnium</i> sp.	28	Western Australia (Hotchkiss, 1963, as <i>L. macropogon</i>)

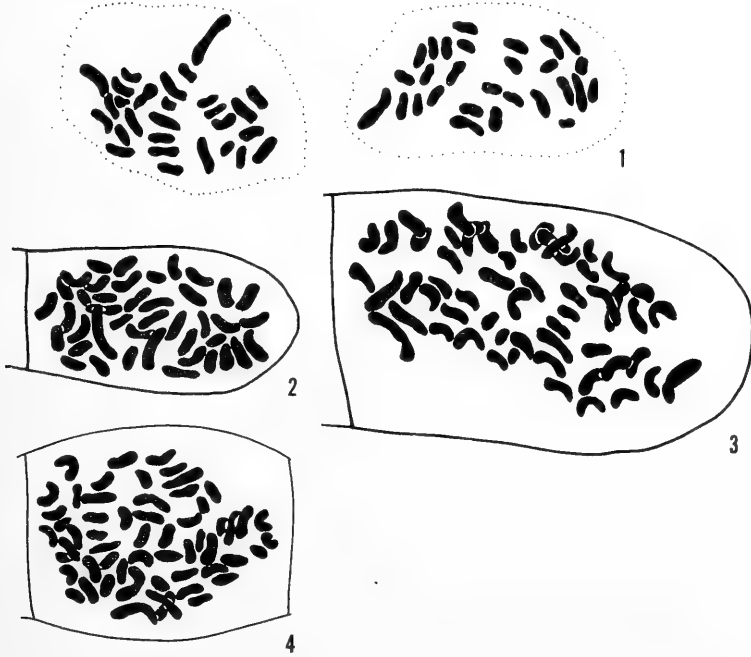
Species with disjunct gametangia

<i>Lamprothamnium succinctum</i> (A. Br. in Asch.) Wood	42	New Caledonia (Hotchkiss, 1965)
<i>Lamprothamnium macropogon</i> (A. Br.) Ophel	56	South Australia (present report)

cytological collections of charophyte materials gathered by R. D. Wood in the Australasian region and described in preliminary reports by Wood (1962*b*) and Hotchkiss (1965), are as follows: WESTERN AUSTRALIA: *Lamprothamnium* sp., Yadgers Brook, 12 miles S of Moora, forming large clump at rock rapids.

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R. D. Wood 60-10-1-5, October 1, 1960; SOUTH AUSTRALIA: *Lamprothamnium macropogon* (A. Br.) Ophel, in one ft. of water, on pipe clay, forming dense carpet under *Ruppia* (?), lagoon near shack, ca. one mi. E of Chinamans Well, 13 mi. SE of Salt Cr., Coorong region. R. D. Wood and C. von der Borsch 60-9-22-1, September 22, 1960. Chromosome number was determined in mitoses in antheridial filaments stained with orcein after fixation in acetic alcohol.



Figs 1-4.

Chromosome complements in *Lamprothamnium* present the appearance of numerous small to medium size chromosomes with about one larger chromosome in every 14 (Figs 1-4). The two new chromosome number determinations in the present report, together with those from the literature, are summarized in Table 1, an enumeration which shows the strongly polyploid nature of the taxa thus far investigated in this genus.

DISCUSSION

The base chromosome number in the Tribe *Chareae* of the Characeae appears to be 14. The new determinations reported here are in accord with this pattern and extend the known chromosome numbers in *Lamprothamnium* to the $n=56$ level. The euploid series of 14, 28, 42 and 56 chromosomes, well known in the large genus *Chara*, is repeated in the 28, 42, and 56 series found thus far in species of the much smaller genus *Lamprothamnium*. It is interesting that the estimate of $n=ca. 50$ for *L. papulosum*, in an early report by Lindenbein (1927) under the name *Lamprothamnus alopecuroides*, has proved to be correct, inasmuch as no number as large as 50 had been proposed for any charophyte up to that time. In Europe several forms of *Lamprothamnium papulosum* (cf. Wood and Imahori, 1965) remain unstudied cytologically. Knowledge of their chromosome number would help clarify their interrelationships.

The combination *Lamprothamnium macropogon* (Braun) Ophel is used here for the plant from South Australia (Wood, 60-9-22-1), with disjunct gametangia and 56 chromosomes. Wood (Wood, 1962a; Wood and Imahori, 1965) designates this taxon as f. *macropogon* (A. Br.) Wood of var. *papulosum* of the 'polymorphic species' *Lamprothamnium papulosum*. The value of disjunct

gametangia as a taxonomic character has been questioned by Wood, but not disproved. The common chromosome number may seem to favour Wood's treatment, but morphological distinctions in the stipulodes and especially in the disjunct (sejunct) gametangia tend to delimit *L. macropogon* as a separate species. On the other hand, the monoecious *Lamprothamnium* with conjoined gametangia (Wood, 60-10-1-5) from Western Australia, previously reported as *Lamprothamnium macropogon* (Hotchkiss, 1963), is designated here simply as *Lamprothamnium* sp. The conjoined gametangia preclude referring this form to *L. macropogon*, while the difference in chromosome number (28 vs. 56) and wide geographical separation are cause for hesitation in assigning it to *L. papulosum* in the absence of abundant study material.

From the data available thus far, the entirely ecorticate, haplostephanous genus *Lamprothamnium* in its cytology appears to be quite far removed from the morphologically similar section of the genus *Chara*, the *Haplostephanae ecorticatae*. It may be noted that the high level of polyploidy in *Lamprothamnium* contrasts sharply with that in *Chara*, *Haplostephanae ecorticatae*, which is almost uniformly at the 14 chromosome level. An exception to this generalization is the monoecious species, *Chara corallina*, reported as $n=42$ by Sarma and Khan (1965). *Chara corallina*, however, appears to be a special case in the *Haplostephanae ecorticatae*, and to bear little relation to the polyploid series in *Lamprothamnium* which begins at the 28 chromosome level. Another distinction may be seen in the lower (14, rarely 28) polyploid levels found in species with disjunct gametangia (and also in dioecious species) throughout the genus *Chara* which contrasts with the higher polyploid levels of the gametangially disjunct species of *Lamprothamnium*.

Cytological data can be correlated with other factors in a preliminary evaluation of the geographical distribution of *Lamprothamnium*. The wide range of chromosome number found in the Australasian region exceeds that reported from elsewhere in the world and includes the lowest number now known in the genus. *Lamprothamnium macropogon* is Australian, *L. succinctum* extends along a well known arc of plant distribution ranging from Australasia through the Indian Ocean to Africa. These considerations, together with a considerable range of morphological variation in the Australasian region, suggest the hypothesis that this area is a centre of distribution for the genus.

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References

- GROVES, J., 1916.—On the name *Lamprothamnus* Braun. *Jour. Bot.*, 54: 336-337.
- HOTCHKISS, A. T., 1963.—A first report of chromosome number in the genus *Lychnothamnus* (Rupr.) Leonh. and comparisons with the other charophyte genera. *PROC. LINN. SOC. N.S.W.*, 88: 368-372.
- , 1965.—Chromosome numbers in Characeae from the South Pacific. *Pacific Sci.*, 19: 31-37.
- LINDENBEIN, W., 1927.—Beitrag zur Cytologie der Charales. *Planta*, 4: 436-466.
- OPHEL, I. L., 1947.—Notes on the genera *Lychnothamnus* and *Lamprothamnium* (Characeae). *Trans. roy. Soc. South Australia*, 71: 318-323.
- SARMA, Y. S. R. K., and KHAN, M., 1965.—Chromosome numbers in some Indian species of *Chara*. *Phycologia*, 4: 173-176.
- WOOD, R. D., 1962a.—New combinations and taxa in the revision of Characeae. *Taxon*, 11: 7-25.
- , 1962b.—Preliminary report on Characeae of Australia and the South Pacific. *Bull. Torrey Bot. Club*, 89: 250-253.
- , and IMAHORI, K., 1965.—A Revision of the Characeae, First Part. Monograph of the Characeae: 1-904. *J. Cramer, Weinheim*.

MOSQUITOES OF TASMANIA AND BASS STRAIT ISLANDS

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(Plates iv-v)

[Read 29 June, 1966]

Synopsis

Twenty-nine species have been recorded from Tasmania, twenty-two from Flinders Island, ten from King Island and four from other small islands of Bass Strait. A new species, *Anopheles tasmaniensis*, and the life history of *Culiseta weindorferi* (Edw.) are described.

The Tasmanian mosquito fauna is closely related to that of southern Victoria. All Tasmanian species either occur in Victoria or have close relatives there. The endemic *Culiseta weindorferi* is closely related to *C. otwayensis* Dobr., and *Aedes cunabulanus* Edw. belongs to a group of the subgenus *Ochlerotatus* which is well represented in Victoria.

Two main elements are represented in the Tasmanian fauna: the southern-Bassian and the northern. The Bassian element is represented by eleven species of *Ochlerotatus*, three species of *Culiseta* and one of the *apiculis* complex of *Neoculex*. The Bassian element may have originated in the tropics and subsequently spread to the northern and the southern temperate regions, being progressively displaced further from the tropics by later evolving groups. The northern element is represented in Tasmania by fourteen species. Species well adapted to cool conditions are widespread but others are confined to the warmer coastal areas or to warmer habitats.

The majority of Tasmanian species are forest mosquitoes and since these have only a restricted ability to disperse across open spaces, it seems that Tasmania received most of the mosquito fauna before separation from the mainland. However, the species which breed in the coastal regions or in the open country may have dispersed to Tasmania, after separation, by the chain of the Bass Strait islands.

The distribution of the two forms of *Ae. andersoni* Edw. suggests that the Grampians form dispersed from the mainland into Tasmania where the typical form evolved and subsequently migrated to the mainland.

The main differences of the Flinders Island fauna from that of Tasmania are (1) the absence from Flinders Island of the two endemic Tasmanian species and also those species which are restricted to special habitats not available on Flinders Island, and (2) the presence of two northern species, *Ae. macmillani* Marks and *M. linealis* Skuse which do not occur in Tasmania, and of two species which are restricted to the coastal regions and the islands with a mild climate (*Ae. clelandi* Taylor and *Ae. stricklandi* Edw.).

The small fauna of King Island reflects the lack of variety of habitats.

INTRODUCTION

Erichson described the first mosquito from Tasmania, *Aedes australis*, in 1842. The description was based on two males and one female sent to him from Van Diemen's Land by A. Schayer. This was followed by Macquart's description of *Aedes nigritorax* in 1847 and *Aedes rubritorax* in 1850. Walker described *Anopheles annulipes* and *Aedes crucians* in 1856, but the latter is conspecific with *Aedes australis* Erichson.

In 1911 Strickland described six species which he found in collections sent to F. V. Theobald by T. L. Bancroft. However, four of these had been already described and only *Tripteroides tasmaniensis* and *Aedes andersoni* (*tasmaniensis* Strickland) were new species. Taylor described *Culiseta littleri* in 1914 and Edwards a further four species in 1926: *Culiseta weindorferi*, *Aedes cunabulanus*, *Aedes luteifemur* and *Aedes purpuriventris*.

Thus during the period 1842-1926 fourteen species were described or recorded from Tasmania. There were no new records until 1948 when D. Lee recorded two more species.

Since 1951 collections from Tasmania and Bass Strait Islands have been made by officers of the Wildlife Survey Section of C.S.I.R.O. (J. H. Calaby, A. L. Dyce, D. L. McIntosh, M. D. Murray and F. N. Ratcliffe) and other entomologists (E. N. Marks, I. Rowley, T. E. Woodward and E. G. Connah). These collections added four species and two subspecies to the Tasmanian fauna (Dobrotworsky, 1953, 1954, 1957 and 1960). By 1960 a total of twenty species and two subspecies had been recorded from Tasmania, four from Flinders Island and two from King Island.

This contribution also incorporated the results of collecting trips by the author to Tasmania (October–November 1961, November–December 1962 and October 1963), to Flinders Island (November 1962 and February 1963) and King Island (November 1963). During these studies 255 breeding places were investigated and larvae collected; almost 2500 adults were collected or reared. In addition to this material I was able to study mosquitoes collected in Tasmania by Dr. M. Littlejohn, and on Bass Strait Islands by Dr. J. A. Thomson, Messrs. S. Murray-Smith and E. Zoski.

The island of Tasmania is largely covered with hills and mountains which are particularly rugged in the western part. Forests cover 47% of the island. The temperate marine climate with rainfall throughout the year creates excellent conditions for the breeding of forest mosquitoes. However, the eastern parts of the island are drier with an average yearly rainfall of below 40 inches, and most of the rain water pools usually become dry during November. The western region of the island has an annual rainfall ranging from 50 to 150 inches, and rain water pools do not dry out throughout the year and provide all year round breeding sites for mosquitoes. However, at higher altitudes the development of larvae would cease during winter where snow may lie for some months.

The low-lying areas are restricted and mostly confined to the north and north-east; they are covered with sclerophyll forest, heath, marshes or tea-tree swamps. Open swamps are rare. Here again in shaded swamps the forest mosquitoes prevail.

A description of the physical features, climate and vegetation is given in Atlas of Tasmania 1965.

The breeding sites of mosquitoes on Flinders Island are less variable than in Tasmania because the mountains are not high and the island does not experience the cold winter conditions such as exist in Tasmania. Frosts are rare and no snow falls occur even on the highest mountains (the highest Strzelecki Peaks are 2,550 feet). The rainfall does not exceed 35 inches per annum, approximately as high as in the eastern part of Tasmania.

The extensive plains with shallow lagoons and swamps provide more habitats for mosquitoes breeding in plain country than in Tasmania.

The major features of King Island are the plateau country, the plains, the swamps and lagoons, and dune formations. The highest hills reach only 600 feet. The island provides a very limited variety of habitats for mosquitoes, and only ten species are recorded there as against twenty-two for Flinders Island.

A full description of Flinders Island is given by Dimmock (1957) and by Guiler *et al.* (1958), and of King Island by Stephens and Hosking (1932) and by Jennings (1959). There is a brief review, of both islands, by Littlejohn and Martin (1965).

DISTRIBUTION AND COMPOSITION OF THE MOSQUITO FAUNA

Five genera of mosquitoes are represented in Tasmania: (1) *Anopheles*—four species, (2) *Tripteroides*—two species, (3) *Aedes*—seventeen species, (4) *Culiseta*—three species and (5) *Culex*—three species (Table 3). The genus *Mansonia* is not recorded from Tasmania but is represented by one species on Flinders Island. Their distribution and abundance are determined by various

environmental factors but particularly by the availability of suitable breeding sites. As would be expected, species which breed in open swamps e.g. *Culex globocoxitus*, *C.p. australicus* and *An. annulipes* are not numerous in Tasmania; they are restricted to low land areas. In contrast to these, species which are associated with forests are numerous and widely distributed. However, forest mosquito species with special requirements are not evenly distributed: *Ae. nigrithorax* and *Ae. silvestris* breed in temporary ground pools in sparse sclerophyll forest; *Tripteroides* and *Ae. notoscriptus* are tree hole breeders.

TABLE 1
Distribution according to habitat of larvae in Tasmania

Species	Number of breeding sites						
	Total	Ground pools		Swamps		Rock pools	Discarded tyres and tins
		More or less exposed to sun	Completely shaded	Grassy	Tea tree		
<i>An. stigmaticus</i>	1		1				
<i>An. annulipes</i>	2		1		1		
<i>An. tasmaniensis</i>	2				2		
<i>T. tasmaniensis</i>	2						2
<i>Ae. (O.) nigrithorax</i>	4	3	1				
<i>Ae. (O.) flavifrons</i>	4		3		1		
<i>Ae. (O.) calcariae</i>	1		1				
<i>Ae. (O.) purpuriventris</i>	3	1	2				
<i>Ae. (O.) luteifemur</i>	17	7	6	2	2		
<i>Ae. (O.) silvestris</i>	6	4	2				
<i>Ae. (O.) nivalis</i>	11	5	5	1			
<i>Ae. (O.) cunabulanus</i>	35	15	17	3			
<i>Ae. (O.) andersoni</i>	37	18	15	2	2		
<i>Ae. (O.) continentalis</i>	5		3		2		
<i>Ae. (F.) alboannulatus</i>	9	7	2				
<i>Ae. (F.) rubrithorax</i>	47	13	31		1	1	1
<i>Ae. (F.) rupestris</i>	4	2				2	
<i>Ae. (P.) postspiraculosus</i>	2		2				
<i>Ae. (H.) australis</i>	1					1	
<i>C. inconspicua</i>	31	6	20	1	4		
<i>C. weindorferi</i>	2		2				
<i>C. fergusonii</i>	26	7	15		4		
<i>C. globocoxitus</i>	2			2			
<i>C. p. australicus</i>	1			1			
	255	88	129	12	19	4	3

Species with a greater capacity for adaptation to cold conditions are able to penetrate to higher altitudes where they breed in moorland and sedgeland country; their larvae are mostly confined there to shallow pools exposed to the sun. These high-altitude species are *Ae. nivalis*, *Ae. cunabulanus* and *Ae. andersoni* (Table 2).

However, for many species which breed in cool ground water, the range of breeding sites is greater than in Victoria. Thus, species such as *C. fergusonii*, *Ae. rubrithorax* and *C. inconspicua* are not restricted to completely shaded pools; because of the lower temperatures prevailing during spring and early summer in Tasmania they are also able to breed freely in pools more or less exposed to the sun (Table 1).

TABLE 2
Distribution of mosquitoes according to altitudes

Localities	Altitude in feet	<i>Aedes</i>														
		<i>cunabulamus</i>	<i>andersoni</i>	<i>continentalis</i>	<i>nealis</i>	<i>siloestris</i>	<i>luteifemur</i>	<i>camporhynchus</i>	<i>purpuriventris</i>	<i>flavifrons</i>	<i>nigrithorax</i>	<i>rubrithorax</i>	<i>alboannulatus</i>	<i>Culiseta inconspicua</i>	<i>Culex fergusoni</i>	<i>Anopheles tasmaniensis</i>
Bridport 10	+	+	+	-	-	+	-	+	+	-	+	-	+	+	-
Sassafras 50	-	+	-	-	-	+	-	-	+	-	+	+	+	+	-
Birralee 50	-	+	-	-	-	+	-	-	+	-	+	+	+	+	+
Lake Leake 2·300	+	+	-	+	+	-	+	-	-	+	+	+	-	-	-
Storey's Creek 3·000	+	+	-	-	-	-	-	+	-	-	+	-	+	-	-
Breona 3·400	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-

TABLE 3
Distribution of mosquitoes in southern Victoria, Tasmania and Bass Strait Islands

Species	Victoria			Bass Strait Islands			
	East Gippsland	Eastern Highlands and West Gippsland	Otway-Portland area	Erith, Deal, Great Dog	King	Flinders	Tasmania
ANOPHELINAE							
<i>Anopheles</i>							
<i>stigmaticus</i>	+	+	+	-	-	+	+
<i>pseudostigmaticus</i>	-	+	-	-	-	-	-
<i>atrripes</i>	+	+	+	-	+	+	+
<i>tasmaniensis</i>	+	-	+	-	-	+	+
<i>annulipes</i>	+	+	+	-	-	+	+
CULICINAE							
<i>Tripteroides</i>							
<i>atrripes</i> (Southern form)	-	+	+	-	-	-	+
<i>tasmaniensis</i>	+	+	+	-	-	+	+
<i>marksi</i>	+	-	-	-	-	-	-
<i>Mansonia</i>							
<i>linealis</i>	+	+	+	-	-	+	-
<i>aurata</i>	+	-	-	-	-	-	-
<i>variegata</i>	+	-	-	-	-	-	-
<i>Aedeomyia</i>							
<i>venustipes</i>	+	+	-	-	-	-	-
<i>Aedes</i>							
<i>procax</i>	+	-	-	-	-	-	-
<i>theobaldi</i>	+	-	-	-	-	-	-
<i>nigrithorax</i>	+	+	+	-	-	+	+
<i>imperfectus</i>	+	+	-	-	-	+	-
<i>flavifrons</i>	+	+	+	-	+	+	+
<i>calcariae</i>	+	+	+	-	-	-	+

TABLE 3—continued

Distribution of mosquitoes in southern Victoria, Tasmania and Bass Strait Islands

Species	Victoria			Bass Strait Islands			Tasmania	
	East Gippsland	Eastern Highlands and West Gippsland	Otway-Portland area	Erith, Deal, Great Dog	King	Flinders		
<i>purpuriventris</i>	..	—	+	—	—	—	+	
<i>clelandi</i>	..	—	+	—	—	+	—	
<i>perkinsi</i>	..	+	—	—	—	—	—	
<i>luteifemur</i>	..	+	+	—	+	+	+	
<i>silvestris</i>	..	+	+	—	—	—	+	
<i>nivalis</i>	..	—	+	—	—	—	+	
<i>camptorhynchus</i>	..	+	+	—	+	+	+	
<i>cunabulanus</i>	..	—	—	—	—	—	+	
<i>andersoni</i>	..	—	+	+	+	+	+	
<i>continentalis</i>	..	+	+	—	—	+	+	
<i>stricklandi</i>	..	—	—	+	+	+	—	
<i>dobrotworskyi</i>	..	+	+	+	—	—	—	
<i>notoscriptus</i>	..	+	+	—	—	+	+	
<i>alboannulatus</i>	..	+	+	+	+	+	+	
<i>rubrithorax</i>	..	+	+	+	—	+	+	
<i>rupestris</i>	..	+	+	+	—	—	+	
<i>tubbutiensis</i>	..	+	—	—	—	—	—	
<i>subbasalis</i>	..	+	—	—	—	—	—	
<i>milsoni</i>	..	+	—	—	—	—	—	
<i>subauridorsum</i>	..	+	+	—	—	—	—	
<i>macmillani</i>	..	+	+	—	—	+	—	
<i>multiplex</i>	..	+	—	—	—	—	—	
<i>postspiraculosus</i>	..	+	+	+	—	—	+	
<i>australis</i>	..	+	+	+	—	+	+	
<i>Culiseta</i>								
<i>victoriensis</i>	..	—	+	—	—	—	—	
<i>drummondii</i>	..	—	+	—	—	—	—	
<i>sylvanensis</i>	..	—	+	—	—	—	—	
<i>hilli</i>	..	+	+	—	—	—	—	
<i>frenchii</i>	..	+	+	—	—	—	—	
<i>otwayensis</i>	..	—	—	+	—	—	—	
<i>inconspicua</i>	..	+	+	+	+	+	+	
<i>weindorferi</i>	..	—	—	—	—	—	+	
<i>littleri</i>	..	—	+	+	—	—	+	
<i>antipodea</i>	..	+	+	—	—	—	—	
<i>Culex</i>								
<i>fergusoni</i>	..	+	+	+	—	+	+	
<i>douglasi</i>	..	+	+	—	—	—	—	
<i>postspiraculosus</i>	..	+	+	—	—	—	—	
<i>pseudomelanoconia</i>	..	+	—	—	—	—	—	
<i>orbostiensis</i>	..	+	+	—	—	—	—	
<i>annulirostris</i>	..	+	—	—	—	—	—	
<i>globocoxitus</i>	..	+	+	+	—	+	+	
<i>pipiens australicus</i>	..	+	+	+	—	+	+	
<i>pipiens molestus</i>	..	+	+	+	—	—	+	
		47	43	31	4	10	22	30

Although most species are well adapted to cool climatic conditions and non-seasonal rainfall, some are distributed in areas with a warmer climate or are confined to habitats with a warmer microclimate e.g. exposed rock pools.

A comparison of the fauna of Tasmania and Bass Strait Islands with that of southern Victoria shows that all Tasmanian species either occur in Victoria or have a close relationship to Victorian species (Table 3). A striking fact emerging from Table 3 is that the mosquito fauna of Tasmania is almost identical with that of the Otway-Portland area of Victoria.

In Tasmania, as in Victoria, the mosquito fauna comprises two major elements, (1) the more ancient southern or Bassian element consisting of the genus *Culiseta*, one group of the subgenus *Ochlerotatus* and the subgenus *Neoculex* (*apicalis* complex) and (2) the northern which is a part of the Indo-Malayan element. This element, which includes a great assemblage of relatively recent successful insects, is represented by *Anopheles*, *Tripteroides*, *Mansonia*, *Culex* and subgenera *Finlaya* and *Pseudoscusea*, and on Flinders Island *Chaetocruomyia*, of the genus *Aedes*.

Previously (Dobrotworsky, 1965) the concept of a southern entry via an Antarctic landmass of the Bassian element in the Australian mosquito fauna was rejected. The detailed study of Tasmanian mosquitoes has not led to any modification of the view that this element entered Australia from the north and was progressively displaced away from the tropics by later-evolving elements.

The migration route of mosquitoes in eastern Australia was probably along the coast and ranges, a route which for the migration of plants has been extremely important and of great antiquity (Burbidge, 1960).

The successful southern dispersal of mosquitoes on the mainland has depended on climate tolerance and adaptability. Some species of *Ochlerotatus* e.g. *Ae. procax* (Skuse) have penetrated just across the Victorian border into East Gippsland, *Ae. perkinsi* Marks has dispersed throughout East Gippsland, while *Ae. imperfectus* Dobr. has penetrated into the Western Highlands as far as Beaufort.

Such pattern of migration can also be observed among mosquitoes of the northern or Indo-Malayan element.

Dispersal to Tasmania raises other problems. Tasmania was joined to Australia, and Port Phillip Bay and Bass Strait were formerly portions of a continuous land surface (Keble, 1946). A land connection between Australia and Tasmania remained until late Tertiary times; Tillyard (1926) believes that the land connection was broken and joined several times. This land bridge has been regarded as the main route for the migration of flora and fauna

Paramonow (1959), however, has questioned the importance of this land bridge. "The ability of an insect to fly or to be carried by wind for very long distances, the presence of a group of islands between Tasmania and Australia forming a bridge between them, are factors nullifying the presence of the strait between Tasmania and Australia." It seems to me that this cannot be applied to all winged insects in spite of many reports of the ability for long distance flights of many of them and the importance of wind in their dispersal. For example, in Canada the adults of tent caterpillar moth (*Malacosma disstriata* Hübner) were carried by the turbulent air associated with cold front for a distance of at least 300 miles in 12 hours (Brown, 1965). Trapping of airborne insects from ships and airplanes has yielded large numbers of insects (Glick, 1939; Gressitt *et al.*, 1960, 1961; Yashimoto and Gressitt, 1960, 1961; Harrell and Yashimoto, 1963; Madison, 1964). The mosquitoes were collected only on few occasions, but there are reports of their being taken at altitudes up to 5,000 feet, and at sea as far as 110 kilometres from nearest land.

It should be kept in mind that the occurrence of active or passive dispersal of insects depends largely on their behaviour and ecology. Insects living in open country or in the upper strata of the forest may be easily carried by winds or may be able to fly long distances. Insects of this type include the southern Victorian mosquitoes: *Ae. camptorhynchus*, *Ae. australis*, *Ae. notoscriptus*, *Ae. macmillani*, *Tripteroides*, *An. annulipes*, *C. globocoxitus* and *C.p. australicus*. These species are potentially able to cross Bass Strait particularly by "jumping" from island to island. The ability of some of these species to breed in salt or brackish water is a further favourable factor helping dispersal across sea barriers. However, the majority of Tasmanian and southern Victorian mosquitoes are ecologically confined to forests and even during swarming they do not fly in

the upper strata. Such mosquitoes usually do not fly out of the forests where they have their breeding sites and are not exposed to strong winds which could carry them for long distances and across water gaps. The unfavourable ecological conditions associated with open and dry land constitute another barrier to the dispersal of many forest mosquitoes. Several common species

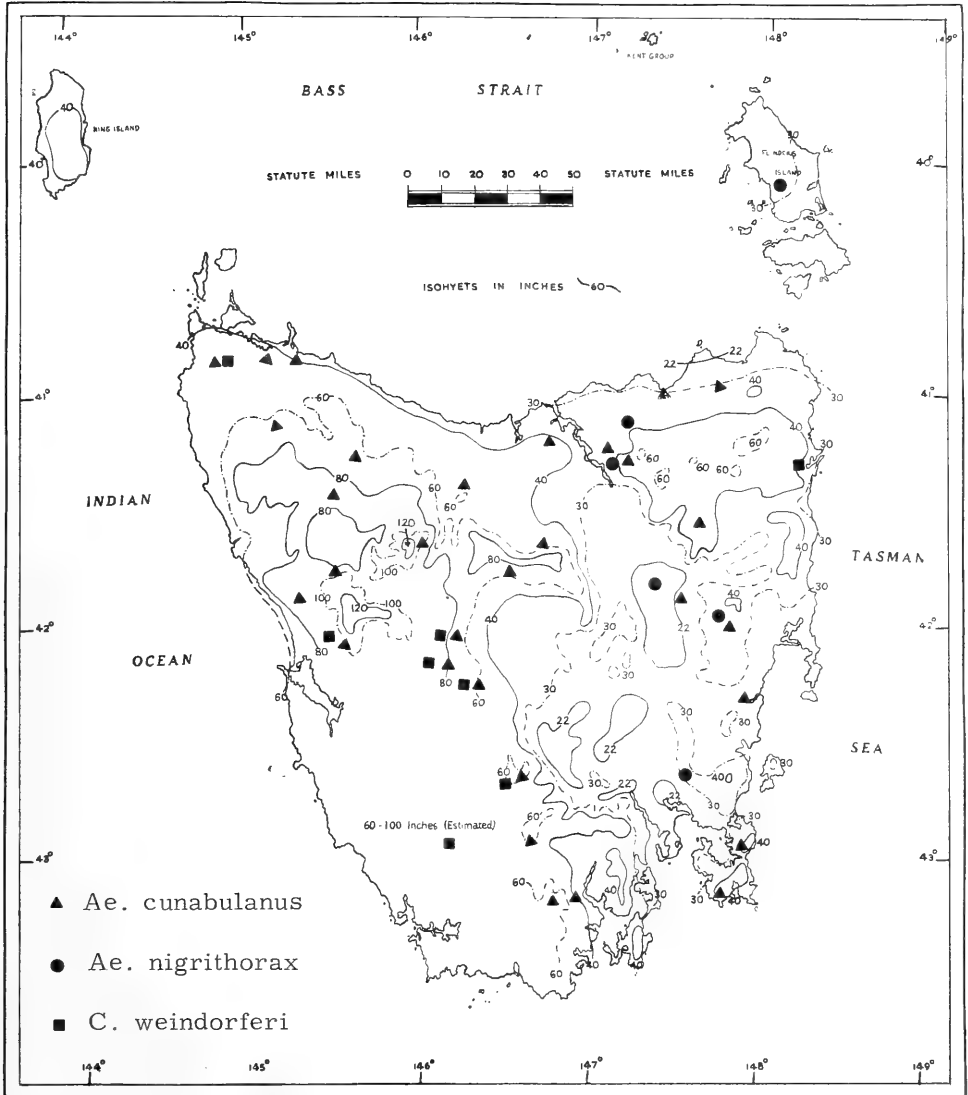


Fig. 1. Distribution of some species of mosquitoes in Tasmania and Bass Strait Islands.

of *Culiseta* widely distributed in the Eastern Highlands of Victoria have not dispersed across the intervening plain into the ecologically favourable Grampians and Otway Ranges.

Quite short stretches of ocean have apparently prevented the dispersal of the common Tasmanian species *Ae. cunabulanus* through the chain of islands to the ecologically suitable Flinders Island, itself only some 35 miles off the Tasmanian coast (Fig. 1). *Ae. cunabulanus* presumably evolved in Tasmania

before the Pleistocene but did not cross the land bridge which joined Tasmania to the mainland during the glacial period. It is difficult to imagine the cause of this failure but it is possible that this species evolved in remote or secluded parts of Tasmania and did not disperse until the disappearance of the land bridge.

While Bass Strait would seem to constitute an impassable barrier to the spread of some mosquitoes, the distribution of others seems to confirm Paramonov's (1959) claim that the main obstacles to the spread of some Victorian insects to Tasmania are climatic and ecological. This may be the explanation of the absence from Tasmania of Victorian species such as *Ae. dobrotworskyi* Marks which occurs in southern Victoria from Genoa to Apollo Bay, and *M. linealis* and *Ae. macmillani* which have reached Flinders Island but are apparently absent from Tasmania. The absence of *C. weindorferi* from the Bass Strait Islands may also be due to climatic factors (Fig. 2).

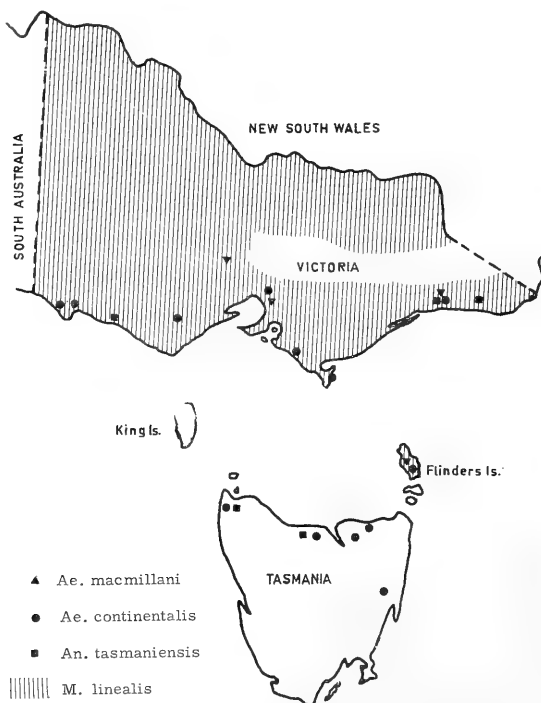


Fig. 2. Distribution of some species of mosquitoes in Victoria, Bass Strait Islands and Tasmania.

It seems therefore that the main migration route was from Victoria to Tasmania. The distribution of *Ae. andersoni* suggests however, that the migration of this species has occurred in both directions. The Grampians form of *Ae. andersoni* is common in the Grampians and is recorded also from a few localities along the Dividing Range to Kiandra in New South Wales. It is likely that this form migrated to Tasmania where the typical form evolved. In Tasmania this form is highly adapted to cold conditions and often breeds at high altitudes (3,000–3,500 feet). On the mainland its distribution is coastal.

The most important differences between the mosquito fauna of Tasmania and the Bass Strait Islands and that of southern Victoria are: (1) absence from Tasmania of the group of northern species which in Victoria are almost entirely confined to East Gippsland. (2) The absence from Tasmania of *Culiseta* species breeding in subterranean waters in tunnels of land crayfishes. These species are common throughout Gippsland. (3) The occurrence in Tasmania

of two endemic species: *Culiseta weindorferi* and *Aedes cunabulannus*. (4) Distribution of *Aedes andersoni* in Tasmanian highlands up to 3,500 feet. (5) The mosquito fauna of Bass Strait Islands is impoverished Victorian fauna.

Paramonov (1959) described the Tasmanian insect fauna as impoverished by comparison with that of Victoria and attributed this condition to the elimination of many species during the Pleistocene glaciation. However, it would seem that the impact of glaciation on the Tasmanian flora and fauna has been exaggerated, for Jennings and Banks (1958) assert that "an ice sheet occurred only in the Central Plateau with cirque and walley glaciers elsewhere". There is no doubt that certain endemic genera of plants became extinct during the most severe phase of glaciation (Burbidge, 1960) and it is possible that some endemic species of mosquitoes suffered the same fate. However, there is no evidence that the Tasmanian mosquito fauna was ever substantially richer than at the present time.

TAXONOMIC ACCOUNT

Family CULICIDAE

Key to genera

Adults

1. Scutellum trilobed, each lobe bearing bristles. Palps in female much shorter than proboscis 2
 Scutellum evenly rounded with marginal setae along it. Palps of females as long as proboscis *Anopheles*
2. (1) Pulvilli present *Culex*
 Pulvilli absent 3
3. (2) Spiracular bristles absent 4
 Spiracular bristles present 5
4. (3) Postspiracular bristles present *Aedes*
 Postspiracular bristles absent *Mansonia*
5. (3) Uniformly brown; base of subcostal vein hairy beneath *Culiseta*
 Black with patches of broad white scales on thorax and abdomen; base of subcostal vein bare beneath *Tripteroides*

Larval (fourth stage)

1. VIIIth abdominal segment without respiratory siphon *Anopheles*
 VIIIth abdominal segment with elongate respiratory siphon 2
2. (1) Distal half of siphon modified for piercing roots of aquatic plants *Mansonia*
 Siphon not modified, normal in shape 3
3. (2) Anal segment with ventral brush (seta 4) reduced to one pair of setae *Tripteroides*
 Anal segment with ventral brush of several tufts 4
4. (3) Siphon with pair of basal setae *Culiseta* (in part)
 Siphon without basal setae 5
5. (4) Siphon with several pairs of ventral tufts *Culex*
 Siphon with a pair of median tufts or setae 6
6. (5) Some of setae plumose; anal segment usually not completely ringed by saddle *Aedes*
 All setae non-plumose; anal segment completely ringed by saddle .. *Culiseta* (in part)

Subfamily ANOPHELINAE

Genus ANOPHELES Meigen

Key to Tasmanian species of the genus ANOPHELES

Adults

1. Wings and legs profusely marked with white scales *annulipes*
 Legs dark scaled 2
2. Wings with some silvery or pale sections of veins. Hind femur entirely dark scaled 3
 Wings entirely dark scaled. Basal four-fifths of hind femur creamy scaled *stigmaticus*
3. Fringe of wings with distinct white section at tip *atratipes*
 Fringe of wings entirely dark *tasmaniensis*

Subgenus ANOPHELES Meigen

ANOPHELES (ANOPHELES) STIGMATICUS Skuse

Anopheles stigmaticus Skuse, 1889, PROC. LINN. SOC. N.S.W., 3: 1758.

This is a small brown species. The basal four-fifths of the hind femora are clothed with creamy scales. It has been recorded from Hobart (Dobrotworsky, 1957). Additional record is: Flinders Island. It also occurs in the mountainous areas of Victoria and New South Wales.

Material examined: 2♂.

ANOPHELES (ANOPHELES) ATRATIPES Skuse

Anopheles atratipes Skuse, 1889, PROC. LINN. SOC. N.S.W., 3: 1755.

This also is a dark brown mosquito. However, the hind legs are entirely dark and the wings have white sections along some veins; the fringe scales at the tip of the wing are white. A single upper sternopleural bristle. The palpi are black and the two basal segments have a rather shaggy appearance (Plate 1).

It is a coastal species not previously recorded from Tasmania or Bass Strait Islands. It has been collected by A. L. Dyce and M. D. Murray at Bridgewater, and by the author at St. Helens and Detention River in Tasmania, and on King and Flinders Islands. It also occurs in all mainland states.

Material examined: 1♂, 14♀.

ANOPHELES (ANOPHELES) TASMANIENSIS n. sp.

Types: The holotype male and three paratype females were bred from larvae collected 29/11/62 at Birralee, Tasmania, and have their associated larval and pupal skins; the allotype and one paratype female were collected at the same locality and date, and eight paratype females were also collected there (27/10/61). The holotype male, allotype female and seven paratype females are in the National Insect Collection, C.S.I.R.O., Canberra. One female paratype is in each of the following collections: National Museum, Melbourne; School of Public Health and Tropical Medicine, Sydney; University of Queensland, Brisbane; British Museum (Natural History), London; U.S. National Museum, Washington.

Distinctive Characters. Adult: A dark species which has pale scales along only some sections of the wing veins. It can be distinguished from *An. atratipes* by the narrower squama scales of the veins, the entirely dark fringe of the wing, the presence of 3-5 upper sternopleural bristles. The two basal segments of the palpi are not shaggy (Plate 1).

Larva: Brown with white dorsal longitudinal stripe on the thorax and abdomen.

Holotype Male. Head: Vertex with pale upright forked scales, becoming black laterally. Frontal tuft white. Tori dark, flagellar segments of antennae pale, but two terminal segments dark; verticillate hairs silver grey. Palps dark scaled; long hairs on segments IV and V, pale. Proboscis black. Thorax: Scutum brown, margins lighter; anterior margin with median and lateral white scale-tufts. Bristles dark. One strong and three weaker upper sternopleural bristles and four lower sternopleural bristles; seven-eight upper mesepimeral bristles. Numerous pale setae in front of wing roots and along lateral edge of scutum. Scutellum light brown with 16 long black setae, and several small pale ones. Legs black, hind femora paler ventrally. Wings: Fringe dark without white section at tip of wings (wing scales partly rubbed, see description of wing venation in allotype female). Knob of haltere brown scaled, with pale stem. Abdomen: Dark brown, almost black, clothed with

numerous pale hairs; scales absent. Terminalia (Fig. 3 *a, b*): Coxite short, blunt, tapering, with long setae and a few scales laterally; inner side of coxite with a long subapical seta curved at its tip. A single stout parabasal spine curved at its tip, arising from an elongate base; ventral lobe of harpago with two short and two longer setae; dorsal lobe with fine broadened setae, four of them in close set row, and one shorter seta arising distally between them and ventral lobe. Style long and slender with minute setae along it; terminal appendage small. Lobes of tergite widely separated, with numerous short setae.

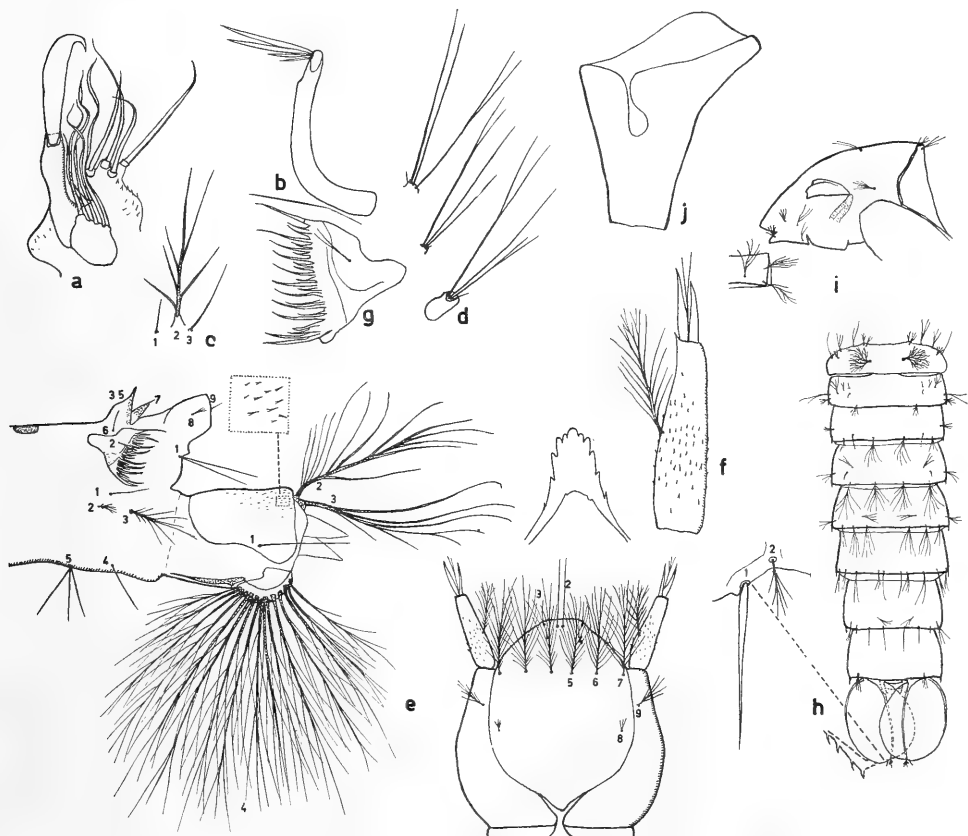


Fig. 3. *Anopheles tasmaniensis* n.sp., *a-b*, adult: *a*, harpago; *b*, phallosome; *c-g*, larva: *c*, prothoracic setae 1-3; *d*, pro-, meso- and metathoracic pleural setae; *e*, head, mentum and terminal segments; *f*, antenna; *g*, pecten; *h-j*, pupa: *h*, abdomen; *i*, cephalothorax and metanotum; *j*, trumpet.

Allotype Female. This differs from the holotype as follows: Tori and first flagellar segment pale, other flagellar segments black. Palps as long as proboscis without labella, black scaled. Scutum dark brown between dorso-central bristles; fossa and lateral area light brown sparsely clothed with small narrow curved pale scales; bristles black, but pale in front of wing roots and along border with pleura. Scutellum with a row of 25 strong black and several smaller pale bristles. 5-6 lower sternopleural bristles; 3 bristles on prealar knob; 10-14 upper mesepimeral bristles. Wings: C, Sc, R₁, R₂, R_s and M₃₊₄, uniformly clothed with dark scales; apical three-quarters of R₃, pale scaled; R₄₊₅ with some pale scales, particularly distally; Cu, pale scaled on basal three-quarters, dark apically; M and An, pale scaled, some black scales basally. Patches of black scales at base of fork R₂ and R₃, and M₁ and M₂, at base R₄₊₅, and M-Cu where it joins Cu.

Paratype Females. The series of 12 paratypes do not show significant variations.

Larva (Fig. 3 *c-g*): Brown with white dorsal longitudinal stripe on thorax and abdomen. Head: setae 2, arising close together, long, stout, single and simple; 3, single, simple; 4, fine, single, simple; 5, 6 and 7 plumose almost equal in length; 8, small, about 4 branched; 9, larger, about 7 branched. Antennae spiculated; seta 1, arising at about mid-length, about three-quarters as long as antenna, plumose. Thorax: Prothoracic setae 1 and 3, single, simple; 2, about 6 branched. Metathoracic palmate setae (1) reduced to branched hair. Abdomen: Segments I-VIII with narrow transverse tergal plate. Pecten with about 24 spines. Anal segment: Saddle covered with fine spicules; seta 1, long, single; 2, about 13 branched; 3, about 7 branched; 4 (ventral brush) of 14-16 plumose setae.

Pupa (Fig. 3 *h, i*): Trumpet broad with almost quadrangle opening, with deep incision. Paddle: without fringe; seta 1, single, stout; seta 2, small, fine, 5-6 branched.

Eggs are illustrated in Plate 2.

Biology: The adults were common in a tea-tree swamp near Birralee, northern Tasmania 27/10/61, but no larvae were found at that date. On the second occasion (29/11/62), this swamp was very shallow and dry in places; several larvae and pupae were collected in the deeper parts.

Distribution. Tasmania: Birralee and Redpa. It also occurs in a coastal belt of Victoria.

Material examined: 1♂, 20♀.

Subgenus CELLIA Theobald

ANOPHELES (CELLIA) ANNULIPES Walker*

Anopheles annulipes Walker, 1846, *Ins. Saund. Dipt.*, 1: 433.

Mackerras (1927), Lee and Woodhill (1944) pointed out the variability of this species in Tasmania as well as on the mainland. Specimens with an entirely black proboscis and others with the proboscis pale on the apical half have been collected in Tasmania.

It has been recorded from Launceston and Low Head (Lee, 1948). Additional records: Bridgewater (A. L. Dyce and M. D. Murray). Little Swanport, St. Patrick's River; King and Flinders Islands. It is widely distributed on the mainland of Australia.

Material examined: 4♂, 1♀.

Subfamily CULICINAE

Tribe SABETHINI

Genus TRIPTEROIDES Giles

Subgenus RACHIONOTOMYIA Theobald

Atripes Group

TRIPTEROIDES (RACHIONOTOMYIA) ATRIPES Skuse

Culex atripes Skuse, 1889, *Proc. Linn. Soc. N.S.W.*, 3: 1750.

A small black mosquito without a white pattern on the scutum; the pleura are densely clothed with white scales.

*For synonymy of this and other species, see Dobrotworsky (1965).

This is a first record of this species from Tasmania. All four specimens examined belong to the southern form of *T. atripes* which have small lateral patches on the tergites visible from above only on segments VI and VII. The females have been taken biting at Lisdillon and Ferntree.

T. atripes also occurs in South Australia, Victoria, New South Wales and Queensland.

Material examined: 4♀.

Caledonicus Group

TRIPTEROIDES (RACHIONOTOMYIA) TASMANIENSIS (Strickland)

Stegomyia tasmaniensis Strickland, 1911, *Entom.*, 44: 249.

This can be distinguished from *T. atripes* by having a band of white scales across the pleuron, and by the pale scaling of the terminal segments of the hind legs.

It is distributed mainly in areas with an annual rainfall higher than 30 inches.

This species has been recorded from: Advent Bay, Bridport, Cradle Valley, Devonport, Eaglehawk, Geeveston, Hartz Mt., King River, Launceston, Mole Creek, Mt. Arthur, Mt. Farrel, Mt. Wellington, New River, St. Patrick's River, Springfield (Edwards, 1924, 1926); Ferntree, Low Head (Lee, 1946, 1948); additional records are: Maydena (D. L. Dyce and M. D. Murray); Derwent Bridge, Renison Bell and Flinders Island. It also occurs in Victoria, South Australia and New South Wales.

Material examined: 6♂, 20♀.

Tribe CULICINI

Genus MANSONIA Blanchard

Subgenus COQUILLETIDIA Dyar

MANSONIA (COQUILLETIDIA) LINEALIS (Skuse)

Culex linealis Skuse, 1899, *PROC. LINN. SOC. N.S.W.*, 3: 1747.

Distinguished by the light-golden longitudinal lines on the dark-bronze scaled scutum and by the white scaled venter with median black patches and black apical border on the sternites.

This species has not been found in Tasmania but occurs on Flinders Island (J. H. Calaby and D. L. Dyce, 2/12/51; N. V. Dobrotworsky, 10/2/63). This is the most southern record of *M. linealis* which occurs in South Australia, Victoria, New South Wales and Queensland.

Material examined: 8♀.

Genus AEADES Meigen

Key to species of the genus AEADES

Adults, female

- 1. Tarsal segments with broad white bands 2
- Tarsi dark scaled, without white bands 10
- 2. (1) Wings mottled with white scales *flavifrons*
- Wings dark scaled or with a few slightly paler scales 3
- 3. (2) Wings with a few slightly paler scales form A
- Wings completely dark scaled 4
- 4. (3) Scutum with longitudinal lines and lyre-shaped pattern *notoscriptus*
- Scutum without such pattern 5

5. (4)	Scutum with patches of white scales ; femora with ochreous preapical ring	<i>alboannulatus</i>	6
	No patches of white scales on scutum ; femora without preapical ring		7
6. (5)	Fifth tarsal segment of hind legs black		8
	Fifth tarsal segment more or less white scaled		8
7. (6)	Venter more or less ochreous, usually with scattered black scales	<i>rubrithorax</i>	
	Venter either black with white lateral patches on sternites, or white with apical black band on sternites	<i>rupestris</i>	
8. (6)	Fifth tarsal segment of hind legs all white ; legs unmottled ; proboscis black scaled		9
	Fifth tarsal segment of hind legs dark scaled apically ; legs and proboscis intensively mottled	<i>camptorhynchus</i>	
9. (8)	Vertex with broad scales ; proboscis short ; anterior half of scutum pale scaled	<i>macmillani</i>	
	Vertex with narrow scales ; proboscis of normal length ; scutum in general dark scaled	<i>calcariae</i>	
10. (1)	Wings mottled, scutum dark, contrasting with white scaled pleura	<i>stricklandi</i>	
	Wings with pale scales only along distal part of vein C and usually also R ; tergites unbanded, IV-VII mottled ; venter with some ochreous scales apically	<i>luteifemur</i>	11
	Wings entirely dark scaled		11
11. (10)	Vertex with broad scales	<i>postspiraculosus</i>	12
	Vertex with narrow scales		12
12. (11)	Scutum with broad margin of pale scales contrasting with dark scales medially		13
	Scutal scaling otherwise		14
13. (12)	Tergites unbanded ; hind femora mottled ; usually patch of broad scales in front of wing roots	<i>andersoni</i>	
	Tergites banded ; hind femora pale scaled on basal three-quarters ; no patch of broad scales in front of wing roots	<i>nigrithorax</i>	
14. (12)	All femora unmottled		15
	At least fore and mid femora mottled		17
15. (14)	Cerci long and narrow	<i>australis</i>	16
	Cerci short and broad		16
16. (15)	Tergites unbanded ; venter more or less purplish	<i>purpuriventris</i>	
	Tergites banded, venter ochreous scaled with some black scales	<i>clelandi</i>	
17. (14)	All femora mottled		18
	Hind femora pale on basal half or two-thirds		19
18. (17)	Proboscis black scaled	<i>cunabulanus</i>	
	Proboscis mottled	<i>continentalis</i>	
19. (18)	Scutal scales medially small, dark bronze ; tergites with white basal bands constricted laterally	<i>silvestris</i>	
	Scutal scales rather large, golden ; tergal bands on segments II-VI straight	<i>nivalis</i>	

Larvae (fourth stage)

1.	Head seta 5, single (rarely 2 branchiae on one side)	2
	Head seta 5 with two or more branches	6
2. (1)	Lateral comb teeth in irregular or triangular patch	3
	Lateral comb teeth in a single row	5
3. (2)	Siphon long slender with index 4·7-5·3 ; seta 1, longer than half length of siphon	<i>postspiraculosus</i>
	Siphon short, seta 1, small	4
4. (3)	Lateral comb teeth of distal row larger than those in basal rows ; saddle covering three-quarters of dorsal part of segment ; upper pair of anal papillae about as long as saddle	<i>notoscriptus</i>
	Lateral comb teeth of equal size ; saddle reduced ; anal papillae very small	<i>australis</i>
5. (2)	Pecten with 1-2 detached spines above seta 1 ; lateral comb of 8-14 spines	<i>nigrithorax</i>
	Pecten without detached spines ; lateral comb usually of 4 spines	<i>stricklandi</i>
6. (1)	Head seta 6, single	7
	Head seta 6, multibranchied	9
7. (6)	Scales of lateral comb fringed, with central long spine ; ventral brush without precratal tufts ; anal papillae short, less than half as long as saddle	<i>clelandi</i>
	Scales of lateral comb fringed, without long central spine	8
8. (7)	Lateral comb patch of less than 36 scales ; siphon index less than 3 ; pecten of thick spines with pale tip	<i>calcariae</i>
	Lateral comb patch of 35-53 scales ; siphon index more than 3 ; pecten spines slender, tip black	<i>flavifrons</i>

9. (6) Antennae at least as long as head or longer; scales of lateral comb fringed, without long central spine; spines of pecten with pale tip; anal papillae unequal, shorter than saddle *purpuriventris*
Antennae shorter than head 10
10. (9) Anal papillae small globular; scales of lateral comb coarsely fringed, without central long spine *camptorhynchus*
Anal papillae elongate, pointed 11
- 11.(10) Lateral comb scales finely fringed 12
Lateral comb scales with 1-4 longer central spines, coarsely fringed basally 14
- 12.(11) Head setae 4, 5 and 6, almost in straight line; prothoracic seta 4 single; 5, 2-3 branched *rupestris*
Head setae 4, 5 and 6, forming triangle; prothoracic seta 5 single 13
- 13.(12) Head setae 4, 5 and 6, forming almost a right-angle with seta 4 well in front of seta 5; prothoracic seta 4, single *alboannulatus*
Head setae 4, 5 and 6, forming obtuse angle, with seta 4 slightly in front of or behind seta 5; prothoracic seta 4, 2-3 branched *rubrithorax*
- 14.(11) Siphon index exceeds 3; pecten of 24-37 close-set, strong, dark spines with paler tip 15
Siphon index usually less than 3; pecten of 16-25 evenly spaced spines with dark tip 16
- 15.(14) Prothoracic setae 1, 2 and 6, single; 3, 4 and 5, 2-branched *andersoni*
Prothoracic setae 1, 2, 4, 5 and 6, single; 3, 2-branched *continentalis*
- 16.(14) Scales of lateral comb with central spine at least twice as long as nearest lateral 17
Scales of lateral comb with 2-4 longer spines of almost equal length *cunabulanus*
- 17.(16) Anal papillae less than half length of saddle *luteifemur*
Anal papillae almost as long as saddle or longer *nivalis*
or *silvestris*

Subgenus OCHLEROTATUS Lynch Arribalzaga

Burpengariensis Section

AEDES (OCHLEROTATUS) NIGRITHORAX (Macquart)

Culex nigrithorax Macquart, 1847, *Dipt. Exot. Supp.*, 2: 9.

This species was originally described from Tasmania and was known only from the type specimen until F. N. Ratcliffe rediscovered it in 1952. Dr. E. N. Marks redescribed the species in 1960.

Ae. nigrithorax is closely related to *Ae. sagax* (Skuse) and can only be distinguished from the latter by the scale pattern on the scutum which is dark bronze medially and creamy, or white, laterally and the hind femora which are pale almost to the apex. Both these traits vary a great deal, particularly the scutal pattern, and in some areas, where the distributions of the two species overlap, it is difficult to separate them. *Ae. sagax* is absent from Tasmania and because of this it is possible to study the range of variation in *Ae. nigrithorax*. For these studies 280 specimens have been collected and examined.

The scutal pattern in *nigrithorax* from Tasmania varies a great deal. Among specimens bred from one pool at Epping, there were some with lateral areas of the scutum clothed with creamy scales and others with almost an entirely dark scutum. The pattern of the hind femora is more constant; all examined specimens had the femora white anteriorly with dark scaling only at the apex (Plate 2 a, b).

Particular attention was paid to the presence of tooth on the claws of hind tarsi; in the *Ae. sagax* from Northern Victoria these are simple. The study of the claws of the hind legs in two Tasmanian populations revealed high variability of this trait. There are specimens with or without tooth on all four claws or with three or two or only one claw toothed (Table 4).

TABLE 4
Variability of the hind claws in Ae. nigrithorax

Locality	Specimens examined	Percentage of specimens showing various distribution of teeth											
		1/1	1/1	1/1	1/0	1/0	1/0	1/1	0/0	0/1	0/0	0/0	0/0
Epping..	222	45.5		15.7		7.7		3.6		10.4		17.1	
Runnymede ..	58	56.9		12.1		5.2		3.4		10.6		12.1	
	280	47.8		15.0		7.1		3.6		10.4		16.1	

Description of fourth stage larva (from Epping): Head broad, seta 4, very small, 2-4 branched; 5, 6 and 8, single; 7, 3-6 branched; 9, 2-branched. Antenna short, about half length of head; seta 1, 3-7 branched. Mentum with 11-13 lateral teeth on each side. Prothoracic setae 1, 2, 4 and 6, single; 3 and 5, single or 2 branched; 7, 3-5 branched. Abdomen. VIIIth segment: lateral comb row of 9-13 spines coarsely fringed basally; seta 1, 4-7 branched; 2 and 4, single; 3, 8-13 branched; 5, 5-8 branched. Siphon index 2.6-3.7, mean 3.1; pecten of 22-29 spines, 1 or 2 detached spines beyond seta 1; seta 1, 3-6 branched. Anal segment: setae 1 and 3, single; 2, 6-10 branched; 4 (ventral tuft) of 16 tufts, 1-2 precratal. Anal papillae lanceolate, about as long as the saddle or longer.

Distribution. It has been found in the dryer eastern part of Tasmania at lower altitudes where it is confined to sclerophyll forests. It has been recorded from Epping (Marks, 1960) and Launceston (Mackerras, 1927). Additional records are: Tasmania: Nunamara, Runnymede, Golconda and Lake Leake; Flinders Island. It occurs also in Victoria, South Australia and New South Wales.

Material examined: 39♂, 275♀.

Flavifrons Section

Aedes (Ochlerotatus) flavifrons (Skuse)

Culex flavifrons Skuse, 1889, Proc. Linn. Soc. N.S.W., (2) 3: 1735.

This species can be recognized fairly easily from others. It has a dark blotch on the wing membrane, mottled wings, mottled femora and tibiae and banded tarsi; the tergites are unbanded. However, *Ae. flavifrons* is a very variable species. The proboscis may be intensively mottled or have only a few pale scales. The scutum may be clothed with light golden scales or clothed mainly with dark bronze, almost black scales with only a few pale golden ones mostly around the bare prescutellar area. Usually all the hind tarsal segments have only basal white bands. However, sometimes there may also be pale scales apically or almost complete apical ring on segments I and II. The mottling of the tergites also varies considerably. Ranging from a scattering of a few pale scales on the terminal segments to an intensive mottling of all tergites; some specimens have tergites VI and VII creamy scaled. The venter may be creamy scaled with a few scattered black scales, or the mottling may be so intensive that the venter appears almost black.

Distribution. This species is particularly common in the northern part of Tasmania. It has been recorded from: Wedge Bay and Mt. Arthur (Edwards, 1924); Eaglehawk Neck, Geeveston, Low Head (Lee, 1948); Advent Bay, Russell Falls, Strahan (Marks, 1964); King Island (Mackerras, 1927). Additional records are: Birrale, Liapootah, Little Swanport, Marrawah, Montumana,

Mt. Field Nat. Pk., Mt. Hartz Nat. Pk., Oonah, Port Arthur, Powranna, Pt. Sorell, Redpa, Sassafras; Flinders Island. It also occurs in Victoria, South Australia and New South Wales.

Material examined: 5♂, 251♀.

AEDES (OCHLEROTATUS) CALCARIAE Marks

Aedes calcariae Marks, 1957, *Pap. Dep. Ent. Univ. Qd.*, 1 (5): 74.

This species has dark scaled wings. The legs are unmottled, the tarsi banded and the terminal segment of the hind tarsus is entirely white. The sternites are pale scaled with basal median and apical lateral black patches.

This is the first record of this species from Tasmania. It has been collected at Carrick, Little Swanport and Nunamara. It also occurs in Victoria and South Australia.

Material examined: 3♂, 4♀.

AEDES (OCHLEROTATUS) PURPURIVENTRIS Edwards

Aedes purpuriventris Edwards, 1926, *Bull. ent. Res.*, 17: 13.

This can be readily distinguished by the black scaled wings and legs, unbanded tarsi, the presence of a dark blotch in the middle of the wing membrane and the partly or wholly purple-scaled venter.

Ae. purpuriventris was originally described from a single female collected at Eaglehawk Neck and rediscovered during the present studies in several localities: Bridport, Liapootah, Little Swanport, Mt. Hartz Nat. Pk., Storey's Creek. It also occurs in Victoria.

Material examined: 16♂, 19♀.

AEDES (OCHLEROTATUS) CLELANDI (Taylor)

Culicada clelandi Taylor, 1914, *Trans. ent. Soc. Lond.*, 1913: 690.

The main distinctive characters are: The scutum uniformly clothed with golden scales; unmottled femora, the unbanded tarsi, the narrow creamy tergal bands and the ochreous venter with some black scales.

This species was originally described by Taylor (1913) from Flinders Island, and later recorded from King Island (Mackerras, 1927), but is not recorded from Tasmania. It also occurs in coastal areas of Western Australia, South Australia and Victoria.

Material examined: 11♀.

Perkinsi Section

AEDES (OCHLEROTATUS) LUTEIFEMUR Edwards

Aedes luteifemur Edwards, 1926, *Bull. ent. Res.*, 17: 112.

A rather light coloured species which can be distinguished by the pale scaling of apical part of the costal vein and at R₁. The hind femora are more or less ochreous with only a few dark scales apically; the tarsi are dark. The tergites are unbanded with scattered, more or less ochreous, scales, particularly on the apical segments.

Most of the specimens collected in Tasmania and King Island are typical. However, some have the distal part of the hind femur mottled with dark scales. A few specimens have all the tergites extensively mottled with ochreous scales. Many specimens collected at Flinders Island are much darker than the typical

ones. Males often have all the scales on the wings dark and the apical half or one-third of the hind femora dark scaled anteriorly. In the dark females the wings have pale scales only on the apex of the subcosta; the hind femora are as in the males but there are always some ochreous scales.

This is a very common species recorded from: Advent Bay, Mt. Farrel, Strahan (Edwards, 1926); Georgetown (Mackerras, 1927); Lake St. Clair (Dobrotworsky, 1960). Additional records are: Birralee, Blackwood, Bridport, Buttlers Gorge, Deloraine, Dundas, Florentine Valley, Frankford, Geeveston, Golconda, Granton, King River, Kamona, Marrawah, Montana, Nunamara, Port Arthur, Pt. Sorell, Queenstown, Redpa, Sassafras, Smithton, Tullah, Zeehan; King and Flinders Islands. It also occurs in Victoria.

Material examined: 10♂, 156♀.

AEDES (OCHLEROTATUS) SILVESTRIS Dobrotworsky

Aedes waterhousei Dobrotworsky, 1960, PROC. LINN. SOC. N.S.W., 85: 57.

A large dark species with unbanded tarsi. The tergites are black with convex bands. The sternites are white scaled with prominent median and apical black patches. It has been recorded from Hobart (Dobrotworsky, 1960). Additional records are: Blackwood, Epping, Lake Leake, Little Swanport, Montana, Powrana. It also occurs in Victoria, South Australia and New South Wales.

Material examined: 11♂, 18♀.

AEDES (OCHLEROTATUS) NIVALIS Edwards

Culex australis Theobald, 1911 (*non* Erichson, 1842), *Mon. Cul.*, 2: 91.

The female is similar to that of *Ae. silvestris* but the scutal scales are golden and larger than in *silvestris*; the tergal basal bands are almost straight. The males are readily distinguished from all other species by having hairy tergites; the only scales present form lateral white patches. In some specimens the basal abdominal bands are reduced to a narrow line.

It has been recorded from: Mt. Wellington (Edwards, 1926), Great Lake (Lee, 1948). Additional records are: Battler's Gorge, Blackwood, Breona, Campbell Town, Derwent Bridge, Granton, Lake Leake, Little Swanport, Poatina, Powrana, Waldheim. It also occurs along the Great Dividing Range in Victoria and New South Wales.

AEDES (OCHLEROTATUS) CAMPTORHYNCHUS (Thomson)

Culex camptorhynchus Thomson, 1868, *Eugenie's Resta Dipt.*, p. 443.

Easily recognized by the uniformly clothing of golden scales on the scutum, the extensive mottling of the proboscis and legs with pale scales, the dark scaled wings and the banded tarsi. The tergal basal bands are convex and the white sternites have median and lateral patches of black scales. It is common in the coastal areas where it breeds usually in brackish waters, but it has also been recorded on occasions breeding in fresh water pools and swamps.

It has been recorded from: Cataract Gorge, Georgetown, Launceston, St. Helens (Edwards, 1924); Burnie, Coles Bay, Ferntree, Fort Direction, Hobart, King River, Sandford, Sassafras (Lee, 1948). Additional records are: Bridgewater (A. L. Dyce and M. D. Murray); Lake Leake, Little Swanport, Port Arthur, Swan Sea; St. Margarets, Sunday (D. L. McIntosh), King and Flinders Islands. It also occurs in Victoria, South Australia, Western Australia and New South Wales.

Material examined: 20♀.

Cunabulanus Section

AEDES (OCHLEROTATUS) CUNABULANUS Edwards

Aedes cunabulanus Edwards, 1924, *Bull. ent. Res.*, 14 : 378.

It has an entirely black proboscis and black tarsi, the scutum uniformly clothed with golden scales and mottled hind femora.

Ae. cunabulanus is a variable species. Two main forms may be recognized :

1. Specimens with broad tergal bands. This form usually has white curved scales on the vertex ; the upright scales are light brown or pale medially, black laterally ; behind the eyes there are two dark patches. The posterior pronotum with elongate white scales below and also in the middle among the narrow curved black ones. The venter is usually entirely white but may have more or less conspicuous dark median, and apical lateral, patches.
2. Specimens without basal tergal bands. The vertex has narrow, curved creamy scales with the upright scales light golden medially, dark laterally ; there may be no dark patch behind the eyes. The elongate white scales on the posterior pronotum are restricted to its lower part. The venter has prominent black patches ; the lateral ones in some specimens joining in the middle, forming apical black bands.

Both these forms often occur together, and the intermediates are common.

This species has been recorded from : Cradle Valley, Ferntree, Mt. Farrel, Mt. Field, Mt. Wellington, St. Patrick, Strahan (Edwards, 1924, 1926) ; Mt. Arthur (Mackerras, 1927) ; Ben Lomond, Great Lake, Lake St. Clair, Ragged Jack Saddle, Upper Blessington, Walls of Jerusalem (Lee, 1948), Gormanston, Moth Creek (Dobrotorsky, 1960). Additional records are : Bridgewater (A. L. Dyce and M. D. Murray) ; Breona, Bridport, Buttler's Gorge, Campbell Town, Derwent Bridge, Eaglehawk Neck, Florentine Valley, Forth Falls, Geeveston, Golden Valley, Granton, Hartz Nat. Pk., Kamona, King River, King William Saddle, Lake Leake, Liapootah, Lilydale, Little Swanport, Mt. Arthur, Nunamara, Parrawe, Patersonia, Port Arthur, Queenstown, Redpa, Renison Bell, Rocherlea, Rosebery, Storey's Creek, Tunel Mt., Waldheim, Wandobe Riv., Waratah, Zeehan. *Ae. cunabulanus* has not been recorded outside Tasmania.

Material examined : 56♂, 330♀.

AEDES (OCHLEROTATUS) CONTINENTALIS Dobrotorsky

Aedes continentalis Dobrotorsky, 1960, *PROC. LINN. SOC. N.S.W.*, 85 : 71.

Rather similar to *Ae. cunabulanus* but can be separated from it by the presence of pale mottling on the proboscis.

This is a coastal species which occurs mainly in the northern part of Tasmania : Birralee, Bridport, Lake Leake, Redpa. It has been also recorded from Flinders Island (Dobrotorsky, 1960) and occurs in Victoria.

Material examined : 11♂, 39♀.

AEDES (OCHLEROTATUS) ANDERSONI Edwards

Andersonia tasmaniensis Strickland, 1911, *Entom.*, 44 : 250.

Easily distinguished by the scutal pattern and the presence of a patch of broad, flat, white scales in front of the root of each wing (the typical form). The hind femora are mottled, the tarsi dark and the tergites unbanded.

Among the typical form collected in Tasmania, a few specimens have a patch of elongate and rather narrow scales in place of the broad scales at the wing roots.

This species has been recorded from : Cradle Valley, Eaglehawk, Geeveston, Mt. Farrel, Mt. Field, St. Patrick (Edwards, 1926); Great Lake, Upper Blessington (Lee, 1948); Boystown Res., Lake St. Clair, Port Davey (Dobrotworsky, 1960) and Flinders Island (Dobrotworsky, 1960). Additional records are : Birrale, Breona, Bridport, Buckland, Campbell Town, Derwent Bridge, Frankford, Golconda, Granton, King William Saddle, Lake Leake, Lebrina, Lilydale, Lisdolon, Montana, Mt. Cameron, Mt. Arthur, Nunamara, Patersonia, Port Arthur, Pt. Sorell, Redpa, Rocherlea, Ross, Sassafras, St. Patrick's River, Storey's Creek, Swan Sea, Wayatinah, Zeehan; King Island. It also occurs in Victoria.

Material examined : 33♂, 107♀.

Stricklandi Section

ÆEDES (OCHLEROTATUS) STRICKLANDI (Edwards)

Grabhamia australis Strickland, 1911, *Entom.*, 44 : 133.

Easily recognized by the dark-bronze scutum contrasting with the white scaled pleura, the dark scaled wings mottled with broad white scales and the dark scaled tarsi.

It was originally described from Flinders Island by Strickland (1911) and later collected frequently there (J. B. Cleland, J. H. Calaby, D. L. McIntosh). It also occurs on King Island, but has not been recorded from Tasmania. *Ae. stricklandi* has a coastal distribution in Victoria, South Australia and Western Australia.

Material examined : 14♀.

Group undetermined

ÆEDES (OCHLEROTATUS) form A

A female reared from a pupa collected in a ground pool at Flinders Island (8/2/63) is probably an undescribed species, but as the male and the larva are unknown its taxonomic status remains uncertain. The main morphological traits of this female are :

Vertex with pale forked and curved scales; palps with pale scales at tip; proboscis dark scaled with admixture of some pale scales on basal three-quarters. Scutum uniformly clothed with pale-golden scales with admixture of some dark scales in fossae and laterally on anterior half. Posterior pronotum with broad dark scales medially and narrow, curved, pale scales below and above. Pleura with broad pale scales; two strong pale lower mesepimeral bristles (on one side). Wing membrane with faint blotch in middle; dark scaled with a few scattered pale scales. Femora dark scaled to base, anteriorly with admixture of a few pale scales, posteriorly more intensively mottled with pale scales, particularly on basal one-third. Tibia dark scaled with some mottling. All tarsal segments with basal white bands. Tergites dark scaled, unbanded with white basal lateral patches; 6th and 7th mottled. Sternites pale scaled with dark apical bands.

Subgenus FINLAYA Theobald

Mediovittatus Group

ÆEDES (FINLAYA) NOTOSCRIPATUS (Skuse)

Culex notoscriptus Skuse, 1889, *PROC. LINN. SOC. N.S.W.*, 3 : 1738.

A small black species with banded tarsi. It is easily recognized by a yre-shaped pattern on the scutum and the banded proboscis.

It has been recorded from Low Head (Lee, 1948). Additional records are : Maydena (A. L. Dyce and M. D. Murray); Epping, Hobart; Flinders Island. It is widespread on the mainland of Australia.

Material examined : 4♀.

Alboannulatus Group

AEDES (FINLAYA) ALBOANNULATUS (Macquart)

Culex alboannulatus Macquart, 1849, *Dipt. exot. Suppl.*, 4 : 10.

A dark species with a mottled proboscis, banded tarsi and a preapical white band or patch on the femora; the venter is white with black median patches.

It has been recorded from : Strahan (Edwards, 1926). Additional records are : Bridgewater, Sandfly (A. L. Dyce and M. D. Murray); Birrale, Carrick, Christmas Hills, Deloraine, Little Swanport, Marawah, Powranna and Bass Strait Islands : Deal (Zosky), King and Flinders. It also occurs in Western Australia, South Australia and in all the eastern states of Australia.

Material examined : 37♂, 52♀.

AEDES (FINLAYA) RUBRITHORAX (Macquart)

Culex rubrithorax Macquart, 1850, *Dipt. exot. Suppl.*, 4 : 9.

Rather similar to *Ae. alboannulatus* but the proboscis is unmottled, there is no preapical white band on the femora, and the venter has an ochreous tint with a mottling of black scales.

One female from Flinders Island differs from all other specimens in having the hind femora dark scaled dorsally almost to base and anteriorly with only a few pale scales.

It has been recorded from : Hillwood, Lindisfarne, Westmoreland (Edwards, 1924), and Flinders Island (Dobrotowsky, 1960). Additional records are : Lake St. Clair, Maydena (A. L. Dyce and M. D. Murray); Orford, Geeveston (E. G. Connah); Bicheno, Birrale, Bridport, Blackwood, Bronte, Buckland, Buttler's Gorge, Carrick, Deloraine, Dunnorlan, Elizabeth Town, Fern-tree, Florentine Valley, Frankford, Hobart, King River, Lake Leake, Lebrina, Lilydale, Little Swanport, Myrtle Bank, Mt. Arthur, Mt. Field Nat. Pk., Mt. Hartz Nat. Pk., Mt. Wellington, Nunamara, Oonah, Osterley, Parrawe, Patersonia, Port Arthur, Powranna, Queenstown, Rocherlea, Rosebery, Sassafras, St. Clair, St. Helens, St. Marys, Storey's Creek, Waldheim, Waratah, Weldborough; North Bruny Island (E. G. Connah), Deal Island (E. Zosky) and King Island. It also occurs in South Australia and all eastern states of Australia.

Material examined : 36♂, 157♀.

AEDES (FINLAYA) RUPESTRIS Dobrotowsky

Aedes rupestris Dobrotowsky, 1959, *Proc. Linn. Soc. N.S.W.*, 84 : 136.

This is similar to *Ae. rubrithorax*, but may be easily separated from it by the pattern on the venter : the sternites are black scaled with basal lateral white patches, or are white scaled with a median patch and an apical black band. This species has not previously been recorded from Tasmania. It has been collected at : North Bruny Island (E. G. Connah); Forth Falls, Huonville, Little Swanport, Rosebery. It also occurs in Victoria and Queensland, and presumably in New South Wales, but it has not been recorded there.

Material examined : 5♂, 12♀.

Subgenus CHAETOCRUIOMYIA Theobald

AEDES (CHAETOCRUIOMYIA) MACMILLANI Marks

Aedes macmillani Marks, 1964, PROC. LINN. SOC. N.S.W., 89 : 131.

A very small stoutly-built species with short proboscis and legs. The anterior half of the scutum is pale, the posterior half dark. The tarsi are banded.

One female was collected by the author at Flinders Island 8/2/63, and this is the most southern record of this species. It also occurs in Victoria and New South Wales.

Subgenus PSEUDOSKUSEA Theobald

AEDES (PSEUDOSKUSEA) POSTSPIRACULOSIS Dobrotworsky

Aedes postspiraculosis Dobrotworsky, 1960, PROC. LINN. SOC. N.S.W., 85 : 261.

A rather small blackish mosquito with banded abdomen and unbanded tarsi. It is easily distinguished from all others by the broad flat scales on the vertex.

This is the first record of this species from Tasmania: Epping, Little Swanport, Powranna, St. Marys. It also occurs in South Australia, Victoria and New South Wales.

Material examined : 19♂, 10♀.

Subgenus HALAEDES Belkin

AEDES (HALAEDES) AUSTRALIS (Erichson)

Culex australis Erichson, 1842, *Arch. Naturgesch.*, 8 : 270.

This is a rather inconspicuous brown species with unbanded tarsi, broad creamy basal bands on the tergites and pale sternites with apical lateral black patches.

At Killiecrankie Bay, Flinders Island, *Ae. australis* behaved as a domestic species, invading houses near the shore; it fed during the night.

It has been recorded from: Eaglehawk Neck (Edwards, 1926), Low Heads (Lee, 1948), Port Davey (Marshall Laird, 1956). Additional records are: Bicheno, Black River, Hobart, Port Arthur, Randalls Bay, and Bass Strait Islands: Deal (E. Zosky), Fisher (J. H. Calaby), Great Dog (J. Thomson), Erith (S. Murray-Smith), King and Flinders. It also occurs along the coast of the Australian mainland from the southern border of Queensland to South Australia and along the southern part of Western Australia.

Material examined : 5♂, 16♀.

Genus CULISETA Felt

Subgenus AUSTROTROTHEOBALDIA Dobrotworsky

CULISETA (AUSTROTROTHEOBALDIA) LITTLERI (Taylor)

Chrysoconops littleri Taylor, 1914, *Trans. ent. Soc. Lond.*, (4) : 702.

It can be distinguished from other species by the pale upright scales on the vertex and by the presence of narrow curved scales on the posterior pronotum.

This species was originally described from a single female from Mt. Arthur, Tasmania. No specimens were collected during the present studies. Apparently it is very rare in Tasmania.

C. littleri also occurs in Victoria and New South Wales.

Subgenus CULICELLA Felt

CULISETA (CULICELLA) INCONSPICUA (Lee)

Theobaldia inconspicua Lee, 1937, PROC. LINN. SOC. N.S.W., 42: 294.

This can be recognized by the dark upright scales on the vertex, the pale scaling of the underside of the proboscis and the bare posterior pronotum.

The swarming of *C. inconspicua* has been observed on Flinders Island (8/2/63). It occurred in a forest glade close to a bush. The swarm appeared just after sunset and consisted of some hundred males, which moved rhythmically in a vertical direction some three to six feet above the ground.

It has been recorded from Sulfur Creek (Dobrotworsky, 1954). Additional records in Tasmania are: Birralee, Bridport, Bronte, Buckland, Carrick, Deloraine, Dunnorlan, Frankford, Geeveston, King River, Lilydale, Montana, Montumana, Moorina, Mt. Field Nat. Pk., Mt. Hartz Nat. Pk., Port Arthur, Pt. Sorell, Myrtle Bank, Redpa, Renison Bell, Rocherlea, Sassafras, Smithton, St. Marys, St. Patrick's Riv., Storey's Creek, Swansea, Waratah and Zeehan; Flinders, King and Great Dog Islands.

C. inconspicua also occurs in Victoria, South Australia and New South Wales.

Material examined: 47♂, 28♀.

CULISETA (CULICELLA) WEINDORFERI (Edwards)

Theobaldia weindorferi Edwards, 1926, Bull. ent. Res., 17: 111.

This species was described in 1926 and has not been collected again until present studies. The discovery of a breeding place in Redpa has made possible the description of the life history of the species.

Edwards in his description stated that the type female differs from the male "in having the upright scales of the head dark". An examination of the types in the National Insect Collection, Canberra, has shown that the female with dark scales on the vertex is actually a different species: *C. inconspicua* described by Lee in 1937.

Distinctive Characters. *The females:* Upright and narrow curved scales on vertex pale; lateral broad scales, white; ocular setae dark. Proboscis and palps black scaled; torus light brown with black setae, scales absent; flagellar segments dark with black setae. Scutum with very narrow dark bronze scales, setae black; scutellum with fine narrow pale scales and seven black border bristles on each lobe. Anterior pronotum with bristles only. Posterior pronotum with a few hair-like scales. Two dark spiracular bristles. Mesepimeron with two dark, strong lower bristles, a patch of fine hairs, very few narrow scales near middle and several bristles on upper part. Tergites clothed with dark scales with violet reflections. Venter with lighter scales. Wings dark scaled. Legs, including tarsi, dark; femora of all legs dark anteriorly to the base.

The male: Palps slightly shorter than proboscis with labella; terminal segment parallel to proboscis. Terminalia (Fig. 4 a, b): Coxites more than twice as long as broad, tapering on distal one-third; basal lobe with a tuft of rather long, curved thick setae. Phallosome simple, oval in shape. Paraproct with three teeth. Lobes of tergite IX distinct, each with 6-8 setae.

Larva (Fig. 4 c, d): Brownish. Head about two-thirds as long as broad. Antennae slightly shorter than length of head; seta 1 arising about three-quarters of length from base, about 19-22 branched. Head setae: 4, moderately long, single; 5, 4-5 branched; 6, single; 7, 3-4 branched; 8 and 9, 2 branched. Mentum with 10-12 lateral teeth. Prothoracic setae 1, 2, 3, 5, 6 and 7, single; 4, 2 branched. Abdomen. VIIIth segment: lateral comb patch of 42-50

fringed scales; seta 1, plumose, 8-12 branched; 2 and 4, single; 3, plumose, 3-5 branched; 5, 2-4 branched. Siphon long, slightly tapering, with index 6.0-7.1; basal seta single; pecten of 3-7 spines. Anal segment: saddle complete ring; seta 1, 1-2 branched; 2, 7-9 branched; 3, 3 branched; 4 (ventral brush) of 15-16 tufts. Anal papillae narrow, pointed, about as long as saddle or slightly longer.

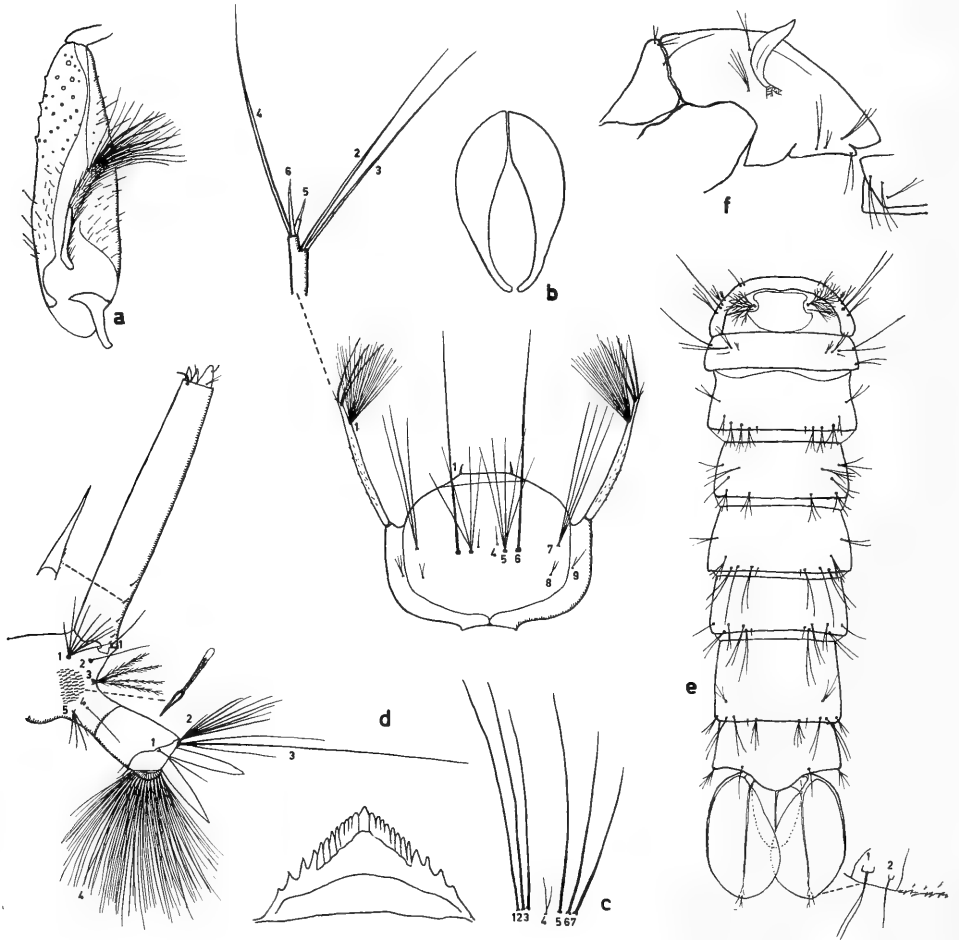


Fig. 4. *Cutiseta weindorferi* Edw., a-b, adult: a, coxite, inner aspect; b, phallosome; c-d, larva: c, prothoracic setae; d, head, mentum and terminal segments; e-f, pupa: e, abdomen; f, cephalothorax and metanotum.

Pupa: Details shown in Fig. 4 e, f.

Biology. This is a day-biting species which attacks man. It is well adapted to a cold climate and continues biting activity at temperatures as low as 11°C.

Its mating behaviour is similar to that of *C. hilli* Edw.; it occurs during the day and the males have been observed in small numbers flying about close to ground. Coupling is usually initiated while both sexes are in flight, and is completed on the grass. Larvae have been found in a pit under an uprooted tree in dense bush.

Distribution. It occurs only in Tasmania, and has been collected at: Lake St. Clair, Maydena (A. L. Dyce and M. D. Murray), Arthur Plains (A. Neboiss); Florentine Valley (M. Littlejohn); Buttler's Gorge, six miles west of King Saddle, Queenstown, Redpa, St. Helens.

Material examined: 63♂, 58♀.

Discussion. *C. weindorferi* is closely related to *C. otwayensis* Dobr. The adults of both species are very similar but the males of *C. weindorferi* have 6-8 setae on each lobe of tergite IX. The larva also are similar, but may be separated by the following traits: in *weindorferi* the mentum has 10-12 lateral teeth (*otwayensis* 13-14); seta 3 of abdominal segment VIII, 3-4 branched (*otwayensis* 5-6), and siphonal index is 6.0-7.1 (*otwayensis* 4.8-5.6). It is likely that *C. otwayensis* differs also in mating habits, and it is not recorded yet as a man-biting species.

Genus CULEX Linnaeus

Piapiens Group

CULEX (CULEX) GLOBOCOXITUS Dobrotworsky

Culex globocoxitus Dobrotworsky, 1953, PROC. LINN. SOC. N.S.W., 77: 357.

This species has the proboscis pale scaled beneath to the tip; the tergites are black scaled with creamy bands unstricted laterally.

It has been recorded from Bothell, Launceston and Middleton (Dobrotworsky, 1953). Additional records are: Bridgewater (A. L. Dyce and M. D. Murray), Cremorne, Granton; Flinders Island. It also occurs in south-western Queensland, New South Wales, South Australia, Victoria and Western Australia.

Material examined: 6♂, 10♀.

CULEX (CULEX) PIPIENS AUSTRALICUS Dobrotworsky and Drummond

Culex pipiens australicus Dobrotworsky and Drummond, 1953, PROC. LINN. SOC. N.S.W., 78: 143.

It can be recognized by: the presence of a few broad white scales on the postspiracular area. The tergal bands are constricted laterally, and there are conspicuous median and apical lateral black patches on the sternites.

It has been recorded from: Bothell, Launceston (Dobrotworsky and Drummond, 1953). Additional records are: Bridgewater, Sandfly and St. Clair (A. L. Dyce and M. D. Murray), Cremorne; King and Flinders Islands. It is widely distributed on the Australian mainland, and has also been recorded from New Caledonia.

Material examined: 22♂, 32♀.

CULEX (CULEX) PIPIENS MOLESTUS Forskal

Culex molestus Forskal, 1775, *Descr. Animalium*, p. 85.

It resembles *C. globocoxitus* but may be distinguished from it by the dark brown scaled tergites and by the fact that the posterior margins of the tergal bands are not sharply defined. The ventral side of the proboscis is dark scaled apically.

It has been recorded from Tasmania (Dobrotworsky and Drummond, 1953).

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References

- BELKIN, J. N., 1962.—“The Mosquitoes of the South Pacific.” (Diptera: Culicidae). University of California Press, 2 vols., 608 and 412 pp.
- BROWN, C. E., 1965.—Mass transport of Forest Tent Caterpillar moth, *Malacosoma distrata* Hübner, by a cold front. *Canad. Ent.*, 97: 1073-1075.
- BURBIDGE, N. T., 1960.—The phytogeography of the Australian Region. *Aust. J. Bot.* 8: 75-212.
- DIMMOCK, G. M., 1957.—Soils of Flinders Island, Tas: *C.S.I.R.O., Division of Soils, Soils and Land Use, Series 23*: 1-68.
- DOBROTORSKY, N. V., 1954.—The genus *Theobaldia* (Diptera, Culicidae) in Victoria. *PROC. LINN SOC. N.S.W.*, 79: 65-78.
- , 1957.—Notes on Australian mosquitoes (Diptera, Culicidae). II. Notes on *Anopheles stigmaticus* Skuse and description of new species of *Anopheles* from Australia and New Guinea. *Ibid.*, 82: 180-8.
- , 1960.—The subgenus *Ochlerotatus* in the Australian Region. III. Review of the Victorian species of Perkinsi and Cunabulanus Sections with descriptions of two new species. *Ibid.*, 85: 53-74.
- , 1965.—“The Mosquitoes of Victoria” (Diptera, Culicidae). Melbourne University Press, 237 pp.
- , and DRUMMOND, F. H., 1953.—The *Culex pipiens* group in south-eastern Australia. II. *PROC. LINN. SOC. N.S.W.*, 78: 131-46.
- EDWARDS, F. W., 1924.—A synopsis of the adult mosquitoes of the Australian Region. *Bull. ent. Res.*, 14: 351-401.
- , 1926.—Mosquito Notes. IV. *Ibid.*, 17: 101-31.
- GLICK, P. A., 1939.—The distribution of insects, spiders and mites in the air. *Tech. Bull. U.S. Dept. Agric.* No. 673, 150 pp.
- GRESSITT, J. L., LEECH, R. E., and O'BRIEN, C. W., 1960.—Trapping of air-borne insects in the Antarctic area. *Pacific Ins.*, 2: 245-50.
- JENNINGS, J. N., and BANKS, M. R., 1958.—The Pleistocene glacial history of Tasmania. *Journ. Glaciol.*, 3: 298-303.
- KEBLE, R. A., 1946.—The sunklands of Port Phillip Bay and Bass Strait. *Mem. nat. Mus. Vict.*, 14: 69-122.
- LEE, D. J., 1948.—Mosquitoes recorded from Tasmania. *Rec. Queen Vict. Mus., Launceston*, 2: 53-6.
- , and WOODHILL, A. R., 1944.—“The Anopheline Mosquitoes of the Australian Region.” Zool. Dept. Univ. Sydney, Monogr. 2, 209 pp.
- LITTLEJOHN, M. J., and MARTIN, A. A., 1965.—The vertebrate fauna of the Bass Strait Islands: I. The Amphibia of Flinders and King Islands. *Proc. roy. Soc. Victoria*, 79: 247-256.
- MACKERRAS, I. M., 1927.—Notes on Australian mosquitoes (Diptera, Culicidae). Part II. The zoogeography of the Diptera. *Aust. J. Sci.*, 12: 157-61.
- LAIRD MARSHALL, 1956.—A new species of Coelomomyces (Fungi) from Tasmanian mosquito larvae. *J. Paras.*, 42: 53-5.
- MARES, E. N., 1960.—Australian mosquitoes described by Macquart. II. Species in Bigot's collection, *Aedes (Ochlerotatus) nigrithorax* (Macquart), *PROC. LINN. SOC. N.S.W.*, 85: 117-20.
- PARAMONOV, S. J., 1959.—Zoogeographical aspects of the Australian Diptero-fauna. *Biogeogr. Ecol. Aust., Monogr. Biol.*, 8: 164-91.
- PRYOR, M. E., 1964.—Trapping of air-borne insects on ships in the Indian Ocean-Antarctic Areas. *Pacific Ins.*, 6: 283-5.
- STEPHENS, C. G., and HOSKING, J. S., 1932.—A soil survey of King Island. *C.S.I.R.O. Bull.* 70: 1-55.
- TILLYARD, R. J., 1926.—“The Insects of Australia and New Zealand.” Sydney. 560 pp.
- YASHIMOTO, C. M., and GRESSITT, J. L., 1960.—Trapping of air-borne insects on the Pacific (Part 3). *Pacific Ins.*, 2: 239-43.
- , ———, 1961.—Trapping of air-borne insects on ships on the Pacific (Part 4). *Ibid.*, 3: 556-8.
- , ———, 1963.—Trapping of air-borne insects in the Pacific-Antarctic area. *Ibid.*, 5: 873-83.

EXPLANATION OF PLATES IV-V

Plate iv

Anopheles atratipes Skuse. a, head; b, wing. *Anopheles tasmaniensis* Dobrotworsky. c, head; d, wing.

Plate v

Anopheles tasmaniensis Dobrotworsky. a, eggs (from Dobrotworsky, 1965, by permission of the Melbourne University Press). *Aedes nigrithorax* Macquart, Epping, Tasmania. Scutum, hind femur and tibia. b, typical form; c, dark form.

NEW TAXA OF *ACACIA* FROM EASTERN AUSTRALIA No. 2

MARY D. TINDALE

Royal Botanic Gardens, Sydney

[Read 15th July, 1966]

Synopsis

Four new taxa of *Acacia* native to Eastern Australia are described. They are all members of the Section *Botryocephalae*.

Due to two impending publications it has been necessary to publish these new species and subspecies prior to my monograph on the *Acacia decurrens* group. The latter group is of great importance in the tanning bark industry.

ACACIA STORYI, sp. nov.

Acaciae filicifoliae affinis, sed differt: ramulis, petiolis et rhachidibus glabris, petiolis ad basin parium infimorum pinnarum glandula singula glabra vel sparse pubescente, saepe etiam glandula singula glabra vel sparse pubescente interjugali praeditis, capitulis pallide flavis, pedunculis glabris, pinnis 8–17–jugis, pinnulis 32–61–jugis, quam in *Acacia filicifolia* glabrioribus.

Allied to *Acacia filicifolia* but differing in the following ways: the branchlets, petioles and rhachises glabrous, the petioles with a glabrous or slightly pubescent gland at the base of the lowest pairs of pinnae, as well as often bearing a glabrous or sparsely pubescent, interjugary gland, the heads pale yellow, the peduncles glabrous, the pinnae 8– to 17–jugate, the pinnules 32–61–jugate, more glabrous than in *A. filicifolia*.

Holotype.—Rockland Spring, 24. miles SSE of Blackwater Township, Leichhardt District, Queensland, Australia, common with *Eucalyptus tereticornis* and *Aristida* spp., erect tree 25 to 30 ft. high, trunk 6 to 9 inches diam. at 5 ft. high, bark smooth grey-green, leaves bipinnate with sparse canopy, pods drooping, Lazarides and Story No. 50, 6/9/1961 (NSW 74764), located in the National Herbarium of New South Wales, Sydney, Australia. *Isotypes*: BRI; MEL; CANB.

This species forms extensive stands on the Blackdown Tableland in Central Queensland on the sandstone plateau in dry sclerophyll forest. It flowers in July and August, the mature legumes occurring on the trees in August and September according to specimens collected by C. H. Gittins.

It is most closely related to *Acacia filicifolia*, both species being characterized by very glaucous, bluish, glabrous, almost straight-sided legumes, by numerous interjugary glands on the rhachises and by fine, narrow, closely spaced pinnules. The latter tend to be more fern-like in these two species than in the other species of the *A. decurrens* group.

ACACIA IRRORATA Sieber ex Spreng., Syst. Veg. 3: 141 (1826), ssp.
VELUTINELLA, ssp. nov.

Acaciae irroratae ssp. *irroratae* affinis, sed costis ramulorum arborum maturarum tuberculis crispato-pilosis carentibus, petiolis et rhachidibus pilis crispatis albis vel luteis tomentellosis, pedunculis pilis paucis albis erectis vel crispatis parce indutis, rhachidum glandulis haud urceolatis, ramulis novellis fusco-luteis vel aurantiacis, foliis 18–35–jugis margine et subtus pilis crispatis albis vel luteis parce indutis, corolla usque dimidiam longitudinem (nec usque tertiam vel quintam partem) divisa, leguminibus angustioribus haud scabridis differt.

Allied to *Acacia irrorata* ssp. *irrorata* but differing in the following characters: the ridges of the branchlets of mature trees without prominent tubercles bearing crisped hairs, the petioles and rachises tomentellose with crisped, white or yellow hairs, the peduncles sparsely clothed with a few, white, erect or crisped hairs, the glands of the rachises not urceolate, the young tips of the foliage dark yellow or orange, the leaflets 18 to 35 pairs, sparingly clothed with white or yellow, crisped hairs on the margin and lower surface, the corolla dissected to half its length instead of $\frac{1}{3}$ to $\frac{1}{5}$ of its length, the legumes narrower, non-scabrous.

Shapely trees about 6 to 10 metres high, the trunk with smooth bark which is dark grey or black with dark grey, horizontal streaks. *Branchlets* ridged, the surface and ridges tomentellose with crisped, slightly matted, yellowish or white hairs, the ribs not tuberculate except in juvenile plants. *Young tips* dark golden yellow, sometimes almost orange. *Leaves*: petiole slightly ridged, 0.7 to 2.5 cm. long, tomentellose, eglandulose or bearing a saccate gland (with a large irregular orifice) between 2 to 6 mm. below the lowest pair of pinnae, clothed as on the branchlets, bearing dark brown, saccate glands between or just below the uppermost 1 to 4 pairs of pinnae. *Pinnae* 7 to 16 pairs, 8.5 to 15 cm. long, 3 to 7 cm. broad, velvety, dark green. *Pinnules* 18 to 35 pairs, 1.5 to 3.5 mm. long, 0.4 to 0.5 mm. broad, the apex obtuse or subacute, the lower surface clothed with whitish, crisped hairs especially towards the margins, the upper surface almost glabrous. *Heads* bright yellow, globose, in racemes or panicles, each head composed of about 20 to 26 flowers, the peduncles slender, ca. 0.1 to 0.2 mm. in diam., clothed with whitish or pale yellow, crisped hairs; buds more or less glabrous. *Bracteoles* 0.7 to 0.9 mm. long, with a broad ciliolate pedicel which is expanded into a pear-shaped, dilated, curved, apical portion clothed with white hairs, but lacking a pronounced apical tuft of hairs. *Calyx* 0.3 to 0.5 mm. long, oboconical, very shortly 5-lobed, yellow, the ribs and the lobes clothed with comparatively short, white crisped hairs except the margin of the lobes where the hairs are stiffer. *Corolla* ca. 1.5 mm. long, yellow, dissected for half its length into 5 acute, narrowly lanceolate lobes, glabrous, the apices and margins granular. *Stamens* numerous, the filaments about 1.7 to 2 mm. long. *Anthers* bilocular. *Ovary* subsessile, very dark brown, more or less oblanceolate, clothed with crisped hairs, 0.5 to 0.6 mm. long and about 0.1 mm. broad. *Style* laterally attached. *Legumes* stalked, coriaceous, non-scabrous, dull, black with brown markings towards the margins, submoniliform, 3.5 to 8 cm. long, 5 to 8 mm. broad. *Seeds* black, glossy to dull, longitudinal in the legumes, the funicle filiform and tightly folded into a loop, then expanded into a tawny pileiform aril on top of each seed, the areole not prominent.

Holotype.—11 miles south of Coffs Harbour, New South Wales, tree 25 ft. high, heavily fruiting, the bark smooth, black with grey horizontal streaks, M. Tindale 11/1960 (NSW 52912), located in the National Herbarium of New South Wales, Sydney.

Isotypes.—K; US; A; MEL.

Distribution.—North Coast of New South Wales.

Habitats.—On rain forest margins or in better class eucalypt forest, sometimes in *Melaleuca* swamps or on hard gravelly ridges.

Chromosome number.— $2n=26$, Voucher specimen: Gills Creek, Kempsey, New South Wales, E. F. Constable 29/5/1964 (NSW 72147). This chromosome count was made by Dr. Barbara Briggs and is published here with her kind permission.

Equivalent synonym.—*Acacia decurrens* (Wendl.) Willd. var. β , see Maiden in Agr. Gaz. N.S.W. 5: 607–8 (1894).

The subspecific epithet *velutinella* refers to the velvety foliage and branchlets which readily distinguish it from ssp. *irrorata*. However juvenile plants of ssp. *velutinella* are characterized by scabrous stems, although as the shrubs

grow older these tubercles disappear. The type subspecies has a much wider distribution than ssp. *velutinella*, as the former ranges from south-eastern Queensland to the North, Central and South Coast of New South Wales, as well as rarely on the North and Central Western Slopes and the Central Tablelands of this State. There are numerous records of ssp. *velutinella* on the North Coast of New South Wales from Dalmorton southwards to Gloucester, whereas ssp. *irrorata* is uncommon in this region. No intermediates have been observed yet, although these two taxa are morphologically close.

In the type subspecies flowering takes place mainly between mid-November and late January, although there are isolated records for February, May, June, July and August (especially in Queensland). Flowering in ssp. *velutinella* occurs in January and February, the legumes maturing from August to November.

ACACIA LEUCOCLADA, sp. nov. ssp. LEUCOCLADA ssp. nov.

Frutex vel persaepe arbor effusa, circiter 4–9 m. (raro usque 15 m.), alta diametro 15–45 cm., cortice arborum maturarum atrobrunneo vel nigro, trunco supra basin ad 3–5 m. aspero et corrugato, ramis juvenilibus levibus, olivaceis et saepe glaucis, cortice arborum parvarum levi et pallide brunneo. *Ramuli* leviter angulati, costis nec tuberculatis nec alatis, glauci, leviter caerulei, nonnunquam glabri sed plerumque pilis brevibus canescentibus incani. *Ramuli novelli* argentei vel albi. *Spiniae* nullae. *Folia*: petiolus circiter 1.5–3 cm. longus, costatus, in plano verticali non applanatus, nonnunquam glaucus, eglandulosus vel prope basin paris infimi pinnarum vel inter has et basin petioli glandula unica mediana ornatus; rhachis 2–8 cm. longa, ut ramuli vestita, plerumque glandula juxta basin omnium parium pinnarum et 2–5 glandulis interjugalibus inter compluria paria pinnarum praedita vel raro 1–2 paribus pinnarum sine glandulis et glandula interjugalibus unica tantum inter paria omnia pinnarum praedita. *Pinnae* 6–16-jugae, 5–12 cm. longae, 4–7.5 cm. latae. *Pinnulae* 17–36-jugae, anguste oblongae vel lineares, 2–5 mm. longae, 0.4–1.2 mm. latae, virides vel caeruleae, subtus vix pallidae, supra glabrae, pilis subappressis, albis, simplicibus, septatis, sparsis per superficiem paginae (plerumque praeter margines) dispersis, apice obtuso. *Capitula* flava, globosa, in racemis vel paniculis disposita, capitulis plerumque 22–26-floris, pedunculis glaucis, pilis appressis, simplicibus, septatis, canescentibus sparse vestitis. *Bractea* ad basin pedunculi, atrobrunnea, fimbria marginali ciliorum alborum et pilis paucis superficialibus ornata. *Bracteolae* 0.8–1 mm. longae, atrorufobrunneae, sursum spathulatae vel peltatae, dense ciliolatae, petiolo angusto, pilis albis lanatis ornato. *Calyx* circiter 0.5–0.7 mm. longus, obconicus, rufobrunneus, tubo lobos aequante vel iis 5-plo longiore, lobis secus costas pilis albis lanatis interdum saepe vel dense vestitus, sed tubo saepe glabro. *Corolla* circiter 1–1.5 mm. longa; petalis tubum aequantibus, glabris vel pilis brevibus, erectis, albis ornatis, margine granulosis. *Staminum filamenta* numerosa, circiter 2–2.2 mm. longa. *Antherae* biloculares. *Ovarium* sessile, castaneum vel atrobrunneum, 0.5–0.8 mm. longum, oblongum vel oblongo-lanceolatum, apice obtuso, apicem et medium versus pilis albis lanatis vestitum. *Stylus* hinnuleus, glaber, ovario 3-plo longior. *Legumina* stipitata, porphyrea vel fusca, leviter vel valde glauca, plerumque submoniliformia, interdum recta, tenuiter coriacea, 3.5–11.5 cm. longa, 6–12 mm. lata, margines versus pilis minutis, fugacibus, albis, rectis, appressis sparse vestita. *Semina* nigra, obscura vel nitida, oblongo-ellipsoidea, in legumine longitudinaliter disposita, funiculo primiv filiformi et stricto vel leviter uncinato deinde in arillum pileiformem eburneum super seminis apicem incrassato, areolo prominente.

A shrub or very often a spreading tree about 4 to 9 m. (or rarely up to 15 m.) high, the d.b.h. of the trunk 15 to 45 cm., with the bark of mature trees dark brown or black, rough and corrugated on the trunk up to 3 to 5 m. from the base, the young branches smooth, olive green and often glaucous, on the

small trees the bark on the main trunk is smooth and light brown. *Branchlets* slightly angled, with non-tuberculate, non-winged ridges, glaucous, slightly bluish, sometimes glabrous but mostly hoary due to short, greyish hairs. *Young tips* silvery or whitish. *Leaves*: petiole ca. 1.5 to 3 cm. long, ribbed, not vertically flattened, sometimes glaucous, eglandulose or with a gland just below the lowest pair of pinnae or mid-way between the latter and the base of the petiole; the rhachis 2 to 8 cm. long, clothed as on the branchlets, usually 1 gland at the base of each pair of pinnae and 2 to 5 interjugal glands between at least several pairs of pinnae or rarely 1 or 2 pairs of pinnae without a gland at their base and with only 1 interjugal gland between each pair of pinnae. *Pinnae* 6 to 16 pairs, 5 to 12 cm. long, 4 to 7.5 cm. broad. *Pinnules* 17 to 36 pairs, narrowly oblong (3:1) to linear (10:1), 2 to 5 mm. long, 0.4 to 1.2 mm. broad, green or bluish, very slightly paler on the lower surface, glabrous above, mostly clothed with rather appressed, white, unbranched, septate hairs scattered over the surface but especially along the margins, the apex obtuse. *Heads* yellow, globose, in racemes or panicles, mostly 22 to 26 flowers in a head, the peduncles glaucous, sparsely greyish hoary with appressed, unbranched, septate hairs. *Bract* at the base of the peduncle dark brown, bearing a marginal fringe of white cilia, as well as some scattered on the surface. *Bracteole* 0.8 to 1 mm. long, dark red-brown, consisting of a narrow stalk clothed with white woolly hairs, expanded into a spatulate or peltate, ciliolate apical portion. *Calyx* ca. 0.5 to 0.7 mm. long, obconical, red-brown, with lobes $\frac{1}{2}$ to $\frac{1}{3}$ the length of the tube, clothed with white woolly hairs on the lobes and sometimes sparsely to densely on the ribs but the tube is often glabrous. *Corolla* ca. 1 to 1.5 mm. long, dissected to about half of its length, the petals glabrous or clothed with short, erect, white hairs, the margins of the petals granulate. *Filaments* of the stamens numerous, ca. 2 to 2.2 mm. long. *Anthers* bilocular. *Ovary* sessile, chestnut or dark brown, 0.5 to 0.8 mm. long, oblong or oblong-lanceolate, the apex rounded, clothed especially towards the apex and middle with white woolly hairs. *Style* fawn, glabrous, often looped, about $2\frac{1}{2}$ to 3 times as long as the ovary. *Legumes* stalked, reddish-brown or brownish grey, faintly to markedly glaucous, usually slightly constricted between the seeds but sometimes almost straight-sided, thinly coriaceous, 3.5 to 11.5 cm. long, 6 to 12 mm. broad, clothed sparsely especially towards the margins with minute, fugacious, white, more or less straight, appressed hairs. *Seeds* black, dull or glossy, oblong-elliptical, longitudinal in the legume, the funicle filiform and straight or slightly hooked, then expanded into a cream-coloured, pileiform aril on top of the seed, the areole usually prominent.

Holotype.—Tunderbrine Creek, Warrumbungle Mountains, A. Correy 3/9/1953 (NSW 25552), located in the National Herbarium of New South Wales, Sydney.

Isotypes: K; A; L; US; G; BRI; AD; UC.

Distribution.—New South Wales: the North, Central and South Western Slopes, rarely on the Northern Tablelands and at Howes Mountain on the border of the North and Central Coast.

Flowering period.—Late July to late September.

Length of Legume Formation.—Approximately 5 months. The mature legumes occur on the trees in November, December and January.

Chromosome count.— $2n=26$. Voucher specimen: 3 miles from Molong, N.S.W., E. F. Constable 24/1/1964 (NSW 78901). This chromosome count was made by Dr. Barbara Briggs (personal communication).

The habit of *Acacia leucoclada* ssp. *leucoclada* is much more open than in *A. dealbata* with which it has been confused in the past. It may be distinguished from *A. dealbata*, as there is a single, prominent, orbicular gland at the base of each pair of pinnae in the latter species but interjugal glands are absent on the rhachis. Both species have glaucous legumes but they are glabrous in *A. dealbata*, whereas in both subspecies of *A. leucoclada* minute, appressed, white hairs are present on their legumes.

ACACIA LEUCOCLADA Tindale ssp. ARGENTIFOLIA ssp. nov.

Acaciae leucocladae ssp. *leucocladae* affinis, sed differt: arbore maiore nonnunquam usque 18 metros alta, ramulis semper dense crispato-pilosis, petiolis rhachidibusque glandulis inconspicuis, angustis, dense crispato-pilosis praeditis, rhachidibus glandula singula prope basin paris summi pinnarum saepe ornatis, etiam inter paria omnia pinnarum 1 vel saepe 2 glandulis raro contiguis, interjugalibus, in rhachide interdum inter paria media pinnarum vel 4 paria infima carentibus.

Allied to *Acacia leucoclada* ssp. *leucoclada* but differing in the following ways: a larger tree sometimes up to 18 metres high, with the branchlets always densely crispato-pilose, with the petioles and rhachises bearing inconspicuous, narrow, densely crispato-pilose glands, with the rhachises often bearing one gland near the base of the uppermost pair of pinnae, also between all the pairs of pinnae 1 or sometimes 2, rarely contiguous, interjugal glands, sometimes these glands absent on the rhachis between the middle pairs of pinnae or between the 4 lowest pairs.

Holotype.—1 mile north of Memerambi, south-eastern Queensland, tree 20 ft. high, with an ironbark type of bark, in fruit, foliage silvery, in red soil, growing along the roadside in cleared country, M. Tindale 31/10/1960 (NSW 52681), located in the National Herbarium of New South Wales, Sydney.

Isotypes.—K; US; A; L.

Distribution.—South-eastern Queensland (the South Burnett district and the Darling Downs) and the Far North Coast of New South Wales (mainly in the *Acacia* Creek-Koreelah districts).

Habitats.—In dry sclerophyll forest, mainly in cleared country, often in red loam, sandy clay or sandy soil, sometimes along the banks of creeks.

Flowering period.—Early July to early September.

Length of Legume Formation.—4 to 5 months, the mature legumes being borne on the trees in November and December.

Chromosome number.— $2n=26$, Voucher specimen: Roseberry State Forest Nursery (96), cultivated, E. F. Constable 27/5/1964 (NSW 78899). (Dr. Barbara Briggs, personal communication.)

The principal diagnostic feature of *A. leucoclada* ssp. *argentifolia* is the barely discernible glands on the petioles and rhachises, which distinguishes this taxon from all other members of the *A. decurrens* group. *A. leucoclada* ssp. *argentifolia* has a more northerly distribution than ssp. *leucoclada*, since it ranges from south-eastern Queensland to the Far North Coast of New South Wales, whereas ssp. *leucoclada* occurs on the Western Slopes, the Northern Tablelands and at Howes Mountain in New South Wales. Probable hybrids between these subspecies have been examined.

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Acacia storyi is named in honour of Dr. R. Story (C.S.I.R.O., Canberra), one of the collectors of the holotype of this species.

THE APPLICATION OF THE NAMES *SERICESTHIS PRUINOSA*
(DALMAN) AND *SERICESTHIS NIGROLINEATA* BOISDUVAL
(COLEOPTERA: SCARABAEIDAE: MELOLONTHINAE)

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(Communicated by Dr. D. F. Waterhouse)

[Read 15th July, 1966]

The name *Sericesthis pruinosa* (Dalman) has been generally applied in collections and in recent literature to a species of melolonthid beetle which is recognisable by its dark brown head, pronotum and scutellum, in combination with elytra of pale yellowish brown, with base and sutural edges darker. Specimens vary in length between 13 and 17 mm. This species is exceedingly common in south eastern Australia and it agrees in all respects with the description of *S. pruinosa* given by Burmeister in 1855, but not with the original description of *S. pruinosa* by Dalman (1823). Dalman described *S. pruinosa* as being of a uniform dark reddish brown colour and length 6 lines (12 mm.). With the kind cooperation of Drs. R. Malaise and E. Kjellander, I have been able to examine the series of six specimens which stand as *S. pruinosa* (Dalman) in the Naturhistoriska Riksmuseum, Stockholm, where Dalman worked nearly one hundred and fifty years ago. The series includes one specimen of *S. nigrolineata* Boisduval, as at present identified, and five of *S. pruinosa* (sensu Burmeister and later workers). The specimen of *S. nigrolineata* bears one label "pruinosa Dalm." in what appears to be the handwriting of Boheman, the insect curator of the Museum from 1841. There are in addition two printed labels, "Nov. Holl." and "Schh.," the latter indicating that the specimen came from the Schönherr collection. None of the other five specimens bears an identification label. Two have printed labels, "Thorey" and "Kinb." and are of later date than Dalman. The other three are labelled "Nov. Holl." and two have printed labels "M. Gall" which may indicate that they came from the Paris Museum.

As the specimen labelled "S. pruinosa Dalm." fits the original description and the other five do not, I believe it to have been the specimen used by Dalman, and I have chosen to make it the lectotype of the species.

Additional evidence on the original and correct application of the name *Sericesthis pruinosa* is provided by the British Museum collection. This includes two specimens bearing the register number 44-12, one of which is a specimen of *S. nigrolineata* Boisduval, labelled "Sericesthis pruinosa D.". The other, a specimen of *S. pruinosa* (sensu Burmeister), is labelled "Sericesthis geminata Macleay", in the same handwriting. The register number indicates that these specimens came to the Museum with the collection of the Entomological Club in March 1844. The identification labels thus provide further evidence of the application of the names in the years following Dalman but before Burmeister's work.

It is therefore established that *S. pruinosa* (Dalman) is the same species as that now known as *S. nigrolineata* Boisduval. *S. pruinosa* was, however described as *Melolontha pruinosa* Dalman, 1823, which makes it a junior homonym of *Melolontha pruinosa* Wiedeman, 1819 (*Lepidiota pruinosa* (Wied.), from Java). The species must therefore assume the name of the oldest synonym, which is *S. nigrolineata* Boisduval. This is a fortunate result as it stabilizes the present use of the name *S. nigrolineata*. The name *pruinosa* Dalman must, however, disappear from use.

The second species, that incorrectly identified as *S. pruinosa* by Burmeister in 1855, was first described by Boisduval in 1835 as *S. geminata*. This synonymy was recognized by Burmeister (1855: 231). Boisduval's types of the species described in the "Voyage de l'Astrolabe" cannot now be located in the Paris Museum but the identifications of the species follow Blanchard and no confusion has arisen. The species which was misidentified by Burmeister as *Sericesthis pruinosa* (Dalman) must now be known as *Sericesthis geminata* Boisduval 1835.

Blanchard (1850) synonymized *Scitala languida* Erichson (1842, *Arch. f. Naturg.*, 1: 168) with *Sericesthis nigrolineata* Boisd. By the courtesy of Dr. K. Delkeskamp, late of the Zoological Museum of the Humboldt University, Berlin, I have been able to confirm this synonymy by reference to the type of *Scitala languida*.

To summarize, the following relationships of the names applied to two common Australian species are established:

SERICESTHIS NIGROLINEATA Boisduval

Sericesthis nigrolineata Boisduval, 1835, *Voyage de l'Astrolabe, Col.*: 206.

Sericesthis nigrolineata (Boisduval), Blanchard, 1851 (1850), *Cat. Coll. ent. Mus. Paris*, 1: 113; Blackburn, 1907, *Trans. roy. Soc. S. Austral.*, 31: 245.

Anodontonyx nigrolineatus (Boisduval), Blackburn, 1907, *Trans. roy. Soc. S. Austral.*, 31: 259, 265.

Melolontha pruinosa Dalman, 1823 (not *pruinosa* Wiedemann, 1819), *Analecta Entomologica*: 53.

Sericesthis pruinosa Blanchard, 1851 (1850), *Cat. Coll. ent. Mus. Paris*, 1: 113.

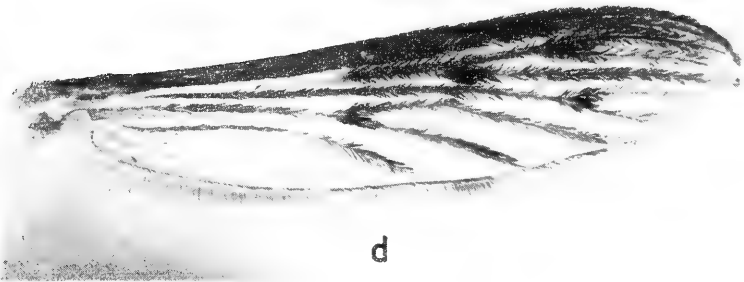
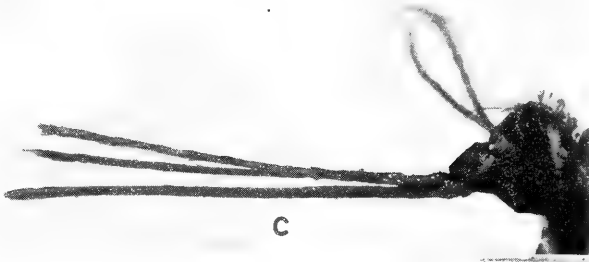
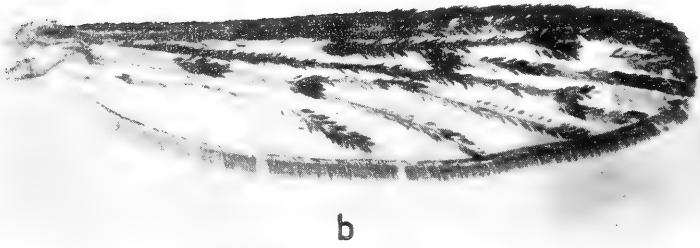
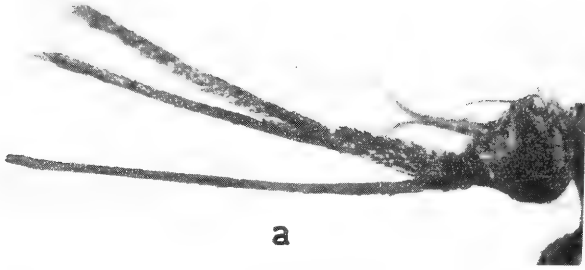
Scitala languida Erichson, 1842, *Arch. f. Naturg.*, 1: 168; Blanchard, 1851 (1850), *Cat. Coll. ent. Mus. Paris*, 1: 113.

SERICESTHIS GEMINATA Boisduval

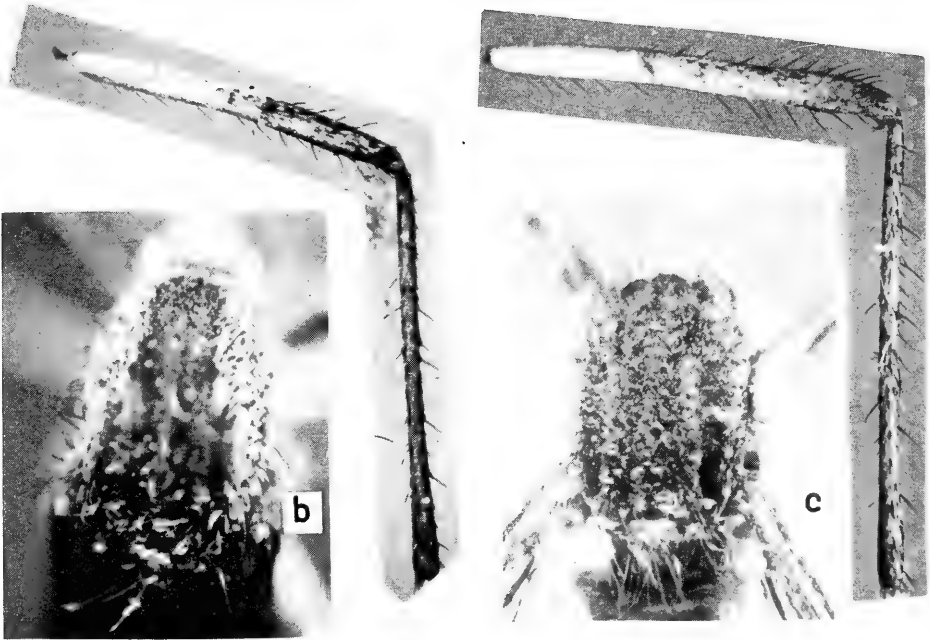
Sericesthis geminata Boisduval, 1835, *Voyage de l'Astrolabe, Col.*: 206; Blanchard, 1851 (1850), *Cat. Coll. ent. Mus. Paris*, 1: 113; Blackburn, 1907, *Trans. roy. Soc. S. Austral.*, 31: 244.

Scitala pruinosa Dalman (*sensu* Burmeister, 1855), *Handb. Ent.*, 4 (2): 231.

It is unfortunate that the result of the foregoing is that the name of a common beetle must disappear and be replaced by *geminata*. It must, however, be recognized that the name *pruinosa* disappears not only as a result of Burmeister's misidentification of the species but also by the rule of homonymy. The only alternative would be an appeal to the International Commission on Zoological Nomenclature to place *Sericesthis pruinosa* (Dalman) on the Official List of accepted names (on the grounds that the name has been much used in the literature), and further to designate as the type of that species a specimen of *S. geminata* Boisduval. The Commission, however, requires strong evidence that confusion will result if the action is not taken and this cannot be claimed in the present case.



Anopheles atratipes Skuse and *Anopheles tasmaniensis* Dobrotworsky.



Anopheles tasmaniensis Dobrotworsky and *Aedes nigrithorax* Macquart.

STUDIES ON THE INHERITANCE OF RUST RESISTANCE IN OATS

IV. EXPRESSION OF ALLELOMORPHISM AND GENE INTERACTION FOR CROWN RUST RESISTANCE IN CROSSES INVOLVING THE OAT VARIETY BOND

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[Read 28th September, 1966]

Synopsis

Segregation for crown rust reaction type was studied in the F_2 and F_3 generations in both seedling and adult plant stages in crosses between the resistant variety Bond and susceptible varieties and in crosses between Bond and the varieties Landhafer, Santa Fe, Trispermia, Mutica Ukraine (Ukraine) and Victoria, all resistant to the prevalent Australian races. The immunity of Bond was conditioned by two dominant genes, acting in complementary fashion, in both stages of growth. However dominance was incomplete at high temperatures, modifying the characteristic F_2 9 resistant : 7 susceptible ratio to a corresponding 5 : 11 ratio. The studies extended the genes for resistance identified in certain of the resistant varieties. Landhafer was found to have a third factor acting in complementary dominant fashion with one of the two complementary Bond factors in conditioning seedling resistance only. A third factor in Santa Fe was a complementary dominant factor to the same member of one of the two Bond factors. It was effective in conditioning resistance in both seedling and adult plant stages. The fifth factor in Ukraine was a third member of the allelic series at one of the Bond loci. Fulghum and Algerian contributed the fourth member of the allelic series at one of the Bond loci and acted in complementary fashion with the second Bond gene to confer adult plant resistance only. Grass clump type segregates were observed in the F_2 generation of the cross between Bond and Landhafer. The segregation ratio suggested the genetic action of an inhibitor gene to a dominant gene for grass clumping.

INTRODUCTION

The oat variety Bond has proved a valuable source of resistance to crown rust (*Puccinia coronata avenae* Erikss.) in North America in breeding improved varieties. It originated in Australia as a selection from a cross made by Pridham at Cowra Experiment Farm between the variety Golden Rain and an offtype of the Red Algerian variety introduced from Algeria. Resistance to most races of crown rust and some races of oat smuts was incorporated into Bond; resistance to the latter diseases apparently was transferred from the Red Algerian parent. Reference to the mechanisms involved in the incorporation of crown rust resistance will be considered later. In addition, Bond possesses the agronomic virtue of stiff straw.

With the increase in prevalence of crown rust races attacking Victoria derivatives in North America and the susceptibility of these varieties to *Helminthosporium* blight (*Helminthosporium victoriarum* Meehan and Murphy) considerable attention was turned about 1945 to the production of commercial varieties deriving resistance from Bond. Several important economic varieties were subsequently released from Bond crosses. However, with the popularity of such derivatives, race 45 of crown rust, capable of attacking Bond and its derivatives, increased tremendously. As a result the varieties Landhafer, Santa Fe and Trispermia have been used more recently in breeding for rust resistance.

In Australia Bond, included in the international differential varietal crown rust set in physiological race surveys, was resistant until 1949, when Waterhouse (1952) isolated two races capable of attacking it from field collections. Investigations by Baker and Upadhyaya (1955) for the period 1953-55 showed that races virulent on Bond were not prevalent and Bond remained a good source of resistance for the breeding of resistant varieties.

In the results presented in the current paper the mode of inheritance of crown rust resistance in Bond was analysed. The factors present in Bond were also shown to interact, or to be allelic, with factors in other resistant and, in certain instances, susceptible varieties. Genetic independence or otherwise between the Bond genes and the stem rust resistance gene (Rd_1) in Richland was also studied.

LITERATURE REVIEW

Crown rust resistance in Bond has been shown to be conditioned by a pair of dominant complementary factors by several investigators (Hayes *et al.*, 1939; Weetman, 1942; Cochran *et al.*, 1945; Ko *et al.*, 1946; Litzenberger, 1949; Kehr and Hayes, 1950; Griffiths, 1953). However, Torrie (1939) obtained an F_2 ratio approximating 11 susceptible : 5 resistant plants, and interpreted the results on the basis of the action of a strong gene in Bond with another masking its effect. At the same time this ratio was explained by Hayes *et al.* (1939) and Ko *et al.* (1946) on the basis of a very weak expression for resistance when both complementary factors in Bond were present in the heterozygous condition.

Modifications of the above reported ratios were observed by certain workers. Apparent segregation of a single factor due to the common presence of one of the complementary Bond genes was reported in crosses between Bond and the varieties Iogold (Hayes *et al.*, 1939) and Santa Fe (Litzenberger, 1949). Whilst Finkner *et al.* (1955) reported the operation of a single factor in Bond from observations on the cross of its derivative, Clinton, with Ukraine, Osler and Hayes (1953) detected the presence of non-identical allelomorphous factors in the variety Santa Fe. Weetman (1942) from field data indicated that resistance in Mutica Ukraine to race I was due to two dominant complementary genes. He suggested that the factors in Ukraine were probably allelomorphous to the Bond genes for resistance.

Inhibition of the factors for resistance in Bond has been reported by certain workers. Richland-Fulghum possessed two complementary inhibitors (Cochran *et al.*, 1945), Ukraine possessed one factor for seedling resistance to race 57 and this gene inhibited the resistance of Clinton against race 109 (Finkner *et al.*, 1955); undetermined factors in S.D. 334 (a Richland derivative) inhibited the resistance of Bond resulting in an F_2 ratio of 15 susceptible : 1 resistant plant (Ko *et al.*, 1946).

Studies on the mode of inheritance of crown rust resistance in the varieties Landhafer, Santa Fe, Mutica Ukraine and Victoria have been reviewed in previous papers in this series (Upadhyaya and Baker, 1960; Upadhyaya and Baker, 1962*b*). Against Australian races Landhafer possessed two factors for adult plant resistance, one of which conditioned seedling or physiological resistance in addition; Santa Fe possessed one factor operative in both seedling and adult plant stages; Mutica Ukraine (henceforth designated as Ukraine) possessed one factor for seedling resistance independent of the three factors for adult plant resistance (two of which acted in complementary fashion). The Victoria type crown rust resistance was conditioned by two linked complementary factors (with a linkage value of 9.6 ± 1.7) in the seedling stage, by two independent factors operative at the adult plant stage only and by one independent factor operative at both stages. The action of the latter factor was inhibited by a linked gene showing approximately 10% recombination with it. One of the factors for adult plant resistance was linked with approximately 10% recombination with the two linked complementary factors for seedling resistance.

Upadhyaya and Baker (1965) studied the relationships of the genes for resistance in the varieties Landhafer, Santa Fe, Trispermia, Ukraine and Victoria to the prevalent Australian races of crown rust. The two factor pairs in Landhafer conditioning adult plant resistance, one of which conferred seedling

resistance in addition, were independent of the factors in the varieties Santa Fe, Trispermia and Victoria. The seedling reaction type of Landhafer was epistatic to those of Trispermia and Victoria. The factor for both seedling as well as adult plant resistance in Santa Fe was independent of the factors in Victoria and epistatic to them. Certain modifying gene(s) resulted in the expression of a reaction type similar to that characteristic of Victoria by suppressing the Santa Fe gene. The Santa Fe factor was considered allelic to the factors in Ukraine and Trispermia. The reaction type of Santa Fe was dominant to that of Trispermia in tests with four races, but with race 203 the Santa Fe gene was inhibited by a pair of complementary factors, one contributed by each variety. The three factor pairs in Ukraine, two acting in complementary fashion, involved in adult plant resistance were independent of the Santa Fe gene. Indirect evidence indicated that the factors conditioning seedling resistance in Santa Fe and Victoria were genetically independent. The independence of the factors responsible for adult plant resistance in Landhafer and Ukraine and likewise the independence of the Ukraine and Victoria adult plant factors could not be established in the absence of studies involving the appropriate crosses.

Upadhyaya and Baker (1962a) showed that the oat varieties Burke and Laggan possessed a single gene (Rd_1) operative against races 2 and 12 of stem rust (*P. graminis avenae* E. and H.).

EXPERIMENTAL RESULTS

The experimental procedure was as set out by Upadhyaya and Baker (1960).

(A) *Studies on Inheritance of Crown Rust Resistance*

Crosses involving Bond with the following varieties were studied:—

Fulghum, Algerian, Burke and Laggan—susceptible to all crown rust races used.

Santa Fe, Landhafer, Ukraine and Victoria—susceptible to only specific races of crown rust.

(a) F_1 Reaction Types and Reactions

The reaction types and reactions of the parents and F_1 's are presented in Table 1.

The adult plant immune reaction and highly resistant reaction seedling type ("0;") characteristic of Bond was dominant or partially dominant in crosses involving specific races where the second parent was susceptible. Likewise where both parents were resistant the immunity or highly resistant reaction type of Bond was usually epistatic or partially so. However, in certain cases a slightly less resistant reaction than either parent was observed in the mature plant stage. Incomplete dominance of the reaction or reaction type of resistant parents was observed in the case of race 203 to which Bond was susceptible.

To field inoculum, comprising a mixture of races, none of which were, however, virulent on Bond the reactions of the F_1 plants in Bond crosses were intermediate or moderately susceptible. In certain cases slightly variable reactions were exhibited among different F_1 plants in the same cross.

(b) *Behaviour of Segregating Generations Involving Races to which only Bond was Resistant*

(1) F_2 Segregation

(i) Seedling tests

Data relating to these tests are presented in Table 2.

In crosses between Bond and Fulghum, Algerian, Burke, Santa Fe and Ukraine a satisfactory agreement between observed and expected results for each F_2 population was observed on the basis of segregation of two dominant complementary factors contributed by Bond. The total segregation of the separate plants in each cross and the grand total for all crosses also agreed

TABLE I
Parental and F₁ seedling reaction types and adult reactions in crosses involving the oat variety Bond

Parent or cross	Seedling reactions to races						Reactions in the adult stage						Field
	203	226	237	237-4	259	286	203	226	237	237-4	259	Field	
Bond	4	0;	0;	0;	0;	0;	S ¹	I	I	I	I	I	
Fulghum	4	4	4	4	4	3	S	S	S	S	S	S	
Algerian	4	4	4	4	4	3	-	-	-	-	-	S (98%)	
Burke	4	4	4	4	4	3	-	-	-	-	-	S	
Laggan	4	4	4	4	4	4	-	-	-	-	-	MS	
Santa Fe	4	;	;	;	;	4	I	I	I	I	I	I	
Ukraine	4	;	;	;	;	4	I	I	I	I	I	I	
Landhafer	;	;	;	;	;	4	I	I	I	I	I	I, MR-Int.	
Victoria	In	In	In	In	;	4	R	R	R	R	R	I (98%)	
F ₁ Fulghum × Bond	-	1	-	-	0;	In	R	R	R	R	R	R	
F ₁ Algerian × Bond	-	0;	-	-	0;	0; -1	-	R	MR	R	R	Int.-S	
F ₁ Burke × Bond	-	0;	-	-	0;	0;	-	R	R	R	R	Int.-R	
F ₁ Laggan × Bond	-	1	-	-	-	-	-	-	MR	R	MR	Int.-S	
F ₁ Santa Fe × Bond	1, 3c	3c	-	-	-	;	-	MR	MR	MR	MR	I, R-MR	
F ₁ Ukraine × Bond	-	0;	-	-	-	0;	R	R	R	R	R	-	
F ₁ Landhafer × Bond	1	0;	0;	2	0;	0; 1=	R	I	-	-	-	Int.-R	
F ₁ Victoria × Bond	2n	0;	1	2-	0; -2-	;-1=	-	I	MR	MR	MR	Int.-R	

¹ I = immune, R = resistant, MR = moderately resistant, Int. = intermediate reaction, S = susceptible.

statistically with the expected 9 resistant : 7 susceptible F₂ seedling ratio. The data for the totals of each cross were also homogeneous. Figures for the crosses Fulghum × Bond and Burke × Bond, tested against race 286, where the frequencies were corrected from F₃ behaviour, are not included in the Table.

TABLE 2

F₂ seedling segregation for crown rust reaction type in crosses involving Bond and certain susceptible varieties

Cross	Crown rust race	F ₂ reaction types			Total	Expected ratio	P value	
		Resistant 0;	1 2-	Susceptible 3-4				
Fulghum × Bond ..	226	119	41	1	122	283	9 Res. : 7 Sus.	0.90-0.80
	259	60	10	-	58	128	9 Res. : 7 Sus.	0.80-0.70
Total		231			180	411	9 Res. : 7 Sus.	1.00
Algerian × Bond ..	226	54	8	-	46	108	9 Res. : 7 Sus.	0.90-0.80
	237-4	30	21	-	50	101	9 Res. : 7 Sus.	0.30-0.20
	286	63	45	2	97	207	9 Res. : 7 Sus.	0.50-0.30
Total		223			193	416	9 Res. : 7 Sus.	0.30-0.20
Burke × Bond ..	259	89	50	2	125	266	9 Res. : 7 Sus.	0.30-0.20
Santa Fe × Bond ..	286	238	80	43	274	635	9 Res. : 7 Sus.	0.90-0.80
Bond × Ukraine ..	226	165	12	-	150	327	9 Res. : 7 Sus.	0.50-0.30
Grand Total		1133 ²			922	2055	9 Res. : 7 Sus.	0.50-0.30
Bond × Victoria ..	259	12	-	16	63	91	5 Res. : 11 Sus. ¹	1.00-0.90
Landhafer × Bond	286	137	13	-	54	204	45 Res. : 19 Sus.	0.50-0.30

¹ Tests conducted at high temperatures modifying expected 9 res. : 7 sus. ratio.

² χ^2_4 heterogeneity for totals of 5 separate crosses=1.96; P value=0.80-0.70.

On this calculated basis the number of resistant and susceptible seedlings were 106.1 and 98.9 respectively (P value=0.20-0.10); in the cross Burke × Bond the corresponding numbers were 184.5 and 114.5 respectively (P value=0.10-0.05). F₂ segregation in the cross Bond × Victoria was studied at high temperatures with daily maxima in excess of 80°F. Under these environmental conditions the doubly heterozygous plants exhibited a "3" reaction type resulting in a 5 resistant : 11 susceptible F₂ ratio with which the observed segregation agreed statistically.

In the cross Landhafer × Bond a ratio very close to 3 resistant : 1 susceptible was obtained. It was found, however, from F₃ studies to be reported later, that an alternative complementary factor from Landhafer interacted with one of the two Bond complementary genes. On this assumption the following genotypes were expected when segregation was studied in tests involving race 286 :

F ₃ (Homozygous resistant)	F ₂ (Resistant) (Segregating)	(Susceptible) (Homozygous susceptible)
1 B _d _a B _d _a B _d _b B _d _b B _d ₁ B _d ₁	2 B _d _a B _d _a B _d _b b _d _b b _d ₁ b _d ₁	1 B _d _a B _d _a b _d _b b _d _b b _d ₁ b _d ₁
2 " " " " " b _d ₁	4 " " " " B _d ₁ b _d ₁	2 " b _d _a " " " "
1 " " " " b _d ₁ b _d ₁	2 " " b _d _b b _d _b " "	1 b _d _a " " " " "
2 " " B _d _b b _d _b B _d ₁ B _d ₁	2 B _d _a b _d _a B _d _b B _d _b B _d ₁ B _d ₁	1 " " B _d _b B _d _b B _d ₁ B _d ₁
1 " " b _d _b " " "	4 " " " " " b _d ₁	2 " " " " " b _d ₁
	2 " " " " " b _d ₁ b _d ₁	1 " " " " " b _d ₁ b _d ₁
	4 " " B _d _b b _d _b B _d ₁ B _d ₁	2 " " B _d _b b _d _b B _d ₁ B _d ₁
	8 " " " " " b _d ₁	4 " " " " " b _d ₁
	4 " " " " " b _d ₁ b _d ₁	2 " " " " " b _d ₁ b _d ₁
	2 " " b _d _b b _d _b B _d ₁ B _d ₁	1 " " b _d _b b _d _b B _d ₁ B _d ₁
	4 " " " " " b _d ₁	2 " " " " " b _d ₁

In the F_2 therefore, a ratio of 45 resistant : 19 susceptible seedlings was expected and a satisfactory fit to this hypothesis was observed.

Relationship of F_2 seedling reaction types to different races was studied in the crosses Fulghum \times Bond and Burke \times Bond where inoculations on the primary leaves were carried out with mixtures of races 226, 259 and 286 and 226, 237 and 237-4 respectively. In no case was any marked variation in reaction type noted in the case of any F_2 seedling, indicating the operation of the same factors in Bond against all races in the mixtures.

(ii) Adult plant tests.

The F_2 segregation data for adult plant behaviour pertaining to the crosses of Bond with Fulghum, Algerian and Laggan are presented in Table 3.

TABLE 3

F₂ segregation for adult plant crown rust reaction in crosses involving Bond and certain susceptible varieties

Cross	Adult plant reactions			Total	Expected ratio	P value
	I ¹	R-MR	MS-S			
Fulghum \times Bond	65	29	35	129	3 Res. : 1 Sus.	0.70-0.50
Algerian \times Bond	82	39	54	175	3 Res. : 1 Sus.	0.10-0.05
Total	215	89	304	304	3 Res. : 1 Sus.	0.10-0.05
Laggan \times Bond	126	45	130	301	9 Res. : 7 Sus.	0.90-0.80

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

These figures confirmed the segregation of the two dominant complementary Bond factors in the cross Laggan \times Bond. However, the data for the other two crosses approximated a 3 resistant : 1 susceptible ratio indicating the action of a non-identical allele to one of the Bond genes in the varieties Algerian and Fulghum, operative in the adult plant stage only. The presence of such a factor in the variety Fulghum was confirmed from studies on the relationship of F_2

TABLE 4

Adult plant reactions of F₂ seedlings classified for reaction type to race 286 in crosses of Bond with Fulghum and Burke

Adult plant reaction	Seedling reaction types							
	Resistant			Susceptible	Resistant			Susceptible
	0 ;	;-1	1-2-	3-4	0 ;	;-1	1-2-	3-4
	Fulghum \times Bond				Burke \times Bond			
I ¹	4	3	-	8	27	-	-	-
R	2	-	1	1	9	15	39	-
MR	2	1	2	1	4	-	4	2
Total	15	(17.0) ²		10 (9.0)	98	(100.0)		2 (0.0)
MS-S	1	1	-	11 (12.0)	-	-	2	27 (29.0)
		2 (0.0)				2 (0.0)		

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Expected values in brackets.

seedling reaction types and adult plant reactions, data for which are presented in Table 4 relating to crosses of Bond with Fulghum and Burke. In the cross Fulghum \times Bond with the operation of such a factor three out of seven susceptible seedlings would be expected to show resistance at the adult plant stage and all the resistant seedlings would be expected to maintain their resistance as mature

plants. From the resistant class of seedlings two were found to give a moderately susceptible mature plant reaction and these on progeny tests showed segregation. Obviously these were incorrectly classified. From among the susceptible seedlings, 10 compared with the nine expected out of 21 gave a resistant reaction due to the operation of the allele from Fulghum. In the cross Burke \times Bond two resistant seedlings out of 100 exhibited a moderately susceptible adult plant reaction and in this case also these were almost certainly due to incorrect classification. Similarly two susceptible seedlings produced moderately resistant adult plants, probably for similar reasons. Otherwise there was close agreement between seedling reaction types and adult plant reactions in this cross. It was thus concluded that the varieties Algerian and Fulghum possessed an effective allele to one of the complementary dominant factors in Bond and that Burke and Laggan carried the recessive allele at this locus.

(2) F_3 Seedling Segregation

Progeny tests were carried out on F_2 plants which had been classified for reaction type or randomly selected. Data for the different crosses are presented in Table 5. The expected reaction in all crosses except Landhafer \times Bond

TABLE 5

F_3 seedling behaviour for crown rust reaction in crosses involving Bond and certain susceptible varieties

Cross	Crown rust races	F_3 behaviour			Total	Expected ratio	P value
		Res. ¹	Seg.	Sus.			
Fulghum \times Bond	226 259 & 286						
(a) ²		3	22	13	38	1 Res. : 8 Seg. : 7 Sus.	0.50-0.30
(b)		11	65	64	140	1 Res. : 8 Seg. : 7 Sus.	0.70-0.50
	Total	14	87	77	178	1 Res. : 8 Seg. : 7 Sus.	0.70-0.50
Burke \times Bond ..	226 237-4 & 237						
(a)		8	57	35	100	1 Res. : 8 Seg. : 7 Sus.	0.30-0.20
(b)		8	70	49	127	1 Res. : 8 Seg. : 7 Sus.	0.50-0.30
	Total	16	127	84	227	1 Res. : 8 Seg. : 7 Sus.	0.20-0.10
Laggan \times Bond ..	226	10	119	109	237	1 Res. : 8 Seg. : 7 Sus.	0.50-0.30
Santa Fe \times Bond	286						
(b)		6	71 ³	72	149	1 Res. : 8 Seg. : 7 Sus.	0.50-0.30
(c)		12	79 ³	72	163	1 Res. : 8 Seg. : 7 Sus.	0.90-0.80
	Total	18	150	144	312	1 Res. : 8 Seg. : 7 Sus.	0.70-0.50
Bond \times Ukraine	286						
(b)		7	63 ³	68	138	1 Res. : 8 Seg. : 7 Sus.	0.50-0.30
Bond \times Victoria	259						
(b)		8	45 ³	56	109	1 Res. : 8 Seg. : 7 Sus.	0.20-0.10
	Grand Total	73	591	537	1201	1 Res. : 8 Seg. : 7 Sus.	0.80-0.70
Landhafer \times Bond	286						
(c)		12	70 ³	30	112	7 Res. : 38 Seg. : 19 Sus.	0.80-0.70

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² (a)=unclassified for F_2 phenotype, (b)=classified for F_2 seedling reaction type, (c)=classified for F_2 adult plant reaction.

³ Some lines in the segregating category showed a preponderance of susceptible plants.

was 1 homozygous resistant : 8 segregating : 7 homozygous susceptible lines. In the Landhafer \times Bond cross the corresponding expected ratio as shown previously was 7 : 38 : 19 respectively. In all cases there was satisfactory agreement statistically between observed and expected results. The confirmation of the predicted ratio in the Landhafer \times Bond cross indicated that Landhafer possessed a dominant factor complementary to one of the two dominant complementary genes in Bond.

In the crosses of Bond with Landhafer, Santa Fe, Ukraine and Victoria certain segregating F_3 lines showed a preponderance of susceptible seedlings. This was probably associated with high temperatures and was observed especially in tests conducted under glasshouse temperature regimes between 75°–85°F.

F_3 segregation was also studied in the progenies of F_2 plants classified for seedling reaction type to race 286 in crosses of Bond with Fulghum and Burke respectively, and these results are presented in Table 6. Good agreement was

TABLE 6

F₃ seedling behaviour for crown rust reaction of F₂ plants classified for seedling reaction type in crosses involving Bond with Fulghum and Burke

F_2 reaction types to race 286							F_3 behaviour to mixture of races					
							226, 259 and 286			226, 237 and 237-4		
							Res. ¹	Seg.	Sus.	Res.	Seg.	Sus.
							Fulghum × Bond			Burke × Bond		
0;	12	28	1	10	29	—
;-1	—	34	—	1	14	—
1-2-	—	4	—	—	39	1
3-4	—	2	59	—	4	29

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

shown between F_2 reaction type and expected F_3 segregation except for two instances, one in each cross, where a resistant F_2 plant gave homozygous susceptible progenies. These were probably errors in F_2 classification. Similarly a few plants classified as susceptible in F_2 gave segregating F_3 progenies. This may have been due to high temperature effects resulting in heterozygous genotypes involving Bond genes being classified as susceptible.

(c) *Behaviour of Segregating Generations Involving Races to which both Bond and the Second Parent were Resistant*

(1) F_2 Segregation

(i) Seedling tests.

The varieties Landhafer, Santa Fe and Ukraine each possessed a single factor for seedling resistance to races to which they were resistant. The F_2 segregation in the cross Landhafer × Bond in tests involving race 286 to which Landhafer was susceptible conformed to 45 resistant : 19 susceptible. Therefore with the operation of one additional dominant factor in Landhafer in tests involving races to which it also was resistant the expected F_2 ratio was 237 resistant : 19 susceptible; if allelism was involved the expected ratio would be modified to a characteristic dihybrid ratio of 15 resistant : 1 susceptible. In the case of crosses between Bond and both Santa Fe and Ukraine the ratio conformed statistically to a 15 : 1 rather than 57 : 7 ratio. Hence against races to which either Santa Fe or Ukraine were respectively resistant a non-identical allele to one of the two complementary factors in Bond was operative. These were alleles rather than identical genes since the factor in Ukraine conferred resistance to fewer races.

The F_2 segregation of the Victoria type of rust resistance in crosses with susceptible varieties was 71.9 resistant : 28.1 susceptible; with the operation of the two complementary Bond factors only 12.3 per cent of plants were expected to be susceptible. Since partial dominance was exhibited by the majority of factors in both Bond and Victoria, the intermediate and resistant classes were grouped together for goodness of fit tests.

TABLE 7
F₂ seedling segregation for crown rust reaction in crosses involving Bond and certain varieties utilising races to which both parents were resistant

Cross	Crown rust race	<i>F₂</i> reaction types				Total	Expected ratio	P value
		0 ; - ;	Resistant ; - 1 -	2 -	Susceptible 3 - 4			
Landhafer × Bond	226	406	19	—	25	237 Res. ¹ ; 19 Sus.	0.20-0.10	
	237	80	17	—	11	237 Res.; 19 Sus.	0.30-0.20	
	237-4	153	27	1	15	237 Res.; 19 Sus.	0.90-0.80	
	259	174	17	—	14	237 Res.; 19 Sus.	0.80-0.70	
Total		813	80	1	65	959 Res.; 19 Sus.	0.50-0.30	
Santa Fe × Bond	226	105	48	13	7	57 Res.; 7 Sus.	0.30-0.20	
	237-4	212	47	—	11	57 Res.; 7 Sus.	0.20-0.10	
	259	299	200	51	32	57 Res.; 7 Sus.	0.50-0.30	
	Total	616	295	64	50	1025 Res.; 7 Sus.	0.10-0.05	
Bond × Ukriane	237-4	192	104	7	20	57 Res.; 7 Sus.	1.00-0.90	
	Total	975	303	—	—	—	—	
Bond × Victoria	226	56	25	11	23	71.9 Res.; 28.1 Sus.	0.02-0.01	
	237-4	80	55	6	23	71.9 Res.; 28.1 Sus.	0.70-0.50	
	286	99	61	32	26	71.9 Res.; 28.1 Sus.	0.90-0.80	
	Total	235	141	49	72	497 Res.; 28.1 Sus.	0.20-0.10	
		425	—	—	—	—	—	

¹ Res. = resistant, Sus. = susceptible.

The data for F_2 seedling segregation in crosses of Bond with Landhafer, Santa Fe, Ukraine and Victoria are presented in Table 7. Statistical tests showed good agreement between observed and expected results except in tests employing race 226 in the cross Bond \times Victoria.

(ii) Adult plant tests.

F_2 generations of crosses involving Bond with Landhafer, Santa Fe and Victoria respectively were classified for mature plant field reactions and the data are presented in Table 8. With the operation of an additional partially dominant factor in Landhafer the expected F_2 ratio in this cross was 1005 resistant : 19 susceptible. In the cross Santa Fe \times Bond a corresponding 15

TABLE 8

F_2 segregation for adult plant crown rust reaction in crosses involving Bond and certain varieties utilising races to which both parents were resistant

Cross	Adult plant reactions					Total	Expected ratio	P value
	Resistant			Susceptible				
	I ¹	R	MR	MS	S			
Landhafer \times Bond	231	28	—	3	5	267	1005 Res. ² : 19 Sus.	0.20-0.10
Santa Fe \times Bond	483	122	18	7	26	656	15 Res.: 1 Sus.	0.20-0.10
Bond \times Victoria ..	273	15	—	2	3	293	97.4 Res.: 2.6 Sus.	0.50-0.30

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Res.=resistant, Sus.=susceptible.

resistant : 1 susceptible ratio was expected ; in the cross Bond \times Victoria the expected percentage of susceptible plants was 2.6 (or seven-sixteenths of 5.92%).

Statistical agreement between observed and expected results was good as shown in Table 8. However it was subsequently observed in progeny tests

TABLE 9

F_3 seedling behaviour for crown rust reaction in crosses involving Bond and certain varieties utilising races to which both parents were resistant

Cross	Crown rust race	Res. ¹ Seg. Sus.			Total	Expected ratio	P value
		Res.	Seg.	Sus.			
Landhafer \times Bond							
(a) ²	259	39	62	6	107	65 Res.: 152 Seg.: 19 Sus.	0.70-0.50
(b)	259	10	15	2	27	65 Res.: 152 Seg.: 19 Sus.	1.00-0.90
	Total	49	77	8	134	65 Res.: 152 Seg.: 19 Sus.	0.70-0.50
Santa Fe \times Bond							
(a)	259	49	62	6	117	7 Res.: 8 Seg.: 1 Sus.	0.80-0.70
(b)		64	74	9	147	7 Res.: 8 Seg.: 1 Sus.	1.00-0.90
	Total	113	136	15	264	7 Res.: 8 Seg.: 1 Sus.	0.90-0.80
Bond \times Ukraine							
(b)	237 & 237-4	51	49	9	109	7 Res.: 8 Seg.: 1 Sus.	0.50-0.30
Bond \times Victoria							
(a)	226 & ..	13	32	6	51	25.5 Res.: 62.2 Seg.: 12.3 Sus.	1.00-0.90
(b)	286 ..	27	59	16	102	25.5 Res.: 62.2 Seg.: 12.3 Sus.	0.70-0.50
	Total	40	91	22	153	25.5 Res.: 62.2 Seg.: 12.3 Sus.	0.70-0.50

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² (a)= F_2 material classified for adult plant reaction ; (b)= F_2 material classified for seedling reaction type.

of the susceptible plants from the cross Landhafer \times Bond that one segregated for the Bond type of resistance and susceptibility, one for the Landhafer type of resistance and susceptibility, whilst one was homozygous resistant for the Landhafer reaction type. This was probably due to the fact that the gene allelic to the dominant complementary factor in Bond was not operative at the adult plant stage. On this hypothesis the expected F_2 ratio was 249 resistant : 7 susceptible; on the sample tested this ratio could not be statistically distinguished from the respective 1005 : 19 ratio previously hypothesized.

Correlated behaviour of F_2 seedlings and adult plants in the cross Bond \times Ukraine is presented later.

(2) F_3 Segregation

Representative samples of plants from each reaction class were tested for random F_2 progeny behaviour in various crosses. The observed and calculated expected frequencies of F_3 lines are presented in Table 9. The expected ratios in the different crosses were as follows :

	Homozygous resistant	Segregating	Homozygous susceptible
Landhafer \times Bond	85	152	19
Santa Fe or Ukraine \times Bond	7	8	1
Victoria \times Bond	25.5	62.2	12.3

Results showed good agreement between observed and expected results and confirmed assumptions that in the different crosses various factors conditioning seedling resistance were operative as follows :

In the cross Bond \times Landhafer, Bond contributed two dominant complementary factors; the variety Landhafer contributed two factors one of which acted in a dominant complementary manner to one of the two factors in Bond, the second being independent and dominant. The varieties Santa Fe and Ukraine also had one independent dominant factor but possessed a complementary allele to one of the two Bond factors. The genes were allelic and not identical for reasons previously indicated. In the cross Bond \times Victoria there were no interactions between the factors contributed by the two varieties and in all six factors were concerned in conditioning seedling resistant in this cross.

(d) *Relationship of F_2 or F_3 Segregating Reactions and Reaction Types to Different Races, Between Segregating Seedling and Adult Plants, and Between F_2 and F_3 Segregating Generations*

(1) F_2 Seedling compared with F_2 Seedling

Inoculations were made on the primary leaf with a rust race to which both parents were resistant, and the secondary leaves inoculated with a race to which only Bond was resistant. The results from such studies involving three crosses are set out in Table 10. In all instances the susceptible classes were susceptible to both races. The majority of seedlings exhibiting an intermediate reaction type on the primary leaf showed full susceptibility on the secondary leaves, indicating that they possessed factors for resistance from the parent other than Bond. Some seedlings from this category, however, showed the Bond reaction type to races to which only Bond was resistant, indicating only partial dominance of the Bond genotype or the action of modifying genes. Considering the total resistant class the expected fractions of F_2 plants susceptible to the second race were thus :

Cross Landhafer \times Bond	—57/237
Cross Santa Fe \times Bond	—24/60
Cross Bond \times Ukraine	—24/60

In all three crosses the deviations were not statistically significant at the 5% probability level.

TABLE 10
Association of F₂ seedling reaction types in Bond crosses between tests involving races to which both parents were resistant and those involving races to which only Bond was resistant

F ₂ reaction types (both parents resistant)	F ₂ reaction types (only Bond resistant)							
	Race 286		Race 286		Race 286		Race 286	
	Resistant	Susceptible	Resistant	Susceptible	Resistant	Susceptible	Resistant	Susceptible
	0 ; - 1	3 - 4	0 ; - 1	3 - 4	0 ; - 1	3 - 4	0 ; - 1	3 - 4
	Landhafer × Bond		Santa Fe × Bond		Bond × Ukraine			
0 ; - ; ; - 1	133 4	28 13	146 2	65 42	24 —	23 7	— —	— —
3 - 4	150 (145·1) ¹	41 (45·9) ²	151 (154·8)	107 (103·2) ³	27 (34·2)	30 (22·8) ⁴	— —	1 1
Total	—	13	—	11	—	—	—	—

¹ Expected values in brackets.

² P value = 0·50-0·30 ; ³ P value = 0·70-0·50 ; ⁴ P value = 0·10-0·05.

One interesting observation was noted in the cross Bond \times Ukraine when F_2 seedlings classified for reaction type to races 237-4 and 226 were reinoculated with race 286 fifty-two days after sowing. All resistant seedlings maintained their resistance whereas of the seedlings susceptible to race 226, 16 out of 28 were resistant to race 286. This shows perfect agreement with the 15.7 resistant plants expected on the assumption that the complementary factors for adult plant resistance in Ukraine were operative at this stage of growth. Presumably the third factor conditioning adult plant resistance in Ukraine was not operative against this race.

(2) F_2 Seedling compared with F_2 Adult Plant

Seedlings classified for reaction type in crosses of Bond with Santa Fe, Ukraine and Victoria were transplanted for observations on adult plant field reactions, and the data are presented in Table 11.

The assumptions relating to gene behaviour in different crosses were:

In the cross Santa Fe \times Bond the factors operative in the seedling stage conditioned adult plant resistance in addition; the complementary allele in Santa Fe, operative in the adult stage only, resulted in all resistant seedlings maintaining their resistance and the susceptible seedling group proving susceptible subsequently.

In the cross Bond \times Ukraine, the seedling resistance Ukraine factor operated against few races only and was ineffective in conditioning adult plant resistance in the field where several races were involved. The three factors in this variety conditioning only adult plant resistance were operative. The complementary allele was also effective in Ukraine (the comparable factors in Fulghum and in Santa Fe behaving similarly), the resistant seedling class producing 21 susceptible adult plants in a population of 960 and the susceptible seedling category 57 resistant plants in a population of 64.

In the cross Bond \times Victoria 56.25 per cent of seedlings maintained their resistance due to the operation of the Bond factors. On the 31.45 per cent resistant due to segregation of factors from Victoria, 0.55 were susceptible and of the 12.3 per cent susceptible seedlings 2.04 were susceptible as mature plants.

From the data presented in Table 11 two plants in each of the crosses Santa Fe \times Bond and Bond \times Ukraine did not behave exactly as expected. The reaction type class “;”-“1” in the cross Bond \times Ukraine was considered to possess the Ukraine type of resistance on the basis of F_3 progeny reaction types. No statistically significant deviations were obtained. No susceptible adult plants were observed in the Victoria type seedling reaction group; however, since in the population examined only 0.8 was expected, this deviation was clearly not significant.

(3) F_2 Seedling compared with F_3 Seedling

Certain F_2 plants were classified for reaction type to races to which both parents were resistant and their F_3 progenies tested against similar races or against a specific race to which Bond alone was resistant. The information obtained in this regard is set out in Table 12 and shows that two plants, one each in the crosses Bond \times Ukraine and Bond \times Victoria, from the resistant F_2 category yielded susceptible progenies in tests involving races to which both parents were resistant. One line in the cross Bond \times Victoria from the susceptible F_2 class segregated with a preponderance of susceptible plants indicating the operation of the factor Vc_2 and its linked inhibitor.

In tests involving races to which Bond alone was resistant the only lack of correlation was that shown when a homozygous resistant line with a reaction type similar to Bond was derived from an F_2 plant exhibiting an intermediate reaction type. Apart from this discrepancy the behaviour of plants of an

TABLE 11
Adult plant reactions of F₂ seedlings classified for reaction type in crosses involving Bond with Santa Fe, Ukraine and Victoria

Adult plant reactions	Seedling reaction types							
	Santa Fe × Bond		Bond × Ukraine		Bond × Victoria			
	0 ;	1-2-	3-4	0 ;	0 ; -1	0 ; -1	3-4	3-4
I ¹ , R, MR	72 (73.0) ²	61 (61.0)	1 (0.0)	72 (74.0)	70 (68.8)	57 (57.0)	13 (16.0)	45 (44.2)
MS-S	1 (0.0)	—	9 (10.0)	2 (0.0)	2 (3.2) ³	—	5 (2.0) ⁴	2 (0.8) ⁵

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Expected values in brackets.

³ P value=0.70-0.50

⁴ P value=0.10-0.05

⁵ P value=0.80-0.70

⁶ P value=1.00.

} χ^2 values corrected for small numbers.

intermediate reaction type was as expected, progenies segregating for Bond genes or homozygous susceptible lines being produced, indicating the presence of factors contributed by the second parent.

(4) F_2 Adult Plant compared with F_3 Seedling

The F_2 segregation pattern in the cross Landhafer \times Bond was based on the operation of five factors, two from Bond and three from Landhafer. Of

TABLE 12

F_3 seedling behaviour for crown rust reaction of F_2 plants classified for seedling reaction type in crosses involving Bond when tested against various races

	F_2 reaction types to races to which both parents were resistant	F_3 behaviour to					
		races to which both parents were resistant			races to which only Bond was resistant		
		Res. ¹	Seg.	Sus.	Res.	Seg.	Sus.
Landhafer \times Bond	Race 226						
	0 ;	6	10	—	1	17	5
	; -1	2	1	—	1	1	1
	3-4	—	—	8	—	—	8
Santa Fe \times Bond	Race 259						
	0 ;	26	40	—	5	58	3
	; -1	33	14	—	—	3	46
	2-	1	23	—	—	—	25
	3-4	—	—	9	—	—	9
Bond \times Ukraine	Race 237-4						
	0 ;	32	27	1	7	61	6
	; -1	17	19	—	—	1	47
	3-4	—	—	12	—	—	16
Bond \times Victoria	Race 237-4						
	0 ;	21	36	—	9	48	2
	; -1	7	8	1	—	3	18
	2-	2	16	—	—	—	18
	3-4	—	1 ²	10	—	—	11

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² Segregating with preponderance of susceptible seedlings.

these one factor in Landhafer conditioned adult plant resistance only. While the susceptible F_2 plants were therefore expected to produce only susceptible F_3 seedling progenies in tests involving races to which both parents were resistant, some resistant F_2 adult plants when similarly tested were expected to yield susceptible seedling progenies. From data presented in Table 13, containing information pertinent to this correlated study, some F_2 susceptible plants gave either homozygous resistant or segregating lines due to segregation of the Bond factors effective against race 286. These were presumed errors in F_2 classification or labelling. Statistically good agreement between observed and expected results in the segregation of resistant F_2 plants was obtained on the basis of expected ratios of 112 homozygous resistant : 608 segregating : 285 homozygous susceptible and 340 homozygous resistant : 608 segregating : 57 homozygous susceptible lines in tests involving races 286 and 259 respectively.

In the cross Santa Fe \times Bond two factors in Bond and two in Santa Fe, one allelic to one of the Bond factors, were effective in conditioning both seedling and adult plant resistance. Hence susceptible F_2 adult plants would be expected to produce homozygous susceptible F_3 lines and resistant plants to yield homozygous resistant progenies or segregating lines in tests involving races to which both parents were resistant. Probably due to misclassification two in the population of 103 resistant plants produced susceptible progenies and of

the 14 susceptible plants three gave segregating progenies. The former two plants were moderately resistant and the latter three moderately susceptible and all were probably minor misclassifications. It was evident, however, that the same factors conditioned both seedling and adult plant resistance in Bond and also Santa Fe.

TABLE 13

F₃ seedling behaviour for crown rust reaction of F₂ plants from the cross Landhafer × Bond classified for adult plant reaction

Adult plant reactions	F ₃ behaviour to						
	races to which only Bond was resistant			races to which both Bond and Landhafer were resistant			
	Res. ¹	Race 286		Res.	Race 259		
I ²	11	Seg. 62	Sus. 15	33	Seg. 48	Sus. 2	
R-MR	—	2	16	2	13	3	
	Total	11	64	31	35	61	5
	Expected	11.8	64.1	30.1	34.2	61.1	5.7
MS-S	—	1	6	1	1	4	

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

In the cross Bond × Victoria, due to the operation of the factors from Victoria conferring mature plant resistance, only one quarter of the total population, in which the proportion of resistant plants was seven-sixteenths, was expected to give susceptible F₃ seedling progenies in tests involving races to which both parents were resistant and similarly one-fifth of the susceptible F₂ class was expected to produce segregating F₃ lines. Of the 209 plants tested from the former class, 21 gave susceptible progenies compared with 21.4 expected. Since only five susceptible F₂ plants were progeny tested, the fact that no segregating line was observed was obviously not a significant discrepancy since only one was expected.

(5) F₃ Seedling compared with F₃ Seedling

In the four crosses involving Bond parentage approximately 25 seeds of each F₃ line were tested to one race to which both parents were resistant and a similar sample tested to a second race to which only Bond was resistant. The various frequencies and interrelationships on the genetic bases previously formulated were as follows :

Cross	Behaviour to races to which both parents were resistant				Behaviour to race to which only Bond was resistant			
					Homo. Res.	Seg.	Homo. Res.	Total
Landhafer × Bond ..	Homo. Res.	28	38	19	85	
	Seg.	—	114	38	152	
	Homo. Sus.	—	—	19	19	
	Total	28	152	76	256	
Santa Fe × Bond and Bond × Ukraine ..	Homo. Res.	4	14	10	28	
	Seg.	—	18	14	32	
	Homo. Sus.	—	—	4	4	
	Total	4	32	28	64	
Bond × Victoria ..	Homo. Res.	6.25	10.25	9.0	25.5	
	Seg.	—	39.75	22.5	62.25	
	Homo. Sus.	—	—	12.25	12.25	
	Total	6.25	50.0	43.75	100.0	

The observed and expected frequencies, in brackets, are shown in Table 14. Since the F_2 population was classified for reaction type to a race to which both parents were resistant, the expected frequencies were calculated separately within the total of each reaction type class to races to which both parents were resistant and not for the overall totals. There was good agreement between observed and expected results in all crosses except Santa Fe \times Bond. In every test homozygous susceptible lines to one race invariably behaved similarly to the second race. One line in each of the crosses Bond \times Ukraine and Bond \times Victoria segregated to the race to which both parents were resistant but was homozygous resistant to the second race. This may have been due to insufficient plants being tested to detect susceptible seedlings in a line actually segregating; in this case the line would be designated erroneously as homozygous resistant.

TABLE 14

Correlation of F_3 seedling crown rust behaviour in Bond crosses between tests involving races to which both parents were resistant and those involving races to which only Bond was resistant

Cross	F_3 reactions to race to which both parents were resistant	F_3 reactions to race to which only Bond was resistant			Total	P value
		Res. ¹	Seg.	Sus.		
Landhafer \times Bond	Race 259			Race 286		
	Res.	12 (15.1) ²	24 (20.6)	10 (10.3)	46	0.50-0.30
	Seg.	—	52 (57.8)	25 (19.2)	77	0.20-0.10
	Sus.	—	—	13	13	
Santa Fe \times Bond	Res.	11 (13.9)	26 (48.9)	60 (34.6)	97	<0.001
	Seg.	—	86 (75.9)	49 (59.1)	135	0.10-0.05
	Sus.	—	—	21	21	
Bond \times Ukraine	Race 237 and 237-4			Race 286		
	Res.	6 (7.1)	25 (25.0)	19 (17.9)	50	0.90-0.80
	Seg.	1 (0.0)	25 (25.3)	19 (19.7)	45	0.90-0.80
	Sus.	—	—	16	16	
Bond \times Victoria	Race 226			Race 259		
	Res.	5 (7.4)	17 (12.0)	8 (10.4)	30	0.20-0.10
	Seg.	1 (0.0)	35 (40.2)	28 (22.8)	64	0.30-0.20
	Sus.	—	—	11	11	

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² Expected values in brackets.

In the cross Santa Fe \times Bond there was a statistically highly significant deviation from the expected results due mainly to an excess in the number of lines homozygous resistant to race 259 and homozygous susceptible to race 286 over that calculated. This is difficult to explain since the number of lines homozygous resistant to both races was close to that expected. The F_3 ratios in tests involving the two races independently from data presented in Tables 5 and 9 also showed good agreement on the basis of the hypotheses proposed.

(B) *Association between crown rust resistance factors in Bond and stem rust resistance factors in Burke and Laggan*

In the crosses Burke \times Bond and Laggan \times Bond 228 and 235 F_3 lines respectively were tested against race 259 of crown rust and a mixture of races 2 and 12 of oat stem rust. The independent behaviour of genes governing crown rust resistance in Bond and the gene (Rd_1) conditioning stem rust resistance in both Burke and Laggan is clear from the data presented in Table 15.

(C) *Inheritance of grass clump habit and its association with the inheritance of crown rust resistance in the cross Landhafer × Bond*

In F_2 adult plants in the cross Landhafer × Bond 49 in a total of 267 plants showed a grass clump habit of growth. These numbers agreed statistically with a ratio of 13 normal : 3 grass clump ($P=0.90-0.80$) suggesting the action of an inhibitor gene to a dominant gene for grass clumping. Similar gene

TABLE 15

Association of F_3 stem rust and crown rust reactions in crosses of Bond with Burke and Laggan

Stem rust behaviour	Crown rust behaviour							
	Res. ¹	Burke × Bond		Total	Res.	Laggan × Bond		Total
		Seg.	Sus.		Seg.	Sus.		
Res. ..	6 (5.4) ²	36 (38.2)	19 (17.4)	61	1 (1.9)	27 (25.6)	23 (23.5)	51
Seg. ..	10 (10.4)	70 (70.4)	38 (33.2)	118	4 (4.8)	61 (63.3)	61 (57.9)	126
Sus. ..	4 (4.2)	37 (30.4)	8 (14.4)	49	4 (2.3)	30 (29.1)	24 (26.6)	58
Total	20	143	65	228 ³	9	118	108	235 ⁴

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² Expected values in brackets based on marginal totals.

³ $\chi^2_4 = 3.56$; $P=0.50-0.30$.

⁴ $\chi^2_4 = 2.43$; $P=0.70-0.50$.

action for grass clump habit has been observed in wheat crosses (McMillan, 1937; Watson, 1943). The independence of genes determining this character from those conditioning adult plant resistance in Bond and Landhafer is shown from the data in Table 16. A number of weak F_2 plants were observed and

TABLE 16

Association of adult plant reaction to crown rust and grass clump habit in the F_2 generation of a cross between Bond and Landhafer

Adult plant reactions	Growth habit		Grass clump	Total
	Normal	Weak		
I ¹	147 (147.1) ²	40 (41.5)	44 (42.4)	231
R-MR	17 (17.8)	7 (5.0)	4 (5.2)	28
MS-S	6 (5.1)	1 (1.5)	1 (1.4)	8
	Total	218	49	267 ³
	Expected ratio	216.9	50.1 ⁴	
	(13 normal : 3 grass clump)			

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Expected values in brackets based on marginal totals.

³ χ^2_4 for independence=1.67; $P=0.90-0.80$.

⁴ $\chi^2_4 = 0.03$; $P=0.90-0.80$.

these may have been heterozygous for the inhibitor gene in the presence of the dominant factor for grass clumping, indicating partial epistasis.

DISCUSSION AND CONCLUSIONS

From the present studies it is evident that the immunity of Bond to Australian races of crown rust in both seedling and adult plant stages was conditioned by two dominant complementary genes. However, dominance was incomplete at high temperatures and the genotype heterozygous for both factors

gave a moderately susceptible reaction type modifying the characteristic 9 resistant: 7 susceptible F_2 ratio to a respective 5: 11 ratio. These findings are in accordance with the observations of other investigators, including Hayes *et al.* (1939) and Weetman (1942). It is proposed to designate these factors as \underline{Bd}_a and \underline{Bd}_b , the line below each symbol indicating complementary gene action. Presumably one gene was contributed by each of the parents, Golden Rain and Red Algerian selection, to the hybrid from which it was selected. Segregation in a cross between Bond and Golden Rain is currently being studied to investigate this hypothesis.

Operation of a single factor was observed in a number of intervarietal crosses involving Bond. In its crosses with Algerian and Fulghum at the mature plant stage monogenic segregation was observed, whilst in crosses with Santa Fe and Ukraine, involving races to which these varieties were also resistant, duplicate factor segregation was noted. Hayes *et al.* (1939) assumed the presence of a common factor in such crosses, Finkner *et al.* (1955) only a single factor in both varieties whilst Osler and Hayes (1953) and Weetman (1942) detected the presence of factors in Santa Fe and Ukraine allelic to one of the Bond genes. The present studies confirmed the latter findings since the complementary factors in Bond were operative in the seedling stage against races to which the second parent was susceptible. It was also evident that the alleles in the varieties Algerian, Fulghum, Santa Fe and Ukraine were not identical since they were operative only against the races to which the respective parents were resistant, either in both seedling and adult plant stages or in the mature plant stage only.

These studies extended the genes for crown rust resistance identified in certain varieties. The complete genotypes of these varieties for crown rust resistance are given below, where non-interacting genes are indicated by numerical suffixes, interacting (complementary) genes given alphabetical suffixes and allelomorphous genes indicated by apostrophe (') marks according to increasing order of reaction type or reaction. Torrie (1939) claimed that Bond possessed one strong gene and that another masked its effect. If Torrie's strong gene in Bond is that designated as \underline{Bd}_a the alleles in the present instance would be relative to the second Bond factor \underline{Bd}_b . Those in Santa Fe, Ukraine and Fulghum would in the proposed terminology be designated as \underline{Bd}_b' , \underline{Bd}_b'' and \underline{Bd}_b''' respectively. Similarly the alternative gene in Landhafer, assumed to act in complementary fashion with \underline{Bd}_a would be designated \underline{Bd}_L . This factor was also operative against race 286 to which Landhafer was susceptible. The complete list of genes, including those documented by Upadhyaya and Baker (1965), in varieties in which additional factors were revealed in Bond crosses are thus:

Landhafer—three factors. One factor (Ld_1) conditioned seedling as well as adult plant resistance. A second factor Ld_2 was responsible for adult plant resistance only and the third factor \underline{Bd}_L was an alternate complementary factor to one (\underline{Bd}_a) of the two complementary Bond factors in conditioning seedling resistance only.

Santa Fe—three factors. One factor (Sf_1) conditioned seedling as well as adult plant resistance. A second factor (\underline{Tr}_a) acting in complementary fashion with \underline{Tr}_b in Trispernia inhibited the action of Sf_1 against race 203 in the seedling stage only. The third factor \underline{Bd}_b' was complementary in action with \underline{Bd}_a and allelic to \underline{Bd}_b . This factor conditioned seedling resistance to races to which Santa Fe was resistant and also resistance in the adult plant stage.

Ukraine—five factors. One factor Sf_1' , allelic with Sf_1 , conditioned only seedling resistance to race 237. Three genes $M\bar{u}_1$, $M\bar{u}_a$ and $M\bar{u}_b$, conferred

adult plant resistance only, the two latter factors acting in complementary fashion. The fifth factor \underline{Bd}_b '' was a member of the allelic series at the \underline{Bd}_b locus.

Fulghum and Algerian—one gene. The \underline{Bd}_b '' member of the allelic series at this locus acted in complementary fashion with the gene \underline{Bd}_a to confer adult plant resistance only.

The genes previously identified in *Trispermia* were Sf_1 '' allelic with Sf_1 , but exhibiting a higher reaction type, and \underline{Tr}_b complementary to \underline{Tr}_a .

No variety used in these studies or those previously reported in this series of papers was resistant to all Australian races of crown rust and the allelism indicated is obviously a barrier in attempts to combine genes from different varieties to provide a more comprehensive genetic basis for resistance in breeding commercial varieties.

The order of epistasis or dominance in the varieties studied in this series of papers was Bond (immune); Landhafer, Santa Fe, Ukraine (highly resistant); *Trispermia*, Victoria (resistant); Fulghum, Algerian, Burke, Laggan (susceptible).

Plants of a grass clump habit were observed in the F_2 generation of the cross Bond \times Landhafer. Coffman (1964) detected dwarf segregates, some apparently of grass clump or grass tuft habit, in certain intervarietal crosses. He considered dwarfing in general to be due to one, two or three gene pairs with various types of interaction when more than one gene was implicated.

References

- BAKER, E. P., and UPADHYAYA, Y. M., 1955.—Physiologic specialisation of crown rust of oats. *Proc. Linn. Soc. N.S.W.*, 80: 340-357.
- COCHRAN, G. W., JOHNSON, C. O., HYENE, E. G., and HANSING, E. G., 1945.—Inheritance of reaction to smut, stem rust and crown rust in four oat crosses. *Jour. agric. Res.*, 70: 43-61.
- COFFMAN, F. A., 1964.—Inheritance of morphologic characters in *Avena*. United States Dept. Agric. tech. Bull. No. 1308.
- FINKNER, V. C., 1954.—Genetic factors governing resistance and susceptibility of oats to *Puccinia coronata* Corda variety *avenae*, F. & L., Race 57. Iowa State Coll. agric. Expt. Stat. Res. Bull., 411: 1040-1063.
- GRIFFITHS, D. J., 1953.—Varietal resistance and susceptibility of oats to crown rust. *Plant Pathology*, 2: 73-77.
- HAYES, H. K., MOORE, M. B., and STAKMAN, E. C., 1939.—Studies of inheritance in crosses between Bond, *A. byzantina* and varieties of *A. sativa*. Minn. agri. expt. stat. tech. Bull. 137.
- KEHR, W. R., and HAYES, H. K., 1950.—Studies of inheritance in crosses between Landhafer, *A. byzantina* L. and two selections of *A. sativa* L. *Agron. Jour.*, 42: 71-78.
- KO, S. Y., TORRIE, J. H., and DICKSON, J. C., 1946.—Inheritance of reaction to crown rust and stem rust and other characters in crosses between Bond, *A. byzantina*, and varieties of *A. sativa*. *Phytopath.*, 36: 226-235.
- LITZENBERGER, S. C., 1949.—Inheritance of resistance to specific races of crown rust and stem rust, to *Helminthosporium* blight and of certain other agronomic characters of oats. Iowa agri. Expt. Stat. Res. Bull. 370.
- McMILLAN, J. R. A., 1937.—Investigations on the occurrence and inheritance of the grass clump character in crosses between varieties of *T. vulgare* (Vill.). Counc. sci. industr. Res. Melbourne, Bull. 104.
- OSLER, R. C., and HAYES, H. K., 1953.—Inheritance studies in oats with particular reference to Santa Fe type of crown rust resistance. *Agron. Jour.*, 45: 49-53.
- TORRIE, J. H., 1939.—Correlated inheritance in oats of reaction to smuts, crown rust, stem rust and other characters. *Jour. agric. Res.*, 59: 783-804.
- UPADHYAYA, Y. M., and BAKER, E. P., 1960.—Studies on the mode of inheritance of Hajira type stem rust resistance and Victoria type crown rust resistance as exhibited in crosses involving the oat variety Garry. *Proc. Linn. Soc. N.S.W.*, 85: 157-179.
- , 1962a.—Studies on the inheritance of rust resistance in oats. I. Inheritance of stem rust resistance in crosses involving the varieties Burke, Laggan, White Tartar and Anthony. *Proc. Linn. Soc. N.S.W.*, 87: 141-147.
- , 1962b.—Studies on the inheritance of rust resistance in oats. II. The mode of inheritance of crown rust resistance in the varieties Landhafer, Santa Fe, Mutica Ukraine, *Trispermia* and Victoria in their crosses with susceptible varieties. *Proc. Linn. Soc. N.S.W.*, 87: 200-219.

- UPADHYAYA, Y. M., and BAKER, E. P., 1965.—Studies on the inheritance of rust resistance in oats. III. Genetic diversity in the varieties Landhafer, Santa Fe, Mutica Ukraine, Trispermia and Victoria for crown rust resistance. *PROC. LINN. SOC. N.S.W.*, 90: 129–151.
- WATERHOUSE, W. L., 1938.—Some aspects of problems in breeding for rust resistance in cereals. *Jour. roy. Soc. N.S.W.*, 72: 7–54.
- , 1952.—Australian Rust Studies. IX. Physiologic race determinations and surveys of cereal rusts. *PROC. LINN. SOC. N.S.W.*, 77: 209–258.
- WATSON, I. A., 1943.—Inheritance studies with Kenya varieties of *Triticum vulgare* Vill. *PROC. LINN. SOC. N.S.W.*, 68: 72–90.
- WEETMAN, I. M., 1942.—Genetic studies in oats of resistance to two physiologic races of crown rust. *Phytopath.*, 32: 19 (abst.).

A NEW CORALLANID ISOPOD PARASITIC ON AUSTRALIAN
FRESHWATER PRAWNS

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[Read 28th September, 1966]

Synopsis

A second species of *Austroargathona* is described from inland New South Wales and Queensland. The species is parasitic on freshwater prawns of the genera *Macrobrachium* (Palaemonidae) and *Paratya* (Atyidae). The type species and only other described species is parasitic on the related prawns of the easterly flowing streams of coastal Queensland and New South Wales.

AUSTROARGATHONA PICTA, sp. nov.

(Figs 1-6)

Non-ovigerous Female. Length up to 11 mm. Very similar in general appearance to *caridophaga* Riek (Riek, 1953) but differing a little in colour intensity and pattern (Fig. 1). Median chromatophore band of pereaeon divided

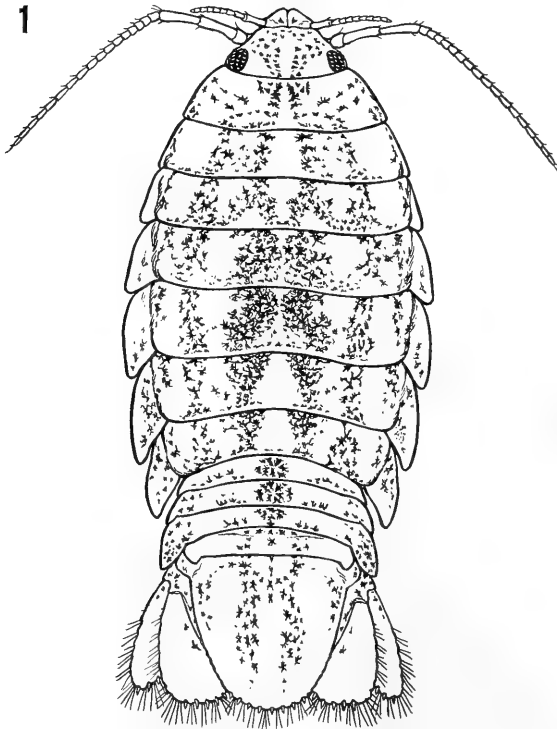
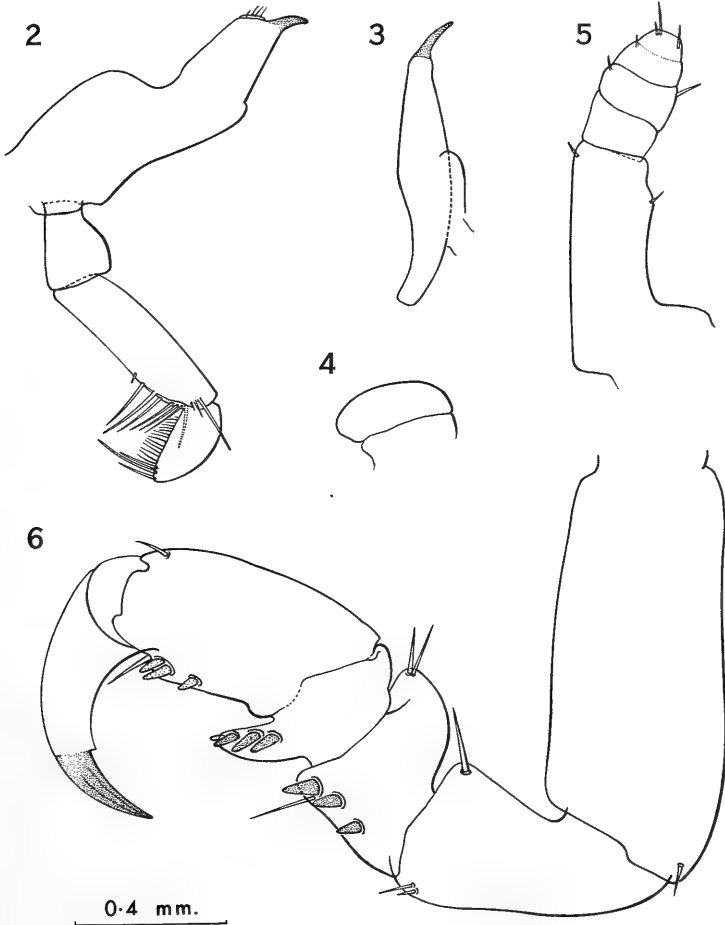


Fig. 1. *Austroargathona picta* sp. nov., Dorsal view $\times 9$.

except on the fourth segment so that there are six indistinct bands except on this one segment. The median two bands of the telson have almost merged so that the telson appears to have a single very wide median band, a distinct,

wide, light laterad area and narrow dark margin. The ramose chromatophores are uniformly pigmented and have sharply defined margins. The cephalon is relatively wider and the eyes less prominent and the lateral margins of the telson are more uniformly convex than in *caridophaga*. Mouthparts distinctive, mandible and second maxilla differing most from those of *caridophaga*.

First and second antenna very similar to those of *caridophaga*, but first article of peduncle of first antenna rather more expanded at base anteriorly; frontal lamina wedge-shaped with a slightly concaved anterior margin and tapering to a rounded point posteriorly; mandibular palp (Fig. 2) with basal



Figs 2-6. *Austroargathona picta* sp. nov. 2. Mandible. 3. First maxilla. 4. Second maxilla. 5. Maxilliped. 6. First peripod.

segment expanded, wider than the following segment, second segment with two series of apical spines, an outer marginal series of seven stout subequal spines, the second the longest, the others gradually shortening distally, but each at least as long as the width of the segment, a very small spine proximal to this series, also a series of three apical spines on the ventral side of the segment, the anterior one much the longest and as long as those of the marginal series, posterior margin of apical segment with a series of about eighteen setae, the distal three very long and stout, with the middle one of these three almost as long as the segment; mandible without a well developed cutting edge, apex

produced into an acute, stout, dark-coloured spine and bearing a series of four fine spines on the median side at the base of the terminal spine, the innermost spine the finest. These spines are less than half the length of the terminal spine and are very fine and transparent. In the description of *caridophaga* the mandible and its palp were inadequately described. They are similar to those in the present species, but the apical spine of the mandible is relatively smaller, and there are apparently only two shorter but stouter mesal spines on the much more narrowed apical lobe. First maxilla (Fig. 3) with tapering base, outer lobe tapering to the acute, distinctly curved, terminal unguis, inner lobe small, rather narrow and with incurved, apex; second maxilla (Fig. 4) small, anterior margin rounded, slightly expanded on the median side (in *caridophaga* the muscle fibres of attachment were confused with the basal structure of the second maxilla so that the structure in the two species is more similar than would appear from the original figures). Coxal plates not quite as acutely pointed and their outer margins more crenulated than in *caridophaga*. Maxilliped (Fig. 5) and first periopod (Fig. 6) similar to those of *caridophaga* but palp of maxilliped more clearly 4-segmented.

Types.—Holotype non-ovigerous female and paratype non-ovigerous females in the Australian Museum Collection.

Type Locality.—Darling River at Bourke, N.S.W.

Distribution.—Darling River at Bourke, N.S.W. (7 Dec. 1959, V. McCristal, 29 Mar. 1960, N. E. Milward and 17 Mar. 1961, J. A. Bishop); Darling River near Gundabooka Bridge (18 Mar. 1961, J. A. Bishop); Darling River, 140 miles downstream from Bourke (18 Mar. 1961, J. A. Bishop); Darling River near Tilpa (19 Mar. 1961, J. A. Bishop); Bogan River, 2 miles e. west of Tarcoon, N.S.W. (23 Mar. 1960, N. E. Milward); Condamine, Q'ld. (10 Apr. 1957, E. F. Riek); Namoi River, near Narrabri, N.S.W. (May, 1961, W. D. Williams); Boonoo Boonoo River, near Tenterfield, N.S.W. (24 May 1961, W. D. Williams), parasitic on cat-fish.

Hosts.—Ectoparasitic on the freshwater prawns *Macrobrachium australiense cristatum* Riek (Palaemonidae) and an undescribed species of *Paratya* (Atyidae). Only at Condamine did the species occur on *Paratya*. The host prawns are restricted to freshwaters. The cat-fish is very probably not a normal host of the species.

The paratypes are all considerably smaller than the holotype. They differ in having only a single fine spine on the median side of the mandible.

It is considered that this species of *Austroargathona* will be found to be widespread in the inland flowing streams of Queensland and New South Wales, for during flooding there is extensive interconnection between the streams. At least one of the host prawns is widespread.

Reference

- RIEK, E. F., 1953.—A corallanid isopod parasitic on freshwater prawns in Queensland. *PROC. LINN. SOC. N.S.W.*, 77: 259–261.

NEW AUSTRALIAN CAVE CARABIDAE (COLEOPTERA)

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[Read 28th September, 1966]

Synopsis

Three new species of cave-dwelling Carabidae are described, viz. *Idacarabus cordicollis* (Tasmania), *Thenarotes speluncarius* (Nullarbor Plain) and *Anomotarus subterraneus* (South Queensland). *A. subterraneus* is of interest in providing a link between the cavernicolous *Speotarus* species and related, surface-dwelling lebiines.

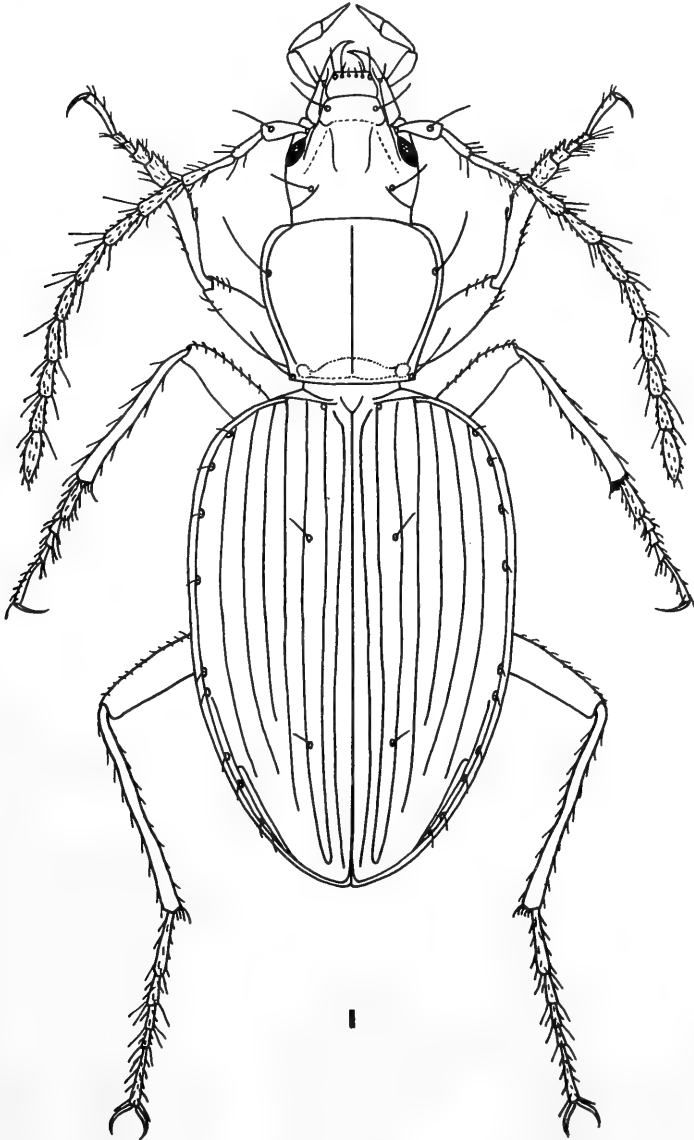


Fig. 1. *Idacarabus cordicollis* sp. n., paratype male.

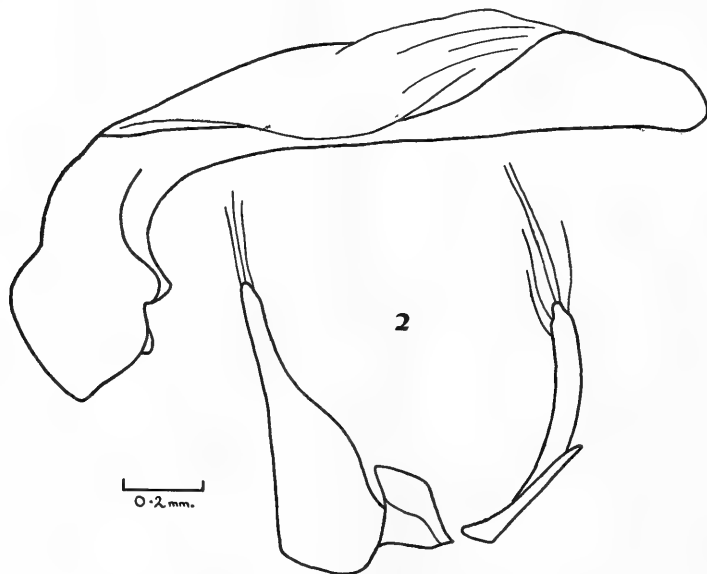
Subfamily MERIZODINAE

IDACARABUS CORDICOLLIS, sp. n.

(Figs 1-2)

Elongate-oval; subapterous; dark piceous, the appendages lighter.

Head ovoid, rather small; eyes small, not prominent; labrum trapezoidal, sexsetose; mandibles slender, acutely pointed; antennae rather long, pubescent from the middle of the third segment. Pronotum cordiform, slightly transverse; anterior and posterior marginal setae present, the latter at the hindangles. Elytra oval, lightly striate; no scutellary striae; humeri effaced; third intervals with two setigerous pores, situated near the third striae. Legs rather long, slender; male anterior tarsi with two basal segments expanded and inwardly



Figs 2-3. Aedeagi in left lateral view. 2. *Idacarabus cordicollis* sp. n. (parameres detached).

dentate. Aedeagus (Fig. 2) with a slender median lobe; parameres dissimilar, the left triangular, trisetose apically, the right styloid, quinquesetose apically.

Length, 5.2-6.4 mm.; max. width, 2.3-2.6 mm.

Type (male) and *allotype* (female).—Tasmania, Newdegate Cave, near Hastings, 13.xi.63 (E. Hamilton-Smith), in the South Australian Museum. Four *paratypes* (both sexes, one immature): King George V Cave, near Hastings, 14.xi.63 (E. Hamilton-Smith) in the South Australian Museum and in the author's collection.

This species is, in reality, the second known member of the genus, for *flavipes* Lea, referred originally and tentatively by its author to *Idacarabus*, has now proved to be a trechine and must therefore be removed to another genus.

Idacarabus cordicollis is less obviously cave-adapted than *I. troglodytes* Lea, the generic type species from Ida Bay Caves, and the two may readily be separated as follows:—

Form elongate; pronotum elongate, lozenge-shaped, the posterior marginal seta wanting; eyes very small; colour castaneous; length 6.5-7.5 mm.	<i>troglodytes</i> Lea
Form less elongate; pronotum slightly transverse, cordate, the posterior marginal seta present at hindangle; eyes larger; colour piceous; length 5.2-6.4 mm.	<i>cordicollis</i> sp. n.

Subfamily HARPALINAE

THENAROTES SPELUNCARIUS, sp. n.

(Figs 3-4)

Mostly brownish-testaceous, the appendages lighter; eyes dark; wings well developed.

Head rather small; eyes prominent, lightly inclosed behind; labrum rectangular, sexsetose; mandibles short, acutely pointed; antennae slender, of average length for the subfamily. Pronotum slightly transverse; anterior angles well marked, subprominent; posterior angles obtuse; sides evenly rounded on front third, then lightly and obliquely contracted to base; base and apex subtruncate; basal foveae scarcely apparent; anterior marginal seta present at front quarter; posterior seta wanting. Elytra elongate-oval, widest a little behind middle, regularly but lightly striate; striae unpunctured; no scutellary striae; third intervals with one setiferous pore, situated against

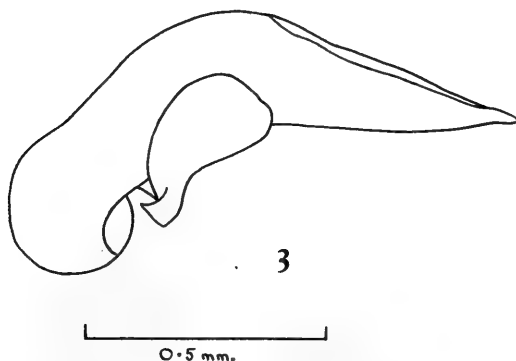


Fig. 3. *Thenarotes speluncarius* sp. n.

the second stria. Legs rather long, slender; tarsi setose above; male anterior and intermediate tarsi expanded and spongiose beneath. Aedeagus (Fig. 4) stout; median lobe tubular, with a dorsal orifice, the apex unarmed; parameres conchoid.

Length, 5-6 mm.; max. width, 2-2.3 mm.

Type (male).—Western Australia, Abrakurrie Cave (Nullarbor Plain), 13.i.64 (P. Aitken), in the South Australian Museum. Fifteen *paratypes* (both sexes), same locality as type, various dates (1960-64) (P. Aitken and E. Hamilton-Smith) in the South Australian Museum and the author's collection.

The placing of this new cavernicolous species in *Thenarotes* Bates (type species *tasmanicus* Bates) must be regarded as provisional, pending an overall revision of the Australian Harpalinae. However, *T. speluncarius* certainly falls within the tribe Pelmatellini, to which the cavernicolous *Notospeophonus* species also belong, but it differs from the latter in possessing setose tarsi and an aedeagus of entirely different form, with no spatulate apex to the median lobe (c.f. Moore, 1964, for aedeagal characters of *Notospeophonus*).

Thenarotes speluncarius has also been collected in Buckalowie Cave and Cave Number 11, of the South Australian portion of the Nullarbor Plain; seven surface-dwelling species, referable to the genus, range over most of the eastern States.

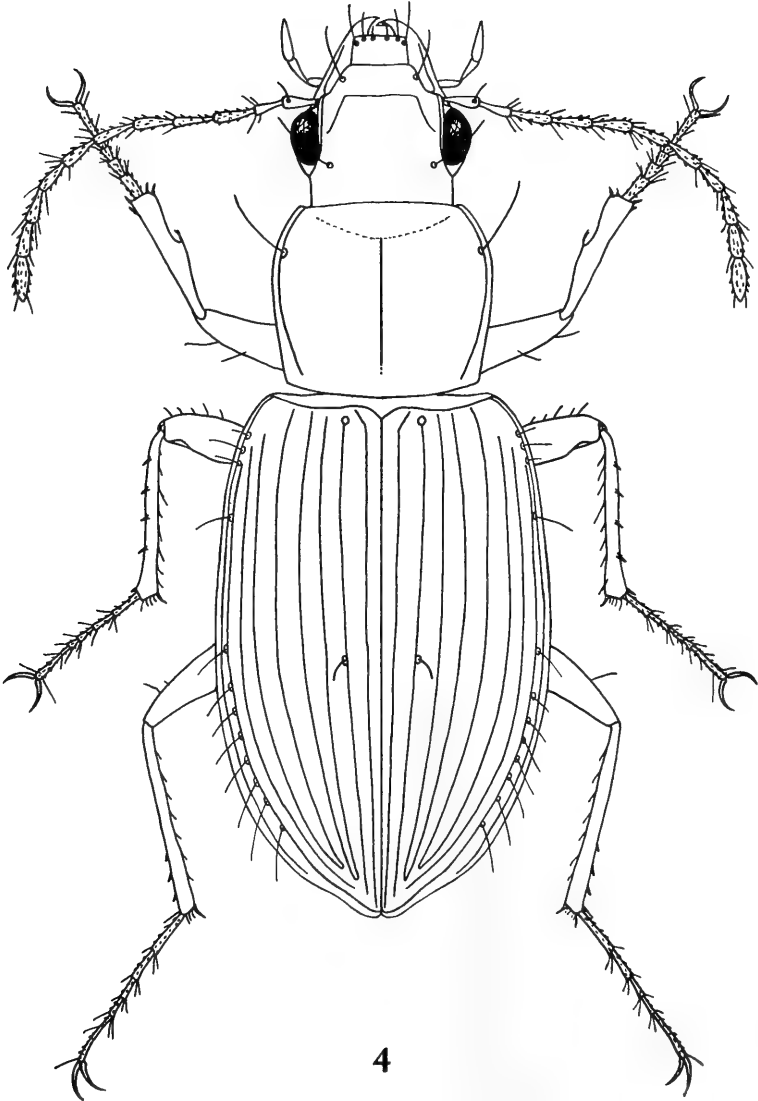


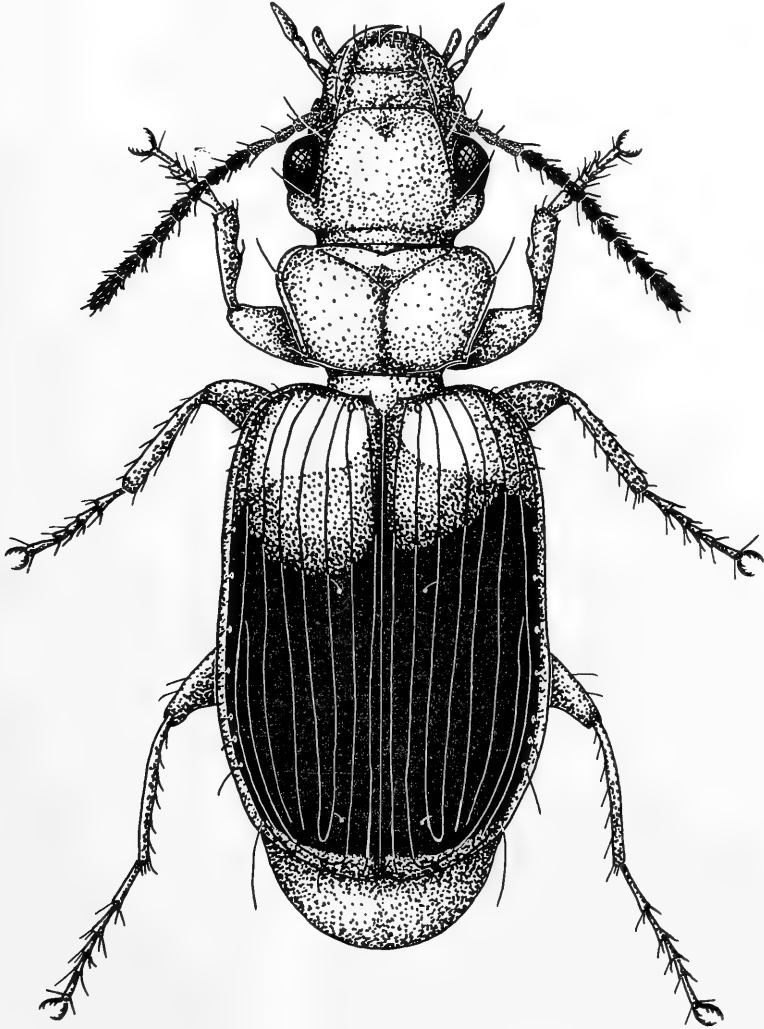
Fig. 4. *Thenarotes speluncarius* sp. n., paratype female.

Subfamily LEBIINAE

ANOMOTARUS SUBTERRANEUS, sp. n.

(Fig. 5)

Form short, depressed, subparallel; fully winged; head, pronotum and appendages brownish-testaceous; eyes black; elytra mostly piceous but humeri widely and margins narrowly brownish-testaceous.



5

Fig. 5. *Anomotarus subterraneus* sp. n., paratype female.

Head large, broad, depressed; eyes large and prominent, inclosed in swollen orbits; neck pronounced; labrum subrectangular, transverse, sexsetose; mandibles short, broad, strongly curved and acutely pointed; antennae short, pubescent from the third segment. Pronotum very transverse, widest at front third; sides strongly rounded from anterior angles to widest part, then strongly contracted and slightly sinuate to posterior angles; anterior and posterior

marginal setae present; anterior angles scarcely apparent; posterior angles obtuse but well marked. Elytra rather short, subparallel, striate, the striae unpunctured; scutellary striae wanting; humeri rounded; third intervals with two setiferous pores, one submedian, the other subapical; apex of abdomen bisetose in male, quadrisetose in female. Legs short but slender; male anterior tarsi lightly dilatate and squamose beneath; claws pectinate. Aedeagus of the normal lebiine type, scarcely differing from those of species of *Speotarus* (Moore, 1964).

Length, 4.6–5 mm.; max. width, 1.8–1.9 mm.

Type (male).—South Queensland, Riverton Cave (in bat guano), 8.ii.64 (E. Hamilton-Smith), in the South Australian Museum. Nine *paratypes* (both sexes, same data as for type) in the South Australian Museum and in the author's collection.

This pretty little species may be recognized within its genus by virtue of its short broad form, large head, and characteristic elytral colour pattern. It is the first-discovered cavernicolous member of the genus and, as such, is of special interest in providing an evolutionary link between the surface-dwelling lebiines and the (so far as is known) exclusively cavernicolous species of *Speotarus*. However, although differing markedly in build from most of its congeners, *A. subterraneus* shows no obvious adaptation to the cave environment. Indeed, the prominent eyes and fully developed wings suggest that the beetle may not be an obligate cavernicole.

Acknowledgement

The author is indebted to Mr. E. Hamilton-Smith for the opportunity to study the interesting material dealt with in this paper.

References

- LEA, A. M., 1910.—On some Tasmanian cave-inhabiting Beetles. *Tasm. Nat.*, 2: 53–58.
MOORE, B. P., 1964.—New cavernicolous Carabidae (Coleoptera) from mainland Australia. *J. ent. Soc. Q'ld.*, 3: 69–74.

ATOPOZOA DEERATA (SLUITER): A DISCUSSION OF THE RELATIONSHIPS OF THE GENUS AND SPECIES

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[Read 26th October, 1966]

INTRODUCTION

The genus *Atopozoa* Brewin 1956 was established for the reception of *Atopozoa marshii* Brewin 1956. The present discussion of the genus and its relations with other genera of the family CLAVELINIDAE Forbes and Hanly is based on a study of larval form, adult colony and zooids of *Atopozoa deerata* (Sluiter), taken in the Gulf of Carpentaria, North Australia, by the C.S.I.R.O. Division of Fisheries and Oceanography while conducting a Prawn Survey in the area.

DESCRIPTION

ATOPOZOA DEERATA (Sluiter)

Distoma deerata Sluiter, 1895, p. 167; *Polycitor coalitus* Sluiter, 1909, p. 23; *Sigillina (Polycitor) coalita*, Michaelsen, 1930, p. 484; *Sigillina deerata*, Hastings, 1931, p. 87.

Records.—Thursday I., Torres Strait (Sluiter, 1895), Malaysia (Sluiter, 1909), Great Barrier Reef (Hastings).

Material Examined.—Gulf of Carpentaria (Prawn Survey St. 1121, C.S.I.R.O. portion only of one colony).

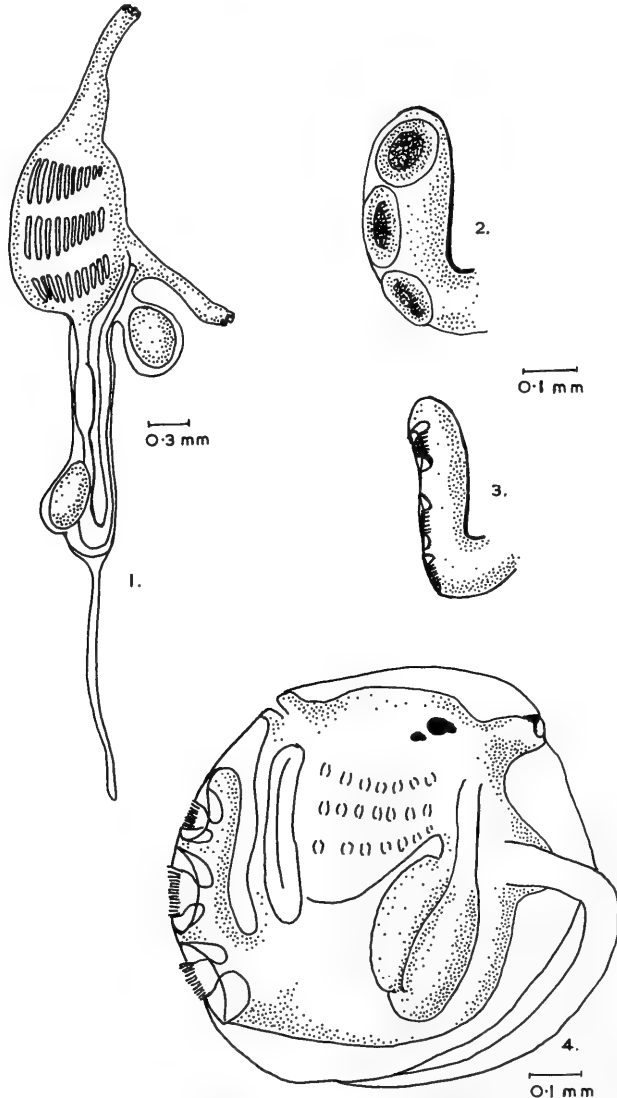
Colony.—Soft, gelatinous; maximum circumference 6 cm., height 8 cm. Surface of colony with furrows up to 1.0 cm. deep dividing surface into irregular areas, or shallow lobes about 4 cm. diameter. Two common cloacal openings observed near apex of colony in furrows protected by overhang of surface lobes. Zooids accumulated in oval-circular areas especially in surface of lobes but also present in base of clefts between lobes.

Common cloacal canals posterior to zooids opening into extensive cloacal spaces separating outer zooid bearing layer of test from central very soft test core. Zooids may be arranged in lines along either side of cloacal canals although this is rather obscure particularly from the surface due to excessive crowding and overlapping of zooids.

Zooids.—(Text-fig. 1). Small, 3 mm. long, excluding long terminal branchial siphon which is as long as thorax. Atrial siphon 6-lobed, long, from posterior third of thorax, directed posteriorly. Zooids arranged in test at angle to surface, with endostyle uppermost, atrial siphon opening into cloacal canals. Three rows of 10 stigmata, anterior row with progressively shorter stigmata dorsally.

Stomach small, spherical, half way down abdomen. A long vascular stolon present, with mesodermal septum. However, no muscles present here as suggested by Michaelsen (1930). Developing embryos at different levels up oviduct, eventually developing to maturity in oviducal pouch, stalked, posterior to atrial siphon; small diverticulum of oviduct in pouch of body wall in mature zooid for reception of embryo as in *Distaplia bermudiensis* (Berrill, 1948, *b*, Text-fig. 5).

Larva.—(Text-figs 2-4). Almost circular, 0.8 mm. long. Papillae carried in vertical line on frontal plate, connected to rest of body of larva by ventral stalk. Papillae unusual, consisting of central circle of adhesive cells depressed into a concavity in the frontal plate which concavity forms a cup like sucker around the adhesive cells. The adhesive cells themselves in mature larvae are carried forward on a stalk but the epidermal cup remains as a concavity in the frontal plate and is never stalked.



- 1.—Zooid.
- 2.—Frontal plate showing papillae developing.
- 3.—Lateral view of frontal plate showing papillae.
- 4.—Mature larva, papillae extruded.

DISCUSSION

The specimen differs from those of Hastings and Sluiter only in the number of common cloacal openings. The colony and zooids also resemble those of *Sigillina vasta* Millar 1962 (also Millar, 1963).

Although the colonies differ and the zooids open directly to the surface, lacking a long atrial siphon and common cloacal system, the zooids of the present species resemble those of:

Atopozoa marshii Brewin, 1956; *Eudistoma vitreus* (Sars) 1851 (see also Berrill, 1948, Millar, 1963b); *Eudistoma mobiysi* (Hartmeyer) 1905 (see also Hartmeyer, 1912, Millar, 1962); *Eudistoma fantasiana* Kott, 1957.

There has been some question on the number of rows of stigmata in *Eudistoma vitreus*, however Millar (1963b) has confirmed the presence of three rows of stigmata in the branchial sac. Berrill (1948) had indicated four rows of stigmata in the larval form, however from his figure it appears that the most anterior row may be from the other side of the branchial sac. All the other species mentioned above have three rows of stigmata. These species, all with three rows of stigmata are unique in the Polycitorinae by virtue of a brood pouch.

Larvae are known for all species except *E. mobiysi* and are all similar: the papillae are not stalked, or only barely stalked, the adhesive cells being accommodated in concavities in the frontal plate as described above for *E. deerata*. In the larvae of *E. vitreus* and *E. deerata* the adhesive cells are maintained in a circular area but in *S. vasta*, *E. fantasiana* and in *A. marshii* the adhesive area has been vertically elongated in a corresponding elongation of the ectodermal concavity and in the latter two species the number of papillae is reduced to two. In larvae of *E. vitreus* and *A. marshii* the frontal plate has not been described as stalked, however it is probable that in more mature larvae it does become so as in *Distaplia* spp. (see Berrill, 1948b for *Distaplia bermudiensis*, Text-figs 11, 12). In mature larvae of *S. vasta*, and *E. fantasiana* the papillae are always carried forward on a stalked frontal plate. The larvae of this group of species are therefore unique in the Polycitorinae due to the stalked frontal plate and sessile papillae.

There are variations in the colonies: *S. vasta* and *E. deerata* have colonial systems; *E. vitreus*, *A. marshii* and some specimens of *E. mobiysi* (Hartmeyer, 1912) have similar colonies with the zooids arranged around a stalked head; *E. fantasiana* and other colonies of *E. mobiysi* have unstalked investing or cushion-like colonies.

Despite these variations the close relationships of zooids and larvae indicate that these species belong in the same genus and the definition of the genus *Atopozoa* Brewin, has been amended to include this group of six closely related species, distinct from other Polycitorinae.

The genus has strong affinities with Holozoinid genera where the larval papillae are also carried forward on a stalked frontal plate, where the papillary stalk is short and thick, and where the larvae develop in a brood pouch. The present group of species differs from the Holozoinae in that they do not always form systems, zooids in many of the species opening to the exterior instead of into a common cloacal system: larval papillae are present in a vertical row and have lost a primitive triradiate arrangement; they have three instead of four rows of stigmata; the atrial siphon persists and has not been modified into a languet. Nevertheless these species demonstrate stronger affinities with the Holozoinae than with the Polycitorinae where they have been accommodated, due only to the presence of three rows of stigmata and an atrial siphon.

Budding in the Holozoinae is from an epicardial extension into the vascular process (Berrill, 1948b) from the posterior end of the abdomen. This enlarges when vegetative reproduction occurs. Hastings (1931) suggests this as the mechanism of budding in the present species which would be expected if the genus does belong with the Holozoinae; rather than budding by the primitive abdominal strobilation of the Polycitorinae. This would explain the variations in the magnitude of the vascular appendage (Sluiter, 1909, p. 25) and suggests

the possibility that certain species of other genera of Polycitorinae, e.g. *Sigillina* and *Hyperiodistoma*, characterized by a well developed vascular stolon, may also belong in the Holozoinae.

It is considered that the genus *Atopozoa* as defined below, and as discussed above is closely related to species of the Holozoinae, and well accommodated in that subfamily. The definition of the subfamily Holozoinae, has been amended (below) to include the genus *Atopozoa*.

CLASSIFICATION

The definitions of the subfamily *Holozoinae* Berrill and genus *Atopozoa* Brewin are modified to accommodate the species as discussed above as follows :

Subfamily HOLOZOINAE Berrill, 1950

Budding from epicardial extension into posterior abdominal vascular extension ; larvae develop in stalked brood pouch ; larval papillae from stalked frontal plate ; zooids with or without atrial siphon ; common cloacal system present or zooids open directly to surface.

Genus ATOPOZOA Brewin, 1956

Atrial siphons present ; zooids open independently or into common cloacal system ; three rows of branchial stigmata ; larval papillae sessile.

Type Species—*Atopozoa marshii* Brewin, 1956

Unfortunately, in the absence of larvae and brood pouch there are no characters of the adult or colony (unless systems are formed) which can distinguish the species from Polycitorinae unless it can be shown that an enlarged vascular stolon indicates that budding always occurs from this area, and this can be correlated with the presence of typical larvae developing in a true brood pouch from the postero-dorsal corner of the thorax. In mature zooids a rudimentary brood pouch is present before it is occupied by the developing embryo.

References

- BERRILL, N. J., 1948a.—Tadpole larvae of ascidians *Polycitor*, *Euherdmania*, *Polysyncrator*. *J. Morph.*, 82 : 355–364.
 ———, 1948b.—Budding and the reproduction cycle of *Distaplia*. *Q. Jl microsc. Sci.*, 89 : 253–289.
 ———, 1950.—The Tunicata. *Ray Soc. Publs.*, 133 : 1–354.
 BREWIN, BERYL, 1956.—*Atopozoa marshii*, a compound Ascidian from Western Australia. *J. Proc. r. Soc. West. Aust.*, 40 (1) : 31–32.
 HARTMEYER, R., 1905.—Ascidians from Mauritius. *Zool. Jb.*, Suppl. viii : 383–406.
 ———, 1912.—Die Ascidien der Deutschen Tiefsee Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'*, 16 (H.3) : 223–392.
 HASTINGS, A. B., 1931.—Tunicata. *Scient. Rep. Great Barrier Reef Exped.*, 4 (3) : 69–109.
 KOTT, P., 1957.—Ascidians of Australia 11. Aplousobranchiata Lahille; Clavelinidae Forbes and Hanly and Polyclinidae Verrill. *Aust. J. mar. freshwat. Res.*, 8 (1) : 64–110.
 MICHAELSEN, W., 1930.—Ascidiae Krikobranchia. *Fauna südwest-Aust.*, 5 (7) : 463–558.
 MILLAR, R. H., 1962.—Further descriptions of South African Ascidians. *Ann. S. Afr. Mus.*, XLVI (VII) : 113–221.
 ———, 1963a.—The larva and affinities of the ascidian *Sigillina vasta* Millar. *Ann. Mag. nat. Hist.*, VI (13) : 204–207.
 ———, 1963b.—The structure and systematic position of the Ascidian *Distomum vitreum* Sars. *Ann. Mag. nat. Hist.*, VI (13) : 386–388.
 SARS, M. (1851).—Beretning om en i Sommeren 1849, foretagen zoologiske Reise i Lofoten og Finmarken. *Nyt Mag. Naturvid.*, 6 : 121–211.
 SLUITER, C. P., 1895.—Tunicaten in Semon, R. Zoologische Forschungsreisen in Australien und den malagischen Archipel. *Denkschr. med.-naturw. Ges. Jena.*, 8 : 163–166.
 ———, 1909.—Die Tunicaten der Siboga Expedition Pt. 2. Die merosomen Ascidien. *Siboga Exped.*, 56b : 1–112.

INHERITANCE OF RESISTANCE TO BUNT IN TURKEY WHEAT SELECTIONS

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Synopsis

The inheritance of resistance to race T-1 of bunt (*Tilletia caries* (DC.) Tul. and *T. foetida* (Wallr.) Liro) was investigated in crosses involving two resistant selections, Turkey C.I. 10095 and C.I. 10097, which were originally made from Turkey Red or South Dakota No. 144 wheat. Studies of F₂ and F₃ generations were made for per cent of bunted plants in crosses between each of these varieties with the susceptible variety Baart and with the resistant varieties Martin, Turkey 3055, Rio and Selection 1403 which are testers for the M, T, R and H major genes respectively, and with the resistant variety Turkey C.I. 10015, possessing only the weak genes X and Y. Both Turkey C.I. 10095 and C.I. 10097 were found to possess weak genes for resistance. To invoke a minimum number of genes to satisfy analyses in all crosses a minor revision of the genotype for Turkey C.I. 10015, as published previously by El Khishen and Briggs, was necessary in that the gene X, and not Y, was considered linked to the $\overline{\text{HMRT}}$ linkage group. On this revised genotype for Turkey C.I. 10015, selection C.I. 10095 was considered to have the major gene R and the two minor genes X and Y, hence the genotype $\overline{\text{RRXX}} \text{YY}$ with regard to bunt resistance, whilst the resistance of C.I. 10097 was considered due to the additive or complementary effect of two weak genes, X, and an independent previously unidentified factor, W, which permitted 37.5% of bunted plants when homozygous and 47.5% when heterozygous. The most satisfactory crossover value for the R and X genes considering all crosses was approximately 10% and the order of linked genes conditioning bunt resistance was determined from appropriate tester crosses as $\overline{\text{HMXRT}}$.

INTRODUCTION

Bunt of wheat (*Tilletia caries* (DC.) Tul. and *T. foetida* (Wallr.) Liro) can generally be effectively controlled by seed treatment. However, Kuiper (1965) described a race of bunt which was not controlled by hexachlorobenzene, the active constituent of several seed-dressing products, and generally accepted throughout the world as one of the most effective fungicides for the control of the disease. This emphasizes the importance of the second method for the control of the disease which is by breeding resistant varieties. The bunt organisms exhibit physiological specialization and no single gene has been identified which will control all races. However Briggs and Holton (1950) showed that a combination of two genes will give effective protection against at least 25 races. In breeding resistant varieties a knowledge of the mode of inheritance of resistance shown by different genes is essential. Investigations on the genetics of resistance to a specific race of bunt will enable resistance genes to be documented and their mode of inheritance studied. As new bunt races are discovered the behaviour of varieties of known genotype can then be tested. Different genes may be required in breeding to incorporate resistance against groups of races of varying pathogenicity to afford protection against all prevalent races. Briggs and his associates at the College of Agriculture, Davis, California have studied the inheritance of resistance in 18 wheat varieties to race T-1 of *T. caries* and in the course of these investigations at least seven genes for resistance have been identified.

LITERATURE REVIEW

Briggs and his coworkers at Davis, California, using a single race T-1 of *T. caries*, have found the Martin gene, M, in nine varieties (Briggs, 1926, 1930*b*, 1931, 1932*a*, 1934; Smeltzer, 1952; Schaller and Briggs, 1955). Briggs (1926) showed that the variety Hussar possessed the Martin gene and a second major gene, H. From a cross between Hussar and the susceptible variety Hard Federation, the H factor was isolated in Selection 1403 (Briggs, 1930*a*). The Turkey gene, T, has been identified in six varieties (Briggs, 1932*b*, 1934, 1936; El Khishen and Briggs, 1945). Analysis of all data accumulated from different crosses between varieties possessing the M and those the T gene indicated that the ratios deviated significantly from those expected on the basis of independent segregation. Briggs (1940) estimated the recombination value between the M and T genes as 34.22 units. A third major gene, R, was identified in two varieties (Stanford, 1941; El Khishen and Briggs, 1945). Stanford concluded that the R and T genes were closely linked with an estimated crossover value of 2.4 map units. From the tester cross results with Martin, the R gene was postulated to lie between the T and M genes. Schaller and Briggs (1955) presented evidence from their own results and from an analysis of combined data of certain previous publications which showed linkage between the H and M genes with a recombination value of 37.2%. The gene order HMRT for the linkage group concerned was established. The H gene would therefore be more than 50 crossover units from the R and T factors.

Four weak resistance genes allowing moderate levels of infection in the homozygous state have been reported. The gene X, in addition to the R and T genes, was identified in a strain of Turkey wheat, C.I. 10016 (El Khishen and Briggs, 1945). This gene accounted for the spreading effect and absence of a definite mode in the susceptible group of F₃ rows in a cross between Turkey C.I. 10016 and the susceptible variety Baart and permitted about 25% of bunted plants when homozygous. El Khishen and Briggs from studies on inheritance of resistance in a related Turkey strain C.I. 10015, concluded that this variety possessed only weak genes -X, and a second factor Y, which when homozygous was postulated to permit about 45% of bunted plants. A deficiency of susceptible rows in tester crosses with Martin, Rio and Turkey, indicated that the Y gene was linked with the HMRT linkage group. Smeltzer (1952) established that bunt resistance in the variety Minturki was governed by two weak genes, U and V. The gene U permitted approximately 42.5% infection in the homozygous state and 55% when heterozygous. Comparable values for the factor V were 35 and 50%. One of these appeared to be closely linked to R and T, but it could not be determined whether U or V was involved in linkage.

MATERIALS AND METHODS

Turkey C.I. 10095 and C.I. 10097 are two out of 12 bunt resistant selections isolated from Turkey Red or South Dakota No. 144 wheat, a hard red winter type, by Kiesselbach and Anderson (1930) at Lincoln, Nebraska. C.I. denotes the accession number of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, United States Department of Agriculture. Originally head selections were made by Kiesselbach and Anderson from bunt free plants in a special planting of the Turkey Red variety heavily inoculated with a collection of *T. foetida* made at Lincoln. With this bunt collection they found an average of 0.6% infected heads in the 10095 Strain and 0.2% infection in Strain 10097 in a series of annual tests over a seven-year period. During these tests the original unselected Turkey Red averaged 30.7% infection with the same inoculum. Turkey C.I. 10015 and 10016 studied by El Khishen and Briggs (1945) were from the same source.

Each of these two resistant varieties under investigation was crossed with the bunt susceptible variety Baart. They were also crossed with the resistant

varieties Martin, Turkey 3055, Rio and Selection 1403, which are testers for the M, T, R and H genes respectively, and with Turkey C.I. 10015, which is the tester for the X and Y genes.

F₃ progenies, produced from non-infected F₂ plants, of the crosses with Baart were grown at Davis, California in duplicate rod rows each containing 80 seeds. Prior to sowing the seed was thoroughly blackened with chlamydo-spores of a race designated as T-1 of *T. caries* from its behaviour on the standard differential set (Rodenhiser and Holton, 1937). This collection has been perpetuated and used at this station since 1919; F₃ progenies of the tester crosses were handled similarly except that they were grown in single rod rows. Inoculated F₂ populations and appropriately spaced parental checks, including rows of the susceptible variety Baart, were included in the nursery.

The plants were pulled when nearly mature and classified as smutted or non-smutted, the former category including plants with any evidence of bunt infection.

EXPERIMENTAL RESULTS

The mean annual percentages of bunt-infected plants observed in parent varieties in the present investigations over a 14 year period at Davis, California, are shown in Table 1. The mean percentage of bunted plants for each variety in all rows in the particular year in which inheritance studies were conducted is also indicated in the Table. Both Turkey C.I. 10095 (henceforth referred to as Turkey 10095) and Turkey C.I. 10097 (henceforth referred to as Turkey 10097) were highly resistant, the highest annual infections being 1.0 and 2.8% respectively. Both strains were consistently more resistant than Turkey C.I. 10015 (henceforth referred to as Turkey 10015), another strain from the same source. Generally Turkey 10095 showed a slightly higher level of resistance throughout comparative tests.

TABLE 1
Percentages of Bunt Infection in Parent Varieties

Variety	Mean of 14 annual tests	Mean of all rows in season of current investigations	
		Turkey 10095 studies	Turkey 10097 studies
Baart	72.1	79.0	82.8
Selection 1403	0.3	0.0	0.0
Turkey 3055	0.9	1.8	1.2
Rio	0.6	1.3	1.7
Martin	0.0	0.0	0.4
Turkey 10015	3.8	4.1	7.3
Turkey 10095	0.3	0.2	—
Turkey 10097	0.6	—	1.1

The F₂ data for all crosses involving both Turkey 10095 and 10097, together with those for parental rows associated with the F₂ populations, are summarized in Table 2. As some genetically susceptible plants always escape infection in such tests and some genetically resistant plants may become infected as shown by Briggs (1926, 1929), F₂ data alone provide inadequately critical information on inheritance. For more accurate genetic analyses F₃ lines were used. The F₂ information, however, does serve to indicate approximately the number of genes involved in the resistant varieties under investigation, especially in the case of major or strong genes, the effect and mode of inheritance of such genes, and also to predict the behaviour of the heterozygous class in the F₃ populations.

TABLE 2
*Percentages of Bunted Plants in the Parent and F₂ Rows
of Crosses Involving Turkey 10095 and Turkey 10097*

Parent or Cross	Number of plants		Percentage of bunted plants
	Total	Bunted	
Turkey 10095	1384	3	0.2
Baart	461	374	81.1
Selection 1403	119	0	0
Turkey 3055	242	3	1.2
Rio	233	4	1.7
Martin	108	0	0
Turkey 10015	129	4	3.1
Turkey 10095 × Baart	1482	394	26.6
Turkey 10095 × Selection 1403	720	48	6.7
Turkey 10095 × Turkey 3055	707	2	0.3
Turkey 10095 × Rio	570	0	0
Turkey 10095 × Martin	692	10	1.5
Turkey 10095 × Turkey 10015	772	0	0
Turkey 10097	1425	17	1.2
Baart	742	621	83.7
Selection 1403	128	0	0
Turkey 3055	202	4	2.0
Rio	174	3	1.7
Martin	78	0	0
Turkey 10015	92	9	9.8
Turkey 10097 × Baart	832	243	29.2
Turkey 10097 × Selection 1403	447	41	9.2
Turkey 10097 × Turkey 3055	528	25	4.7
Turkey 10097 × Rio	594	10	1.7
Turkey 10097 × Martin	523	19	3.6
Turkey 10097 × Turkey 10015	306	19	5.9

The distributions of F₃ rows of crosses involving Turkey 10095 and 10097 are tabulated in Table 3 together with the distributions of the appropriate parental rows associated with the F₃ progenies. These distributions are shown by 5% classes with a separate classification of completely immune lines into a 0% class.

Two weak factors, X and Y, additive in effect, were postulated by El Khishen and Briggs (1945) to be responsible for the resistance shown by Turkey 10015. A related strain Turkey C.I. 10016 (henceforth referred to as Turkey 10016) was considered by them to possess the factor X, in addition to the major R and T genes. As will be shown subsequently the presence of weak factors in both Turkey 10095 and 10097 was inferred from segregation in crosses with tester varieties but primarily from the pattern of distribution of F₃ rows in their crosses with the susceptible variety Baart.

Weak or minor genes cannot be distinguished and documented with the same precision as major genes unless they are each first isolated into separate lines, which then can be intercrossed. On the basis of inheritance studies conducted in this manner, a decision then may be possible as to whether or not each gene is different and distinct.

Obviously until such procedures are adopted a minimum number of minor genes should be invoked which will satisfy and reconcile segregation patterns exhibited in all crosses involving varieties where weak genes are considered to be operative. This principle was applied in the case of the four Turkey selections, two in the current investigations, all from the same source studied at the California station.

TABLE 3
Distribution of Parental and F₃ Rows of Crosses Involving Turkey 10095 and Turkey 10097 into 5 Percent Classes for Bunt Infection

Parent or Cross	Distribution of rows by 5 percent classes																	Total number of rows					
	0	-5	-10	-15	-20	-25	-30	-35	-40	-45	-50	-55	-60	-65	-70	-75	-80		-85	-90	-95	-100	
Turkey 10095 ..	20	4																				24	
Baart ..																						13	
Selection 1403 ..	3																					3	
Turkey 3055 ..	2	3																				5	
Rio ..	1	4																				5	
Martin ..	3																					3	
Turkey 10015 ..	3																					3	
Turkey 10095 × Baart ¹	5	38	19	6	11	13	18	15	20	19	15	6	3	6	7	6	6	4	6	2		225	
Turkey 10095 × Turkey 10095 ×																							
Selection 1403 ..	37	19	12	12	5	7	2	1	2	1	1											100	
Turkey 10095 × Turkey 3055 ..	173	56	12	4	2	1	1					1										250	
Turkey 10095 × Rio ..	183	52	4	2	1																	242	
Turkey 10095 × Martin	44	25	11	7	2	1	1	2	2	1	2	2						1				99	
Turkey 10095 × Turkey 10015 ..	73	26	1																			100	
Turkey 10097 ..	15	12																				27	
Baart ..																						15	
Selection 1403 ..	3																					3	
Turkey 3055 ..	2	3																				5	
Rio ..	1	4																				5	
Martin ..	3																					3	
Turkey 10015 ..	3																					3	
Turkey 10097 × Baart ¹	2	14	18	15	15	20	15	30	22	20	14	10	15	8	6	7	8	4				243	
Turkey 10097 × Turkey 10097 ×																							
Selection 1403 ..	15	18	11	13	10	10	8	4	7	1	2	1	3	1								104	
Turkey 10097 × Turkey 3055 ..	30	75	74	42	17	9	3	1														251	
Turkey 10097 × Rio ..	83	110	54	10	5	4	1	1	1													269	
Turkey 10097 × Martin	34	28	25	9	2	4	2	1														106	
Turkey 10097 × Turkey 10015 ..	14	19	41	23	5	2																104	

¹ Mean of duplicate rows only included.

To implement this objective some minor modifications in the analyses of Turkey 10015 and 10016 as proposed by El Khishen and Briggs (1945) were considered necessary. The evidence for these and the steps which were followed in arriving at appropriate modified genotypes for these Turkey strains were as follows:

(a) Although transgressive segregation for bunt susceptibility was recorded in the current investigations in the cross Turkey 10097 \times Turkey 10015 no susceptible F_3 rows were obtained. However some F_3 rows showed 20–25% infection, which suggests that these varieties have in common the stronger, or X, gene of the two (X and Y) reported by El Khishen and Briggs in 10015, since the factor X, when homozygous, was considered to permit 22.5% infection.

(b) In the case of both Turkey 10015 and 10097, segregation producing susceptible F_3 lines occurred as expected in their crosses with Selection 1403 on the hypothesis that the H gene in Selection 1403 is more than 50 crossover units from the factors for resistance in these Turkey strains. In the case of the genetic testers for the M, R and T genes (which have previously been demonstrated to be genetically linked) a consistent deficiency of susceptible F_3 progenies was evident on the assumption of independent gene segregation in crosses involving these testers with both Turkey 10015 and 10097. The segregation pattern observed in both strains was parallel with each tester cross as a comparison of Table 3 in the present publication and Table 3 in the paper of El Khishen and Briggs shows, allowing for the fact that the level of infection in the susceptible Baart check rows was some 10 to 17% higher in their tests. It is probable, therefore, that if both Turkey 10015 and 10097 have the gene X in common, this factor is linked with the $\overline{\text{HMRT}}$ linkage group. The absence of moderately susceptible rows in the cases of Rio (R) and Turkey (T) tester crosses with Turkey 10097, and in the case of the Turkey (T) tester cross with Turkey 10015, further indicates a close linkage between the X with the R and T genes respectively. Unless this close linkage is assumed a reasonably high proportion of F_3 progenies heterozygous for X and lacking other genes for resistance would be expected; these lines would, on the degree of infection postulated for the heterozygous Xx condition, be expected to show approximately 60% infection. No F_3 row with such a high infection percentage was actually observed in these crosses.

(c) That some slight revision would be required in the genetic analysis of Turkey 10016 as published by El Khishen and Briggs is indicated from these observations. The present hypothesis which slightly modifies their analysis is that Turkey 10016 has both the X and Y genes in addition to the major R and T genes, with X, as previously indicated, and not Y being in the $\overline{\text{HMRT}}$ linkage group. Although it is realized that the same precision in genotype analysis where minor factors are implicated cannot be expected from the degree of segregation observed in tester crosses other experimental evidence supports the conclusion outlined for the genetic constitution of Turkey 10016. No F_3 rows showing more than 10% infection were reported by El Khishen and Briggs in the cross 10015 \times 10016. On the basis of linkage between X and the R and T genes with 10% crossing over between R and X (a value finally decided upon from analyses of Turkey 10015, 10016, 10095 and 10097 hybrids with tester varieties) 12 such rows would have been expected.

On the postulated order for the M, R and T genes proposed by Stanford (1941), since X appears to be fairly closely linked with M as well as R, the X gene lies between $\overline{\text{M}}$ and R but closer to the latter, the gene order in the linkage group being thus $\overline{\text{MXRT}}$. For all classes a crossover value of 10% between X and R gave the best overall fit between observed and expected results for the cross Turkey 10016 \times Baart and also for the tester cross of this variety with Martin. Values consistent with previously known information were assigned to F_3 rows derived from different F_2 genotypes and values which might reasonably

be expected on gene interaction assigned in other cases. The theoretical distribution for the cross Turkey 10016 \times Baart was calculated by the method to be indicated in the discussion under hybrids involving Turkey 10095. The χ^2_{14} value for agreement between observed and expected results was 6.83, giving a P value between 0.95–0.90. The revised genotype of Turkey 10016 was thus considered to be $\overline{XXRRTT} YY$.

ANALYSIS OF GENOTYPE OF TURKEY 10095 IN RELATION TO BUNT RESISTANCE

The distribution of the means of duplicate F_3 rows on the basis of 5% class intervals for the cross Turkey 10095 \times Baart is shown in Figure 1. This curve is based on per cent of rows in each class out of the 225 rows actually tested. The per cent distribution was adopted so as to serve as a basis for comparison with previous similarly depicted distributions. It will be seen that there are two minimum points on the curve—at the midpoints 12.5% and 57.5% respectively. The curve has, in general, features similar to those published by Briggs (1936) for the distribution of F_3 rows in crosses involving certain Turkey varieties and Baart in which segregation was due to the action of a single incompletely dominant gene present in these Turkey varieties. The main differences are that the heterozygous class shows a more general spreading distribution with absence of a pronounced modal class, and that there is also a definite spreading effect with lack of a definite mode for the susceptible group. This latter effect indicates the segregation of one or more weak genes. Furthermore, if 12.5 and 57.5% are taken as minima on the basis of the action of a single gene there are obviously too few susceptible rows for the single gene hypothesis to be statistically satisfactory. Again if the minima at 12.5 and 57.5% are taken to indicate the separation of the F_3 lines into a monohybrid 1:2:1 ratio, the infection percentage in the then heterozygous group of F_3 rows should approximate the F_2 percentage infection. The mean per cent infection in the F_3 rows in the cross Turkey 10097 \times Baart with between 12.5 and 57.5% of bunted plants was 34.9, compared with a corresponding F_2 population infection of 26.6% as indicated in Table 2. This further suggests that the segregation observed was due to the effect of one or more weak genes as well as a major gene for resistance.

Information as to the identity of these genes is obtained from an analysis of F_2 and F_3 data on crosses between Turkey 10095 and tester varieties. Segregation producing susceptible F_2 plants and F_3 rows was obtained in crosses involving Selection 1403, Turkey 3055 and Martin, indicating the H, T and M genes respectively were not present in Turkey 10095. However, the absence of any segregation in both the F_2 and F_3 generations of Rio and Turkey 10015 crosses with Turkey 10095 indicates that the strong gene is the Rio (or R) gene and that the weak gene (or genes) is one (or both) of those present in Turkey 10015 (X and/or Y). No susceptible F_2 plants or segregating F_3 rows were produced in the two crosses indicated. With R as the major gene for resistance the presence of one or more weak genes in addition is also necessary to account for the low F_2 infection of 26.6% in the cross with Baart. Stanford (1941) found in the F_2 of a Rio \times Baart cross 45.6% infected plants, which was confirmed by the heterozygous F_3 lines averaging 51.4% infection.

The presence of both X and Y as weak genes is favoured for the following reasons, the evidence being briefly summarized for each point:

(a) More susceptibility in the F_2 and F_3 generations of the cross between Turkey 10095 and Turkey 10015 would be expected if only either X or Y was present. Computations show that with the stronger or X gene alone present, 1/16 of the F_2 plants of this cross would be homozygous XX in genotype, with this as the only gene for bunt resistance. The previous behaviour of this gene indicated that F_3 rows derived from such genotypes produce approximately 22.5% infected plants. Also certain other genotypes would be expected to

produce F_3 lines with a mean infection above 5%. Computations based on the presence of the Y gene alone with 10% crossing over between the R and X genes indicate that only 0.2% of F_3 rows would possess the homozygous Y gene alone for resistance. However, 4.5% would be expected to be derived from plants of the genotype $RrXx YY$ with a predicted amount of infection based on factor interaction of approximately 25.0%. A similar percentage of rows would be derived from $rR\bar{X}x YY$ F_2 plants with a somewhat higher predicted F_3 infection percentage. Finally 40.5% of F_2 plants would possess the R and X genes in repulsion and calculations assess an infection of approximately 10% in F_3 rows derived from such plants. The fact therefore that such a large proportion of F_2 plants theoretically produces F_3 lines which would be expected above the 10% infection level supports the hypothesis based on the presence of both X and Y as weak resistance genes.

(b) Although behaviour resulting from the interaction of genes conditioning bunt resistance cannot be predicted it would not be expected that either X or Y in conjunction with the R gene would confer the low level of F_3 infection (26.6%) observed in the cross Turkey 10095 \times Baart, since Stanford (1941) has shown that the R gene when heterozygous permits about half the plants to become infected.

(c) An analysis of the comparison between observed and expected results for F_3 data of the cross Turkey 10095 \times Baart indicates that both the X and Y weak genes are present in the former variety. Assuming firstly that only the genes R and X are present in Turkey 10095 and linkage with a crossover value of 10% between them, then 56 F_3 rows would be expected above the 55% infection level from the two genotypes $rr\bar{X}x$ (85% similar to susceptible Baart) and $rR\bar{X}x$ (62.5%), whereas only 40 were actually observed. Of the 56 expected lines in this category, 46 would be considered to have approximately 85% infection, whereas only 24 were observed above 70% infection. A comparison likewise between observed and expected results for the distribution of F_3 rows was made on the assumption that the independent R and Y genes alone were present in Turkey 10095. This comparison was entirely satisfactory in the resistant classes and also those showing above 55% infection, the calculated figure for the former group being 56.7 and the latter 46.7, compared with observed numbers of 68 and 40 respectively. However, if the F_2 infection of 26.6% is used in predicting the behaviour of the doubly heterozygous class in the F_3 the genotype $Rr YY$ would be expected to be slightly more resistant than this. When the genotypes $Rr Yy$ and $Rr YY$ (3/8 of the population) are normally distributed on this basis, the observed 30–35% classes have a corresponding surplus. The χ^2_{11} value for all infection classes was 39.86, with a corresponding P value of <0.01 .

For these reasons the genotype of Turkey 10095 was considered to be $R\bar{R}X\bar{X} YY$ with regard to genes conditioning bunt resistance.

On this hypothesis a comparison was made between observed and expected results for the distribution of the 225 F_3 duplicate rows of the cross Turkey 10095 \times Baart. The 10% crossover value between R and X previously postulated for Turkey 10016 in the introduction to this Section gave a satisfactory fit and the analysis in the cross with Baart and also with the tester varieties was not improved by varying the crossover value between them. The Y gene was considered independent of the other two. That rather close linkage exists between R and one of the weak genes was also shown by a comparison of observed and expected results with independent behaviour of these three genes. Under this latter condition only 17.5 of the 225 F_3 rows would be expected to exhibit above 55% infection which is in serious disagreement with the 40 rows actually observed in this category. Linkage with 10% crossing over between R and X was finally adopted then, since, considering the four varieties postulated to contain the X gene—Turkey 10015, Turkey 10016, Turkey 10095 and Turkey

10097—best agreement was obtained between observed and expected results using this value. On this basis the proportion of F_2 genotypes, the number of F_3 rows expected from each out of the total of 225 and the per cent of bunt expected in F_3 rows from the different genotypes are indicated in Table 4.

The values assigned to the different genotypes in general were very close to those previously reported. The mean of the Baart checks sown throughout the F_2 and F_3 rows in the cross Turkey 10095 \times Baart was 81.9 with a standard error of 1.35%. The mean $+2.18$ times (the t value at the 0.05 probability level for 12 degrees of freedom) the standard error is therefore $81.9 + 2.94$ or 84.84%, with 85 as the closest integer. The value of 85% thus used for the $rrxx\ yy$ genotype, which would be expected to be similar to Baart, did not therefore differ significantly from the 81.9% mean for Baart and gave a better agreement than the actual Baart mean for the most susceptible class; F_3 rows produced from different genotypes involving X and Y without the R gene were assigned values by El Khishen and Briggs (1945), and these values were followed in general in assigning values to the F_3 rows derived from such genotypes, except that the values for $Xx\ yy$ and $xx\ Yy$ were approximately 10% lower than assigned by these authors. The mean of the Baart checks to which their data refer was 93.5%, however, compared with 79.0% in the present investigation. It is logical therefore to lower the infection level of the genotypes $Xx\ yy$ and $xx\ Yy$ which confer little resistance on F_3 lines accordingly by a somewhat less amount than the difference in the Baart checks in the two years under comparison. The values for the other genotypes involving X and Y without R were identical to or within 2.5% of those postulated by El Khishen and Briggs. The genotype containing R in the heterozygous condition alone was ascribed a value of 50.0, a figure suggested by Stanford (1941).

Information on the F_3 behaviour of the triple heterozygote was obtained from F_2 data. The mean infection in the F_2 was 26.6%. A much better agreement between observed and expected results was secured by assigning a higher value to rows derived from this genotype in the F_3 . The standard error

$\sqrt{\frac{pq}{n}}$ of the F_2 based on 1,482 plants was 1.15%. The upper 95% fiducial limit was 28.85% and a value of 29.0% (the nearest integer) was assigned to the F_3 triple heterozygote. The most complete agreement between observed and expected results was secured by giving this genotype a value of around 35%, but this would have differed significantly from the 26.6% observed. No attempt was made to assign values to the different F_3 rows indicated as resistant although it is recognized that these would differ slightly in resistance. Any genotypes containing R in the homozygous condition would be expected to show a mean not exceeding that of Rio (1.3%), whilst those containing the $XX\ YY$ genotype (2.66 rows) would exhibit a mean of 4.1% similar to Turkey 10015. On a binomial distribution for these mean percentages all would be expected to fall below 10% infection and the resistant genotypes were arbitrarily assigned to the 0-5 and 5-10 per cent classes

With regard to the other genotypes although no positive evidence is available on gene interaction, values were assigned which seemed logical on the behaviour of these genes independently. Except for the triple heterozygote the various genotypes permitting bunt were assigned mean values which were multiples of 2.5%. Further refinement would have resulted in a closer agreement between observed and expected results, but this did not seem justified as it would have added little further significant information in the present instance. A difference in reaction of genotypes with the R and X genes in the coupling and repulsion phases respectively would be expected and is indicated in Table 4.

Frequency distributions were calculated for all genotypes other than those classified as resistant in Table 4. For means above 10% this was done by using the means indicated and the standard errors for each mean derived from the formula, $s = \sqrt{\frac{pq}{n}}$, where p and q are the infection percentages expressed proportionately, and n is the mean number of plants per duplicate row or 111.5

TABLE 4

Proportion of F₂ Genotypes Expected, Number of F₃ Rows Expected out of a Total of 225, and Percent of Bunt Expected in F₃ Rows of Turkey 10095 × Baart
(Based on linkage between R and X genes with 10% crossing over)

F ₂ genotype and proportion expected	Number of F ₃ rows expected	Mean percent of bunt expected in F ₃ rows	F ₂ genotype and proportion expected	Number of F ₃ rows expected	Mean percent of bunt expected in F ₃ rows
$\frac{RX}{RX} \frac{Y}{Y}$ 0.0506	11.39	Resistant	$\frac{rX}{R_x} \frac{Y}{Y}$ 0.0013	0.29	12.5
$\frac{RX}{RX} \frac{y}{Y}$ 0.1013	22.79	Resistant	$\frac{rX}{R_x} \frac{y}{Y}$ 0.0025	0.56	20.0
$\frac{RX}{RX} \frac{y}{y}$ 0.0506	11.39	Resistant	$\frac{rX}{R_x} \frac{y}{y}$ 0.0013	0.29	27.5
$\frac{R_x}{RX} \frac{Y}{Y}$ 0.0112	2.52	Resistant	$\frac{r_x}{R_x} \frac{Y}{Y}$ 0.0112	2.52	25.0
$\frac{R_x}{RX} \frac{y}{Y}$ 0.0225	5.06	Resistant	$\frac{r_x}{R_x} \frac{y}{Y}$ 0.0225	5.06	42.5
$\frac{R_x}{RX} \frac{y}{y}$ 0.0112	2.52	Resistant	$\frac{r_x}{R_x} \frac{y}{y}$ 0.0112	2.52	50.0
$\frac{rX}{RX} \frac{Y}{Y}$ 0.0112	2.52	Resistant	$\frac{rX}{rX} \frac{Y}{Y}$ 0.0006	0.14	Resistant
$\frac{rX}{RX} \frac{y}{Y}$ 0.0225	5.06	7.5	$\frac{rX}{rX} \frac{y}{Y}$ 0.0013	0.29	12.5
$\frac{rX}{RX} \frac{y}{y}$ 0.0112	2.52	10.0	$\frac{rX}{rX} \frac{y}{y}$ 0.0006	0.14	22.5
$\frac{r_x}{RX} \frac{Y}{Y}$ 0.1013	22.79	20.0	$\frac{r_x}{rX} \frac{Y}{Y}$ 0.0112	2.52	34.0
$\frac{r_x}{RX} \frac{y}{Y}$ 0.2025	45.56	29.0	$\frac{r_x}{rX} \frac{y}{Y}$ 0.0225	5.06	52.5
$\frac{r_x}{RX} \frac{y}{y}$ 0.1013	22.79	40.0	$\frac{r_x}{rX} \frac{y}{y}$ 0.0112	2.52	62.5
$\frac{R_x}{R_x} \frac{Y}{Y}$ 0.0006	0.14	Resistant	$\frac{r_x}{r_x} \frac{Y}{Y}$ 0.0506	11.39	45.0
$\frac{R_x}{R_x} \frac{y}{Y}$ 0.0013	0.29	Resistant	$\frac{r_x}{r_x} \frac{y}{Y}$ 0.1013	22.79	70.0
$\frac{R_x}{R_x} \frac{y}{y}$ 0.0006	0.14	Resistant	$\frac{r_x}{r_x} \frac{y}{y}$ 0.0506	11.39	85.0

plants in the present instance. The proportion of each genotype which lay in the successive class intervals around the mean was then calculated on the basis of a normal distribution from the ratio $\frac{\text{deviation}}{\text{standard error}}$. Distributions with

means of 7.5 and 10% were calculated on the basis of a binomial distribution in each case according to the formula $(p+q)^n$. Comparisons showed that with regard to means above 10% the normal distribution very closely approached the binomial distribution and was accordingly used. These frequency distributions account solely for sampling errors and probably underestimate the errors involved in distributing the rows of each genotype since no account is taken of environmental effects. The separate distributions of the genotypes concerned are shown in Table 5, as well as the total number of rows expected in each 5% infection class, by taking the combined values of the separate distributions.

The comparison between observed and expected distributions is shown in Figure 1, indicating the per cent of rows in each infection class. The chi-square test for comparison of observed and expected number of F_3 rows in each class is presented in Table 6. In this test the resistant rows in the 2.5% and 7.5% classes were grouped together as the expected rows had been assigned in this way in these classes. Classes with expected numbers less than five were grouped with an adjacent class or classes to give an expected number greater than five. The total χ^2_{13} value was 11.8205, giving a probability value between 0.70 and 0.50.

The proposed genotype for Turkey 10095 will now be considered in a comparison of observed and expected results in tester crosses other than those involving Rio and Turkey 10015, which have previously been considered. In calculating expected distributions in these instances the order of the linked genes was taken as Turkey (T), Rio (R), X and Martin (M) in conformity with the relationship suggested by Stanford (1941) in assessing the linkage between the M, R and T genes. The map distances T-R, R-X and X-M on the basis of 10% crossing over between R and X were taken to be 2.4, 10 and 20 crossover units respectively. These figures, especially for the X gene, are considered to be only approximate but are in close agreement with the figure of 34.22% given for the linkage between the Martin and Turkey genes (Briggs, 1940) and the estimate of 2.4% linkage between the Rio and Turkey genes made by Stanford. In any case, the map distance between M and T should perhaps be increased as the intervening genes allow the detection of double crossing in this region, but further refinement does not seem necessary concerning this point at this stage in view of the uncertainty of the extent of linkage between R and X.

As indicated in Tables 2 and 3 segregation occurred in tester crosses with Selection 1403, Turkey and Martin, indicating that neither the H, T or M genes respectively were present in Turkey 10095. In the cross with Selection 1403, two F_3 rows were observed with above 60% infection whilst computations show that 4.08 would be expected in this category, derived from the three genotypes—completely susceptible, Xx and Yy. Although the gene H is on the same chromosome as X, they are probably more than 50 crossover units apart, on the data of Schaller and Briggs (1955), and are therefore genetically independent. A binomial distribution calculation shows that the probability of obtaining a deviation as great as or greater than that observed through chance alone is 0.34. A chi-square test was not used as one of the expected classes was less than five. As expected, less segregation occurred in the crosses involving the T and M genes on account of linkage with R and X. In the test cross with Martin 1 row above 60% was recorded and three above 45%, the computed values being 0.78 and 1.78 respectively; obviously the agreement between observed and expected results in the former case is entirely satisfactory, and on the basis of a binomial distribution the probability of obtaining a deviation as great as or greater than that observed through random sampling was 0.43

TABLE 6

χ^2 Test for Comparison of Observed and Expected Number of F_3 Rows for the Cross Turkey 10095 \times Baarti, for the Several Bunt Infection Classes Indicated

Bunt infection class	Number observed Rows	Number expected Rows	Deviation	χ^2
0- 5	43	43.00	-2.89	0.1287
5- 10	19	21.89		
10- 15	6	4.10	2.07	0.2870
15- 20	11	10.83		
20- 25	13	17.88	-4.88	1.3319
25- 30	18	22.85	-4.85	1.0294
30- 35	15	19.51	-4.51	1.0425
35- 40	20	15.35	4.65	1.4086
40- 45	19	15.41	3.59	0.8363
45- 50	15	10.28	4.72	2.1672
50- 55	6	5.11	0.89	0.1550
55- 60	3	2.61	2.44	0.9076
60- 65	6	3.95		
65- 70	7	9.19	-2.19	0.5219
70- 75	6	8.69	-2.69	0.8327
75- 80	6	3.39	1.47	0.2533
80- 85	4	5.14		
85- 90	6	4.91	2.29	0.9184
90- 95	2	0.78		
95-100	0	0.02		
Total	225	224.89		11.8205 ¹

¹D.f. = 13, P = 0.70-0.50.

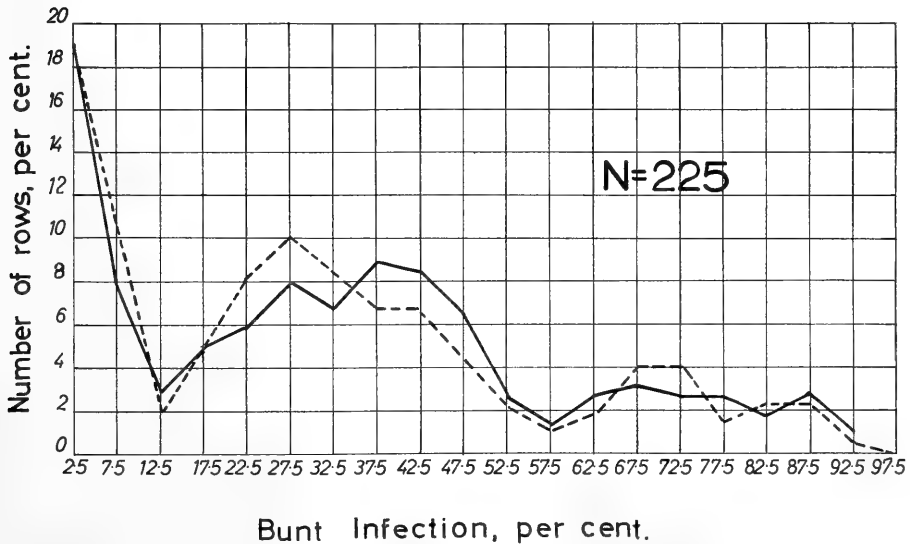


Fig. 1.—Observed percentage distribution of F_3 rows of the cross Turkey 10095 \times Baart for bunt infection (solid line) compared with theoretical distribution (broken line).

in the second comparison. With the tester cross involving Turkey 3055 the close linkage between the T, R and X genes gives a low probability of F₃ rows above 60% infection being produced, only one row in about 15,000 being computed to fall into this infection range. However above 40% 0.69 rows out of 250 tested derived from various genotypes—completely susceptible, Xx, Yy, Xx Yy, Tt, Rr, YY and Rr Yy, which would reasonably be expected to fall above this infection point—would be theoretically expected, whilst as shown in Table 4 one was actually observed in the 55–60 infection class.

The postulated genotype for Turkey 10095, $\overline{RRXX} YY$, with 10% crossing over between the R and X genes, with regard to bunt resistance therefore gives satisfactory statistical agreement between observed and expected results in crosses both with Baart and tester varieties of known genetic constitution for bunt resistance.

ANALYSIS OF GENOTYPE OF TURKEY 10097 IN RELATION TO BUNT RESISTANCE

An analysis of the genotype of Turkey 10097 indicated that its resistance was due to the additive or complementary effect of two weak genes, one being the X factor and the second a previously unidentified factor, designated W. The distribution of the per cent of F₃ rows in the cross Turkey 10097 × Baart is shown in Figure 2. The presence of two weak genes in Turkey 10097 was necessary to account for the F₂ infection of 29% in its cross with Baart and for the spread of F₃ rows in the same cross. With the X gene alone, the predicted behaviour would give an F₂ infection of approximately 60% with a corresponding grouping of F₃ rows in the intermediate class around this mean, with one-fourth of the rows, comprising the completely susceptible group, above this figure. As indicated in Table 2 and Figure 2 this hypothesis falls far short of fitting the observed results. The absence of a maximum point in the group of resistant F₃ classes indicates that the factor W must confer little resistance even in the homozygous condition.

TABLE 7

Ratio of F₂ Genotype, Number of F₃ Rows, and Mean Percent of Bunt in F₃ Rows Postulated for the Cross Turkey 10097 × Baart, the X and W Factors Being Independent

Ratio of F ₂ Genotype	Number of F ₃ Rows	Mean Percent of Bunt in F ₃ Rows
1 XX WW	15.19	1.0
2 XX Ww	30.38	9.0
2 Xx WW	30.38	20.0
4 Xx Ww	60.75	32.5
1 XX ww	15.19	22.5
2 Xx ww	30.38	60.0
1 xx WW	15.19	37.5
2 xx Ww	30.38	47.5
1 xx ww	15.19	80.0
Total	243.03	

The X and W genes were considered independent and the values assigned the mean percentage of bunt expected in the F₃ rows in the various genotypes in the cross Turkey 10097 × Baart are indicated in Table 7, together with the number of F₃ rows expected for each genotype. Of the various values assigned the W gene, those which gave the best agreement between observed and expected results indicated a value of 40% infection in F₃ rows for homozygous WW and 50% for the heterozygous Ww condition. The values assigned XX and Xx were 22.5 and 60.0% respectively, compared with corresponding values of

TABLE 8
Theoretical Distributions of F₃ Rows of Turkey 10097 × Baart for the Several Genotypes Indicated
 (Means used for genotypes are indicated in Table 7)

Bunt infection class	Genotype										Expected rows (Number)	Observed rows (Number)	Expected rows (Percent)	Observed rows (Percent)
	XX WW	XX Ww	Xx WW	Xx Ww	XX ww	Xx ww	xx WW	xx Ww	xx ww	xx ww				
0-5	15.07	2.30	0.01								17.38	16	7.15	6.58
5-10	0.12	16.22	0.41		0.06						16.81	18	6.92	7.41
10-15		10.57	3.71	0.03	0.81						15.12	15	6.22	6.17
15-20		1.24	11.05	0.55	3.68						16.53	15	6.80	6.17
20-25		0.04	11.05	4.26	6.09			0.01			21.61	20	8.89	8.23
25-30			3.71	14.57	3.68			1.14	0.03		23.13	15	9.52	6.17
30-35			0.41	21.93	0.81			3.62	0.39		27.16	30	11.18	12.35
35-40			0.01	14.57	0.06	0.01		5.31	2.42		22.38	22	9.21	9.05
40-45				4.26		0.10		3.62	7.18		15.16	20	6.24	8.23
45-50				0.55		1.00		1.14	10.32		13.01	14	5.35	5.76
50-55				0.03		4.51		0.17	7.18		11.89	10	4.89	4.12
55-60						9.56		0.01	2.42		11.99	15	4.93	6.17
60-65						9.56		0.39	0.03		9.96	8	4.10	3.29
65-70						4.51		0.03			4.75	6	1.95	2.47
70-75						1.00					2.86	7	1.18	2.88
75-80						0.10					5.63	8	2.32	3.29
80-85						0.01					5.54	4	2.28	1.65
85-90											1.86	0	0.77	0.00
90-95											0.21	0	0.09	0.00
95-100											0.01	0	0.00	0.00
Total	15.19	30.37	30.36	60.75	15.19	30.36	15.19	30.36	30.36	15.22	242.99	243	99.99	99.99

22.5 and 62.5% in the case of Turkey 10095. Tests involving the two Selections were conducted in different seasons, the corresponding completely susceptible genotypes being assigned values of 80 and 85% respectively. Hence some slight reduction in the value assigned the heterozygous Xx condition might reasonably be expected in the cross Turkey 10097 × Baart.

The mean infection in the 15 Baart checks throughout the F₂ and F₃ rows of the cross was $83.8 \pm 1.49\%$. The lower 95% fiducial limit was 80.6% and a value of 80% for the completely susceptible xx ww genotype was adopted rather than the mean for the Baart checks as better agreement between observed and expected results was secured. Similarly in the case of the double heterozygous genotype the upper 95% fiducial limit value of 32.3% for the F₂ mean of $29.2 \pm 1.58\%$ was used in distributing F₃ rows from this genotype. The double homozygous resistant genotype was assigned a value of 1.0% similar to the mean of Turkey 10097. The two remaining genotypes XX Ww and Xx WW were assigned values which might reasonably be expected from the interaction of the genes concerned.

The theoretical distributions of F₃ rows in the various genotypes were calculated as in the case of Turkey 10095. The theoretical distribution of the F₃ rows for each genotype is shown in Table 8, together with the computed total number for each infection class. The chi-square test for comparison of observed and expected numbers of F₃ rows for the different infection classes is shown in Table 9, the P value being 0.70-0.50. The theoretical distribution is compared graphically with the observed distribution in Figure 2. The genotype XX WW for Turkey 10097 thus gives satisfactory agreement between observed and expected results for the distribution of F₃ rows of the cross Turkey 10097 × Baart, when the indicated values are assigned to F₂ genotypes.

The postulated genotype for Turkey 10097 will be considered in its behaviour in tester crosses in greater detail. In the cross Turkey 10097 × Selection 1403, 3/64 of the F₃ population, derived from the genotype $\bar{h}h\bar{x}\bar{x} ww$ (completely susceptible) and $\bar{h}hXx ww$ (60% infection) would be expected to exhibit more than 55% infection. In 104 rows tested four such rows were observed compared with 5.07 expected. On the basis of a chi-square test this comparison gives a P value between 0.70-0.50. With 20% crossing over between X and M, 2.25% of the F₃ rows in the Martin cross, derived from similar genotypes to those above, would be expected above the 55% infection class. In 106 rows observed, one was found in the 50-55% infection class. If this is considered to belong to the category above 55%, the probability on a standardized normal variate test of such a deviation being due to chance alone is 0.52. In the case of the cross involving Turkey 10015, as previously indicated, the infection range with the X gene in common would be expected to extend up to 20-25% in F₃ rows and two rows were actually observed in this infection class. The distribution of infection in F₃ rows around a mean of approximately 10% substantiates the theory that independent segregation of the W and Y genes occurred in this cross with the X gene present in both varieties.

A comparison of observed and expected results in the case of tester crosses with Turkey 3055 and Rio was not entirely satisfactory however. Assuming the same gene order for the T, R, X and M genes as employed in the case of the Turkey 10095 tester crosses, 3.5 F₃ rows of the 251 tested in the cross with Turkey 3055 would theoretically exhibit approximately 60% infected plants. No rows showing more than 30-35% infection were recorded. Similarly three F₃ rows in the tester cross with Rio would be expected to be derived from F₂ plants heterozygous for the X gene alone, theoretically showing 60% infected plants in such lines. One segregate was recorded in each of the 35-40 and 40-45% infection classes.

However the fact that no moderately susceptible F₃ lines corresponding to those expected from appropriate genotypes in the case of both the Turkey

TABLE 9

χ^2 Test for Comparison of Observed and Expected Number of F_3 Rows for the Cross Turkey 10097 \times Baart for the Several Bunt Infection Classes Indicated

Bunt infection class	Number observed Rows	Number expected Rows	Deviation	χ^2
0- 5	16	17.38	-1.38	0.1096
5- 10	18	16.81	1.19	0.0842
10- 15	15	15.12	-0.12	0.0010
15- 20	15	16.53	-1.53	0.1416
20- 25	20	21.61	-1.61	0.1199
25- 30	15	23.13	-8.13	2.8576
30- 35	30	27.16	2.84	0.2970
35- 40	22	22.38	-0.38	0.0065
40- 45	20	15.16	4.84	1.5452
45- 50	14	13.01	0.99	0.0753
50- 55	10	11.89	-1.89	0.3004
55- 60	15	11.99	3.01	0.7556
60- 65	8	9.96	-1.96	0.3857
65- 70	6	4.75	5.39	3.8176
70- 75	7	2.86		
75- 80	8	5.65	2.37	0.9977
80- 85	4	5.54		
85- 90	0	1.86	-3.62	1.7197
90- 95	0	0.21		
95-100	0	0.01		
Total	243	243.00		13.2146 ¹

¹ D.f. = 15, P = 0.70-0.50.

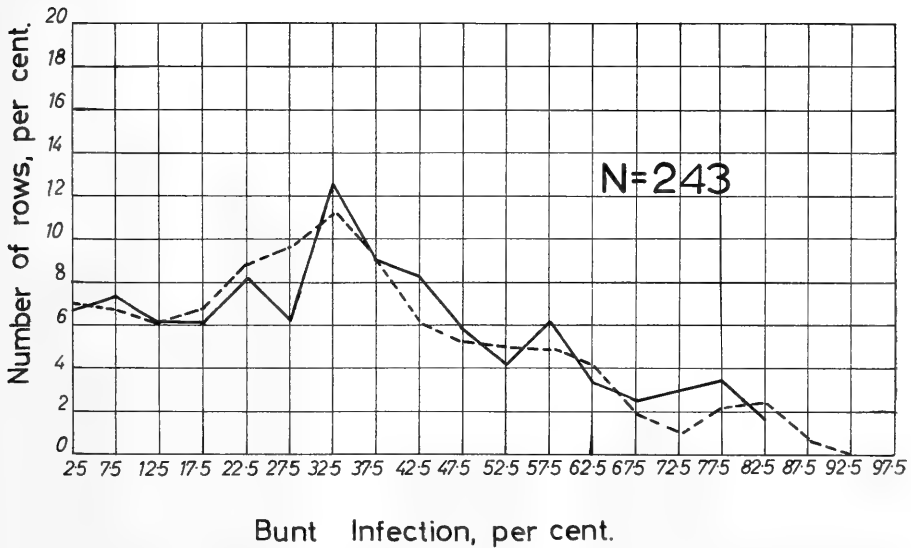


Fig. 2.—Observed percentage distribution of F_3 rows of the cross Turkey 10097 \times Baart for bunt infection (solid line) compared with theoretical distribution (broken line).

3055 and Rio tester crosses was not statistically significant at the 0.05 probability level on the basis of a standardized normal variate test. In any case all tester crosses involving Turkey 10097 were sown in a section of the nursery where low bunt infection was recorded in the Baart check rows. Under these circumstances the infection in segregating rows would also be expected to be lower. Hence the two weak genetic factor genotype (XX WW) for Turkey 10097 gave satisfactory agreement between observed and computed distributions also in tester crosses, and this genotype is therefore proposed for this Turkey strain.

DISCUSSION

Weak genes for bunt resistance have been reported by El Khishen and Briggs (1945), Smeltzer (1952) and in the current investigations. These are genes which are presumably incompletely dominant in all instances where they have been postulated to operate and which when homozygous permit up to 45% of plants (in the case of the Y gene) to become infected with bunt. The gene X in this category was found to be associated in the present studies with the $\overline{\text{HMRT}}$ linkage group and was presumably located between the M and R genes but closer to R, with which it showed approximately 10% recombination. Smeltzer found one of the two weak genes (U or V), which he identified in Minturki, also associated with the same linkage group. Crosses between Minturki and other varieties possessing postulated weak genes, however, were not available in his or the current investigations and the relationship between the genes in Minturki and other weak genes could not be established. Presumably U or V may be identical with X.

Verification of the postulated genotype for Turkey 10097, where two weak genes are invoked, would necessitate initially isolation of the two separate homozygous genotypes carrying resistance genes in F_3 lines exhibiting the appropriate levels of infection from a cross with a susceptible variety such as Baart. Final proof would depend on the isolation of homozygous highly resistant or immune F_3 lines due to gene interaction when these two genotypes were crossed.

It might also reasonably be expected that isolated weak genes similar to those proposed in these studies might be found alone in certain instances. Tisdale *et al.* (1925) in investigations on varietal resistance in hard red spring, hard red winter, soft red winter and white classes of wheat found that certain varieties and strains in all these classes consistently showed between 10 and 30% infected heads in a series of tests at different stations over a period of two years or longer. The percentage of bunted plants would undoubtedly be higher than this, but there are definite indications that genes permitting only a moderate number of infected plants were responsible for the observed varietal reactions. Likewise El Khishen and Briggs (1945) reported that unpublished data of Mackie and Briggs in 1920 showed that six out of 956 varieties and strains of wheat tested had a bunt infection of between 20 and 25% indicating the presence of a weak gene similar in effect to the X factor. Similarly varieties showing around 40 to 50% infection would indicate the presence of genes similar in effect to the W or Y factors. The group of Turkey wheat selections from the same source as those studied in the present investigations possess weak genes either entirely or in combination with strong ones as they have been discovered in Turkey 10015, 10016, 10095 and 10097. The presence of weak genes in combination with a strong one (R) has been postulated in Turkey 10095 and this parallels the presence of weak genes in combination with the R and T genes in Turkey 10016.

Previous investigations on Turkey types and strains of wheat have revealed that, in spite of general morphological similarities, they differ considerably in genotype for bunt resistance. Sherman and Cooperatorka have been found

to possess the Martin gene, Turkey 1558, 1558B, 2578, 3055 and Oro the T gene, Rio the R gene, Turkey 10015 the X and Y genes, Turkey 10016 the R, T, X and Y genes and Minturki the U and V genes. Therefore all except the H gene have been found in wheats of this type. Hence the unique genotypes reported in Turkey 10095 and 10097 in the present instance are not unexpected. Clark and Bayles (1935) reported that Turkey is the name applied to a rather morphologically similar group of wheats introduced at different times from widely scattered and isolated areas of the Crimea region in Southern Russia into the United States. Morphologically distinct strains given varietal nomenclature have been isolated from these wheats and all strains of this variety have been noted as lacking uniformity. Evans and Janssen (1922) reported that South Dakota 144 wheat from which the selections currently studied were made followed the general historical pattern of introduction from the northern areas of the Crimea, whence it was introduced into Kansas about 1875, and was subsequently given the accession number which it bears by the South Dakota Agricultural Experiment Station. In tests reported by Kiesselbach and Anderson (1930) significant differences in cold survival and minor differences in heading and ripening dates were observed among the selections of South Dakota 144, indicating physiological differences.

Since the genotypes of Turkey 10015, 10095 and 10097 were different at Davis, California using a single race of bunt, it might reasonably be expected that they would not behave in an identical manner to different bunt races. The only tests on the differential behaviour of these varieties are those reported by Kiesselbach and Anderson. To race VI of *T. foetida*, Turkey 10015 showed 8.9% infection whilst the infections in Turkey 10095 and 10097 were higher, being 25.0 and 21.7% respectively. To race X (*T. caries*) both Turkey 10095 and 10097 were immune but Turkey 10015 showed 7.3% infection. There was little differential behaviour between Turkey 10095 and 10097 and in only two instances were minor differences reported. To one collection of *T. foetida* 10095 showed 4.7% infection whilst 10097 was immune; in the case of one collection of *T. caries* the respective reactions were immunity and 4.2% infection. Tests against several races of the pathogens with varieties known to possess the same gene for resistance to one race will frequently reveal the presence of additional resistance factors. On this basis Holton and Briggs (1950) presented evidence indicating that Martin possessed at least two genes for resistance to a combination of physiologic races of *T. caries* and *T. foetida*. Schaller, Holton and Kendrick (1960) showed that a second gene (M_2) in Martin was inherited independently of M and was also different from M in being incompletely dominant in inheritance. The varieties Baart and Federation, susceptible to race T-1, apparently possessed the M_2 gene, since their race reactions were identical to that of the isolated M_2 gene from Martin.

The type of gene interaction whereby a combination of two weak genes are postulated to confer high resistance or immunity to a pathogen is of interest. The interaction may be an additive effect or may involve complementary gene action. The crown rust resistance of the oat variety Bond has been found to be based on complementary dominant gene interaction (Baker and Upadhyaya, 1966 (in press)). From Bond the two factors concerned have been isolated in separate lines (Baker, 1966 (in press)).

The phenotypes shown by wheat plants when seed inoculated with the bunt organisms is obviously the result of a complex interaction between genotype and environment. Invariably some genotypically susceptible plants do not manifest bunt symptoms. On the other hand Briggs (1929) indicated that genetically resistant plants, as indicated by progeny tests, occasionally may become infected. He demonstrated also the presence of minor genes which modify bunt resistance. Little is known of the mechanism in the host conferring resistance in bunt. A pertinent observation is that if the maturity of the resistant variety Florence is delayed by cutting back the initially formed

spikes, occasional late maturing tillers show bunted grains (Waterhouse, personal communication). This suggests that a differential growth rate between the host and pathogen after infection confers resistance. In this connection there is also lack of knowledge on the significance of the fact that all tillers in a susceptible plant frequently do not show bunt symptoms. Until basic information is obtained on the nature of bunt resistance in wheat it is impossible to specify the phenomena whereby a homozygous genotype may, in the case of weak genes, permit a moderate percentage of plants to fail to manifest bunt symptoms or those whereby a heterozygous genotype in the case of certain strong genes, such as the R factor, permits approximately only half the plants to show symptoms at maturity.

Genotype and environment interactions might reasonably be expected to be more variable in the case of weak genes. In this connection Smeltzer (1952) found that Minturki (possessing the weak genes U and V) in one season showed an average infection of 20.7%, with a range of from 3.8 to 38.9% in individual rows, the previous highest annual average infection over several seasons being 3.2%. He suggested that the physiology of the plants was disturbed by severe winter conditions in the season showing high average infection such that there was a breakdown in the resistance mechanism in Minturki. Environmental effects on host-pathogen relationships have been reviewed by Tapke (1948) in the case of smuts.

Five genes (H, M, X, R and T) for resistance to the one race of bunt have been placed by linkage studies on the same chromosome. It may be argued that the R and T genes which are similar in effect and mode of inheritance represent the same gene which differs in its chromosomal site due to a small inversion so that the two genes are no longer at the same locus on the chromosome. However, Sutherland and Jodon (1934) obtained an average of 4% of bunt in 1930-32 with Rio and 60% with Turkey C.I. 1558. At the same time in the absence of more critical evidence this could be accounted for by the presence of a second gene in Rio. The other three genes (H, M and X) clearly differ from one another and from the R and T genes from their reaction to a single race with regard to the level of infection they permit, their mode of inheritance with regard to dominance or the fact that they exhibit a differential reaction to certain races.

Sears, Schaller and Briggs (1960) by monosomic analysis placed the M gene on chromosome XIII (2A). Hence the five linked genes of the seven definitely identified conditioning resistance to race T-1 are located on this chromosome belonging to the A genome in hexaploid wheats and contributed by a prototype of the present-day diploid wheat species, *Triticum aegilopoides* (Link) Bal. This evidence suggests that diploid *Triticum* species may possess previously unrecorded genes for bunt resistance capable of being transferred by amphidiploidy to hexaploid wheat. Several investigators have reported that *T. monococcum* L. ($2n=14$) is generally highly resistant to bunt, but a few instances are noted where it was quite susceptible. It is also of interest that *T. timopheevi*, Zhuk. containing the A and a modified B genomes, was immune to all bunt races to which it was tested by Rodenhiser and Holton (1945).

It is possible that weak genes which have been identified in Turkey wheats on the basis of their segregation pattern to race T-1 may confer immunity to certain races of bunt in the Crimean area. It is also feasible that they may confer immunity to new races as they arise in North America and elsewhere. Hence, although somewhat more difficult to manipulate in a breeding programme on their behaviour to race T-1, they may well have a place in breeding for resistance to particular races of the pathogens. In this connection combinations of single genes may afford protection against numerous physiologic races identified on the accepted differential varieties. Briggs and Holton (1950) concluded that the Martin and either the Turkey or Rio genes together gave

protection against all 25 then known races. For this reason Selection C.I. 12242, which was assumed to possess both the Rio and Martin genes, was resistant to all races. Schaller and Briggs (1953) reported that two genes (M and T) in combination afforded protection against 25 out of 31 races then recognized.

A combination of the five linked genes (H, M, X, R and T in this order on the chromosome) would provide a potent resistance against all bunt races. The genotype of Turkey 10016 includes the genes T, X and R. By a backcrossing programme involving Turkey 10016 and Martin, using the former variety as the recurrent parent and selecting for resistance to a race such as L-8 or T-16, which is virulent on Turkey 10016, but incapable of attacking varieties possessing the M gene (Briggs and Holton, 1950), the genes M, X, R and T could be combined. If a race capable of attacking this combination was detected but to which Hussar was resistant due to the H gene which it possesses, the latter gene could then be incorporated similarly by backcrossing. At the present time there is apparently no bunt race to which Hussar owes its resistance to the combined effect of the M and H genes, and to which Turkey 10016 is susceptible. With the estimated linkage values between these genes it should be possible by crossing Hussar and Turkey 10016 to combine at least the R or T genes with either the M or H genes by selection in segregating generations which are tested with appropriate races. The predicted amount of crossing over would permit their combination in a variety with little difficulty. Once the HMXRT linkage group was established in a homozygous dominant condition in a well-adapted variety the backcross technique could be used in a practical breeding programme. Since monosomic series are available in many agronomic varieties currently cultivated commercially, cytogenetical techniques could also be employed to substitute the chromosome with all the linked genes into these varieties.

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References

- BAKER, E. P., 1966.—Isolation of complementary genes conditioning crown rust resistance in the oat variety Bond. *Euphytica*, (in press).
- BAKER, E. P., and UPADHYAYA, Y. M., 1966.—Studies on the inheritance of rust resistance in oats. IV. Expression of allelomorphism and gene interaction for crown rust resistance in crosses involving the oat variety Bond. *PROC. LINN. SOC. N.S.W.*, (in press).
- BRIGGS, F. N., 1926.—Inheritance of resistance to bunt, *Tilletia tritici* (Bjerk.) Winter, in wheat. *J. agr. Res.*, 32 : 973-990.
- , 1929.—Factors which modify resistance of wheat to bunt, *Tilletia tritici*. *Hilgardia*, 4 : 175-181.
- , 1930a.—Inheritance of the second factor for resistance to bunt, *Tilletia tritici*, in Hussar wheat. *J. agr. Res.*, 40 : 225-232.
- , 1930b.—Inheritance of resistance to bunt, *Tilletia tritici*, in White Odessa wheat. *J. agr. Res.*, 40 : 353-359.
- , 1931.—Inheritance of resistance to bunt, *Tilletia tritici*, in hybrids of White Federation and Banner Berkeley wheats. *J. agr. Res.*, 42 : 307-313.
- , 1932a.—Inheritance of resistance to bunt, *Tilletia tritici*, in hybrids of White Federation and Odessa wheat. *J. agr. Res.*, 45 : 501-505.
- , 1932b.—Inheritance of resistance to bunt, *Tilletia tritici*, in crosses of White Federation with Turkey wheat. *J. agr. Res.*, 44 : 131-136.
- , 1934.—Inheritance of resistance to bunt, *Tilletia tritici*, in Sherman and Oro wheat hybrids. *Genetics*, 19 : 73-82.
- , 1936.—Inheritance to resistance to bunt, *Tilletia tritici*, in hybrids of Turkey wheats, C.I. 1558B and 2578. *Hilgardia*, 10 : 19-25.
- , 1940.—Linkage between the Martin and Turkey factors for resistance to bunt, *Tilletia tritici*. *J. Amer. Soc. Agron.*, 32 : 539-541.
- BRIGGS, F. N., and HOLTON, C. S., 1950.—Reaction of wheat varieties with known genes for resistance to races of bunt, *Tilletia caries* and *T. foetida*. *J. Amer. Soc. Agron.*, 42 : 483-486.

- CLARK, J. A., and BAYLES, B. B., 1935.—Classification of wheat varieties grown in the United States. U.S. Dept. Agric. Tech. Bull. 459.
- EL KHISHEN, A. A., and BRIGGS, F. N., 1945.—Inheritance of resistance to bunt (*Tilletia caries*) in hybrids with Turkey wheat selections C.I. 10015 and 10016. *J. agr. Res.*, 71: 403-413.
- EVANS, A. T., and JANSSEN, G., 1922.—Winter wheat in South Dakota. S. Dak. agric. Expt. Stat. Bull. 200.
- KIESSELBACH, T. A., and ANDERSON, A., 1930.—Breeding winter wheats for resistance to stinking smut. Nebr. agr. Expt. Stat. Res. Bull. 51.
- KUIPER, J., 1965.—Failure of hexachlorobenzene to control common bunt of wheat. *Nature*, 206: 1219-1220.
- RODENHISER, H. A., and HOLTON, C. S., 1937.—Physiologic races of *Tilletia tritici* and *T. levis*. *J. agr. Res.*, 55: 483-496.
- , 1945.—Distribution of races of *Tilletia caries* and *Tilletia foetida* and their relative virulence on certain varieties and selections of wheat. *Phytopath.*, 35: 955-969.
- SCHALLER, C. W., and BRIGGS, F. N., 1955.—Linkage relationships of the Martin, Hussar, Turkey and Rio genes for bunt resistance in wheat. *J. Amer. Soc. Agron.*, 47: 181-186.
- SCHALLER, C. W., HOLTON, C. S., and KENDRICK, E. L., 1960.—Inheritance of the second factor for resistance to bunt, *Tilletia caries* and *T. foetida*, in the wheat variety Martin. *J. Amer. Soc. Agron.*, 52: 280-282.
- SEARS, E. R., SCHALLER, C. W., and BRIGGS, F. N., 1960.—Identification of the chromosome carrying the Martin gene for resistance of wheat to bunt. *Canad. J. Genet. Cytol.*, 2: 262-267.
- SMELTZER, D. G., 1952.—Inheritance of resistance to race T-1 of *Tilletia caries* in Minturki and Cooperatorka wheats. *J. Amer. Soc. Agron.*, 44: 529-533.
- STANFORD, E. H., 1941.—A new factor for resistance to bunt, *Tilletia tritici*, linked with the Martin and Turkey factors. *J. Amer. Soc. Agron.*, 33: 559-568.
- SUTHERLAND, J. L., and JODON, N. E., 1934.—Resistance of wheat varieties at Moccasin, Montana and North Platte, Nebraska. *J. Amer. Soc. Agron.*, 26: 296-306.
- TAPKE, V. F., 1948.—Environment and the cereal smuts. *Bot. Rev.*, 14: 349-412.
- TISDALE, W. H., MARTIN, J. H., BRIGGS, F. N., MACKIE, W. W., WOOLMAN, H. M., STEPHENS, D. E., GAINES, E. F., and STEVENSON, F. J., 1925.—Relative resistance of wheat to bunt in the Pacific coast states. U.S. Dept. Agric. Bull., 1299.

RHINONYSSINE NASAL MITE INFESTATIONS IN BIRDS AT MITCHELL RIVER MISSION DURING THE WET AND DRY SEASONS

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Synopsis

The tropical Mitchell River Mission has a sharply defined wet and dry season each year, almost 90% of the annual average rainfall of 48 inches falling between December and March. Collections of birds during each season showed no obvious difference either in terms of absolute numbers or species composition, except for a slightly broader spectrum in the "dry" (59% of the species were seen in both seasons, 25% only in the "dry" and 16% only in the "wet"). Any disparity is explainable by (i) natural factors such as seasonal migration and nomadism; and (ii) sampling bias: the country is largely impassable in the "wet", and, paradoxically, it is therefore easier both to collect water-birds in the "dry" and perching birds in the "wet".

This constancy is paralleled by the rhinonyssine mite populations in the nasal passages of these birds. The same mite genera and species are present in both seasons, and infestation rates and numbers of mites *per* infested bird are constant. Of 108 species of birds examined, 43 had nasal mites; the proportion in the "wet" was 28/77 and in the "dry" 29/82. Of 841 individual birds examined, 129 had nasal mites; the proportion in the "wet" was 65/476 and in the "dry" 64/365. The average number of mites in an infested bird was five in the "wet" and four in the "dry". These overall statistics could reflect the relatively constant microclimate in the warm, moist nasal passages compared with the extremes outside, where noon shade temperatures over 100°F and relative humidities below 20% are common in the "dry".

A list of the 128 species of birds recorded at the Mission is appended, showing the species recorded, or likely to be recorded as harbouring rhinonyssine nasal mites.

INTRODUCTION

The belief of Victorian virologists that Murray Valley encephalitis had infiltrated from north Queensland stimulated a survey of human sera for neutralizing antibodies to MVE. This showed their highest incidence around the Gulf of Carpentaria, and the Mitchell River Mission was selected for intensive study. The virus has since been isolated from mosquitoes caught there, and periodical visits have confirmed the significance of the area, where a field station has recently been opened (20th Annual Report, Queensland Institute of Medical Research, 1965).

In an expansion of this programme, several species of birds have already been shown, by direct isolation of viruses, to act as reservoirs of infection. The study of blood-sucking arthropods other than mosquitoes as possible natural vectors is also contemplated, but this will be hampered for some time by the infant state of systematics in almost all groups concerned. As a beginning, the intranasal mites of birds are receiving attention.

The present note, a comparison of the bird faunas and their intranasal mite populations in the "wet" and the "dry", is based on 10 weeks intensive field collecting, divided almost equally between the dry seasons (October-November) of 1964 and 1965, and the wet seasons (March-April) of 1965 and 1966. Results to date have been most gratifying, and a wealth of new records and species is under study (Domrow, 1966, and in ms.).

THE LOCALITY

To summarize Standfast (1965), the Mitchell River Mission cattle station (15°28'S, 141°40'E) is centred 16 miles from the west coast of Cape York Peninsula in a very flat, low-lying area of tropical tussock grassland and tropical woodland. It is typified by scrubby eucalypts and many coarse grasses, with fresh-water mangrove (*Barringtonia gracilis*)* and cabbage-tree palms (*Livistona australis*) common along the water-courses. The annual rainfall averages 48 inches, of which 42 inches fall between December and March. During the "wet", the rivers and creeks flood and large areas of low-lying country become fresh-water swamps, which, overgrown with the ubiquitous and very dense and tall grasses, provide a breeding ground for a wide variety of water-birds. During the "dry", this grass largely dies (or is burnt) away, leaving much bare earth, while the creeks are restricted to a series of water-holes, and the swamps recede to form small lagoons or dry out completely. These residual pools, with their meagre fringe of greenery, become the foci of the activities of large numbers of birds, which come to water throughout the day—this is not surprising as frequently the shade temperature exceeds 100°F and the relative humidity falls below 20% at noon.

THE BIRDS

Tables 1 and 2 are confined to the birds I have actually examined for nasal mites, and provide a comparison between the "wet" and the "dry". In both, the host data are broken down to ordinal level. Table 1 is concerned with the numbers of species of birds examined and found infested. Table 2 details the total numbers of birds examined, the numbers found infested and the numbers of mites *per* infested bird.

TABLE 1

Numbers of species of birds examined and found infested with Rhinonyssinae at Mitchell River Mission

Order	Species examined				Species infested			
	"Wet"	"Dry"	Both	Total	"Wet"	"Dry"	Both	Total
Columbiformes	4	4	2	6	3	2	1	4
Gruiformes		1		1				
Podicipiformes		1		1		1		1
Charadriiformes	5	9	4	10	2	4	2	4
Ciconiiformes	10	6	6	10		2		2
Anseriformes	2	6	2	6		1		1
Pelecaniformes	1	2		3				
Falconiformes	6	3	3	6	1	1	1	1
Strigiformes	1	1		2				
Psittaciformes	4	7	4	7	2	3	2	3
Caprimulgiformes	1	1	1	1				
Coraciiformes	6	5	5	6	4	2	1	5
Cuculiformes	6	2	2	6	2	1	1	2
Passeriformes	31	34	22	43	14	12	6	20
Total	77	82	51	108	28	29	14	43

It is evident, both in terms of species composition and absolute numbers of individual birds, that the "wet" fauna parallels the "dry" very closely (there are several large and permanent water-holes in the area), but with a slightly broader spectrum in the "dry". This is confirmed by consulting the complete list below of the birds now known to occur at Mitchell River: 75 (59%) of the 128 species were listed in both seasons, with 32 (25%) noted only in the "dry" against 21 (16%) only in the "wet". However, although it is impossible

* Given in error as *Nauclea orientalis* by Standfast.

to give a clear-cut explanation in every case—the predatory and water-bound faunas, for example, while nomadic, are undoubtedly more uniform than indicated—there are two factors which would tend to emphasize this slight difference.

The first comprises real, or natural differences of two main types. The dry season component includes a group of migratory species (*Myristicivora*, *Mesoscolopax*, *Erolia*, *Stiltia*, *Scythrops* and *Myiagra*), which, travelling south in September-October and returning north in March-April, could also be expected at the Mitchell River Mission in the "wet". However, other members of this group (*Halcyon sancta*, *Cacomantis variolosus* and *Chalcites*) have been noted only in the "wet", and *Eudynamys* and *Edoliisoma* in both seasons. Also, many (particularly a large group of nectar-feeders, e.g., lorikeets and honey-eaters) are nomadic, being dependent on flowering plants etc.: *Barringtonia* and eucalypts were both flowering profusely in the "dry" of 1965. The mistletoe bird, *Dicaeum*, is another example: this small bird "undertakes extensive seasonal movements coincident with the fruiting of the [mistletoe] plants. This may be in spring, summer, autumn, or winter, in different areas" (Keast, 1961).

The second is an unreal difference due to collecting bias. This is the direct result of climatic conditions. In the "wet", the roads are closed even to light traffic, and the swamps are overgrown with dense grass and reeds in excess of eight feet tall. Tables 1 and 2 bear out the paradoxes that it is easier both to obtain water-birds in the "dry" (95 of 25 species v. 55 of 18 species) and perching birds in the "wet" (421 of 59 species v. 270 of 57 species). Further, it is impossible to reach the sea by overland in the "wet", so *Larus*, *Haematopus* and *Haliastur indus* have been noted only in the "dry".

THEIR NASAL MITE PARASITES

From Tables 1 and 2, the infestation rates (Rhinonyssinae only) are also remarkably similar. Omitting host species examined only in the dry season, and the Cuculiformes, of which only inconclusive numbers were examined, the types of birds infested, the numbers infested and the numbers of mites *per* infested host remain virtually unchanged from the "wet" to the "dry".

TABLE 2

A seasonal comparison of infestation rates by Rhinonyssinae in birds at Mitchell River Mission

Order	Number examined		Number infested		Mites/infested bird	
	"Wet"	"Dry"	"Wet"	"Dry"	"Wet"	"Dry"
Columbiformes	32	32	5	4	3(3)	2(2)
Gruiformes		7				
Podicipiformes		2		1		1(1)
Charadriiformes	20	41	5	9	4(3)	6(6)
Ciconiiformes	19	13		2		16(15)
Anseriformes	15	28		1		2(2)
Pelecaniformes	1	4				
Falconiformes	24	8	5	2	6(4)	4(1)
Strigiformes	1	1				
Psittaciformes	62	61	4	6	4(-)	4(4)
Caprimulgiformes	1	2				
Coraciiformes	44	18	15	2	4(3)	10(-)
Cuculiformes	17	4	2	1	20(-)	1(1)
Passeriformes	240	144	29	36	4(4)	3(2)
Total	476	365	65	64	5(3)	4(3)

In the final column, unbracketed figures are derived from the total number of mites present; bracketed figures apply only to sexually mature mites—the adjustment is not great. Dashes indicate that figures are unavailable, certain common mites having been deep-frozen in the field for subsequent inoculation studies. The bracketed figures for Passeriformes are, for this reason calculated from only 26 birds in the "wet" and 31 in the "dry".

The constancy in seasonal occurrence of birds extends to the genera and species of their mite parasites, which are now treated under an ordinal arrangement of those hosts known to occur in both seasons. Host-specificity is marked in the Rhinonyssinae.

Double rhinonyssine infestations, while not unknown elsewhere in Queensland (Domrow, unpublished data), have not been noted at Mitchell River, although occasional mixed infestations—Rhinonyssinae (Mesostigmata) and Speleognathinae (Prostigmata)—are on record. However, speleognathines tend to inhabit portions of the nasal cavities different from those preferred by rhinonyssines.

COLUMBIFORMES : The two species of mites recorded (*Mesonyssus geopeliae* and *M. ocyphabus*) are members of a widespread and characteristic group of *Mesonyssus* species peculiar to pigeons (Fain, 1962 ; Wilson, 1964 ; Domrow, 1965).

CHARADRIIFORMES : Both genera and species of mites noted (*Rhinonyssus himantopus* and *Larinyssus benoiti*) are widespread parasites of waders (Strandtmann, 1959 ; Domrow, 1966).

FALCONIFORMES : The one species collected, *Ptilonyssus cerchneis*, also occurs in falcons in Africa, U.S.A. and U.S.S.R. (Fain, 1957 ; Strandtmann, 1962 ; Bregetova, 1964).

PSITTACIFORMES : All three species of mites recorded (*Mesonyssus trichoglossi*, *M. kakatuae* and *M. aprosmicti*) are members of a group of *Mesonyssus* species restricted to this order of birds (Wilson, 1964 ; Domrow, 1964).

CORACIFORMES : The two species of *Mesonyssus* (*M. daceoae* and *M. halcyonius*) recorded from Alcedinidae are close relatives of the species known from African members of this family (Fain, 1957, 1960 ; Domrow, 1965). *Merops*, a bee-eater (Meropidae), is parasitized by a species of *Ptilonyssus*, *P. triscutatus*, previously known from this host genus only in Europe and Africa (Fain, 1957).

CUCULIFORMES : The species of *Sternostoma*, *S. cuculorum*, taken from cuckoos at Mitchell River was originally recorded from the same host family in Africa (Fain, 1957).

PASSERIFORMES : Apart from *Sternostoma thienponti* and *Sternostoma* sp. from *Cracticus* and *Neositta* respectively, and *Ruandanyssus* sp. from *Artamus*, the remaining 13 species from 17 birds belong to *Ptilonyssus* (or the closely related *Passeronyssus*). These will not be listed in detail, but where overseas hosts have been recorded for these species, they have been closely related indeed to the Australian ones.

DISCUSSION

One explanation for this remarkable constancy of parasite populations throughout the year would seem to lie in the clemency of the warm, moist microclimate afforded by the nasal passages of the host, compared with the extremes outside. On the other hand, with small arthropods bound absolutely to water, e.g., mosquitoes, the wet season fauna differs radically from the dry, when standing waters stagnate and specialized habitats such as temporary pools, tree-holes and leaf axils dry out.

From Table 2 it was seen that the incidence of immature stages in both the "wet" and the "dry" was low, necessitating only minor adjustment to the overall numbers of mites *per* infested host to express their presence. Both sets of figures are given, however, to stimulate enquiry into the question whether the mite populations fluctuate at other times of the year. Further, the tenacity with which these delicate, weakly sclerotized mites keep to their specific microhabitat (see *Addendum*), coupled with their low numbers at the periods studied, presents the possibility that the restricted collecting periods may have tapped only maintenance populations, and not have coincided with reproduction peaks.

A LIST OF MITCHELL RIVER BIRDS

As both the wet (W) and dry (D) seasons are considered above, my own data have been slightly augmented by the incorporation of Standfast's preliminary list (1965) of the dry season fauna, on which I have the following comments.

It is doubtful if more than one species of crow (*Corvus ceciliae*) occurs at the Mission: eye-colour varies tremendously from white, through parti-coloured (blue and white), to dense blue-black, while the down of all specimens is uniformly white. With this one deletion (*C. bennetti*), I have had a further 41 of Mr. Standfast's species in the hand and would accept them, with two reservations.

Firstly, the smaller of the two species of cuckoo-shrikes occurring at the Mission admittedly appears white-breasted in the field, but in the hand it is distinctly grey-tinted and identifiable as *Coracina papuensis* rather than *C. hypoleuca*.

Secondly, the birds pointed out to me by Mr. Standfast as "banded plovers" proved in the hand to be Australian pratincoles (*Stiltia isabella*), not *Zonifer tricolor*.

Of the remaining 15 species, I can confirm seven by sighting, track or call (*Dromaius*, *Burhinus*, *Xenorhynchus*, *Pelecanus*, *Haliastur indus*, *Falco cenchroides* and *Scythrops*), but have not noted the others (*Alectura*, *Phaps*, *Porphyrio*, *Dupetor*, *Alcyone*, *Cyrtostomus*, *Aegintha* and *Ptilonorhynchus*).

I can now add another three orders (Podicipiformes, Strigiformes and Caprimulgiformes) and 72 species to this list. Of these, five (*Synoicus*, *Larus*, *Haematopus*, *Himantopus* and *Notophox pacifica*) are based on adequate sightings in the field and the remainder on specimens in the hand. These latter, in cases of doubt, were sent to the Queensland Museum, where Mr. D. P. Vernon kindly checked them against reference skins. I do not think many species, at least of land birds, remain undetected in the area, but I have glimpsed snipe, swifts, swallows and possibly a fantail. The following arrangement is that of the 9th edition [1958] of Leach's *An Australian Bird Book*. The rhinonyssine mite species printed in italics have been recorded at Mitchell River, while those in Roman type may be expected to occur there, having been recorded from the indicated host elsewhere in Australia (or New Guinea in the case of *Anas superciliosa*, see Wilson, 1964).*

CASUARIIFORMES		
<i>Dromaius novaehollandiae</i>	WD	
GALLIFORMES		
<i>Alectura lathamii</i>	D	
<i>Synoicus australis</i>	WD	
COLUMBIFORMES		
<i>Myristicivora spilorrhoea</i>	D	<i>Mesonyssus</i> sp. "A"
		<i>Mesonyssus</i> sp. "B"
<i>Geopelia placida</i>	WD	<i>Mesonyssus geopeliae</i>
<i>Geopelia cuneata</i>	WD	
<i>Geopelia humeralis</i>	WD	<i>Mesonyssus geopeliae</i>
<i>Phaps chalcoptera</i>	D	<i>Mesonyssus phabus</i>
<i>Geophaps scripta</i>	W	<i>Mesonyssus ocyphabus</i>
<i>Ocyphaps lophotes</i>	W	<i>Mesonyssus ocyphabus</i>
		<i>Mesonyssus columbae</i>
GRUIFORMES		
<i>Porphyrio melanotus</i>	D	
<i>Grus rubicundus</i>	WD	

* Since writing this, I again visited Mitchell River for three weeks in October-November 1966, adding eight more species to the list, making 136 in all. These additions are indicated by "d" in the central column.

PODICIPIFORMES

<i>Podiceps ruficollis</i>	D	<i>Rhinonyssus poliocephali</i>
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CHARADRIIFORMES

<i>Chlidonias hybrida</i>	WD	
<i>Sterna bergii</i>	d	<i>Larinyssus orbicularis</i>
<i>Larus novaehollandiae</i>	D	
<i>Haematopus ostralegus</i>	D	
<i>Erythrogonys cinctus</i>	D	<i>Rhinonyssus himantopus</i>
<i>Lobibyx miles</i>	WD	<i>Rhinonyssus himantopus</i>
<i>Charadrius alexandrinus</i>	d	<i>Rhinonyssus coniventris</i>
		<i>Rhinonyssus minutus</i>
<i>Charadrius melanops</i>	WD	<i>Rhinonyssus himantopus</i>
<i>Himantopus leucocephalus</i>	D	<i>Rhinonyssus himantopus</i>
<i>Recurvirostra novaehollandiae</i>	d	
<i>Numenius madagascariensis</i>	d	
<i>Mesoscolopax minutus</i>	D	
<i>Limosa limosa</i>	W	
<i>Erolia ruficollis</i>	d	<i>Rhinonyssus</i> sp.
<i>Erolia acuminata</i>	D	
<i>Irediparra gallinacea</i>	WD	
<i>Stiltia isabella</i>	D	<i>Larinyssus benoiti</i>
<i>Burhinus magnirostris</i>	WD	
<i>Eupodotis australis</i>	WD	

CICONIIFORMES

<i>Threskiornis molucca</i>	WD	
<i>Threskiornis spinicollis</i>	WD	
<i>Plegadis falcinellus</i>	WD	
<i>Platalea regia</i>	W	
<i>Platalea flavipes</i>	W	
<i>Xenorhynchus asiaticus</i>	D	
<i>Egretta intermedia</i>	Wd	
<i>Egretta alba</i>	WD	
<i>Notophox novaehollandiae</i>	WD	<i>Mesonyssus belopolskii</i>
<i>Notophox pacifica</i>	Wd	
<i>Notophox picta</i>	WD	<i>Mesonyssus belopolskii</i>
<i>Nycticorax caledonicus</i>	WD	
<i>Dupetor flavicollis</i>	D	

ANSERIFORMES

<i>Anseranas semipalmata</i>	WD	
<i>Nettapus pulchellus</i>	WD	
<i>Dendrocygna arcuata</i>	D	<i>Rhinonyssus rhinolethrus</i>
<i>Tadorna radjah</i>	WD	
<i>Anas superciliosa</i>	D	<i>Rhinonyssus rhinolethrus</i>
<i>Anas gibberifrons</i>	D	

PELECANIFORMES

<i>Phalacrocorax sulcirostris</i>	WD
<i>Phalacrocorax melanoleucus</i>	WD
<i>Anhinga novaehollandiae</i>	WD
<i>Pelecanus conspicillatus</i>	WD

FALCONIFORMES

<i>Accipiter fasciatus</i>	Wd	
<i>Aquila audax</i>	WD	
<i>Haliaeetus leucogaster</i>	WD	
<i>Haliastur sphenurus</i>	WD	
<i>Haliastur indus</i>	D	
<i>Milvus migrans</i>	WD	
<i>Falco berigora</i>	WD	<i>Ptilonyssus cerchneis</i>
<i>Falco cenchroides</i>	WD	<i>Ptilonyssus cerchneis</i>

STRIGIFORMES

<i>Ninox novaeseelandiae</i>	W	<i>Rhinoecius cooremani</i>
<i>Ninox connivens</i>	D	

PSITTACIFORMES

<i>Trichoglossus moluccanus</i>	WD	<i>Mesonyssus trichoglossi</i>
<i>Psitteuteles versicolor</i>	D	
<i>Calyptorhynchus banksi</i>	WD	<i>Mesonyssus kakatuae</i>
<i>Kakatoe galerita</i>	WD	
<i>Kakatoe roseicapilla</i>	WD	<i>Mesonyssus kakatuae</i>
<i>Kakatoe sanguinea</i>	D	
<i>Aprosmictus erythropterus</i>	WD	<i>Mesonyssus aprosmicti</i>

CAPRIMULGIFORMES

<i>Podargus strigoides</i>	WD
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CORACIFORMES

<i>Eurystomus orientalis</i>	WD	
<i>Alcyon azurea</i>	D	
<i>Dacelo leachi</i>	WD	<i>Mesonyssus daceloeae</i>
<i>Halcyon pyrrhopygia</i>	WD	<i>Mesonyssus halcyonus</i>
<i>Halcyon sancta</i>	W	<i>Mesonyssus halcyonus</i>
<i>Halcyon macleayi</i>	WD	<i>Mesonyssus halcyonus</i>
<i>Merops ornatus</i>	WD	<i>Ptilonyssus triscutatus</i>
		<i>Sternostoma cooremani</i>

CUCULIFORMES

<i>Cuculus saturatus</i>	W	
<i>Cacomantis pyrrhophanus</i>	WD	<i>Sternostoma cuculorum</i>
<i>Cacomantis variolosus</i>	W	<i>Sternostoma cuculorum</i>
<i>Chalcites plagosus</i>	Wd	
<i>Scythrops novaehollandiae</i>	D	
<i>Eudynamys orientalis</i>	WD	
<i>Centropus phasianinus</i>	WD	

PASSERIFORMES

<i>Hirundo neoxena</i>	d	<i>Cas angrensis</i>
		<i>Ptilonyssus echinatus</i>
<i>Microeca fascians</i>	WD	<i>Ptilonyssus microecae</i>
<i>Microeca flavigaster</i>	WD	<i>Ptilonyssus microecae</i>
<i>Rhipidura leucophrys</i>	WD	<i>Ptilonyssus macchurei</i>
		<i>Sternostoma laniorum</i>
<i>Myiagra rubecula</i>	D	<i>Sternostoma laniorum</i>
		<i>Ruandanyssus terpsiphonei</i>
<i>Seisura inquieta</i>	D	<i>Ptilonyssus terpsiphonei</i>
<i>Coracina novaehollandiae</i>	WD	<i>Ruandanyssus terpsiphonei</i>
<i>Coracina papuensis</i>	WD	
<i>Edoliisoma tenuirostre</i>	WD	
<i>Lalage tricolor</i>	WD	<i>Ptilonyssus cractici</i>
		<i>Ruandanyssus terpsiphonei</i>
<i>Smicrornis flavescens</i>	Wd	
<i>Gerygone palpebrosa</i>	WD	<i>Ptilonyssus</i> sp.
<i>Cisticola exilis</i>	WD	
<i>Malurus melanocephalus</i>	WD	<i>Ptilonyssus maluri</i>
<i>Artamus cinereus</i>	WD	<i>Ruandanyssus</i> sp.
<i>Grallina cyanoleuca</i>	WD	<i>Ptilonyssus grallinae</i>
<i>Pachycephala rufiventris</i>	WD	<i>Ptilonyssus motacillae</i>
		<i>Ruandanyssus terpsiphonei</i>
<i>Gymnorhina tibicen</i>	Wd	<i>Ptilonyssus cractici</i>
		<i>Sternostoma thienponti</i>
<i>Cracticus nigrogularis</i>	WD	<i>Sternostoma thienponti</i>
<i>Cracticus quoyi</i>	WD	<i>Sternostoma thienponti</i>
<i>Neositta striata</i>	W	<i>Sternostoma</i> sp.
<i>Climacteris melanota</i>	d	
<i>Dicaeum hirundinaceum</i>	D	<i>Ptilonyssus dicaei</i>
<i>Pardalotus rubricatus</i>	W	
<i>Cyrtostomus frenatus</i>	D	<i>Ptilonyssus cinnyris</i>
<i>Meliphaga albogularis</i>	W	<i>Ptilonyssus meliphagae</i>
<i>Myzomela pectoralis</i>	WD	<i>Ptilonyssus gliciphilae</i>
<i>Gliciphila fasciata</i>	D	
<i>Gliciphila indistincta</i>	D	<i>Ptilonyssus gliciphilae</i>
<i>Conopophila albogularis</i>	d	
<i>Meliphaga fusca</i>	W	
<i>Meliphaga flava</i>	WD	<i>Ptilonyssus stomioperae</i>

<i>Stomiopera unicolor</i>	WD	<i>Ptilonyssus stomioperae</i>
<i>Entomyzon cyanotis</i>	WD	<i>Ptilonyssus philemoni</i>
<i>Philemon citreogularis</i>	D	<i>Ptilonyssus philemoni</i>
<i>Mirafra javanica</i>	WD	<i>Ptilonyssus capitatus</i>
<i>Steganopleura bichenovii</i>	WD	
<i>Donacola castaneothorax</i>	WD	
<i>Aegintha temporalis</i>	D	
<i>Bathilda ruficauda</i>	W	
<i>Poephila atropygialis</i>	WD	
<i>Poephila personata</i>	WD	
<i>Poephila gouldiae</i>	W	<i>Sternostoma tracheacolum</i>
<i>Oriolus flavocinctus</i>	WD	<i>Ptilonyssus trouessarti</i>
<i>Sphecotheres flaviventris</i>	WD	<i>Ptilonyssus sphecotheris</i>
<i>Chibia bracteata</i>	WD	<i>Passeronyssus dicruri</i>
<i>Ptilonorhynchus violaceus</i>	D	
<i>Chlamydera nuchalis</i>	WD	<i>Ptilonyssus sphecotheris</i>
<i>Corvus ceciliae</i>	WD	

Acknowledgements

Our Institute is most grateful to the Anglican Mission at Mitchell River for many courtesies. The Government Botanist, Mr. S. L. Everist, kindly identified the *Barringtonia* from a kodachrome: its foot-long, pendulous, red inflorescences are conspicuous in the "dry".

References

- BREGETOVA, N. G., 1964.—Some problems of evolution of the rhinonyssid mites. Report presented at the First International Congress of Parasitology. *Nauka*, 1-7.
- DOMROW, R., 1964.—The genus *Mesonyssoides* in Australia (Acarina: Laelapidae). *J. ent. Soc. Qd.*, 3: 23-29.
- , 1965.—New laelapid nasal mites from Australian birds. *Acarologia*, 7: 430-460.
- , 1966.—Some mite parasites of Australian birds. *Proc. Linn. Soc. N.S.W.*, 90: 190-217.
- FAIN, A., 1957.—Les acariens des familles Epidermoptidae et Rhinonyssidae parasites des fosses nasales d'oiseaux au Ruanda-Urundi et au Congo belge. *Ann. Mus. roy. Congo belge*, 60: 1-176.
- , 1960.—Acariens nasicoles récoltés par le Dr. F. Zumpt en Rhodésie du Nord et au Transvaal. Description de trois espèces nouvelles. *Rev. Zool. Bot. afr.*, 62: 91-102.
- , 1962.—Les rhinonyssides parasites des pigeons (Acarina: Mesostigmata). *Rev. Zool. Bot. afr.*, 65: 305-324.
- KEAST, A., 1961.—Bird speciation on the Australian continent. *Bull. Mus. comp. Zool. Harv.*, 123: 305-495.
- STANDFAST, H. A., 1965.—Notes on the birds of Mitchell River. *Qd. Nat.*, 17: 91-94.
- STRANDTMANN, R. W., 1959.—New records for *Rhinonyssus himantopus* and notes on other species of the genus. *J. Kansas ent. Soc.*, 32: 133-136.
- , 1962.—A ptilonyssid mite from the sparrow hawk, *Falco sparverius* (Acarina: Rhinonyssidae). *Proc. ent. Soc. Wash.*, 64: 100-102.
- WILSON, N., 1964.—New records and descriptions of Rhinonyssidae, mostly from New Guinea (Acarina: Mesostigmata). *Pacific Insects*, 6: 357-388.

ADDENDUM

Since writing the above, it has become desirable to explain the method of collection, and to detail the parasitope of these mites. All the material was taken after the classical method outlined by Fain (1957), the premier student of these mites: "*La récolte des Acariens a été pratiquée généralement peu de temps après la mort de l'Oiseau . . . le bec est largement ouvert. Au moyen d'une paire de ciseaux à mors fins on découpe le palais, le plus près possible du bec et sur une grande longueur de façon à bien exposer la région qui correspond aux narines. Les tissus excisés sont . . . examinés ultérieurement . . . Pour examiner les narines par l'intérieur il est souvent nécessaire de disséquer les cornets situés profondément ou les lamelles cornées qui cachent plus ou moins leur orifice interne . . .*"

Les Rhinonyssidés vivent . . . dans les narines, on peut cependant les rencontrer aussi dans le mucus qui recouvre les cornets, mais ils ne s'aventurent jamais très loin à l'intérieur des fosses nasales . . . les Rhinonyssidés sont animés de mouvements lents et ne se déplacent probablement que très peu."

The same author (1965, *Ann. Parasit. hum. comp.*, 40 : 317-327) continues : "De toutes les formes d'acariase interne, la plus répandue est celle des voies respiratoires. On la rencontre principalement chez les Mammifères et les Oiseaux, mais elle existe aussi chez les Serpents, les Batraciens et même chez certains Invertébrés tels que les Mollusques pulmonés . . . Tous ces Acariens des voies respiratoires sont spécifiques, non seulement en ce qui concerne l'hôte, mais encore pour la région souvent très limitée qu'ils occupent dans l'appareil respiratoire . . . Les Acariens de la . . . famille . . . des Rhinonyssidae sont hémaphages comme la plupart des Mésostigmates ectoparasites dont ils dérivent probablement. On les rencontre . . . dans les régions antérieures des fosses nasales, mais uniquement sur les parties les plus vascularisées des cornets. Une espèce cependant (*Sternostoma tracheacolum* a envahi les bronches et les poumons où elle se nourrit d'ailleurs également de sang."

Any tendency, therefore, based only on clinical veterinary experience with this species (it causes severe respiratory complications in cage birds, see Murray, 1966, *Aust. vet. J.*, 42 : 262-264), to believe that rhinonyssine mites in general are endoparasites whose major populations occur in the deeper respiratory organs (tracheae, bronchi, lungs and air sacs), with only the fringe of those populations evident in the nasal passages, should be resisted. Avian nasal mites are just that, and all specialists I have questioned on this point agree, having dissected birds in the field, that rhinonyssines are not found, except as rarities and *S. tracheacolum* apart, in the internal respiratory tract (see also Maa and Kuo, 1965, *J. med. Ent.*, 1 : 395-401).

By this method it is possible to collect virtually every mite present in the nasal passages of each bird. The population data given above are therefore both quantitative and at least suggestive that the populations of these delicate mites are independent of the two major macroenvironmental factors, relative humidity and temperature. Nor does it seem likely that these factors would affect the mite populations by way of their hosts, since avian organ systems are capable of considerable physiological regulation, even in extreme climatic conditions (Thomson, 1964, "A New Dictionary of Birds", Nelson, London—see entries on drinking, excretion, heat regulation, respiratory system, etc.).

To conclude, rhinonyssine mites are essentially the sole occupants of a specialized parasitope affording an unchanging microclimate and a food supply of constant quality. Reasonably stable populations are therefore not inconsistent with this situation. However, I know of no published data to support this, and so let the original text stand.

Corrigenda

These Proceedings, Vol. 90, Part 2, page 199, line 11 from bottom, for "pale-yellow robin, *Eopsaltria capito*" read "lemon-breasted flycatcher, *Microeca flavigaster*". Page 208, line 9, for "*Callistemon*" read "*Barringtonia gracilis*". Also amend host data accordingly in *Synopsis* and captions to Figs 28 and 29.

INTRASPECIFIC POLYPLOIDY IN
HYPOPTERYGIUM ROTULATUM (HEDW.) BRID.

HELEN P. RAMSAY

School of Biological Sciences, University of Sydney

(Plates vi-ix)

[Read 30th November, 1966]

Synopsis

Intra specific polyploid races with chromosome numbers of $n=9$, 18, ca. 27 and 36 were discovered in plants of *Hypopterygium rotulatum* growing mixed together on the same log at Mt. Wilson, and a population with $n=18$ was located a mile away.

Cytological behaviour at meiosis was studied, and morphological characteristics of the plants were compared.

Spore mother cells with normal meiosis were found in all chromosome races, but some higher polyploids showed a high proportion of irregularities.

Few morphological differences between the various plant groups were detected. Some increase in the size of spore mother cells and greater variability in size of spores occurred in high polyploids. The leaf cells were more variable and longer in the plants with chromosome numbers of $n=18$ and 36.

Plants with a chromosome number of $n=9$ were dioecious while the others were monoecious.

INTRODUCTION

The HYPOPTERYGIACEAE is a well-defined tropical family of mosses, *Hypopterygium* being the largest genus with about 70 species (Brotherus, 1924). *Hypopterygium rotulatum* (Hedw.) Brid. in the sub-genus Eu-hypopterygium, section Pseudo-Tamariscina, is a very variable species (Sainsbury, 1955) evident from the large number of specimens described originally as separate species but now moved into synonymy. The upright almost dendroid gametophytes are produced from a creeping secondary protonema, a number of plants arising along its length. Some of the plants are perennial although new gametophytes arise from the protonema, or new shoots form from the old plants each year. The complanate arrangement of the leaves, and the ventrally placed amphigastria characterize this family. *H. rotulatum* has been recorded in the literature as dioecious (Brotherus, loc. cit.) each female gametophyte bearing several capsules, usually only one from each perichaetium.

Shimotomai and Koyama (1932) obtained a mitotic count of $n=18$ from gametophyte tissue in the synoecious species *H. japonicum* Mitt. belonging to the sub-genus Eu-Hypopterygium, section Aristifolia. No other chromosome numbers have been recorded for this family.

MATERIALS AND METHODS

The specimens of *Hypopterygium rotulatum* (Hedw.) Brid. were collected from two areas about one mile apart at Mt. Wilson, N.S.W. at an altitude of about 3,200 ft. in shaded rainforest. The majority were growing on a log which was covered for more than six feet on its sides and underneath by *H. rotulatum* and *Pterygophyllum dentatum*. Plants of *Hypopterygium* were growing on rotting logs, earth and rocks on the banks of a stream. As some variation in the sizes of plants was noticed, groups of plants were kept separate. Specimens were

kept in glass dishes for two to three weeks in the laboratory until meiosis was completed, then plants were pressed. These voucher specimens have been retained in the Ray Herbarium, Botany Department, University of Sydney (for numbers see Table 1).

Smear preparations of meiotic stages in spore mother cells were obtained using the method outlined in Ramsay (1964, 1966). Drawings and photomicrographs were made using Zeiss microscope equipment and phase contrast microscopy as in Ramsay (1966) and are reproduced here at a magnification of $\times 2,700$ for drawings and at quoted magnifications for the photomicrographs.

OBSERVATIONS

In Table 1 it can be seen that a series of chromosome numbers was obtained for the 12 different groups of plants of *Hypopterygium rotulatum* examined. The chromosome numbers of $n=9$, 18 ca. 27 and 36 represent a polyploid series in plants growing in the same locality and in close proximity.

The results deal separately with the chromosome numbers and behaviour at meiosis, and with the comparison of taxonomic features of plants from each of the chromosome groups.

TABLE 1
Chromosome numbers in Hypopterygium rotulatum

Date Collected	Voucher* Number	Sex	Chrom. Number	Locality	Figures	Plates
16-4-64	8/64	D	9	Log, waterfall	1	VI.1
6-9-65	36/65	D	9	Log, waterfall	2-3	VI.2
16-4-64	8a/64	M	18	Log, waterfall	4, 6	VI.3
1-5-64	33/64	M	18	Happy Valley	5	VI.4
	33a/64					
	33b/64					
1-5-64	22/64	M	ca. 27	Rocks, waterfall	7-9	—
16-4-64	8d/64	M	ca. 27	Log, waterfall		VI.5-11
16-4-64	8e/64	M	36	Log, waterfall	10-11	VII.1-3
16-4-64	8b/64	M	36	Log, waterfall	—	—
16-4-64	8c/64	M	36	Log, waterfall	—	VII.4
16-4-64	8f/64	M	36	Log, waterfall	—	VII.5-8
16-4-64	16/64	M	36	Rocks, waterfall	—	—

M=monoecious. D=dioecious. All specimens were collected from Mt. Wilson (3,200 ft.) in New South Wales.

* Specimens deposited in the Ray Herbarium, Botany Department, University of Sydney.

CYTOLOGICAL BEHAVIOUR

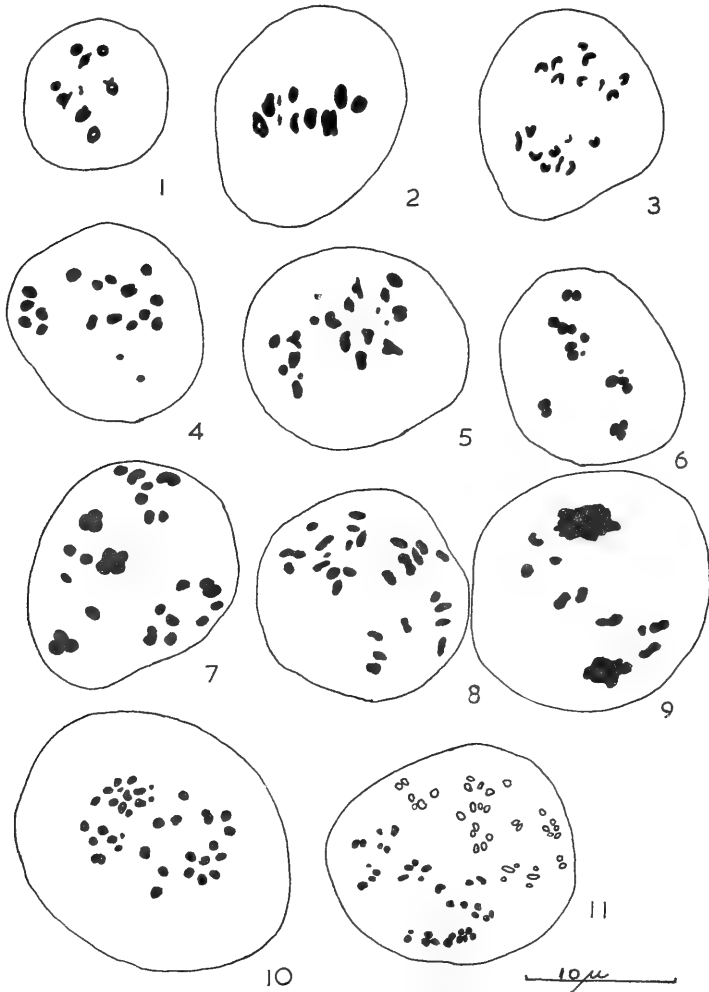
H. rotulatum (8/64, 36/65) $n=9$ (Text-figs 1-3. Plate VI, 1-2).

Both these dioecious populations were collected from the same log, the former in April, 1964, the latter in September, 1965 (Table 1). A chromosome number of $n=9$ was observed at Metaphase I of meiosis (Text-figs 1-2. Plate VI, 1-2). Eight of the bivalents were of almost uniform size, but one was smaller and disjoined precociously in the majority of cells (Text-fig. 2). Its size and precocious behaviour are similar to that found in a number of other mosses (Vaarama, 1953, 1956, Steere, 1954, *etc.*, Yano, 1957, Khanna, 1960, *etc.*, and Ramsay, in a number of Australian mosses unpubl.).

At Anaphase I, nine chromosomes were observed to pass regularly to each pole (Text-fig. 3). Tetrad formation was normal and no lag of chromosomes was seen.

Heteropycnosis or precocious staining of part of the nucleus, usually in the form of an open ring, was visible at early prophase of meiosis. However, it was much less pronounced than in many other mosses *e.g.*, *Bryum*, *Rhizogonium*,

etc. (Ramsay, unpubl.). Even in dioecious species no evidence was found of a large bivalent which separated precociously and could be related to the possible sex chromosomes described in some other mosses *e.g.*, *Macromitrium* (Ramsay 1966), *Pogonatum* (Yano, 1955, 1957), *etc.*



Meiosis in spore mother cells of *Hypopterygium rotulatum* $\times 2,700$. 1, 8/64 M-I, $n=9$, note small bivalent; 2-3, 36/65. 2, M-I, $n=9$, note small bivalent separating precociously; 3, A-I small chromosome distinct at each end; 4, 8a/64 M-I, $n=18$, note two small bivalents; 5, 33a/64 M-I, $n=18$, note similarity to fig. 1 but twice the number; 6, 8a/64 M-I, secondary association of bivalents; 7-9, 22/64. $n=27$; 7, multivalents or secondary association of some bivalents; 8, 27 bivalents at M-I; 9, T-I, note 9 lagging univalents or bivalents; 10-11, 8e/64, $n=36$; 10, M-I, 36 bivalents visible including four small ones; 11, A-I.

H. rotulatum (8a/64, 33/64, 33a/64, 33b/64) $n=18$ (Text-figs 4-6. Plate VI, 3-4).

The first of these populations was collected on the same log with the previous ones, but the other was found about one mile downstream in Happy Valley (Table 1). Both had 18 bivalents at metaphase of meiosis, consisting of 16 similar in size, and two small precociously disjoining ones. Comparison of

bivalents in Plate VI, 1-2 ($n=9$) and Plate VI, 3 ($n=18$) suggests that the latter is made up of 2×9 chromosomes. The gametophytes of these must therefore be diploid.

Although the populations had the same chromosome number, it was noticed that in 8a/64 secondary association with two or more bivalents associated together at metaphase I was common in dividing cells (Plate VI, 3). During meiosis irregularities observed included univalents left out at telophase I and clumping of groups of chromosomes off the metaphase I plate. Chromosome balance was obviously unstable in this group of plants.

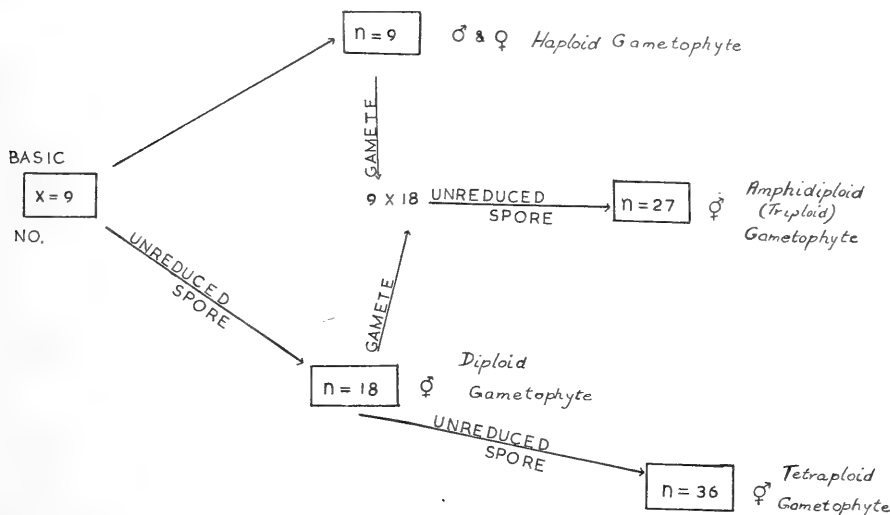


FIG 12

Possible origin of chromosome races in *Hypopterygium rotulatum*.

However, meiosis in 33/64, 33a/64 and 33b/64 was normal and a very small percentage of cells behaved irregularly. All the plants in this chromosome group on further examination were found to be monoecious, the antheridia being borne in separate perichaetia in the axils of leaves just below the archeogonial 'inflorescences'.

The mitotic chromosomes examined by Shimotomai and Koyama (1932) in the synoecious species *H. japonicum* consisted of 16 large and two small chromosomes, and compare in relative sizes to those in *H. rotulatum* with $n=18$.

H. rotulatum (22/64, 8d/64) $n=ca. 27$ (Text-figs 8-9. Plate VI, 5-11).

Meiosis in the spore mother cells of the above groups of plants revealed approximately 27 bivalents at metaphase I. Some had been collected from the same log at Mt. Wilson (Table 1). Only an approximate chromosome count could be obtained, for although some cells had $n=27$ (Text-fig. 8. Plate VI, 6) clumping, irregularities and multivalent formation or secondary association made it difficult to interpret divisions (Plate VI, 7-10). A maximum of 32 including possible univalents or dissociated bivalents was found and none gave a number as high as 36. Some side views of metaphase I showed a regular arrangement of bivalents on the equator, and anaphase I revealed no lagging chromosomes in a number of the spore mother cells, but others (Text-fig. 9. Plate VI, 11) had as many as nine univalents or bivalents left out at end of anaphase I. Normal tetrads with four equal nuclei were produced in some

spore mother cells, although many contained large and small nuclei, or chromosomes lying loosely in the cytoplasm even after the spores had been differentiated.

H. rotulatum (8e/64, 8b/64, 8c/64, 8f/64, 16/64) $n=36$ (Text-figs 10-11. Plate VII, 1-8).

Table 1 shows that some of these plants also came from the same location at Mt. Wilson. Their chromosome number was found to be $n=36$.

Meiosis was almost regular in 8e/64 although some secondary association was noticed at metaphase I. Separation of chromosomes at anaphase I proceeded normally and lag was infrequent. Tetrad formation appeared normal.

In other populations behaviour at meiosis was very irregular. Secondary association of bivalents was common (Plate VII, 4-6), bivalents and univalents lay off the metaphase I plate, lag at anaphase I (Plate VII, 7) was frequent and unequal distribution of chromosomes to nuclei at telophase I and telophase II resulted in irregular tetrads with only three nuclei, or with more than four usually unequal in size. It is unlikely that any viable spores could result from such behaviour.

Some breakdown at meiosis might have been due to the excessive numbers of chromosomes or bivalents struggling for position on the equator at metaphase, so that groups of chromosomes, unable to manage this successfully, formed themselves into nuclei containing univalents as well as whole bivalents.

Heteropycnosis at early prophase in the polyploids was identical with that in the haploids (Plate VII, 1), no comparable increase in amount or number of heteropycnotic regions being observed.

COMPARISON OF TAXONOMIC CHARACTERS

A summary of the features of the plants examined is set out in Table 2. Photographs of the leaves and cells of the leaves are found in Plates VIII and IX. The leaves illustrated were taken from side shoots between the middle and the base of the shoot. The gametophyte plants used for these measurements bore several sporophytes, at least two having been examined cytologically. Photomicrographs of cells were taken towards the mid-leaf near the end of the nerve.

So that comparison of gametophyte characters could be made in plants with different chromosome numbers, it was assumed that the chromosome number of the gametophyte corresponded to the haploid chromosome number (i.e. $n=9$ or 18, 27, 36, etc.) obtained at meiosis in the attached capsules. Since all capsules on each plant used had the same chromosome number it seemed reasonable to suppose this to be true, in the absence of mitotic counts. Some of the possible variations in the chromosome numbers of gametophytes giving rise to capsules containing the various chromosome numbers are suggested in the discussion, and the need for actual mitotic counts of gametophyte cells has already been emphasized. Some comments on the methods used for obtaining the measurements are described below.

Height of Gametophyte plants. The total height included distance from ground level to the apex of the leafy branches but did not include the sporophyte

Leaf size. The average lengths (not including the point) and breadths (in the mid-leaf) of ten leaves and amphigastria were obtained.

Cell size. Twenty cells were examined from areas corresponding to the photographs in Plate IX.

Spore mother cells and spore size. Diameters of 20 spores and 20 spore mother cells were measured. Since the spore mother cells were squashed, an area in which the cells were evenly spread was chosen for measurements to give more real comparisons. It was not possible to calculate volumes since the diameter of the squashed cells did not correspond to the original diameter.

TABLE 2
Comparison of morphological characteristics of Hypopterygium rotulatum

Voucher Number	Chrom. Number n=	Height of gametophyte cm.	Sex	Leaf Size mm. l × b	Amph. Size mm. l × b	Cell Size		Diam. S.M.C. μ	Spore Size μ
						Leaf μ l × b	Amph. μ l × b		
8/64	9	2-2.5	♂ and ♀	1.0 × 0.7	0.5 × 0.5	3.8 × 2.4 ± 0.05	3.7 × 2.3	0.99	12-14
33/64	18	2-2.8	♂ +	1.1 × 0.7	0.6 × 0.6	4.9 × 2.6 ± 0.4	3.7 × 2.4	1.61	11-12
22/64	27	1.5-2.0	♂ +	0.93 × 0.7	0.5 × 0.5	3.7 × 2.4 ± 0.2	3.8 × 2.5	1.44	10-13
8f/64	36	1.8-2.0	♂ +	1.05 × 0.8	0.6 × 0.6	4.4 × 2.6 ± 0.5	4.25 × 2.0	1.65	10-16

Amph. = amphigastria. S.M.C. = spore mother cells. l = length. b = breadth.

The results set out in Table 2 give some indication of the features most likely to be of use in further investigations, particularly of gametophytes from which mitotic counts could be obtained. Although the leaves and amphigastria showed little difference in gross size in the various groups of plants studied, the leaf cells in particular showed increase in length and greater variation in plants with chromosome numbers of $n=18$ and 36 . In Plate IX the numbers of cells in a given area appear to be greater in the haploid and triploid and fewer but larger in the diploid and tetraploid. It has been pointed out by Lewis (1961) that decrease in numbers of cells may account for apparently little change in overall size of some polyploids.

The length of setae and size of capsules was similar in all chromosome races, and measurements were not therefore included in Table 2. However, a clear difference in the sizes of spore mother cells can be seen in Table 2, and by comparison of the Text-figures and Plates of the various chromosome forms. Spore size data shows a greater variation in the sizes of spores in polyploids. It is interesting to note that the characters examined in plants with a chromosome number of $n=ca. 27$ (22/64) were much closer to the 'original haploid' (i.e. plants with $n=9$) than to the others.

It appears, therefore, that increase in the length of the cells of the leaf, an increase in the size of spore mother cells and a greater range of variation in the size of spores are features which reflect the increase in chromosome numbers in the various plants. Other characters remained much more stable throughout the groups.

DISCUSSION

Polyploidy in Mosses. Before chromosome numbers in mosses had generally been investigated polyploid gametophytes were produced experimentally by apospory (É. and Ém. Marchal, 1911) in *Bryum caespiticium* and *B. argenteum*. Later Wettstein (1923-1924, 1928) produced a series of polyploid gametophores in *Bryum* by treatment of the protonema, or of the spore mother cells at meiosis in *Funaria*. Auto- and amphidiploid races were produced in several mosses e.g. *Funaria hygrometrica* $n=14$ to 28 and 56 ; the polyploid population of *Bryum caespiticium* $n=10$ was called *B. corrensi* with $n=20$; *Amblystegium serpens* from $n=12$ to 24 ; and *Physcomitrium pyriforme* from $n=18$ to 36 and 72 .

Increasing numbers of naturally occurring inter- and intra specific polyploids are being reported as the chromosome numbers of mosses from many parts of the world become known (Wylie, 1957; Steere and Anderson, 1954; Khanna, 1960; Yano, 1957 *a, b, c, etc.*). Examples include *Atrichum undulatum* (Hedw.) P. Beauv. (Lowry, 1954) with $n=7, 14$ and 21 , *Mnium* spp. (Lowry 1948) $n=6, 12$ *Tortula princeps* De Not. $n=12, 24+1$ and $36+2$ (Steere, 1954; Steere *et al.*, 1954) *Philonotis socia* Mitt. (Yano, 1957*a*) with $n=6$ and 12 and *Octoblepharum albidum* Hedw. with $n=13$ and 26 (Khanna, 1960). They represent species from many families. *Octoblepharum albidum* was analyzed by Khanna (1960) who found no qualitative differences between the plants in external characteristics such as leaf size, size of leaf cells, *etc.* Some differences in spore size were noted, although overlapping occurred, and from his drawings it appears that the spore mother cells were larger in the polyploid.

The majority of the examples of intraspecific polyploidy represent different populations in different localities e.g. *Tortula mucronifolia* $n=12$ and 24 , *Drepanocladus uncinatus* $n=12$ and 24 , *Distichium capillaceum* $n=14$ and 28 (Anderson and Crum, 1958). The spore mother cells of the latter were found to be larger in the diploid, although the spores were similar in size.

One particularly interesting series of interspecific polyploids exists in the genus *Bryum*, where the chromosome numbers of $n=10, 20, 30, 40$ and 50 were discovered in Alaskan species by Steere (1954).

Lewis (1961) has summarized the work of Wettstein (1940) on the relationship of cell size and volume in artificially induced auto- and allo-polyploids. "Generally an increase in size of cells, organs and individuals follows recently induced polyploidy but the extent of such increases varies. The effect is not uniform over the entire polyploid range, cell size usually decreasing, or ceasing to increase especially in the more hybrid polyploids" (Lewis, loc. cit.). In the auto-polyploids of *Physcomitrium pyriforme* cell size was shown to increase with increase in chromosome number, particularly in the leaf. A negative correlation was found between the initial number of chloroplasts and their number, following doubling of the chromosome numbers (Lewis, 1961). The number of cells in the polyploid organism may be less, so that increase in cell size may not lead to an increase in the size of the organ (Darlington from Lewis, 1961).

A significant feature of size relations of polyploids to normal plants is that recently produced polyploids may show distinct variations but natural polyploids do not. Wettstein (1937) observed that in an artificial diploid strain of *Bryum caespiticium* which he called *B. corrensi*, the size of cells and other morphological characters were much larger in the newly produced polyploid, but gradually decreased over a period of 11 years until they had reverted to the size of the original haploid cells etc. During the same period meiosis and spore production also became normal, although very irregular in the newly produced diploid. The stabilization of cell size and other characters and the establishment of normal spore production were found in the original plants after 11 years, in clones produced vegetatively during this time, and in successive generations produced from the first fertile spores.

Khanna (1960) suggested that polyploid populations of *Octoblepharum albidum* were in a state of reversion to haploid size since variations in the cell size, spore size etc. between the diploid and haploid plants were not constant. Meiotic behaviour in auto-polyploids of maize, studied in detail by Giles and Randolph (1951), showed a reduction in multivalent frequency at meiosis in successive generations, until within 10 years meiotic behaviour had reverted to normal.

Apart from influencing the autosome number, polyploidy must also affect sex balance in dioecious species, whether sex is determined by a sex chromosome or a gene complex on autosomes. Doubling of the chromosome number can occur in several ways in mosses such as regeneration from gametophyte cells in which breakdown of mitosis doubles the chromosome number, by apospory from cells of the seta or capsule, or by reconstituted nuclei in spore production at meiosis. The latter would result in the production of monoecious plants.

It has been found generally that polyploids are monoecious (Mehra and Khanna, 1961; Anderson, 1964, for summaries) and apospory is probably the most important factor in the evolution of polyploidy in mosses. The chromosomes of such polyploids would have more affinity for their exact replicas than related chromosomes which may bear other alleles, and secondary association of bivalents might occur more frequently than multivalent formation.

Polyploidy in Hypopterygium rotulatum.

The area from which the plants of this species was collected has been re-visited at frequent intervals in an attempt to repeat the results, and to study the whole population in greater detail. Unfortunately, 1965 and 1966 have been drought years with unusually low rainfalls, particularly in the summer months. In 1965 plants did not regenerate in large numbers, although protonema and old and immature plants were present in the winter months. Very few capsules were produced, and the only chromosome number obtained was $n=9$ in a few capsules in September (earlier investigations had been carried out in April, 1964). The population is again showing considerable growth and archegonia and antheridia are being produced. Dioecious and monoecious forms are

present, although only a few capsules have been found in 1966, but meiosis has not been detected. Drought could again influence fertilization in these plants. The population is obviously maintained by vegetative means.

The necessity for water to carry the sperm to the ovum, especially in dioecious species, is a controlling factor for fertilization. Monoecious forms which allow self fertilization would be able to overcome this if a thin film of water were present, and the antheridia and archegonia were placed close together and ripened simultaneously. The genetic disadvantage of selfing is the establishment of strict homozygosity. Isolating mechanisms such as protandry, or self incompatibility with their genetic advantages of outbreeding, are disadvantages if fertilization depends rigidly on sufficient water at the correct time.

Taxonomic descriptions of *H. rotulatum* state that it is dioecious, whereas the majority of plants examined in this study were found to be monoecious.

The populations which showed almost normal meiosis such as 33/64, 8e/64 and also produced normal looking spores may have resulted from self fertilizations. Cross fertilization in an area where such a variety of chromosome numbers were present would be particularly hazardous. Some of the possible crosses within such a population are set out in Table 3.

TABLE 3

	Egg		Sperm	Expected meiotic behaviour
n=9	9	×	9	normal pairing
	9	×	18	9 pairs, 9 univalents, or trivalents
	9	×	27	9 pairs, 18 univalents or multivalents according to affinities
	9	×	36	9 pairs, 27 multivalents or univalents
n=18	18	×	18	18 pairs, normal behaviour
	18	×	9	9 pairs, 9 univalents or multivalents

The ovum may have some control over which sperm are acceptable. Other controls may be affected by the genetic affinities of the two nuclei. In some plants sporophytes reached the stage of differentiation into capsules, or almost to formation of the spore mother cells, then shrivelled up. No environmental factor causing this could be found, as such plants were growing among those with well-developed capsules. They may have been the result of irregular fertilizations.

Wettstein (1940) mentions that *Bryum corrensii* did not produce sporophytes, which matured to form capsules and spores, for several years. During the first few years after the development of this experimental polyploid, embryo sporophytes developed only for a short time and capsules were not formed. Within 11 years normal sporophytes were regularly produced.

From these studies it is clear that polyploid gametophytes must exist among the haploid plants of *Hypopterygium rotulatum*, although mitotic counts are needed for confirmation. A scheme setting out the possible origins of the various chromosome numbers is set out in Text-figure 12.

Evidence for such a scheme comes from the apparent duplication of complements in plants with n=9 and those with n=18 most obvious in the doubling of the number of minute bivalents. The four small bivalents in plants with n=36 (8e/64) points to a further doubling from n=18. All the polyploids are monoecious, while haploids are dioecious, as would be expected if the new numbers had resulted from failure of reduction in spores at meiosis. Plants with a chromosome number of n=27 could result from fusion of gametes with chromosome numbers of n=9 and 18, followed by reconstitution at meiosis, giving rise to unreduced spores.

The results of this investigation appear to be the first in which a population of mosses growing in close proximity show such high grades of intra specific polyploidy. The levels of polyploidy correspond to tetraploids, hexaploids, and octoploids in Angiosperms.

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References

- ANDERSON, L. E., 1964.—Biosystematic evaluation of the Musci. *Phytomorphology*, 14: 27–41.
- , and CRUM, H., 1958.—Cytotaxonomia Studies on mosses of the Canadian Rocky Mountains. *Nat. Mus. Canada, Bulletin* 160: 1–89.
- BROTHERUS, V. F., 1924.—In Engler and Prantl, *Die natürliche Pflanzenfamilien* Ed. 2, Vol. 11. Leipzig.
- GILES, A., and RANDOLPH, L. F., 1951.—Reduction of quadrivalent frequency in auto-tetraploid maize during a period of ten years. *Amer. Jour. Bot.*, 38: 12–17.
- KHANNA, K. P., 1960.—The haploid and spontaneous diploid race in *Octoblepharum albidum* Hedw. *Cytologia*, 25: 334–341.
- LEWIS, K. R., 1961.—The genetics of Bryophytes. *Trans. brit. bryol. Soc.*, 4: 111–130.
- LOWRY, R. J., 1948.—A cytotaxonomic study of the genus *Mnium*. *Mem. Torrey bot. Club*, 20(2): 1–42.
- , 1954.—Chromosome numbers and relationships in the genus *Atrichum* in North America. *Amer. Jour. Bot.*, 41: 410–414.
- MARCHAL, É., 1920.—Recherches sur les variations numériques des chromosomes dans la série végétale. *Mem. Acad. roy. Belg. Cl. Sci.*, Ser. 2, 4: 3–108.
- , and Ém., 1911.—Aposporie et sexualité chez les mousses III. *Bull. roy. Acad. Belg. Cl. Sci.*: 750–778.
- MEHRA, P. N., and KHANNA, K. P., 1961.—Recent cytological investigations in mosses. *Res. Bull. Panjab Univ.*, 12: 1–29.
- RAMSAY, Helen P., 1964.—The chromosomes of *Dawsonia*. *The Bryologist*, 67: 153–162.
- , 1966.—Sex chromosomes in *Macromitrium*. *The Bryologist*. (in press.).
- SAINSBURY, G. O. K., 1955.—“A hand book of the New Zealand mosses”. *Roy. Soc. N.Z. Bull.*, 5: 412.
- SHIMOTOMAI, N., and KOYAMA, Y., 1932.—Geschlechtschromosomen bei *Pogonatum inflexum* Lindb. and chromosomenzahlen bei einigen anderen laubmoosen. *Jour. Sci. Hiroshima Univ.*, (B2) 1: 95–101.
- STEELE, W. C., 1954.—Chromosome number and behaviour in Arctic mosses. *Bot. Gaz.*, 116: 93–133.
- , 1958.—Evolution and speciation in mosses. *Amer. Nat.*, 42: 5–20.
- , ANDERSON, L. E., and BRYAN, Virginia S., 1954.—Chromosome studies on Californian mosses. *Mem. Torrey bot. Club*, 20: 1–75.
- VAARAMA, A., 1954.—On the characteristics of the spontaneous bivalent race of *Funaria hygrometrica*. *Arch. Soc. Vanamo*, 9: 395–400.
- WETSTEIN, F. VON, 1923, 1924.—Kreuzungsversuche mit multiploiden moosrasen. *Biol. Zentralbl.*, 43: 71–82, 44: 145–168.
- , 1924.—Morphologie und physiologie des formwechsels der moose auf genetischer grundlage. I. *Z. indukt. Abstamm.—u. Vererb. Lehre*, 33: 1–236.
- , 1928.—Morphologie und physiologie des formwechsels der moose auf genetischer Grundlage. II. *Bibl. Genet., Leipzig*, 10: 1–216.
- , 1940.—Experimentelle untersuchungen zum artsbildungs problem. III. *Ber. deutsch. bot. Ges.*, 58: 374–388.
- WYLLIE, Ann P., 1957.—Chromosome numbers of mosses. *Trans. brit. bryol. Soc.*, 3: 260–278.
- YANO, K., 1957.—a. Cytological studies on Japanese mosses. I. Fissidentales, Dicranales, Grimmiiales, Eubryales. *Mem. Fac. Educ. Niigata Univ.*, 6: 1–31.
- , 1957.—b. Cytological studies on Japanese mosses. II. Hypnobryales. *Mem. Takada Branch Niigata Univ.*, 1: 85–127.
- , 1957.—c. Cytological studies on Japanese mosses. III. *Ibid.*, 1: 129–259.

EXPLANATION OF PLATES VI-IX.

Plate vi

Hypopterygium rotulatum, meiosis in spore mother cells, $\times 2,200$. 1-2, M-I, $n=9$, note small bivalent disjoined in 2. 3-4, M-I, $n=18$. 3, secondary association in 8a/64. 4, 18 bivalents in 33/64 includes two small ones (tiny spots are excess stain). 5-10, $n=ca. 27$ various stages of meiosis. 5, premetaphase stage before chromosomes are fully contracted, multivalents indicated by arrows. 6, M-I, ca. 27 bivalents showing. 7-8, side view M-I, showing bivalents left off the plate. 9, clumping of chromosomes at M-I. 10, secondary association or multivalents at M-I. 11, late A-I, showing lagging chromosomes, one bivalent in centre not disjoined.

Plate vii.

Hypopterygium rotulatum, meiosis in spore mother cells of populations with $n=36$ chromosomes, $\times 2,200$. 1, heteropycnosis in polyploid. 2-3, M-I, $n=36$, fairly regular arrangement on the metaphase plate. 4-6, M-I, secondary association, clumping in five and six, while a ring is clear in four. 7, T-I, lag of univalents. 8, tetrad of spores, note chromosomes left in cytoplasm.

Plate viii.

Hypopterygium rotulatum, leaves from plants with different chromosome numbers, $\times 30$. 1' plants with $n=9$ (8/64). 2, plants with $n=18$ (33/64). 3, plants with $n=27$ (22/64). 4' plants with $n=36$ (8f/64).

Plate ix.

Hypopterygium rotulatum, cells of leaves in Plate VIII, $\times 350$. 1, cells from plants with $n=9$ (8/64). 2, cells from plants with $n=18$ (33/64). 3, cells from plants with $n=27$ (22/64). 4, cells from plants with $n=36$ (8f/64).

HIGHLANDS PEAT OF THE MALAYAN PENINSULA

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Synopsis

The factors responsible for the formation of highland peat on the Malayan Peninsula are mentioned together with analytical results for a peat from Gunong Erau, Malaya.

The highland peat of the tropics is quite a distinct formation from the peat found on the lowlands. In contrast to the extensive lowland peat (two million acres in the Malayan Peninsula, 40 million acres in Indonesia) highland peat is found in isolated areas on the tops of mountains where the underlying rock is quite acidic.

Mohr in 1922 stated after examination of the Hjang-Plateau in Besoeki, Indonesia, "Man findet dort merkwürdigerweise Stellen mit einer Art von bleichem Torf bedeckt welche sich halten kann unter Einwirkung der Kombinationen von niedriger Temperatur und des Unterwasserstehens."

In 1930 Vageler maintained that only those mountain peats formed from Sphagnum were genuine Highmoors. This would appear to be too rigid a classification. Tropical highmoors contain Sphagnum moss but in Malaya, at least, there is also present forest vegetation which, however, does not reach the full development of the lowland forest and does contribute material for the formation of peat.

In Indonesia, highmoor peats are formed in Sumatra, Toba-Ebene, 1,450 m. (4,750 ft.); in Java, at Gedeh, Telaga-Saät, 1,400 m. (4,570 ft.), Dieng Plateau, 2,000 m. (6,500 ft.); in Celebes, at Lindessee, 1,000 m. (3,260 ft.).

Many of the craters of Indonesian mountains contain swamps in which peat forms. In addition to *Sphagnum* and *Juncus prismatocarpus* R.Br., swamp grasses and Cyperaceae grow on the banks (von Faber, 1927).

This type of peat present in the tropics is found in many parts of the world and is typical of Europe and other areas with temperate climates. They occur in Australia in humid localities, usually in parent materials of low base status and the vegetation is often dominated by Cyperaceae (Stephens, 1949-50).

On the Malayan Peninsula highmoor peat is formed at altitudes greater than 1,500 m. (4,900 ft.), usually on relatively bare quartzite or acid granite ridges (Scrivenor, 1931) having a typical vegetation of montane ericaceous forest with sphagnum and lichens on the ground (Wyatt-Smith, 1954).

The montane ericaceous forest occurs above 1,500 m. (4,900 ft.) on exposed ridges and consists of dwarfed vegetation carrying masses of epiphytes. The main species present are: FAGACEAE, *Pasania lampadaria*, *Pasania rassa*; ERICACEAE, *Pieris ovalifolia*, *Vaccinium* spp. *Rhododendron* spp.; ELAEOCARPACEAE, *Elaeocarpus masterii*; MYRTACEAE, *Eugenia* spp., *Rhodamnia cinerea*, *Tristania merguensis*; THEACEAE, *Ternstroemia japonica*, *Anneslea crassipes*; SYMPLOCACEAE, *Symplocos* spp.; RUTACEAE, *Astrophyllum montanum*, *Tetradomia tetrandra*; GUTTIFERAE, *Garcinia* spp.; AQUIFOLIACEAE, *Ilex* spp.; MYRSINACEAE, *Myrsine posteriana*; LAURACEAE, *Phoebe declinata*; PENTAPHYLACACEAE, *Pentaphyllax arborea*; BUXACEAE, *Buxus* spp.

Peat forms a layer on the ground to a maximum depth of about 5 cms. but will accumulate to greater depths in rock crevasses. It is not associated

with swamps or ponds, and its accumulation is due to the continually humid conditions and low temperatures preventing oxidation of the plant material and to the presence of very acid rock underlying it.

Samples of peat were taken from Gunong Erau in the Cameron Highlands at the height of approximately 1,960 m. (6,400 ft.). Here the daily average temperature ranges from 14.1-23°C. (57.6-73.4°F.), the relative humidity at 1 p.m. is greater than 98% throughout the year, while the total rainfall is 2,687 mm. (105.5 inches) and the lowest average rainfall in any month is 129 mm. (five inches). There was no visible difference in the samples which were of a reddish brown colour. The results of analysis are given in Table 1.

TABLE 1
Analysis of peat from Gunong Erau

Sample depth	pH	Ash content % (on dry basis)	Loss on ignition % (on dry basis)
0-20 cm. (0-8 inches) ..	2.0	2.6	97.4
20-40 cm. (8-16 inches) ..	2.0	2.3	97.7
40-60 cm. (16-24 inches) ..	2.3	7.3	92.7

The pH was determined on dried peat in IM.KCl with a soil KCl ratio of 1 to 5.

Humus fractions were determined according to the procedure of Konanova, 1961, and are given in Table 2.

TABLE 2
Humus fraction (Percentage of dry weight of sample)

Sample depth	Humic + Ulmin	Hymato- melanic acid	Crenic + Apocrenic acids	Humic + Ulmic acids
0-20 cm. (0-8 inches) ..	25.0	14.6	55.4	5.0
20-40 cm. (8-16 inches) ..	30.0	10.4	53.0	7.3
40-60 cm. (16-24 inches) ..	25.0	18.5	47.5	9.0

The low ash contents and pH's of all the samples are striking. There is a slight decrease in acidity and increase in ash content with increase in depth.

Analysis of similar material at the University of Liverpool (Burgess, 1966) showed that it contained degradation products characteristic of humic acid found under broad-leaved forests in Europe (Burgess, *et al.*, 1964).

The similarity to peat material from temperate regions is not unusual, since the climate of the Cameron Highlands of Malaya is temperate and the vegetation is similar to heath vegetation.

References

- BURGESS, N. A., HURST, H. M., and WAKKENDEN, B., 1964.—The phenolic constituents of humic acid and their relation to the lignin of the plant cover. *Geochem. et Cosmochim. Acta.* 28: 1547-1554.
- BURGESS, N. A., 1966.—Private communication.
- FABER, F. C., VON, 1927.—“Die Kraterpflanzen Javas Welterreden”.
- KONANOVA, M. M., 1961.—Soil Organic Matter. (Pergamon Press, Oxford).
- MOHR, E. C. J., 1922.—“De grond van Java en Sumatra”. (Amsterdam).
- SCRIVENOR, J. B., 1931.—“The Geology of Malaya”. (Macmillan, London).
- STEPHENS, C. G., 1949-50.—Comparative morphology and genetic relationships of certain Australian, North American and European soils. *J. Soil. Sci.*, 1(2): 124-129.
- VAGELER, P., 1930.—“Grundriss der tropischen und subtropischen Bodenkunde”. (Berlin).
- WYATT-SMITH, J., 1954.—Forest types in the Federation of Malaya. *Malay Forester*, xvii: 83-84.

ABSTRACT OF PROCEEDINGS

ORDINARY MONTHLY MEETING

30th MARCH, 1966

Dr. R. C. Carolin, President, in the chair.

The minutes of the last Monthly Meeting (24th November, 1965) were taken as read and signed.

The following were elected Ordinary Members of the Society: Messrs. A. A. Martin, B.Sc.(Hons.) Rand., University of Melbourne, Parkville, Victoria; and R. E. Wass, B.Sc.(Hons.) (Q'ld.), Department of Geology and Geophysics, University of Sydney.

The Chairman announced that library accessions amounting to 50 volumes, 495 parts or numbers, 15 bulletins, 13 reports and 10 pamphlets, total 583, had been received since the last meeting.

The Chairman drew the attention of members to a Seminar on The Bush Fire Problem in Public Lands to be conducted at Leura on 16th and 17th April under the auspices of the National Trust of Australia (N.S.W.).

PAPERS READ

(By title only, an opportunity for discussion to be given at the April Ordinary Monthly Meeting)

1. The composition, occurrence and origin of lerp, the sugary secretion of *Spondylaspis eucalypti* (Dobson). By R. Basden.
2. Seeds and fruit of the Goodeniaceae. By R. C. Carolin.
3. The breeding biology and larval development of *Hyla jervisiensis* (Anura: Hylidae). By A. A. Martin and M. J. Littlejohn.

ORDINARY MONTHLY MEETING

27th APRIL, 1966

Dr. R. C. Carolin, President, in the chair.

The minutes of the last Monthly Meeting (30th March, 1966) were read and confirmed.

The Chairman announced that the Council had elected the following office-bearers for the 1966-67 session: Vice-Presidents: Dr. D. T. Anderson, Miss Elizabeth C. Pope, Mr. G. P. Whitley and Professor J. M. Vincent; Honorary Treasurer: Dr. A. B. Walkom; Honorary Secretary, Mr. R. H. Anderson.

The Chairman referred to the retirement of Dr. W. R. Browne from the position of Honorary Secretary and to his great services to the Society in this and other capacities.

The Chairman announced that library accessions amounting to 15 volumes, 158 parts or numbers, 1 bulletin, 1 report and 1 pamphlet, total 176, had been received since the last meeting.

The Chairman reminded members that there would be no Ordinary Monthly Meeting in May.

PAPERS READ

1. Fungi attacking seeds in dry seed-beds. By D. M. Griffin.
2. On the species *Fenestella horologia* Bretnall and *Minilya duplaris* Crockford. By R. Wass.
3. Two new species of Permian Brachiopods from Queensland. By R. Wass.

EXHIBIT

Mr. A. G. Khan (a visitor introduced by Dr. I. V. Newman) exhibited embryos of *Podocarpus* species grown in agar culture. Fully grown embryos, excised under aseptic conditions from the surface-sterilised seeds, were cultured aseptically on two culture media differing chiefly in that one had coconut milk and a greater number of growth-factors. The culture tubes were kept at room temperature. Dry *P. elatus* R. Br. seeds were supplied by the Forestry Commission (from low-temperature storage). The embryos from these seeds were cultured on 26th March last and are still dormant on April 27, not showing any growth on the surface of either medium. Full size green *P. falcatus* R. Br. seeds were collected from the Royal Botanic Gardens, Sydney, on 14th April, 1966, and their embryos were cultured on the same day. By 27th April the embryos are showing significant growth on the surface of both media, the cotyledons having turned green and the roots appearing. The embryos from the same collection of *P. falcatus* R. Br. seeds when submerged in either of the two culture media remained dormant.

LECTURETTE

Miss Elizabeth C. Pope, Australian Museum, Sydney, gave a lecturette on the fauna of the intertidal reefs at Darwin, Northern Territory, illustrated by colour transparencies.

ORDINARY MONTHLY MEETING

29th JUNE, 1966

Dr. R. C. Carolin, President, in the chair.

The minutes of the last Monthly Meeting (27th April, 1966) were read and confirmed.

The following were elected Ordinary Members of the Society: Dr. John Child, M.A., B.Comm. (N.Z.), D.Phil. (Oxon.), Gladesville, N.S.W.; Messrs. G. A. Holloway, Australian Museum, Sydney; and A. G. Khan, Surry Hills, N.S.W.

The Chairman announced that Dr. C. G. Hansford, who had been a member of the Society since 1952, had died at Uvongo Beach, Natal, South Africa, on 18th February, 1966.

The Chairman announced that library accessions amounting to 31 volumes, 301 parts or numbers, 10 bulletins, 7 reports and 6 pamphlets, total 355, had been received since the last meeting.

The Chairman announced that the next Ordinary Monthly Meeting will be held in the Main Hall of Science House on Friday, 15th July, at 7.45 p.m., immediately preceding the Sir William Macleay Memorial Lecture to be delivered at 8 p.m., by Professor D. G. Catcheside, D.Sc., F.R.S., the subject being "The Centenary of Mendel".

The Chairman also announced that there will be no Ordinary Monthly Meeting in August.

The Chairman referred to the retirement of Dr. A. B. Walkom as Honorary Secretary and to his valuable services to the Society over many years. A vote of thanks to Dr. Walkom was carried by acclamation.

The Chairman announced the appointment of Dr. M. F. Day as a Trustee of the Kosciusko State Park and referred to the satisfaction of the Society at such action.

PAPERS READ

1. The Rhabdiphoridae (Orthoptera) of Australia. Part 4. A new genus from South Australia. By Aola M. Richards.
2. Notes on three recently proposed Australian Tertiary echinoid genera. By G. M. Philip.
3. Chromosome numbers in *Lamprothamnium*. By A. T. Hotchkiss.
4. Mosquitoes of Tasmania and Bass Strait Islands. By N. V. Dobrotworsky.

NOTES AND EXHIBITS

Mr. G. P. Whitley contributed a note on announcements of the formation of the Linnean Society of New South Wales in *The Sydney Morning Herald* newspapers of October and November, 1874. On 30th October, 1874, page 4, appeared :

"SCIENCE OF NATURAL HISTORY.—A preliminary meeting of gentlemen interested in the study of natural science was held yesterday in the boardroom of the Free Library, and, after some discussion, the following resolutions were carried unanimously:—'That a society for the cultivation of the science of Natural History in all its branches be now formed, under the name of "The Linnean Society of New South Wales", and that all those whose names are signed to the papers now before the meeting shall be, and are, the original members of such society.—That the annual subscription shall be £1 ls., payable on the 1st January of each year; and that all members joining after the close of the present year shall pay an entrance fee of £1 ls., in addition to their annual subscription.—That the officers of the society shall consist of a president, vice-president, secretary, treasurer, and a council of six.—That the following gentlemen be requested to accept the respective offices:—President, Mr. Macleay; vice-president, Sir W. Macarthur; secretary, Captain Stackhouse; treasurer, Mr. Burton Bradley.—That a committee, consisting of the president, Mr. Stephens, and Dr. Alleyne, be appointed to draw up rules to lay before the adjourned meeting this day week, to make inquiries respecting a room for the use of the society, and generally to have full powers to conduct the affairs of the society until the election of the Council.—That the above-mentioned committee be instructed to draw up and distribute, according to their discretion, a circular, giving full information as to the nature and aims of the society, and inviting the co-operation of all interested in the study of natural history.—That a concise account of the proceedings of this meeting be forwarded to the Sydney daily newspapers, and that an advertisement be inserted in each, stating the time and place of the next meeting.' The meeting was then adjourned till next week."

The above paragraph was repeated in the *Herald* of 31st October, page 6.

On page 5 of the 5th November issue, the *Herald* announced that the Linnean Society of New South Wales was to meet that afternoon to consider draft rules, and there is a brief account of the meeting in *The Sydney Morning Herald*, 6th November, 1874, page 5.

Newspapers have been consulted at the Public Library of New South Wales.

LECTURETTE

An illustrated lecturette entitled "Plants in Iceland" was given by Dr. D. J. Anderson, School of Biological Sciences, Department of Botany, University of Sydney.

ORDINARY MONTHLY MEETING

15th JULY, 1966

Dr. R. C. Carolin, President, in the chair.

The minutes of the last Monthly Meeting (29th June, 1966) were taken as read and confirmed.

The Chairman announced that library accessions amounting to 13 volumes, 185 parts or numbers and 3 bulletins, total 201, had been received since the last meeting.

The Chairman announced that there will be no Ordinary Monthly Meeting in August.

PAPERS READ

(By title only, an opportunity for discussion to be given at the September Ordinary Monthly Meeting)

1. The application of the names *Sericesthis pruinosa* (Dalman) and *Sericesthis nigrolineata* Boisduval (Coleoptera: Scarabaeidae: Melolonthinae). By E. B. Britton. (Communicated by Dr. D. F. Waterhouse.)
2. New taxa of *Acacia* from eastern Australia. No. 2. By Mary D. Tindale.

ORDINARY MONTHLY MEETING

28th SEPTEMBER, 1966

Dr. R. C. Carolin, President, in the chair.

The minutes of the last Monthly Meeting (15th July, 1966) were read and confirmed.

The following were elected Ordinary Members of the Society: Mrs. Denise D. Clyne, Turramurra, N.S.W.; Mr. B. A. Conroy, Leichhardt, N.S.W.; Miss Judith H. Ford, Mosman, N.S.W.; Miss Lois J. Lovedee, B.Sc., East Gosford, N.S.W.; Mr. Ahmed Mahmood, M.Sc., University of Karachi, Karachi-32, West Pakistan; and Mr. G. L. Miklos, Hunter's Hill, N.S.W.

The Chairman announced that Mr. George N. Baur had been elected a member of Council in place of Professor S. Smith-White.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1967, from qualified candidates. Each applicant must be a member of this Society and be a graduate in Science or Agricultural Science of the University of Sydney. The range of actual (tax-free) salary is, according to qualifications, up to a maximum of \$A3,200 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 2nd November, 1966.

The Chairman announced that library accessions amounting to 39 volumes, 318 parts or numbers, 19 bulletins, 16 reports and 17 pamphlets, total 409, had been received since the last meeting.

PAPERS READ

1. Studies on the inheritance of rust resistance in oats. IV. Expression of allelomorphism and gene interaction for crown rust resistance in crosses involving the oat variety Bond. By E. P. Baker and Y. M. Upadhyaya.

2. A new corallanid isopod parasitic on Australian freshwater prawns. By E. F. Riek.

3. New Australian cave Carabidae (Coleoptera). By B. P. Moore.

LECTURETTE

A lecturette entitled "Dolphins and small whales in the Solomon Islands and New Guinea waters", illustrated by still and movie films, was delivered by Dr. W. H. Dawbin, School of Biological Sciences, University of Sydney.

ORDINARY MONTHLY MEETING

26th OCTOBER, 1966

Dr. R. C. Carolin, President, in the chair.

The minutes of the last Monthly Meeting (28th September, 1966) were read and confirmed.

Mr. B. F. Clough, B.Sc.Agr., Sydney University; Mr. S. W. L. Jacobs, Pymble, N.S.W.; Dr. Patricia Mather (née Kott), University of Queensland, St. Lucia, Queensland; Mr. J. W. Patrick, B.Sc.Ag., Sydney University; and Miss Eileen F. Pyne, B.Sc., Strathfield West, N.S.W., were elected Ordinary Members of the Society.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1967, from qualified candidates. Each applicant must be a member of this Society and be a graduate in Science or Agricultural Science of the University of Sydney. The range of actual (tax-free) salary is, according to qualifications, up to a maximum of \$A3,200 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 2nd November, 1966.

The Chairman announced that library accessions amounting to 18 volumes, 135 parts or numbers, 3 bulletins, 4 reports and 2 pamphlets, total 162, had been received since the last meeting.

PAPERS READ

1. *Atopozoa deerata* (Sluiter): a discussion of the relationship of the genus and species. By Patricia Kott (Dr. Patricia Mather).
2. Inheritance of resistance to bunt in Turkey wheat selections. By E. P. Baker.

LECTURETTE

An illustrated lecturette entitled "Phylogeny and Evolutionary Patterns in the Flowering Plant Family Dipsacaceae" was delivered by Professor F. Ehrendorfer, Director, Institute of Systematic Botany, and Botanic Gardens, University of Graz, Austria.

ORDINARY MONTHLY MEETING

30th NOVEMBER, 1966

Dr. R. C. Carolin, President, in the chair.

The minutes of the last Monthly Meeting (26th October, 1966) were read and confirmed.

The following were elected Ordinary Members of the Society: Mr. R. A. Boyd, B.Sc., University of New England, Armidale, N.S.W., and Mr. E. H. Hault, B.Sc.(Hons.), University of New England, Armidale, N.S.W.

The Chairman announced that the Council had appointed Miss Alison K. Dandie, B.Sc.(Hons.), to a Linnean Macleay Fellowship in Botany for one year from 1st January, 1967.

The Chairman referred to the death on 6th October, 1966, of Mr. Melbourne Ward, who had been a member of the Society since 1930.

The Chairman announced that library accessions amounting to 19 volumes, 248 parts or numbers, 14 bulletins, 23 reports and 9 pamphlets, total 313, had been received since the last meeting.

PAPERS READ

1. Rhinonyssine nasal mite infestations in birds at Mitchell River Mission during the wet and dry seasons. By R. Domrow.
2. Intraspecific polyploidy in *Hypopterygium rotulatum* (Hedw.) Brid. By Helen P. Ramsay.
3. Highlands peat of the Malayan Peninsula. By B. R. Hewitt.

NOTES AND EXHIBITS

Mr. Ellis Troughton (Hon. Science Associate at the Australian Museum) exhibited the skull of the adult ♂ holotype of the New Guinea Highland Dog, *Canis hallstromi* (*Proc. roy. zool. Soc. N.S.W.*, May, 1957), from the Huri-Duna country, Southern Highlands district of Papua. Received at Taronga Park Zoo in March, 1957, the original pair produced a series of litters, invariably black at birth, resulting in some variability in adult coloration.

There are several references to a small native dog in New Guinea with a yodelling call, from as far back as 1842 in the *Colonial Magazine*. The first skin and skull to reach the Queensland Museum were collected by the Lieut. Governor, Sir Wm. MacGregor, in 1897, at 7,000 ft. on Mt. Scratchley in Papua.

The specimen was the subject of a rather misleading colour description, and unduly dingo-like photo of the stuffed skin, provided by De Vis (*Ann. Qld. Mus.*, 10, 1911). Subsequently Professor Wood Jones (*American Journ. Mamm.*, X, 1929) published a description and figure of the skull, concluding that it provided definite evidence "that the Papuan Dog is a very definite race, possessing a relatively large upper carnassial tooth . . . and differing widely in its characters from the dogs of certain other Pacific Islands". He also stressed the need for study of additional material before the breed became too hybridized.

Wood Jones did not confirm his diagnosis with a specific or racial name so that his paper has been generally overlooked. Therefore, in view of the persistence of such distinctive characters in the original pair and their progeny at Taronga Park, confirmed by personal examination of the skull and skins in the Queensland Museum, the unusual course of specifically naming the living pair, within two months of arrival at Taronga Park, obviated the inevitable inference that the progeny were subject to captive hybridization. The term "feral" was used in Wood Jones' racial definition, but the term may be applied too casually in discrediting the New Guinea Highland Dog as a mere variation of the mainland Dingo, currently estimated as existing for about 22,000 years in its present form. More probably, the New Guinea Dog was a prehistoric inhabitant of the rain-forests of the Atherton Tableland and, by subsequent deployment over the more arid regions, became the actual progenitor of the Australian Dingo.

Mr. A. G. Khan exhibited photographs and photomicrographs concerning the nodulation of roots in three species of *Podocarpus*. Photographs showed the rooted cuttings bearing nodules in sterile culture of *P. elatus* R.Br. ex Endl., *P. spinulosus* (Sm.) R.Br. ex Mirb., and *P. lawrencei* Hook f., the last mentioned one being the most prolific in nodule and adventitious root formations. Photomicrographs showed the development of nodule and lateral root on naturally growing infected plants. The cortical tissue of the nodule produced in sterile culture is devoid of any endophyte which eliminates infection as a cause of the nodulation. This is strengthened by the anatomical features of young nodule and young lateral root, both of which arise endogenously but differ in their cellular configuration. The nodule lacks any appearance of an apical meristem pattern of cells and has an endodermis over-arching its vascular tissue, whereas the lateral root shows an apical meristem pattern of cells and has an open-ended endodermis.

Prof. T. G. Vallance exhibited his copy of George Shaw's "Zoology of New Holland" (London, 1794) and a MS letter from Shaw to the artist James Sowerby giving instructions for an illustration in the book. The letter (undated) contains the following passage:

"Dr. Shaws Compts. to Mr. Sowerby & informs him that the quadruped intended for the ensuing No. of the New-Holland Zoology is now at Mr. Wilson's, & if Mr. S. will send a messenger for it he may have it at his own house for some days, which will be necessary, in order to study its several attitudes, & to give as elegant a figure of it as possible. It is an Opossum with the aspect of a Squirrel, & is a very beautiful animal . . . Mr. S. will take notice that the tail is strongly prehensile, & may therefore be represented in such a manner as to shew that particular, unless it shd. be thought to interfere with the elegance of the plate; But the best way will be to make several sketches, in different attitudes.

It is to be fed with bread & milk. It is nearly torpid by day, but very active by night. Care must be taken to express well & clearly the lateral membrane of the sides & feet, as in the flying Squirrel . . ."

The animal referred to in the letter appears in Tab. XI of Shaw's book, where it is identified as *Didelphis sciurea*, the Squirrel Opossum.

Dr. R. C. Carolin showed a film, prepared by himself and Mr. R. J. Oldfield, demonstrating pollinating mechanisms in Australian native plants. It showed pollination by birds and insects in the families Proteaceae, Myrtaceae, Stylidiaceae, Papilionaceae and Dilleniaceae. Numerous insects were shown working flowers in their own distinctive ways, some clearly pollinating flowers, whereas the insects of others could have had no effect in this direction. The explosive mechanism of *Conospermum* was illustrated.

Mr. S. W. L. Jacobs exhibited photographs illustrating the distribution of starch in transverse sections of fresh grass leaves. Poöideae show general starch distribution, whereas in Panicoideae and Eragrostoideae starch formation is restricted to the parenchymatous sheath around the vascular bundle. In *Triodia*, where the photosynthetic tissue is more restricted, this starch-forming sheath surrounds the chlorenchyma rather than the vascular bundle. It is suggested that the parenchymatous sheath is, functionally, more connected with the chlorenchyma than with the conducting tissue.

LIST OF MEMBERS.

(15th December, 1966)

ORDINARY MEMBERS.

(An asterisk (*) denotes Life Member.)

- 1940 Abbie, Professor Andrew Arthur, M.D., B.S., B.Sc., Ph.D., c.o. University of Adelaide, Adelaide, South Australia.
- 1940 *Allman, Stuart Leo, B.Sc.Agr., M.Sc., 99 Cumberland Avenue, Collaroy, N.S.W.
- 1965 Anderson, Derek John, Ph.D., School of Biological Sciences, Botany Building, Sydney University.
- 1959 Anderson, Donald Thomas, B.Sc., Ph.D., School of Biological Sciences, Department of Zoology, Sydney University.
- 1964 Anderson, Mrs. Jennifer Merciana Elizabeth, B.Sc.Agr., Macleay Museum, Sydney University.
- 1922 Anderson, Robert Henry, B.Sc.Agr., 19 Kareela Road, Chatswood, N.S.W.
- 1963 Ardley, John Henry, B.Sc. (N.Z.), School of Public Health and Tropical Medicine, Sydney University.
- 1927 *Armstrong, Jack Walter Trench, "Cullingera", Nyngan, N.S.W.
- 1952 Ashton, David Hungerford, B.Sc., Ph.D., 92 Warrigal Road, Surrey Hills, E.10, Victoria.
- 1912 Arousseau, Marcel, B.Sc., 229 Woodland Street, Balgowlah, N.S.W.
- 1962 Bailey, Peter Thomas, B.Sc., C.S.I.R.O., Division of Wildlife Research, P.O. Box 109, City, Canberra, A.C.T.
- 1961 Bain, Miss Joan Maud, M.Sc., 18 Onyx Road, Artarmon, N.S.W.
- 1949 Baker, Eldred Percy, B.Sc.Agr., Ph.D., Department of Agricultural Botany, Sydney University.
- 1962 Ballantyne, Miss Barbara Jean, B.Sc.Agr., N.S.W. Department of Agriculture Private Mail Bag No. 10, Rydalmere, N.S.W.
- 1959 Bamber, Richard Kenneth, F.S.T.C., 113 Lucinda Avenue South, Wahroonga, N.S.W.
- 1950 *Barber, Professor Horace Newton, M.S., Ph.D., F.A.A., School of Biological Sciences, Department of Botany, University of N.S.W., P.O. Box 1, Kensington, N.S.W.
- 1960 Barber, Ian Alexander, B.Sc.Agr., School of Biological Sciences, Department of Zoology, Sydney University.
- 1955 Barlow, Bryan Alwyn, B.Sc., Ph.D., School of Biological Sciences, The Flinders University of South Australia, Bedford Park, South Australia.
- 1965 Basden, Ralph, M.Ed., B.Sc. (Lond.), F.R.A.C.I., A.S.T.C., 183 Parkway Avenue, Hamilton, N.S.W.
- 1960 Batley, Alan Francis, A.C.A., 123 Burns Road, Wahroonga, N.S.W.
- 1954 Baur, George Norton, B.Sc., B.Sc.For., Dip.For., 3 Mary Street, Beecroft, N.S.W.
- 1935 *Beadle, Professor Noel Charles William, D.Sc., University of New England, Armidale, 5N, N.S.W.
- 1946 Bearup, Arthur Joseph, B.Sc., 66 Pacific Avenue, Penshurst, N.S.W.
- 1940 Beattie, Joan Marion, D.Sc. (née Crockford), 2 Grace Avenue, Beecroft, N.S.W.
- 1964 Bedford, Geoffrey Owen, B.Sc., c/- C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
- 1961 Bedford, Miss Lynette, B.Sc., School of Biological Sciences, Department of Zoology, Sydney University.
- 1952 Bennett, Miss Isobel Ida, Hon. M.Sc., School of Biological Sciences, Department of Zoology, Sydney University.
- 1964 Bertus, Anthony Lawrence, B.Sc., Biology Branch, N.S.W. Department of Agriculture, Private Mail Bag, No. 10, Rydalmere, N.S.W.
- 1948 Besly, Miss Mary Ann Catherine, B.A., School of Biological Sciences, Department of Zoology, Sydney University.
- 1961 Bishop, James Arthur, Department of Genetics, The University of Liverpool, Liverpool 3, England.
- 1964 Blackmore, John Allan Philip, LL.B. (Syd. Univ.), 25 Holden Street, Ashfield, N.S.W.
- 1958 Blake, Clifford Douglas, B.Sc.Agr., Ph.D., Faculty of Agriculture, Sydney University.
- 1941 Blake, Stanley Thatcher, D.Sc. (Q'ld.), Botanic Gardens, Brisbane, Queensland.
- 1960 Bourke, Terrence Victor, B.Sc.Agr., c/- Department of Agriculture, Stock and Fisheries, Popondetta, Papua.
- 1946 Brett, Robert Gordon Lindsay, B.Sc., 7 Petty Street, West Hobart, Tasmania.
- 1960 Brewer, Ilma Mary, D.Sc., 7 Thornton Street, Darling Point, Sydney.
- 1955 Briggs, Miss Barbara Gillian, Ph.D., 13 Findlay Avenue, Roseville, N.S.W.
- 1924 Browne, Ida Alison, D.Sc. (née Brown), 363 Edgecliff Road, Edgecliff, N.S.W.
- 1911 Browne, William Rowan, D.Sc., F.A.A., 363 Edgecliff Road, Edgecliff, N.S.W.
- 1949 Burden, John Henry, 1 Havilah Street, Chatswood, N.S.W.

- 1931 *Burgess, Professor Norman Alan, M.Sc., Ph.D., Professor of Botany, University of Liverpool, Liverpool, England.
- 1959 Burgess, The Rev. Colin E. B. H., Parks and Gardens Section, Department of the Interior, Canberra, A.C.T.
- 1962 Burgess, Ian Peter, B.Sc.For., Dip.For., The Forestry Office, Coff's Harbour, N.S.W.
- 1960 Cady, Leo Isaac, P.O. Box 88, Kiama, N.S.W.
- 1959 Campbell, Keith George, D.F.C., B.Sc.For., Dip.For., M.Sc., 17 Third Avenue, Epping, N.S.W.
- 1927 Campbell, Thomas Graham, Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
- 1934 *Carey, Professor Samuel Warren, D.Sc., Geology Department, University of Tasmania, Hobart, Tasmania.
- 1949 Carne, Phillip Broughton, B.Agr.Sci. (Melb.), Ph.D. (London), D.I.C., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
- 1956 Carolin, Roger Charles, B.Sc., A.R.C.S., Ph.D., School of Biological Sciences, Department of Botany, Sydney University.
- 1957 Casimir, Max, B.Sc.Agr., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag, No. 10, Rydalmere, N.S.W.
- 1936 *Chadwick, Clarence Earl, B.Sc., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W.
- 1956 Chambers, Thomas Carrick, M.Sc. (N.Z.), Ph.D., Botany School, University of Melbourne, Parkville, N.2, Victoria.
- 1966 Child, John, M.A., B.Comm. (N.Z.), D.Phil. (Oxon.), 48 Milling Street, Gladesville, N.S.W.
- 1959 Chippendale, George McCartney, B.Sc., 4 Raoul Place, Lyons, A.C.T.
- 1947 Christian, Stanley Hinton, Malaria Research Unit and School, Kundiawa, Eastern Highlands, Territory of Papua and New Guinea.
- 1932 *Churchward, John Gordon, B.Sc.Agr., Ph.D., "Shady Trees", Clarktown Avenue, Mount Eliza, Victoria.
- 1946 Clark, Laurance Ross, M.Sc., c.o. C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
- 1961 Clarke, Miss Lesley Dorothy, 4 Gordon Crescent, Eastwood, N.S.W.
- 1947 Clarke, Mrs. Muriel Catherine, M.Sc. (née Morris), 122 Swan Street, Morpeth, N.S.W.
- 1901 Cleland, Professor Sir John Burton, M.D., Ch.M., C.B.E., 1 Dashwood Road, Beaumont, Adelaide, South Australia.
- 1966 Clough, Barry Francis, B.Sc.Agr., School of Biological Sciences, Department of Botany, Sydney University.
- 1966 Clyne, Mrs. Denise Dorothy, 7 Catalpa Crescent, Turrumurra, N.S.W.
- 1956 Cogger, Harold George, M.Sc., Australian Museum, College Street, Sydney.
- 1946 Colless, Donald Henry, Ph.D. (Univ. of Malaya), c.o. Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
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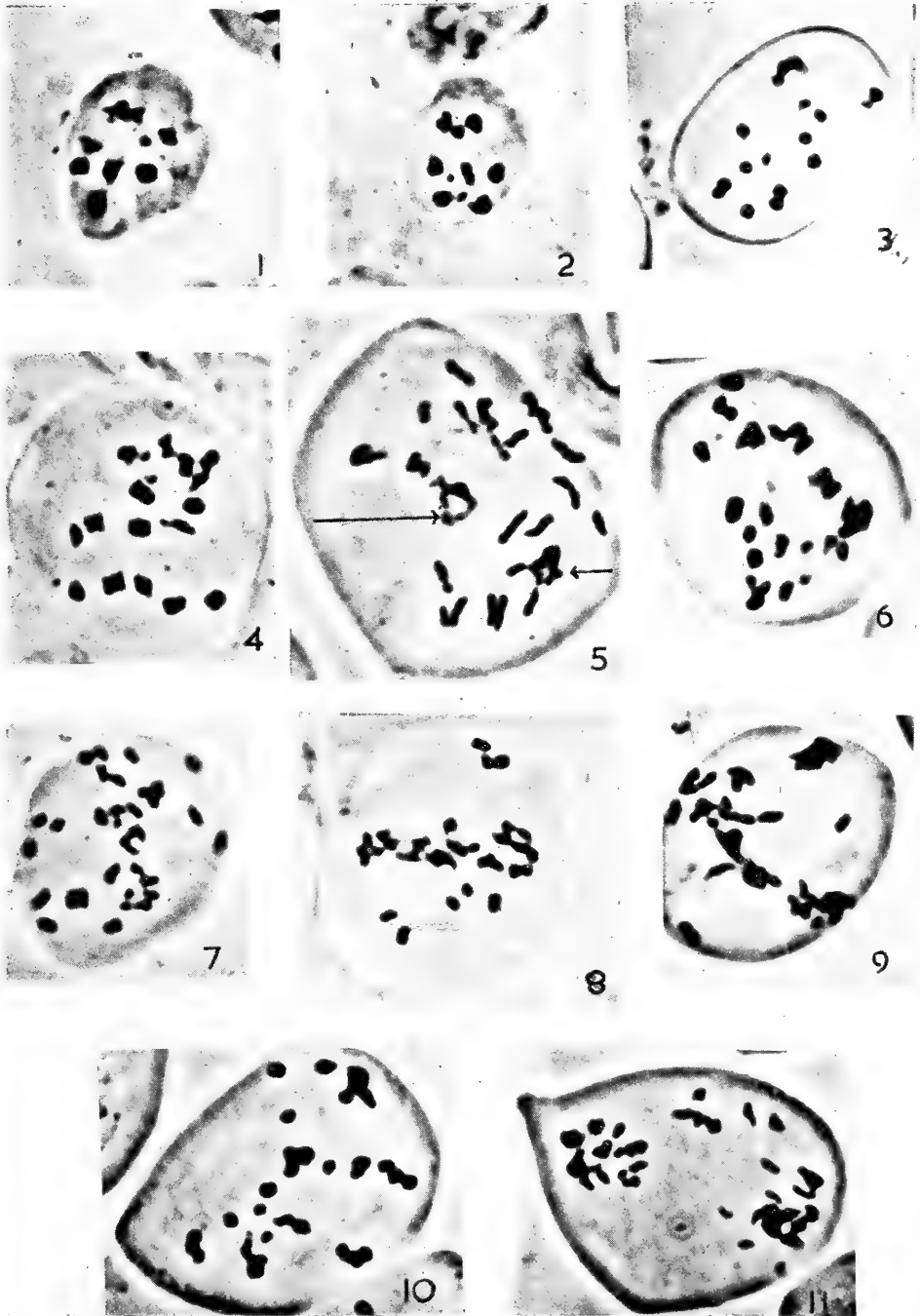
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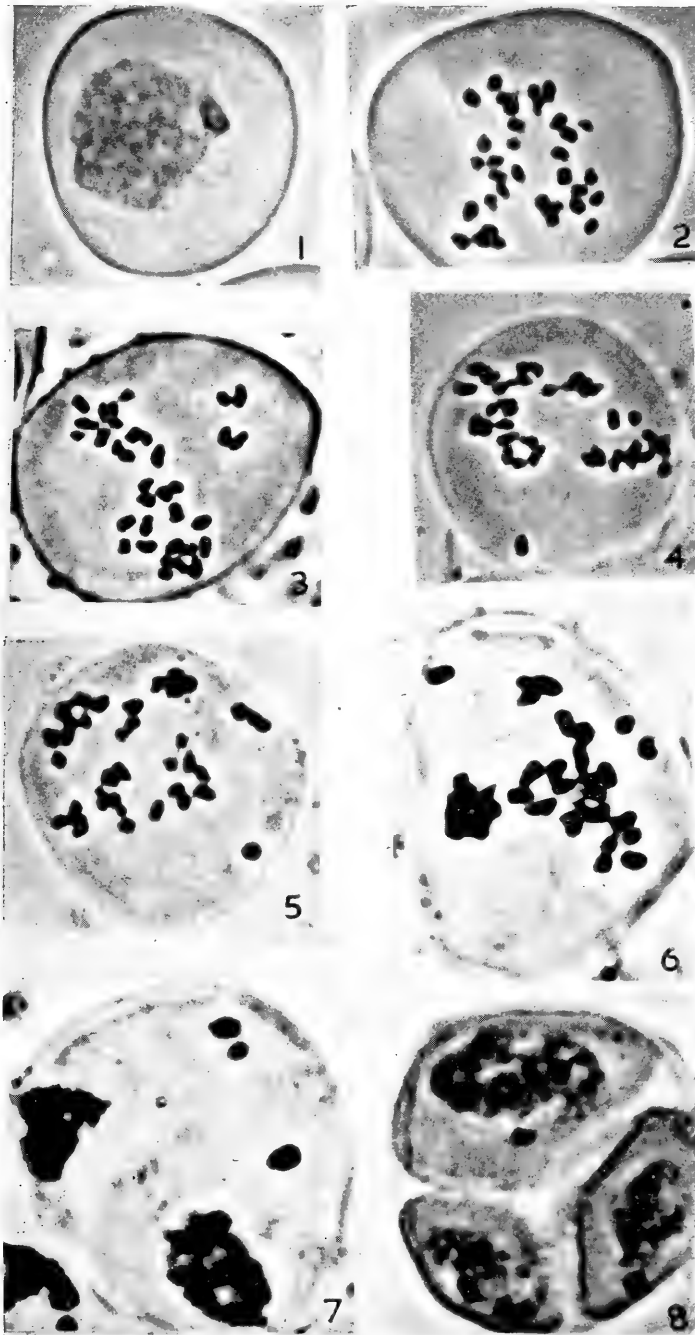
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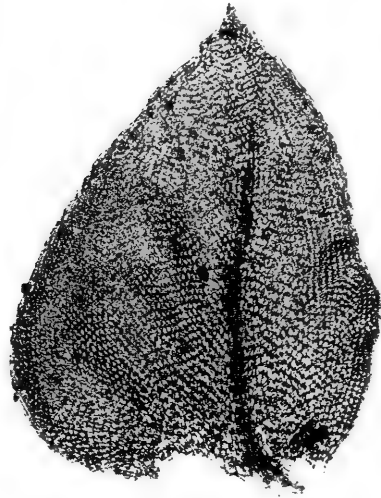
Hypopterygium rotulatum, meiosis in spore mother cells $\times 2,200$.



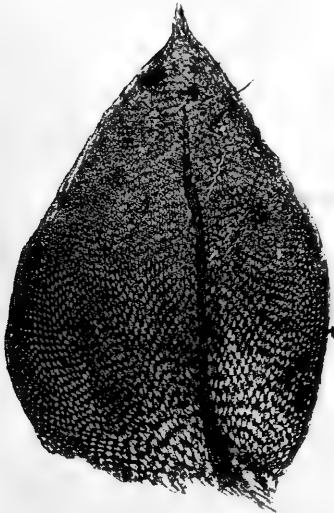
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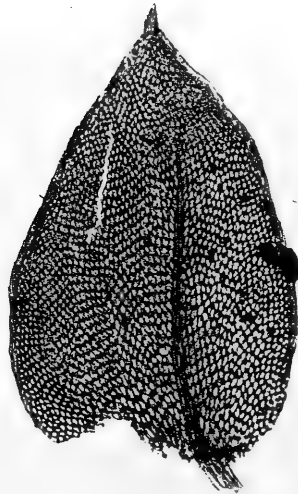
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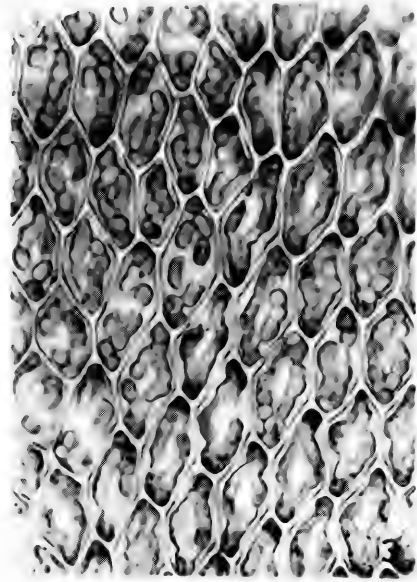
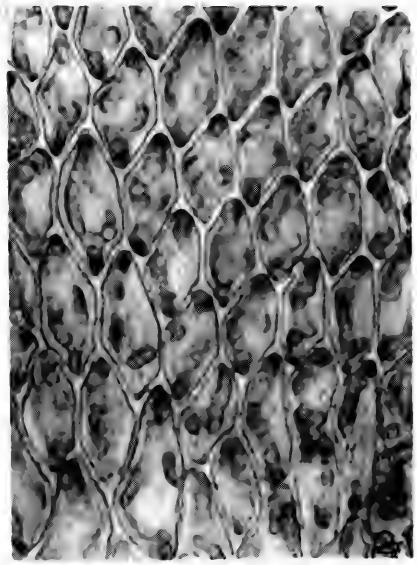
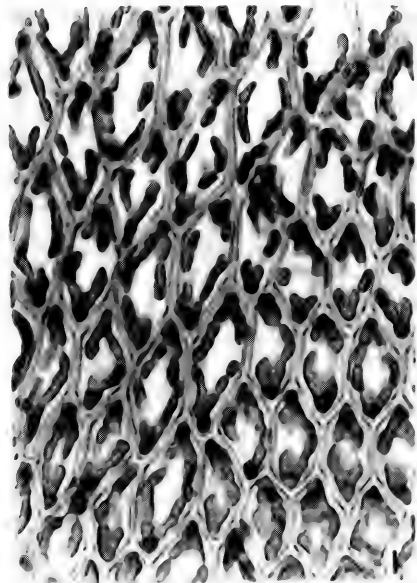


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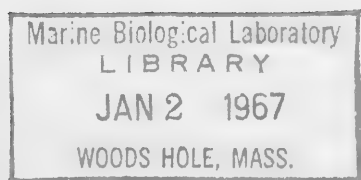
Hypopterygium rotulatum, leaves.



Hypopterygium rotulatum, cells of leaves.

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Founded 1874. Incorporated 1884

“ For the cultivation and study of the science of Natural History in
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