(*Issued 1st September, 1961.*)

Vol. LXXXVI. **No. 395.**
Part 1.

THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1961

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Part 1 (pp. 1-168).

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

With seven plates.
[Plates i-vii.]

SYDNEY

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The Linnean Society of New South Wales

LIST OF OFFICERS AND COUNCIL, 1961–62.

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NOTICE

Sets of the PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALES (except First Series, Volumes I-VI, 1875-1881), and separate Parts, may be purchased from the Society, Science House, 157 Gloucester Street, Sydney. Separate Parts may be obtained also from David Nutt, 41 Colebrooke Row, London, N.1. The stock of First Series, Volumes I-VI, is strictly limited and some Parts of these Volumes are out of print.

From 1st March, 1954, the price of each complete volume will be £3 10s., plus postage. (All previous price lists are cancelled.)

INDEX TO VOLUMES I-L OF THE PROCEEDINGS [Issued 15th February, 1929]. Pp. 108. Price 5s.

THE MACLEAY MEMORIAL VOLUME [Issued 13th October, 1893]. Royal 4to, ii to 308 pages, with portrait, and forty-two plates. Price £1 1s.

DESCRIPTIVE CATALOGUE OF AUSTRALIAN FISHES. By William Macleay, F.L.S. [1881]. A few copies only. Two volumes and supplement. Price £2 2s.

THE TRANSACTIONS OF THE ENTOMOLOGICAL SOCIETY OF NEW SOUTH WALES, 2 vols., 8vo. [Vol. I (complete in five parts, 1863-66), price 70s. net, Parts 2-5 10s. each; Vol. II (complete in five parts, 1869-73), price 30s. net, or single Parts 7s. 6d. each.]

SUBSCRIPTION: £3 10s. per annum; postage 4s.

ANNUAL GENERAL MEETING.

29th March, 1961.

The Eighty-Sixth Annual General Meeting was held in the Society's Rooms, Science House, Sydney, on Wednesday, 29th March, 1961.

Dr. I. V. Newman, President, occupied the chair.

The minutes of the Eighty-Fifth Annual General Meeting, 30th March, 1960, were read and confirmed.

In the absence of the Honorary Treasurer (Dr. A. B. Walkom) the Honorary Secretary (Dr. W. R. Browne) presented the balance sheets for the year ending 28th February, 1961, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A., and his motion that they be received and adopted was carried unanimously.

Report on the Affairs of the Society for the Year.

In presenting the report on the affairs of the Society to be taken as read, the President said: "The promotion of the progress and welfare of our Society is a matter for much thought in these days. We are a generalized Society in a time of specialization—a Society with roots in amateur soil, but shooting into an atmosphere of professionalism. Let us not forget that the professional specialist in one discipline is but an amateur in other disciplines. Thus the possibility of boredom at our meetings is high. Personally, I find some interest somewhere at some time in every meeting; and this is my experience in similar societies in the four countries in which I have lived. But boredom is in large part a matter of the will. If one is prepared to be interested, I am confident the interesting will appear. Cross-references in thought and new light on principle and method can come from papers in an alien discipline. There is an obligation on the readers of papers to present them suitably, on members of other disciplines to be present, for an intelligent question out of ignorance can stimulate valuable discussion, and on members of the relevant disciplines to be present for the discussions. For, the more of us there are together the more interesting we can be. To stimulate interest, the Council made several changes this year. Authors are now told the time allotted for presenting their papers; the synopses appear in the notice of the meeting; an indication of the fields of discussion on papers is given in the report of the meeting. For myself, I felt that a concise statement of 10 or 12 lines from the author of a paper read in title, giving to the President the purpose, background or context of the paper, would have enabled the President to evoke some comment, if not discussion, on some of these papers.

"My final point to put forward about the welfare of our Society is the idea that here we meet other disciplines in discussion and friendship, here we meet and can help to establish younger scientists in the scientific community, and here we can bring together the professional specialist, the professional generalist, and the interested layman. A difficult task? Of course; but nothing worthwhile for a Society can be done without effort of body or mind by the individual member.

"The thanks of the Society are due to Miss G. Allpress, our Assistant Secretary, for her careful attention to the business and library work throughout the year, and for compiling the material for the Report on the Affairs of the Society. We continue to be in a great debt of gratitude to the Honorary Secretaries, Dr. W. R. Browne and Dr. A. B. Walkom, who so successfully guide the affairs of the Society. Dr. Walkom, as

Honorary Treasurer and Honorary Editor, has placed the Society in a financial position for advancement and has continued to give us a PROCEEDINGS with an enviably high standard of production. It is to these two devoted honorary officers that the Society in recent years has owed its continuance as a successful organization. I would thank the members of Council and Committees for their co-operation in maintaining the Society's activities during the year."

The Society's PROCEEDINGS for 1960, Vol. 85, Parts 1 and 2, were published in 1960 and Part 3 in March, 1961. Volume 85 consists of 403 pages, 10 plates and 324 text-figures. An increase in the charges for printing the PROCEEDINGS commencing with Vol. 85, Part 3, was made in October, 1960. The regulations governing Linnean Macleay Fellowships were revised by the Council on 21st September, 1960.

During the year twenty-two new members were added to the list, one ordinary member and one corresponding member died, five members resigned and two were removed from the list of members. The numerical strength of the Society at 28th February, 1961, was: Ordinary Members, 238; Life Members, 31; Corresponding Member, 1; total, 270.

Lecturettes were given at the following meetings: April, Environmental Adaptations in Australian Reptiles, by Mr. H. G. Cogger; July, Notes on the Vegetation of Nigeria, by Dr. G. K. Berrie; September, The Natural History of New Caledonia, by Miss Elizabeth C. Pope; October, Genetical and Biological Studies in the Western Australian Country-side, by Messrs. S. H. James and W. J. Peacock; November, An Entomologist Abroad, by Mr. K. E. W. Salter. The discussions which followed added greatly to the interest of the proceedings. We express our thanks and appreciation to the lecturers.

On 29th June, 1960, the Second Sir William Macleay Memorial Lecture, entitled "Bridging the Gap between Race and Species" (see PROC., 85 (3): 322-327), was delivered by Dr. Th. Dobzhansky to a large audience.

Library accessions from scientific institutions and societies on the exchange list amounted to 1,912 compared with 2,076 in the previous year. Loans from the library to members and institutions were as numerous as in the previous year. Exchanges of publications were arranged with the following: Laboratory of Water Biology, Polish Academy of Sciences, Cracow, Poland; Saugar University Botanical Society, Saugar, India; Office de la Recherche Scientifique et Technique Outre-mer, Paris, France; The National Geological Library, Peking, China; The Institute of Palaeontology, Academia Sinica, Nanking, China; Ohio Herpetological Society, Columbus, Ohio, U.S.A.; Centro de Estudios Zoologicos, Faculdade National de Filosofia, Universidade do Brasil, Rio de Janeiro, Brasil. Commencing from 1961 the Council decided to subscribe to "Australian Plants" (published by the Society for Growing Australian Plants, Picnic Point, N.S.W.). At the request of the Royal Microscopical Society, London, owing to limitation of the library facilities of that Society, the exchange of publications with this Society was terminated with the volumes for 1960. A copy of "The Royal Society. Its Origins and Founders", edited by Sir Harold Hartley, was purchased for the Society's library.

The total net return from the Society's one-third ownership of Science House for the year was £1,383/10/2.

The President and Mrs. Newman attended, as official guests, the annual celebration in May, 1960, of the landing of Captain Cook at Kurnell.

The Society was represented by Dr. I. V. Newman and Mr. E. Troughton at the Conservation Conference on 13th August, 1960. The President, on behalf of the Council, subscribed to a resolution to the Premier sponsored by the National Parks Association of New South Wales, urging *inter alia* that all national parks, reserves and other areas of nature conservation be brought under the responsibility of one Minister of the Crown and that a unified authority for management and training of officers be set up.

The Society, supported by the Royal Society of New South Wales and the Royal Zoological Society of New South Wales, suggested the names of two scientists for the nomination to one vacancy on the Kosciusko State Park Trust, without success.

A donation was made to the Trust of "The Muogamarra Sanctuary" in recognition of the valuable work being done by it.

Linnean Macleay Fellowships.

Mr. W. J. Peacock, B.Sc., was appointed to a Fellowship in Botany for one year as from 1st January, 1961. Mr. Peacock's programme of research is the development of work in two fields: (1) a survey of cytological conditions in the Goodeniaceae with particular studies of certain situations in the family: (*a*) interchange hybridity in *Brunonia australis*, (*b*) tetrad segregation in *Leschenaultia* and (*c*) development of polyploidy in *Dampiera*, and (2) the study of basic chromosome sub-structure using irradiation and similar techniques.

We wish Mr. Peacock every success in his research.

Linnean Macleay Lectureship in Microbiology.

Dr. Y. T. Tchan, Linnean Macleay Lecturer in Microbiology, University of Sydney, spent the greater part of the year on study leave in Europe, working chiefly in Denmark and France. In Denmark the work was on electron microscope study of the cytology of *Azotobacter*, in collaboration with Dr. H. L. Jensen (former Macleay Bacteriologist) at the Statens Planteavls-Laboratorium, Lyngby, Prof. Maalø at the Microbiological Institute, Copenhagen, and Dr. Birch-Andersen at the State Serum Institute, Copenhagen. In France Dr. Tchan worked on nitrogen fixation at the Pasteur Institute, Paris.

Obituaries.

The following deaths during the year are recorded, with regret:

James Joscelyn Lawrence, M.Sc., Ph.D., died on 26th May, 1960, of leucaemia. He was virologist at the School of Public Health and Tropical Medicine, Sydney, and had made many contributions to both animal and human epidemiology and parasitology. His special interest at first was zoology, but later he was able to turn with success to bacteriology and virology. Dr. Lawrence had a wide knowledge of many scientific fields. He joined the Society in 1946, and in that year he contributed one paper to the PROCEEDINGS and one with Mr. A. J. Bearup.

Theodore Cleveland Roughley, B.Sc., F.R.Z.S., of Vaucluse, Sydney, who had been a member of the Society since 1925 and a Corresponding Member since 1957, died suddenly on 14th January, 1961, at Tuggerah, N.S.W. Mr. Roughley was born at Ryde, N.S.W., in 1888, educated at Sydney High School and Sydney University, was zoologist at the Technological Museum, Sydney, for twenty-eight years (1911-1939), and Superintendent of N.S.W. Fisheries from 1939 to 1952. He wrote a number of books, including "Fish and Fisheries of Australia", "Fishes of Australia and their Technology" (1916), "Cult of the Goldfish" (1933), "Wonders of the Great Barrier Reef" and "Aeronautical Work of Lawrence Hargrave". He published two papers in the Society's PROCEEDINGS, one in 1926, and "The Life History of the Australian Oyster (*Ostrea commercialis*)" in 1933. For the work represented by the latter paper the University of Sydney granted him the degree of Bachelor of Science. He lectured in the U.S.A. in 1945 and 1946 on Australia's Great Barrier Reef, and his ability to analyse fish-industry problems led to his investigating the oyster industries of the U.S.A. and the United Kingdom in 1956. Mainly owing to his efforts, New South Wales oyster production has greatly increased since 1915; he was responsible for the development of the fish-canning industry in Australia. Mr. Roughley was President of the Microscopical Society of New South Wales, Vice-President of the Aquarium Society, President of the Royal Zoological Society of New South Wales 1934–1936, President of the Great Barrier Reef Game Fishing and Angling Club in 1937, and President of this Society 1938–1939. Mr. Roughley served on the Council from 1931 to 1956. He was a keen and skilful bowler and golfer, and his hobby was the collection of books and works of art.

Presidential Address.

Pattern in the Meristems of Vascular Plants: A Review of Shoot Apical Meristems of Gymnosperms, with Comments on Apical Biology and Taxonomy, and a Statement of Some Fundamental Concepts. (For full text see pages 9–59.)

The declaration of types for the apices of the shoots of vascular plants is precluded by incompleteness of the records of the internal structure and behaviour. Wide coverage in the literature makes the Gymnosperms a suitable group for review. On the basis of illustrations in the literature covering the group, with a few angiosperms added, and all arranged at a common magnification in taxonomic and ontogenetic sequence, comments are made and fundamental concepts are proposed.

The larger the general apex, the less convex it is. The larger the apex, the more complicated and the less clearly defined is the cellular pattern. Vacuolation increases generally away from the tip and the surface; and cell size is the resultant of rates of enlargement and division. High vacuolation accompanies both dormancy and cessation of growth. Degree of vacuolation is the resultant of vacuolation rate and division frequency. Primary augmentation, longitudinal or transverse, provides surface for many primordia, and is not a type feature. Apical limits are not indicated by primordia (incidents in total apical activity), but should be indicated by some form of curve which is concave upwards. Wall directions in cellular pattern should be related to Sachs' *original* concepts of periclines and anticlines, and patterns so derived should be recognized as largely physiological in origin.

The fundamental concepts are to meet the fact that apical cells are not directly recognizable in the shoot apices of seed plants. 1. Attending to the centre of the initiation, *there are three basic types of apex*: the *Duplex Apex*, with two superposed initiating regions whose side walls are perpendicular to the surface, the outer region (of one or more tiers) dividing with new walls only parallel with the side walls, the inner region (of only one tier) dividing with walls parallel with both side and lower (horizontal) walls (cf. tunica-corpus topography); the *Simplex Apex*, with one initiating region, like the inner region of the Duplex Apex; the *Monoplex Apex*, with one initiating region—the apical cells of classical form, inwardly pointed. In these founts of cellular structure originating the general meristem, one division of initial initiates increase in both length and breadth for the Monoplex Apex, but two divisions of initial are required for this in the Simplex Apex and the inner region of the Duplex Apex, while in the outer region of the Duplex Apex divisions of initial only increase breadth (surface). 2. The *Continuing Meristematic Residue* is a logical necessity, alone inheriting the initial function from its mother initial cell(s) and handing on, each cell of it, the initial function to only one of each pair of daughter cells, and it is the initiating region of the three basic types of apex. It is a concept of precision, and involves differential division. It is the "apical cells", whether they are directly recognizable or not. The concept of *anneau initial* as initiator is rejected. A search for apical cells in seed plants is not pointless. 3. *Cellular pattern expresses the compounding of rates and orientations of physiological processes.* The visible cellular pattern results from process patterns of rates and orientations which express the presence patterns of chemical concentrations and physical intensities. The chemical and physical entities involved are supplied under gradient patterns of translocation from the location pattern of founts of origin. Cellular structure, passing back from the apical summit as a fixed point of reference, behaves in visible pattern according to the part of the physiological pattern it occupies at the time. But also patterns in relation to the summit may change with time (dormancy—activity changes and changes in tunica-corpus topography). 4. *Physiology and Phylogeny meet in the relating of the evolution of the three basic types of apex* to the origin of the major taxa of vascular plants.

In conclusion: The *Continuing Meristematic Residue* (apical cells, in the apex) is a reality, whether directly observable or not. There are only three fundamental types of apex in the shoots of vascular plants—*Monoplex*, *Simplex* and *Duplex* types of apex. Cellular structure changes as it "passes back" through the physiological pattern.

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

President: J. M. Vincent, D.Sc.Agr., Dip.Bact.

Members of Council: S. J. Copland, M.Sc.; Lilian Fraser, D.Sc.; F. V. Mercer, B.Sc., Ph.D.; S. Smith-White, D.Sc.Agr.; H. S. H. Wardlaw, D.Sc., F.R.A.C.I.; and A. R. Woodhill, D.Sc.Agr.

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

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

LINNEAN SOCIETY OF NEW SOUTH WALES.

GENERAL ACCOUNT. Balance Sheet at 28th February, 1961.

LIABILITIES.	£ s. d.	£ s. d.
Accumulated Funds—		
Amount received from Sir William Macleay during his lifetime ..	14,000 0 0	
Further sum bequeathed by his will	6,000 0 0	
		20,000 0 0
Contingencies Reserve		15,899 1 4
		35,899 1 4
Current Liabilities—		
Bookbinding Account	1,127 10 1	
Income Account	1,116 14 0	
Suspense	79 9 10	
		2,323 13 11
		£38,222 15 3

ASSETS.	£ s. d.	£ s. d.
Fixed Assets—		
Commonwealth Loans, at cost ..	15,048 10 0	
Debentures:		
Metropolitan Water, Sewerage and Drainage Board, at cost	6,344 7 6	
Science House (one-third share), at cost	14,835 4 4	
		36,228 1 10
Current Assets—		
Cash in hand	10 0 0	
Commercial Banking Co. of Sydney, Ltd.	1,984 13 5	
		1,994 13 5
		£38,222 15 3

INCOME ACCOUNT. Year ended 28th February, 1961.

	£ s. d.	£ s. d.
To Salary		754 0 0
„ Printing Proceedings	1,625 15 11	
„ Printing Reprints	461 5 6	
„ Blocks	307 15 2	
		2,394 16 7
„ Insurance		11 6 10
„ Postage	104 2 10	
„ Petty Cash	28 9 7	
		132 12 5
„ Audit	16 16 0	
„ Printing and Stationery	148 9 8	
„ Expenses	110 18 7	
„ Cleaning	66 13 6	
„ Bank Expenses	2 15 3	
„ Library	26 1 5	
„ Sir William Macleay Memorial Lecture	36 6 0	
		408 0 5
„ Transfer to Contingencies Reserve		1,500 0 0
„ Balance to 1961-62		1,116 14 0
		£6,317 10 3

	£ s. d.	£ s. d.
By Balance from 1959-60		1,115 17 5
„ Subscriptions		
1960-61	426 6 0	
Arrears	23 2 0	
In Advance	16 16 0	
		466 4 0
„ Entrance Fees		25 4 0
„ Interest		1,102 4 0
„ Science House		1,383 10 2
„ Rent		39 3 4
„ Sales		736 4 0
„ N.S.W. Government Grant		200 0 0
„ Fellowships Account (surplus income at 28th February, 1961, transferred)		682 7 4
„ Bank Expenses		4 13 3
„ Sale of Reprints		558 8 3
„ Postcard Sales		1 12 6
„ Donation		2 2 0
		£6,317 10 3

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, 1961, 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, 1961, as shown by the books. Certificates of the investments have been inspected.

Sydney, 10th March, 1961.

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

A. B. WALKOM,
Hon. Treasurer.
2nd March, 1961.

LINNEAN SOCIETY OF NEW SOUTH WALES.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

Balance Sheet at 28th February, 1961.

LIABILITIES.	£ s. d.	ASSETS.	£ s. d.	£ s. d.
Accumulated Funds—		Fixed Assets—		
Amount bequeathed by Sir William Macleay ..	35,000 0 0	Commonwealth Loans, at cost ..	30,447 15 0	
Surplus Income Capitalized	22,824 16 11	Debentures:		
		Metropolitan Water, Sewerage and Drainage Board, at cost	18,156 14 9	
		Rural Bank of N.S.W., at cost	2,172 15 0	
		Loan on Mortgage	6,035 0 0	
				56,812 4 9
		Current Assets—		
		Commercial Banking Company of Sydney Ltd.		1,012 12 2
	£57,824 16 11			£57,824 16 11

INCOME ACCOUNT. Year ended 28th February, 1961.

	£ s. d.		£ s. d.
To Salary of Linnean Macleay Fellow	233 6 8	By Interest	2,282 7 4
„ Balance, being Surplus Income transferred to General Account	682 7 4		
„ Capital Account	1,366 13 4		
	£2,282 7 4		£2,282 7 4

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, 1961, 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, 1961, 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, 10th March, 1961.

A. B. Walkom,
Hon. Treasurer.

2nd March, 1961.

LINNEAN SOCIETY OF NEW SOUTH WALES.

BACTERIOLOGY ACCOUNT.

Balance Sheet at 28th February, 1961.

LIABILITIES.	£ s. d.	£ s. d.	ASSETS.	£ s. d.	£ s. d.
Accumulated Funds—			Fixed Assets—		
Amount bequeathed by Sir William Macleay	12,000 0 0		Commonwealth Loans, at cost	15,318 2 6	
Accumulated Income Capitalized	6,310 0 0		Debentures:		
Research Fund	10 0 0		Metropolitan Water, Sewerage and Drainage Board, at cost	800 0 0	
		18,320 0 0	Loan on Mortgage	2,200 0 0	
Current Liability—					18,318 2 6
Income Account at 28th February, 1961		279 17 6	Current Assets—		
			Commercial Banking Company of Sydney Ltd.		281 15 0
		£18,599 17 6			£18,599 17 6

INCOME ACCOUNT. Year ended 28th February, 1961.

	£ s. d.		£ s. d.
To University of Sydney (towards salary of Lecturer)	895 0 0	By Balance from 1959-60	196 8 0
„ Balance to 1961-62	279 17 6	„ Interest	978 9 6
	£1,174 17 6		£1,174 17 6

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, 1961, 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, 1961, 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, 10th March, 1961.

A. B. Walkom,
Hon. Treasurer.

2nd March, 1961.

PRESIDENTIAL ADDRESS.

PATTERN IN THE MERISTEMS OF VASCULAR PLANTS.

II. A Review of Shoot Apical Meristems of Gymnosperms, with Comments on Apical Biology and Taxonomy, and a Statement of Some Fundamental Concepts.

By I. V. Newman, Department of Botany, University of Sydney.[1]

(Plates i-ii; ten Text-figures.)

[Delivered 29th March, 1961.]

Synopsis.

The fragmentary nature of the records of the topography of the general apical region of shoots of vascular plants in regard to season, age, plastochrone and life cycle precludes the declaration of apical types on these bases. Nor has relative size been adequately considered. The small numbers, varied habit, and wide coverage in literature make the gymnosperms a suitable field for review. On the basis of illustrations of apices from works covering the whole group, reproduced at a common magnification in taxonomic and ontogenetic sequence, together with apices of some angiosperms, comments are made and fundamental concepts advanced.

Comments. 1. *Size and Form*: The larger the general apex, the less convex it is. 2. *Size and Cellular Pattern*: The larger the apex, the more complicated the cellular pattern and the less definite the internal boundaries. 3. *Vacuolation and Size of Cells*: Vacuolation generally increases away from the tip and the surface: size is a resultant of enlargement rate and division frequency in any region. 4. *Vacuolation and Dormancy*: High vacuolation accompanies both dormancy and termination of growth, but with potentialities still available in the former. 5. *Vacuolation and Pattern*: Vacuolation seen is the resultant of rate of vacuolation and frequency of cell division; the "central mother cell" zone may be a physiological incident, not a formal feature. 6. *Augmentation and Type of Apex*: Increase of primary structure by cambial type of augmentation (longitudinal or transverse) provides surface for appearance of numerous primordia, and is not a type feature. 7. *Extent and Size of Apex*: There is yet no satisfactory demarcation of the apex for precise expression of size. Limits should form a curve with focal point near the superficial centre. Primordia are incidents in the total apical activity, and are not valid marks of apical limits. 8. *Pattern and Direction of Partition Walls*: Direction is better related to morphogenetic curves (parallel with or perpendicular to them) and not to the surface, returning to Sachs' periclines and anticlines. Such pattern fluctuates with physiological changes.

Fundamental Concepts: These are to meet the situation that apical cells are not directly recognizable in the shoots of seed plants.

1. *Three Basic Types of Apex*: Confine attention to the centre of initiation, for the general meristem is under a variety of subsequent physiological influences. The *Duplex Apex* has two superposed initiating regions, only "anticlinal" partitioning in the outer, both "anticlinal" and other-directional partitioning in the inner, commonly giving the tunica-corpus topography (angiosperms). Side walls of initial cells are perpendicular to the surface. The *Simplex Apex* has one initiating region as the inner region of the Duplex Apex (gymnosperms). The *Monoplex Apex* has one initiating region—the apical cell(s) of classical form with side walls meeting at a point or line and with partitioning parallel with the inclined side walls. These concepts propose a fount of cellular structure originating the general meristem. One initial division in the Monoplex Apex initiates increase in both length and breadth, but this requires two initial divisions in the Simplex Apex and the inner region of the Duplex Apex, while initial division in the outer region of the Duplex Apex initiates increase only in breadth (surface).

2. *The Continuing Meristematic Residue*: A logical necessity, this is the initial cell(s), dividing differentially to form continuing meristematic residue (next generation of initials) and tissue mother-cell(s) (sister cells of the former). It is the initiating region of the basic

[1] Formerly of the Botany Department, University of Ceylon, and the Division of Forest Products, C.S.I.R.O., Melbourne.

types of apex—monoplex in the massive-tissued cryptogamic plants, simplex in the gymnosperms and some "fern allies", duplex in the angiosperms. A concept of precision involving differential division, it leaves freedom to interpret, independently of taxonomy, the general apical meristem on a physiological basis under the gradient of cell senescence. It is the "apical cell" (or cells) validly termed on function, not to be restricted to a particular appearance. Evidence is given suggesting presence of apical cells not generally recognizable (gymnosperms and angiosperms); methods of search are proposed. Argument and evidence are given against the "initial ring" (*anneau initial*) as initiator of structure. The search for apical cells in seed plants is not pointless.

3. *Cellular Pattern, the Structural Expression of the Compounding of Differential Rates and Orientations of Physiological Processes*: Three levels of phenomena lie in causative sequence: visible pattern (cellular) resulting from process patterns (rates and orientations) expressing presence patterns (concentrations and intensities) of chemical and physical entities. Entities are supplied under two levels of phenomena: gradient patterns (translocation) and location pattern (founts of origin). Referred to the apical summit, the patterns may be regarded as fixed in space (over short periods, at least). Cellular structure passing back through them appears and behaves in visible pattern appropriately to the part of the combined physiological pattern it may occupy at the time. But, with the same reference point, patterns may change in time, as in the onset of dormancy and in relational changes in tunica and corpus (which are of topographical, not formal, significance).

4. *Physiology and Phylogeny Meet*: Structure and activity of the basic types of apex appear related to the evolutionary origin of the major taxa of vascular plants. If apical cells are universally present through logical necessity, the phylogenetical problem concerns their changes in kind, number of kinds, and manner of partitioning. These are, genetically, mutations, and are of such far-reaching effects and associations that, morphologically, they suggest terms currently rejected by geneticists—macromutation and macroevolution.

Conclusion: The *Continuing Meristematic Residue* (apical cells in the apex) is a reality, whether directly discernible or not. There are only three fundamental types of apex in the shoots of vascular plants—*Monoplex, Simplex* and *Duplex* types of apex. Cellular structure changes as it "passes back" from the fount of initiation through the "frame" of physiological pattern fixed in regard to that fount.

Introduction.

The study of cellular structure and activity in apical meristems of vegetative shoots of vascular plants has become prominent during the last thirty years. The taxonomic coverage is now so wide that authors have attributed taxonomic significance to types of apex. After looking for comparisons and relationships in the many records, it seemed to me that too little recognition has been given to mere size, to age of plant, and to seasonal cycle. Apices of some different sorts of plants are so greatly different in size that the "mechanics" of the one must be very different from the "mechanics" of the other. In many cases, the records, particularly in the gymnosperms, are unspecified or fragmentary—to a degree that makes comparison dubious.

A little recollection of one's own casual observation of growing plants and the results of their apical activity will make it obvious that any one apex has not constant activity, but undergoes a greater or lesser range of seasonal variation which may be both quantitative and qualitative—rate of production and kind of appendage. The few thorough histological studies that cover the seasonal cycle extend the statement to the outward form and internal structure of the apex. Between apices at different parts of the one plant, differences may occur in size, in rate and kind of productive activity, and in outward form. These differences we might expect to be reflected in internal structure. This approach to the apex as a "going concern" may be called "the biology of the apex". Cautionary references to biological factors have been made by M. A. Johnson (1951, p. 189), though he does not pursue this aspect fully into a critique of the records, in his valuable, detailed review of work on Gymnosperms. A similar requirement of caution is implied by Popham (1951, pp. 263–4) in discussing his proposed types of apex. Philipson (1949, p. 37) points out the need for study of seasonal changes in apical structure; and Reeve (1948), throughout his paper on the tunica-corpus concept in dicotyledons, brings out the importance of variations of apical structure during ontogenetic development. Korody (1938) had carefully followed the seasonal cycle of cellular pattern in the very tip of the growing point of some conifer

stems. Indeed, as long ago as 1890, Duliot emphasized the biological aspect, insisting that it was only useful to work with actively growing apices collected during the warm season; for, in the stationary buds of winter, the cells are quiescent, with walls equally thickened, so that cell lineages are not traceable for studying histogeny in apical meristems by relative thickness of cell walls. Recently, de Silva has thoroughly studied seasonal variation of zonation in the vegetative apex of *Cycas circinalis* (1954*a*) and the histological difference between the vegetative and male reproductive phases of the apex of *Cycas rumphii* (1954*b*).

The outstanding disclosure of recent work on apical meristems of vascular shoots has been that a variety of cellular patterns exists. The "taxonomy of the apex" would be the attribution of particular patterns or particular modifications of fundamental patterns to particular taxonomic groups. But, until very recently, many of the records have been so fragmentary or even of material of unidentifiable origin in regard to seasonal cycle, plastochrone, and chronological age of the individuals examined, that there has been no safe basis for taxonomic designation of types of cellular pattern.

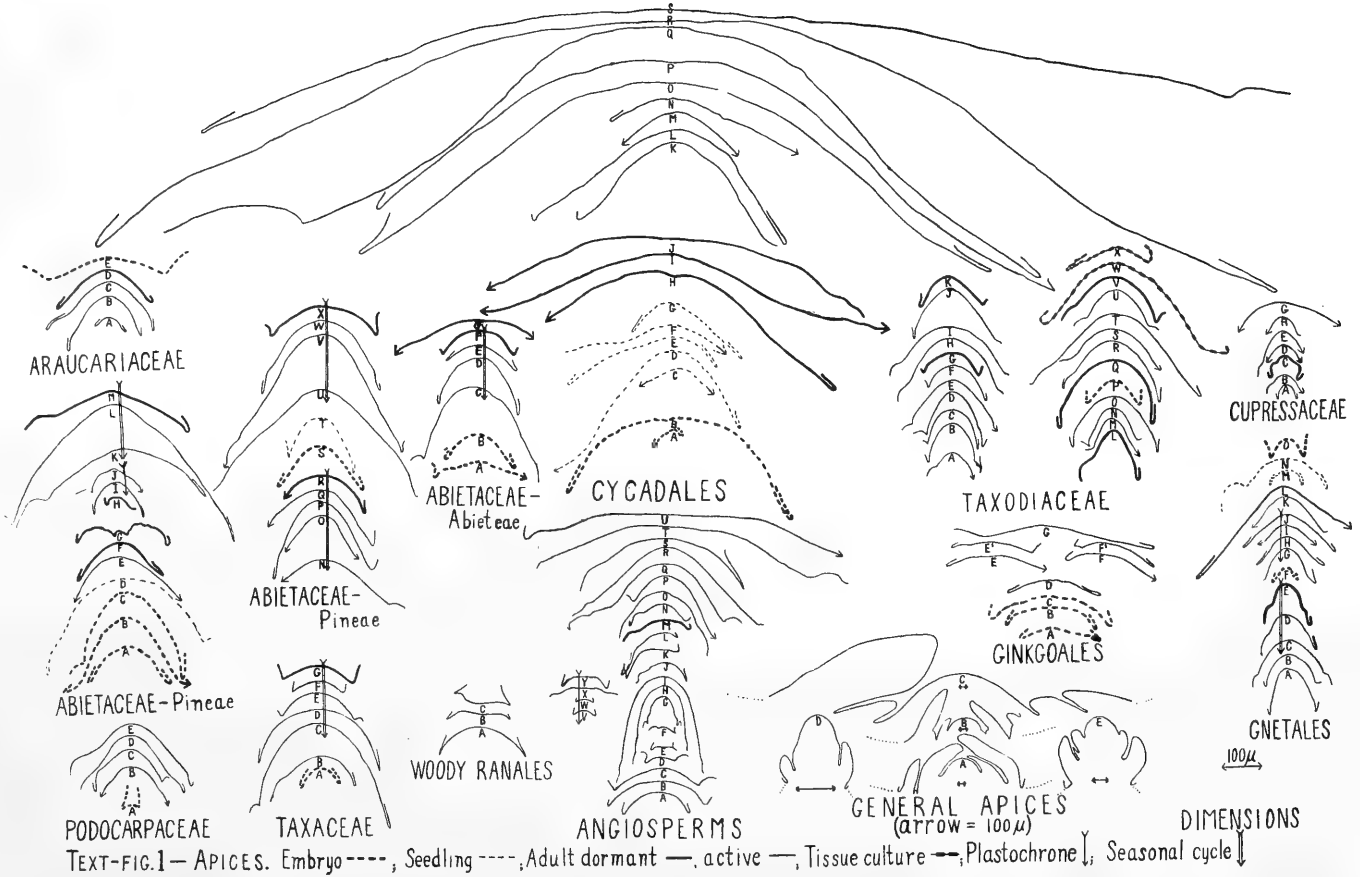
This paper is primarily a summary and critique of records, having in mind the biologic situations suggested above and some of the physiological implications of the revealed patterns. Descriptive attention is concentrated on the gymnosperms, for, taxonomically, these have been widely covered in apical research (at least one record from each of the nine taxa, classically recognized as families (Chamberlain, 1935)).[2] In size and outward form of the apex, type of appendage, habit of the whole plant, and type of seasonal cycle, they present differences ranging from one extreme to the other in the several features. All this being within a relatively small taxonomic and numerical extent, the group is a suitable ground for cross-checking the effect of size on pattern and form, and of these three, together with age and the seasonal cycle, on taxonomy.

The method of work was as follows: from all available illustrations showing cellular structure of Gymnosperm apices (up to 1952), suitable figures (preferably photomicrographs) were selected and photographed so as to be at a common magnification. Any effect of mere size on pattern or form could then be more readily discerned. The resulting photographs were arranged in columns according to the families (as in Chamberlain, 1935),[2] to reveal possible taxonomic features, and within each column in an ontogenetic sequence—mature embryo, seedling, dormant adult, active adult—or in stages of plastochrone to reveal any effect of stage in life-cycle or seasonal cycle or growth cycle. The simple seasonal cycle is the fluctuation between more and less activity in producing the one kind of lateral, with the commonly occurring extreme expression as the alternation between active and dormant phases. In the complicated seasonal cycles with more than two phases and more than one type of lateral produced, their active phases present a range of different kinds of activity and histological patterns. Such cycles complicate the presentation and its interpretation. A selection of Angiosperm apices was included for comparison.

The full range of illustrations was presented in an unpublished paper to Section M, Botany, at the Sydney Meeting of the Australian and New Zealand Association for the Advancement of Science in August, 1952, under the title "The Biology and Taxonomy of Cellular Pattern in Vascular Shoot Apices". The paper now appearing brings the matter up to date with inclusion of more recent work.

To reproduce the whole of the above arrangement, with cellular detail or even pattern clearly visible, is not practicable; but the relative sizes and forms of apical contour are shown in Text-figure 1 of outlines from the photographs at uniform magnification. Each extends so far as to include the youngest primordium (or its axil)

[2] That is, the living families Cycadaceae (now the order Cycadales composed of three families as proposed by L. A. S. Johnson, 1959), Ginkgoaceae (or order Ginkgoales), Gnetaceae (preferably the order Gnetales) and the families of Coniferales (pp. 226-9) based on Eichler's account in Engler and Prantl's "Die Natürlichen Pflanzenfamilien", 1889. Apart from the name Abietaceae instead of Pinaceae, the species mentioned fit the families as arranged and named in Pilger's account in the 1926 edition of that work.



Text-fig. 1.—Contours of apices from photographic reproductions of published illustrations (× 50 approx.). For explanation see text and Table 1. Wherever the illustration outlined ends laterally without indicating a primordium, the outline ends with an arrowhead.

TABLE 1.

Data for the Apices shown in Text-figure 1.

(Together with data for additional apices exhibited at the A.N.Z.A.A.S. Congress in 1952 and others entered for record purposes.)

The information is set out in columns as follows:

1. The distinguishing sign of the apex: Capital letters refer to the apices in the figure. † means that the illustration was shown at the 1952 A.N.Z.A.A.S. Congress but is not in the figure. * means an illustration published since 1952 relevant to the purpose of the figure.
2. Taxonomy. The family (or order) and the specific name of the plant. The Coniferales are respectively headed by family names (see footnote 2).
3. Biology. E=embryo. S=seedling. A=adult, active. D=adult, dormant. Concise data on age, plastochrone, and seasonal cycle are added in some cases. To economize space, the time sequence was run down the figure, where cycles were available; for ease of location, the lettering was run up the figure from the family name. Plastochrones and seasonal cycles are indicated by single- and double-shafted arrows, respectively, beside the letters in figure and table.
4. Author.
5. Date.
6. Number of illustration in original publication (plate number in roman figures, figure number in arabic figures) and whether photomicrograph (P) or line-drawing (L). Where magnification of the original was not given or was doubtful, the symbol "?×" appears.

Except for the General Apices and where indicated in column 6, all apices referred to in the table (except those distinguished by an asterisk alone in column 1) were photographically reproduced from the originals at a common magnification of ×250, the outlines traced and arranged and the whole reduced to about ×50 in Fig. 1. In the case of the General Apices, as overall shape was the chief feature, they were geometrically reproduced at the smallest magnification suitable for each one.

Note that the species listed below are not necessarily the only species referred to in the articles cited.

1	2	3	4	5	6
	CYCADALES				
A	*Zamia integrifolia*	E	M. A. Johnson	1939	7, L
B	*Macrozamia moorei*	E	,,	1944	8, P
C	*Encephalartos frederiiciguilielmi*	S	,,	,,	3, L
D	*Macrozamia spiralis* (probably now to be called *M. communis*)[3]	S	,,	,,	7, P
E	*Zamia floridana*	S	Foster	1939	13, L
F	*Microcycas calocoma*	S 1-year	,,	1943	12, P
G	*Cycas revoluta*	S	Foster	1939	I, 2, P
H	*Encephalartos lehmanii*	D lateral bud	M. A. Johnson	1944	4, P
I	,, *villosus*	D?	,,	,,	5 P
J	*Microcycas calocoma*	D	Foster	1943	11, P
K	*Cycas revoluta*	A	,,	1939	I, 6, P
L	*Macrozamia spiralis*[3]	A	M. A. Johnson	1944	9, P
M	*Zamia umbrosa*	A	,,	1939	6, L
N	*Bowenia serrulata*	A	,,	1944	6, P
O	*Microcycas calocoma*	A	Foster	1943	7, P
P	*Dioon edule*	A	,,	1941*b*	3, P
Q	*Cycas revoluta*	A young, unexpanded	,,	1940	6, P
R	,, ,,	A large plant, crown of megasporophylls unexpanded	,,	,,	10a, P
S	,, ,,	A bud, unexpanded	,,	,,	12, P

[3] M. A. Johnson states that his material had been collected and identified by the late Professor A. A. Lawson, the seedlings as *M. spiralis* and the adult as *M. corallipes*. On the basis of a reference in *Index Kewensis* to a proposed synonymy, he used for the adult plant the specific epithet *spiralis* (p. 31), which is now known to have priority for it. The distinct species that has been commonly known as *spiralis* is now to be called *communis* (the seedlings of M. A. Johnson's material). For the nomenclatural problem see L. A. S. Johnson, 1959, pp. 98 and 104.

TABLE 1.—*Continued.*

Data for the Apices shown in Text-figure 1.—Continued.

1	2	3	4	5	6
	GINKGOALES				
A	*Gingko biloba*	E "bud in axil of cotyledon"	Sprecher	1907	49, L
B	,, ,,	E	,,	,,	7, L, ×?
C	,, ,,	E	Lyon	1904	XXXIII, 10, P
D	,, ,,	A terminal, short shoot	Gunckel & Wetmore	1946	5, P
E	,, ,,	A long shoot, 22nd April	Foster	1938	XXVII, 2, P, ×60
E′	,, ,,	A long shoot, 18th April	,,	,,	XXVII, 1, P, ×60
F	,, ,,	A spur shoot, 29th April	,,	,,	XXV, 2, P, ×60
F′	,, ,,	A spur shoot, 15th April	,,	,,	XXV, 1, P, ×60
G	,, ,,	A spur shoot	,,	,,	5, L
	ARAUCARIACEAE				
A	*Dammara* (=*Agathis*) *australis*	A	Duliot	1890	XIII, 8, L
B	*Araucaria cunninghamii*	A	Griffith	1952	7, P
C	,, *excelsa*	A	,,	,,	6, P
D	,, ,,	D	,,	,,	10, P
E	,, *brasiliana*	E	Strasburger	1879	XXI, 78b, L
	ABIETACEAE—Pineae				
A	*Larix decidua*	E	Schopf	1943	IV, 71, P
*	,, ,,	D-A long shoot, seasonal cycle as for M→K or X→U, below	Frampton	1960	8, L
B	*Pinus strobus*	E	Spurr	1949	22, P
C	,, ,,	E	Skrobishevski	1873	VI, 14, L, ×?
D	,, *taeda*	S	Davis	1949	2, P
E	,, *murrayana*	A	Lewis & Dowding	1924	12, L, ×?
F	*Pinus montana*	D	Korody	1938	22, L
G	,, *cemboides* var *monophylla*	D spur shoot	Doak	1935	25 I,L
*H	,, *lambertiana*	D dwarf shoot, end needle formation	Sacher	1955	9, L
∧ *I	,, ,,	A dwarf shoot, mid plastochrone, cataphyll formation	,,	,,	3, L
∧ *J	,, ,,	A dwarf shoot, end (=begin.) plastochrone, cataphyll formation	,,	,,	5, L
∧ *K	,, ,,	A near end new bud formation (Oct.)	,,	1954	7, P
*L	,, ,,	A new bud formation (May-September)	,,	,,	6, P
∧ *M	,, ,,	D winter bud (the three foregoing match apices O→R and U→X, above)	,,	,,	5, P
∧ N	*Picea engelmannii*	A (D?) end leaf formation, September	Lewis & Dowding	1924	5, L, ×?
O	,, *excelsa*	A	Duliot	1890	2, L
P	,, ,,	A elongating before leaf primordia begin.	Korody	1938	21, L
Q	,, *canadensis*	A beginning bud formation	Lewis & Dowding	1924	2, L, ×?
∧ R	,, *excelsa*	D	Korody	1938	19, L
S	*Pseudotsuga taxifolia*	E	Allen	1947	9, L
T	,, ,,	S 1 month	,,	,,	11, L
∧ U	,, ,,	A late leaf formation	Sterling	1946	18, P
V	,, ,,	A apex lengthens	,,	,,	15, P
W	,, ,,	A cataphylls begin	,,	,,	13, P
∧ X	,, ,,	D	,,	,,	17, P
†	,, *douglasii*	D(?) end leaf formation late September	Lewis & Dowding	1924	6, L, ×?

TABLE 1.—*Continued.*

Data for the Apices shown in Text-figure 1.—Continued.

1	2	3	4	5	6
	ABIETACEAE—Abieteae				
A	*Cedrus libanotica*	E	Buchhold & Old	1933	4A, L
B	*Abies balsamea* (?)	E	Hutchinson	1924	XX, 23, L, ×?
C	,, *venusta*	A vigorously expanding	Foster	1939*a*	I, 7, P
D	,, *concolor*	A 2nd growth begins	Korody	1938	8, L
E	,, ,,	A 1st growth cataphylls	,,	,,	7, L
F	,, ,,	D	,,	,,	6, L
G	,, *pectinata*	D(?)	Groom	1885	XVI, 1, L, ×?
†	,, *lasiocarpa*	D(?) Sept. (*cf.* N, in AB.-Pin., above)	Lewis & Dowding	1924	9, L, ×?
	TAXODIACEAE				
A	*Cryptomeria elegans*	A	Duliot	1890	XIII, 10, L
B	,, *japonica*	A	Cross	1941	23, P
C	,, ,,	A	,,	,,	5, L
D	*Taiwania cryptomerioides*	A small lat.	,,	1943*a*	3, P
E	,, ,,	A vigorous	,,	,,	6, P
F	*Athrotaxus selaginoides*	A	,,	,,	1, P
G	*Taxodium distichum*	D deciduous	,,	1939	13, L
H	,, ,,	A expanding deciduous	,,	,,	IX, 1, P
I	,, ,,	A expanding, permanent	,,	,,	IX, 3, P
†	,, ,,	A	Groom	1885	XVI, 4, L
J	*Cunninghamia lanceolata*	A	Cross	1942	10b, P
K	,, ,,	D	,,	,,	3, L
L	*Sequoiadendron*	D lateral	,,	1943*b*	7, P
M	,,	A weak lateral	,,	,,	11, L
N	,,	A stronger lateral	,,	,,	12, L
O	,,	A vigorous leading	,,	,,	13, L
P	*Metasequoia glyptostroboides*	E	Sterling	1949*b*	19, P
Q	,, ,,	D	,,	,,	16, P
R	*Sequoia sempervirens*	A leafy lateral	Crafts	1943	6, P
S	*Sequoia sempervirens*	A branch of leader	Cross	1943*b*	4, P
T	,, ,,	A leader	Crafts	1943	2, P
U	,, ,,	A leader end of dorm.	Cross	1943*b*	3, P
V	,, ,,	D leader	Sterling	1945	10, P
W	,, ,,	On tissue culture	Ball	1950	19, P
X	,, ,,	,, ,,	,,	,,	17, P
	CUPRESSACEAE				
A	*Libocedrus decurrens*	A	Duliot	1890	XIII, 13, L
B	*Frenelia* (=*Callitris*) *australis*	A	,,	,,	XIII, 17, L
C	*Cupressus horizontalis*	D	,,	,,	XIII, 15, L
D	,, ,,	A	,,	,,	XIII, 11, L
E	*Chamaecyparis pisifera*	A	M. A. Johnson	1951	8, L
F	*Juniperus phoenicea*	A	Duliot	1890	XIII, 16, L
G	,, *communis*	A	Groom	1885	XVI, 6a, L, ×?
	PODOCARPACEAE				
A	*Phyllocladus alpinus*	E	Holloway	1937	XXXIII, 50, L
B	*Podocarpus longifolia*	A	M. A. Johnson	1951	5, L
C	*Podocarpus totara*	A	Jackman	1960	8, P
D	*Phyllocladus trichomanoides*	A from strong well-developed branch	,,	,,	7, P
E	*Dacrydium biforme*	A (has no dormant phase)	,,	,,	1, L
	TAXACEAE				
A	*Taxus cuspidata*	E	Sterling	1949*a*	12, L
B	,, *baccata*	A	Louis	1935	VIII, 66, P
C	*Torreya californica*	A beginning leaf formation	Kemp	1943	16, P
D	,, ,,	A end cataphyll formation	,,	,,	15, P
E	,, ,,	A beginning cataphyll mation	,,	,,	13, P
F	,, ,,	A? shoot expanding. [is not apex still D?]	,,	,,	12, P
G	,, ,,	D	,,	,,	11, P

TABLE 1.—*Continued.*

Data for the Apices shown in Text-figure 1.—Continued.

1	2	3	4	5	6
	GNETALES				
A	*Ephedra altissima*	A small lateral	Gifford	1943	10, P
B	,, ,,	A permanent shoot, maximum growth	,,	,,	8, P
∧ C	,, ,,	A permanent shoot, maximum growth	,,	,,	3, L
D	,, ,,	A permanent shoot, early growth	,,	,,	6, P
∧ E	,, ,,	D permanent shoot	,,	,,	9, P
F	*Gnetum gnemon*	E	Bower	1882	XXV, 13, L
∧ G	,, ,,	A minor axis, maximum area (?)	M. A. Johnson	1950	9, L
H	,, ,,	A minor axis, medium area (?)	,,	,,	12, P
I	,, ,,	A minor axis, minimum area	,,	,,	10, L
∧ J	,, ,,	A major axis, maximum area	,,	,,	1, L
K	,, ,,	A major axis, near maximum area	,,	,,	8, L
L	,, ,,	D	Bower	1882	XXV, 14, L
M	*Welwitschia mirabilis*	S 2 months, short axis	Rodin	1953	15, P
N	,, ,,	S 1 week, long axis	,,	,,	14, P
O	,, ,,	E	Strasburger	1879	XXII, 91, L
	ANGIOSPERMS				
A	*Coleus blumei*	A	Popham *et al.*	1948	1, P
B	*Myrica californica*	A	Reeve	,,	1, P
C	*Chrysanthemum* hybrid	A	Popham *et al.*	,,	2, P
D	*Lonicera caprifolium*	A	Flot	1906	II, 2, P
E	*Syringa vulgaris*	A	Priestley	1929	III, P
†	*Garrya elliptica*	A & E	Reeve	1948	16 & 19, P
F	*Arabidopsis thaliana*	A	Vaughan	1952	L
G	*Phragmites communis*	A	Duliot	1891	III, 1, L
H	*Elodea densa*	A	Stant	1952	VIIIA, P
I	*Hippuris vulgaris*	A	Louis	1935	IX, 77, P
J	,, ,,	A	Duliot	1890	XVIII, 6, L
†	,, ,,	A " quite young "	de Bary	1884	1, L
K	*Salix laevigata*	A	Reeve	1948	11, P
L	*Salix laevigata*	A	Reeve	1948	12, P
M	*Liriodendron tulipifera*	D	Millington & Gunckel	1950	8, P
N	*Castanopis californica*	A	Reeve	1948	5, P
O	*Convallaria majalis*	A	Stant	1952	2, L
P	*Acacia longifolia*	A	Boke	1940	II, 1, P
†	,, ,,	Flower	Newman	1936	II, 1–4, P
Q	*Washingtonia filifera*	A	Ball	1941	4, P
R	*Phoenix canariensis*	A 10 years	,,	,,	1, P
†	,, ,,	E	,,	,,	10, P
†	*Trachycarpus excelsa*	A	,,	,,	5, P
S	*Opuntia cylindrica*	A	Boke	1941	2, P
T	*Echinocereus reichenbachii*	A	,,	1951	7, P
U	*Trichocereus spachianus*	A	,,	1941	1, P
↑ V	*Vinca rosea*	A minor axis near maximum area	Cross & Johnson	1941	17, P
W	,, ,,	A minor axis, minimum area	,, ,,	,,	15, P
X	,, ,,	A old major becomes minor at leaf initiation	,, ,,	,,	20, P
∧ Y	,, ,,	A major axis, maximum area	,, ,,	,,	19, P
	WOODY RANALES				
A	*Trochodendron aralioides*	A	Gifford	1950	24, P
B	*Pseudowintera axillaris* var. *colorata*	A	,,	,,	19, P
C	*Drimys lanceolata*	A	,,	,,	16, P
	GENERAL APICES				
A	*Washingtonia filifera*	A	Ball	1941	8, P
B	*Opuntia cylindrica*	A	Boke	1941	4, P
C	*Microcycas calocoma*	A	Foster	1943	7, P
D	*Gallium cruciata*	A	Flot	1906	25, L
E	*Torreya californica*	A near end leaf formation	Kemp	1943	9, L

shown in the original. Where possible, the uppermost primordium on the opposite side of the apex is shown. Each outline is placed with the axis of the upper pith vertical, and the youngest primordium to the left (inverted if necessary). The biological features are indicated by different types of line, occasional vertical sequence, and vertical lines, as explained in the Figure and at the top of Table 1. The nature and sources of these outlines and other illustrations not represented are given in Table 1 which provides information to enable the reader to make for himself analyses and comparisons of the data. Plate i, similarly explained by Table 2, gives examples of cellular patterns.

This arrangement immediately reveals a major difficulty in comparing illustrations in the literature. In many cases, the original does not include a primordium; or, it is not clear whether the uppermost primordium in it is the youngest on the apex; in decussate types, it may not even be recorded in which longitudinal plane the section is cut; frequently the records are taxonomically and biologically fragmentary; and, particularly in older records, magnifications may be omitted or be not definite. Despite these deficiencies in the records, some features stand out and may be noticed here. But it should also be remembered that each author comes to his work with his own background of experience and that the manner of origin of the material and the *degree of his acquaintance* with it, are peculiar to the material *he* is describing. I have gained the impression that variation and incompleteness in these matters, rather than real variety of phenomena, lie behind many differences in terms used, descriptions given and interpretations made. Moreover, reviewers seem to me to have leaned too heavily on authors' verbal descriptions and interpretations, and not sufficiently on the phenomena illustrated.

For this reason, in the survey portion of this paper I have considered the texts almost only as necessary for finding the biological and manipulative data and the sources of material relevant to the sections of apices illustrated in the papers. The following comments and the fundamental concepts subsequently proposed are based, therefore, not on authors' verbal descriptions and interpretations of phenomena, but on what are, as nearly as possible under the circumstances, observations of the phenomena themselves.

But, what does one mean by "the apex" of a shoot? How much of the far end of a shoot does the apex occupy? As will be seen, attempts have been made to give it precise limits; yet in usage the authors often overstep those limits. It is rather as with the summit of a mountain: one reaches the summit; one climbs up the summit; the summit is flat, pointed or rounded; the last 50 feet of the summit is almost perpendicular. Just which then is the summit? So with the apex, there are greater and lesser regions implied in different contexts. In Text-figure 1 and in several places later, the term "General Apex" is used to cover the stem region of what might be termed the bud. The unqualified term apex commonly refers to the bare region above the latest primordia, sometimes including one or more primordia. Though precision of terms is desirable, because of the complications present I do not feel prepared to essay a precise definition, and so the term "apex" in this paper has more a qualitative than a quantitative reference. I hope the context will make the usage clear in each instance, and that the total discussion will pave the way for future precision in use of the term.

Some Comments on the Records.

1. size and form.

The larger the general apex, the less convex it is; and it may even be concave peripherally. This is shown in comparing the cycads with the rest of the gymnosperms, and the Cactaceae and Palmaceae (Text-figure 1 angiosperms, S, T, U and Q, R, respectively) with the rest of the angiosperms. Palms, succulents, and some of the cycads, illustrated in Text-figure 1 (especially general apices, A, B and C, respectively), all possess stems with massive "primary" tissues, and show a form of general apex that is a nearly flat or slightly concave expanse with a central more or less conical

TABLE 2.

Data and Explanations for the Apices shown in Plate i.

The data and explanations for the illustrations of apices of vegetative stems shown in Plate i are set out in columns as follows: 1, the distinguishing letter in the figure; 2, the name of the plant and reference to its position in Text-figure 1, if any; 3, chief features to be noticed, with annotations; 4, author, date and number of illustration in original publication; roman figures are plate numbers, arabic figures are figure numbers.

1	2	3	4
A	*Sequoia sempervirens* TAXODIACEAE S	A small apex of a branch of a leader shoot. Shows one, possibly two, discrete periclinal (" tunica "?) layers, with other periclines. The system of anticlines is evident, as is also the " focal group " (central mother cells) about the common focus of the two systems. (Cf. Sachs, 1878, pp. 52–58, and our Text-figure 2.) A leaf primordium is partly included at the right.	Cross 1943*b* 4
B	*Chrysanthemum morifolium* Cf. ANGIOSPERMS C	A relatively large apex for an angiosperm; early part of plastochrone. Same general pattern as for A, but with discrete periclines more numerous. The part of the anticline system immediately undercupping the focal group, where cell division appears more frequent, is designated by the authors as the " zone of cambial-like cells " (arrows) (p. 479) (cf. also A, D, H, I).	Popham and Chan 1950 3
C	*Lonicera caprifolium* ANGIOSPERMS D	Decussate type, probably minor axis. The section was cleared in *eau de Javelle* that the walls be unobscured. Same general pattern as for A, despite the flatness (discrete periclines, 3 or 4), but anticlines not showing clearly. Author describes discrete initiation of layers from " assises initiales ": *ie*, epidermis; *ic*, cortex; *iv*, vascular cylinder; *im*, medulla.	Flot 1906 II, 2
D	*Vinca rosea* ANGIOSPERMS V	Decussate type, minor axis near maximum area. Same general pattern as for A (discrete periclines 2, focal group only 1 (?) cell). Note anticline-pericline angle is not right-angle in upper part. This figure gives even stronger hint of " cambial zone " than does B.	Cross and Johnson 1941 17
E	*Cymodocea aequorea*	Drawing designed to show cell lineages, upon which the author identifies a single apical cell (*i*) originating all the structure within the epidermis which has its own initial (*ep*). He describes this as like an epidermis covering a gymnosperm apex (cf. F, H, I here) which possesses an apical cell (p. 317). *f*, leaf primordium; *s*, latest segment from the apical cell of the sub-epidermal mass.	Duliot 1890 XIV, 6
F	*Pseudotsuga taxifolia* ABIETACEAE— Pineae U	" Mamillary " apex, late leaf-formation. Differs from A in that outermost pericline is probably not discrete at apex (i.e. " no tunica "). Deep zone in anticline system with great activity in cell division (" cambium-like zone " or " eumeristem " of the author, p. 745) that gives longitudinal augmentation of surface on which many primordia appear (only one or two upper ones shown on either side of the figure).	Sterling 1946 18

TABLE 2.—*Continued.*

Data and Explanations for the Apices shown in Plate i.—Continued.

1	2	3	4
G	*Washingtonia filifera* ANGIOSPERMS Q GENERAL APICES A	Type with concave general apex bearing central, conical projection, on base of or beside which primordia arise (cf. K). At first sight similar to A, but with 2 or possibly 3 discrete periclinal layers. Slight appearance of cambial zone undercupping focal group. Cell arrangement above focal group may suggest, slightly, Sachs' " cap-layering " (1879, p. 202, " Kappenschichtung ") with co-axial, outward-fanning anticlines (cf. K and Text-figure 3). The " primary thickening meristem" giving lateral augmentation, appears at bottom left.	Ball 1941 4
H	*Torreya californica* TAXACEAE C	Beginning of leaf formation; youngest primordium on the left. Differs from A in that there is no *discrete* pericline (typical gymnosperm arrangement, i.e. " no tunica present "; focal group at the surface). Anticlines not prominent; suggestion of cambial zone at centre and right.	Kemp 1943 16
I	*Gingko biloba* GINKGOALES F	Spur shoot. Very clear pattern of the type in H. Periclines and anticlines distinct, but towards the sides clearly not intersecting at right angles (cf. B, D). This is one of Foster's classical pictures demonstrating departure of gymnosperms from tunica-corpus arrangement.	Foster 1938 XXV, 2
J	*Echinocereus reichenbachii* ANGIOSPERMS T	Despite its size, this apex shows essentially the same arrangement as in A, with 1 (possibly 2) discrete periclinal layers. The curvature of the periclines and anticlines is very broad, as is also the " focal group ". The author's Figure 6, not suitable for reproducing here, shows an extensive " primary thickening cambium " (giving lateral augmentation), the inner edge of which is shown at the left of this figure. Two leaf primordia are shown—left and right. There is no clear indication of a cambial zone undercupping the focal group.	Boke 1951 7
K	*Dioon edule* CYCADALES P	Despite the size (magnification ¼ that of D and ½ that of the remainder) and internal diffuseness of this apex, the eye can extract the appearance of periclines and anticlines, but with different systems above and below the focal group—even the surface layer is not discrete. The region below shows the usual confocal system, but the region above the focal group reminds one of the type of cell arrangement described by Sachs as coaxial and called by him " cap-layering " (" Kappenschichtung ") (1879, p. 202). See Text-figure 3 here and cf. G. Lateral augmentation by a " primary thickening cambium " is shown at the right of the figure.	Foster 1941*b* 3

TABLE 2.—*Continued.*

Data and Explanations for the Apices shown in Plate i.—Continued.

1	2	3	4
L	*Aspidium filix mas* FERN	Adult dormant apex, above any leaf primordia (one ramentum appears on the left). The active apex has a much flatter form and the sides of the apical cell may be curved to meet at a point, and not straight as here.	Hofmeister 1857 VI, 8
M	*Pinus lambertiana* ABIETACEAE—Pineae I	Dwarf shoot in mid-plastochrone during cataphyll formation. For size, it should be compared with long shoot outlines of the same species (Text-figure 1 ABIETACEAE—Pineae K–M). It is introduced to illustrate the doubtfulness of forcing on it zonal descriptions appropriate to larger apices, such as the long shoot apices of the same species outlined in Text-figure 1, whose cellular structure resembles that of *Pseudotsuga taxifolia* shown as component F of this Plate ii.	Sacher 1955 3
N	*Podocarpus totara* PODOCARPACEAE C	Main (shoot or branch) apex in active growth. Included for comparison of indefiniteness of pattern with tendency to uniformity of tissues in a small apex.	Jackman 1960 8

projection. The tissues and primordia, for some way towards the periphery of this expanse, are in a state of immaturity such as is found for only a relatively short distance down the flanks of the markedly convex form of general apex (see Comment 6). In most of the cycads, the illustrations copied did not extend far towards the periphery of the general apex. It should be recognized that the cycads as a whole are not satisfactorily recorded, as it is often not clear whether the apex figured is of seedling, active adult or dormant adult, and, if active, what is the stage of activity. de Silva (1954*a*) has now made a comprehensive seasonal study in *Cycas circinalis*. In decussate apices the plane of the vertical section should always be considered with care, as it will make a marked difference to the form presented (see in Text-figure 1 GNETALES, G-K, and ANGIOSPERMS, V-Y, the major and minor axes being at right angles to one another in relation to the latest formed primordia). Under this heading may be mentioned also the range of form in one family, exemplified by the outlines of some Podocarpaceae shown in Text-figure 1 PODOCARPACEAE, B, C, D, E, and TAXODIACEAE, A, B, E, F, J, O, T.

2. SIZE AND CELLULAR PATTERN.

The larger the apex, the more complicated is the cellular pattern and the less clearly defined are the boundaries within it. Comparison of the *Ginkgo* apex (Pl. i, fig. I) with cycad apices (Pl. i, fig. K) shows both these features; and comparison of cycads with other gymnosperm families (e.g., Pl. i, figs A, F. H) shows the greater complexity in the larger apices. Many of the gymnosperm apices do not have a clear "tunica-corpus" organization, particularly among the cycads; whereas most angiosperm apices are of the "tunica-corpus" type.[4] But also, as clearly shown by Text-figure 1, angiosperms have small apices compared with cycads. These small angiosperm apices (e.g., Pl. i, figs B-E) are very neat in the simplicity of pattern and sharpness of boundaries. It is noteworthy that in the large apices of the Cactaceae (Pl. i, fig. J) the boundaries are obscure and there is a hint of approach to a simple cycad appearance in the pattern;

[4] This very frequent difference was clearly expressed and illustrated by Duliot in 1890 and 1891 (though he did not use the terms "tunica" and "corpus"), in papers that merit close study by all students of the apical meristem. This will be referred to in later sections of the present paper.

and in the Palmaceae (Pl. i, fig. G) the large apices show complexities suggestive of cycads in the manner of production of their large primary structure (see Comment 6; and cf. the illustration of the apex of *Echinopsis* in Wardlaw's paper (1952*b*, Fig. 1) and the record for *Xanthorrhoea media* by Staff (1961)). At the other end of the scale, smallness of size may lead to weakness of pattern such as recorded for the dwarf-shoot apex of *Pinus lambertiana* in comparison with the long-shoot apex (Sacher, 1955, p. 786). Obviously, there is scarcely room for display of pattern in the dwarf-shoot apices outlined in components H, I, J of the ABIETACEAE-Pineae in Text-figure 1 in comparison with the long-shoot apices outlined in components K, L, M, etc., of the same series. That is, there would not be the room for the enlargement with vacuolation that gives the characteristic appearance of the central mother cell group prominent in the long-shoot apex and the apices of many other plants.

3. VACUOLATION AND SIZE OF CELLS.

Degree of vacuolation, as distinct from size of cells, appears to increase basipetally and centripetally. The size attained by the cells in any one region will be the integrated result of the rates of partition and enlargement of cells at that location. One of the causes of the appearance of pattern in the apex is that this integration does not always produce a size gradient of constant sign or slope with successively greater distance from the central extremity backwards and from the surface inwards. This appears prominently in the cycads. For example, we may consider that if, in a restricted region, rate of partition is relatively low or rate of enlargement relatively high, then the region will have large cells such as are described under the term "central mother cells" (see Pl. i, figs I and K). Unless the two rates are varied correlatively, stresses are liable to be set up between this region and its surroundings due to its excess or deficiency of volume. Are the frequently reported large inter-protoplast distances of this central mother-cell zone a sign of such a deficiency (for I suppose that in a meristem, the size of the cell must be taken as the size of the protoplast, no rigid secondary wall being present)? The lower rate of partition, leading to fewer and larger cells, would require less wall material than is produced by that mass of protoplasm. These "thickened" walls may then be deposition of *surplus* wall material (whatever its chemical nature) in strain cracks, and not be due to the metabolic activity of the region *favouring* carbohydrate accumulation as suggested by Johnson (1951, p. 192). (The generally accepted view that cell-size and vacuolation are at least in part related is, of course, recognized.)

4. VACUOLATION AND DORMANCY.

By comparison with the active apex, the dormant apex tends to show a high degree of vacuolation close to, if not actually in the superficial layer, both terminally and laterally. The subsequent resumption of cell division by these highly vacuolate cells of the dormant apex emphasizes what is implicit in Comment 3: that the meristematic cell is not inherently devoid of vacuoles. Dormancy in these apices is obviously associated with a minimum (even absence) of cell division. Now, suppose even a low rate of vacuolation continues while partition rate falls to or near to zero; as dormancy supervenes, all the cells in the summit region of the apex may become highly vacuolate. This appears to be the case in the dormant apices covered by this review. It is in line with the account of the cessation of growth at the floral apex presented by the author for two species of *Acacia* (Newman, 1936, pp. 65–7, 75) and illustrated by Tepfer (1953, Pl. 76, fig. *b*, and Pl. 79, fig. *a*) for *Ranunculus repens*.

Attainment of the dormant state and the termination of growth may therefore follow the same course in the changing relationship between rates of vacuolation and partition. But the *metabolic* changes involved, as cells attain adulthood, proceed to completion in the termination of growth, whereas they only *remain unexpressed* in the attainment of dormancy. In the terms of Prat (1945, p. 614 onwards, or 1951, p. 699 onwards) cell senescence is complete, with latent potentiality now zero in the (formerly) initial region of the flower that has ceased growth; whereas cell senescence is only partial, with latent potentiality still significant, in that region of the vegetative apex

that has become dormant. Admittedly, rejuvenescence may occur in the summit region of the floral apex after fertilization occurs; but morphologically, should this not be regarded as a new sequence? The concept that flower is primary and fruit a secondary elaboration requires further study in view of Stopp's (1952, p. 906) strongly argued contention, supported by gross morphological observations, that flower and fruit are two phases of *one* continuous development. A number of apices not specified as dormant have been described with a vacuolate initial region, in both angiosperms and gymnosperms. Partanen and Gifford (1958) mention this for an active apex of *Pinus lambertiana*. This condition may be related to slower partition rate in these particular cases.

5. VACUOLATION AND PATTERN.

From Comment 4, it is clear that when one is using vacuolation in description of pattern, care must be taken to make comparison only with that which is biologically comparable. Indeed, Baranetzky in 1900 (pp. 325–7) raised the question of the morphological relevance of an apparent pattern due to what would be included today under the concept of physiological gradient. Referring to the irregular group of cells that terminate the central cylinder (the central mother cells of many current descriptions), he pointed out that location at the common focal region of two curved systems of apparent cell layers leads to their irregularity (see Text-fig. 2, here), and that this with the earliness of their enlargement gives an *appearance, only*, of zonal differentiation. And such a differentiation, as (morphologically) characterized by Hanstein (1868), Baranetzky regarded as more an appearance than a reality.[5] This point could lead into a discussion of the semantics of description in our work on apices. Much as it is needed, I would not care to enter on it here. But a warning should be raised against anything but a most cautious use of vacuolation in attributing taxonomic or typologic significance to a cellular pattern. Thus the difference in pattern recorded by Sacher (1955, p. 786) between apices of long and dwarf shoots of *Pinus lambertiana* (see Comment 2, above), which is expressed as absence of clear differentiation of a "central mother cell" zone (due to absence of marked enhancement of cell size and vacuolation), is not a difference in apical type. It merely expresses a difference due to the different mechanical situation (cf. Plate i, figure F, of *Pseudotsuga taxifolia* which is very close in size and organization to *Pinus lambertiana* long-shoot with Plate i, figure M, of *Pinus lambertiana* dwarf-shoot).

6. AUGMENTATION AND TYPE OF APEX.

One may express the prime function of the apical meristem as the provision of a stage upon which the appendages may enter and play their part, and as a *milieu* in which differentiation for adult function of the stem may take place. In some plants there appears a phenomenon of augmentation of that stage and *milieu* before or during that entry and differentiation. This augmentation may be transverse or longitudinal. I suggest that in discriminating fundamental types of apex, and even taxonomic types, it be neglected.

Transverse augmentation provides meristematically for a primary structure large in cross-section. This is shown clearly in the case of the palms where augmentation is brought about by what Ball (1941*b*) calls a "primary thickening meristem", extensively shown in his figure 8 of *Washingtonia filifera* and in detail of its inner margin at the left of his figure 4 of that species (reproduced here as Plate i, figure G). A similar feature is observable over a wide taxonomic range of seed plants, exemplified as follows.

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[5] (p. 326): "Le groupe situé à l'extrémité du plérome de Hanstein n'est que le foyer des deux systèmes de courbes suivant lesquelles sont disposées les cellules du méristème primitif. Les cellules de la partie central de la tige, qui, comme je l'ai dit, commencent a s'élargir de meilleure heure que les autres peuvent prendre avec cela une forme moins regulière (Voy. Hanstein, *loc. cit.*, fig. 1, 3), ce qui contribue encore à leur distinction plus nette des assises qui les recouvrent (périblème). Tout cela mène à la conviction, que la visibilité des couches de Hanstein est un phénomène plus apparent que réel, et qui n'est pas l'expression d'une loi géometrique." In his reference to two systems of curves, this author follows Sachs (1878) (see below—end of next to last paragraph of Comment 8), who referred to this irregular group of cells as the "focal group" (p. 83).

Cycad apices illustrated are represented by that of *Dioon edule* (Pl. i, fig. K). It is suggested by descriptions and illustrations of Cactaceae (e.g., the margins of Plate i, figure J of *Echinocereus reichenbachii*, but not so clearly in some of Boke's earlier figures—1941). Among Monocotyledons it is shown, not only for Palmaceae but also for others with apices relatively very broad for their length, by Helm (1936, especially Figs 1 of *Crinum moorei* and *Galanthus nivalis*, 8 and 9 of *Livistona chinensis*, and 11 of *Iris* sp.) and by Staff (1961) in *Xanthorrhoea media*). Despite the wide taxonomic separation of these plants, the same effect is gained by essentially the same method. It would appear that the primary structure to be achieved is so large that an extra-large apical meristem with some normal sequence is not competent to produce the needed volume of tissue before completion of the normal primary differentiation would have stopped the increase. Contrast the general apices in Text-figure 1.

Longitudinal augmentation is clearly displayed in *Pseudotsuga taxifolia* (Text-figure 1 ABIETACEAE—Pineae, cf. V with W) in the production of dormant buds provided with a *large* number of primordia that will be merely expanded at the beginning of the next season's growth. The biological requirement here is the rapid production of length of apical axis on which more and more primordia may appear, without the first formed members of the set, or the axis in their neighbourhood, attaining the adult condition that would be expected at that distance in plastochrones in a normal type of apex. The method used for this is the activity of what Sterling (1946, p. 745) describes as a "cambium-like 'receptacular meristem'" which broadens and lengthens the apex. (Broadening is inevitable by the curved contour of the meristem.) This zone, set back a little from the summit of the apex, undercups the region where central mother cells may be described, occupies the whole width of the axis, and its partitions are formed more frequently lying tangentially to curves that are concave towards the summit of the apex (see Pl. i, fig. F). Sterling, giving this zone the unfortunate term "eu-meristem", refers to similar, but less obvious, appearances in palms and some other monocotyledons (Ball, 1941, and Helm, 1936) and suggests it is an amplification of similar appearances in *Ginkgo* (Foster, 1938) and *Sequoia* (Sterling, 1945, and Cross, 1943*b*—see Pl. i, fig. A here). The occurrence in both angiosperms and gymnosperms of an upwardly concave, *axis-wide* zone with more or less prominence of new partitions being formed tangentially to the curve of the zone is becoming more frequently recorded under the term "cambial-like zone" (cf. Pl. i). Popham and Chan (1950, p. 479) have described it as waxing and waning during the plastochrone in the apex of *Chrysanthemum morifolium* (see Pl. i, fig. B, here). They regard it as rare in angiosperms and associated only with large apices (p. 482). But Vaughan (1952) illustrated such a zone in the minute apex of *Arabidopsis thaliana* (compare F and C, in Text-fig. 1, ANGIOSPERMS). Full plastochronal studies may reveal the zone more frequently, if not universally, in angiosperms, but with various intensities. From Popham and Chan's account, one might suggest that the cambial zone extends the apex longitudinally to receive the origin of the next primordium, and then diminishes to zero. (This brings echoes of the "*anneau initial*" of Plantefol—1947. See later in "*A search for Apical Cells.* Finding the Evidence".) Whether the cambial zone, so prominent in *Pseudotsuga*, is a distinct feature or merely a greatly increased development of a regular, but usually relatively obscure feature, is not clear, for that is the only clear example of such augmenting activity that I have been able to locate fully described. It is suggested in Sacher's figure (1954, Fig. 6) of *Pinus lambertiana* "new bud", but is not the prominent feature shown in *Pseudotsuga taxifolia* (Pl. i, fig. F); however, it might be more prominent in later activity of the "new bud" of *Pinus lambertiana*. Its augmenting activity in producing this type of dormant bud irrupts into the usual sequential system of maturing primordia, to provide for the production of many appendage primordia without the maturation of the earlier primordia which would be proper to the type to which the apex otherwise belongs.[6]

[6] It may be that the appearance referred to for *Ginkgo, Sequoia, Arabidopsis* may be just a clearer manifestation than usual of a universal feature, namely, Sachs' anticline system referred to in Comment 8. Possibly then the spectacular appearance in *Pseudotsuga taxifolia* is really a maintenance, over a longer interval, of the physiological conditions governing the anticline system.

It would be instructive to study apices in closely related taxa, differing in the presence and absence of the phenomenon of augmentation, to see if the type of organization were otherwise the same. Even more appropriate for study would be species with presence and absence of augmentation at different periods of the life cycle (not of season or plastochrone), as they may be susceptible of experimental study. The resting bud of *Pinus* contains very many primordia held at early stages, but such buds may not appear till at least the second year. Seedlings of *Pinus* devoid of resting buds are under observation in another connection, and may incidentally provide information on this question.

7. EXTENT AND SIZE OF THE APEX.

Scientists appear committed to the doctrine that description is the nearer perfection (and the knowledge greater), the more fully it is expressed in quantity and number. Thus, we find in the literature attempts to express the size of the apex quantitatively. Obviously, this is of no comparative value unless the apices concerned are biologically comparable. Unfortunately this is the case far less than might be supposed from the freedom with which comparisons are made in the literature. Still more obviously, no comparisons are valid unless there is agreement about what it is that shall be measured. There seems to have been some agreement (cf. M. A. Johnson, 1951, p. 189) that the apex for purposes of measurement is composed of that tissue which is above the transverse plane passing through the upper edge of insertion of the latest primordium. There is no space in this preparatory paper to discuss this foundational problem at length, but I would offer the following concise comments:

(*a*) The (growing) apex is a co-ordinated, patterned system of cells functioning as a whole for the production of the primary structure of the axis and the institution of appendages.

(*b*) With progress of time, the pattern remains relatively constant in form, but the cellular material involved in the space occupied by that pattern changes continually, much as the form of a wave in the sea is constant, but the water involved in it changes continually. This concept may also be applied to the component processes that go to establish the pattern, such as the rates of partition, vacuolation and enlargement.

(*c*) The appearance of a new element in the pattern (a primordium) at one restricted, peripheral region cannot be held as disrupting the integrity of such a co-ordinated patterned system, which may be regarded as moving onward continuously (like a sea wave) rather than by jumps. This is clearly implicit in the descriptions and discussions of authors; for, whatever they may do about measuring the apex, they invariably imply, if they do not recognize, that co-ordinated system and its activity, without reference to the level of the latest primordium below which it inevitably extends.

(*d*) In the case of an apex of the extreme form of that of *Elodea*, *Hippuris*, etc. (cf. Text-fig. 1 ANGIOSPERMS, H, I. J), the apparently current designation of the apex for measurement can do little violence to the concept of the integrated system. But the method's weakness is exposed by its *reductio ad absurdum* in some decussate plants where, immediately after inception of a pair of opposite primordia, the apex, by that definition, consists of the outer part only of the superficial layer, not one of whose cells is wholly included in the measured apex (cf. Text-fig. 1 ANGIOSPERMS, X, and Pl. i, fig. D). How extremely absurd is this measurement for the case of a concave apex where the value will be unreal? The complete irrelevance of such a measurement is beautifully shown by the figures given by Gifford (1950; see here Text-fig. 1 WOODY RANALES) for *Drimys*, *Pseudowintera* and *Trochodendron* with concave, flat, and markedly convex apices, respectively.[7]

[7] In connection with quantitative correlation between size of organ and size of parent shoot, in which size of apex was considered significant, Reed (1927, p. 88) refers to the difficulty in measuring the apex. Sinnott (1921, pp. 395-399), in studying that correlation, regarded the cross-sectional area of the pith of the internode on the parent stem, below the attachment of the organ, as a suitable measure of the size of apex at the time of origin of the organ. This is, in effect, the size of the cross-sectional area within the procambial ring at the conclusion of the enlargement phase of primary growth. As a basis of comparison it neglects the contour form of the apex, but will always give a real value.

(*e*) If it is possible or desirable to set definite, measurable limits to apices, they should be in the form of curves with focal points near the superficial centres of the apices. Only by some such concept could we avoid completely unreal situations in dealing with apices having nearly flat or concave surfaces, as in the cases mentioned above, in some Cycads (e.g., Foster's illustration of *Cycas revoluta*, 1940, Figs 8 and 3, in comparison with others), *Ginkgo* (Text-fig. 1 GINKGOALES, E), *Vinca* (Text-fig. 1 ANGIOSPERMS, V-Y, and Pl. i, fig. D), etc. In these, indeed, the alignment of walls, from "anticlinal" at the lateral surface to "periclinal" (in relation to the central surface) in the central region, strongly suggests such curves.[8]

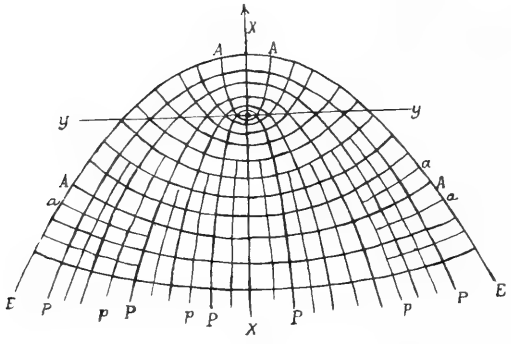
(*f*) In Comment 2 it was suggested that size may affect the incidence or definiteness of pattern. Restriction of attention to the rigidly defined apex, i.e., above the last formed primordium, eliminates, not only what may be really a functional part of the apex, but also "resources" which may significantly affect the apex as a functional unit. So that one should always have, at least in the background of thought, a unit corresponding to what was earlier in this paper entitled "the general apex". In this connection, and thinking of pattern, compare the possible "central mother cell" situations in Plate i, figures C, I, M and N, where C, alone, approaches the representation of a general apex.

8. PATTERN AND THE DIRECTION OF PARTITION WALLS.

Comment 7(*e*) raises the matter of designating the direction of partition walls. They are commonly described as anticlinal, periclinal or random. The terms anticlinal and periclinal are commonly taken to suggest a relation to the surface. This may be confusing to our thought if we invariably, though perhaps unconsciously, assume that relation to be in any way causal. Only close to the surface of large apices or in the whole of very small apices would it be possible to imagine that the existence of the surface of the apex has a directive effect, whether by mechanical restriction of cell shape between cuticle and expanding inner tissues, or by metabolic gradients, as of tension of oxygen or carbon dioxide. But within the apex it would appear more likely that partition will derive its polarity from other gradients of various physiological entities. The weight of evidence now suggests the distal centre of the apex, or axially near to it, as the source or focus of such entities and their gradients. Equal concentrations or intensities, we would expect to lie on concave upward curves described about such a focus, gradient lines being normal to such curves. The apices of *Vinca*, *Ginkgo* and others (Pl. i, figs D, I, etc.) show strong suggestions of such curves. Walls lying along the curves close to the top and near the lateral surface are commonly described as anticlinal, and those near the mid-line have been described as periclinal, having in mind the surface at the tip of the apex. But the walls in both of these locations obviously lie identically with relation to some curve or other described about a focus near the distal centre of the apex. Majumdar's (1942) photomicrograph (Pl. I, Fig. 3) and interpretative drawing of it (Text-fig. 6*a*) clearly show such relationships of cells to "morphogenetic curves".

The appearance of curves (those under reference and another set lying concave downwards), emphasized by Baranetzky (1900—see Comment 5, above), was clearly presented by Sachs in 1878 (pp. 52–8 and Pl. III and IV), with a discussion of essentially the same problem of designation of wall direction (p. 54). Sachs, in proposing (p. 58) the terms "*periclinal wall direction*" and "*anticlinal wall direction*", placed the periclinal directions as being curved in a like sense to the surface ("in gleichem Sinne wie die Oberfläche des Organes gekrümmt sind"), and the anticlinal directions as being such

[8] Whaley (1939, p. 445), for purposes of comparing volumes, defines the "apical meristem" as "that region at the stem tip in which the cells are meristematic, non-vacuolate and essentially isodiametric . . ." These terms are practically incapable of being assigned accurate limits, but will make possible reasonably approximate comparisons of that which is comparable, regardless of the form of the apex. But the definition does not do justice to the apex in its total activity, for, suppose "meristematic" here means "dividing", there are regions of undoubted "meristematic" character where the cells are prominently vacuolated, in particular, the commonly reported "central mother cell" group.



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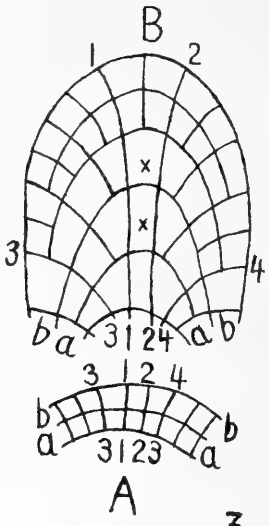


3

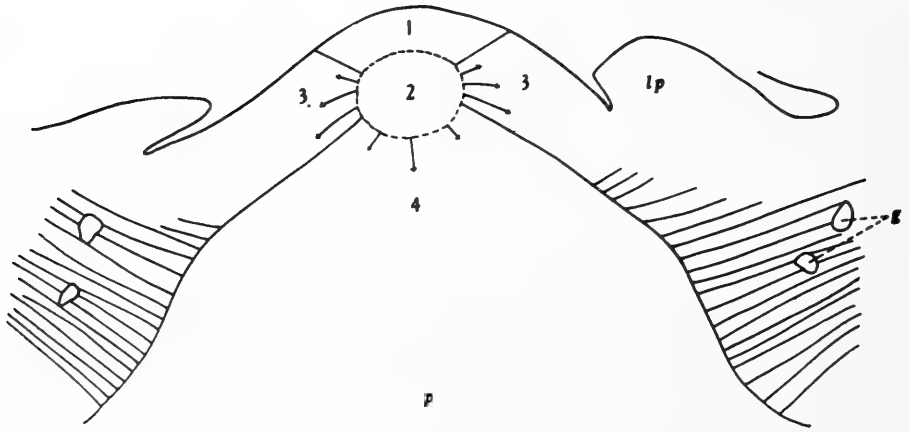


Fig. 2. Diagram, based on figure 3, representing the zonal structure of the shoot apex in *Dioon edule*, and its relation to the differentiation of foliar organs and stem tissues. The summit of the apex is occupied by Zone 1 which represents the ultimate point of origin of all other tissues. Directly beneath this zone, and derived from it, is found the prominent obovoid *zone* of *central mother cells* (Zone 2), from the base of which, by a renewal in the rate of cell division, is derived the active zone of *rib meristem* (Zone 4). This zone basally matures into the massive pith (P) of the shoot axis. The flanks of the apex represent the zone of *peripheral tissue* (Zone 3). The outer portion of this zone originates directly from cells of Zone 1 while the inner region, like the rib meristem, is derived from the zone of central mother cells. Foliar primordia (L. P.), as well as the cortex, are produced by Zone 3. The curved, parallel lines beneath the leaf primordia represent the position of the cambium-like zone of tissue, derived from Zone 3 and responsible for the outward and upward elevation of the crowded foliar organs of the bud. The transverse "leaf-trace girdles" (G) originate in this tissue.

4

Text-figs 2-4.—Reproductions of authors' explanatory diagrams.

Text-fig. 2. Photographic reproduction of Sachs' figure showing confocal periclines and anticlines (1878, Pl. III, fig. 1), his "normal layering" (1879, p. 202) in its simplest form. The reader must exclude from the mind any idea that the lines actually represent cell walls themselves, or that the focus is the necessary or only place of origin of cell production.

Text-fig. 3. Tracing of Sachs' figure showing co-axial periclines with anticlines, his "cap-layering" (1879, Pl. V, fig. 4 and p. 202). The same caution applies as for Text-figure 2; and it should be clearly recognized that the figure does *not* represent structure continually emanating forward from the line *a-a* as stationary base-line, whereby figure A expands as figure B; but structure emanating backward from *b-b* as advancing base-line. Since, the further along the line *b-b* to either side of the centre, the less is the tangential increment of its length, the fan-like nature of the pattern does not indicate forward *movement from* a stationary, constant source, but backward *relationship of* an advancing, widening source.

Text-fig. 4. Photographic reproduction of Foster's (1941*b*) figure 2 with its legend, explaining his figure 3 which is reproduced here as Plate i, figure K. This legend should be compared with the explanation offered below from a different point of view (3rd and 4th paragraphs of section "Pattern in Space" in the discussion of the 3rd of the "Fundamental Concepts").

that their curvature is contrary to that of the surface and of the periclines, cutting them at right angles with a system of orthogonal trajectories ("deren Krümmungen derjenigen der Oberfläche des Organs, sowie auch den periclinen Richtung entgegengesetzt sind, indem sie diese . . . rechtwinkelig schneiden, also ein system . . . orthogonaler Trajectorien für jene darstellen"). These quotations and Sachs' figures, together with the evidence of some of the illustrations in Plate i, here, emphasize that "periclinal" and "anticlinal" walls strictly are not always respectively parallel with and perpendicular to the *surface*. Moreover the morphogenetic curves do not necessarily show the geometrical simplicity (with orthogonal intersections) of Sachs' theoretical "constructions", e.g., his Fig. 1 on Pl. 3, a fact which he recognized clearly himself (p. 82). (See here, also, Plate i, figures B, D, I, and Text-figure 7A″, where the pericline-anticline intersections near the surface are far from orthogonal.)

To complete the background to this question of pattern and direction of cell walls, reference should be made to Sachs' (1879, p. 202) proposal for two types of cell arrangement in growth, remembering that in this paper and a previous one (1878) he repeatedly insisted (e.g., p. 46) that overall growth is primary, cell division and arrangement are secondary. (Contrast the recent expression by Esau (1953, p. 75): ". . . synthesis of new living substance is a fundamental *part of* the process of the formation of new cells by division" [my italics]; such a precedence being rejected by Sachs, 1878, p. 75.) The first type, with "common layering" ("gewohnliche Schichtung"), is where periclines and anticlines are confocal and are concave downwards and upwards, respectively, in regard to the axis of growth (see Text-figure 2, here, and compare the components of Plate i, except perhaps figures G and K). The second type, with "cap-layering" ("Kappenschichtung"), is where periclines and anticlines are coaxial and are concave inwards and outwards, respectively, in regard to the growth axis (Text-figure 3, here, and compare figures G and K[9] of Plate i). The type with *common layering* characterizes the ordinary growing stem apex, that with *cap layering* characterizes the root cap, early stages of primordia, and other situations where a local excess of growth is occurring (Sachs, 1879, pp. 202, 204).

Without following these lines of thought to the end, it seems desirable to suggest that, to avoid the philosophical risk of using the terms periclinal and anticlinal as fixedly related in direction to the surface, we should seek to replace them, where suitable, with terms expressing normal and tangential relationship to curves described about an appropriate focus (but on occasion in relation to an axis). This would return essentially to the concepts of "periclinal" and "anticlinal" put forward by Sachs. But in relation to apices with "normal layering", it would be with the following change at least. Whereas he set forth first the periclinal system and then on the basis of that the (often less prominent) anticlinal system of wall directions, we would probably prefer to establish first the system that is concave upwards (Sachs' anticlines), based on the histological gradients radiating from the focus, and then the system that is concave downwards (Sachs' periclines), derived from the first, and possibly also partly from the presence of the surface.

Some Fundamental Concepts.

If the foregoing comments are well founded, the work on apices to date is largely haphazard exploration of some easily accessible or outstanding features. The time is ripe for systematized surveying. From the Comments, it is clear that there will be many fascinating physiological aspects in that survey. On the basis of the many illustrations available to me, and on the general line of the foregoing argument, I would suggest three fundamental concepts that (with others that may be established) should be the foundation of future inquiry into apical organization.

The one point on which there has tended to be general agreement in this field is that: In *all* the ferns (Filicales of Scott, 1909, p. 616, and Bower, 1923; Filicineae of Eames, 1936, p. 401; Filicopsida of Newman, 1947 and 1949), the horse-tails

[9] See below, third paragraph of the section "Pattern in Space", in the discussion of the third "Fundamental Concept".

(Sphenopsida of Scott, 1909, pp. 616–7), the Psilopsida (of Eames, 1936, pp. 114, 330, 405) and *many* of the club-mosses (Lycopsida of Eames, 1936, pp. 401–3), the apices that have been examined possess one (mostly) or up to about four *clearly observable* "apical cells" of a characteristic shape which is more or less *pointed in the basipetal direction*; whereas in seed plants or Phanerogamic Tracheophyta (Spermatophyta of Scott, 1909, p. 616, Rendle, 1930, p. 32, and Eames, 1936, p. 401; or Spermatopsida of Newman, 1947 and 1949), after some early claims for it, *no* clearly observable apical cell came to be recognized.[10] Seeing that there must be some fount of origin, some source of supply of cells for the tissue structure, it has generally been stated that there is an ill-defined, undifferentiated region of initiation in apices of seed plants. As investigations have proceeded, particularly in gymnosperms, differentiation and definiteness have become recognized more and more. Even 70 years ago, Duliot (1890, 1891) clearly and explicitly described a single apical cell (not of the accepted typical form) for the adult vegetative shoot of conifers and Gnetales, and a vertical series of initial cells (2–5 in number) for various angiosperms. Flot (1905, 1906, 1907) presented substantially the same story for some angiosperms, though he referred to an initial *layer* ("assise initiale"; see Pl. i, fig. C, and Text-fig. 7A″, here) rather than as Duliot did to an initial *cell* ("cellule initiale"; see Pl. i, fig. E, here). There is still, however, a general denial for these plants of the existence of "apical cells" in the sense used for the cryptogamic Tracheophyta, the Bryophyta and the massive Phaeophyceae.[11] It is therefore to meet the situation in the seed plants that the following fundamental concepts are proposed.

1. THREE BASIC TYPES OF APEX.

Focusing attention on the words and interpretative diagrams of authors, one may see with M. A. Johnson (1951, p. 202) four types of apex in gymnosperms; or with Popham (1951; see Text-fig. 5, here) seven types of apex in vascular plants (Tracheophyta) of which three (I, II, III) are found in "pteridophytes" or Cryptogamic Tracheophyta, three (III, IV, V) in gymnosperms, and two (VI, VII) in angiosperms. Thus, at least five types of apex are to be found in seed plants. But if we recognize the significance of the biological factors referred to in the above comments, and give our attention to the untouched illustrations (chiefly photomicrographs) presented by some of the authors, I believe there can be effected a reduction of the number to three basic types, of which the additional ones listed are modifications. Chiefly on the basis of Comments 2 and 3, M. A. Johnson's Cycadophyte and Ginkgophyte types become essentially similar; and on the basis of Comments 2, 3 and 6, his Coniferophyte type joins them. This leaves the tunica-corpus type as a second main type. Popham's type III (re *Cycas revoluta*) becomes as his type V on the basis of Comments 2 and 3; on the basis of Comment 6, his type IV joins with his type V (and III); his types VI and VII are united as essentially a tunica-corpus organization; and thus for the seed-plants, Popham's five types become two main types. These two fundamental types of apex to which the variety of seed-plant apices can be reduced I have called the *Simplex* and *Duplex* Apices. This differentiation of types is based on a consideration of the (restricted) region of cell initiation as abstracted from the general region of cell division which arises from it. A variously restricted region of cell initiation has been recognized by a number of authors under names such as "apical initial group" (Foster, 1938, p. 536, in *Ginkgo*), "central initial cells" (Majumdar, 1942, p. 60, in *Heracleum*), "central initial zone" (Philipson, 1947, p. 187, in *Succisa praetensis*, and 1949, p. 26, for many dicotyledons), "primordial meristem" (Reeve, 1948, p. 65, for several dicotyledons) and "initial cells" (Stant, 1952, p. 117 and Pl. VIII, A and B, for the tunica of some

[10] To take an early example, cf. Jost (1907, p. 280): "The stem-apex of the Phanerogam is more complicated still. Here we find no predominant apical cell to which all the other cells may be referred; the apex consists, on the other hand, of a group of many cells."

[11] To take a late example: Esau (1953, pp. 92-103) recognizes the necessity for the existence of "apical initials" (distinguished from "apical cells" by their lack of morphological distinction and by being "more or less numerous"), but still leaves them as indefinitely circumscribed groups in one or more layers in vertical series.

monocotyledons). Esau (1953, pp. 92–103) gives a clear exposition of current views and work relating to the nature and variety of this region of cell initiation. I am not aware, however, of the precise proposition of these two of the basic types being made elsewhere. By the incidence of various patterns of rates of the processes involved in partition and growth in the general apical meristem thus arising, apices of *either* basic type may come to present *similar* general patterns of tissue and activity, or apices of the same basic type may come to present *different* general patterns of tissue and activity.[12]

This paper is chiefly concerned with gymnosperms and their implications for vascular plants in general. But the picture should be completed by pointing out that Popham's type I makes a modification of the Simplex Apex as the third basic type which I would call the *Monoplex* Apex which is characteristic of the "Pteridophyta", and provides us with the classical apical cell.

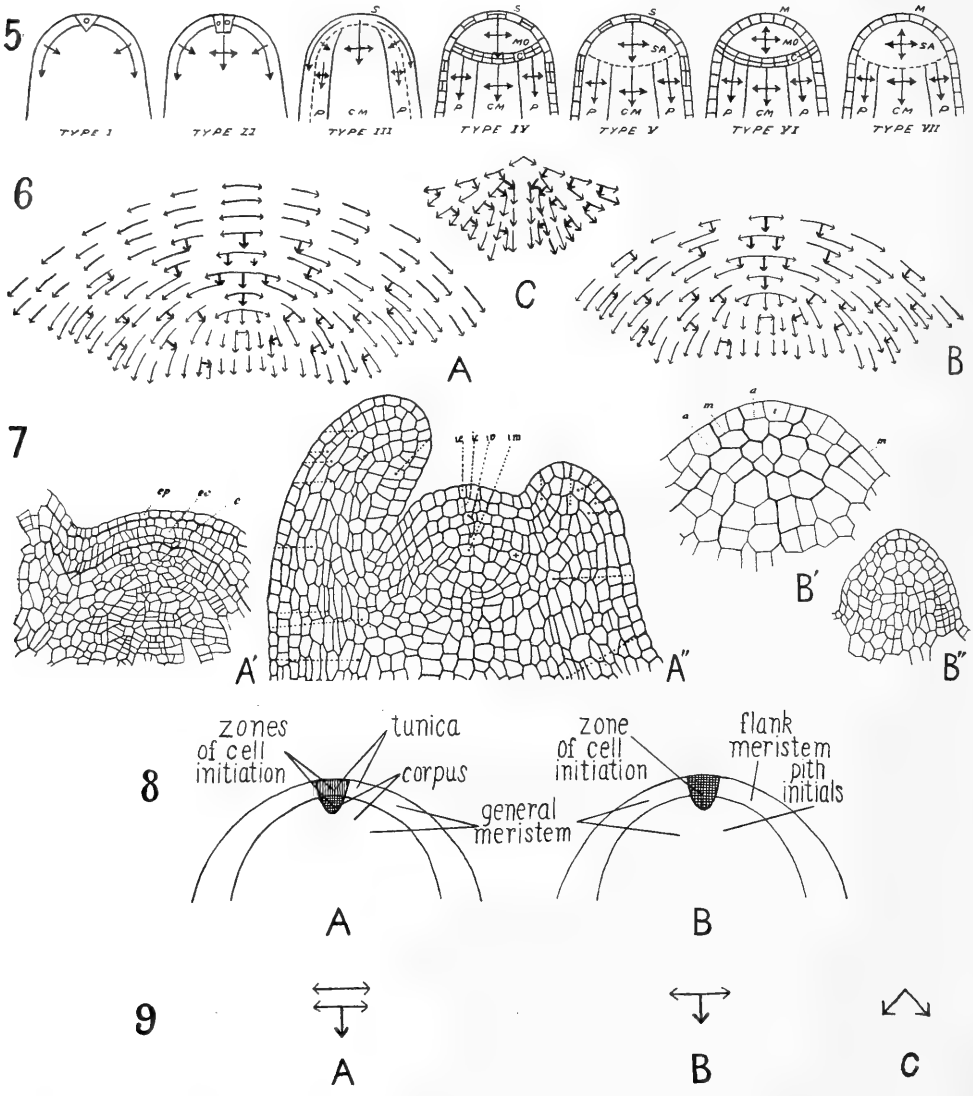
The Duplex Apex.

The Duplex Apex represents the type, classically described for the angiosperms, to which the term *tunica-corpus* is now regularly applied. As generally used to include more than the actual regions of initial cells, this term, *tunica-corpus*, implies the presence of two initiating regions which are genetically distinct (once they have been differentiated early in the ontogeny of the plant or lateral organ of the plant). The tunica-corpus concept was formulated by Schmidt (1924) on the observation that in the apical region there was an outer zone of tissue in which partition walls were strictly "anticlinal" (by this, surface alone being increased), forming a "tunic" covering the "corpus", the whole inner zone, in which partition walls were in various directions not predominantly "anticlinal" (by this, volume being increased). Other workers have described the same phenomenon in a variety of terms and complexities (e.g., Priestley and Swingle, 1929; Schüepp, 1926; Louis, 1935, etc.); but Schmidt's simple terms have gained acceptance. It is also generally recognized that the tunica may consist of one or more layers, the several layers being genetically discrete. I would emphasize that the tunica-corpus concept is usually applied to the general region of cell division (the total meristematic region), whereas the terms I am proposing are referable only to the region of cell initiation.

In the Duplex Apex, *therefore, there are two discrete, but axially contiguous centres of cell initiation. The cells of the outer centre undergo partition only perpendicular to the surface, and may extend one or more layers in depth from the surface. The inner centre of cell initiation, whose cells undergo partition not constantly in any one sense in regard to the surface, is sub-contiguous to the outer centre.* This clear distinction between the partition behaviour of the two initiating centres is usually the basis of the difference in appearance and genetical discreteness of the tunica and the corpus zones of the general apical meristem. The general meristematic region of a duplex apex may be represented schematically as in Text-figure 6A.[13] The arrows represent the general direction of *displacement* (relative to fount of cellular structure) of the cells in the various zones and layers, as cell division goes on during the general meristematic activity of the apex. In tunica-corpus terms, the diagram represents a three-layered tunica covering a relatively massive corpus. This situation was clearly described by Duliot (1890, 1891) for a number of angiosperms. He recognized a vertical series of initiating centres: from the lowest one, cells emanated laterally and basally; from the upper ones, which ranged in number from 1 to as many as 4, cells emanated only

[12] The authors just mentioned have also recognized the existence of a variety of patterns appearing in the derived general apical meristem. These patterns may be taken as corresponding to the concept of morphogenetic fields. The reader will find much stimulation of thought to relate this matter of patterns of rates (as referred to here) and cells (as referred to in Comment 5 (*b*) under a wave simile) to the presentation of the genetical and "field" aspects of morphogenesis given by Professor C. W. Wardlaw in chapters 9-11 and 18-19 of his book "Phylogeny and Morphogenesis" (1952*a*).

[13] The diagram suggests one, only, of a number of possible partition patterns in the cellular structures after they emanate from the initiating centres.



Text-figs 5-9.—Diagrams and examples of pattern in apices of vascular shoots.

Text-fig. 5. Popham's (1951) seven types; reduced copy from his figure 1, with this explanation: "Diagrammatic representations of longisections through shoot apices illustrating the seven principal types of organization found among vascular plants. (S, surface meristem; M, mantle; MO, central mother cells; C, cambium-like zone; SA, sub-apical initials; CM, central meristem; P, peripheral meristem.)"

Text-fig. 6. The three proposed basic types of apex in vascular shoots; diagrams of the general meristematic regions of apices: A, Duplex, B, Simplex, and C, Monoplex. The arrows in these diagrams represent the *direction of displacement* from the superficial centre, or from the surface of the apex, imposed on cells by the enlargement and divisions that formed them or by the division of others nearer those locations. For simplicity, only the effects of divisions with anticlinal and periclinal partition are presented. In A, are three separate outer layers of periclinal displacement produced by only anticlinal partitioning ("tunica") covering a central region with both directions of displacement ("corpus"). In B, the outer separate layers are absent, the whole apex resembling the inner region alone of A. In C, notice the early discrimination into two halves, compared with later (or no?) discrimination in A and B. (The different thickness of arrows has no other significance than as a guide to the eye.)

laterally, the cell layers usually remaining discrete for some distance from the centre (cf. Pl. i, fig. E, with only 1 upper layer, and Text-fig. 7A′ with at least 3 upper layers). The same clear presentation of the phenomena was given by Flot (1906) in part of a paper directed primarily to other matters (see Text-fig. 7A″). The descriptions by Duliot and Flot are fully referable to the concept presented here.[14] Dermen (1945, pp. 387–9) approaches it even more nearly in describing (for Cranberry) separate "primary histogenetic layers", the innermost one showing both periclinal and anticlinal divisions in contrast to anticlinal only in the outer layers. The Duplex Apex is possibly universal in angiosperms, and is present in some gymnosperms (among conifers and Gnetales).

The Simplex Apex.

After the establishment of the tunica-corpus concept in popular favour, reports began to appear of departures from it, chiefly in the form of descriptions of occasional periclinal partitions in the tunica, even in its outermost or single layer (sometimes still entitled the "dermatogen"). But Koch (1891)[15] is commonly recorded as having already described in Pinaceae a meristematic mantle covering a meristematic medulla, both derived from a superficial group of "mother cells". The matter was brought to a head by descriptions of "periclinal" partitions in the surface layer at the very centre of the apex: in *Abies concolor* and *Picea excelsa* by Korody (1938), in *Ginkgo biloba* and *Cycas revoluta* by Foster (1938 and 1939, respectively), and in *Zamia* spp. by M. A. Johnson (1939, p. 194). However, this kind of partitioning was an essential part of Duliot's (1890) presentation of the conifer apex possessing a single superficial apical cell that frequently possessed parallel lateral walls (cf. Text-fig. 7B′), and such a cell had already been specifically figured for *Abies balsamea* by Dingler in 1886 (Pl. I, fig. 10) and tentatively interpreted as dividing by walls parallel with and perpendicular to the surface in his Fig. 10*a* (a figure of the same kind as my Text-figure 10D). Dingler's figures are reproduced here as Plate ii, figures E and E′. Subsequent work by a number of authors has confirmed this revelation that in many gymnosperms, at least at the cell initiation centre, there is no disposition of the cells as a tunica, i.e., the outer centre of cell initiation present in the duplex apex is not represented. Here, there is only one centre of cell initiation; it is like the inner centre of the duplex apex, but is located at the surface.

[14] These two authors deserve careful attention for their descriptions of the phenomena of histogenesis in the apex. Probably, too rigid interpretative attributions of mature tissues to particular layers or even to segmentations in the primordial meristematic region have led to the value of their descriptive work being overlooked.

[15] Cited after M. A. Johnson, 1951, p. 193. Note the precedence of Duliot.

Text-fig. 7. Photographically reproduced figures illustrating the cellular appearance of the two types of apex; × 240, approx., except perhaps B″ (cf. also Plate i). A′, *Poterium sanguisorbe,* of duplex type, showing four discrete outer layers ("tunica"); initial regions marked as *ep* for epidermis, *ec* for cortex, *c* for central cylinder (Duliot, 1890, Pl. 17, fig. 8). A″, *Phytolacca abyssinica,* of duplex type, showing three discrete outer layers ("tunica"); initial regions marked as *ie* for epidermis, *ic* for cortex, *iv* for vascular cylinder (note, this includes one of the outer discrete layers), *im* for medulla (Flot, 1906, Pl. 2, fig. 1). B′ and B″, *Araucaria excelsa* (Duliot, 1890, Pl. 13, figs 6 and 7); B′, active apex of simplex type and, according to Duliot, with a single initial cell (*i*); B″, dormant apex with walls of uniform thickness and *appearing,* as Duliot cautioned, to have two discrete layers covering a central cylinder. (For differential thickness of walls leading to Duliot's identification of initial cells, cf. also Pl. i, fig. E.)

Text-fig. 8. Diagrams correlating the duplex and simplex with the tunica-corpus and common gymnosperm types of apex. A, duplex type with two zones of cell initiation, the differentiation continuing in the general meristem as tunica-corpus. B, simplex type with one zone of cell initiation, the general meristem differentiating into at least two main zones, flank meristem and pith initials, not markedly different from a form of tunica-corpus. The monoplex type may be taken in provisionally under a form like B.

Text-fig. 9. Diagrams of the initiating centres or founts of cellular structure of the duplex (A), simplex (B) and monoplex (C) types of apex, expressed in directions of displacement. These are the minimum terms of expression of Text-figs 6A, B and C.

In the Simplex Apex, *therefore, there is one centre of cell initiation; it is located at the surface of the apex and its cells undergo partition not constantly in any one sense in regard to the surface and it is only one layer in depth.* The general meristematic region of a simplex apex may be represented schematically as in Text-figure 6B, with the same conventions as for the duplex apex. In tunica-corpus parlance, the diagram represents a corpus devoid of a tunica, an interpretation for apices among gymnosperms which was proposed in such terms, first by Buder (1928, p. (20)) and then supported by Korody (1938). But, as long ago as 1890, Duliot explicitly presented such a conception (see Pl. i, fig. E, where the "tunica" is 1-layered, and Text-fig. 7A′, where it is 3- or 4-layered). As one example among many is his description, in *Tradescantia*, of the epidermis and cortical initials as distinct and of the central cylinder having an "initiale . . . qui se comporte comme la cellule terminale unique d'une tige de conifère" (p. 321). In his conclusion (p. 346) he makes this possession of one or more discrete layers lying across the summit of the apex a characteristic of angiosperms, separating them from the gymnosperms which possess no such discrete layers there. We know today that there are exceptions to this general statement.[16] The simplex apex appears characteristic of Cycads and *Ginkgo* and is prevalent among the Conifers.

The Monoplex Apex.

This is the type of the Classical concept of the apical cell—commonly an inverted pyramid, or portion of one, but in any case either with the two side walls meeting in a line or more than two meeting in a point. The initiating centre is commonly one, or in some cases, only a few cells with inclined side walls. In the divisions in these initial cells, the new walls are parallel with the inclined walls, and subsequent divisions in the early production of tissue tend to be parallel with or perpendicular to that inclination, as can be easily observed in many a text-book illustration, or as shown for *Aspidium filix-mas* in Plate i, Figure L from Hofmeister (1857).

In the Monoplex Apex, *therefore, there is one centre of cell initiation; it is located at the surface of the apex and its cells undergo partition only in a direction parallel with the inclined walls (the outer walls if there are two or more cells in the group) and it is only one layer in depth.* The general meristematic region of a monoplex apex may be represented schematically in Text-figure 6C. As with the simplex apex, the general meristem arising from this basic type may show, sooner or later, some functional arrangement resembling tunica and corpus, and appropriate studies might even reveal augmentation phenomena, particularly for increasing the breadth of the general apex. But in many cases comparable interpretation appears not to be possible. An examination of ferns and other Cryptogamic tracheophytes from this point of view would be rewarding.

The Significance of These Types.

Text-figures 6A, B and C are highly abstracted diagrams showing the result, in the first two, of only anticlinal and periclinal partitions, and in the third of partitions only parallel with and perpendicular to the (initial) apical cell partition. In the "corpus" derived from the duplex type and in the general meristem derived from the simplex and monoplex types, often there is much greater variety in the direction of partition. Another point with which these diagrams do not deal is the histological pattern that appears in the general meristem as a result of differences in rates and directions of partition, in rates and directions of cell enlargement, and in rates of vacuolation, as they vary severally from place to place.

Underlying the above analysis is the abstraction of a region of cell initiation (a fount of cellular structure) from the general apical meristem. In the duplex apex

[16] Duliot (1890, pp. 298-9) raises a caution regarding the seasonal condition of the apex; and illustrates, in *Araucaria excelsa*, the active apex with a superficial initial cell (i.e., of simplex type) and a dormant apex with two discrete layers covering a central cylinder (suggesting a 2-layered tunica covering a corpus, i.e., of duplex type). See here, Text-figures 7B′ and B″.

there are two centres comprising this region (or fount), differing in the character of their activity. In the simplex and monoplex apices there is only one centre. In the duplex apex the general meristem derived from that fount maintains the characteristics of this difference in the typical tunica-corpus zonation, as suggested in Text-figure 8A. In the simplex apex, whatever be the histological pattern of the meristem derived from the fount of cellular structure, most authors describe, at the least, an outer zone whose cells more or less resemble in character and arrangement the cells of a tunica and an inner zone whose cells similarly more or less resemble the cells of a corpus. Instead of those terms, it is common to find such terms as "flank meristem" and "pith initials", respectively. This is suggested in Text-figure 8B. Were similar descriptive studies made of the monoplex apex (which might be taken in under Text-figure 8B), it is not at present clear to me whether the functional appearance of a tunica-corpus-like organization could be discerned.

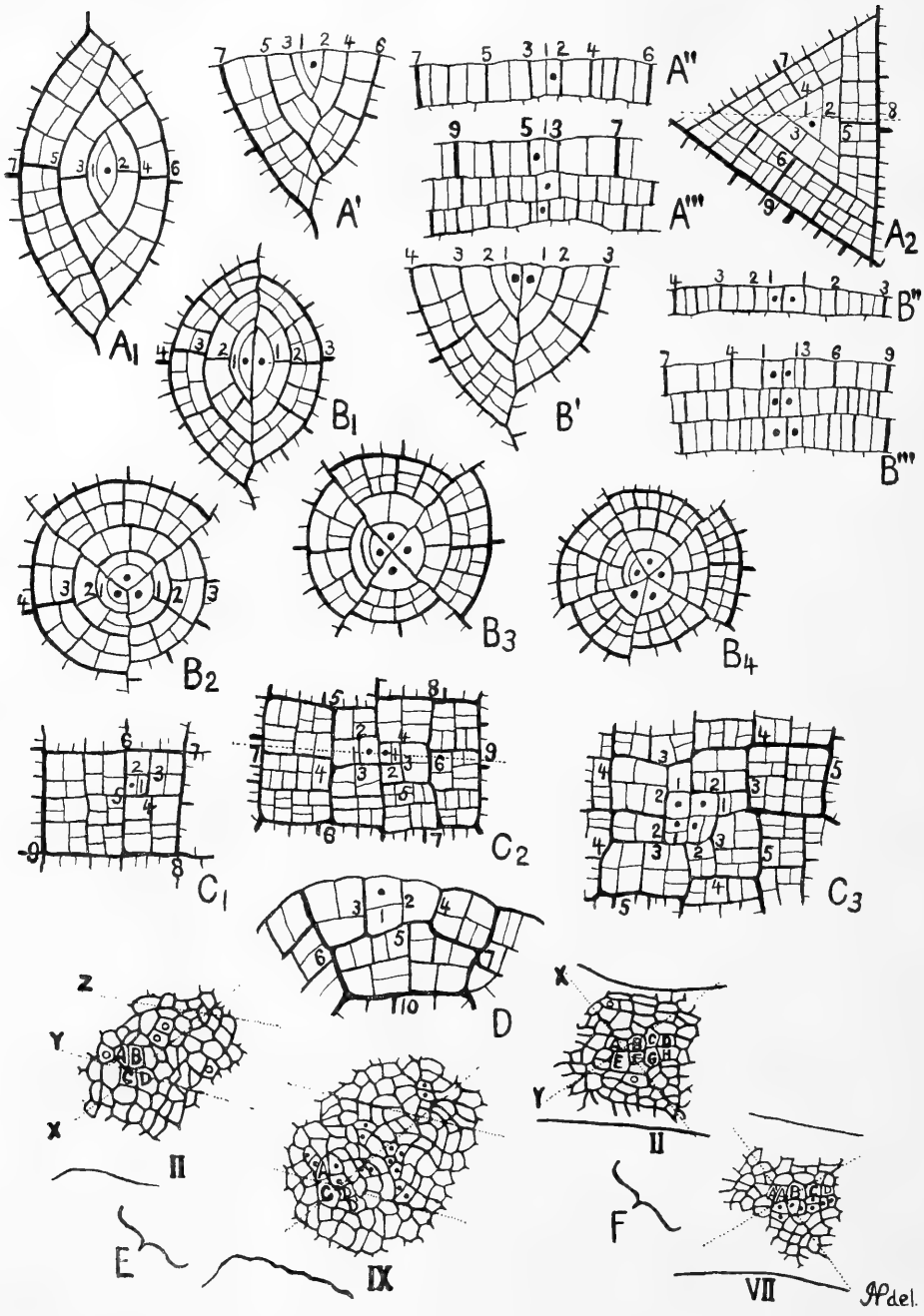
2. THE CONTINUING MERISTEMATIC RESIDUE.[17]

A Logical Necessity.

It has been emphasized that the arrows in Text-figures 6A, B and C represent the direction of displacement of cells from the fount of cellular structure (cell initiation centre). It will be noticed that double-ended arrows parallel to the surface in A and B occur only in a single axial row, and that all arrows perpendicular to the surface are inwardly directed—none outwardly. This is to emphasize the fact, not always clearly presented in the literature, that when cells divide they cannot "give off" derivatives towards the (superficial) centre or the initiation centre of the apex—one of the products is by that division located further from the centre (both by space and number of cells) than was the parent cell at its own formation. Any division occurring in a cell situated between a given cell and the centre of the apex will inevitably displace that given cell away from the centre of the apex. If, as the given cell, we take cells, from either side, successively nearer the centre of the apex, then, logically we reach a limit where there are no cells between the given cell(s) and the centre of the apex. For, either the given cell is itself at that point, or the common wall of two given cells is there, or (approaching from more than two opposed directions) the common angle of more than two given cells is there. The expression, then, of Text-figures 6A, B and C, in minimum terms, or alternatively, the representation of the initiation regions of Text-figures 8A (2 zones) and 8B (1 zone, applicable to 6B and C) would be as in Text-figures 9A, B and C which represent the initiation centres (founts of cellular structure) of the duplex apex, simplex apex and monoplex apex, respectively.

In the limiting case where the given cell is central, we have a single cell whose activity, as classically expressed, is "cutting off cells alternately to either side". This is typically shown in the apical cell of a fern leaf (the appearance closely resembling the central region of the fern stem shown in Plate i, figure L); but the case we are imagining is not necessarily of that characteristic shape. Now, at each division of such a cell, all the progeny of one of the two daughter cells will ultimately (after some meristematic generations) become adult. The other daughter cell will undergo a division of the same kind as its parent, i.e., all the progeny of one of the two resulting grand-daughter cells will ultimately (after some meristematic generations) become adult, the other grand-daughter cell undergoing a division of the same kind as its parent cell and grand-parent cell. Thus, onwards, indefinitely, there will be a *continuing meristematic residue*, not all of whose progeny will ultimately become adult. This means that this cell, holding for its short existence as an individual the "office" of continuing meristematic residue, undergoes a differential division such that one of its daughter cells takes over (or inherits) the "office" and undergoes a similar differential division, while the other daughter cell does not take over (or inherit) the office, undergoes a division not of that differential character, and, if a term is needed,

[17] This was the chief point of the unpublished paper at the ANZAAS Congress in 1952 and was mentioned in Part I of this series (Newman, 1956*a*, p. 17).



Text-fig. 10.—Cellular structure at the apex derived from different numbers and forms of apical cell composing the continuing meristematic residue. Figures A-D (no particular magnifications) are theoretical constructs, with the apical cells marked by black dots. In these figures the cell wall thickness is varied on the principle that at each cell division each daughter protoplast secretes its own new primary wall completely around itself, so that walls representing the present boundary of a former tissue mother cell will be considerably thicker than any walls of the contained derived cells, whose walls will be variously thick. Similarly, the further removed such a boundary wall is from the continuing meristematic residue, the thicker it will be, till cell division ceases in that neighbourhood. For the basic assumption see

may be called "*tissue mother-cell*" (a term in corresponding use in describing cambial activity).

Such is a description in general terms of the activity of a single initiating cell commonly described as dividing to one side and the other alternately, as shown in surface diagram in Text-figure $10A_1$. Whether the sides of the cell are inclined to meet at a point away from the surface of the apex (the monoplex type) or are parallel with one another in vertical section of the apex (tunica portion of the duplex type) will determine whether the resultant cellular structure occurs in depth (Text-fig. 10A′) or in a single layer (Text-fig. 10A″). Respectively, these alternatives are manifested by the growing apex of the typical fern leaf and by the activity in a selected longitudinal plane in a typical "tunica" layer of angiosperms and some gymnosperms (the central region of Plate i, figure L, of a stem resembles the appearance in the fern leaf and for tunica see Plate i, figures A, E). In the second alternative there may be a number of such initiating cells vertically superposed, according to the number of layers in the "tunica" (Text-fig. 10A‴, and cf. Pl. i, figs B-D, G, J, and Text-figs 7A′, A″).

Sanio (1873, p. 57), Giltay (1882, p. 438), Priestley and Scott (1939, p. 538), Wardrop (1952) and Newman (1956*a*, pp. 10-11). Right-angled partitioning was used for simplicity. The initial partitions from each apical cell are numbered separately in increasing age, on the side of them away from the relevant apical cell. Figures E-F (× 160, approx.) are from living apices, taken from Part I of this series.

A_1—Surface view; single bi-convex apical cell dividing to either side alternately. A′—L.S. of A_1 where the apical cell has the side walls meeting at a point (or line) (monoplex apex); numbering of partitions corresponds to A_1. A″—L.S. of a case like A_1, but with the apical cell side walls parallel, division producing width but no increase in length; same numbering of initial partitions as for A_1, but with more subdivisions. A‴—L.S. of a three-layered tunica of a duplex apex; one apical cell in each layer; numbers for outer layer only and as though the section passed just above the level of partition 4 in C_1; absent are the numbers of partitions parallel to the plane of section. A_2—Surface view; single apical cell with three sides dividing to each side in rotation; L.S. through the dotted line would appear like A′, according to shape of the apical cell, but the numbers of the "initial" partitions would be in different order.

B_1—Surface view; two plano-convex apical cells with common plane wall, each dividing with partition parallel to its outer wall. B′—L.S. of B_1 where the apical cells have the side walls meeting the common wall (monoplex apex); numbering of partitions corresponds to B_1. B″—L.S. of a case like B_1, but with the apical cells' side walls parallel, division producing width but no increase in length; same numbering of initial partitions as for B_1, but with more subdivisions. B‴—L.S. of a three-layered tunica of a duplex apex; two apical cells in each layer; numbers are for the outer layer only and as though the section passed through the dotted line in C_2. B_2, B_3 and B_4—Surface views; three, four and five apical cells, respectively, whose side walls all meet at a common angle; numbering of initial partitions for only two of the apical cells in B_2; L.S. through these would appear as described for B′ and B″.

C_1—Surface view; single rectangular apical cell dividing in two directions at right angles, the two directions being necessary to increase the surface in two dimensions (cf. the "one direction" in each apical cell in A_1 and B_{1-4}, a difference analogous to that between monoplex and simplex apices in regard to increase in both length and breadth, i.e., in two dimensions in any median longitudinal plane); L.S. view in a plane just above partition 4 and as for an outer tunica layer is shown by the numbered upper row in A‴. C_2—Surface view; two rectangular apical cells with common wall, each dividing in two directions at right angles; L.S. view in the plane of the dotted line and as for an outer tunica layer is shown by the numbered upper row in B‴. C_3—Surface view; four rectangular apical cells with a common angle, each dividing in two directions at right angles; cf. the *Coleus* apex in F, below (wall ages not shown), and the photograph of a surface section of *Echinocereus reichenbachii* apex shown in Plate ii, figure B, where variety in wall thickness is well shown and original tissue mother cell boundaries appear.

D—L.S. of a simplex apex with one apical cell, where the most recent partition is "periclinal"; numbering is only for partitions perpendicular to the plane of section; partitions 8 and 9 are not included in the figure; cf. *Torreya californica* apex shown in Plate i, figure H, and *Araucaria excelsa* active apex shown in Text-figure 7B′.

E—Surface view of the first and last components (II and IX) in figure 6 of Part I of this series (Newman, 1956*a*), shown here at a higher magnification. For explanation see text: "A search for apical cells. Finding the evidence."

F—Surface view of the first and last components (II and VII) in figure 8 of Part I of this series (Newman, 1956*a*), shown here at a higher magnification; cf. C_3, above. For explanation see text as for E.

The line of argument in the paragraph before last applies also, with appropriate verbal changes, when, in selecting the given cells successively nearer the superficial centre of the apex, we approach from more than two directions around it. In the limiting case, the given cell itself, with more than two sides, is at the superficial centre of the apex, and will, as classically described, "cut off cells successively parallel with its lateral faces". This is typically shown in a three-sided apical cell of a fern stem, as in the surface diagram, Text-figure $10A_2$; but the cases we are imagining are not necessarily confined to that typical shape and number of sides. Whether the lateral walls of this initiating cell are inclined to meet at a point away from the surface of the apex (monoplex type in a typical fern stem as in Plate i, fig. L) or are parallel with one another in vertical section of the apex (tunica part of the duplex type in angiosperms and some gymnosperms), will determine whether the resultant cellular structure occurs in depth (Text-fig. 10A′) or in a single layer (Text-fig. 10A″ for one cell or 10A‴ for superposed cells giving several discrete layers). The Text-figures illustrating vertical sectional views are as in the last paragraph, but now we are observing only a selected plane in a three-dimensional process.

In the foregoing presentation, the limiting cases were single cells. Selecting given cells successively nearer the superficial centre of the apex from two opposed, or more than two, directions, the limiting cases may be two cells with a common wall or a group of more than two with a common angle. The activity of these groups is classically expressed as "cutting off cells from their outer faces". The same verbal forms apply in stating these cases as for the case of the single cell in the second paragraph of this section, except that the daughter cells which undergo the same differential division as the parents are always those next the common wall or common angle. Thus, onwards, indefinitely, there will always be two cells with a common wall or a group of cells with a common angle as a *continuing meristematic residue*, of each of whose component cells, not all the progeny will ultimately become adult. This means that the cells, together holding for their short existence as individuals the "office" of continuing meristematic residue, are in common contact by a wall, where there are two only, or by an angle, where there are more than two. (Of several possible variants, one will be indicated in the later reference to the living *Coleus* apex in the section on "*A Search for Apical Cells*".)

Such is a description, in general terms, of the activity of a group of two or more initiating cells having either a common wall or common angle, commonly described as dividing towards the side away from the common wall or angle, as shown in surface diagrams in Text-figures $10B_1$ and $10B_{2-4}$, respectively.[18] Whether the outer sides of the cells are inclined to meet away from the surface of the apex (monoplex type), or are parallel with the common wall or angle (tunica part of the duplex type), will determine whether the resulting cellular structure is produced in depth, as in the stem of some massive fern allies, e.g., Marattiales, and in the Fucales among the Algae (Text-fig. 10B′), or in a single layer, as in the typical tunica layer of angiosperms and some gymnosperms (Text-fig. 10B″). In the second case, there may be a number of such groups of initiating cells vertically superposed, according to the number of layers in the tunica (Text-fig. 10B‴; and see the reproduction of Duliot's figures as Pl. i, fig. E, and Text-fig. 7A′; cf. also Flot's figures reproduced as Plate i, Figure C, and Text-figure 7A″).

As indicated above, the forms of apex represented superficially by Text-figures $10A_{1,2}$, $10B_{1-4}$ and longitudinally by Text-figures 10A′ and 10B′ are well known in Cryptogamic Tracheophyta. But in the Phanerogamic Tracheophyta, or Seed Plants, since Duliot's (1890, 1891) work, there appears to have been no confidently affirmed record of any recognizable appearance at the stem apex of adult plants that could be represented, particularly in vertical section, by such figures or an approach to them.

[18] This description, more than for the single initial, implies spatially rigid inheritance of "office" between successive continuing meristematic residues, raising the question whether such initial cells are morphological entities or are functional incidents due to chance of location. See the section *"A Search for Apical Cells,* Status and Name".

Vertical sections illustrated for plants described with tunica, however, are consistent with components A″, A‴, B″, B‴ of Text-figure 10, since absence of any characteristically basally pointed shape would make the cells of the continuing meristematic residue not directly identifiable. Text-figures $10C_{1-3}$ showing imaginary constructs for 1-, 2- and 4-celled residues in superficial view, simplified to rectangular partitioning for diagrammatic treatment, in harmony with the principles given above, are not inconsistent with recorded appearances of the surface of "tunica" types of apex. The longitudinal views would be as in Text-figures 10A″, A‴, B″, B‴.

So far, production of structure in depth has only been referred to in connection with the monoplex apex with its basipetally pointed initials that have inclined walls laterally or on the outer side (i.e., away from the common wall or angle of a group). For the types with "parallel" lateral walls, production of structure in depth involves also partitions of the continuing meristematic residue parallel with the apical surface. This is suggested, for a single-celled residue only, with only rectangular partitioning for simplification, in Text-figure 10D, where the latest partition of the continuing meristematic residue is shown as parallel with the surface (cf. Dingler's (1886) tentative scheme in his fig. 10*a*, shown as Plate ii, Figure E′). This applies to the corpus, alone, of duplex types—for example, Johnson's (1950) Fig. 9 of *Gnetum gnemon*, Duliot's (1890) figures of *Sagittaria sagittaefolia* (Pl. 15, Fig. 6) and *Euonymus europaeus* (Pl. 18, Fig. 9)—and to the apex itself of simplex types—for example, the figures here of *Torreya californica* with two such cells (Pl. i, fig. H) and *Ginkgo biloba* (Pl. i, fig. I), and Korody's (1938) Fig. 11 of *Abies concolor*.

Spatial Implications and their Significances.

In summing up the activity of apices with the three basic types of continuing meristematic residue, there are certain spatial implications and their significances that might be mentioned in passing.

In the Monoplex type, only the one initial-cell partition initiates increase in both length and breadth. The prefix in the type name is to recall this oneness. This is the type of apex that is predominant in the more massive-tissued cryptogamic plants—some Phaeophyceae among the Algae, the Bryophyta, and the majority of the Cryptogamic Tracheophyta.

In the Simplex type, two initial-cell partitions in different directions (at right-angles approximately) are required to initiate increase in both length and breadth. Though the two directions of division are needed, yet there is still only the one "layer" in the initiating centre, and to that extent the organization is simple—hence the title for the type. This is a type of vegetative shoot apex prominent in gymnosperms and present in some Cryptogamic Tracheophytes, in some of which there may be fluctuations and transitions between monoplex and simplex types as described in the genus *Lycopodium* by Härtel (1938).

In the Duplex type, initial-cell partition takes place in two or more "layers", the innermost behaving as the simplex type to initiate increase in length and breadth, while in the outer layer(s) initial-cell partitions, being only perpendicular to the surface, can initiate increase only in surface area to clothe the increasing inner tissues. Because there are the two forms of initial activity, the prefix indicating twoness appears in the title for the type. This is the type of vegetative shoot apex at present appearing to be characteristic of the angiosperms, but also found in a few gymnosperms. But in some cases there are fluctuations between duplex and simplex types in seasonal or plastochronal sequence. (See, for example, Duliot, 1890, pp. 298–9, for *Araucaria excelsa* for seasonal sequence and a suggestion of it also for *Lycopodium complanatum*—Härtel, 1938, figs 14–19.)

Obviously, here are some profound physiological problems related to major classification in the Plant Kingdom and to the underlying phylogeny. What physiological differences—metabolic or genetic—lead to the difference between the angle the side walls of initial cells make with the surface (or is it with the axis?); how in racial

history did one form become changed into the other, monoplex into simplex? What is the physiological condition restricting initial-cell partitions to be only perpendicular to the surface, leaving the sub-adjacent layer not so restricted; and how in racial history did the one change into the other, simplex into duplex? These questions open a profound field of research—the biochemistry and biophyics of growth at the apex.

A Concept of Precision.

The concept of the continuing meristematic residue focuses into precision through logical necessity a trend of thought variously expressed by a number of authors—with less restriction to the classical concept by such as the three following: M. A. Johnson (1939, pp. 193–5) illustrates forty "initial cells" in *Zamia* spp., each dividing to form tetrads as a characteristic, and states that "it is only the ones at the exact apex that continue to supply cells throughout the life of the plant and which are thus the true apical initials". This tetrad-forming tendency, as stated for each cell, does not readily fit in with the above presentation of the continuing meristematic residue, nor are Johnson's figures fully convincing on that point. Duliot (1890, p. 290) clearly expressed the existence of a single apical cell in adult apices of gymnosperms, drawing this conclusion from a study of 20 genera (p. 308[19]). In the angiosperms, he clearly recognized a central cylinder with a single initial or apical cell (sometimes two) that behaves as does the single initial of a conifer shoot itself (p. 321[19]). This was, for example, in *Tradescantia martensii*, and lay beneath the distinct cortex and epidermis layers (cf. also Plate i, figure E here of *Cymodocea aequorea* where the one initial cell provides the cortex as well as the central cylinder). Among dicotyledons, he describes *several* superposed "histogènes", each with its single initial cell ("cellule terminale génératrice"), as in *Potentilla splendens* (his figure Pl. 17, fig. 7). Korody (1938), who appears to have been unaware, unfortunately, of Duliot's work, moves towards precision in the concepts used, defining as "initials", in the strict sense, those "independent source cells of the *form elements*, namely, of the tunica layers and of the corpus, lying directly in the apical point" (my translation[20]). The initial cells lying in storey-fashion, it is the lowest one or group that provides the corpus (p. 38). These "initials" (source-cells—*Ursprungszellen*) would correspond to what I have called continuing meristematic residue, and have referred to, from a functional point of view, as the fount of cellular structure. The "form-elements" (*Bildungselement*) would be the cells of what I have called the general meristem, the first in any line of cell generations of which is the tissue mother-cell (sister to the continuing meristematic residue).

This concept of the continuing meristematic residue renders precise, by logical necessity, the essential idea behind Majumdar's (1942) concept of the (indefinite group of) "central initial cells" as a "self-perpetuating meristem" (p. 60), but, rejecting his description of this meristem as a broad inverted cone (p. 61) would restrict it to fewer cells. Dermen (1945) recognized (p. 387) at the upper central region of the apical "dome" of Cranberry three "primary histogenetic layers" with an activity such as I have attributed to a duplex apex. He refers (p. 389) to a few cells in each layer "exactly or approximately at the central point in the curvature of the apical dome" as having "the function of carrying on the histogenetic continuity of each layer". These cells being usually more than 4-sided in vertical view, "not more than three cells as a rule, can be located in the very central point simultaneously and maintain a central position on the curvature of the dome as the cells divide and the stem grows forward. Therefore a tissue derived from each histogenetic layer will arise from one, two or three cells." Dermen's account is very close to the chief point made about this feature in the present paper, which is that the *indefinite* region of initiation of cellular structure

[19] From Duliot (1890): (p. 308) ". . . la tige des Gymnospermes s'accroît . . . par une cellule terminale, tantôt pyramidale, tantôt prismatique, mais toujours unique." (p. 321) ". . . initiale . . . qui se comporte comme la cellule terminale unique d'une tige de conifère . . ."

[20] From Korody (1938, pp. 37-38): "Den Terminus "Initialen" werden wir nur in seiner strengen Begrenzung für die unmittelbar am Scheitelpunkt gelegenen selbständigen Ursprungszellen der *Bildungselemente*, also der Tunicaschichten und des Corpus benutzen. . . ."

proposed by some authors is replaced by a single cell or a precise group of cells—logically necessary, if not visibly recognizable.[21]

Foundational to the precision of the concept of the continuing meristematic residue is the proposition of the differential division of an initial cell. It is *not* a case of *a persistent* cell (or cells) continuing to cut off a succession of daughter cells, retaining its parent status the while, as seems to be implied in Dermen's description given above, but of a succession of differential divisions wherein ability to undergo such a differential division is handed on to only one of the two daughter cells to which the initial cell is amplified. Prat (1945)[22] has strongly opposed the commonly held idea that one or a group of initial cells "gives rise" indefinitely to cells that differentiate, while itself continuing indefinitely meristematic, an idea whose current expression may be found in Esau's textbook on Plant Anatomy (1953, pp. 75 and 92[23]). Prat denies that an "initial cell" "gives rise to" other cells, after each of which actions it continues its autonomous life; for the other cell is always the *sister* and not the daughter of the now initial cell, its contemporary—the property of being an initial descending in inheritance to one of the daughter cells, to the exclusion of the other (p. 581). He thus points out the differential nature of the division of the initial cell in relation to the meristematic and metabolic qualities inherited through it.[24] The initial cell is completely juvenile, that is, fully potent. One of its daughter cells inherits that condition; the other does not, is less juvenile and begins a line of cell generations progressively less juvenile and more differentiated—a line of increasing realization of differentiation and of decreasing potentiality yet available, thus following a rising gradient of cell senescence. It is because the polarity of this gradient of cell senescence is strictly orientated that initials remain in a constant, morphological position—apical, intercalary or basal[25] (see pp. 581 and 614, *et seq.*). (The terms differentiation, meaning "the progressing towards the adult state", and its counterpart "dedifferentiation", meaning "the returning towards the juvenile state", seem to me to be unfortunate, despite their growing popularity. The term "differentiation" should be restricted to the coming into existence of a state of variety *among* objects that were formerly in a state of uniformity. The reverse would apply for "dedifferentiation".)

Bünning (1952), discussing polarity in relation to plant morphogenesis, stresses the differential nature of division of initial cells and its indication of polarity in

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[21] There is the same logical necessity of a single initial in each radial row of secondary vascular tissue, whether its derivatives mature with or without further divisions, and whether the term cambium applies to the ring of such initials alone (the continuing meristematic residue) or to all their immature derivatives as well. Mischke (1890, pp. 67-8), contending against the idea of several initials, recorded the observation of the single initial and divisions in the derived tissue-mother-cells; and Beijer (1927, p. 633) was also emphatic on *one* initial in each radial row. In a recent paper (Newman, 1956*a*), I have claimed to identify in the radial row in the Cambial Zone of *Pinus radiata* that cell which at the moment was holding the office of initial cell. This hereditary concept was not in Beijer's presentation: "eine Zelle die immer im Cambium bleiben wird".

[22] Prat has presented a condensed English language version of this paper with enlarged bibliography in two parts—I (1948) and II (1951). The original paper, more lively in expression, more stimulating to thought, is strongly recommended. Pages given in this paragraph are from the original. The English version pages appear in brackets in the following list: p. 581 (1948, p. 623), 582 (1948, p. 623), 614 (1951, p. 699).

[23] Respectively: "Thus, in active meristems a continuous separation occurs between cells that **remain** meristematic—the *initiating cells*—and those that develop into the various tissue elements—the *derivatives* of the initiating cells" and "An *initial*, or initiating cell (p. 75), is a cell that **remains** within the meristem indefinitely by combining self-perpetuation with addition of cells to the plant body". [Bold-face type mine.]

[24] Page 582: "Le premier grand fait est que la cellule initiale entre en division *inégale*, l'une de ses filles retenant certaines propriétés, (dont la faculté de division indéfinie) tandis que l'autre en manifeste de différentes, notamment celle de se spécialiser chimiquement et de devenir progressivement incapable de se deviser."

[25] Absence of such polarity of cell senescence, with consequent diffuse growth, is normal, above unicellular organization, only in filamentous colonial algal types (throughout, if floating, e.g., *Spirogyra*, *Melosira*; away from holdfast, if attached, e.g., *Ulothrix*), thin laminae away from holdfast (e.g., *Ulva*, adult *Porphyra*) and cell aggregates of bacteria and Myxophyceae.

protoplast structure. If, in a usually polarized meristem, structural polarity disappeared from the protoplasts or the polarity were functionally compensated, the subsequent irregular cell mass would be an unorganized tumour (pp. 106–9). Prat's concept of the gradient of cell senescence is a collective idea integrating the various gradients of polarity that take their cue from that first differential division in the initial cell.

Words begin to fail us here; for the co-ordinates of our language must be three for the space dimensions, one for the time dimension and one or more for the dimensions of constitution, a total of at least five dimensions. Slowly we are building up adequate forms of expression—at present we still grope for verbal counterparts of the realities we strive to express. To speak of an "initial cell" catches and holds still something that properly only exists as progressing, so that, while we hold it still, we lose its full meaning and nature. My term, "continuing meristematic residue", is an attempt to retain the idea of progression as a characteristic of the object—as motion is characteristic of the image on the cinema screen. The term "initial cell", as it were, only catches the progression in a stilled mid-phase—as the still image of one frame of the film on the cinema screen catches the motion in mid-step.

One could continue indefinitely, in the manner of Text-figure 10, constructing logical schemes on paper to cover the various possible arrangements of the continuous meristematic residue and the derived general meristem, and discussing the logical relations of gradients and directions of polarity involved. One could also interpret against the logical constructs the appearance of stilled cellular structure in killed apices. But it would be more profitable to return from logic to life.

A Search for Apical Cells.

Status and Name.

The attempt to create on paper schemes for the partitioning of such continuing meristematic residues as do not have a characteristic and recognizable cell shape or form shows readily how "apical cells" have failed to be accepted for seed plants. For example, in his classic monograph on the meristem, Schüepp (1926, p. 38), in defining an apical cell, included size and form as distinguishing characteristics (cited from Schopf, 1943, p. 60). Those who look for a typical shape will quickly deny its existence; those who will accept a non-typical shape are forced to make identification *by inference from presumed* activity. As shown above, the existence of continuing meristematic residue (momently expressed as initial cell or cells) is logically inescapable—there *must* be "apical cells". Yet some, while admitting the existence of initial cells in the apex, question their morphological permanence and continuity. Three prominent lines of argument for this denial may be exemplified.

Foster (1941*a*, p. 348), summing up work on seed plants, and having in mind the spectacular work on *Ginkgo* and cycads initiated by him, emphasized that no visually recognizable "cell or group of cells seems to dominate" the zone of initiation, and doubted whether the "initial" cell or cells are "important" or even constant in number, form and division sequence.

Ball (1946) made two vertical cuts crossing at right-angles where the apical cells should be. Four new *separate* apices arose from the quadrants. He argues: "No central group of initial cells in the original shoot apex is essential to the function of that meristem; this operation destroyed the central cells. The lateral cells of the shoot apex are able to function as initials and to grow and produce all parts of a normal shoot." (This work was repeated for or included in a later paper with similar conclusions—Ball, 1948, p. 255.) In view of the normal institution of initials from lateral cells of the shoot apex at the origin of primordia of leaves and branches, this emergency institution really supports the logical necessity of the initial cells—the continuing meristematic residue.[26]

Dermen (1945, pp. 389–390) argued for variation in number and for change of individual status of initials from his study of colchicine-induced, polyploid, periclinal

[26] One recalls Sachs' (1878, 1879) emphasis that growth is primary, and the features of cell partitioning are secondary.

chimaeras. On this basis he claimed that cells could cease function, and others could assume function, as initials. Thus the function would be tied, not to a particular cell lineage, but to a particular location, the status of initial being, incidentally, not genetically, acquired.

This view, presented by Dermen and at least implied in argument, as by Foster and Ball, is summed up by Esau (1953, p. 93) as: ". . . a cell is an initial, not because of its inherent characteristics, but simply because of its particular position in the meristem, a position that cannot be considered permanent." But this conflicts logically with her earlier statements[23] about the initials *remaining* "meristematic" in contrast to their "derivatives", and *remaining* "within the meristem indefinitely by combining self perpetuation with . . ." If there is to be any reality in the concepts of gradient of cell senescence (Prat, 1945) and of polarity in initials, particularly protoplast polarity (Bünning, 1952, p. 107), the continuity must be primarily morphological and only secondarily positional. Esau's dilemma arises from failure to recognize Prat's contention that an initial is NOT *a permanent cell* stuttering off the beginnings of cellular structure, but is ONE *of two daughter cells* formed under differential division (inheritance). It would be resolved by use of such a term as continuing meristematic residue. Thus, paradoxically, what we are seeking to locate are not particular, permanent cells, but particular permanent lines of genetical descent, momently embodied in what we call initial cells, such a line being capable in normalcy and emergency, of institution *de novo* just as must always be done in the embryo. This line of argument applies also in cambial, intercalary and basal meristems, but is irrelevant to diffuse growth.

There has also been dispute over what to call these initiating cells, particularly in the apex when they are without obvious structural differentiation. Popham (1951, p. 253) not only denies them the title, "apical initials", where no structural difference or regular, fixed scheme of segmentation is clearly to be seen, but will not even recognize them as a "separate and distinguishable growth zone". This confusion of idea is present in the earliest work, as where Dingler (1882) clearly recognized classical type apical cells in embryos and seedlings and leaf primordia of some gymnosperms, but, in some older shoot apices, says no apical cell is visible, and shows in longitudinal view on his Plate III, the apical centre occupied by rectangular appearing cells for active *Juniperus communis* (Text-fig. 17) and dormant bud of *Abies balsamea* (Text-fig. 19), yet is so fixed on the classical idea that his theoretical construct, as for *Picea excelsa* (Text-fig. 20), shows the inverted pyramidal apical cell. But surely, it is the function of being the fount of origin of cellular structure for which the cells should be titled. As Prat (1945, p. 581, or 1948, p. 623) has emphasized, the function of initiation is not confined to the apex—meristem may also be intercalary or basal. Whichever it is, its initiating cells share the one characteristic, differential feature of division in providing a line of descent restricted to one, only, of each of the successive pairs of daughter cells—the continuing meristematic residue. Thus, Korody's (1938, p. 37) term, "initial cell" (*sensu stricto*), may be generalized to apply in intercalary, basal or apical meristems. The term "apical cell" may then (for historical continuity, instead of "apical initial") be retained for such initials (of whatever form) maintained at an apex by a basipetally increasing gradient of cell senescence. The special shapes and fixed regular schemes of partition in the cryptogamic plants have been a great convenience to botanists in their studies, but should not therefore be accorded exclusive terminological significance.[27]

Finding the Evidence.

An account of a small research on the living apex, done during about three weeks in 1952 at Sydney, was to have appeared at this point. Circumstances arose which made it appropriate to publish that work separately in a paper which became Part I

[27] One might also point out that if a horizontal plate of cells can be called "apical cells", as in Marattiales and Fucales, for example, there is no logical reason why the term could not be applied to a vertical line, column, or plate of cells (cf. Text-figs 10A‴, B‴).

of this series (Newman, 1956*a*), and which complements some of the discussion in this paper. The salient features of that work are appropriate at this point.

The 1956 paper records the microscopical study under vertical illumination of the living apex to observe cell partitioning in the surface layer. The hope was to see if there are "apical cells" in seed plants. The apices were cut off with about 8–12 mm. of stem, were kept standing in tap water and, having chlorophyll present in the stem, were expected not to need nourishment for the several days of the observation. *Tropaeolum majus*, a plant with spiral (alternate) phyllotaxy, showed growth of leaf primordia, and in nine days showed about 40 partitionings over a radius of 4–5 cells at the tip of a leaf primordium and about 30 partitionings over a rectangle of about 14 × 9 cells around and about the apical centre of the stem. *Coleus* sp., a plant with decussate phyllotaxy, showed growth of leaf primordia, and in four days showed about 17 partitionings over a rectangle of about 11 × 8 cells around and about the apical centre of the stem. It might also be mentioned that several apices of scaly buds of *Pinus radiata* long shoots were successfully observed in a pilot study and the cell pattern at the apex photographed over several days, at the Division of Forest Products, C.S.I.R.O., Melbourne, in 1955. The apices were dormant (mid February and May—see Newman, 1956*b*), and no partitioning was recorded, as shown in Plate ii, figure D_{1-4}.

The leaf primordium of *Tropaeolum* showed at the apparent apical centre a division of a cell, one of whose daughter cells appeared to be central in a pattern (including its sister cell) that somewhat resembled the pattern in which the parent cell was central. This suggests a single apical cell for the leaf primordium.

For the stem apex of *Tropaeolum majus*, the first and last components (II and IX) of the original figure 6 are reproduced here as Text-figure 10E. The four cells ABCD at the intersection of the guide lines X and Y are at the apical centre as identified in the former paper. By the time of component IX, cell A may have enlarged slightly and changed shape; cell B has divided just before the drawing was made; cell C has enlarged and should soon divide; cell D divided on the first day of observation and is represented in component IX by its daughter cells—D and D′. Note that D′ has already enlarged, suggesting the approach of division, while its sister cell has remained small and is interpreted as belonging to the continuing meristematic residue. This would harmonize with the requirement that, cell size at division remaining constant, frequency of division must increase with increasing displacement from the initiating centre.[28] Thus BCD may be the continuing meristematic residue for the outer tunica layer of this apex. Compare the similar group shown in Plate ii, figure A, from Dermen's (1945) study of Cranberry and in my pilot study on *Pinus radiata* (Pl. ii, fig. C).

For the stem apex of *Coleus* sp., the first and last components (II and VII) of the original figure 8 are reproduced here as Text-figure 10F. As this is a decussate apex with rectangular outline, the length of the rectangle alternating in directions at right angles with the sequence of plastochrones, one looks for a continuing meristematic residue of rectangular form. The cells ABCDEFGH, in two rows in component II, may be considered for this office. Component VII shows A had divided (this was on the second day) to A and A′, while E, F, G and H had each divided (this was about the third or fourth day), as indicated by the pairs of cells with small dots. On the line of argument followed in establishing the logical necessity of the continuous meristematic residue (or apical cells), the direction of the partition in cell F precludes the whole row of four pairs of cells being that continuous meristematic residue. It is, however, consistent with the following alternative compositions: ABEF, CDGH, BCFG, or BCDFGH. Compare the similar double row of cells in the decussate *Ephedra monostachya*, of whose apical cell nature Dingler was uncertain in 1886 (see here Pl. ii, fig. F) and in the not-decussate *Pinus radiata* as seen in my pilot study shown in Plate ii, figure D_{1-4}, though three cells at the left of the group suggest Figures A and C.

[28] An idea not sufficiently regarded by those who describe inactivity of the cells at the region where apical cells would be (Plantefol, 1947, and his followers; also Camefort, 1951 and 1956*a* and *b*, and Chouinard, 1959).

Further than the suggestions for *Tropaeolum* and *Coleus*, the evidence could not take us. Though apical cells were not clearly demonstrated, the observations for only two or three times as long should provide some approach to a confident interpretation.

Just as that paragraph had been written in the third (and final) draft of this paper, there arrived *Phytomorphology* containing Ball's (1960) paper on "Cell divisions in living shoot apices". The excellent conditions and facilities for his work enabled him to use sterile technique, a complicated culture solution including, among other items, giberellin, coconut milk, and micro-elements for ensuring good growth of the severed apices. His observations were entirely with automated cinemaphotomicrography and modern vertical illumination equipment and extended over two years. This is not the place to enter into a detailed discussion of the paper, but to consider what contributions it makes to the study of the living apex. Lupin apices were observed for periods of up to 20 days with continuous photography, but were declared to be unsuitable because of lack of photographic contrast between cell contents and cell walls, the rapidity of cell divisions, and the nutations that altered the angle of presentation of the apical dome. These difficulties were not marked in the cases of *Vicia faba* and *Asparagus officinalis*, which were observed for from 5–10 days, the longest sequence illustrated covering just under 5 days. *Tropaeolum majus* was declared unsuitable for photography as it was devoid of chloroplasts in the apices, for the green colour imparted thereby to cells is "essential for successful photography of the apex" (p. 377). There was no noticeable green colour in the apices of *Pinus radiata* photographed in my pilot study of them at the Division of Forest Products in Melbourne and shown here in Plate ii, figures C and D_{1-4}, where they appear reasonably amenable to photography, despite the use of essentially the same methods of illumination as for my 1956*a* paper.[29] Details of that work are given in the explanation of the figures. Ball's work with elaborate apparatus and complicated culture medium is a welcome confirmation of what I had done with Sydney tap-water and vertical illumination improvised from a milk-bottle top. My observations did not last as long as the 20 days of some of his [29]. However, the longest period *illustrated* by Ball with divisions identified (just under five days) is for *Vicia faba* in his figures 4–17. His pessimistic conclusion is: "No cells can be regarded, on the basis of the present observations, as initial cells or apical cells of a shoot apex. No pattern of division could be ascertained in the superficial cells of the apices" (p. 292). But, if one looks closely only at the *Vicia faba* series of figures, there is more hope. It is clear that at the beginning of the series the apex is canted away from the observer by growth of the tissue underlying the primordium to the lower side, so that central cells of the apex will not be those now appearing central in figure 4 (cells numbered 1), but cells higher in the figure. As the series progresses and maximal area is attained about the time of Figure 13, where the apex seems obviously to be viewed vertically and is in sharper focus than the primordium, below, the cell 3 appears central, and even suggests an hexagonal form (allowing for the poor resolution). The subsequent figures suggest the institution of a leaf primordium on the upper side of the figure, with canting of the apex towards the observer, so that the cell 3 no longer appears central and even appears slightly smaller (because of the canting). This is the only cell of those numbered which has not divided. Divisions have occurred, according to the numbering on the figures, above, below and to the left of it, and I think that photos at some intervening times would show that divisions had occurred to the right of it. To me, cell 3 is a strong candidate for apical cell status. It is a great pity that the records do not extend further than this, just short of the point which my observations may have reached with the leaf primordium of *Tropaeolum*, but a little further

[29] In the first paragraph of his paper, Ball refers to my method as "crude"—"improvised" would sound better—and as being "inadequate because it provided no suitable culture medium and no means of photomicrography". It was the circumstances under which I was working and the geometrical features of the object—not the method—which decided me against photomicrography (my paper, p. 4). It should also be pointed out that the Sydney tap-water and the inner resources of the severed shoot-ends provided observation time of 9 days for *Tropaeolum* and 4 days for *Coleus*, with growth and divisions recorded throughout.

than they reached with the two stem apices. I feel that there *is* a hint of a pattern of division; and that there is encouragement to proceed further with this work. One further comment is that the rigid optical conditions for the automated cinemaphotomicrography compel a lack of precision in the records. When there is little contrast in the object, varying the direction of illumination, altering the condenser aperture, or varying the focus may reveal structure to the *directly observing eye* that is not visible with unvarying illumination to the camera. I think that, to adopt a term from the commercial world, "personalised" observations by photomicrography, or even by camera-lucida drawing, will in this matter get us on further, and faster, than will completely automated cinemaphotomicrography.

I am aware of only one other work examining the undamaged living apex—an exhibit about examining the apex of tomato plants by Dr. G. Hussey at the 1960 Nottingham (England) Conference of the Society for Experimental Biology. The work is not yet published.

A geometrical approach may be made through cell arrangement by the methods of Lewis (1943), who considered the number of side-walls a cell should have in various circumstances, and the consequent number of "rays" at the lateral "vertices" (the common angles between three or more cells). The surface cells of a regular cylindrical stem will average exactly six sides each, with only 3-rayed vertices. Considering the apex of the stem as a hemisphere, if all vertices are 3-rayed, the apex must be deficient in six cell-sides. If this deficiency "is locally concentrated, an apical cell becomes conspicuous"; but it "may be widely distributed, yielding a growing point with several initials . . ." (p. 768). Ball (1960, pp. 388–392) claims this to be impossible to determine, as the anticlinal walls in the surface layer of the apical dome are revealed by his photographs to be all of "curved, rounded appearance", except when just laid down. But in this he seems not to have allowed for the inclination of the cells as they pass on to the slope of the apex with time, for the convexity of the upper (outer) wall which, on the slope, may even be what is photographed; nor, particularly, to have allowed for the obscuring of angles by the poor resolution of the photographs as shown by his illustrations. Note the clear hint of angularity in the vertically viewed cell 3 in his figure 13.

The search for apical cells would be pointless under the concepts of Plantefol (1947), Buvat (1952) and Lance (1952) that the apical centre (initial region) is inactive or so quiescent that it plays no significant part in vegetative growth, structure arising further back from the "*anneau initial*", the "initial ring"—a self-perpetuating meristem. Evidence contrary to this central apical inactivity and the self-perpetuation of the initial ring was given in my previous paper (1956*a*), which, as to apical activity, has now been amply confirmed by the above work of Ball (1960). These concepts of the quiescent apical centre and of the initial ring and the evidence in rebuttal were based on angiosperms. The supporters of those concepts have been adding evidence from gymnosperms, to support the initial ring as initiator of structure. Guerindon (1954) followed Lance (1952) in the use of distribution of mitoses in seedlings of *Pinus pinaster*. Camefort (1954) used a technique for identification of ribonucleic acid to locate the prominent nucleoprotein concentration (indicating activity) in the region of the initial ring, in contrast to its scarcity in the "apical initial" zone. Later (1956*a*), he published an extensive review and research paper on gymnosperm apices in which he claimed to entrench the concept of the initial ring as initiator, by cytological techniques describing the organelles of the cells as revealing the various tissues of the apex, by the distribution of mitoses, and by distribution of the nucleic acids. And, further, he claimed that the initial ring is a self-perpetuating meristem, with only incidental contribution of cells from the apical initial zone (pp. 82–83). This is also presented in a shorter paper (Camefort, 1956*b*), largely extracted from the former. Arguments against this self-perpetuating aspect were advanced in my previous paper. Now, Partanen and Gifford, in 1958, used autoradiography by phosphorus-32 in *Pinus lambertiana* to show synthesis of deoxyribonucleic acid (indicating immanent

mitoses) in several nuclei, concurrently, in the central region of the apex, the nuclei involved being located by a phase contrast image of the same longitudinal section of the apex.[30].

Continued search, then, for apical cells in seed plants is not pointless; and it should follow these four lines: (1) direct microscopical observation of the sequence of partitioning in the living apex; (2) traditional study of sections to trace cell lineages by wall character; (3) electron microscope study to see whether apical cells are recognizable by any difference in fine structure compared with their sister cells (tissue mother cells)—a study at the level of organization revealed by the work of Buvat (1958) for example, on the fine structure of chondriomes, membranes, plasmodesms, etc., in apical meristems; (4) geometrical studies of cellular pattern following the methods of Lewis (1943).

3. CELLULAR PATTERN, THE STRUCTURAL EXPRESSION OF COMPOUNDED DIFFERENTIAL RATES AND ORIENTATIONS OF PHYSIOLOGICAL PROCESSES.

The Levels of Phenomena in Causative Sequence.

Cellular pattern in the apical meristem can be analysed into a number of components, such as cell size, cell shape, orientation of cell shape, vacuolation (or its converse, "density" of cytoplasm), etc. As mentioned previously (Comments 3, 4, 7*b*, etc.), these components themselves may be the expression of the interaction of physiological processes, often in their aspects of rates. Thus, for example, size of cell in a region will be the expression of the rate of enlargement together with the rate (frequency) of partition, varying *with* the former and *inversely to* the latter; and shape of cell will have added to the factors governing size a factor relating to direction—an orientating factor. The physiological processes underlying cellular pattern appear, then, in two forms—rate and orientation. (This calls to mind the two types of response to stimulus—nastic and tropic.) The general view today is that such physiological processes are determined by physiologically active entities that occur in concentrations or intensities, respectively chemical or physical.

We thus have three levels of phenomena that are in causative sequence: (1) the *visible* (*cellular*) *pattern* which is the result of (2) a number of *process pattern* (rates and orientations) which are the expressions of (3) a number of *presence patterns* (concentrations and intensities). The existence of these three levels of pattern should be constantly in our minds when discussing the structure and activity of the apical meristem, lest we fall into errors of inference or of (self-) deceptive verbiage.

The presence pattern of concentrations and intensities will approximate to the concept of the morphogenetic field, being less abstract, perhaps, than the "field" concept. To be present at any point, unless it originates *in situ*, an entity must be translocated from a fount of origin, by diffusion or cytoplasmic streaming or both for chemical entities, or by some form of energy transfer for physical entities. Whether by spreading in space or by loss through usage, concentration or intensity will decrease with distance from the fount of origin. Thus, gradients will appear, which, from the point of view of any particular location, will really be expressions of the rate of supply of the entities. Here then we have two more levels of phenomena: (4) translocation of entities expressible as *gradients* and (5) the *founts of origin* of these entities.

[30] Loiseau (1960) has concluded that since destruction of the apical centre (apical initials) with initial ring undamaged can be followed by uninterrupted morphogenetic activity, therefore apical initials are not indispensable—the essential activity being confined to the initial ring (pp. 284-291). But earlier (pp. 254-261) he reports continued growth and organ formation following total destruction of the initial ring with the apical centre undamaged. The reported delay in morphogenetic activity (cf. p. 254 with p. 291) is naturally due to the greater area of damage. Surely the initial ring is not indispensable. Wardlaw (1957) reviewed the problem of the initial ring *vs* the apical centre and concluded that the French work needed better relation "to the well substantiated body of evidence on apical ontogeny, organisation and re-activity that has accrued from experimental and other investigations" (p. 228). Wardlaw records me as observing that "divisions do take place in the apical initial cells" (p. 225); but I only claimed to be on the brink of such an observation (see fourth paragraph, above).

The first three levels of phenomena—visible, presence, and process patterns—play roles in the total causative sequence different in a sense from those played by the remaining two levels of phenomena—gradients and founts of origin. The first three are of executive or guiding nature; the last two are in the nature of supply.[31]

The subject is richly complex, as founts of origin of entities vary in number, location and productivity; and, as far as materials are concerned, in some cases precursors and components must pass through the established pattern to the fount of origin of the entity. The great volume of relevant experimental and theoretical data now available but not yet integrated or fully understood is a temptation to the speculative production of hypotheses. However, it is hoped that the analysis just presented, though not devoid of speculation and hypothesis, will, if only by provoking contradiction, contribute to the understanding of apical activity. But there are still two aspects of cellular pattern as expressions of the compounding of rates and orientations that are worth further study. These aspects are the relations to space and time.

Pattern in Space.

In Comment 7*b*, it was suggested that the pattern might be looked on as a non-travelling frame in which cellular structure became involved in passing by, much as the sea-water is a non-travelling substance in which the wave form becomes involved in passing by. This is at first sight a curious inversion of ideas—in popular view of the sea, the material (water) stays while the immaterial (configuration or wave) passes on; but here, it is the immaterial (the pattern) which stays while the material (the cellular structure) passes on. Difficulty with this imagery may be resolved when we remember that any idea of motion must be relative to some point of observation. If we took such a point at a fixed position on a wave curve, the sea-water would appear to move past it, or if we took the whole wave pattern as our frame of reference, the sea-water would appear to be passing from part to part of the pattern. In the case of the apex, we must stabilize our thought by selecting some point of observation; for this, the superficial centre would serve most appropriately.

Over relatively short periods of time, the pattern at the first three levels in the causative sequence (*see* the fifth paragraph, above) remains stationary in relation to that observation point. The present discussion will assume this (movement of the pattern in relation to this point will be considered later). This proposed view involves thinking, not of the apex growing onwards while adding cellular structure to existing structure, but rather of cellular structure moving away from a fount of origin and becoming involved successively in the parts of the pattern that may lie in its path.[32] Some such mental orientation as this is needed to enable us to describe validly the structure and activity of the apex and, subsequently, such features of differentiation as the origin of stem procambium and its relation to primordia and procambia of laterals. The ideas set out above, together with the mathematical situation involving time-lapse between divisions and the sizes of cells in different regions, are not adequately recognized by Camefort (1956*a*) in reaffirming the Plantefol School's relegation of the apical initial region to a status of insignificance. Consequently, this School erects one *visibly* prominent component, *along the line of* a functionally integrated pattern of development, into a false pre-eminence as initiator.

[31] The concepts of fields and of gradients, with copious reference to literature, is discussed by Wardlaw, 1952, Ch. XIX. General problems of relative rates of division and enlargement and of polarity in relation to partitioning are discussed by Sinnott (1938).

[32] This difference in viewpoint for relative motion of wave and material involved in it is well shown by reference to Sinnott and Bloch's (1939, pp. 629-630) description of elongation in root cells: 'as though there were a "wave" of elongation rolling down the root, reaching its crest in one end of the cell first and then passing on to the other, the amplitude of the wave extending over the whole region of elongation'. The concept presented in the present paper is of that wave being stationary in relation to the apex, with cellular structure passing into its influence and then beyond, so that the part of the cell first to reach the crest of the wave is that part that is "basal" (furthest from the apex), as described by Sinnott and Bloch (whose "downwards" means "towards the apex").

The foregoing concept can be tested against a particular case, such as the apex of *Dioon edule* shown in Plate i, figure K, which is reproduced and reduced from Foster's magnificent illustration (1941*b*, Fig. 3). Cellular pattern is immediately obvious, and careful study will show that it can be broken down into components as suggested above. The outline of appearance pattern is shown in Text-figure 4, which is Fig. 2 of Foster's paper together with Foster's explanation. We are not concerned with the functional destination of the parts of the pattern, nor is the object to dispute the author's interpretation, but to make a test description. Under the concepts of the present paper, the fount of origin of the cellular structure will be a small continuing meristematic residue, probably of simplex type, at the superficial centre of Foster's Zone 1. There can be no continuing meristematic residue functioning in Zone 2, the so-called central mother cells. The fan-like appearance of Zone 1 could be ascribed to a constant frequency of transverse partition from the surface inwards, with a rapidly decreasing frequency of longitudinal partition from the surface inwards, while enlargement rate is constant over the area. There is some hint that the partition rate in the superficial layer may be less than that within, leading to slightly larger cells occupying it. Conversely, the partition rate may be the same, but the enlargement rate greater. In the region of the "central mother cells" (Zone 2) of Foster, it appears that either the partition rate is less or the enlargement rate is greater, or both conditions obtain, leading to the large size of the cells. What we must guard against is any thought of this region as a constant group of "mother" cells. Any individual cell of this group is constantly receding from the fount of origin, and, in time, it or its progeny will have moved to another region of the physiological pattern from the point of view of processes—the second level in the causative sequence (sixth paragraph above). Here, it or its progeny will behave appropriately to that region of the pattern, with probably similar rates of transverse and longitudinal partitioning in a shallow upper region of Zone 4, at first, but with longitudinal partition rate rapidly lessening with continued recession from the fount of origin. Possibly a slight increase in rate of enlargement goes with increasing distance from the fount of origin in this zone. The reader may apply comparable descriptive methods in the Zones 3, but I doubt whether there should be any suggestion that they have "arisen" from the sides of the "central mother cell" group. This description is an attempt; it is probably debatable; but I hope it is an incitement to critical observation of literature.

The concept of the cells (and their derivatives) undergoing displacement from a fount of origin in the apical centre has been elaborated by Schüepp (1952, pp. 593–4) for the even more strikingly patterned apex of *Microcycas calocoma* as it was described and brilliantly illustrated by Foster (1943). Schüepp's geometrical analysis is a most important contribution to methodology of interpretation of apices, and emphasizes the danger of thinking that the direction followed by the human eye in its viewing of sectioned tissues is always a true indication of the realities of growth movement and cellular displacement. The resemblance to Sachs' "cap layering" is an optical phenomenon, not a phenomenon of growth, in *Dioon* and *Microcycas*, above (see Text-fig. 3).

The zones of the pattern visible in apices in longitudinal section, as marked in Text-figure 4 (and subzones that may be discernible), when considered in three dimensions, seem to have forms approximating to figures obtainable by the revolution of various conic section curves about their axes. The co-ordinates of points on these curves we can imagine to be connected by equations whose terms would represent the various components of the process pattern. In cross-sectional view, however, the regions of the pattern will be annular and, in this sense, susceptible of treatment along the line of Turing's (1952) treatment of morphogen concentrations in terms of waves. His concept of stationary waves on a ring may be relevant to determining the differentiation of procambial strands (as viewed vertically) from the surrounding maturing parenchyma (pith, cortex, and medullary rays). This assumes that the differentiation at the determined regions occurs equally in the one transverse plane,

at the one time, at any particular level.[33] If procambia are correlated with leaf initiation, such a stationary wave concept would also apply to it in the case of whorled leaves. And Turing has suggested this (p. 68)[34] with the modification of annular to polygonal symmetry.

The spiral sequence of primordia is perhaps covered by Turing's concept (p. 67, (*e*)) of sets of waves travelling in opposite directions round a ring. This is a "pattern" ring at constant distance from the apical point of reference and hence progressing in space with the passage of time. The compounding of such waves into "peaks" and "depressions" at regular successive angular intervals could signal the initiation of procambium and/or leaf primordium at the successive plastochrones of the spiral phyllotaxy. More complicated situations could readily be imagined. Such "waves on a ring" involve a vertical projectional aspect. But, in relation to vascular origins, for example, caught momentarily in lateral view of a medium longitudinal plane, the patterns appear as in Kaplan's Figure 20 (1938, p. 259). After some time in this sector, the pattern would switch to a new position of temporary rest (stationary wave) in that sector, but, having a fixed spatial relation to the summit of the apex, would be at a higher level in relation to the base of the plant since the apex is advancing. Such patterns can be pictured as revolving by jumps about the vertical axis, while moving forward. Occupancy of a particular position would last for a plastochrone. (Cf. Newman, 1936, p. 71, and Majumdar, 1942, p. 62, for a similar conception in relation to primordial origin.)

In the spiral or whorled phyllotaxies, the form and histogenetic activity of the continuing meristematic residue seem unlikely to have any relation to the quantitative expression. But in decussate forms there might be a close relation. If, for example, in *Coleus* apex (Text-fig. 10F) that residue was ABEF and the apex is achieving maximum area, enlarging to left and right, we would expect partitioning to increase the number of cells towards these directions rather than at right angles to them. With new primordia instituted left and right at the end of the plastochrone, we know that in this type of apex maximum area is then built in the direction lying up and down (on this illustration). The first thought is that this is due to a switch of the direction-of-partition rates through 90°, in the continuing meristematic residue. But it could be a change through 90° of the location of excess partition rates in the general meristem in the region called "*anneau initial*" (initial ring) by the Plantefol school.[35] This could be considered either an oscillatory change or a travelling wave phenomenon (Turing, 1952, p. 67, (*b*) and (*d*) combined or (*e*)).

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[33] It cannot be too strongly emphasized that, in the "differentiation of procambium", it is the surrounding tissues that are differentiating—to parenchyma. The procambium remains meristem. Priestley (1930*a*, p. 58, and 1930*b*, p. 103) describes the compression of the procambial cells between the pith and cortex, which appear, in some cases at least, to have an enhanced rate of enlargement, while in the procambium the rate remains unchanged. The cells of the latter are thus *pulled out* in length by the surrounding tissue, and the little changed volume is provided for by decrease in cross-sectional area. Though he does not show longitudinal views, Helm's (1932) transverse sectional views of the origin of procambia in a number of vascular plants approximate to this idea, though his own suggestion (p. 124) favours longitudinal divisions of cells to produce the small cross-sectional area. If transverse division rate remains low in the procambium compared with the vacuolating-dividing pith and cortex, its cells, by their own enlargement and further passive stretching, become individually very long compared with the neighbouring parenchyma cells. In vertical aspect this also will fit into the concept of stationary waves in a ring. (Note the contrasting ideas here of active compression alone—Priestley, 1930*a*, p. 62—and, at least some, passive stretching to account for the form of the cells.)

[34] Reputedly whorled organs may not truly be contemporaneous or co-planar in origin. In *Doryanthes excelsa* and *Acacia baileyana* (Newman, 1928, pp. 505 and 509; 1933, p. 151) "whorled" floral organs are described as arising in (spiral) sequence. Careful examination will reveal that many "opposite" leaves may not be ontogenetically truly opposite.

[35] Camefort (1956*a*), in the second part of his important paper on gymnosperm apices, relates phyllotaxy to the concept of the initial ring. There is no space for discussion of this here.

Pattern in Time.

The last example introduced the idea of a change of pattern in time. It was apparently an oscillatory change of orientation. There are changes which occur in the pattern with time, but also in relation to the observation point. Two examples will be discussed: change in pattern as dormancy develops and as orientation of partition varies.

Institution of Dormancy.

Dormancy has already been referred to in Comment 4, with emphasis on the occurrence of vacuolation. It is introduced here from the point of view of the change of pattern with time. On the basis of Comment 4, appearance pattern in the active apex shows a degree of vacuolation, high in mature primary tissues, becoming less and less, progressively towards the superficial centre of the apex (subject to some local variations, e.g., "central mother cells" of cycads, etc.). As the apex attains dormancy, the region of high vacuolation advances nearer to the superficial centre, and may even include that region. Conversely, we may say that the region showing density of cytoplasm progressively contracts about the superficial centre of the apex and may even contract to zero. In terms of process pattern, this appearance shows the region of high vacuolation rate advancing towards, even to include, the superficial centre; or, alternatively, it shows the region of appreciable partition rate contracting about the superficial centre, even to the point of elimination. It should be remarked that the first of these latter alternatives implies inhibition of partitioning. One might go on to analyse this change with time in terms of presence pattern: concentrations and intensities increasing or decreasing and gradients becoming more or less steep. To go further without a basis of observation and experiment in some detail would stretch the hypothetical and speculative to excess.[36]

Change in Orientation of Partition.

Orientation of partition has been discussed in Comment 8 in regard to the validity of some descriptive terms commonly used. Here will be discussed, by way of example, change with time in the relation of tunica and corpus. This is the change with time in the relation of that outer region in the pattern, where the partition walls are constantly tangential to upwardly concave morphogenetic curves described about the superficial centre as focus, to that inner region, where partition walls are not constantly in any one direction. The partitions in the tunica are commonly described as "anticlinal", taken as implying perpendicularity to the surface; but such is not always true, for in the apex of *Vinca rosea* shown in Plate i, figure D, there is clearly no perpendicular relation to the surface, but a clear tangential relation to morphogenetic curves. (See Comment 8 and the references there to Sachs in 1878 and Barenetzky in 1900.)

It is a commonplace in the literature for the tunica to be described with a different number of layers in different apices. Remembering that the classical concept of the tunica-corpus organization implies a duplex apex, we recognize the superposed continuing meristematic residues of both regions as an axial column of length varying according to the number of tunica layers. The morphogenetic curves may therefore be regarded as having their "focus" as a line rather than a point. They will therefore be more or less elongated in the axial direction. In terms of process pattern, the variety in numbers of tunica layers means that the rate of partition orientated other than tangentially to these morphogenetic curves is zero for a variety of depths from the surface, leaving partitions to be only tangential to these curves. Therefore, when it is recorded that in the one plant the number of tunica layers decreases with time, we envisage a change in the process pattern, whereby the region of that zero rate of other than (morpho-

[36] The presence or absence of an appearance of differentiated, vacuolate "central initial cells", "central initial zone", or "primordial meristem", as described by Majumdar (1942, p. 60) Philipson (1949, pp. 25-26) and Reeve (1948, p. 65), respectively, does not affect the general line of the argument. It should be mentioned that Camefort (1956*a*, p. 82) sees the changes to and from dormancy as involving the initial ring almost exclusively, the apical centre having no significance.

genetically) tangential partitioning contracts towards the superficial centre of the apex (or towards the surface?). That is, the region of mingled "periclinal" and other directional divisions advances and may, at least in theory, occupy the superficial centre of the apex, the tunica being eliminated. Because the tunica-corpus concept has been more prominently in our minds for some years, and the other type of seed-plant apex is of more recent promulgation, we are inclined to view the direction of progression as that just given. It is logically as reasonable to view the appearing and increasing of a tunica as arising by the reverse progression—the appearance and enlargement away from the superficial centre of a zone in which the rate of mingled "periclinal" and other directional divisions is zero while the rate of anticlinal division is not zero. As long ago as 1890, Duliot (pp. 298–299), without using the terms current today, described this last progression as the apex of *Araucaria excelsa* passes from the active to the dormant condition (and naturally, *vice versa*). In the terms of the continuing meristematic residue, we have, in the first view, a change from duplex to simplex type of apex, and in the reverse view a change from simplex to duplex.

4. The Meeting of Physiology and Phylogeny.

A phylogenetic trend has already been suggested in the part of the paper dealing with the three basic types of apex. Buder (1928), in outlining the work of his school of apical studies, had already indicated the trend in "Cormophyta" from the single apical cell to "absence" of apical cell and, in the latter case, from one "initial" in gymnosperms to two, three, or four "initials" in storeyed layers in the tunica-corpus apex of angiosperms. (Note the avoidance of the term "apical cell" unless the classical shape is present.) In my terms, this is the phylogenetic trend from monoplex to simplex to duplex apex, the common thread through all being the differential division undergone by the one cell only or by each of a very few commonly contiguous cells to produce continuing meristematic residue (which repeats the differential division) and tissue mother cell (which is at the beginning of Prat's gradient of cell senescence).

Camefort (1956*a*, p. 86), discarding significance of apical initials, has made the common thread in the phylogenetic series the presence of the "initial ring", the trend being bound up with the relationships between this ring, the differences in the apical zone, and the extent of tunica organization. I feel, for reasons given earlier, that the initial ring has not the permanent morphological flavour he would accord it in the apex. It is rather a mathematical concomitant of apical growth in a more or less massive structure. Camefort (p. 82) advances a record to show that for every mitosis observed in the apical centre, there are 100 in the initial ring. But, taking the apex as a conic form (to which many gymnosperm apices approach), it is not difficult to find relative volumes for the two regions of the order of 1:50; and then, allowing for the frequent size ratio of cells as about 2:1, one would expect the number of mitoses in apical and initial ring zones to be in the ratio of the order of about 1:100. But, also, for example, in the massive Brown Alga, *Hormosira banksii*, judging from the figures given by Osborne (1948) there could be produced figures of distribution of mitoses such as Plantefol and his school use for substantiating the concept of the initial ring, the "*anneau initial*". This feature, then, is without phylogenetical, only general physiological significance.

If the apical cell is a logical necessity, its occurrence is universal in apical growth and the phylogenetical question is not whether it is or is not present, but what changes have taken place in its form and activity in the course of evolution? In this connection, it should be emphasized that, once one accepts the duplex type of apex, the number of superposed initials with only anticlinal divisions (commonly the number of tunica layers) is not of much, if any, phylogenetical significance, but is an expression of the physiological situation at the moment. And beyond this, I suggest that the very tunica-corpus organization, itself, is a topographical description of an appearance in the general meristem characterized by differences in disposition of cell partitions irrespective of the basic type of apex (continuing meristematic residue). Obviously it is almost inevitable with the duplex type. Thus, occasional divisions in the "tunica"

that are periclinal (e.g., Cross, 1939*b*, figs 17, 18) do not deny this as tunica; and Reeve (1948, p. 73) warns against formalism in interpreting tissue patterns such as that of tunica-corpus. Thus I doubt the validity of Hamann (1960, p. 404) referring to, say, the third tunica layer as, phylogenetically speaking, derived from an "unstable" corpus layer; or the validity, even for reasons of comparison with other species of a genus, of designating what *appear entirely* as inner tunica layers to be corpus layers. The principle that the tunica-corpus concept is of topographical value only is strongly expressed by Rauh and Reznik (1953, p. 237), and I would emphasize that this topography is the visible expression of the current or immediately preceding physiological situation.

Though the tunica-corpus topography may vary, be constant, or be simulated in the general meristem derived from any of the three basic types of apex, there remains the marked difference in organization of these three apical types—monoplex, simplex and duplex. Here is the central problem posed by phylogeny to physiology. How arose the differences in partitioning of apical cells so that: some, as in ferns, etc., have partitioning always inclined to the apical surface or axis (i.e., parallel to the inclined side walls that meet inwardly at a point or line); some, as in many gymnosperms and the corpus of angiosperms, have partitioning in two directions, parallel with the horizontal, inner (lower) wall and parallel with the side walls that are perpendicular to the apical surface; and some, as for the tunica of angiosperms,[36] have partitioning in directions only parallel with the side walls that are perpendicular to the apical surface? The last two, at least on paper, can be explained by changing gradients of entities controlling "anticlinal" and "periclinal" partitioning. They stand together over against the first one as fundamentally different.

Certain implications confront us. Earlier arguments were based on the idea that this apical neighbourhood, if not the apical cells themselves, is the source or focus of gradients in the control of development. This sounded well at the time, but it now demands thought: firstly, as to the mechanism underlying the sourcehood; secondly, as to the relation of over-all phylogenetic changes to the changes in this source of the controls of development. I can do little more than say that these problems are there to be faced, and that I hope this paper will help to set a background against which they may be considered.

As to the mechanism underlying the sourcehood of the apical cells (or central zone): This will tax to the utmost all our modern techniques of electron microscopy, phase contrast microscopy, the use of labelled elements to trace the origin and synthesis of chemical entities such as nucleic acids and enzymes, micromanipulation *in vivo*, etc., but all applied within smaller and smaller regions of tissue or cell. The procedures applied and the evidence acquired would be, in effect, for the study of the machinery of essentiality, in the apical cell as regulator. This regulating function has been claimed for it in ferns by Wardlaw (1955, p. 399), who wrote, "in the ferns, the apical cell is not only the focal point in the distal meristem but is essential for the continuing regulated growth and regulated morphogenetic activity of the shoot apex", where the characteristic developments of primordia and leaf form are not due to the direct action of substances produced from the apical cell, but more probably "are mediated through the organisation and physiological activity of the apex as a whole, the intact apical cell being a central and essential element of this complex reaction system". We must seek through research in other regions of the Plant Kingdom, the corroborative detail demanded by this general and challenging statement. One of my main theses is that, if such a situation exists in the ferns regarding the apical cell, it must exist in the gymnosperms, angiosperms, and some "fern allies" where the apical cells, not having the classical form, are not directly identifiable, though they must inevitably be present.[37]

[36] For simplicity of argument in this paragraph, derivation of tunica-corpus organization from duplex apex is assumed.

[37] A valuable historical and critical review, particularly about micrurgery, is given by Loiseau (1960). Wardlaw (1960) has given a brief general discussion of problems and approaches to the organization of the apex for shoot production.

Thus we pass to the relation between over-all phylogenetic changes and changes in the form and arrangement of apical cells. This problem is wide open to thought and investigation. Does the change in body form from fern type to gymnosperm type have any connection with the physiological changes involved in the difference between the apical cell with inclined side walls meeting at a point, and the apical cell with parallel side walls joined by an "additional" wall lying parallel with the surface, and with the accompanying requirement of two directions of initial division instead of one? Does the change in body form from gymnosperm type to angiosperm type have any connection with the physiological changes involved in the difference between the presence of only *one* type of apical cell having partitions occurring both perpendicular to and parallel with the surface, and the presence of *two* types of apical cell superposed—the one as before, the other lacking the physiological features determining the occurrence of walls parallel with the surface?[38] Alternatively, the problem of the changes in basic type of apex may possibly be a problem of change in location of the focal point for a system of morphogenetic curves. Suppose such a curve, representing one from Sachs' anticline system (see Text-fig. 2), meets the apical surface at two points (in L.S. of the apex) about one cell-width apart. If the focal point is well within the superficial cell layer, the lateral "anticlinal" partitions (tangential to the curve) will be inclined to the surface and meet inwardly at "a point", as in the Monoplex Apex. If the focal point is near the bottom of the superficial cell layer, the lateral "anticlinal" partitions (tangential to the curve) will approach parallel relationship (perpendicular to the surface) and a lower "anticlinal" partition can appear to join them (parallel with the surface), as in the Simplex Apex. If the focal point is further and further back, out of the surface layer, there appear one or more outer cell layers with "anticlinal" partitions (tangential to the curve) *only perpendicular* to the surface and one innermost cell layer at the focal region with partitioning like that in the Simplex Apex—namely, the tunica and corpus initial regions of the Duplex Apex.

It is necessary to be cautious at the end, when we look at the genetics rather than the phyletics of phylogeny. Where we have been speaking of change from one type of apex to another, we have been speaking of genetical mutation. But at first sight these are not "small" mutations such as the introduction of crinkling into a petal or a change of length in the hair of a fly; they are "large" mutations covering extensive differences in plant form accompanying the apical changes. Expressed in terms that do not appeal widely today to geneticists, we may be dealing with, not micromutations accumulating to microevolution by producing new specific and subspecific taxa, but with macromutations leading by jumps to macroevolution by sudden new appearances of taxa of high rank. As proposed by Goldschmidt (e.g., 1952*a* and *b*, 1953), the macromutation involves the appearance of a mutant gene or gene complex that acts early enough in embryology to alter radically or to change completely the nature of the organ involved—a homoeotic mutation. This, supported by the presence of modifiers, provides what, I suggest, might be thought of as a "constellated" mutation—the macromutation—which forms a workable system. Goldschmidt conceives, thus, the rare, sudden appearance of new high-ranking taxa—division, order, family—which by micromutations are gradually diversified into more and more taxa of lower rank. Commonly current genetics is strongly opposed to this, claiming there is only one kind of mutation and evolution in this connection, and the battle seems to have died down in their favour. Moreover, the determinate growth of animals facilitates interpretation of mutations in terms of the time of application in the course of a single embryological development; but this is not so easily done in the case of the higher plants with indeterminate growth and what one might call a repetitive embryological development at the growing apex.

I am not competent to enter the genetical field of battle around the idea of macroevolution. The point for us here is that in these changes of apical cell type, expressed in differences of form, arrangement and partitioning, and which seem to be related to

[38] Perhaps the words "change . . . from . . . to . . ." may be too old-fashioned for some phylogeneticists. They may substitute "difference between . . . and . . ."

phyletic differences in morphology, we are dealing with mutations—whether single or "constellated"—which could be prizes over which that battle of evolutionary genetics might flare again. Only when the battle is won would the labels on the prizes be finally known.

Conclusion.

Setting aside these debatable points, I would close by affirming three convictions.

Firstly: There exists the continuing meristematic residue which is the initiator of cellular structure and which, in the apex, may be called the apical cell or cells, whether directly discernible by shape, or not. Its existence is logically necessary. It is not a permanent cell or cells, but an hereditary line of cells, each of which, from its institution by division of the previous office-holder till it divides, itself, holds the office of continuing meristematic residue (or apical cell).

And secondly: As to types of apex in vascular plants, no sound analysis can be based on the general meristem which is under such varied and varying physiological influence; but there are only three fundamental types, based on the activity and arrangement of the continuing meristematic residue—the monoplex apex, the simplex apex, and the duplex apex, as described in the foregoing pages.

And thirdly: Cellular structure may be regarded as though "flowing" back from a fount of origin (the continuing meristematic residue) in the distal centre of the apex. The appearance of the cellular structure shows a pattern, at any moment, determined by the physiological pattern which is fixed in regard to the fount of origin as point of reference.

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EXPLANATION OF PLATES I-II.

Plate i.

Selected photographic reproductions of vegetative stem apices illustrated by various authors. The plants are listed below with the approximate magnifications of the figures; with the exception of E, L and M, they represent photomicrographs. The detailed descriptions and sources of the figures are given in Table 2; they are all of adult plants in active growth.

A, *Sequoia sempervirens* × 120. B, *Chrysanthemum morifolium* × 120. C, *Lonicera caprifolium* × 120. D, *Vinca rosea* × 240. E, *Cymodocea æquorea* × 120. F, *Pseudotsuga taxifolia* × 120. G, *Washingtonia filifera* × 120. H, *Torreya californica* × 120. I, *Ginkgo biloba* × 120. J, *Echinocereus reichenbachii* × 120. K, *Dioon edule* × 60. L, *Aspidium filix-mas* × 120. M, *Pinus lambertiana* (dwarf shoot) × 120. N, *Podocarpus totara* × 120.

Plate ii.

Reproductions and originals showing cellular pattern at the apical centre of several plants Except for E, E^1 and F, they are or represent photomicrographs.

A.—A vertical view of possible apical cells from Dermen's study of Cranberry (1945, fig. 3). Compare figure C here and Text-figure 10E or $10C_{2-3}$. × 500.

B.—A vertical view of the central region of the apex from Boke's study of *Echinocereus reichenbackii* (1951, fig. 9). This can show a great area of cells because of the breadth of the apex (see Plate i, Figure J) which would make for a more extensive following of cell lineages than in the narrower apices (cf. A, C and D_{1-4} here and the L.S. aspect of apices on Plate i). Note the general resemblance of the appearance here to the theoretical construct in Text-figures $10C_2$ or C_3. × 250.

C.—An original photograph by reflected light of the living scaly apex of the long shoot of *Pinus radiata*. The illumination was as for the earlier study of living apices (Newman, 1956*a*), except that a round-bottomed 500 c.c. flask containing a dilute solution of cuprammonium hydroxide was used as a combined condenser and heat filter. The microscope was one of the common kinds and the camera a Leitz camera attachment. The plates used were Kodak Super XX. The apex was prepared by cutting off the tip of the investing scales and removing the inner immature scales till the apical dome was revealed at the bottom of a protective cup formed by the truncated remaining outer scales. It was necessary to add a plasticine collar to raise the effective rim of this cup. The scaly bud cut off just below the investing scales was held in position on the bottom of the culture vessel with plasticine. Tap-water (Melbourne) was used without supplement. The photograph shown is the best sample from a series of four taken over one and two-thirds days without sign of cell division—the apex was approaching dormancy as the time of year was mid-February. Note the three centrally placed cells forming a group resembling that shown for Cranberry in figure A of this Plate and comparable, possibly, with the central cells in *Tropaeolum* shown in Text-figure 10E. × 160.

D_{1-4}.—As for C, in all respects, except that these are the four members of a complete series from another apex taken over two and two-thirds days in May, when dormant. The cell arrangement at first sight resembles that shown for *Coleus* (Text-figure 10F) and for *Ephedra monostachya* (this Plate, Fig. F). This may be accidental (*Pinus* is not decussate like those plants) and attention should be given to a group of three at the top (left) of the prominent double row, more resembling figure C of this Plate. × 160.

E.—A reduction of Dingler's (1886) figure 10 of L.S. of the apex of *Abies balsamea*, showing absence of a pyramidal apical cell. Dingler's tentative identification of the apical cell is shown by the small dot, which, in the original, is a v. Compare Text-figure 10D. × 250.

E′.—Dingler's (1886) theoretical figure 10a giving his *tentative* interpretation of the division sequence of a not pyramidal apical cell to give the cell pattern shown in his figure 10 (figure E on this Plate). He numbers the walls in inverse order of age. This figure has not been reduced in reproduction.

F.—A reduction of a surface view of the apex of *Ephedra monostachya* from Dingler's (1886) figure 8. This, from a decussate plant, is to be compared with the apex of *Coleus* shown in Text-figure 10F. Dingler was uncertain whether to attribute apical cell status to the four cells w, x, y, z. The biconvex cell at the right was interpreted as apical cell in a leaf primordium. × 250.

NEW AND LITTLE-KNOWN LAELAPTIDAE, TROMBICULIDAE AND LISTROPHORIDAE (ACARINA) FROM AUSTRALASIAN MAMMALS.

By Robert Domrow, Queensland Institute of Medical Research, Brisbane.

(Sixty-two Text-figures.)

[Read 29th March, 1961.]

Synopsis.

Seventeen new species of mites parasitic on Australasian marsupials, rodents and bats are described in the families Laelaptidae, Trombiculidae and Listrophoridae. Two previously unknown males are also described, and additional host and locality data for 23 little known species are given.

In the Laelaptidae, nine new species are described: *Haemolaelaps quartus,* n. sp., from a rat-kangaroo, *Aepyprymnus rufescens,* New South Wales; *Haemolaelaps ulysses,* n. sp., from a ring-tailed possum, *Pseudocheirus peregrinus laniginosus,* Victoria; *Laelaps breviseta,* n. sp., and *L. mackerrasi,* n. sp., from the allied rat, *Rattus assimilis,* north Queensland; *Laelaps calabyi,* n. sp., from a native mouse, *Pseudomys higginsi,* Tasmania; *Neolaelaps vitzthumi,* n. sp., from a fruit-bat, *Pteropus scapulatus,* Northern Territory; *Pneumonyssus dentatus,* n. sp., from a marsupial mouse, *Antechinus flavipes godmani,* and a scale-tailed rat, *Melomys cervinipes,* north Queensland; *Raillietia australis,* n. sp., from the common wombat, *Phascolomis mitchelli,* New South Wales; *Trichosurolaelaps harrisoni,* n. sp., from the musk rat-kangaroo, *Hypsiprymnodon moschatus,* north Queensland.

New records are given for *Australolaelaps mitchelli, Gymnolaelaps annectans, Haemolaelaps domrowi, H. marsupialis, Hirstionyssus musculi, Ichoronyssus aristippe* (male described for first time), *Laelaps assimilis, Mesolaelaps antipodianus, M. australiensis, M. bandicoota, M. sminthopsis, Neolaelaps spinosus, Peramelaelaps bandicoota, Spinolaelaps miniopteri, Trichosurolaelaps crassipes, T. emanuelae* and *T. striatus.*

In the Trombiculidae, two new species are described: *Trombicula alicola,* n. sp., from a bat, *Rhinolophus megaphyllus*; *Neotrombicula comata,* n. sp., from a marsupial bandicoot, *Isoodon macrourus.*

New records are given for *Guntherana andromeda, G. philippensis, G. cassiope* and *G. kallipygos.*

In the Listrophoridae, six new species are described: *Austrochirus mcmillani,* n. sp., from a marsupial bandicoot, New Guinea; *Austrochirus trouessarti,* n. sp., from a marsupial mouse, *Antechinus flavipes godmani,* north Queensland; *Cytostethum mollisoni,* n. sp., from a rat-kangaroo, *Potorous tridactylus,* Tasmania; *Cytostethum clibanarius,* n. sp., from a rat-kangaroo, *Aepyprymnus rufescens,* north Queensland; *Cytostethum parvum,* n. sp., and *C. moschati,* n. sp., from the musk rat-kangaroo, *Hypsiprymnodon moschatus,* north Queensland.

New records are given for *C. promeces* and *C. pseudocharactum,* the male of the latter being described for the first time.

During the past two years, Dr. J. L. Harrison, at the Institute's Field Station, has been studying the ecology of the small mammals of the Innisfail district in north Queensland, as part of a wider investigation of the epidemiology of leptospirosis in that area. It has been an integral part of this work that collections of ectoparasites have been made from the mammals brought into the laboratory, the result being a very large collection, which has come to me for study. It has included numerous new species, some of which are described here as a preliminary to a distributional analysis of the material.

The opportunity has also been taken to include a number of other new species and new host and distributional records in these families, based mainly on material received from Mr. J. H. Calaby, C.S.I.R.O. Wildlife Section, Canberra, and Dr. Bruce McMillan, School of Public Health and Tropical Medicine, Sydney.

Family LAELAPTIDAE.

The family is taken in the sense of Vitzthum (1940–43), and the genera and species are arranged alphabetically.

Genus Australolaelaps Womersley.

Australolaelaps mitchelli Womersley, 1956.

A second record of this species, originally described from the dama pademelon, *Thylogale eugenii* (Desmarest) (Macropodidae) in South Australia, is eleven females from the black-striped wallaby, *Protemnodon dorsalis* (Gray), Mt. Lindesay, S.E.Q., 24.iv.1960, J. H. Calaby and party.

Genus Gymnolaelaps Berlese.

Gymnolaelaps annectans Womersley, 1955.

This species is probably a nidophile rather than a true parasite, and may prove to belong in *Laelapsis* Berlese. It was originally recorded from the nests of mutton birds, and associated with *R. rattus* (Linné). I have since seen the following material: 1♀ off rabbit (*Oryctolagus cuniculus* (Linné)), Exmouth, N.S.W., 17.v.1955, E. J. Waterhouse; 1♀ off rabbit, "Cherry Hill", Uralla, N.S.W., 2.vi.1955, E.J.W.; 1♀ off hare (*Lepus europaeus* Pallas), Chiswick, 10 miles south of Armidale, N.S.W., 5.vii.1955, E.J.W.; 5♀♀ from *R. norvegicus* (Berkenhout), Unley Park, S.A., ACC 240, 19.xi.1950, R. V. Southcott.

Genus Haemolaelaps Berlese.

Haemolaelaps domrowi Womersley, 1958.

This species was originally described from the long- and short-nosed bandicoots, *Perameles nasuta* Geoffroy and *Isoodon macrourus* (Gould)[1] (Peramelidae), from Queensland, and has since been recorded from *I. m. moresbyensis* (Ramsay) and another bandicoot, *Peroryctes raffrayanus raffrayanus* (Milne-Edwards) from Papua by Domrow 1958*a*). I have since seen a further four females from *I. m. moresbyensis*, within five miles of Port Moresby, Papua, Sept. 1959, I. Cook, while the following records extend the known southward range: numerous specimens, *I. macrourus*, Tooloom, N.S.W., 19.viii.1960, J. H. Calaby; 3♀♀, *Perameles gunnii* Gray, Guildford Junction, Tasmania, 21.iv.1959, B. C. Mollison.

Haemolaelaps marsupialis Berlese, 1910.

This species was originally described from a bandicoot from Sydney, and has since been recorded from *Perameles nasuta* and *Isoodon macrourus* from Queensland by Womersley (1958). The following records extend the known range southward: 9♀♀, *I. macrourus*, Tooloom, New South Wales, 20.ii.1960, J. H. Calaby; 29♀♀, *Perameles gunnii*, Guildford Junction, Tasmania, 21.iv.1959, B. C. Mollison; 14♀♀, *I. obesulus* (Shaw), Maydena, Tas., 17.xii.1959, T. Anderson.

Haemolaelaps quartus, n. sp. (Figs 1–2, 8).

Types: Holotype female in Division of Entomology, C.S.I.R.O., Canberra, in Hoyer's medium; from a rat-kangaroo, *Aepyprymnus rufescens* (Gray) (Macropodidae), Peacock Creek, Bonalbo, N.S.W., 8.viii.1960, J. H. Calaby.

Female.—A large, stout species, length of idiosoma 980μ in slightly distended specimen.

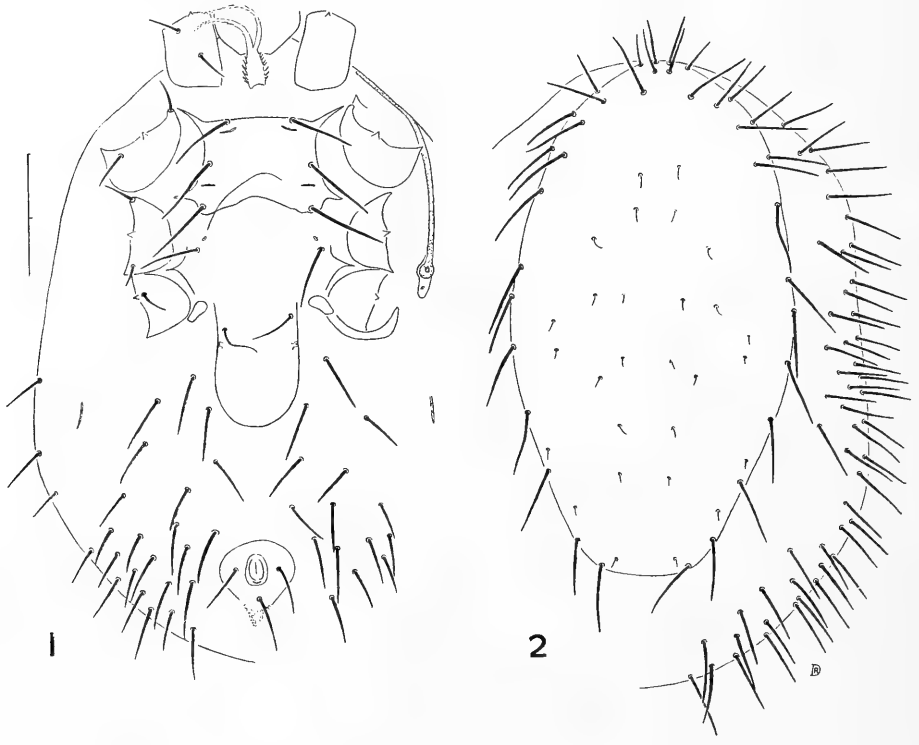
Dorsum: Dorsal shield without distinct reticulate striae (as are the ventral shields), rather small, leaving a broad band of lateral and posterior cuticle uncovered. Setae on dorsal shield of two distinct types, the 18 lateral pairs being four to five times as long as the 14 minute discal pairs. Dorsal cuticle very hairy, with about 50 setae on each side.

Venter: Sternal shield rather weak, with lateral and posterior margins concave; with six setae and four well-marked lyriform pores. Metasternal setae and pores present. Genital plate much reduced, its margin discernible by the cessation in cuticular striae rather than by a definite edge. It extends only as far as the second pair of ventral setae usurped by the genitoventral plate in *Laelaps*. One pair of rather short genital setae are present. Genital operculum longitudinally striate at level of metasternal complex, and reaching forward over posterior border of sternal shield. Anal plate

[1] The nomenclature of this species and *I. obesulus* (Shaw) is discussed by Mackerras and Mackerras (1960).

roundly arched anteriorly, but more angular posteriorly; with three subequal anal setae as figured. Ventral cuticle with weakly defined metapodal plates, and about 25 pairs of setae. Peritremes reaching forward to level of coxae I; stigmata simple; peritremalia extended slightly behind stigmata, with a pore, but not fused with articulatory lunule behind coxae IV.

Legs: Coxal setal formula 2.2.2.1, all setae being completely unmodified. Without stronger setae dorsally on femora I & II. Most setae on legs, posterolateral body cuticle, and margins of dorsal shield minutely barbed. Setae on sternal and genital plates nude, but those on anal plate also barbed.



Text-figs 1-2.—*Haemolaelaps quartus*, n. sp. Female. 1, Venter; 2, Dorsum. (In all figures, one division of the scale equals 100μ.)

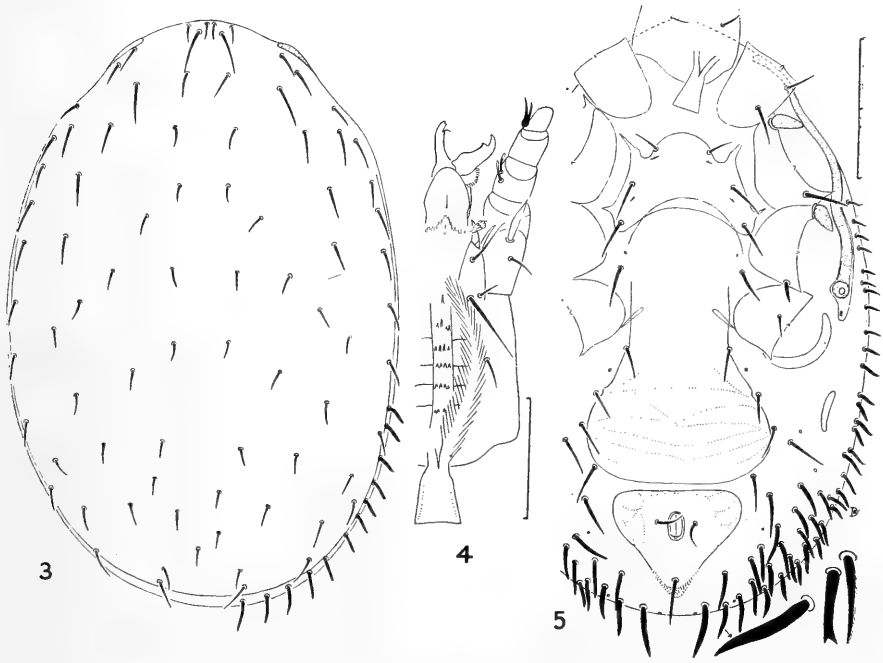
Gnathosoma: Tritosternal base strongly barbed laterally; laciniae normal, extending forward to base of hypostome. All hypostomal and gnathosomal setae subequal, except rather smaller outer posterior hypostomals. Labial cornicles not as strongly developed as in *Laelaps*. Salivary stylets present. Deutosternum with seven groups of 1–4 minute denticles. Palpi slender, with bifurcate tarsal claw. Two setae on inner face of genu clavate (this character is also present at least in *H. marsupialis* and *H. domrowi*). Chelicerae as in genotype; movable finger with two weak teeth, and surrounded basally by weakly defined corona; fixed finger edentate, with flagelliform, but basally slightly inflated pilus dentilis.

Notes.—Haemolaelaps quartus, n. sp., is the fourth species to be assigned to the *marsupialis* complex as treated by Womersley (1958). These four species are all Australian, and are characterized by the strongly barbed tritosternal base, and the flagelliform pilus dentilis. The three known species (*H. marsupialis* Berlese, genotype; *H. flagellata* Wom.; *H. domrowi* Wom.) have 39 pairs of setae on the dorsal shield, and a well-developed genital plate (noticeably expanded behind coxae IV, and extending back as far as the third pair of ventral setae usurped by the genitoventral shield in *Laelaps*).

In *H. quartus*, there are only 32 pairs of setae on the dorsal shield, and the genital plate is scarcely expanded at all behind coxae IV (extending back only as far as the second pair of ventral setae usurped in *Laelaps*).

HAEMOLAELAPS ULYSSES, n. sp. (Figs 3–5).

Types: Holotype female in Queensland Museum, Brisbane, and two paratype females each in Department of Zoology, University of Melbourne; British Museum (Natural History), London; U.S. National Museum, Washington, D.C. All seven specimens are in Hoyer's medium, and were taken from the ears of a ring-tailed possum, *Pseudocheirus peregrinus laniginosus* (Gould) (Phalangeridae), Warramate Hills, near Lilydale, Victoria, J. A. Thomson, 17.vii.1960.



Text-figs 3-5.—*Haemolaelaps ulysses*, n. sp. Female. 3, Dorsum; 4, Gnathosoma; 5, Venter, with insets showing posterolateral body seta and two setae from femur IV. These are at twice the scale indicated for the gnathosoma.

Female.—A pale brown, well-sclerotized species with idiosoma 814–847μ (av. 829) long.

Dorsum almost entirely covered by dorsal shield, except for extremely narrow posterolateral strip. All dorsal setae short and evenly tapering, arranged in regular pairs, except in posterior quarter; about 40 pairs of setae are present on the shield. Marginal cuticle with about 12 pairs of stronger setae similar to those on venter.

Venter: Sternal shield small, and of characteristic shape. Anterior margin with two semicircular concavities outside sternal setae I, but strongly arched medially. Posterior margin also strongly concave. The usual three pairs of setae and two pairs of pores are present on the shield. Metasternal setae and pores free in cuticle. A pair of weak internal sclerotizations are present between coxae IV. Genitoventral plate expanded behind coxae IV, with only one pair of setae on the shield, but closely flanked by another three pairs. Anal plate large, and well sclerotized, with anus and three anal setae as figured. Both the genital and anal shields bear linear striations as shown. Metapodal plates well marked, elongate. Ventral cuticle with

several minute sclerotized plaques, and about 45 pairs of strong setae. The lateral setae are spinose, but more posteriorly the setae are peculiarly curved. Peritremal structures typical of the genus, and not fused with articulatory lunule behind coxae IV.

Legs rather stout, with stronger setae on tarsi II-IV. All tarsi with caruncle and two claws. Femora I & II without elongate setae dorsally. Anterior seta on coxae II & III much expanded, and very blunt. Otherwise undistinguished, except for several apically bifurcate setae along the anterodorsal face of the central segments of all four legs.

Gnathosoma: Tritosternal base not dentate laterally; laciniae strongly ciliated. Labial cornicles fairly well developed. Hypostomal and gnathosomal setae as figured. Deutosternal groove with five transverse rows of about four denticles each, and a single anterior denticle. Hypostomal processes, epipharynx, and salivary stylets as figured. Chelicerae with both digits dentate; fixed digit with weak pilus dentilis. Palpi undistinguished, except for clavate setae on genu, and foliate seta on trochanter. Palpal claw two-tined.

Notes.—Haemolaelaps ulysses, n. sp., may be immediately recognized by its peculiar sternal shield, its large genital and anal shields, and the setation of the coxae and palpal trochanter. In these respects, it is not typical of the genus *Haemolaelaps*, although it falls here both in Strandtmann and Wharton's (1958) and Tipton's (1960) keys.

Genus Hirstionyssus da Fonseca.

Hirstionyssus musculi (Johnston, 1849).

The following specimens have been identified according to Bregetova (1956): 6♀♀, *Mus musculus* Linné, Mt. Tyson, near Toowoomba, Queensland, 30.vii.1959, E. H. Derrick (associated with *Mesolaelaps australiensis* Hirst); 1♀ and 1 nymph, *Rattus rattus*, Yarralumla, Australian Capital Territory, 7.iii.1960, J. H. Calaby. The specimens recorded from *M. musculus* by Womersley (1956) as *H. arcuatus* (Koch, 1839) are also conspecific with the above material.

Genus Ichoronyssus Kolenati.

Ichoronyssus aristippe Domrow, 1959 (Figs 6, 7).

Types: Allotype male in Queensland Museum, Brisbane, collected with one nymph of the same species, and three nymphs of a related, but much hairier species, on the type host, a bat, *Miniopterus schreibersii blepotis* (Temminck) (Vespertilionidae), Bonalbo Colliery, Bonalbo, N.S.W., 17.viii.1960, J. H. Calaby.

Male.—About same size as female, idiosoma 696μ long in somewhat distended condition.

Dorsum: Dorsal shield parallel-sided in anterior three-quarters, but tapering and truncate posteriorly; with pattern of reticulate striae and pores. Sixteen pairs of elongate marginal setae are present on the shield, one pair less than is usual in the female. In addition, there are normally sixteen minute discal setae present (one of these is absent in the allotype, but these minor variants are to be expected). Marginal cuticle not as hairy as in female, with only six setae on each side.

Venter: All ventral shields with reticulate striae. Intercoxal shield terminating roundly at level of posterior margin of coxae IV; with five pairs of setae and three pairs of pores. Ventral shield irregular in outline, and fused posteriorly with anal shield; with two pairs of usurped setae. Anal shield also irregular in outline, elongate, and with usual three setae and barbules as shown. Ventral cuticle with fourteen setae arranged 8.6. Peritremes reaching forward to middle of coxae II; peritremalia fused with articulatory lunule behind coxae IV.

Legs: Femora and genua I & II with one or two stronger setae dorsally. Coxae II-IV with crescentic striae in posterior half. Anterodorsal process on coxae II with retrorse spine on external edge, as in female.

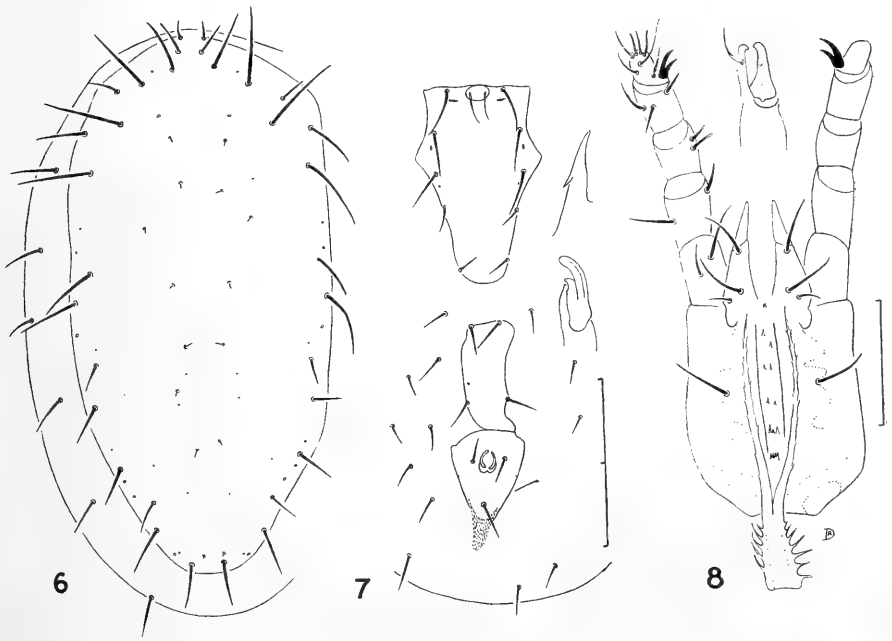
Gnathosoma: Palpal trochanter modified on ventro-internal margin. Chelicerae with fixed finger weak and edentate. Movable finger with single weak tooth. Spermatodactyl somewhat longer than movable finger, and curved apically.

Nymph.—The stage originally illustrated is the protonymph, and has four platelets between the antero- and posterodorsal shields. On the posterodorsal shield, the posterior pair of setae set outside the larger pair may be somewhat stronger than figured.

Genus Laelaps Koch.

Laelaps assimilis Womersley, 1956.

This species is common on the type host, the allied rat, *Rattus assimilis* (Gould), in Queensland. The following are new hosts and localities: numerous specimens of both sexes from *R. assimilis*, Palen Ck., S.E. Queensland, 18.v.1960, I. Cook and R.D.; *R. lutreolus velutinus* (Thomas), Florentine Valley, Tasmania, 7.vii.1959, B. C. Mollison; *R. l. velutinus*, Depot Bridge, Maydena, Tas., 7.ix.1959, B.C.M.



Text-figs 6-7.—*Ichoronyssus aristippe* Domrow. Male. 6, Dorsum; 7, Venter, with insets showing chelicera and anterodorsal process of coxa II. These are at twice the indicated scale.
Text-fig. 8.—*Haemolaelaps quartus*, n. sp. Female. Gnathosoma.

Laelaps brevisèta, n. sp. (Figs 9–11).

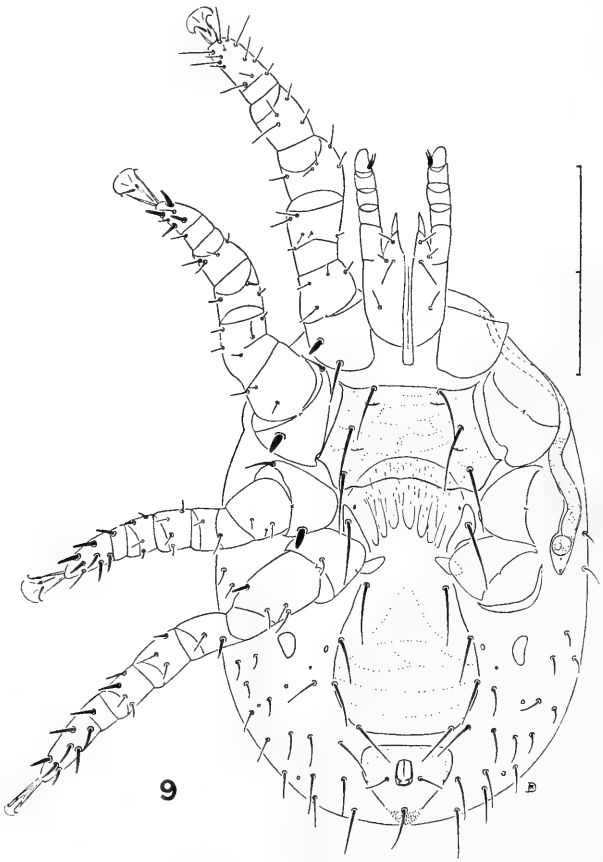
Types: Holotype female in Queensland Museum, Brisbane, and one paratype female in Queensland Institute of Medical Research, Brisbane. Both these specimens are in Hoyer's medium, and were collected on an allied rat, *Rattus assimilis* (Gould) (Muridae), trapped alive in rain-forest, Dinner Ck., near Innisfail, north Queensland, 23.ix.1959, J. L. Harrison. An additional seven paratype females have been distributed between this Institute; British Museum (Natural History), London; U.S. National Museum, Washington, D.C. These are in polyvinyl alcohol-lactophenol, and were taken from the same host and locality, 21.x.1959, 16.xii.1959, and 19.v.1960, J.L.H.

Female.—A rather small, broadly oval species, with stout legs. Length of idiosoma in mounted specimens 490–517μ.

Dorsum: Dorsal shield broadly oval, covering entire dorsum except for extremely narrow lateral strip; with 39 pairs of setae. All these setae are very short, except for

the verticals and the extreme posterior pair. On the disc, the setae are barely one-quarter as long as the interval between their bases. A regular system of pores is present.

Venter: Sternal shield wider than long, with posterior margin weakly concave and slightly irregular; with usual six setae and four pores. Metasternal setae set on distinct platelets, but metasternal pores free in cuticle. With pair of oval internal sclerotizations between coxae IV. Genitoventral plate as wide as long (see Domrow, 1958*a*), with setae barely as long as interval between their bases. Genital operculum striate, reaching forward to level of sternal setae III. Anal plate narrowly separated from genitoventral plate, broad, and with setation as figured. Metapodal plates distinct.



Text-fig. 9.—*Laelaps breviseta*, n. sp. Female. Venter.

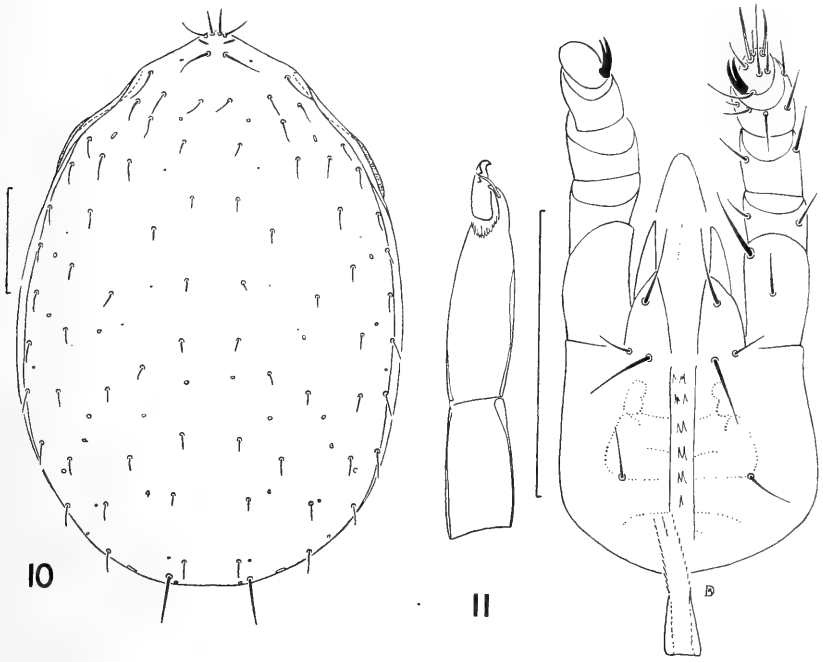
All ventral plates with striae as figured. Ventral cuticle with about 15 pairs of setae, which increase in length posteriorly. Peritremalia not extending around posterior margin of coxae IV; with two small pores.

Legs: Coxal setal formula 2.2.2.1, the anterior seta of coxae I and the posterior setae of coxae II and III being markedly thickened and spine-like. Femora I & II dorsally with two and one longer setae, respectively. Tarsi II-IV with spinose setae. All tarsi with caruncle and two claws.

Gnathosoma: Tritosternum apparently normal. Outer posterior pair of hypostomal setae about half as long as other two pairs, which are also slightly longer than the gnathosomal pair. Deutosternum with about five duplex denticles, and one single denticle posteriorly. Labial cornicles well developed. Epipharynx evenly tapering, but

slightly rounded distally; groove not reaching apex. Chelicerae typical. Palpi undistinguished, with bifurcate tarsal claw.

Notes.—In my key (1958*a*) to the Australasian species of *Laelaps*, *L. breviseta* comes nearest to *L. nuttalli* Hirst. It may be easily separated from this species by the relative proportions of the dorsal, genitoventral and anal shields, and by the great disparity in size of the dorsal and genitoventral setae.



Text-figs 10-11.—*Laelaps breviseta*, n. sp. Female. 10, Dorsum; 11, Gnathosoma.

LAELAPS CALABYI, n. sp. (Figs 12–17).

Types: Holotype female, allotype male, and four paratypes of each sex in Division of Entomology, C.S.I.R.O., Canberra. These specimens are all in Hoyer's medium, while a further 80 paratype females and eleven paratype males in spirit, together with a few nymphs, have been distributed among Queensland Institute of Medical Research, Brisbane; South Australian Museum, Adelaide; South African Institute for Medical Research, Johannesburg; British Museum (Natural History), London; U.S. National Museum, Washington, D.C. These specimens are all from three native mice, *Pseudomys higginsi* (Trouessart) (Muridae), Dawson Settlement, Tasmania, 19.vi.1959, J. H. Calaby; Florentine Valley, Tas., 6.vii.1959, B. C. Mollison; Maydena, Tas., 8.vii.1959, B.C.M.

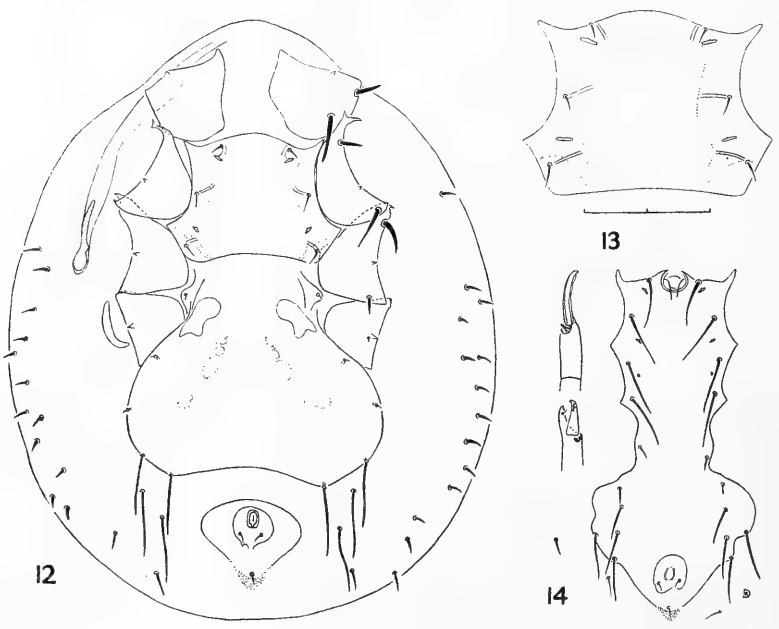
A further four females, four males and two nymphs from the first collection are in polyvinyl alcohol-lactophenol, and have not been included in the type series.

Female.—A dark, very broad, and almost subcircular species. Specimens of this sex may be rather sharply divided into two groups on size. The smaller averages 884μ (range 847–902), the larger averages 1,338μ (range 1,298–1,364). An occasional specimen may be smaller still, e.g., 792μ, or intermediate in size, e.g., 1,177μ. These measurements are the length of the idiosoma, taken from freshly mounted and little compressed material.

Dorsum: Dorsal shield emarginate posterolaterally, and somewhat truncate posteriorly; with 34 pairs of setae, all of which are very short except the posterior pair. A broad marginal band of cuticle is left uncovered, and bears five to seven pairs of

short setae. The inner half of this band, especially in larger specimens, is sclerotized, and quite distinct from the almost colourless outer half.

Venter: Sternal shield particularly well sclerotized marginally; slightly convex anteriorly and slightly concave posteriorly. With six very short setae and four pores as figured. Metasternal setae minute, but set on well-marked metasternal plates. Metasternal pores not detected. With internal sclerotization between coxae IV as figured. Genitoventral plate grossly expanded behind coxae IV, noticeably broader than maximum width of sternal plate, and slightly concave posteriorly. Anterior two pairs of genitoventral setae minute, and posterior two pairs very much longer. Anal plate about as broad as long, with three small subequal setae. Ventral cuticle with two pairs of sinuous setae like those on posterior half of genitoventral plate, in addition to 14 or 15 pairs of short spinose setae. Peritremal plate extending forward to beyond coxae I, but peritremes themselves abbreviated, and lying above coxae III.



Text-figs 12-14.—*Laelaps calabyi*, n. sp. Female. 12, Venter of smaller form; 13, Sternal plate of larger form; 14, Male holoventral shield, and chelicerae of both sexes.

Legs: Coxal setal formula 2.2.2.1, those on I-III all somewhat thickened, while that on IV is very minute. One very long seta dorsally on femora I, and one or two stouter setae on femora I & II and genu I.

Gnathosoma: Tritosternal base narrow, merging into two slender ciliated laciniae, which reach the level of the anterior hypostomal setae. All three pairs of hypostomal setae and gnathosomal pair subequal. Deutosternum with file of about six single denticles. Labial cornicles well developed. Epipharynx slightly clavate, uniformly spiculate ventrally, and with dorsal groove reaching apex. Chelicerae and palpi as usual.

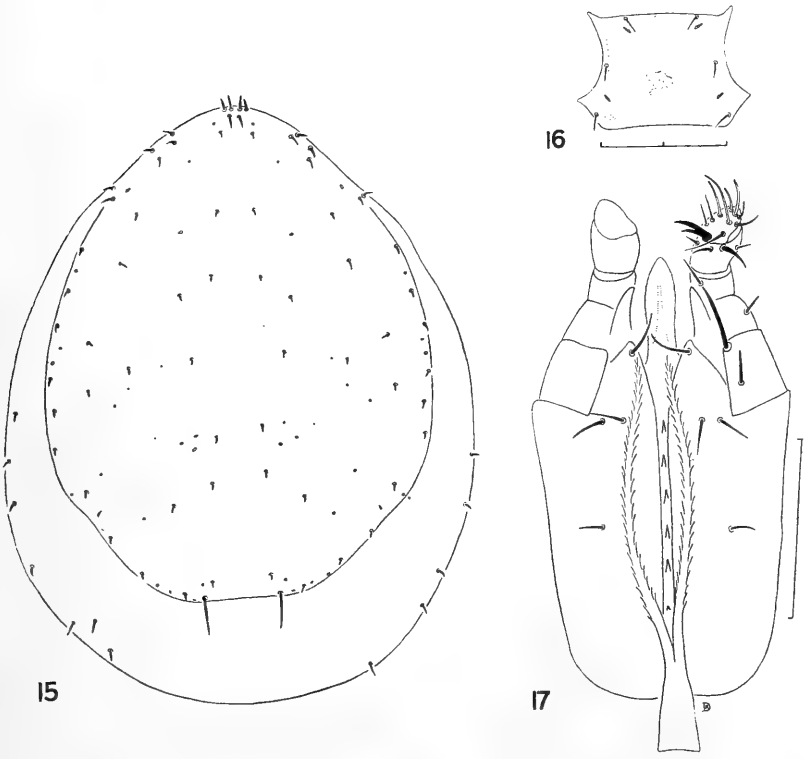
Male.—Length of idiosoma 704–1,034μ.

Dorsum as in female.

Venter: All ventral plates fused to form holoventral plate. Sternal and metasternal setae long and subequal. Genital and first pair of usurped ventral setae much shorter. Four pairs of long sinuous usurped ventrals are also present. One or two pairs of short setae are present on the ventral cuticle.

Legs and gnathosoma as in female, except for chelicerae. Spermatodactyl apparently tubular, about as long as middle segment of chelicerae, and weakly curved.

Notes.—Laelaps calabyi, n. sp., is closely related to *L. finlaysoni* Womersley, which was also described from native mice (*Pseudomys apodemoides* Finlayson and *P. minnie* Troughton), but in South Australia. I am grateful to Messrs. H. M. Hale and H. Womersley for the opportunity to examine three females and one male from the type series of *finlaysoni*. The two species share the following characters: peritremes much abbreviated; dorsal setae minute; anterior two pairs of genitoventral setae minute; setae on coxae I-III well developed, but that on IV minute; metasternal setae minute;



Text-figs 15-17.—*Laelaps calabyi*, n. sp. Female. 15, Dorsum of smaller form; 16, Sternal plate of a particularly small specimen; 17, Gnathosoma.

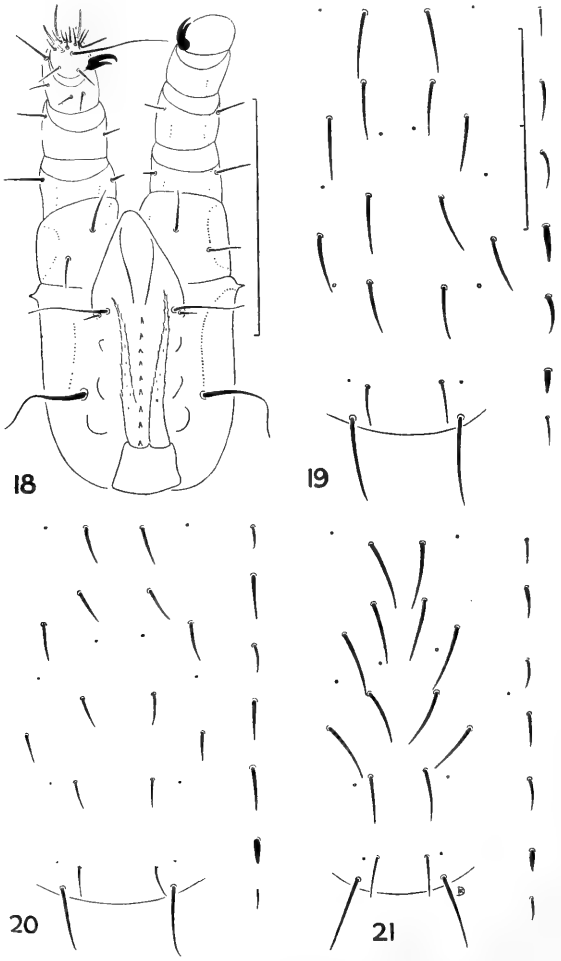
peculiar texture of sternal shield. They may also, however, be readily separated by several characters—the width of the genitoventral plate relative to that of the sternal plate; the proportions of the anal plate; and the length of the postanal seta relative to that of the adanals.

The occurrence of two sizes of females in *L. calabyi* has been noted above, but may be further analysed here. In the three series examined, the number of normal and giant specimens were respectively 13/1, 13/25 and 16/18. Only three specimens fell outside the two ranges. A similar phenomenon occurs in the related species *L. rothschildi* Hirst, but here the small form occurs almost exclusively on rats of the genus *Melomys*, while the giant form occurs on *Uromys*.

L. rothschildi is classified by Strandtmann and Wharton (1958) as a *Mysolaelaps*, and *L. calabyi* would also key out here in their system. However, they list *finlaysoni* as a *Laelaps*. I am not convinced that *Mysolaelaps* merits generic rank.

LAELAPS MACKERRASI, n. sp. (Fig. 20).

Types: Holotype female and five paratype females in Queensland Museum, Brisbane, from an allied rat, *Rattus assimilis* (Gould) (Muridae), rain-forest, Dinner Ck., near Innisfail, north Queensland, 10.vi.1959, J. L. Harrison. Thirty-one paratype females from the same host, habitat and locality have been distributed among the Queensland Institute of Medical Research, Brisbane; Division of Entomology, C.S.I.R.O., Canberra; South Australian Museum, Adelaide; South African Institute for Medical Research, Johannesburg; British Museum (Natural History), London; U.S. National Museum, Washington, D.C. The entire type series is in polyvinyl alcohol-lactophenol.



Text-fig. 18.—*Neolaelaps vitzthumi*, n. sp. Female. Gnathosoma.

Text-figs 19-21.—*Laelaps* spp. Posterior portion of dorsal shield of female, together with coxal setae. 19, *L. southcotti* Domrow; 20, *L. mackerrasi*, n. sp.; 21, *L. habrus* Domrow.

Female.—Generally as in *L. southcotti* Domrow, 1958*a* (Fig. 19), but somewhat smaller. Length of idiosoma in mounted specimens 660–682μ.

Dorsum: Dorsal shield with 39 pairs of setae, and regular pattern of pores. Setae on posterior half of disc 32–41μ long, i.e., one-half to two-thirds as long as the interval between them.

Venter: Genitoventral plate distinctly longer (165–178μ) than broad (147–156μ); width between fourth pair of setae 94–103μ, but occasionally as narrow as 80μ. Successive genitoventral setae longer than interval between them.

Legs: Coxal formula 2.2.2.1. All coxal setae unexpanded and tapering, except posterior seta on coxae III, which is distinctly thickened and spinose. Tarsi II-IV with several stronger setae. Femora I and II with two and one seta respectively on dorsal surface, which are twice as strong as adjacent setae.

Gnathosoma: Inner pair of posterior hypostomal setae twice as long as other two pairs. Gnathosomal pair intermediate in size. Deutosternal groove with about six denticles in single file, although the anterior denticle may be double. Labial cornicles well developed. Epipharynx tapering, with groove along entire length. Chelicerae, palpi and tritosternum as in *L. breviseta*, n. sp.

Notes.—I had for some time confused this species with *L. southcotti*, since both have simple setae on coxae I. However, the two species may be recognized by the relative lengths of the dorsal setae, and the armature of coxae II, as figured above. *L. southcotti* parasitizes the giant scale-tailed rat, *Uromys caudimaculatus* (Krefft), while *L. mackerrasi* is a parasite of the allied rat, *Rattus assimilis* (Gould). Another close relative is *L. habrus* Domrow, 1958*a* (Fig. 21), described from a bandicoot from Papua. All these three species have 39 pairs of dorsal setae, as do *L. nuttalli* Hirst, 1915, *L. assimilis* Womersley, 1956, *L. wasselli* Domrow, 1958*a*, and *L. breviseta*, n. sp., above.

Genus Mesolaelaps Hirst.

Mesolaelaps antipodianus (Hirst, 1926).

This species was originally described from *Perameles nasuta* from Sydney, and has since been recorded from *P. gunnii* (Victoria), *Isoodon obesulus* (South Australia), and rabbits (Tasmania) by Womersley (1937, 1956). I have since seen the following material: very numerous specimens from *P. nasuta*, Mt. Nebo, S.E. Queensland, 1.xii.1958, E. H. Derrick; 2♀♀, *I. obesulus*, Maydena, Tas., 17.xii.1959, T. Anderson.

Mesolaelaps australiensis Hirst, 1926.

This common species has been recorded from a variety of hosts in Australia, including the echidna, *Tachyglossus aculeatus acanthion* (Collett) (Tachyglossidae), the numbat, *Myrmecobius fasciatus* Waterhouse (Myrmecobiidae), the bandicoots *Perameles gunnii*, *P. nasuta*, and *Isoodon macrourus*, *Rattus lutreolus* (Gray), a "dasyurid", "rats" and "mice" (Womersley, 1937; Domrow and Smith, 1956; Domrow, 1958*a*). A further record is 12♀♀ from a native cat, *Dasyurus quoll* (Zimmermann), Maydena, Tasmania, 3.i.1959, B. C. Mollison.

Mesolaelaps bandicoota (Womersley, 1956).

This species was originally described from *I. macrourus* in S.E. Queensland. A further record from the same host is eighteen females, Tooloom, N.S.W., 19.viii.1960, J. H. Calaby.

Mesolaelaps sminthopsis (Womersley, 1954*b*).

This species is apparently restricted to dasyurid marsupials. It was originally described from *Sminthopsis leucopus* (Gray) in Victoria, and has since been recorded from *Antechinus flavipes* (Waterhouse) in Queensland by Domrow and Smith (1956). I have since seen 4♀♀, *A. flavipes*, Tuggolo State Forest, New South Wales, 21.iii.1960, J. Bromell; 4♀♀ (a fifth specimen was lost), *A. flavipes*, Wartook, Victoria, ACC 657, 5.i.1948, R. V. Southcott.

Genus Neolaelaps Hirst.

Neolaelaps spinosus (Berlese, 1910).

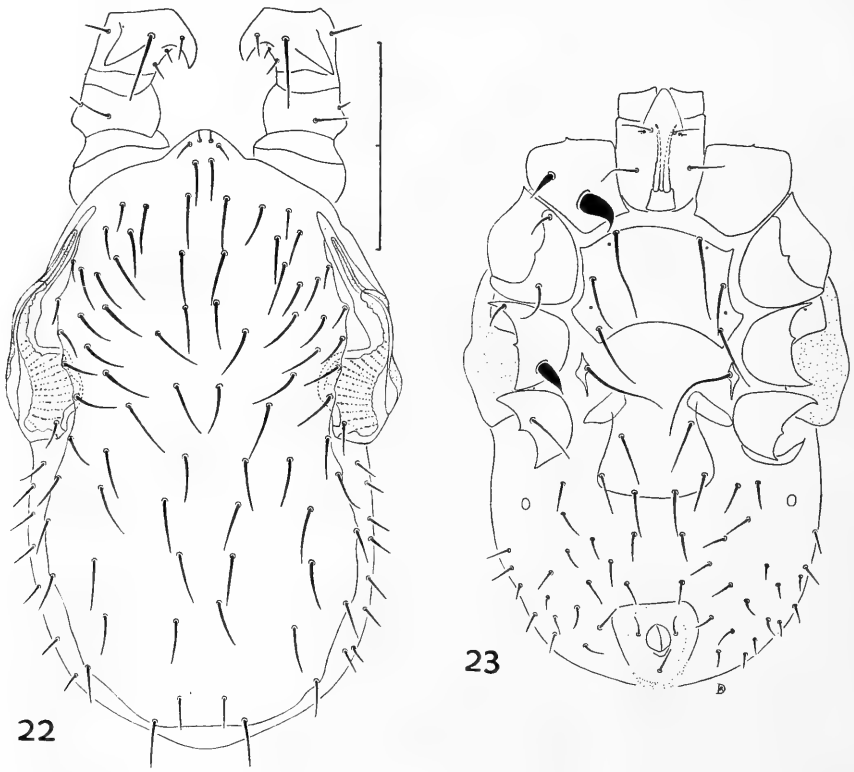
This species was originally described from fruit-bats of the genus *Pteropus* in Ceylon, Borneo, Java and Ambon. In addition to the material recorded from *P. conspicillatus* Gould in north Queensland (Domrow, 1958*a*), I have since seen two series of interest. The first of these was examined by the courtesy of Dr. B. McMillan. He told me that he was collecting parasitic Diptera from large black *Pteropus* at Poronbus, New Ireland, 7–10.viii.1958, and later noticed many mites in the tubes containing the

flies. These proved to be 146 specimens of all stages of *N. spinosus*. A total of fourteen flies was present in the tubes.

The second series has a similar history, and came from Dr. R. V. Southcott. He writes "this batfly had about twelve mites running over its dorsum. Fly and mites put into alcohol." I was only able to find two mites in the dried out tube, and these also proved to be Berlese's species. They have the same collection data as *N. vitzthumi*, n. sp., below, which was found "swarming" on the dead bat, "especially upon the dorsum of the ears".

NEOLAELAPS VITZTHUMI, n. sp. (Figs 18, 22–23).

Types: Holotype female and two paratype females in South Australian Museum, Adelaide. Twenty paratype females have also been divided between the collections of the Queensland Institute of Medical Research, Brisbane; Dr. R. V. Southcott, Adelaide; South African Institute for Medical Research, Johannesburg; British Museum (Natural



Text-figs 22-23.—*Neolaelaps vitzthumi*, n. sp. Female. 22, Dorsum; 23, Venter.

History), London; U.S. National Museum, Washington, D.C. The type series is in Hoyer's medium, and was collected from a fruit-bat, *Pteropus scapulatus* Peters (Pteropodidae), Adelaide River, Northern Territory, Australia, M 49, 10.vi.1943, R.V.S.

Four females and one nymph in polyvinyl alcohol-lactophenol, with the same collection data, have also been examined, while I have also seen a further three females in the South Australian Museum, *Pteropus gouldii* Peters, Townsville, Q., n.d., F. H. Taylor.

Female.—A stout-bodied, fairly well sclerotized species, with idiosoma in mounted specimens 539–572μ long.

Dorsum: Dorsal shield single, covering most of dorsal surface, except for narrow posterolateral strip. Lateral margins of shield noticeably concave as a result of enlargement of stigmata. Forty pairs of evenly arranged setae are present, as figured.

Marginal cuticle with about eight pairs of setae. Peritremes somewhat abbreviated, terminating at level of posterior margin of coxae I, and somewhat thickened in basal half. This thickened part merges quickly into an immense stigma, which is clearly open to the exterior. The texture of the stigmata is as figured.

Venter: Sternal plate wider than long, with evenly convex anterior margin, and evenly concave posterior margin. Three pairs of slender setae and two pairs of small pores are present on the shield. Metasternal plates fairly well developed, each with a long slender seta. Metasternal pores not detected. Genito-ventral shield a little expanded, but truncate behind coxae IV; with three pairs of setae. Anal plate roundly triangular, with anal setae arranged as figured, the postanal seta not being basally expanded. Ventral cuticle with about 20 pairs of short setae and two small metapodal plates.

Legs: Coxal formula 2.2.2.1. Coxae I with two spines, the posterior by far the stronger, and both merging into minute apical filament; coxae II with two normal setae; coxae III with normal anterior seta, but with strong posterior spine; coxae IV with normal seta. All trochanters with long slender seta on ventral surface. Genua and femora I & II each with one longer seta dorsally; femora III & IV each with one stronger seta dorsally. Femora I also with two strong retrorse spurs dorsally. Legs otherwise undistinguished.

Gnathosoma: Palpi fairly stout, with two-tined tarsal claw, and setation as figured. Only two pairs of hypostomal setae detected, the outer pair being much shorter than the inner pair. Gnathosomal setal pair slightly swollen basally, and with distal half very fine. Deutosternal groove with about nine denticles in single file. Tritosternum with rather broad base; laciniae evenly tapering, and very shortly barbed.

Deutonymph.—Length of idiosoma 407μ in mounted specimen.

Dorsum: Dorsal shield single, eroded midlaterally at level of stigmata, and indistinct posterolaterally; with about 33 pairs of setae. Stigmata and peritremes indicative of adult form.

Venter: Intercoxal shield terminating at level of posterior margin of coxae IV, with four pairs of setae, and a fifth pair set in cuticle very near posterior angle. Ventral cuticle with about 20 pairs of setae, including one much longer pair near posterior angle of anal shield, which is rather more elongate than in adult.

Legs and gnathosoma as in adult, but spinose setae on coxae I and III and gnathosomal setal pair rather weaker. Femora I with two incipient but distinct blunt tubercles dorsally.

Notes.—Neolaelaps vitzthumi, n. sp., is abundantly distinct from the other member of the genus, *N. spinosus* (Berlese). The two species may be separated by the armature of the gnathosoma, coxae I & III, femora I and anal shield; the structure and size of the stigmata; and the shape of the tritosternal laciniae.

Genus Peramelaelaps Womersley.

Peramelaelaps bandicoota Womersley, 1956.

This species was originally described from bandicoots from S.E. Queensland. The first extra-Australian record is 18♀♀, 30♂♂ and 2 nymphs from *Isoodon macrourus moresbyensis*, within five miles of Port Moresby, Papua, September, 1959, I. Cook.

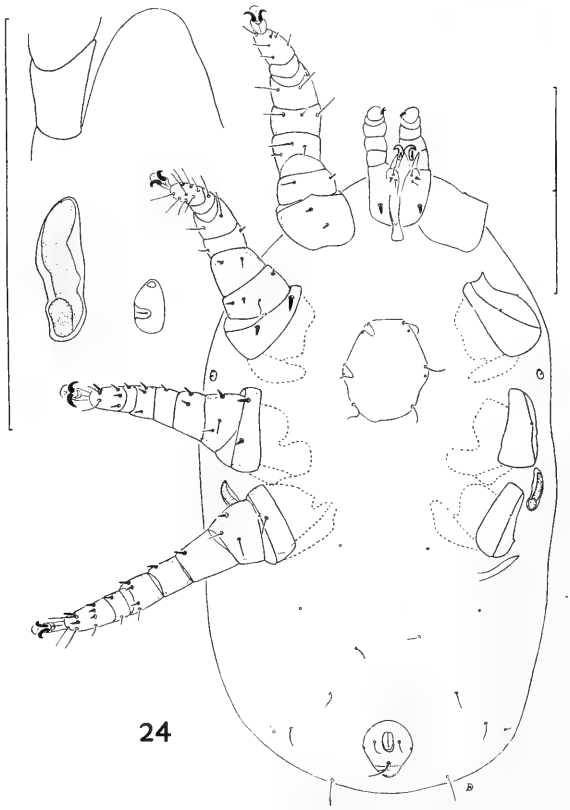
Genus Pneumonyssus Banks.

Pneumonyssus dentatus, n. sp. (Figs 24–26).

Types: Holotype nymph and one paratype nymph in Queensland Museum, Brisbane; also one paratype nymph each in Queensland Institute of Medical Research, Brisbane; British Museum (Natural History), London; and U.S. National Museum, Washington, D.C. The type series is in Hoyer's medium, and was collected in the nasal passages of a marsupial mouse, *Antechinus flavipes godmani* (Thomas) (Dasyuridae), trapped alive in rain-forest at 1,200′, Palmerston National Park, 20 miles west of Innisfail, north Queensland, 10.vi.1960, J. L. Harrison.

A further 85 nymphs in polyvinyl alcohol-lactophenol have been examined, but are not included in the type series. These are all from scale-tailed rats (Muridae) as follows: 71 from one *Melomys cervinipes* (Gould), secondary forest, Danbulla, Atherton Tableland, north Queensland, 13.viii.1958, J. L. H. and I. Cook; and 14 from two *M. cervinipes*, rain-forest at 1,200′, Palmerston National Park, 5–6.iii.1959, R.D. One of the latter two rats also had an intranasal species of *Walchia* (Trombiculidae) present.

Protonymph.—A large and sluggish species, creamy coloured, with short legs, and normally much distended. Length of idiosoma about 548–590μ in somewhat flattened specimens.



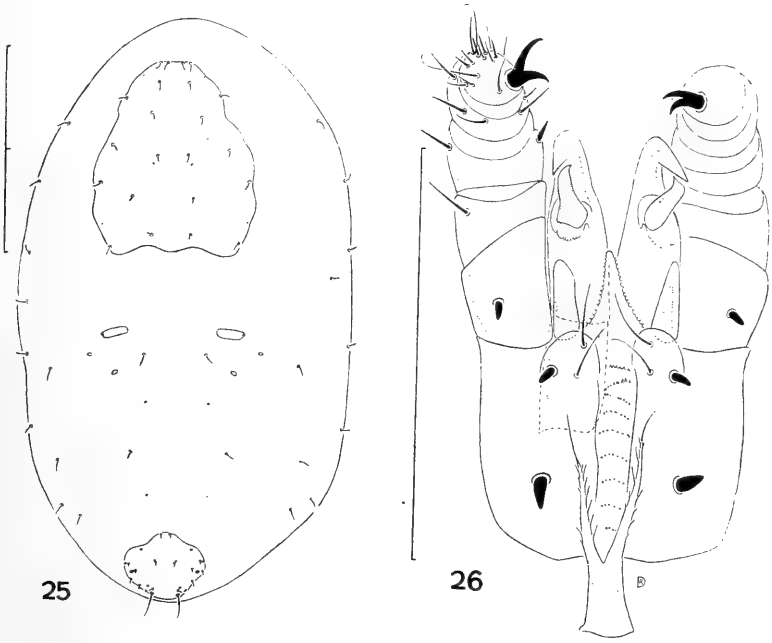
Text-fig. 24.—*Pneumonyssus dentatus*, n. sp. Protonymph. Venter, with insets showing tectum, peritreme, and plaque between coxae II and III.

Dorsum: Two weakly sclerotized dorsal shields present. Anterior shield larger, with irregular lateral margins, but evenly triconvex posterior margin; with 11 pairs of short setae and a few paired pores. Posterior shield strongly convex on all four sides, with seven (occasionally only six) pairs of minute setae, and one pair of much larger setae posteriorly. Small pores (one lateral pair especially distinct) are also present on the shield. Between the two shields are six platelets (the larger anterior pair having a pore in the exterior angles), two pairs of pores, and two transverse rows of four setae. Eight pairs of marginal setae are present.

Venter: Sternal shield subhexagonal, situated between coxae II and III; with three pairs of setae and two pairs of pores. Ventral cuticle behind coxae IV with four pores and ten setae. Anal plate rounded anteriorly, but with straighter posterior margins. Paired anal setae set near middle of anus, and weaker than postanal seta. Peritremes much abbreviated, lying above and between coxae III and IV. In a similar position between coxae II and III is a small sclerotized plaque.

Legs: Coxal setal formula 2.2.2.1, those on coxae I-III being spinose. Setae on legs III and IV also generally spinose. No longer setae dorsally on femora I & II. All tarsi with caruncle and two strong claws. All coxae except I with strongly sclerotized internal apodemes; coxae IV flanked posteriorly by sclerotized articulatory lunule.

Gnathosoma: Tritosternum well developed, but with laciniae not very long. Inner two pairs of hypostomal setae slender, but posterior pair and gnathosomal pair much thickened, and spine-like. Deutosternum with about nine irregularly arranged transverse rows of denticles. Labial cornicles quite well developed. Epipharynx as figured. Chelicerae stout, and extremely well sclerotized. Fixed digit with tip sharply recurved; without pilus dentilis. Movable digit sharply pointed distally, articulated in socket with



Text-figs. 25-26.—*Pneumonyssus dentatus,* n. sp. Protonymph. 25, Dorsum; 26, Gnathosoma.

several minute indications of a corona on ventral margin. Palpi stout, with spinose seta on trochanter, and large bifurcate tarsal claw. Tectum with very distinct, and strongly sclerotized, arched anterior edge.

Notes.—The adults of this remarkable species remain undetected, though the nasal passages of numerous animals have been examined (Domrow, 1961). The species is placed in the genus *Pneumonyssus* purely on ecological grounds.

Genus Raillietia Trouessart.

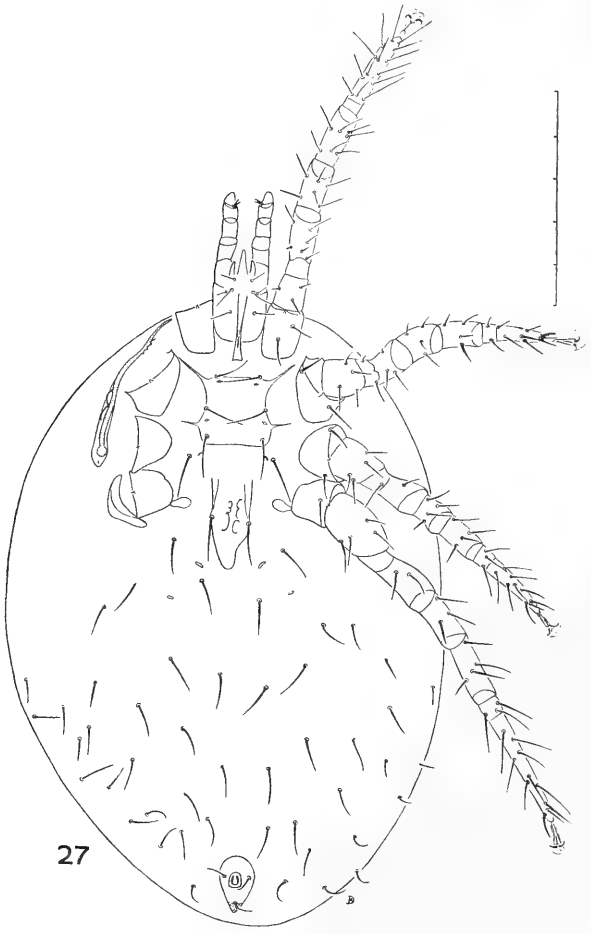
Raillietia australis, n. sp. (Figs 27–29).

Types: Holotype female in Division of Entomology, C.S.I.R.O., Canberra, and one paratype female in British Museum (Natural History), London. Both specimens are in Hoyer's medium, and were collected in the ears of a common wombat, *Phascolomis mitchelli* (Owen) (Vombatidae), Brindabella Road, A.C.T.-N.S.W. border, 24.v.1960, J. H. Calaby.

Female.—A large, creamy coloured, and weakly sclerotized species, greatly distended in appearance. Idiosomal length unavailable because of distortion.

Dorsum: Dorsal shield small, elongate-oval, and covering only the mid-portion of the anterior half of the dorsum. With 32 or 33 pairs of slender setae which increase in length posteriorly. In the specimen not illustrated, the two setae marked Y are

replaced on both sides by a single seta. In the same specimen, an additional short seta is present on one side at the location marked X. As the posterior pair of long marginal setae is preceded by a much shorter pair of setae on the shield proper, it seems that this represents the entire scutal complex. Nor has any postdorsal shield been noted. A regular pore-system is present, and the shield is further marked by a regular series of areolations indicating muscle insertions. The number of setae on the dorsal cuticle in the specimen illustrated is about 25 pairs; of these, the anterior pair is very small.



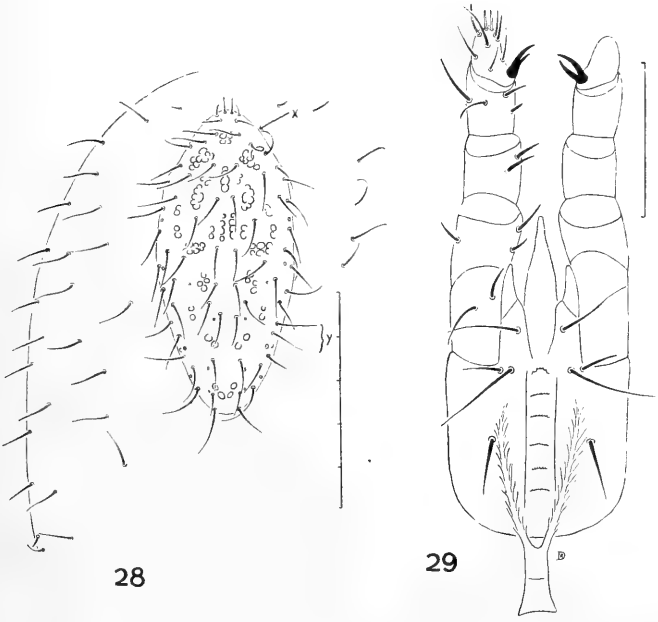
Text-fig. 27.—*Raillietia australis*, n. sp. Female. Venter.

Venter: Sternal shield reduced, and slightly longer than wide, with angles attenuated between coxae I & II and III & IV. With usual six setae and four pores. Metasternal setae and pores free in cuticle. With pair of internal sclerotizations between coxae IV. Genital plate reduced, irregular in outline, with two setae and areolations as on dorsal shield. Genital operculum indistinct. Anal plate arched anteriorly, and straight-sided posteriorly; with central anus and three subequal setae. Ventral cuticle with four platelets behind genital shield, and 23–25 pairs of setae. Peritremes reaching forward to level of coxae I, with crescentic markings as shown, and not extending posteriorly around coxae IV.

Legs: Coxal setal formula 2.2.2.1, all setae being slender and completely unmodified. All four pairs of legs slender, and with undistinguished setation. Femora I and II

without stronger setae dorsally. All tarsi with caruncle and two claws. An articulatory lunule flanks coxae IV posteriorly. Coxae II with small pointed process on antero-dorsal margin.

Gnathosoma: Tritosternum well developed, but with rather short laciniae. Hypostomal setae very slender, the anterior and inner posterior pairs being subequal, and about twice as long as the outer posterior pair. The gnathosomal pair are slightly thicker, and almost as long as the anterior hypostomals. Deutosternum with about six transverse rows of denticles. Labial cornicles present, but not very strong. Epipharynx slender, minutely spiculate, tapering distally. Chelicerae not clear, but well sclerotized, and with apically hooked and well-formed digits. Cheliceral teeth are, however, probably absent. Palpi slender, with bifurcate claw.



Text-figs 28-29.—*Raillietia australis*, n. sp. Female. 28, Dorsum; 29, Gnathosoma.

Notes.—This species has been assigned to the genus *Raillietia* partly on ecological grounds, but it does agree well with Strandtmann and Wharton's diagnosis (1958). An examination of male specimens should decide the matter. *R. australis* may be easily separated from the ear-mite of cattle, *R. auris* (Leidy), by the gnathosomal details, the relative sizes of the ventral shields, and the degree of setation of the body cuticle. A third species, *R. hopkinsi* Radford, has been described from an African waterbuck, but is apparently much closer to *auris* than to *australis*.

Genus Spinolaelaps Radford.

Spinolaelaps miniopteri (Zumpt and Patterson, 1952).

One female from a bat, *Miniopterus schreibersii blepotis*, Bonalbo Colliery, Bonalbo, N.S.W., 17.viii.1960, J. H. Calaby. The synonymy of this species is discussed by Till (1960); it occurs on bats both in South Africa and Australia.

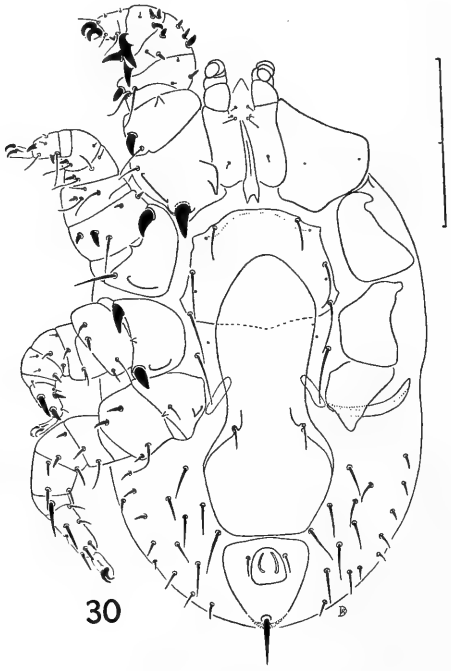
Genus Trichosurolaelaps Womersley.

Trichosurolaelaps crassipes Womersley, 1956.

In addition to two paratype females, I have lately been able to examine the two series from the collection of Dr. R. V. Southcott recorded by Womersley (1956). These comprise in all 20♀♀ and 7♂♂. I can now say that, in the male, the dorsal shield is longitudinally striate, the dorsal setae bladed, and the peritremes abbreviated, being

situated above coxae III. Nevertheless, the species may be recognized by the characteristic shapes of all ventral shields in both sexes, as well as by the attenuated peritremes peculiar to the female.

All these specimens are from the brush-tailed possum, *Trichosurus vulpecula* (Kerr) (Phalangeridae), as is a single deutonymph, Unley Park, South Australia, 28.vi.1954, ACC 680, R.V.S. by Berlese funnel. In this nymph, the dorsal shield is entire, with minute discal setae, and longitudinal striae. The peritremes are much abbreviated, not much longer than the diameter of the stigmata. Many body setae are bladed. Intercoxal shield with five pairs of setae, and terminating at level of posterior margin of coxae IV. Coxal armature as in adult, but slightly weaker.



Text-fig. 30.—*Trichosurolaelaps harrisoni,* n. sp. Female. Venter.

Trichosurolaelaps emanuelae Domrow, 1958*a*.

Apart from the original series from the New Guinea bandicoot, *Echymipera kalubu kalubu* (Lesson), I have since seen 18♀♀ and 6♂♂ from two bandicoots, Bengaragum Village, Maprik area, N.G., 28.i.1960, M. Willis and J. Wannan, and 1♀ from *Rattus exulans* (Peale), Korefeigu Village, Goroka area, N.G., 11.i.1960, M.W. and J.W. These specimens were examined through the courtesy of Dr. B. McMillan.

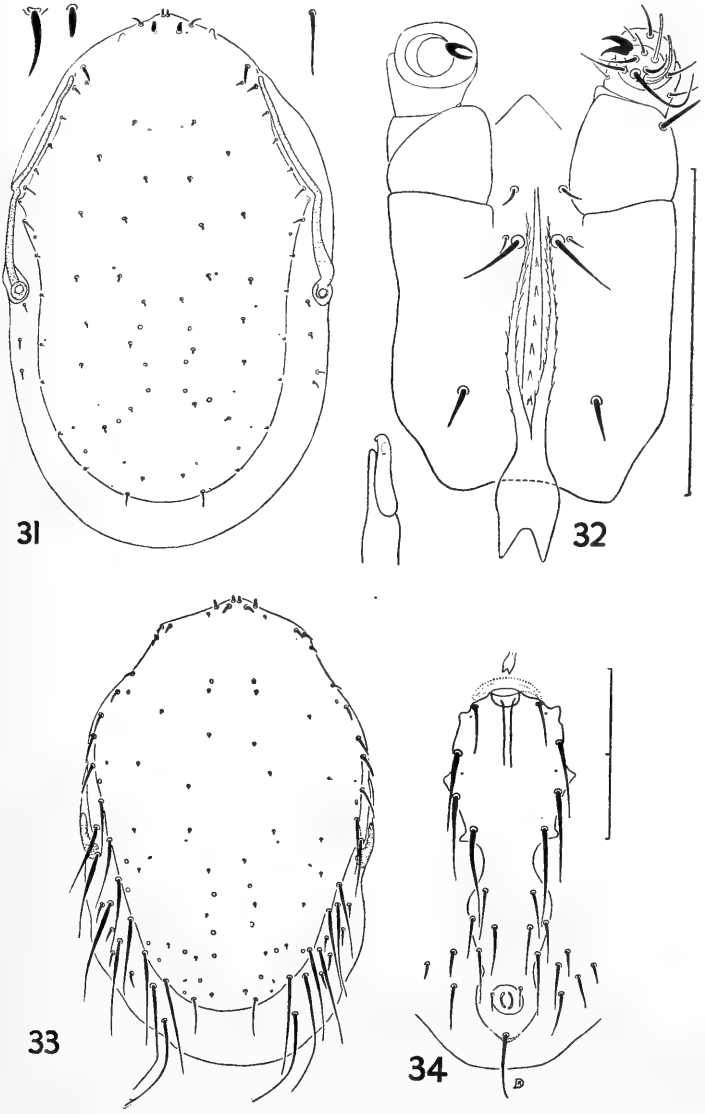
The females agree well with the original description, as do the males, but in the latter sex, the dorsal setae are variable. The disparity in length between the discal and marginal setae may be either more, or less, marked than illustrated.

Trichosurolaelaps harrisoni, n. sp. (Figs 30–34).

Types: Holotype female and allotype male in Queensland Museum, Brisbane, in Hoyer's medium. Forty-five paratype females, and one paratype male in spirit have been divided between the Queensland Institute of Medical Research, Brisbane; Division of Entomology, C.S.I.R.O., Canberra; South Australian Museum, Adelaide; South African Institute for Medical Research, Johannesburg; U.S. National Museum, Washington, D.C.; and British Museum (Natural History), London. All these specimens, and five nymphs, were collected on two musk rat-kangaroos, *Hypsiprymnodon moschatus*

Ramsay (Macropodidae), trapped alive in rain-forest, Dinner Ck., near Innisfail, north Queensland, 30.vi.1960 and 4.viii.1960, J. L. Harrison.

A further three females in polyvinyl alcohol-lactophenol have been examined, but are not included in the type series. These are from the same host, trapped in rain-forest on hills (altitude less than 1,000′) immediately behind Etty Bay, near Innisfail, 6.viii.1958, J.L.H.



Text-figs 31-32.—*Trichosurolaelaps harrisoni*, n. sp. Female. 31, Dorsum, with insets of stronger setae from femur and trochanter I, and femur II (from left to right); 32, Gnathosoma (palpi deflexed), with inset of chelicera.
Text-figs 33-34.—*Trichosurolaelaps harrisoni*, n. sp. Male. 33, Dorsum; 34, Holoventral shield.

Female.—An oval, well sclerotized species with short thick legs. Length of idiosoma in mounted material about 605μ.

Dorsum: Dorsal shield covering most of dorsal surface, wider and slightly irregular in outline in anterior half, but evenly rounded posteriorly; with two small tubercles

near vertex. Vertical setae six in number, somewhat thickened. Lateral setae in 15 pairs, of which the anterolaterals and extreme posterior pair are strongest. Disc of shield with 14 pairs of setae. A regularly arranged series of pores is present. Texture of shield minutely granular. Dorsal body cuticle with a few pairs of simple setae. Peritremes with lateral stigmata, and dorsolateral peritremes, which reach forward to level of coxae I. Peritremalia not extending posteriorly around posterior margin of coxae IV.

Venter: Sternal plate subquadrate, with convex anterior margin, straight lateral margins, and medially convex posterior margin; with usual three pairs of setae and two pairs of punctate pores. Metasternal setae and pores free in cuticle. With two elongate-oval, internal sclerotizations between coxae IV. Genital plate also subquadrate, widest immediately behind coxae IV. With two anterolateral striae giving insertions of genital setae a pedunculate appearance as in *T. crassipes* Womersley. Genital operculum reaching forward to level of sternal setae II, evenly rounded, and with striate appearance. Anal plate triangular, with very slightly rounded sides. Anterior margin as wide as posterior margin of genital shield. Anus set in anterior half, and flanked by two adanal setae, which are much weaker than the postanal seta. Ventral cuticle with about 16 pairs of setae, which decrease in length marginally.

Legs: Coxal setal formula 2.2.2.1, the posterior seta on coxae I, the anterior seta on coxae II, and both setae on coxae III being greatly thickened and spine-like. In addition, coxae I and IV have a pointed, backwardly-directed process near their inner margins, while coxae I, II and III have a distinct sclerotized ridge along their posterior margins. With lunate articulatory sclerotization behind coxae IV. Coxae II with pointed process on anterodorsal margin. Most leg segments with strong spinose setae, some especially so, e.g., trochanter and telofemur I. Tarsus I with one, and tarsus II with two small pointed processes; tibia and genu I with strong retrorse spinose process on posterior margin. Femur and trochanter I each with a stronger seta dorsally; femora II with a longer seta dorsally. All tarsi with caruncle and two claws, those of tarsi I being the strongest.

Gnathosoma: Tritosternal base strongly sclerotized, and bipartite posteriorly; merging into two ciliated laciniae, which extend forward to level of hypostomal setae. Inner posterior pair of hypostomal setae the strongest. Gnathosomal setae intermediate in size. Deutosternum with about six denticles in single file. Chelicerae quite slender, fixed digit not dentate, but movable finger weakly hooked apically, and with weak tooth on margin. No fringe of setulae was seen surrounding the insertion of the movable finger. Palpi undistinguished; tarsus with bifurcate claw.

Male.—Slightly smaller, and less rounded than the female. Length of idiosoma in mounted material 506μ.

Dorsum: Dorsal shield wider in anterior half, with eight vertical setae and 15 pairs of lateral setae, which steadily increase in length posteriorly, except the extreme posterior pair which are scarcely half as long as the subposterior pair. Disc with 13 or 14 pairs of minute setae, the pattern, as well as that of the pores, being slightly irregular posteriorly. Dorsal marginal cuticle with several elongate setae interspersed with short spinules. All the longer dorsal setae are bladed basally as in *T. striatus* Domrow. Likewise, the dorsal shield is finely longitudinally striate as in that species. Peritremes much abbreviated, situated above coxae III and IV.

Venter: All ventral plates fused to form holoventral plate. Genital aperture in convex anterior sternal margin. All ventral setae subequal, except sternal setae II and III and the metasternals, which are much stronger than the others. Sternal and metasternal pores as in female. Ventral area scarcely broader than anal area, with three pairs of usurped ventral setae. Anal area much as in female. Ventral cuticle with three to five pairs of setae.

Legs and gnathosoma essentially as in female. Chelicerae not clearly visible, but not grossly modified.

Notes.—The insertions of the genital setae of *T. quadratus*, n. sp., show some resemblance to those of *T. crassipes* Womersley, the genotype, but in other characters,

e.g., the peritremes, it is more closely related to *T. striatus* Domrow. It may be separated from this species in the female by the armature of the coxae, the shape of the genital shield, and the relative lengths of the posterior pair of setae on the dorsal shield. In the male, the two species may be separated by the coxal armature, the shape of the holoventral shield, and the relative lengths of the sternal, metasternal, and the posterior pair of setae on the dorsal shield.

Trichosurolaelaps striatus Domrow, 1958*a*.

This species was originally described from the ring-tailed possum, *Pseudocheirus peregrinus laniginosus* (Gould), from Queensland. The following additional material has since been examined: 13♀♀, 2♂♂, *P. convolutor* (Oken), Glenora, Tasmania, 2.vi.1960, B. C. Mollison. There is a further series from a Tasmanian ring-tail in the South Australian Museum, Adelaide.

Family TROMBICULIDAE.

Five species with expanded sensillae have already been described from Innisfail, in the genera *Guntherana* and *Ascoschöngastia* (Domrow, 1960*b*, 1960*c*). An intranasal species of *Walchia* is being described by Col. R. Traub (in ms), while the remaining new species (with filamentous sensillae) is described below.

Genus Trombicula Berlese.

Trombicula alicola, n. sp. (Figs 35–39).

Types: Holotype larva and one damaged paratype larva in Queensland Museum, Brisbane, in polyvinyl alcohol-lactophenol. Both specimens were collected on the hind margin of the wings of leaf-nosed bats, *Rhinolophus megaphyllus* Gray (Rhinolophidae), in a cave, Bramston Beach, north Queensland, 27.vii.1959, J. L. Harrison coll.

Larva.—A small, weakly sclerotized species, idiosoma barely exceeding 400μ in mounted, engorged specimens. Body cuticle annulate.

Body setation: Dorsal setae cylindrical and barbed, arranged 2.8.6.6.6.4. Humeral setae 34, middorsal setae 27, caudal setae 23μ long. Ventral setae irregularly arranged, about 50 in number, those adjacent to anus being 17μ long. Coxal setae 1.1.1; sternal setae 2.2.

Gnathosoma: Cheliceral bases very stout, but cheliceral blades missing in both specimens. Galeal setae fine and nude. Palpal coxal setae long, with about five slender ciliations. In addition to the usual ventroexternal tarsala, the palpal formula is b. b. bbb. B+4b. Subterminala absent. Palpal claw with three prongs.

Scutum almost square, but slightly wider than long. Lateral margins parallel; anterior margin ever so slightly concave, but a little convex around insertion of AM; posterior margin shallowly convex. AL not set on shoulders, and slightly in front of AM; PL set in extreme posterolateral angles. PL and AM subequal, and longer than AL. SB much closer to level of PL than that of AL. Sensillae filamentous, short, branched except on basal third. Punctae present. The scutal standard data are given below. Eyes double, diameter of anterior lens 14μ.

Legs all seven-segmented. All tarsi with basal bar, and caruncle and two claws. The specialized setation is as follows: *Tarsus I* with pretarsala, subterminala, parasubterminala, tarsala 19μ long, and microtarsala. *Tibia I* with two tibialae and microtibiala. *Genu I* with three genualae and microgenuala. *Tarsus II* with pretarsala, tarsala 16μ long, and microtarsala. *Tibia II* with two tibialae. *Genu II* with genuala. *Tibia III* with one mastiseta. *Genu III* with two mastisetae.

Standard data in micra of larval scutum of T. alicola.

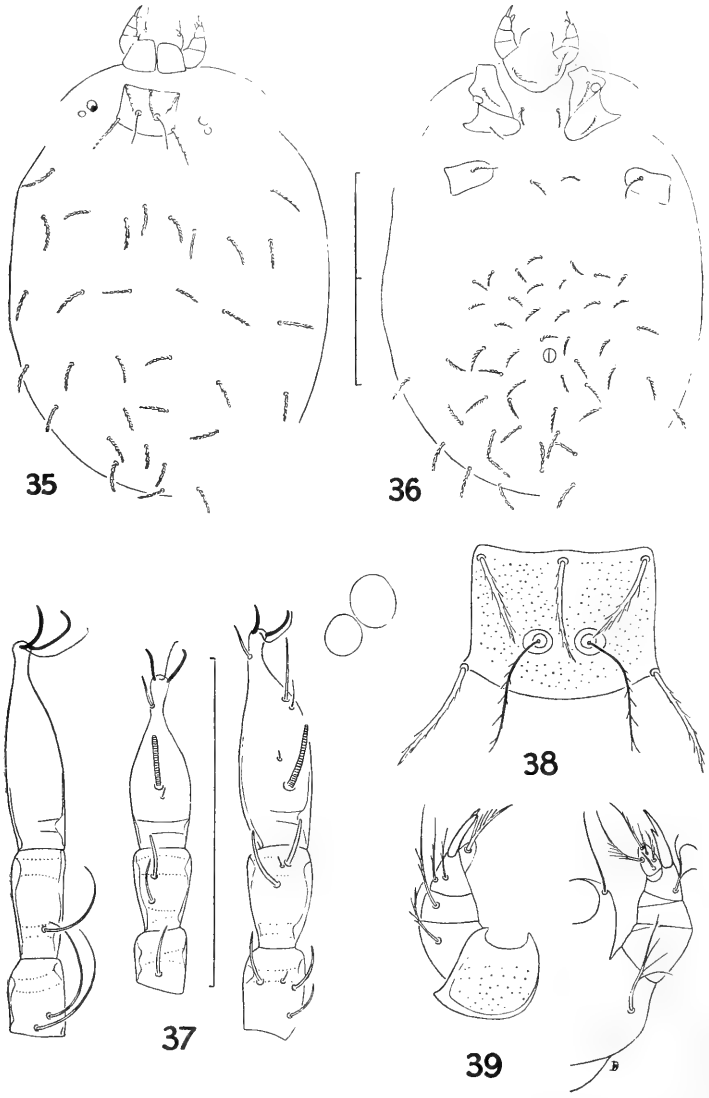
AW	PW	SB	ASB	PSB	SD	AP	AM	AL	PL	Sens
49	58	15	29	17	46	34	34	27	36	39

Notes.—*T. alicola*, n. sp., appears closely related to *T. insolli* Philip and Traub, 1950, described from a Malayan bat, *Eonycteris spelaea*. The two species may be separated by the setation of the palpi, dorsum, and legs III.

Genus Neotrombicula Hirst.

Neotrombicula comata, n. sp. (Figs 40–44).

Types: Holotype larva in Division of Entomology, C.S.I.R.O., Canberra, and one paratype larva each in British Museum (Natural History), London, and U.S. National Museum, Washington. All three specimens are in polyvinyl alcohol-lactophenol, and



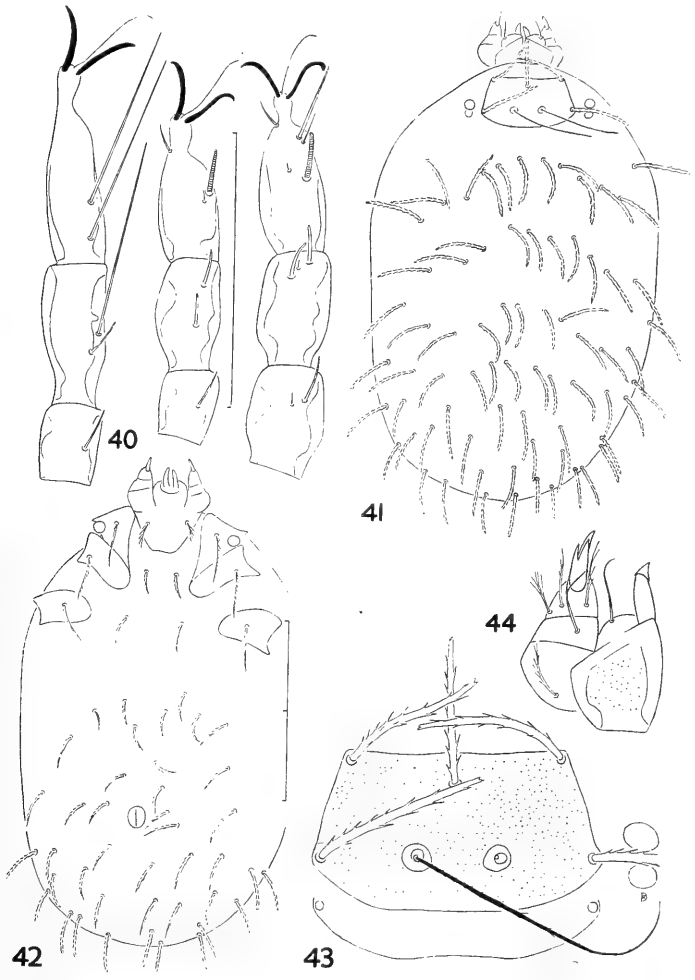
Text-figs 35-39.—*Trombicula alicola*, n. sp. Larva. 35, Dorsum; 36, Venter; 37, Specialized setation of legs I-III (right to left); 38, Scutum and eyes; 39, Dorsal and ventral views of gnathosoma (left to right).

were collected from among a mass of chiggers "attached in a concentric area about one inch in diameter around the base of the scrotal stalk" of a short-nosed bandicoot, *Isoodon macrourus* (Gould) (Peramelidae), Tooloom, N.S.W., 19.viii.1960, J. H. Calaby.

Associated chiggers were *Trombicula mackayensis* Womersley, 1954*a* (in large numbers), and occasional specimens of *Neotrombicula thylogale* (Womersley, 1954*a*) and *Guntherana* (*Derrickiella*) *perameles* (Womersley, 1939).

Larva: A medium sized, and well sclerotized chigger, with idiosoma 440–506μ long in mounted, engorged specimens. Body cuticle annulate.

Body setation: Dorsal setae cylindrical and barbed, arranged 2.10–12.10.12.10–12+24. Humeral setae 65–70, middorsal setae 49–52, caudal setae 47–50μ long. Ventral setae irregularly arranged, about 40 in number, those near anus being 36–40μ long. Coxal setae 1.1.1; sternal setae 2.2.



Text-figs 40-44.—*Neotrombicula comata*, n. sp. Larva. 40, Specialized setation of legs I-III (right to left); 41, Dorsum; 42, Venter; 43, Scutum and eyes; 44, Dorsal view of gnathosoma.

Scutum transversely rectangular. Anterior and lateral margins almost straight. Posterior margin shallowly convex, but very weakly concave medially in one specimen. AL not on shoulders, and well in front of level of AM. AM and AL subequal, but shorter than PL. SB in line with PL. Sensillae filamentous, finely barbed. Punctae present. The scutal standard data are given below. Eyes double, diameter of anterior lens 13–14μ.

Legs all seven-segmented. The specialized setation is as follows: *Tarsus I* with pretarsala, subterminala, parasubterminala, tarsala 17μ long, and microtarsala. *Tibia I* with two tibialae and microtibiala. *Genu I* with genuala and microgenuala. *Tarsus II*

with pretarsala, tarsala 16μ long, and microtarsala. *Tibia II* with two tibialae. *Genu II* with genuala. *Tarsus III* with two mastitarsalae. *Tibia III* with tibiala and mastitibiala. *Genu III* with genuala.

Standard data in micra of larval scutum of N. comata.

AW	PW	SB	ASB	PSB	SD	AP	AM	AL	PL	Sens
74	97	28	36	18	54	37	52	54	60	107
76	98	30	38	19	57	38	54	57	65	—
79	100	31	39	20	59	38	58	55	66	—

Notes.—Neotrombicula comata, n. sp., is a member of the *novaehollandiae* complex as discussed by Womersley (1954*a*). It may be easily distinguished from the four species already included (*thylogale*, *derricki*, *antechinus*, and *novaehollandiae*) by its extremely heavy body setation.

Genus Guntherana Womersley and Heaslip.

Guntherana andromeda (Womersley, 1954*a*).

This species was originally described from free-living larvae collected in S.E. Queensland. I have since seen the following material from the ears of two species of wallabies: two larvae from *Thylogale thetis*, Mt. Tamborine, 10.v.1960; twelve larvae from *Protemnodon dorsalis*, Mt. Lindesay, 24.iv.1960, all collected by J. H. Calaby and party. Associated species (except for several *G. cassiope* and *Acomatacarus* sp. larvae) are discussed below.

Guntherana philippensis (Philip and Woodward, 1946), n. comb.

This species was originally described from *Rattus* spp. in the Philippines, and Womersley (1952) recorded specimens collected from *Onychogalea* in the Northern Territory. These latter specimens are not in good condition, and I was unwilling (1960*b*) to accept this species as Australian. However, the recent recovery of 46 larvae in the ears of another macropodid host (*P. dorsalis*, Mt. Lindesay, 24.iv.1960) confirms Womersley's record. *G. philippensis* has six setae in the first dorsal row, and may be immediately separated from its two near relatives (*G. andromeda* and *G. parva*) by its characteristically shaped scutum. The anterolateral scutal excavations are also present in *G. antipodiana*.

Guntherana kallipygos (Gunther, 1939).

A variety of rats and bandicoots have been recorded as hosts for this species, but the following is the first record from a macropodid—two larvae, *T. thetis*, Mt. Lindesay, 24.iv.1960.

Family LISTROPHORIDAE.

Genus Austrochirus Womersley.

Austrochirus mcmillani, n. sp. (Figs 45, 62).

Types: Holotype male in School of Public Health and Tropical Medicine, Sydney, and one paratype male in British Museum (Natural History), London. Both specimens are in Hoyer's medium, and were collected on a marsupial bandicoot (Peramelidae), Bengaragum Village, Maprik area, New Guinea, 28.i.1960, M. Willis and J. Wannan.

Male.—A strongly sclerotized species, with body (including capitulum) approximately 528μ long.

Dorsum: Postcapitular shield simple, broader in posterior third, with uniform punctae in an arch-like pattern; flanked by four setae, of which the posterior two are the stronger. Middorsum with several transverse annulations medially, and scaly laterally. Posterior portion covered by weakly scaled cuticle, with four short setae in transverse row anteriorly, and two weak and four long flagelliform setae posteriorly. Posterolateral zones weakly sclerotized.

Venter: Genitalia preceded by four minute discs. Intromittent organ short, and flanked posterolaterally by two crescentic sclerotized supports, each of which bears a single seta. Anus subterminal, elongate, and flanked by two minute suckers and

setae, all of which are surrounded by a sclerotized frame. A further pair of setae are set between the genitalia and the anus. Caudal lobe transparent marginally, with four weakly defined lobules, and four pairs of flagelliform setae.

Legs: Legs I and II typical of genus. Usual two pairs of striate clasping zones present, with a pair of setae between them. Apodemes III arched and strongly sclerotized, preceded by usual three pairs of setae, one pair of which is flagelliform. Legs III greatly enlarged. Basal movable segment with single seta. Mid two segments almost completely fused, but with division noticeable on inner aspect; with seta in dorsodistal angle. Tarsus III with six simple setae arranged as figured, together with very strong seta dorsobasally. With four setae between apodemes III and IV.

Text-fig. 45.—*Austrochirus mcmillani*, n. sp. Male.

Apodemes IV also strongly arched, with T-shaped extension running forward, so that the arms of the T appear to fuse with the posterior edge of apodemes III. A further inverted V-shaped sclerotization, the arms of which are expanded distally and provided with a seta, is also associated with apodemes IV. Legs IV also enlarged, slightly more so than legs III. Three basal movable segments as in legs III, but without setae. Tarsi IV with about five short setae as shown, and stronger seta dorsobasally. Tarsi III and IV with blunt, subapical processes, and well developed pulvilli.

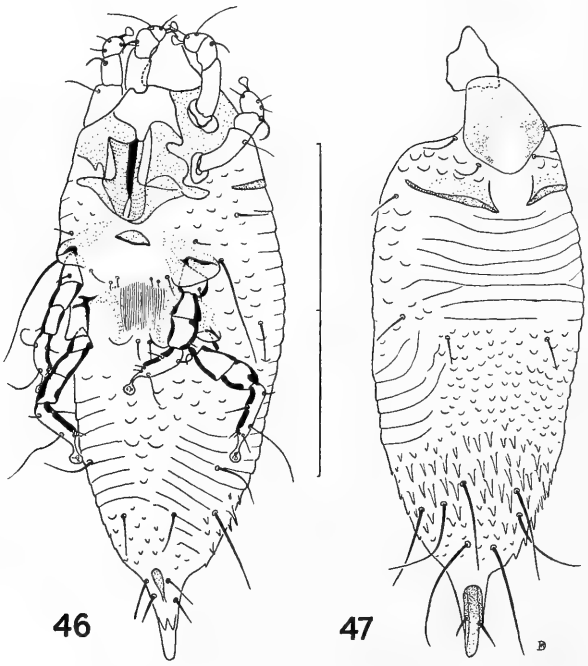
Notes.—Austrochirus mcmillani, n. sp., is a member of the *queenslandicus* species group as defined by Domrow (1960*a*), and is also from a peramelid host. Its postcapitular shield, and the structure of the posterior legs, genitalia, and caudal lobe will separate it easily from the other two known members of this group—*A. queenslandicus* Womersley, 1943 (Fig. 61) from short- and long-nosed bandicoots (*Isoodon macrourus* and *Perameles nasuta*), and A. *filmeri* Domrow, 1960*a*, from the bilby (*Macrotis lagotis*).

The specific identity of the host of *A. mcmillani* is unknown, but it was associated with *Trichosurolaelaps emanuelae* Domrow, 1958*a*, whose type host is *Echymipera kalubu kalubu* (Lesson).

AUSTROCHIRUS TROUESSARTI, n. sp. (Figs 46–48).

Types: Holotype female and allotype male in Queensland Museum, Brisbane; one paratype male each in South Australian Museum, Adelaide; British Museum (Natural History), London; U.S. National Museum, Washington, D.C. All five specimens are in polyvinyl alcohol-lactophenol, and were collected from marsupial mice, *Antechinus flavipes godmani* (Thomas) (Dasyuridae), rain-forest at 1,200 feet, Crawford's Lookout, Palmerston National Park, north Queensland, 18.iii.1959 and 10.vi.1960, J. L. Harrison and R.D.

Female.—A small, almost white, and delicately sclerotized mite with body 380μ long from tip of gnathosoma to end of caudal process.



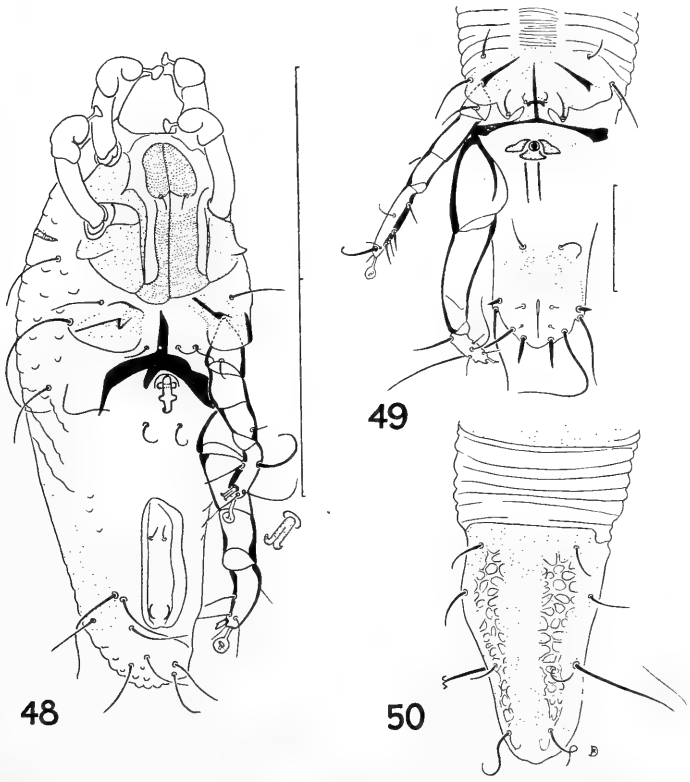
Text-figs 46-47.—*Austrochirus trouessarti*, n. sp. Female. 46, Venter; 47, Dorsum.

Dorsum: Postcapitular shield flanked posteriorly by two pairs of subequal setae; anterior half evenly and weakly punctate, but posterolateral fields each with a tapering strip of heavy punctae. Accessory lobes present, strongly sclerotized along their posterior margins, and marked anteriorly with crescentic striae. Body cuticle divided rather sharply into three distinct zones of differing texture—transverse striae, crescentic striae, and elongate papillae; with four shorter setae between the first two zones, and eight rather larger setae arranged 6.2 across the third. Apex of opisthosoma produced into a slender, dorsally sclerotized process bearing two stiff setae.

Venter: Cuticle mainly marked with crescentic striae, but transversely striate posterolaterally. Genitalia preceded by two short, and four minute setae; with zone of fine longitudinal striae between two backwardly-directed bands of sclerotized cuticle, each of which is followed by a lobule and a short seta. Anus subterminal, near base of caudal process; flanked by four subequal setae, and preceded by two pairs of slightly longer setae, the anterior pair of which is more widely set than the posterior.

Legs: Legs I and II typically atopomeline, slightly flattened, and with strongly recurved seta dorsally. Caruncles present. Clasping apparatus also typical, although the anterior zone of striae, and the pair of setae behind it, are not visible. Coxae III separated by transverse suboval sclerotized bar; anterior margins preceded by an inner minute seta, and an outer very long seta, above which is a third seta. Legs III and IV each with four movable segments. Basal and penultimate segment of leg III each with single seta. Tarsi with setation typical of genus.

Male.—Rather smaller, but slightly more heavily sclerotized than female. Length of body including capitulum 283–312μ.



Text-fig. 48.—*Austrochirus trouessarti*, n. sp. Male. Venter.
Text-figs 49-50.—*Cytostethum mollisoni*, n. sp. Male. 49, Venter; 50, Dorsum.

Dorsum: Anterior half exactly as in female; posterior half without terminal process, and covered by small papillae of uniform size.

Venter: Anterior half as in female. Genitalia set immediately behind apodemes of leg IV. Intromittent organ as figured, recurved distally, with hook directed inwardly. Two simple setae behind genitalia. Anal plaque elongate, with two small setae anteriorly, and possibly with two discs posteriorly. Opisthosoma slightly sclerotized posterolaterally, with four pairs of stronger setae; papillate terminally, with two pairs of weaker setae.

Legs: Legs III as in female, but slightly stronger, and with strong bifid seta with diverging prongs near apex of tarsus. Legs IV rather stronger still, with distinct subapical process near caruncle.

Notes.—*A. trouessarti*, n. sp., is the second known member of the *sminthopsis* species group as defined by Domrow (1960*a*). Both species are from phascogalines.

and are characterized by the possession of papillate cuticle and accessory lateral lobes to the postcapitular shield. The new species may be recognized by three characters—the three types of dorsal cuticular texture, the long posterodorsal setae, and the peculiar caudal process. None of these characters is present in *A. sminthopsis* Womersley, 1954*b*, also collected on a marsupial-mouse, *Sminthopsis crassicaudata* (Gould), but in arid country in south-east South Australia.

This species is named for the late Dr. E. L. Trouessart, who named (1893) the first Australian atopomeline, *Campylochirus chelopus* Tr., a parasite of the Tasmanian ring-tailed possum, *Pseudocheirus convolutor* (Oken). Fifty years were to pass before a second species was described (Womersley, 1943), and sixty-three before *C. chelopus* was seen again (Domrow, 1956*b*).

Genus Cytostethum Domrow.

Cytostethum promeces Domrow, 1956*a*.

One male, *Potorous tridactylus*, Maydena, Tas., 27.vi.1960, B. C. Mollison. This is the type host, but the previous records are from Queensland.

Cytostethum pseudocharactum Domrow, 1956*a* (Fig. 60).

Types: Allotype male and two paratype males in Queensland Museum, Brisbane, from the type host, *Potorous tridactylus*, Maydena, Tas., 27.vi.1960, B. C. Mollison. Eight females were also taken. In Hoyer's medium.

Male.—A well sclerotized, stout-bodied species, with length of idiosoma (including gnathosoma) about 642μ in mounted material. Dorsally and anteriorly essentially as in female.

Venter: Genitalia set between basal movable segments of legs IV; intromittent organ short, preceded by four small discs and two setae. Anus longitudinal, flanked by three pairs of small discs, and preceded by two setae, and two transverse sclerotized rods. Posterior body lobe a narrow, transparent marginal strip, preceded by the heavily sclerotized body margin, which bears five pairs of setae, two pairs of which are flagelliform.

Legs: Legs III as in female. Apodemes IV united medially with longitudinal strut, and preceded by four small setae. Legs IV much enlarged, and heavily sclerotized. Central two movable segments only weakly divided ventrally. Tarsi IV strong, with six setae and much reduced caruncle.

Cytostethum mollisoni, n. sp. (Figs 49–52).

Types: Holotype female, allotype male, and two pairs of paratypes in Division of Entomology, C.S.I.R.O., Canberra; one pair of paratypes each in British Museum (Natural History), London, and U.S. National Museum, Washington, in Hoyer's medium. All these, together with very numerous other specimens in spirit, were collected on a rat-kangaroo, *Potorous tridactylus* (Kerr) (Macropodidae), Maydena, Tasmania, 27.vi.1960, B. C. Mollison.

Female.—A slender, but well sclerotized species, with body (including gnathosoma and terminal process) 660–682μ.

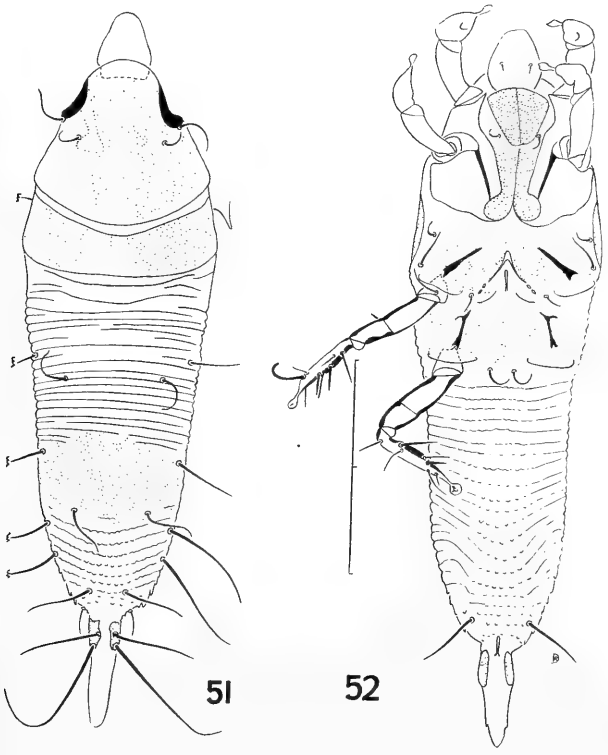
Dorsum: Anterodorsal shield slightly longer than wide, with texture as figured, and four setae. Middorsal shield concave anteriorly to accept convex posterior margin of preceding shield; with a seta in each anterior angle. Middorsum with band of about 16 simple annulations bearing transverse row of four setae. Postdorsal shield wider than long, poorly defined, with four setae; followed by about seven minutely dentate annulations, and eight setate. End of body produced into distinct terminal process, which is sclerotized basolaterally, and bears four setae.

Venter: Genitalia set between coxae III, followed posteriorly by four minute discs, a pair of setae, and two sclerotized longitudinal strips, the apices of which bear a further pair of setae. Two specimens carry a single elongate ovum in the opisthosoma, 214×53 and $224 \times 58\mu$ long. Cuticle with about 20 minutely dentate annulations and two posterior setae. Anus longitudinal, and set just behind these two setae.

Legs: Legs I and II and clasping organ typical of subfamily. Leg III with seta on basal and penultimate movable segment. Tarsi III and IV with eight and seven setae respectively, as figured for other species from *Potorous* (Domrow, 1956*a*).

Male.—Also a slender form, but smaller than female. Length of body including gnathosoma 511–539μ. Terminal process absent. Anterior half of body as in female. Middorsal shield followed by only six annulations. Postdorsal shield covering end of body completely, areolate laterally, with eight shorter and two longer setae.

Venter: Genitalia set between legs IV. Intromittent organ short, flanked anteriorly by two sclerotized bars, and followed by two elongate sclerotized strips. Posterior body lobe marked off by semicircular line preceded by two setae; with two sclerotized plaques, four minute setae and anus discally, and four flagelliform and four spine-like setae marginally.



Text-figs 51-52.—*Cytostethum mollisoni*, n. sp. Female. 51, Dorsum; 52, Venter.

Legs: Legs III as in female. Legs IV thickened, and with central two movable segments weakly divided ventrally. Tarsus IV with five setae, two sub-terminal processes, and much reduced caruncle.

Notes.—*C. mollisoni*, n. sp., is the sixth characteristic form of *Cytostethum* to be described from *Potorous tridactylus*. At least three (and probably five) forms have been found on the one individual host, so it seems unlikely that they are simply seasonal or ecological variants within a single species.

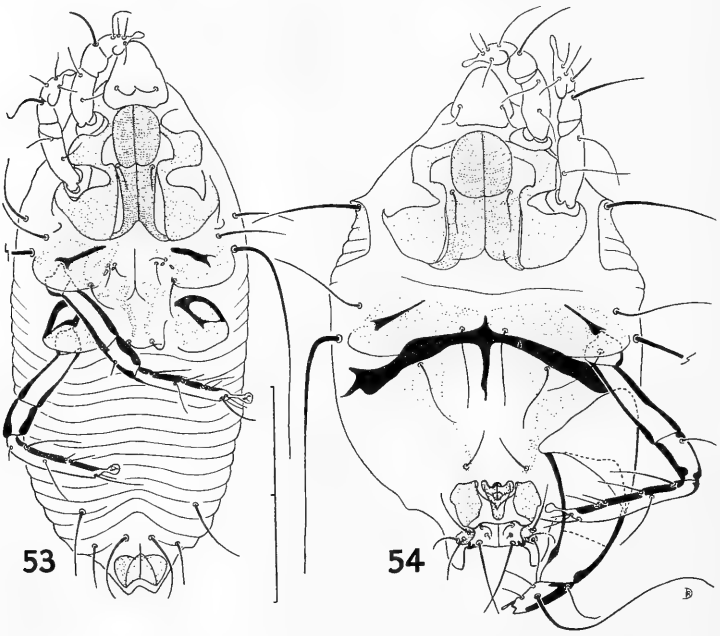
The males of five of these forms are known, and in each the genitalia, caudal lobe, and modified (clasping) legs IV are quite different. All six female forms are likewise immediately recognizable morphologically, and ova have been seen in four. Thus, although the six forms are sympatric, they are morphologically quite distinct, and apparently reproductively isolated. The recognition of all six forms as full species therefore seems justified.

CYTOSTETHUM CLIBANARIUS, n. sp. (Figs 53–56).

Types: Holotype female, allotype male, and one pair of paratypes in Queensland Museum, Brisbane. These specimens are in polyvinyl alcohol-lactophenol, and were collected on a rat-kangaroo, *Aepyprymnus rufescens* (Gray) (Macropodidae), found dead on the road near Herberton, north Queensland, 9.iv.1959, R.D.

Female.—A large, cream coloured, and fairly well sclerotized mite, 518–565μ long from tip of gnathosoma to end of opisthosoma.

Dorsum: Postcapitular shield partly covering gnathosoma, subcircular, finely punctate except for a strip across anterior margin; flanked posteriorly by four subequal setae. Behind these structures is a second, transverse shield, which is finely punctate and without setae. About ten transverse cuticular annulations follow on the middorsum. The annulations in the posterior third are interrupted by two weakly separated median shields; the more anterior is weakly sclerotized and with a seta in each



Text-figs 53-54.—*Cytostethum clibanarius*, n. sp. 53, Venter of female; 54, Venter of male.

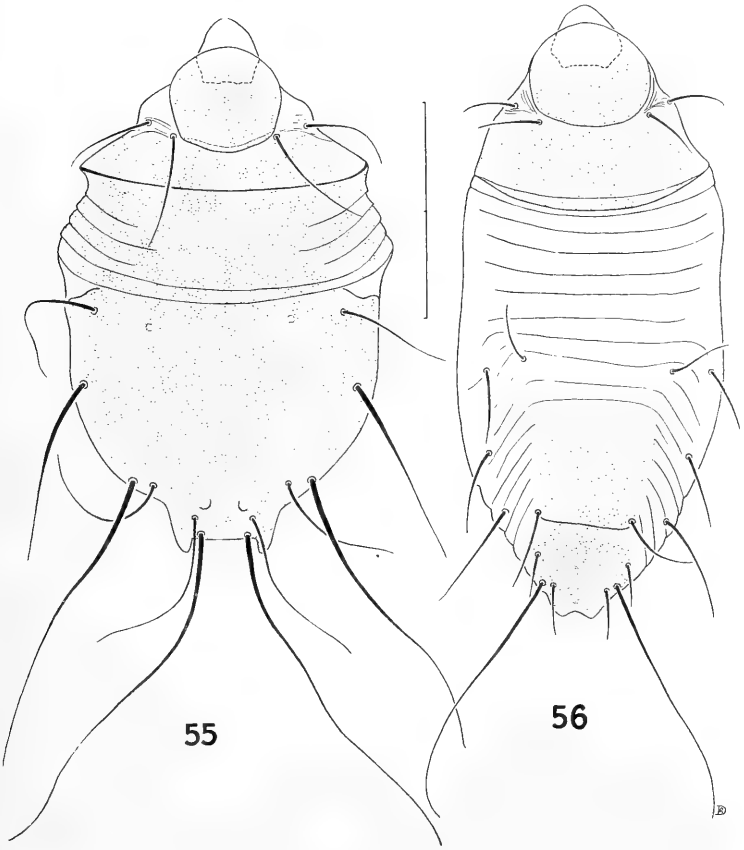
posterolateral corner, while the posterior is strongly sclerotized, and bears three pairs of setae, the central pair being exceedingly long. Four further pairs of setae, which increase in length posteriorly, are set in the lateral annulations on either side of these posterior shields.

Venter: Gnathosoma, legs I and II, and clasping apparatus between coxae I and II typically atopomeline. Genitalia between coxae III, with two pairs of minute suckers and setae. A third pair of setae is situated nearby on the inner posterior angles of coxae III. Genitalia followed by two backwardly-directed punctate strips, which terminate near a pair of setae between coxae IV. Anus subterminal, between two slight caudal lobes; preceded by six setae arranged 2.4. Ventral cuticle with about fourteen transverse annulations behind legs IV.

Legs: With a smaller, and a very much larger seta above coxae III, and a further seta above these (in life, the large seta is stretched out at right angles to the body, but has been depicted as adpressed to save space). Posterior margins of coxae III and IV flap-like, covering part of basal movable segments of legs III and IV. Penultimate segment of legs III with a single seta, but basal movable segment

apparently without one. Tarsi III and IV with eight and seven setae respectively, arranged as in the other species of the genus (Domrow, 1956*a*).

Male.—A very dark brown, heavily sclerotized, and squat mite, with body 460–492μ long from tip of gnathosoma to end of caudal processes. Postcapitular shield as in female, but flanked by setae which are about twice as long. Second dorsal shield wider, but not as deep as in female. Middorsum covered by extremely heavily sclerotized cuticle, which has about four annulations laterally. This band of cuticle



Text-figs 55-56.—*Cytostethum clibanarius*, n. sp. 55, Dorsum of male; 56, Dorsum of female.

is of the same appearance as the dorsal shields. Posterior half of idiosoma covered entirely by postdorsal shield, with two blunt caudal processes posteriorly, and six pairs of setae laterally. Of these setae, the pair between the caudal processes, and the third pair in front of them, are extremely long.

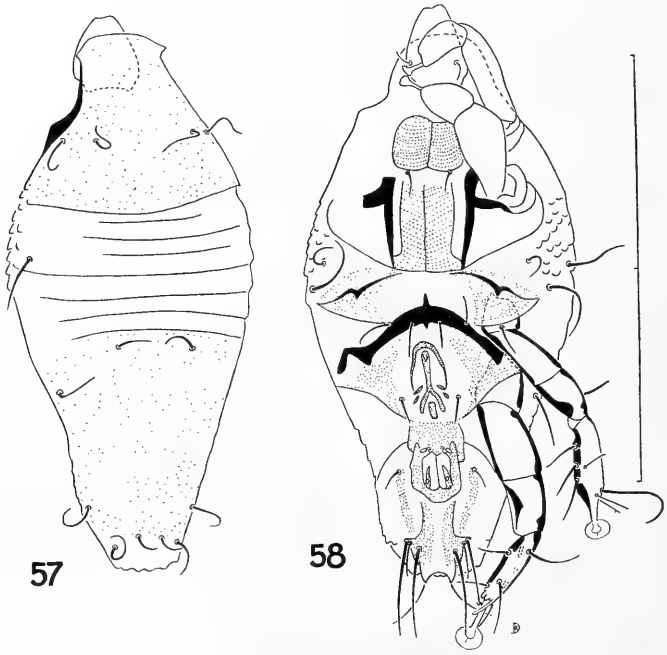
Venter: Anterior half of body as in female. The dorsal band of heavily-sclerotized, annulate cuticle encroaches slightly onto the ventral surface at the level of the posterior half of the clasping apparatus; a strong seta is set in each anterior angle. Genitalia near posterior end of body, with short intromittent organ guided between two lateral sclerotizations. Anus subterminal, flanked on each side by three pairs of setae, and a tubercle bearing a further three setae.

Legs: Legs III as in female, but with a seta on basal movable segment. Coxal apodemes IV very heavy, and united medially with a longitudinal strut. Two sclerotized strips run back to terminate near a seta as in female. Legs IV very stout, with

second and third movable segments fused ventrally, and only weakly divided dorsally. Tarsus IV with minute unexpanded caruncle and four setae, of which the ventrolateral is extremely long as in *C. promeces* Domrow.

CYTOSTETHUM PARVUM, n. sp. (Figs 57–58).

Types: Holotype male and one paratype male in Queensland Museum, Brisbane; one paratype male in British Museum (Natural History), London, and two paratype males in U.S. National Museum, Washington. All specimens are in Hoyer's medium, and were collected on a musk rat-kangaroo, *Hypsiprymnodon moschatus* Ramsay (Macropodidae), rain-forest, Dinner Creek, near Innisfail, north Queensland, 30.vi.1960, J. L. Harrison.



Text-figs 57-58.—*Cytostethum parvum*, n. sp. Male. 57, Dorsum; 58, Venter.

Male.—A very small, but well sclerotized species, with body (including capitulum) 258–268μ long.

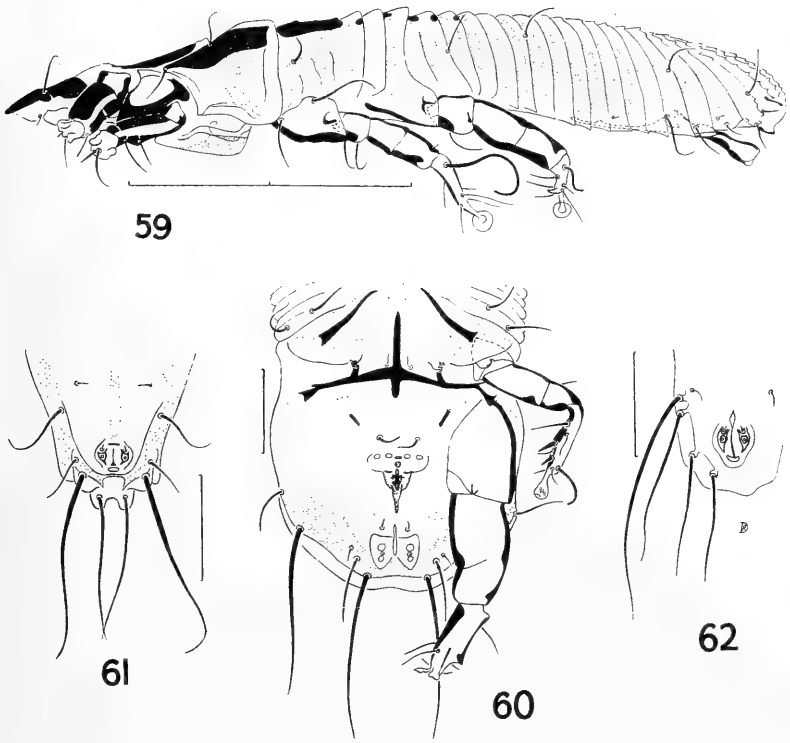
Dorsum: Postcapitular shield completely merged into a second, more posterior sclerotization, so that the four postcapitular setae are set in a transverse line across the combined shield. Middorsum with about seven transverse annulations. Posterior half of dorsum covered with weakly sclerotized cuticle, with four setae anteriorly, and six setae arranged 2.4 posteriorly. Extreme posterior margin weakly scalloped.

Venter: Legs I and II, and clasping organ typical of genus. Genitalia between legs IV. Intromittent organ in shape of inverted Y, with apex recurved; preceded anteriorly by sclerotized arch, and posteriorly by several short sclerotized rods and two setae. Anus elongate, surrounded by particularly heavily sclerotized framework, which bears two minute setae anteriorly. This structure is flanked posterolaterally by two elongate sclerotizations, which bear a seta anteriorly. Still further back, and more medially, are a further two longitudinal sclerotizations, into which are inserted three pairs of setae, the apices of which merge into two small, pointed, and projecting terminal processes. These processes obscure the insertions of a further pair of setae.

Legs: Apodemes III not united medially; preceded by scaly cuticle bearing usual three pairs of setae. Legs III unexpanded, with four movable segments. Basal and penultimate movable segments each with single seta. Tarsus III with six short setae and much stronger subapical seta. Apodemes IV arched, and united medially in short longitudinal rod; flanked by four setae. Legs IV slightly incrassate; three basal movable segments without setae. Tarsus IV with about five setae, and about three blunt subterminal processes. Caruncles III and IV not reduced.

CYSTOSTETHUM MOSCHATI, n. sp. (Fig. 59).

Types: Holotype male and allotype female in Queensland Museum, Brisbane, and two paratype females in British Museum (Natural History), London. All specimens are in Hoyer's medium, and were collected from musk rat-kangaroos, *Hypsiprymnodon moschatus* Ramsay (Macropodidae), rain-forest, Dinner Creek, near Innisfail, north Queensland, 30.vi.1960 and 4.viii.1960, J. L. Harrison.



Text-figs 59-62.—*Cytostethum* and *Austrochirus* spp. 59, *C. moschati*, n. sp., Lateral view of male, all tarsi appear somewhat foreshortened; 60, *C. pseudocharactum* Domrow, Venter of male; 61, *A. queenslandicus* Womersley, Caudal lobe of male, amended; 62, *A. mcmillani*, n. sp., Caudal lobe of male.

Male.—A well sclerotized, very elongate species; length of body including capitulum 544μ. Capitulum, legs I and II and clasping apparatus typical of subfamily. Only the posterior pair of striate clasping organs are visible in lateral view, but these are preceded by a pair of setae and the anterior pair of claspers. Postcapitular shield apparently simple, followed immediately by two broader shields of characteristic texture. The first of these additional shields carries the usual four postcapitular setae, and is punctate centrally. The second additional shield carries a single pair of setae, and is punctate except for a clear patch in the upper anterior angle. About five minute sclerotizations follow along the middorsum. Opisthosoma strongly annulate,

with about 22 annulations, the posterior few of which are serrate. Four pairs of setae are present laterally, while the genitalia and anus are flanked by a further seven pairs. Genitalia set well behind legs IV, elongate, and as figured. Anus terminal, with two internal sclerotized rods.

Legs: Apodemes III typical, preceded by usual three pairs of setae (the most dorsal pair is the pair on the second additional shield), and with four setae between them. Legs III with four movable segments, the penultimate one of which bears a short seta. Tarsi III elongate, with about five weak setae, and a very strong seta dorsobasally. Apodemes IV typical, with two setae between them. Legs IV somewhat enlarged. Three basal movable segments without setae. Tarsi IV with about five weak setae, a stronger dorsobasal seta, and a subapical process. Caruncles III and IV not reduced.

Female.—Very similar to male, but with relatively larger opisthosoma. Length of body (including capitulum) 602μ. About the same number of annulations are present as in the male. Legs III and IV not enlarged. Tarsi III and IV with dorsobasal seta not enlarged, and similar to other tarsal setae.

Notes.—The preceding three new species are placed in the genus *Cytostethum* with some hesitation. Apart from the two members of the *perkinsi* group (genus *Austrochirus*, see Domrow, 1960*a*), the males of nine other atopomeline species from phalangeroids are now known. These belong in the genera *Campylochirus* Trouessart, 1893, *Cystostethum* Domrow, 1956*a*, and *Atellana* Domrow, 1958*b*. All these forms show wide variation in dorsal shield pattern, but have remarkably similar posterior legs in the male. Thus legs III are simple as in the female, while legs IV are greatly modified and enlarged. This character they share with the *perkinsi* group. The following five points should therefore be considered in allocating the above three new species:

1. The new species have macropodid hosts, as do the known species of *Cytostethum*.

2. The *perkinsi* group is at present quite homogeneous, and restricted to phalangerids.

3. I have recently had two series of atopomelines from *Thylogale* (Macropodidae), the type host genus of *Neolabidocarpus* Gunther, 1942, but have been unable to identify the one described species. I am, however, reasonably certain that its males will prove to have legs as described above.

4. The genera *Campylochirus* and *Atellana* each contain a single characteristic species parasitic on phalangerids.

5. Still another monotypic listrophorid genus, *Chirodiscus* Trouessart and Neumann, 1890, will probably prove to be an atopomeline from Australia.

Thus the course likely to cause least confusion is to take a broad view of *Cytostethum*, and to leave the other groups as compact as possible.

Acknowledgements.

I am first of all most grateful to the many collectors and donors listed in the text for the opportunity to examine this interesting material. Many thanks are further due to Mr. H. Womersley for his kind advice and extracts from the literature; to Dr. I. M. Mackerras for his criticism of my manuscript; to Mr. J. Nelson for the identification of *Pteropus scapulatus;* and to Miss P. Nicholas for her careful typing.

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SEED COAT ANATOMY AND TAXONOMY IN EUCALYPTUS. III.*

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(Plate iii; Text-figures 40–47.)

[Read 29th March, 1961.]

Synopsis.

Series Miniatae: The two species, *E. miniata* and *E. phoenicea,* which alone comprise the Series, have a number of points in common. These are the hemitropous seed without a raphe, an obsolete or missing cuticle, the suberized inner integument, no chalaza cork and the high number (up to six or seven or even nine) of small vascular bundles arranged in a semicircle along the upper chalaza border. They differ with regard to the sclerification of the epidermis, suberization of the hilum and occurrence of sclereid and crystal idioblasts.

Series Tetrapterae: The common features of *E. tetraptera, E. forrestiana* and *E. erythrandra* are: seed hemitropous with short raphe, outer cuticle missing, inner integument not suberized, nucellus cutinized. *E. steedmanii* does not fit into this Series because of its entirely different testa structure.

Series Clavigerae: This Series as formulated by Blake is a natural one. Seed hemitropous without raphe, strongly compressed dorsiventrally and thin, orbicular to ovate in outline. Outer cuticle well preserved, inner integument not suberized but partly resorbed and vascular system of various patterns. The embryo cotyledons have oxalate druses only in the large aleurone grains of the epidermis, sharing this particular location with all Corymbosae and species of *Angophora.*

Series Corymbosae: The seed is hemitropous and without a raphe, being either flattened dorsiventrally and wingless (Subseries Ochrophloiae and Maculatae) or laterally with a long terminal wing which is missing in very few cases (Subseries Setosae, Gamophyllae, Eucorymbosae and Neocorymbosae). *E. trachyphloia* with wingless seed compressed dorsiventrally would better be placed on this basis in the Ochrophloiae instead of the Neocorymbosae. The outer integument is multilayered with the cuticle well preserved, the inner integument not suberized but partly resorbed. Oxalate druses are present in the cotyledons as in the Clavigerae.

Series MINIATAE Blakely.

The seed is hemitropous, dorsiventrally compressed and smooth in *E. phoenicea* (resembling *E. baileyana* and its relatives) and with strong ribs in *E. miniata* (similar to *E. erythrocorys*).

The *outer integument* is mostly multilayered on the ventral side and predominantly two-layered on the back; the outer cuticle is faintly discernible or missing.† The cells of the outer epidermis of *E. miniata* have thick anticlinal walls, the thickenings sometimes hourglass-like (Fig. 40*b*) with cutinized middle lamellae. In ribs and hilum rim they are perpendicularly elongated, some of them having periclinal divisions. In contrast, the epidermal walls of *E. phoenicea* are thin, though sclereids (with horse-shoe shaped thickenings) may occur here too, mainly restricted to the hilar and micropylar region (Fig. 40*a*). The sclereids in both species are lignified and heavily impregnated with tannins. There are sclereid idioblasts in the integumentary parenchyma on the ventral side of *E. miniata*, mostly close to the crystal layer and in radial alignment with the chalaza. The inner epidermis is a typical crystal layer, the cells with a thick bottom (the morphological outer wall) accommodating small crystals ensheathed by a cellulose

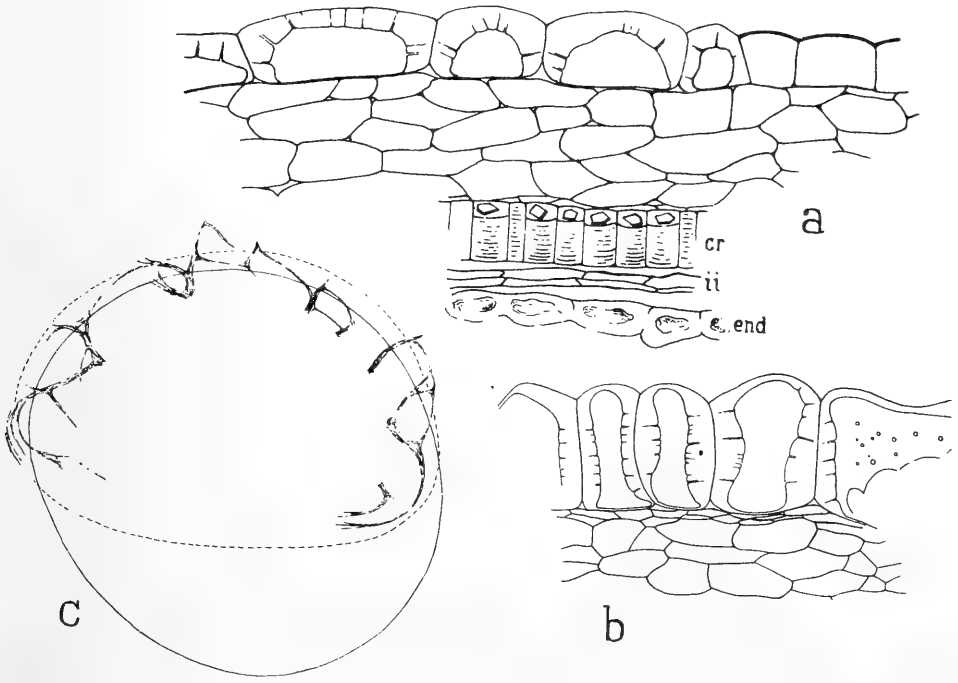
* See Part I, Proc. Linn. Soc. N.S.W., 1958, 83, Part 1: 20-32; and Part II, *ibidem,* 1959, 84, Part 2: 278-291.

† In *E. phoenicea* minute patches of a very thin "crust" can be discerned on the surface. Its chemical nature will be examined later in connection with similar occurrences in other species.

membrane. In most of the *E. phoenicea* seeds the crystal layer at the rim of the chalaza is in-folded against itself so that in surface view (best examined from inside) the double layer of crystal-bearing cells forms a "collar" of variable width around the chalaza, as illustrated in Figure 45*a* for *E. haematoxylon*. In *E. miniata* lignified sclereid idioblasts were occasionally observed, intercalated between the somewhat smaller non-lignified cells of the crystal layer.

The *inner integument* is suberized and projects beyond the rim of the crystal layer into the "window", this projection being of variable width with a smooth, wavy or jagged contour.*

Chalaza. The parenchymatous tissue within the gap in the crystal layer and inner integument is neither suberized nor lignified, therefore the so-called "chalaza cork" is (as in *E. tetrodonta*) missing. Crystal-bearing idioblasts with uneven, often reticulate thickenings accommodating one or two ensheathed crystals per cell were seen in the centre of the chalaza of *E. miniata* only.



Text-fig. 40*a-c*.—*a*, *b*, trans. sect. through the outer integument showing sclerified epidermal cells: *a*, *E. phoenicea*, horse-shoe shaped thickenings in the micropylar region, 350×; *b*, *E. miniata*, some thickenings hour-glass-like, 230×. *c*, *E. miniata*, vascularization pattern, 23×. The dotted line limits the chalaza region, the solid line the hilum.

Hilum. It overlaps to a great extent (sometimes completely) the chalaza (Fig. 40*c*), is sharply circumscribed by a raised rim of sclereids in *E. miniata*, whereas in *E. phoenicea* sclereids may occur in more or less dispersed groups (very rarely confluent to form a complete sclerified frame) around the hilum. In *E. miniata* about two superficial layers are lignified and suberized. The occurrence of cells characteristically arranged in groups of four indicates that cell divisions were still in progress when suberization took place (Pl. iii, fig. 3). *E. miniata* is a further case of metaplasy by suberization of the hilum, at least *pro parte*, because only that part of it which overlaps the chalaza is

* These projections are particularly prominent in *E. phoenicea* and they are the reason why in sections through the chalaza close to its periphery the inner integument may be seen as a continuous layer separating the chalazal tissue from the nucellar.

completely suberized while in the remaining part not all cells have suberin lamellae. In *E. phoenicea* no such suberization is encountered and the protection of the scar is dependent solely on deposits of tanniniferous substances.

Vascularization. The high number of small bundles entering the chalaza is characteristic for both species: up to 6 in *E. phoenicea*, up to 9 in *E. miniata*. The more of them present the more tender and shorter they are. They are arranged in a semicircle, their entrance close to the upper border of the hilum (Fig. 40*c*).

These two species are considered—on grounds other than seed structure—as closely related and the broader features of seed coat anatomy are in accord with this view. The anatomical discrepancies in such characters as epidermis structure, occurrence of sclereid and crystal idioblasts and suberization of the hilum suggest these features must be used with caution for taxonomic purposes.

S. T. Blake (p. 335) advocates grouping together of the Miniatae and *E. baileyana* and its relatives. However, the testa structure does not help to substantiate this suggestion. Nevertheless as far as our investigations have gone these two species show no closer affinity with any other groups of species so far examined and any hint of closer affinity from seed coat anatomy must await the completion of the study of the whole genus.

Series TETRAPTERAE Blakely.

In this Series Blakely lists in the 1935 edition of "A Key to the Eucalypts" only *E. tetraptera*, but in an addendum to the description of *E. steedmanii* he says, "I have proposed a new Series—Tetrapterae, for the reception of the three species . . .", which he implies are *E. tetraptera*, *E. forrestiana* and *E. steedmanii*.

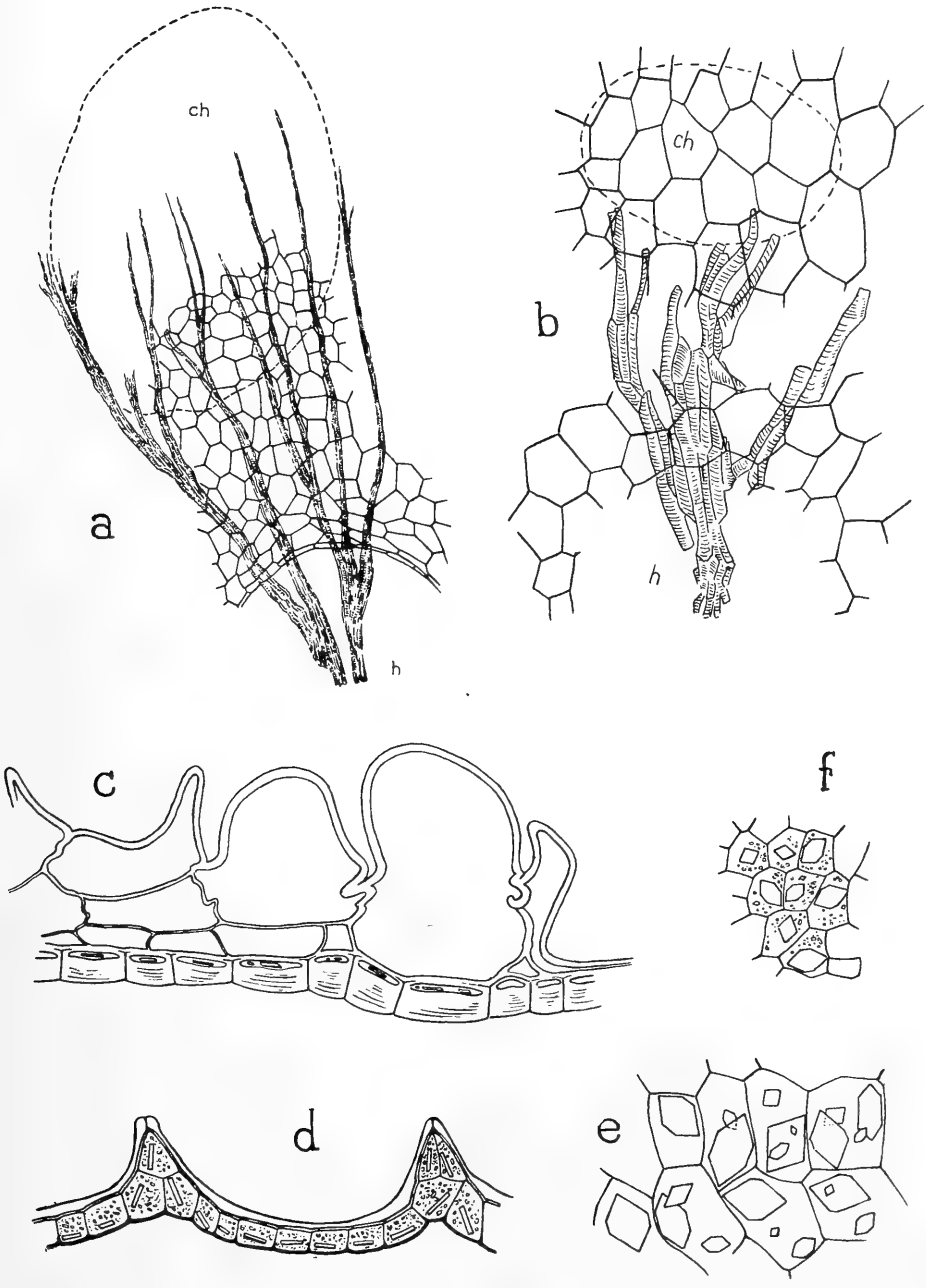
The editors of the second edition, 1955, place *E. erythrandra* also in the Series Tetrapterae in accordance with the notes accompanying the description of this species, but in spite of Blakely's notes concerning *E. forrestiana* under *E. steedmanii* which they include in the Tetrapterae in this edition, they still retain *E. forrestiana* in the Series Contortae where it was placed by Blakely in the (1935) first edition.

The three species *E. tetraptera*, *E. steedmanii* and *E. erythrandra* are dealt with together and at the same time the relationship to *E. forrestiana* is particularly considered.

The seeds are hemitropous, but in contrast with Eudesmiae, Miniatae, Clavigerae and Corymbosae the hilum is some distance below the chalaza, therefore the vascular bundle has to run to some extent through the outer integument, forming a short raphe, before reaching the chalaza (Fig. 41*a*). The outer cuticle is missing, the tender inner integument is not suberized. The chalaza cork is always present and its middle lamellae are lignified. In view of the tenderness of this tissue the limit between the middle lamella *sensu stricto* (that is, the intercellulary substance alone) and the primary wall is obscure and it may be that the lignification affects both. The suberin pellicle forming the secondary wall can be isolated easily and stained.

This type of suberization combined with lignification was called by A. Meyer and his students "Metakutisierung" (metacutization) (see H. Müller, 1906; also E. Gauba, 1926).

Remnants of the nucellar tissue (the cells empty and obliterated) are present, often amounting to a considerable quantity. A striking feature is the extensive wall cutinization of its outer layers, especially in the proximity of the chalaza (Pl. iii, fig. 1). Fatty substances synthesized and released by the protoplasts of these cells accumulate not only on the surface of the nucellus to form finally a cuticle (coalescing with that of the inner integument), but also impregnate the periclinal and anticlinal walls up to six or more layers deep. This intramembranous cutinization is more or less continuous only in the outermost layers. Seen in section it is gradually reduced further into broken lines, granules and dots, which are more and more widely spaced the more distant they are from the surface (atypical cutinization). If we interpret this teleologically we could consider it as a substitute for the unsuberized inner integument (suberized in



Text-fig. 41*a-f*.—*a*, *b*, vascularization patterns: *a*, *E. tetraptera*, 75×; *b*, *E. steedmanii*, 220×. *c*, *d*, outer integument in trans. sect., 350×: *c*, *E. tetraptera*; *d*, *E. steedmanii*. *e*, *f*, crystal layer in surface view, 350×: *e*, *E. tetraptera*; *f*, *E. steedmanii*.

Eudesmiae, Miniatae, Renantherae). Thus, having fulfilled its role as a nutritive tissue, the nucellus is converted to a tissue protecting the embryo.

The (black) seeds of *E. tetraptera* and *E. erythrandra** are morphologically identical and differ (in our sample) only in the size. There is a narrow circumferential wing, built up by the two integuments, and a system of folds (or narrow wings) on the ventral side, most of them radiating towards the raised hilum-chalaza region. However, Gardner (1940–41) considers *E. erythrandra* as a hybrid between *E. tetraptera* and *E. angulosa*. From our seed investigation it can be anticipated that no evidence of such a hybrid origin can be expected, because the seed structure of the putative parents is very similar in the salient characters.

On the other hand, Blakely (Key, p. 74–75), though listing *E. forrestiana* in the Section Platyantherae, Series Contortae, has pointed to some affinities with the Tetrapterae. This suggestion is supported by the conformity of their external and anatomical seed structure. The same set of anatomical criteria is also encountered in *E. stoatei*. The suggestion by L. A. S. Johnson (*in litt.*)—on other grounds than seed structure—of a close relationship with *E. tetraptera*, has support also from our investigation. *E. steedmanii*† is an exception because of its entirely different outer integument. There is no testa expansion into wings or folds and the surface is finely honeycombed by transversely elongated pits in longitudinal alignment on the back and in rows radiating towards the hilum on the ventral side. This sculpture is due to the sunken outer walls of the large epidermal cells and (in cross section) to the undulate course of the underlying crystal layer. This type of ornamentation is encountered—as a test at random showed—in several Sections, e.g., *E. spathulata*, *E. torquata*, *E. intertexta* (Section Macrantherae), in *E. sideroxylon* (Section Terminales) and in *E. viridis* (Section Porantheroideae). Further examples are given by Grose and Zimmer (1958) and illustrated in surface view in their fig. X on page 7. Our Figure 41*d* shows the anatomical structure in sectional view.

It is also worth mentioning that in *E. tetraptera* and *E. erythrandra* each cell of the crystal layer contains besides one large ensheathed crystal a few smaller ones, all geometrically well shaped (Fig. 41*e*), whereas in *E. steedmanii* there is only one large crystal surrounded by a considerable number of crypto-crystalline granules (Fig. 41*f*).

Another fact suggesting the exclusion of *E. steedmanii* from the Tetrapterae is the shape of the cotyledons, which are reniform in *E. tetraptera* and *E. erythrandra*, but—as a germination test showed—deeply bisected in *E. steedmanii*.

It is interesting that C. A. Gardner (*in litt.*), using other evidence, quite independently from our investigation, arrived at the same conclusion. In his opinion *E. steedmanii* should be placed in the Series Cornutae, close to *E. spathulata*. We examined *E. spathulata* and the seed structure agrees precisely with that of *E. steedmanii*, even with regard to seemingly trifling characters, as, for instance, the occurrence of crystal idioblasts (with crystal plus granules) in the integumentary parenchyma of the ventral side.

There is still another problem with regard to the position of the Series Tetrapterae. Blakely puts it between the Eudesmiae and Miniatae on the one side, and Clavigerae and Corymbosae on the other. These four Series have, contrary to the Tetrapterae, no raphe at all and therefore an entirely different vascularization pattern. This could be considered as a minor character, but it is significant that the seed of the Xylocarpae (*E. macrocarpa*, *E. pachyphylla*, *E. pyriformis*) agrees well in all salient characters (wings, short raphe, unsuberized inner integument, heavy cutinization of the nucellus) with the Tetrapterae, though the cotyledon shape is quite different: reniform in the Tetrapterae and bisected in the Xylocarpae. Of course, there is—as with the widespread

* The seed was obtained through E. F. Martin and was collected from a cultivated tree at Bulgunnia Station homestead, 50 miles west of Mt. Eba (South Australia), by T. Gray in October, 1957.

† Authentic seeds of *E. steedmanii* were received from C. A. Gardner, Government Botanist, Perth.

occurrence of honeycombed seeds—always the question as to which characters arise independently in different unrelated groups, and which are phyletic, expressing true affinities. More facts are still needed before a definite answer can be given.

Series CLAVIGERAE (Maiden) S. T. Blake.

S. T. Blake separates seven species from Blakely's Corymbosae, uniting them into the Series Clavigerae. Most of them occur in relatively remote parts of northern Australia, and this and the fact that they shed seeds quickly after ripening accounts for the difficulty in obtaining sufficient quantities for examination. We have had a good quantity only of *E. papuana*, *E. tessellaris* and *E. confertiflora*, whereas the results of three other species, *E. clavigera* (Darwin, 1.12.1915, Hill 364), *E. grandifolia* (Burrundie, N.T., 5.11.1915, Jensen 352) and *E. aspera* (Roy Hill, W.A., 8.5.1958, Burbidge 6043), are based on one or two seeds obtained from authentic dried specimens. It is plain in these latter cases the examination could not be extended to all anatomical and histochemical details; nevertheless from those examined in detail and because of the consistency of the group we believe we have obtained an adequately accurate picture of the seed structure in this Series.

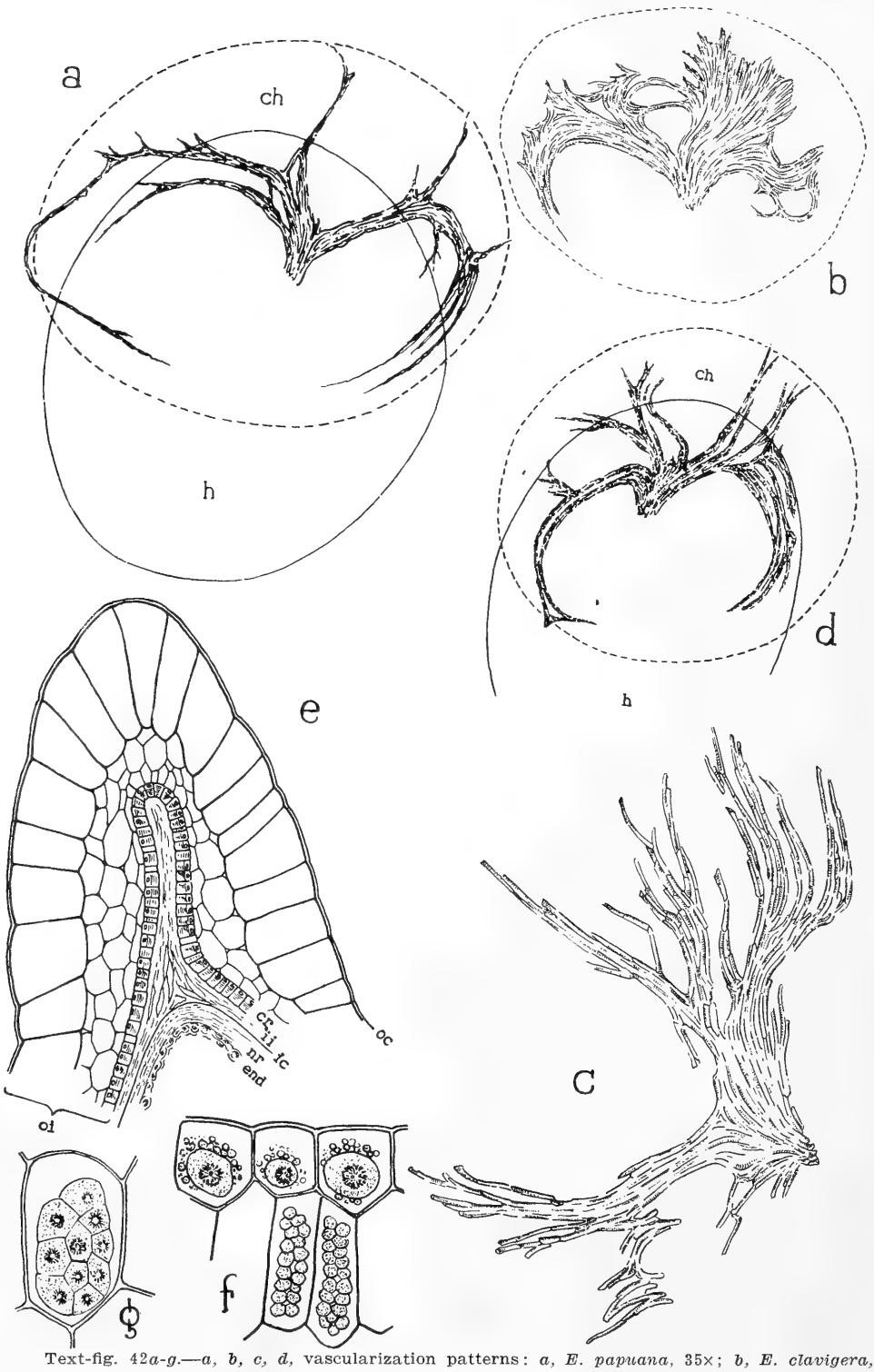
The seeds are hemitropous, strongly compressed dorsiventrally and therefore thin, flat or concave-convex, orbicular or ovate in outline, and with a narrow firm or tender circumferential border. From the point of view of dissemination these seeds would be called in German terminology "Scheibenflieger" (when orbicular) or "Scheibendrehflieger" (when ovate).

The *outer integument* is multilayered on the ventral side, but on the back reduced to three and here and there to two layers only (Fig. 43*d*). The outer cuticle is well preserved. The epidermal cells are thin walled, but some with thicker walls may be interspersed (*E. papuana*, *E. confertiflora*). They contain either amorphous reddish-brown deposits or are filled with a yellowish or reddish solution which is precipitated by potassium dichromate, copper acetate or formalin. Rhodamin gives a blue flocculent precipitate, ferric salts stain the contents dirty green or blue, and osmic acid inky blue to black. These reactions point to tannins. Both solution and solid deposits assume a brilliant ruby-red colour with vanillin-HCl, indicating the presence of a phenol, very probably of phloroglucin, and may be considered as phloroglycotannoids. In *E. papuana* most of the epidermal cells are filled with a solution, easily extracted by water or alcohol, and a few only have solid deposits. The latter were the only type seen in *E. confertiflora*.* The proportion of cells containing solution to those with solid deposits varies within the species and generally it can be said that the greater the amount of these deposits the darker the seed colour, which varies from light brown to black. In *E. papuana* the small epidermal cells surrounding the exostome are crystal-bearing, the walls being either thin (Fig. 43*a*) or sclerified to such a degree that the crystals become embedded in the wall thickenings (Fig. 43*b*). This encasement can be complete, but more frequently the uneven wall thickenings form only a "pocket" around the crystal. Besides this ergastic envelope the crystals have also their own alloplasmic sheath originating probably from a cellulosic degeneration of the protoplast (Fig. 43*c*). Mechanical elements in the integumentary parenchyma are rather rare, but can be seen for instance beneath the hilum scar in *E. papuana*. Sclereids forming an uninterrupted layer between the two epiderms on the dorsal side were seen only in *E. aspera*.† The inner epidermis is a typical crystal layer with thick outer walls (crystal sclerenchyma), leaving but little space for the crystals.

The *inner integument* is tender, not suberized and here and there resorbed. The inner cuticle was seen to be almost smooth in *E. clavigera* and *E. confertiflora*, with

* These deposits were still undissolved in sections kept for one month in water and in alcohol.

† We had only one seed for examination. Though the embryo was apparently of normal structure, some anomalies in shape and size of the seed and its venation pattern give rise to some doubt whether this occurrence of sclereids is a peculiar and constant character in this species. Heavy sclerifications in the testa are common in seed which is sterile or inviable for some reason or other.



Text-fig. 42*a-g.*—*a*, *b*, *c*, *d*, vascularization patterns: *a*, *E. papuana*, 35×; *b*, *E. clavigera*, 23×; *c*, *E. confertiflora*, 60×; *d*, *Angophora intermedia*, 35×. *e*, trans. sect. through the circumferential border of *E. papuana*, 150×. *f*, *g*, oxalate druses in the aleuron grains of the embryo cotyledons, 730×: *f*, in the upper epidermis of *E. papuana*; *g*, in a mesophyll cell of *E. tetraptera*.

short ribs in *E. papuana* and with few but very long projections (up to eight layers deep) into the radial walls of the nucellus in *E. tessellaris* and *E. grandifolia* (see Pl. iii, fig. 5, of *E. gummifera*).

The circumferential border of the seed is built up by both integuments and is relatively thick in *E. papuana* (Fig. 42*e*) and *E. confertiflora*, but very thin in *E. tessellaris*. In *E. grandifolia* we saw also the inner cuticle, the nucellar tissue and even some endosperm penetrating to some extent into the border.

The *hilum* overlaps the chalaza and the vascular bundle enters directly into it, whereupon it ramifies, forming discrete strands of variable thickness, the two outermost the strongest, and with an arcuate course along the chalaza border (*E. papuana*, Fig. 42*a*; *E. grandifolia*). In *E. confertiflora* the strands are very loose and their arrangement varies. They are turned upwards (like antlers, Fig. 42*c*), or spread horizontally or the outermost bent down. In the two seeds of *E. clavigera* examined (Darwin, 1.12.1915, Hill 364) the tracheids were flatly spread, like a fan, covering a great portion of the chalaza (Fig. 42*b*). Commonly one single bundle enters the chalaza, but in *E. confertiflora* we saw sometimes two and even three separate bundles.

The *chalaza cork* has lignified middle lamellae and is filled with dark tanniniferous deposits. This seems to be a general rule for the whole genus, only very few exceptions having been observed hitherto. In *E. confertiflora* (from Port Moresby, Papua) most of the seed (but not all) have a considerable amount of a mineral deposit in the chalaza parenchyma around the tracheids. There are granules, loose or aggregated into grape-like clusters, crystals, partly or completely corroded, but well-shaped intact crystals of tetragonal bipyramids occur too. Sulphuric acid converts them all on the spot in clusters of needle-shaped crystals of calcium sulphate. Consequently they belong to the trihydrate of calcium oxalate whose crystals belong to the tetragonal system. It is interesting to see both hydrates in adjacent tissues: the monoclinic monohydrate in the crystal layer, the tetragonal trihydrate in the chalaza.

Remnants of nucellus and endosperm are present, the former multilayered, the latter mostly as a single strongly compressed layer.

Morphologically and anatomically the seeds of the Clavigerae agree in all essential characters with those of *Angophora*. There is also the same occurrence of amorphous and dissolved phloroglycotannoids in the epidermal cells. A further remarkable feature relates to the location of cluster crystals (druses) of calcium oxalate in embryo cotyledons. In the Eudesmiae, Miniatae and Tetrapterae they are confined to mesophyll cells (Fig. 42*g*). In the Clavigerae (and as will be shown later in the Corymbosae too) they are found exclusively in the epidermis. Here each cell contains some small aleurone grains (without any inclusion) surrounding one very large "solitaire" in which one druse of considerable size is embedded (Fig. 42*f*). This applies only to the upper epidermis, whereas in the lower the occurrence of very small druses is not so constant. The Clavigerae and Corymbosae have this peculiar distribution of cluster crystals in common with *Angophora* (*A. intermedia*, *A. cordifolia*, *A. costata*).

The above results show in review that the seed structure in its essential traits supports the opinion that the Series Clavigerae, as formulated by Blake, is a natural one.

Series CORYMBOSAE (Benth.) Maiden. (23 species examined.)

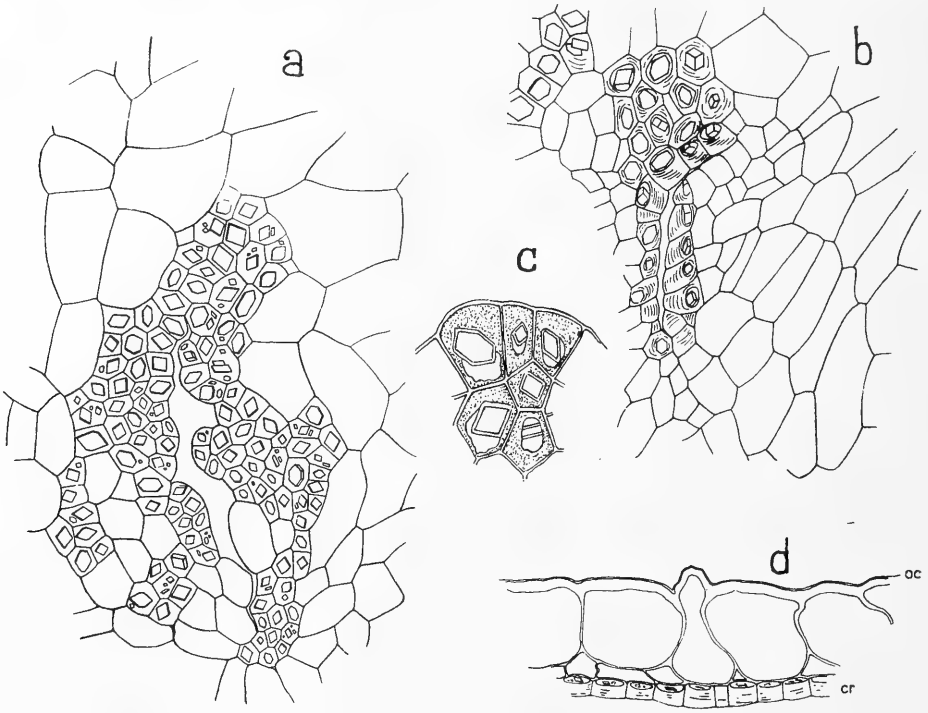
Seed hemitropous, compressed either dorsiventrally and then wingless, or laterally when (with very few exceptions) it is furnished with a long terminal wing.

The *outer integument* is multilayered, though in some species the epidermis on the dorsal side may lie directly upon the crystal layer (e.g., *E. trachyphloia*, *E. jacobsiana*). Where the surface is wrinkled, the outer integument appears in cross sections more or less deeply lobed, e.g., *E. abbreviata* (Fig. 44*c*), *E. foelscheana*, *E. latifolia*.

The outer cuticle is always well preserved.

The epidermal cells are rectangular in cross section, somewhat perpendicularly elongated or even palisade-like towards the edges (Subseries Maculatae), and then some of them are horizontally divided. The outer walls are commonly rather thicker and some of them lignified (e.g., in *E. setosa*, *E. terminalis*, *E. ficifolia*, *E. bleeseri*).

In most of the Setosae and Eucorymbosae the epidermal cells have (like some subepidermal cells) uneven thickenings on the inner and side walls (Fig. 44*b*). They are all filled with light or dark reddish-brown tanniniferous substances, either dissolved or as amorphous deposits, often glasslike (Ochrophloiae, Maculatae), and either readily or scarcely soluble in water or alcohol.* $FeSO_4$ stains inky blue, vanillin-HCl ruby red. They may be classified as phloroglycotannoids. The conspicuous deposits on the outer walls of *E. calophylla* (Fig. 44*a*) deserve particular consideration. They are unique among the Corymbosae. Petit has recorded and illustrated them in his Fig. 19 on page 48. He mentions their mucilaginous aspect and noticed also a brownish substance



Text-fig. 43*a-d*: *E. papuana.*—*a, b, c,* crystal-bearing epidermal cells around the open exostome in surface view: *a,* the cells thin walled, 175×; *b,* the cells sclerified, 230×; *c,* a group of them after treatment with HCl to remove the crystals, 350×; their shape is preserved perfectly by their alloplasmic envelope which is embraced by the (stippled) secondary uneven wall thickenings (ergastic envelope). *d,* trans. sect. through the outer integument, dorsal side, 230×.

in the lumen. Netolitzky (p. 240) suggests that the wall deposits are probably the so-called "inclusions". We examined seed gathered ourselves from a natural stand (Dwellingup, W.A.) with the following results:

Cross sections show considerable deposits on a thick outer wall and part of the side walls, adhering firmly to the walls and occupying about one-third to one-half of the cell cavity (Fig. 44*a*). After swelling is induced a fine and dense lamellation is revealed together with simple or ramified pit canals. In very thin sections the outer layers appear nearly colourless, but, due to a gradually intensified impregnation with dark substances, the colour of the subsequent layers changes from light brown to almost black in the innermost. Chloroiodide of zinc stains the light lamellae pure blue, the heavily impregnated inner ones dirty blue. IKI (iodine + potassium iodide) alone does not stain them, but the addition of sulphuric acid produces under strong swelling a dark to blackish-blue staining. Cuprammonia dissolves them. Boiling in 2 per cent.

* In sections of *E. foelscheana*, kept for a month in water and in alcohol, most of the deposits were still undissolved.

HCl for two hours causes no hydrolysis. All these reactions point to cellulose as the ground substance.

The impregnating substance responds to tannin reagents. In very fine sections the nearly colourless outer lamellae remain unstained with $FeSO_4$, the brownish inner ones become greenish or olive-green. The three reagents considered as reliable indicators of phloroglycotannoids (which are characteristic for the "inclusions"), vanillin-HCl, p-dimethylaminobenzaldehyde-H_2SO_4 and KOH, have no effect except for some bleaching with KOH. It is concluded from the above reactions that the wall deposits have a cellulosic ground substance impregnated with tannins but not with phloroglycotannoids. In water these deposits show no noticeable swelling,* but after treatment with Eau de Javelle (to remove the tannins), followed by washing with water, they swell markedly, filling the whole cavity. Alcohol contracts these masses to their original volume. We have already encountered the same wall deposits—though less conspicuously—in the Renantherae, Series Occidentales (*E. marginata*, *E. staerii*, *E. sepulcralis*) and have considered them as membrane-mucilage impregnated with tannins.

The chemical behaviour of the yellowish or brick-red material secreted in the cavity of the epidermal cells is quite different. It is also present in all parenchyma cells of the outer integument. Vanillin-HCl or p-dimethylaminobenzaldehyde-H_2SO_4 gives a brilliant ruby-red colour constantly.

The impregnated parenchyma walls are also stained pink or red, while $FeSO_4$ stains (in thin sections) these walls and the contents pure inky blue, often with a tinge of violet. Here we are dealing obviously with the same tannin derivatives, the phloroglycotannoids, we have already encountered in the Clavigerae.

Integumentary parenchyma is quite generally initiated by divisions in both epidermal layers (predominantly in the outer one), though when fully developed this origin is seldom recognizable. Only in some sections of *E. ptychocarpa* the three outermost layers demonstrated clearly their formation from the outer epidermis by periclinal and anticlinal partitions (Fig. 44*b*). Phloroglycotannoids as deposits and wall impregnation are very common. Sclereid idioblasts were seen in *E. gummifera* and *E. terminalis*.

Crystal layer. Various deviations from the typical structure were occasionally observed.

(1) It is, for instance, not unusual that cells of this layer at the chalaza border are without crystals.

(2) Patches of empty cells within this layer are a regular feature in *E. trachyphloia* (from Belmont, Brisbane) and also frequent in *E. ptychocarpa*.

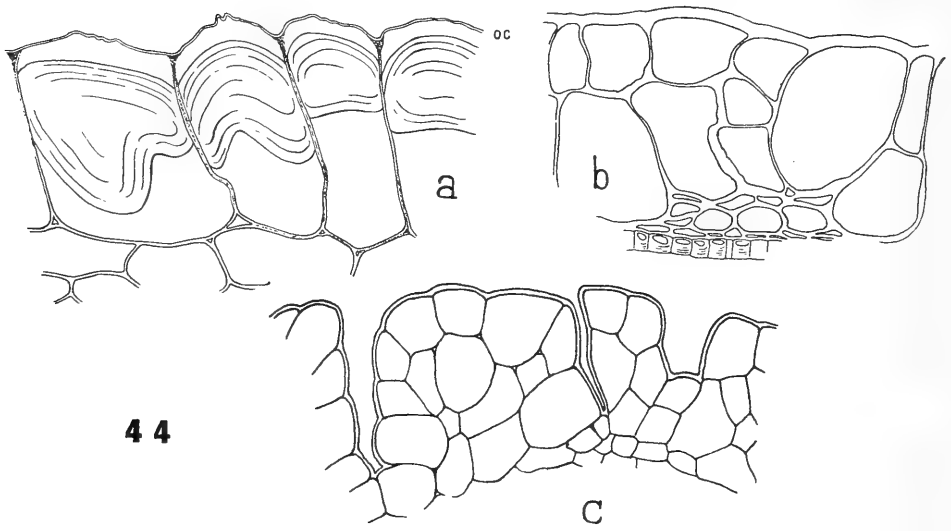
(3) In *E. haematoxylon* and *E. maculata* the crystal layer is occasionally infolded against itself at the rim of the chalaza so as to reverse the orientation of the crystal-bearing cells (Fig. 45*a*). As previously mentioned, this is quite common in *E. phoenicea*.

(4) An occasional doubling of the crystal layer in patches anywhere along its course may occur, the additional layer being adjacent to the outer face of the basic crystal layer. The crystal-bearing cells may have the same orientation (*E. latifolia*, *E. abbreviata*, Fig. 45*b*), or are inverted (*E. ferruginea*, Fig. 45*c*).

The *inner integument* in many species is in some places more or less resorbed and—except at its base on the chalaza border—not suberized. The inner cuticle (coalescent with that of the nucellus) is always present, either (in cross sections) with short ribs or, especially near the chalaza, with long projections penetrating sometimes up to twelve layers deep into the anticlinal walls of the nucellus (Pl. iii, fig. 5). In longitudinal sections they appear as narrow wavy strips quickly decreasing in width.

Wings. The presence of a long terminal wing is characteristic of certain groups of the Corymbosae and unique in the genus. This wing, usually about as long as the body, is the result of an extension of the outer integument, but without the participation of the crystal layer, and causes the seed to move spirally during dissemination ("Schraubenflieger"). Its formation is strictly confined to species with seed flattened or

* Mucilages are known which scarcely swell in water, e.g., that of *Cinnamomum cassia*.



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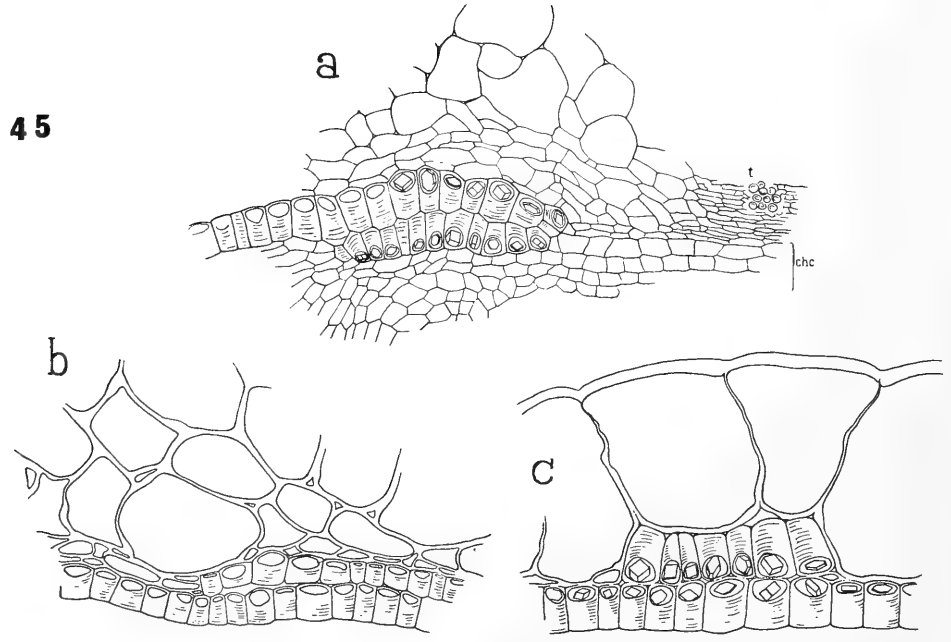

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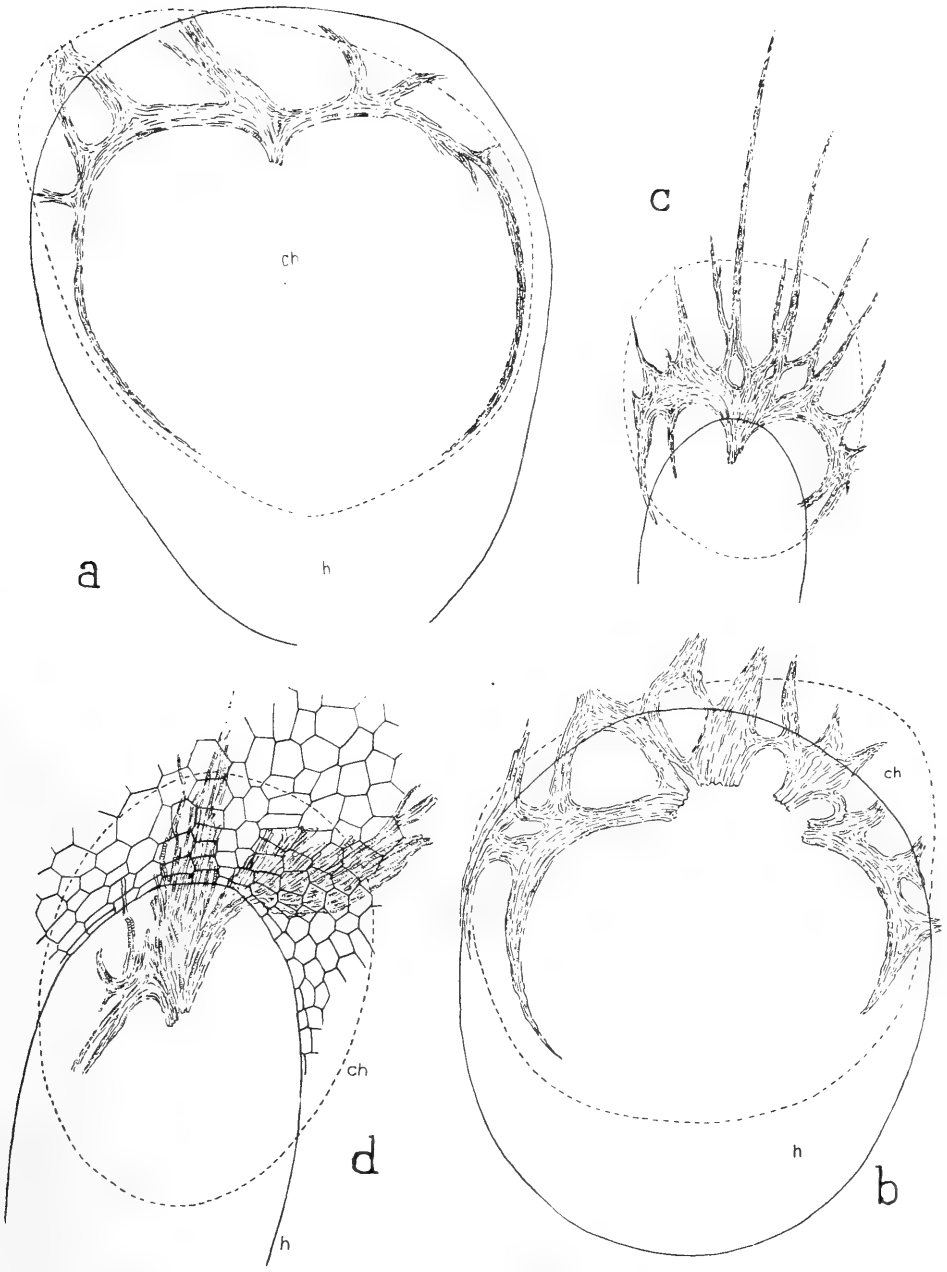
Text-fig. 44*a-c*.—Part of outer integument in trans. sect.: *a, E. calophylla,* 230×, epidermal cells with wall deposits; *b, E. ptychocarpa,* 150×, showing origin of some integumentary parenchyma from the outer epidermis by periclinal and anticlinal divisions; *c, E. abbreviata,* 90×, outer integument lobed.

Text-fig. 45*a-c*.—Occasional doubling of the crystal layer, 230×: *a, E. haematoxylon,* crystal layer infolded against itself at the rim of the chalaza; *b, E. abbreviata,* the additional layer (crystals omitted) with the same orientation; *c, E. ferruginea,* the short additional layer with inverse orientation of the crystal-bearing cells.



Text-fig. 46*a-d*.—Vascularization patterns: *a, E. calophylla,* 15×; *b, E. haematoxylon,* 15×; *c, E. abbreviata,* 23×; *d, E. dichromophloia,* 75×.

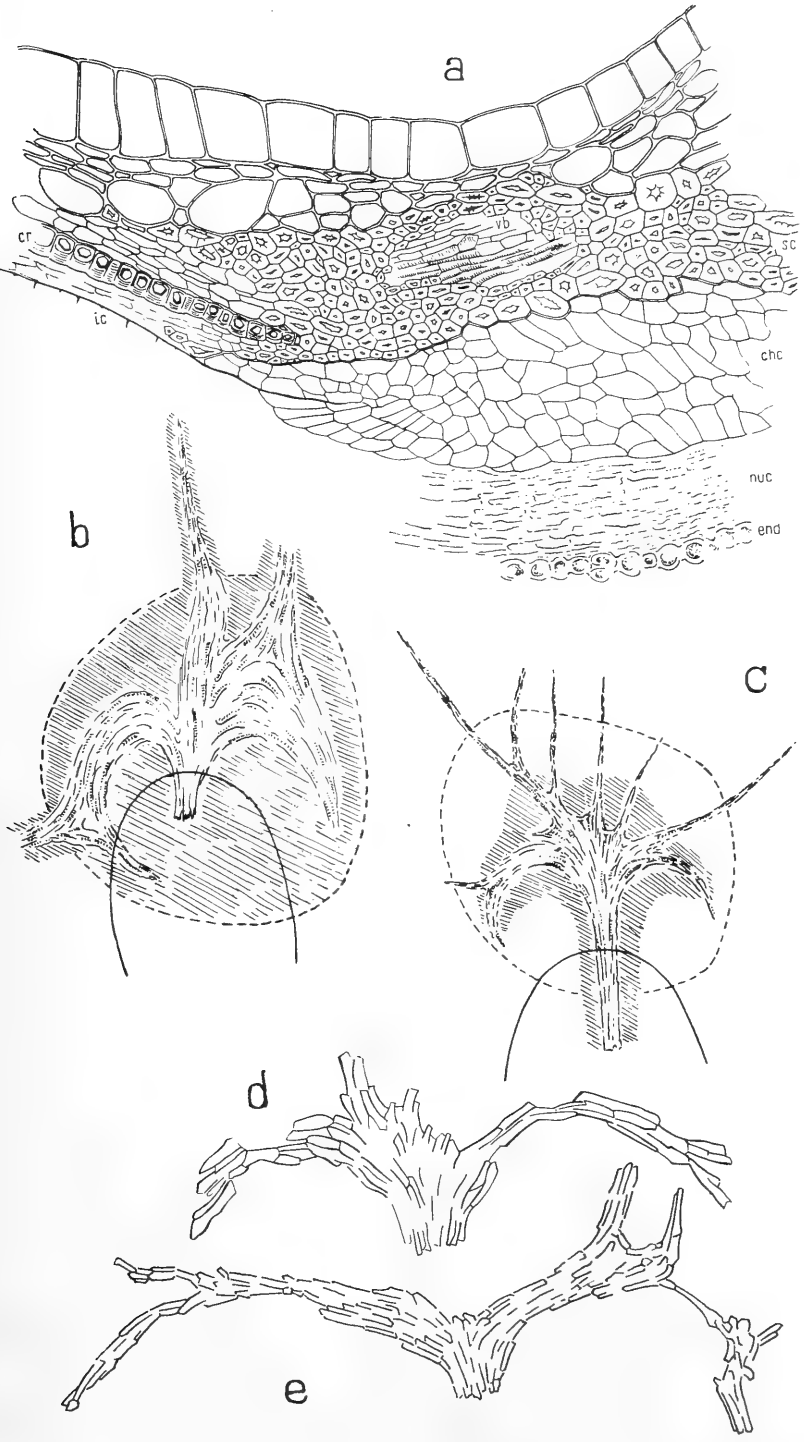
compressed laterally, thus excluding the Subseries Ochrophloiae and Maculatae which have dorsiventrally flattened wingless seed. On the winged seeds the hilum and chalaza are located on one flank more or less close to the inner edge.* The wing shape varies sometimes within the species, is frequently flat and ligulate, sometimes spoon-like or even boat-shaped. If the seed is very strongly compressed so that hilum and chalaza are lodged on the narrow inner edge, then the wing is folded. Adopting some of S. T. Blake's adjustments to Blakely's grouping we see that all species belonging to the Setosae (3), Gamophyllae (1) and Eucorymbosae (6) are furnished with a wing (*E. collina* is considered by Blake of doubtful validity as a species). In the Neocorymbosae (12) six species have a long terminal wing, in *E. gummifera* it is small, in *E. haematoxylon*—if present—rudimentary, and it is missing in *E. calophylla*, but they all have laterally compressed seed. *E. trachyphloia* is out of step in this Subseries, its wingless seed being dorsiventrally flattened. Thus, whilst in the first three Subseries of the Corymbosae all species have winged seeds, the fourth includes a few with missing or imperfect wings. Bentham (III, 1888) has already pointed out that this character appears to be of little value if we consider, for instance, the two allied species *E. calophylla* and *E. ficifolia*. These are closely similar in every other respect, differing from each other mainly in their wingless or winged seeds. In our opinion it is not so much the wing but the shape of the seed body (flattened laterally or dorsiventrally) which, apart from other characters, expresses affinity or lack of it in these species. If this character is of taxonomic value then it supports a readjustment in the placing of *E. trachyphloia*. It is noteworthy that Jacobs (1935) suggested some affinity with *E. jacobsiana* placed by Blakely in the Subseries Ochrophloiae of which all species have dorsiventrally flattened seed.

The *chalaza* accommodates the conducting tissue, of which some patterns (though at times variable even in the same species) are illustrated in Figures 46 and 47. The poor vascularization in *E. trachyphloia* (Fig. 47*d*) is remarkable and reminiscent of that in *E. jacobsiana* (Fig. 47*e*, type material), consisting mainly of two more or less curved branches. Of course, this poor vascular supply may be due to the size of the seeds (3–3½ mm.) which are the smallest among the Corymbosae. Nevertheless, the similarity of the patterns could perhaps also lend some support for the transfer of *E. trachyphloia* from the Neocorymbosae to the Ochrophloiae. With regard to the relative position of xylem and phloem a few observations of cross sections may be mentioned. In *E. ficifolia* and *E. calophylla* amphicribral bundles were seen sometimes, but as a rule collateral bundles are prevalent with the phloem on the outside of xylem (*E. latifolia*, *E. ptychocarpa*, *E. foelscheana*) and in *E. setosa* occasionally on its inside. In *E. watsoniana* and *E. setosa* the phloem was sometimes in a position lateral to the xylem. These differences are probably due to a variation in the arrangement of the two bundle components in different levels of its course, from the large still undivided bundle at its base to the terminal veinlets.

In many species of the Neo- and Eucorymbosae the conducting tissue is embedded in a small-celled, tannin-impregnated tissue, obliterated beyond recognition. In the Maculatae it runs in a solid, thick plate of sclereids (Fig. 47*a*, *b*).

Occurrence of sclereids in the chalaza is often encountered. They are either dispersed or forming a more or less closed layer of variable thickness, adjacent to the chalaza cork and beneath the vascular system. In *E. calophylla* this layer is only one to two cells thick, in *E. ferruginea* four to seven. Their occurrence in *E. trachyphloia* is not constant. In seeds we collected at Belmont (Brisbane) the sclereids are abundant and dispersed all over the chalaza, but quite absent in seeds from Beerburrum. A gradual increase of sclereids from species to species can be observed in the Ochrophloiae.

* In the description of the winged Corymbosae Maiden (VII, 105 ff.) comments on the position of the hilum in relation to the *endosperm* (!), e.g., "hilum about the centre of the endosperm", "hilum on the upper half of the endosperm", etc. Now, the hilum is a scar on the testa which envelops nucellus, endosperm and embryo. The nucellus is multilayered and the endosperm generally a single layer of cells. They both extend completely around the inner side of the testa and surround the embryo. What Maiden has in mind is undoubtedly the proper *seed body* (without the wing) and not the *endosperm*.



Text-fig. 47.—*a, E. maculata,* trans. sect. through the chalaza region, 230×. (Bundle strand *vb* embedded in the sclerenchyma plate *sc.*) *b-e,* vascularization patterns: *b, E. maculata,* 35×; *c, E. watsoniana,* 35×; *d, E. trachyphloia,* 175×; *e, E. jacobsiana,* 175×.

The shaded parts in *b* and *c* show the extent of sclerification around the conducting tissue. The broken line limits the chalaza.

E. bloxsomei is devoid of them. In *E. torrelliana* and *E. eximia* conspicuously pitted sclereids are loosely arranged, singly or in groups, in the lower part of the chalaza. In *E. peltata* and *E. watsoniana* (Fig. 47*c*) they form a solid layer one to three cells thick. A further step leads to the Subseries Maculatae where the highest degree of sclerification is achieved. Here, the mechanical tissue extends over the whole chalaza, embedding completely, as just mentioned, the conducting tissue and accompanying the bundles to their very ends beyond the chalaza (Fig. 47*a*, *b*).

All these mechanical elements are formations of the chalazal tissue. However, in *E. watsoniana* there are also sclereids as part of the conducting tissue. In cross sections through the lower still undivided part of the bundle the xylem is surrounded by a crescent-shaped plate of sclereids which on the phloem side are only scattered. The fact that these mechanical cells can be already discerned on the bundle stump protruding from the hilum is evidence enough for their origin.

The closure of the chalaza (on its inside) is as a rule accomplished by a tender lignified and suberized tissue, filled with tanniniferous deposits staining ruby-red with vanillin-HCl. As previously mentioned, the designation of this tissue as "chalaza cork" is not quite appropriate. Using this term is only a matter of convenience. It is not a cork in the sense of the phellem originating from a phellogen. It is not exclusively derived from chalazal tissue, because nucellar tissue too can take part in its formation; finally it may not be suberized. These facts are best illustrated by the following examples.

A cross section through the chalaza cork of *E. calophylla* shows in its outer part thick-walled, pitted and lignified cells interspersed among the thin-walled suberized ones, thus somewhat reminiscent of the occurrence of sclereids within the phellem of some plant species. Here and there the lignified cells may be arranged more compactly along the periphery of the chalaza cork (Pl. iii, fig. 4).

In *E. haematoxylon* the outer part consists of lignified and suberized cells arranged in orderly parallel rows whilst the inner part consists of irregularly disposed suberized, but not lignified, nucellar cells passing at the circumferential chalaza border into merely cutinized nucellus cells.

Finally, we remember that in the Miniatae, for instance, there is neither suberization nor lignification in that part of the chalaza which in other species is generally occupied by a suberized tissue.

The *hilum* overlaps the chalaza to a lesser or greater degree. In *E. calophylla* and *E. haematoxylon* it is almost entirely so (Fig. 46*a*, *b*). Suberization was observed in *E. setosa* (Darwin, W. Bateman, Dec., 1957), but was sometimes only patchy and restricted to that part which overlaps the chalaza (Pl. iii, fig. 2). Small groups of suberized cells were also seen in *E. terminalis* (Ayers Rock, N.T., 4.6.56, N. Forde, 134).

Nucellus and endosperm. Remnants are always present, the former multilayered, the cells empty and obliterated, the latter generally as a single layer.

Oxalate druses. As in the Clavigerae and species of *Angophora*, they are confined to the epidermis of the embryo cotyledons and embedded only in the large aleurone grains.

The results obtained from this anatomical review of the testa of the Corymbosae support the erection of two groups on the basis of seed shape.

(1) Seed laterally flattened or compressed: Subseries Setosae, Gamophyllae Eucorymbosae and Neocorymbosae. This would roughly correspond with Maiden's "Terminaliptera", but including *E. calophylla* and *E. gummifera*. Nearly all the species have a long terminal wing which, however, is of restricted taxonomic value as revealed by the two closely related species *E. calophylla* and *E. ficifolia*.* On the other hand the

* The two species have nevertheless some other remarkable differences in their testa structures. The considerable wall deposits in the epidermal cells of *E. calophylla* are missing in *E. ficifolia* (as well as in all other Corymbosae). The chalaza cork of *E. ficifolia* is a uniform tender suberized tissue which in *E. calophylla* is, as already mentioned, interspersed with sclerified but not suberized cells — a structure not yet encountered among the species hitherto examined.

testa structure is of no help in providing confirmatory evidence for the separation of Blakely's Subseries based on morphological characters of other organs.

(2) Seed compressed dorsiventrally: Subseries Ochrophloiae and Maculatae. This would cover Maiden's "Naviculares" (except *E. calophylla* and *E. gummifera*). The seeds are wingless, but in some species bordered by a tender narrow membrane sometimes a little enlarged on the upper (or also lower) end of the seed. The Maculatae are undoubtedly a well defined group for which the testa structure too provides clear evidence, especially by the embedding of the vascular system in a thick plate of sclerenchyma tissue. This character links the Maculatae with the Ochrophloiae, where from species to species a gradual increase in the sclerification of the chalazal tissue can be observed, culminating in *E. watsoniana*, but without reaching the extent seen in *E. maculata* and *E. citriodora*.

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(Additional to those cited in Part I, Proc. Linn. Soc. N.S.W., 1958, 83, Part 1, p. 31, and in Part II, *ibidem*, 1959, 84, Part 2, p. 291.)

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EXPLANATION OF PLATE III.

(Cork tissue, cuticles and cutinized walls brown.)

1, *E. tetraptera*, trans. sect. of the chalaza, 180×, showing the chalaza cork and the cutinization of the nucellus. 2, *E. setosa*, part of the trans. sect. through the hilum-chalaza region, 140×. 3, *E. miniata*, part of surface view of the hilum with two entering bundles and the sclereid rim, 90×. 4, *E. calophylla*, central part of the "chalaza cork" in trans. sect., 230×. The outer part lignified, the inner suberized. 5, *E. gummifera*, nucellus in trans. sect., 350×, showing the inner cuticle and the cutinized anticlinal walls.

THE EFFECTS OF FOREST FIRES ON THREE SPECIES OF STICK INSECTS (PHASMATIDAE PHASMATODEA) OCCURRING IN PLAGUES IN FOREST AREAS OF SOUTH-EASTERN AUSTRALIA.

By K. G. Campbell, Forestry Commission of N.S.W.

(Plate iv.)

[Read 26th April, 1961.]

Synopsis.

The effect on three species of phasmatids of forest fires, both "wild" or bushfires and controlled burning, practised as a sylvicultural technique in Forestry, is studied. Two field experiments using a controlled fire were carried out at Wedding Bells State Forest near Woolgoolga, N.S.W. (where *C. tessulatus* (Gray) is present) and at Konangaroo State Forest, near Jenolan, N.S.W. (where *P. wilkinsoni* Macleay and *D. violescens* (Leach) occur) in order to study the effect of such fires on the egg stage of these insects. The results of these were analysed and the conclusions reached as to their effects on this stage are presented.

Bushfires which occurred during 1957 in the Jenolan and Hanging Rock-Nundle State Forest areas were studied to determine their effects in the nymphal and adult stages of the stick insects and the results are discussed.

Conclusions drawn from the results of these experiments, field studies and observations made are as follows: (1) That unless a fire consumes the litter on the forest floor down to the mineral earth there will be little deleterious effect on either eggs containing developing embryos or the larvae of the *Myrmecomimesis* sp. wasp; (2) Fires affecting the nymphal or adult stages can operate as a destructive factor having a long-term depressant effect on phasmatid populations and can modify the forest stand to such an extent as to reduce such populations to a very low density; (3) That the effects of such fires will be dependent on a number of factors, including the intensity of the fire, the condition and type of the forest stand, and the litter on the forest floor.

Introduction.

Three species of stick insects occur in plague numbers in the forests of south-eastern Australia. The biology of *Ctenomorphodes tessulatus* (Gray) has been studied by Hadlington and Hoschke (1959) and that of *Didymuria violescens* (Leach) by Campbell (1960) and *Podacanthus wilkinsoni* (Macleay) by Richards (1953) and Campbell (1960).

The possible use of fire as a control measure was mentioned by Froggatt (1923) and since then its merits have been discussed without any effort being made to ascertain the truth of his proposition or the probable results of such a course of action.

In present-day forest practice "burning" presupposes that the fire will be "controlled" and not a "wild" or uncontrolled bushfire, although the effects of the latter are also considered in this paper.

Eggs of *C. tessulatus*, after being oviposited during the summer and early autumn, may be present on the forest floor for about six months and those of *P. wilkinsoni* and *D. violescens* for up to eighteen months or more. During this stage there may be several periods in autumn, winter and possibly early spring when controlled burning may be practicable and safe.

The active feeding stages (nymph and adult) are present during the spring, summer and early autumn and the safe use of fire as a possible control depends on the local weather and climatic conditions.

During the nymphal stage early spring is usually the only time when fire can be used safely unless the summer is wet or cool and then it may be impossible to light a fire in the forest for this purpose. It is usually unsafe to attempt the use of fire as a possible control during the adult life of the insects.

A "wild" fire may occur at any period of the year when conditions are favourable and from the point of view of its effect on a phasmatid population (or the individuals comprising it) it is of no consequence whether the fire is controlled or not. (The severity or consequences of a fire often have no relation to its classification.)

In an attempt to ascertain the effect of a controlled fire on the egg stage of these insects, two experiments were carried out. To assess the effect of a "wild" fire on both the egg and nymphal stages, sampling was done before and after the fire and subsequent observations were made also.

The experiments involving controlled burning of the undergrowth and surface litter on the forest floor were carried out:

(1) On Wedding Bells State Forest No. 360, near Woolgoolga in northern New South Wales, where eggs of *C. tessulatus* were present amongst the litter, on 20 and 21/5/57; and

(2) At Konangaroo State Forest No. 750, near Jenolan, N.S.W., on the central highlands, where eggs of *P. wilkinsoni* and *D. violescens* were present, on 11 and 12/7/57. The weather conditions during late autumn and early winter made these small controlled fires possible and safe.

Wedding Bells State Forest.

Procedure.

The area selected was in Compartment 6, at an altitude of 500 ft. It was triangular in shape, being bounded on two sides by roads and a firebreak was constructed by hoeing along its third side to prevent the fire from spreading.

The overstorey trees on this portion were *E. gummifera* (Gaertn.) Hochr. (bloodwood), *E. acmenioides* Schau. (white mahogany), *E. maculata* Hook. (spotted gum) and *E. paniculata* Sm. (grey ironbark), with an intermediate storey of *Casuarina torulosa* Ait. (rose sheoak) and an understorey of leguminous and proteaceous shrubs and grasses.

The area was divided into four roughly equal blocks, and within each block five samples of litter down to (but not including) the mineral earth were collected at random. Each sample was one square yard in extent and all were beneath the crown projection of an overstorey tree.

After the fire was out and the area was cool, another twenty samples were collected. Each was the same size and immediately adjoining one of the previous samples.

All samples were later sieved and the eggs removed manually for examination under a low power stereo-microscope.

Conditions of Burn.

Weather conditions were warm and dry, the day cloudless and the litter very dry. Maximum shade temperature (measured in the open) was 78°F. at 2 p.m.

The fire was lit around the perimeter of the area and allowed to burn inward. From a fire protection viewpoint a good "controlled burn" was obtained and practically all grass, leaves and small fallen branches were reduced to ashes. However, the surface litter was burnt down to the mineral earth in a very patchy manner. There were no extensive areas of mineral soil exposed although the fire was hot enough to ignite the fibrous bark of a mahogany and sparks were carried by the wind beyond the road where spot fires were started.

Konangaroo State Forest.

Procedure.

The area selected, enclosed by a fire trail, was near the northern boundary of the forest adjoining the Jenolan State Park and east of the Oberon-Kanangra Walls Road at an altitude of 4,200 feet (see Pl. iv, fig. 1).

Overstorey species were *Eucalyptus radiata* Sieb. (peppermint), *E. viminalis* Labill. (manna gum), *E. dalrympleana* Maiden (mountain gum), *E. pauciflora* Sieb.

(snow gum), *E. dives* (Gaertn.) Hochr. (red bloodwood) and *E. fastigata* D. & M. (brown barrel), an understorey of *Eucalyptus* regeneration, *Lomatia myricoides*, *Pteridium aquilinum* (bracken fern), *Acacia falciformis* and *Dianella revoluta* was present with ground cover of *Poa* sp. (snow grass). This represents an example of Costin's (1954) *E. fastigata-E. viminalis* alliance.

Fourteen litter samples each one square yard in area were collected at random down to, but excluding, the mineral earth, before the fire was lit. After the area had cooled another fourteen samples were collected at random and the eggs later removed and examined as described above.

Conditions of Burn.

Weather conditions were dry but cool, 70°F. maximum in shade, as the sky was overcast with medium altitude cloud. The perimeter of the area was set alight and the fire allowed to burn inward. The fire burnt unevenly, but the areas from which the samples were taken (beneath the crown projection of trees with a reasonably heavy leaf litter and less grass than in the open) were in many cases well burnt and the mineral earth exposed.

Results.

The results of examination of the eggs collected from the samples are summarized in Table 1.

Table 1.

Total Number of Eggs Collected Before and After Controlled Burning.

	Advanced Embryos.		Undeveloped Embryos.	Parasitized Eggs.	Diseased or Deteriorated Eggs.	Total Eggs.	Empty Shells.	Grand Total.
	Live.	Dead.						
Wedding Bells S.F. (*C. tessulatus*) (20 plots)								
Before burning	13	1	9	225	759	1007	3449	4456
After burning	10	2	1	175 (9b)	925(1b)	1123	3486	4609
Konangaroo S.F. (*P. wilkinsoni*) (14 plots)								
Before burning	3	1	4	22	22	52	304	356
After burning	0	0	4 (4b)	0	9 (1b)	13 (5b)	166	184
(*D. violescens*) (14 plots)								
Before burning	1	0	15	27	59	102	920	1022
After burning	0	0	4 (1b)	12 (5b)	26 (3b)	42 (9b)	475 (42b)	568

" b " denotes burnt—i.e. contents affected by fire though state of egg still discernible.

Details are given in Appendix I and II.

C. tessulatus.

Analysis of the figures indicates that the burning had no significant effect on the eggs containing advanced embryos. Eggs in which embryonic development was at a very early stage and the larvae of the parasitic wasp *Myrmecomimesis* sp. present within the phasmatid eggs (Hadlington and Hoschke 1959) were significantly affected.

P. wilkinsoni and D. violescens.

In the case of both species, all classes of eggs were significantly affected by the fire.

Discussion.

The effects of the fire are apparently proportional to the amount of heat to which the eggs are exposed. These effects are influenced by: (*a*) Intensity of the fire; (*b*) Rate of spread of the fire; (*c*) Nature and quantity of litter on the forest floor; (*d*)

Conditions of the litter; (*e*) Disposition of the eggs in the litter; (*f*) History of defoliation of the area.

Defoliation at Wedding Bells S.F. had been extensive and the needles—branchlets with scale-like leaves—of *Casuarina* sp. as well as fragments of *Eucalyptus* sp. leaves covered the ground. The amount of litter covering the eggs depends largely on the time of oviposition and the rate of defoliation. Eggs with advanced embryos would be most deeply covered by litter as they were oviposited during defoliation. It is assumed that parasitized eggs in the litter, and probably less deeply covered by it, would be those most easily detected by the wingless *Myrmecomimesis* female. Eggs with little embryonic development were probably laid most recently and covered only by a small amount of litter.

At Wedding Bells the fire spread quickly over the area, burning the top surface of the litter but not affecting it except in localized spots to any depth. Eggs nearest the surface were affected significantly but a proportion of parasitized eggs and those deeply buried in the litter were undamaged.

At Konangaroo the fire was not as satisfactory a control burn as the one at Wedding Bells as it did not destroy the small or medium-sized branchlets. However, it did burn more slowly and thoroughly and generally burned the surface litter down to the mineral soil particularly, as mentioned earlier, where this was mainly composed of fallen leaves and bark. As all of the samples were collected under the crown projection of a tree, and the litter there had a higher proportion of this debris, the fire was usually most intense in these situations. However, it was a very uneven burn and large patches were left untouched. This slow fire which destroyed litter down to the soil damaged all classes of eggs significantly and even burnt empty shells which represented past populations and were deepest buried in the litter.

Effects of Fire on Nymphs and Adults.

Nymphs are present in spring and early summer and adults during summer and early autumn. In the highlands where plagues of these insects may occur, weather conditions must necessarily be dry and warm for a fire to spread extensively. Burning during such conditions, except for special purposes, is not favoured, because of the difficulty of control and emphasis is placed rather on the prevention and suppression of fire at these times. Consequently, no experimental burning was attempted during such conditions, for these obvious reasons.

During the early summer of 1957, however, "wild" fires burnt extensive forested areas near Jenolan and Nundle and various observations and records of their effects on the phasmatids were made.

Egg surveys to estimate the probable densities of phasmatid populations had been made in the Nundle group of forests, where plague numbers had been predicted as a result of these surveys (Campbell, 1960). Large numbers of nymphs of *P. wilkinsoni* were present as expected on Tuggolo, Tomalla and Nundle State Forests during the spring and early summer of 1957. Moderate numbers were present during the same period over portions of the Jenolan area.

Nundle Area.

During early November, 1957, partial defoliation of the trees was visible and the insects were in the second to fourth instars. On 17th November a "wild" fire burnt most of Tuggolo State Forest and subsequently portions of Tomalla and Nundle State Forests; it was not brought under control until 2nd December.

Conditions were very warm and dry and fire control operations were hampered by the steepness and inaccessibility of the terrain. The fire not only burnt along the ground but also burnt in the crowns of the trees in many cases (a "dependent-crown" fire). Litter, undergrowth and the crowns were consumed over extensive areas. On Tuggolo State Forest the fire, fanned by a strong southerly wind, burnt strongly at night as well.

The tree crowns within all these forests were mainly composed of epicormic shoots and these were present on many stems as a result of refoliation after previous severe defoliation by phasmatids in 1955/56. Where the insects were numerous they were present on the shoots on the stems as well as in the crown of the trees.

The fibrous bark of species such as *E. obliqua* and *E. laevopinea* and epicormic growth assisted the fire to reach the crowns.

Effects of Fire and High Temperatures.

The fire affected the phasmatids in various ways: (1) by direct destruction; (2) by "knock-down" from heat or smoke followed by burning of undergrowth or litter onto which the insects fell; and (3) by killing by high temperature without direct contact with the fire.

The insects can withstand high temperatures for short periods without being killed, although at both Epping and Hurstville (suburbs of Sydney, N.S.W.) when the ambient air temperature reached 108°F. in the shade for an hour or so on 20th December, 1957, deaths of *D. violescens* and *P. wilkinsoni* (held in wire mesh cages) ensued. *C. tessulatus* withstood this temperature (unpublished reports Hadlington and Campbell, 1957).

During December, 1951, it was observed that adults and nymphs of *P. wilkinsoni* were killed at Nundle S.F. while crossing bare open ground (a bush fire was burning at this time) and specimens kept in the cabin of a truck in which the temperature was recorded at 150°F. lived for 15 minutes (personal communication, P. Hadlington).

Table 2.

Total Numbers of Eggs of P. wilkinsoni *Collected by Sampling on Tuggolo S.F. Before and After the Fire of 1957.*

	Number of Sites Sampled.	Advanced Embryos.		Undeveloped Eggs.	Parasitized Eggs.	Diseased or Deteriorated Eggs.	Total.	Empty Shells.	Grand Total.
		Live.	Dead.						
Before fire 1957..	9	217	0	100 (1)	91	346 (7)	754 (8)	386 (60)	1140 (68)
After fire 1959 ..	6	3	1 (1)	2	0	14	20 (1)	87 (1)	107 (2)

Figures in brackets denote eggs of *D. violescens*.

In 1957 it was observed that temperatures which scorched (and so killed) leaves also killed *P. wilkinsoni*, but some survivors fed for at least a week after a part of their abdomen was burnt off.

Adult insects are disturbed by smoke and will move from the tree crowns by falling or flying in advance of any marked increase of ambient temperature caused by the approach of a fire, thus increasing the chances of their destruction by flames or heat. In 1951, at Nundle, phasmatids were observed to be killed by heat 400 yards in advance of a fire.

In 1957 fire caused almost complete destruction of the phasmatid *P. wilkinsoni* population which was present in very high density on Tuggolo State Forest, as is illustrated by comparison of the numbers of eggs obtained by sampling this forest in 1957 and 1959. The sites were chosen quite at random — those sampled in 1959 do not coincide in every instance with those of 1957 — details are given in Appendix III.

A potential phasmatid population at eclosion within the range of 3,000-360,000 nymphs per acre was predicted in 1957 and in 1958 a population at eclosion within the limits of 9,000-110,000 nymphs per acre could be expected. In other words, severe to total defoliation would be expected over the whole of this forest in 1957 and some defoliation, serious only in very localized situations, would occur in 1958 also.

Prior to the fire in 1957 serious defoliation was occurring as predicted and observations made revealed a pattern of population density which agreed satisfactorily with the forecast made (Campbell, 1960).

After the fire it was difficult to find a live phasmatid, even in areas where tney had been most numerous, and there was no doubt of the extremely high mortality which had been caused as a direct and indirect result of the fire.

In 1959 the area was again sampled and examination of the eggs obtained indicated that a population of between 0-6,000 to the acre could be expected in 1959/60 and between 0-3,000 per acre in 1960/61. Observations made in 1960 confirmed the forecast for that year.

These figures and observations strengthen the observations made in 1957 of the catastrophic effect of the fire on the phasmatid population in this forest.

By the end of April, 1958, it was difficult to distinguish between the burnt and unburnt portions of the forest, as defoliation, by the phasmatids, of the unburnt area was almost total. The main observable difference was the blackened trunks and lack of any undergrowth in the burnt areas. Recovery of the trees in the burnt area has also been more rapid than those in the area defoliated by the insects.

Jenolan Area.

Damage to the forests of this region by phasmatids (mainly on areas not dedicated as State Forest) was, and is, probably the most serious of any in the various localities affected (see Pl. iv, figs 2, 3).

Both *P. wilkinsoni* and *D. violescens* have occurred in very large numbers during recent years and large numbers of many *Eucalyptus* species have been killed and others severely damaged by defoliation over many thousands of acres. Most of the timber is of little commercial value, but much of the area represents a portion of the high rainfall area of the catchment for the new Warragamba Dam on the Wollondilly River in New South Wales (Holford, 1959).

Serious landslip and erosion occurred soon after because of removal of the Eucalyptus canopy by defoliation on the very steep country around Jenolan. This was later minimized by stabilization of the area by the growth of tree regeneration, herbs and grass cover.

Early in November, 1957, a severe uncontrolled fire burnt large areas of forested land supporting fairly dense populations of phasmatids either as nymphs feeding on the foliage or as egs present amongst the forest litter. This fire burnt for several weeks until controlled near Jenolan Caves on 30/11/57. As a result of this fire, which resulted in the destruction of the stabilizing ground cover, as well as defoliation of the remaining live *Eucalyptus* sp., severe land slip and erosion again occurred on the steep slopes.

Very high mortality of the phasmatid population occurred and in 1959/60 (when high numbers would normally have been expected) it was difficult to find, even by careful searching, a few phasmatids where they had been previously abundant. This region, throughout which very dense populations of phasmatids occurred, extending along the forested highlands from Wallerawang to Wombeyan, N.S.W., now contains only one small area where phasmatids are now present in high numbers. This is situated about five miles north-west of Wombeyan Caves, N.S.W., on the Great Dividing Range. This area was not burnt in 1957.

Discussion.

It appears from the evidence available, that forest fires have considerable and important effects on phasmatid populations. The most obvious effect is that of destruction of large numbers of phasmatids. Occasionally the environment is modified to the extent of changing it completely to one in which the species cannot persist, as repeated firing of the forest area will convert it into open savannah or grassland for varying periods of time.

During the current plagues of *P. wilkinsoni* (Campbell, 1960) fire has caused a crash of the population in three instances. In the case of this insect which was

extremely numerous in the Duncan's Creek area of Nundle S.F., a severe fire occurred in 1951. Since then the density of the population has been very low indeed and has not since built up to plague proportions. During 1957 when numbers were very high in the State Forests of Nundle, Tomalla and Tuggolo and in the Jenolan area, serious fires occurred as mentioned previously.

Since then numbers have been very low in all areas burnt over by these fires.

The other population crashes are attributable to exhaustion of the food supply at Nundle during 1952 and 1957 (Campbell, 1960). The only areas where *P. wilkinsoni* is abundant at present are those which were not burnt in 1951, or 1957, or which were not completely defoliated in 1957. There was a recovery of the population in the areas where the crash occurred, due to the exhaustion of food at Nundle in 1952, during the period 1953-1957 but there has been no recovery to date of the population in the Duncan's Creek area after the 1951 fire. The effects of fire are probably longer lasting than the effects of exhaustion of the food supply.

This wild fire described above occurred during the end of the nymphal stage of the phasmatids; the adult insects are knocked down by smoke and there is no evidence to suggest they are any less susceptible than the nymphs.

The effects of fires occurring when the phasmatids are in the egg stage are far more complex. These are influenced by the weather conditions, condition and type of the undergrowth and forest litter, and the disposition of the eggs within the litter and on the forest floor, as well as the stage of development of the embryo.

It is also possible that non-lethal high temperatures may disturb the normal development of the embryo and cause eclosion of the nymphs at a time when it would not generally occur. *P. wilkinsoni* was unusually abundant, in small unburnt localities, in the summer of 1958/59, following the 1957 fire at Jenolan, but present in low numbers in the summer of 1959/60 when it was anticipated that they would be abundant.

The effects of fire on the cleptid wasp egg-parasite may be completely destructive (Hadlington and Hoschke, 1959) but, as with the unparasitized eggs, the effects are complex.

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EXPLANATION OF PLATE IV.

1.—Area controlled burned on left-hand side of car. Note some trees still living in this section — Konangaroo State Forest. (Photo, K. G. Campbell.)

2, 3.—Trees defoliated completely and repeatedly by phasmatids killed outright — Konangaroo State Forest. (Photo, P. Hadlington.)

Appendix I.

Konangaroo Burning Experiment.

Site No.	Before Burning—11/6/57.																After Burning—12/6/57.															
	Advanced Embryos.				Undeveloped Embryos.		Parasitized Eggs.		Diseased Eggs.		Total.		Empty Shells.		Grand Total.		Advanced Embryos.				Undeveloped Embryos.		Parasitized Eggs.		Diseased Eggs.		Total.		Empty Shells.		Grand Total.	
	Alive.		Dead.														Alive.		Dead.													
	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.	P.	D.
1	—	—	—	—	—	—	3	6	2	11	5	17	28	108	33	125	—	—	—	—	—	—	—	—	3 (1b)	—	3	—	31	15	35	15
2	—	—	—	—	—	—	2	1	2	4	4	5	32	37	36	42	—	—	—	—	—	—	—	1 (1b)	3	4	3 (1b)	5 (1b)	49	40	52	46
3	1	1	—	—	—	6	2	3	3	3	6	13	73	29	79	42	—	—	—	—	—	—	—	—	—	—	—	—	9	13	9	13
4	—	—	—	—	1	2	3	3	4	—	8	5	27	36	35	41	—	—	—	—	—	1	—	5 (1b)	1	4 (1b)	1	10	12	14	13	26
5	—	—	—	—	—	1	—	3	1	7	1	11	7	40	8	51	—	—	—	—	—	—	—	—	—	2	—	2	15	68	15	70
6	1	—	—	—	1	3	4	6	1	22	7	31	41	188	48	219	—	—	—	—	—	—	—	—	1	—	1	10 (2b)	6	24	7	24
7	—	—	—	—	—	—	—	—	—	2	0	2	14	96	14	98	—	—	—	—	—	—	—	—	—	1	—	1	1	7	1	8
8	—	—	—	—	—	1	3	3	1	1	4	5	6	17	10	22	—	—	—	—	—	—	—	—	—	1	—	1	4	39	4	40
9	1	—	1	—	1	1	1	—	3	3	7	4	24	48	31	52	—	—	—	—	—	—	—	—	—	2	—	2	5	26	5	28
10	—	—	—	—	—	1	—	1	—	3	0	5	3	50	3	55	—	—	—	—	—	—	—	—	—	2 (1b)	—	2 (1b)	2	5	2	8
11	—	—	—	—	—	—	2	1	—	1	2	2	5	12	7	14	—	—	—	—	—	—	—	1	—	2	—	3	6	73	6	76
12	—	—	—	—	—	—	—	—	1	—	1	0	6	24	7	24	—	—	—	—	—	—	—	—	—	1	—	1	3	11	3	12
13	—	—	—	—	—	—	2	—	4	2	6	2	17	108	23	110	—	—	—	—	4 (4b)	1	—	2	—	3	4 (4b)	6	19	59 (10b)	27	75
14	—	—	—	—	1	—	—	—	—	—	1	0	21	127	22	127	—	—	—	—	—	2 (1b)	—	3 (3b)	1	4 (1b)	1	9 (5b)	4	81 (32b)	5	127
	3	1	1	—	4	15	22	27	22	59	52	102	304	920	356	1022	—	—	—	—	4 (4b)	4 (1b)	—	12 (5b)	9 (1b)	26 (3b)	13	42 (9b)	166	475 (42b)	184	568

Note: (b) denotes burnt, i.e. contents affected by fire though state of egg still discernible.
P = *P. wilkinsoni.*
D = *D. violescens.*

APPENDIX II.

Wedding Bells State Forest.

Site No.	Before Burning—20-21/5/57.								After Burning—20-21/5/57.							
	Advanced Embryos.		Undeveloped Embryos.	Parasitized Eggs.	Diseased or Deteriorated Eggs.	Total.	Empty Shells.	Grand Total.	Advanced Embryos.		Undeveloped Embryos.	Parasitized Eggs.	Diseased or Deteriorated Eggs.	Total.	Empty Shells.	Grand Total.
	Live.	Dead.							Live.	Dead.						
1a	—	—	—	8	41	49	102	151	—	—	—	3	38	41	144	185
b	—	—	—	6	32	38	152	190	—	—	—	2	37	39	126	165
c	—	—	1	—	18	19	52	71	—	—	—	2	24	26	115	141
d	—	—	—	1	7	8	78	86	—	—	—	37 (1b)	44	81 (1b)	255	337
e	—	—	—	12	34	46	108	154	—	—	—	6 (1b)	76	82 (1b)	205	288
Total 1 ..	—	—	1	27	132	160	492	652	—	—	—	50 (2b)	219	269 (2b)	845	1116
2a	1	—	—	4	13	18	155	173	—	1	—	8 (6)	68	77 (6b)	316	399
b	—	—	1	11	5	17	170	187	—	—	—	2	77	79	306	385
c	—	—	—	—	—	0	62	62	—	—	—	3	70	63	198	261
d	—	—	—	34	68	102	276	378	1	—	—	17	73 (1b)	91 (1b)	172	264
e	—	—	—	2	27	29	125	154	2	1	—	22	60	85	321	406
Total 2 ..	1	—	1	51	113	166	788	954	3	2	—	52 (6b)	338 (1b)	395 (7b)	1313	1715
3a	—	—	—	8	34	42	176	218	—	—	—	—	7	7	41	48
b	—	—	—	22	86	108	219	327	1	—	1	4	19	24	105	130
c	1	—	1	29	68	99	337	436	—	—	—	9 (1b)	65	74 (1b)	130	205
d	—	—	1	7	19	27	76	103	1	—	—	11	17	29	100	129
e	—	—	—	4	12	16	152	168	2	—	—	29	32	63	238	301
Total 3 ..	1	—	2	70	219	292	960	1252	4	—	1	53 (1b)	140	197 (1b)	614	813
4a	3	—	3	13	9	28	201	229	—	—	—	3	9	12	60	72
b	1	—	—	6	58	65	104	169	—	—	—	4	83	87	204	291
c	2	1	1	15	26	45	152	197	1	—	—	5	56	62	207	269
d	1	—	—	19	80	100	347	447	1	—	—	6	19	26	100	126
e	4	—	1	24	122	151	405	556	1	—	—	2	61	64	143	207
Total 4 ..	11	1	5	77	295	389	1209	1598	3	—	—	20	228	271	714	965
Total ..	13	1	9	225	759	1007	3449	4456	10	2	1	175 (9b)	925 (1b)	1132 (10b)	3486	4609

(b) denotes burnt, i.e. contents affected by fire though state of egg still discernible.

APPENDIX III.

Figures of Egg Dissections of Survey made 3–6/6/1957: Tuggolo State Forest (P. wilkinsoni).

Site No.	Advanced Embryos.	Developing Embryos.	Undeveloped Eggs.	Parasitized Eggs.	Diseased and Deteriorating Eggs.	Total.
1	1	—	6	—	9	16
2	4	—	9	—	16 (1)	29 (1)
3	11	—	7	3	41 (3)	62 (3)
4	29	—	9	10	39 (1)	87 (1)
5	4	—	6	7	8	25
6	15	—	3	4	5	27
7	13	—	16	13	15 (1)	60 (1)
8	119	—	36 (1)	45	197 (1)	402 (2)
9	13	—	8	9	16	46
Total	217	—	100 (1)	91	346 (7)	754 (8)

Egg Survey 14–17/9/1959—Tuggolo State Forest.

Site No.	Developed Embryos.		Undeveloped Embryos.	Parasitized Eggs.	Diseased or Deteriorated Eggs.	Total.	Empty Shells.	Grand Total.
	Live.	Dead.						
1	—	1	—	—	1	2	16	18
2	1	—	1	—	3	5	4	9
3	—	—	—	—	1	1	2	3
4	2	— (1)	1	—	6	9 (1)	45 (1)	54 (2)
5	—	—	—	—	1	1	8	9
6	—	—	—	—	2	2	12	14
Total ..	3	1 (1)	2	—	14	20 (1)	87 (1)	107 (2)

Figures in brackets denote eggs of *D. violescens*.

ANTHONY MUSGRAVE, 1895–1959.

(*Memorial Series No. 18.*)

(With Portrait, Plate v.)

The sudden death at home, from heart attack, of Mr. Anthony Musgrave, Curator of Entomology at the Australian Museum, Sydney, on 4th June, 1959, is mourned by all his colleagues and by a wide circle of friends.

Only two evenings before his death Mr. Musgrave had delivered the Froggatt Memorial Lecture at the Naturalists' Society of New South Wales in his usual high-spirited way. He enjoyed lecturing just as his audience enjoyed listening to him and none there present suspected this was his swansong. The lecture epitomized his main interests: his zealous devotion to natural history; painstaking study of all aspects of his subject matter (historical, zoological and botanical); his extensive reading and verification of sources, and his ability to produce lantern slides of great technical excellence and beauty. He had studied art under Julian Ashton, and used to illustrate his early scientific papers with his own drawings. He was active in the field and almost every year would spend some time in the bush collecting insects, writing detailed observations and photographing anything likely to be of later use.

Anthony Musgrave was born at Cooktown, Queensland, on 9th July, 1895, and was educated at Hayfield Preparatory School, Homebush, and at the Church of England Grammar School, North Sydney. He joined the staff of the Australian Museum as a cadet on 7th February, 1910. "Your salary", he was informed, "will be at the rate of Twenty-six pounds (£26) per annum, payable monthly. The Trustees make no promise as to future increases, and its continuance is dependent on the necessary funds being voted by Parliament . . . " Five years later, when, as Entomologist's Assistant he was receiving £90 a year, he was further advised, "You must be prepared to suffer reductions, if required. Those who are now granted slight increases must specially note this as they may possibly be the first to suffer if such should unfortunately be necessary." After a year in the Museum library, Musgrave, still in his teens, was appointed assistant (in the place of Rex Bretnall) to the then entomologist, "Scientific Assistant" W. J. Rainbow. At school Musgrave had excelled at English, Latin and French, but now he studied Zoology as well at the Sydney Technical College, later proceeding to Professor S. J. Johnston's lectures at the University of Sydney. He passed the necessary examinations but did not take a full course for a degree. On 1st June, 1920, after Rainbow's death, Musgrave was appointed Entomologist, a title later altered to Curator of Entomology. A portrait of him at that time appeared in the Sydney newspaper, *Sun*, 19th June, 1920. He had been a keen member of the Linnean Society of New South Wales since April, 1920, sometimes exhibiting specimens at its meetings, and was a member of its subcommittee on Phenological Observations. He joined the Royal Zoological Society of New South Wales in 1920 and was a member of its Council from 1920 to 1935, was elected President in 1929–1930 and a Fellow in 1933. He had contributed papers to that Society's publications from 1917 to just before his death and several others are in the press. He was also a Fellow of the Royal Entomological Society of London and a member of the Royal Australian Historical Society from 1950, serving on the Council of the last-named in 1956 and 1957.

He had a wide interest in and knowledge of insects and arachnida, but chose to specialize in Hemiptera and Diptera (notably Nycteribiidae), spiders and ticks. Above all, he was keen to analyse and card-catalogue the vast literature on Australasian and Pacific entomology. His bibliographical work was amazingly detailed; not only

would he personally check every reference to every available book and paper, but he determined exact dates of publication, and recorded biographies of their authors and the routes and dates of scientific expeditions upon which insects and arachnida were collected. Musgrave's monumental *Bibliography of Australian Entomology 1775–1930 with Biographical Notes on Authors and Collectors* was published by the Royal Zoological Society of New South Wales in 1932 and was kept up-to-date on cards. It is hoped that it will be possible to publish not only the manuscript addenda to that work, but also his card-index bibliography of Pacific entomology and his manuscript check-lists of Australian arachnids and weevils. For about twenty years, Mr. Musgrave compiled all the zoological entries for *Australian Science Abstracts* until they ceased publication in 1957. Musgrave's 1932 *Bibliography* was evidently the model for H. M. Whittell's *Literature of Australian Birds* (1954) and David Miller's *Bibliography of New Zealand Entomolgy* (1956).

Musgrave wrote articles for both the first (1925) and second (1958) issues of the *Australian Encyclopaedia* and contributed many papers to the *Australian Museum Magazine* and the proceedings of scientific societies. Nearly two hundred titles appear in the list of his publications. Besides bibliography, these cover such subjects as arachnida (especially venomous spiders), various insects, accounts of his collecting trips, separate biographies of entomologists,* historical papers, book reviews, and notes on photography and collecting techniques. He wrote a history of his native Cooktown for the Royal Australian Historical Society, and was a joint author of the comprehensive Index (1958) to the articles, authors and illustrations in the first forty-two volumes of that Society's *Journal.*

Beginning with a youthful survey of the insects of the Sydney Botanic Gardens for Rainbow and with an official trip to the Barrington Tops, New South Wales, in 1916, Musgrave carried out field work in every State of the Commonwealth except Western Australia and the Northern Territory and he had visited New Guinea, the Great Barrier Reef and Lord Howe Island. In 1934 he journeyed overseas to England and Ireland. Although on leave, he slaved at entomology and bibliography almost every day and night, as is attested by his very detailed diary; he also completed many short biographies of arachnologists. He represented the Trustees of the Australian Museum at the Museums Association conference at Bristol in July, 1934, and enjoyed a visit to Europe with his kind friends, Mr. and Mrs. F. J. Griffin, before returning to Australia via the United States. Colonel Griffin has recalled their meeting in his sympathetic notice of Musgrave in the *Journal of the Society for the Bibliography of Natural History* 3 (7), October, 1960: 381.

Anthony Musgrave placed himself at the disposal of his country in both World Wars, applying for enlistment at Victoria Barracks in 1916, but he was not required for active service. In 1940, he contributed a considerable sum to the Commonwealth Treasury for National Defence purposes. He studied First Aid and in 1941 was a Warden, prepared to act under the National Emergency Services of New South Wales. From March, 1942, till September, 1945, N.303655 Driver Anthony Musgrave served on part-time war service in the Australian Military Forces (8th V.D.C. Battalion).

Musgrave's entire professional life was spent in the service of The Australian Museum where it is fittingly proposed to name a new reading room in the library (to which he gave so many books and papers) in his memory.

He trained a series of assistants: Mr. T. G. Campbell (now of C.S.I.R.O. Division of Economic Entomology, Canberra), the late K. C. McKeown, the late Nancy B. Adams, Mr. D. K. McAlpine, Miss P. Goodwin (now Mrs. R. Ford), Mr. Peter Rawlings and Miss Romola Wilkinson.

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* These were: Adams, 1955; Baum, 1946; Bertram, 1928; Corbet, 1948; Dodd, 1924; French, 1933; Froggatt, 1937; Hopson, 1928; Horn, 1946; Lea, 1932; Middleton, 1951; Phillips, 1938; Rainbow, 1920; Shaw, 1931; Sherborn, 1932; Stephen, 1931; Stuart, 1948 and 1955 (two references); Tonnoir, 1940; Turner, 1949; and Waterhouse, 1930 and 1951 (two references).

He disliked publicity. His name hardly ever appeared in newspapers and he declined radio and television interviews, yet he identified thousands of specimens for a regular, sometimes overwhelming, stream of museum visitors. He was not greatly interested in the social or welfare-work of the museum staff, yet everyone respected him for his helpfulness, which was generously at their disposal whenever required. Golf had been his favourite weekend relaxation. He was fond of good plays, ballet and music and knew by heart and sang many of Gilbert and Sullivan's lyrics which, like *Punch*, appealed to his rich sense of humour. Apart from the tremendous amount of reading his bibliographical researches entailed, he found time to delve widely in the literature of travel and philosophy and, as for fiction, he told me that of all the novels he had read, Talbot Mundy's *Om* had made the greatest impact on him.

Musgrave never married and is survived by his sister, Mrs. Frances Hatton; a niece, Mrs. Peter Coombs, and cousins.

In his Presidential Address to the Royal Zoological Society of New South Wales, Mr. Musgrave divided the history of Australian entomological research into three periods: the Fabrician (1770–1830), the Westwoodian (1831–1861) and the Macleayan (1862–1929). Insofar as one man can influence such a grand scheme as the whole of Australian entomology, zoologists of the future, in view of Anthony Musgrave's ordering of the scattered literature on this subject, might well consider the designation of a Musgravian period from 1930 to 1959.

Anthony Musgrave was descended from an old and distinguished North of England family whose coat of arms with its annulets he bore. "The Musgraves", says Burke's *Genealogical History of the Dormant . . . Peerages of the British Empire*, "are said to have come originally from Germany, and to have been Musgraves or Lords Marchers there". Banks tells the following story of their good fortune in obtaining an alliance with the imperial family. "The emperor had two great generals, who made court to his daughter at the same time . . . to decide the matter [he] ordered the two heroes to run at the ring for her (an exercise then in use); it so happened that this Musgrave (one of the contending generals) had the fortune to pierce the ring with the point of his spear; by which action he gained her for a reward . . . and had 'six annulets, or' given him for his coat of arms . . . From this marriage issued that Musgrave who . . . accompanied William the Conqueror into England, and was the founder of the Musgraves in this country."

Baron Musgrave (A.D. 1350) was active in border struggles against the Scotch and descended from him were the Musgraves of Eden Hall, Cumberland, created Baronets in 1611, and two other lines of baronets. The famous 13th century Syrian glass beaker, known as the "Luck of Edenhall", a relic of the Musgrave family, was featured in *The Museum Journal* for February, 1959. The lineage of our Anthony Musgrave can be linked from Burke's *History of the Colonial Gentry* to William Musgrave who settled in Montserrat in the 18th century.

Three gentlemen each with the name Anthony Musgrave distinguished themselves in Australia, so a few notes on the family may not be out of place and may simplify matters for future historical students.

First, the one in whose memory these lines are written, Mr. Anthony Musgrave (1895–1959), Fellow of the Royal Entomological and Zoological Societies.

Second, his father, the Hon. Anthony Musgrave,* C.M.G. (1849–1912), a Deputy Commissioner and later Government Secretary of British New Guinea.

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* Mr. Musgrave's sister (Mrs. Frances Hatton) has a 1907 photograph of her father which was reproduced on the Address to him (also in her possession) printed at Port Moresby and presented to him by Chief Judicial Officer J. H. P. Murray and fourteen others on 16th May, 1908, an outstanding example of Papuan printing (see *Notes of Proceedings at the Presentation . . . to the Hon. A. Musgrave, C.M.G.* . . . 1908, printed at the "Beacon" Office, Cooktown, 7 pages, in which his career was summarized). Biographical particulars of the Hon. A. Musgrave were also given in the *Telegraph* newspaper, Brisbane, for 4th December, 1908, and 8th June, 1912.

The third Anthony Musgrave, the one after whom the Musgrave Ranges in Central Australia were named, was Sir Anthony Musgrave, G.C.M.G. (1828–1888), great-uncle of our entomological colleague, who had been Governor of several Colonies, also of South Australia and Queensland.* Mr. Anthony Musgrave's father was private secretary to his uncle, Sir Anthony, in various parts of the world.

On his mother's side, our late friend's ancestry can be linked to William Colles, (born 1585) of the 13th century family of Worcester county (Glascott, J. H., and Rev. W. Morris Colles, *The Pedigree of the Family of Colles in Ireland*, printed for private circulation by Spottiswoode, London, 1886).

For help received during the preparation of this Memorial Notice, I wish to thank Mrs. Frances Hatton, the librarians of the Australian Museum, Public and Mitchell Libraries, Sydney; Mr. David McAlpine and Miss Kathleen Pope of the Australian Museum; Mr. C. E. Chadwick of the Department of Agriculture, Sydney, and Mrs. G. Frewer. Colonel Francis J. Griffin kindly sent me a reprint of his notice of Anthony Musgrave from the *Journal of the Society for the Bibliography of Natural History* 3(7), 1960: 381 with its excellent portrait of our late friend.

[A full bibliography of Musgrave's writings, so far published, appeared in the Proceedings of the Royal Zoological Society of New South Wales, 1958–59 (published 1961), pages 12–20.]

G.P.W.

* C. A. Bernays gave a biography and portrait in an article entitled "Sir Anthony Musgrave, G.C.M.G." in the *Brisbane Courier* newspaper for 16th December, 1922. See also the *Australian Encyclopaedia*, 1958.

SUPPLEMENTARY NOTE TO A REVISION OF THE AUSTRALIAN RUTELINAE (COLEOPTERA: SCARABAEIDAE).

By P. B. Carne.

[Read 29th March, 1961.]

Synopsis.

The validity of *Amblyterus simplicitarsus* Carne, described from a single male, is confirmed by the examination of additional specimens of both sexes. Plesioallotypes of both this species, and *A. clypealis* Ohaus, are designated.

Introduction.

Since his revision of the Australian Rutelinae was published (Carne, 1958), the author has seen a large volume of additional material. Several undescribed species and one possibly new genus have been noted, but the specimens so far available are not considered adequate for their description. The purpose of the present note is to describe the opposite sexes of two species of *Amblyterus* Macleay that were previously known from a single sex only.

Amblyterus simplicitarsus Carne.

Amblyterus simplicitarsus Carne, 1958, *Aust. J. Zool.*, 6 (2): 226.

♂. The original description, based on a single specimen, requires slight modification. Length 13–15 mm. Pronotum with basal ridge continuous, disk sometimes with a distinct median longitudinal impression. Elytron with 3rd interval appreciably costate, 5th and 7th only rarely so. Fore tibial teeth subequal; hind tibia only rarely with proximal carina developed. Pygidium with long erect hairs over most of disc, especially numerous at sides.

♀ Length 16–17 mm. Clypeal disc swollen but with marginal ridge distinct and with dorsal profile similar to that of ♂. Clypeofrontal suture transverse but scarcely discernible. Pronotum more strongly convex, sides evenly rounded. Fore tibial teeth variable: broad and heavily sclerotized in one example, less robust and similar to those of ♂ in two others. Pygidial vestiture relatively sparse.

Specimens examined: 2 ♂♂, 2 ♀♀ (one designated as a plesioallotype) (BM); 1 ♂ (National Museum, Melbourne); 1 ♂, 1 ♀ (Division of Entomology Museum). All labelled "Queensland, Challenger Expedition, 85–44".

The type locality of the species is the Clarence River district of north-eastern New South Wales.

Amblyterus clypealis Ohaus.

Amblyterus clypealis Ohaus, 1904, *Stettin. ent. Ztg.*, 65: 165; Carne, 1958, *Aust. J. Zool.*, 6 (2): 227.

Specimens of a female *Amblyterus* from south-eastern Queensland were found to agree with that labelled as a cotype of *clypealis* by Ohaus. A study of the associated males confirmed both the validity of the species and its close relationship to *A. tarsalis* Lea.

♂. Length 15½–17½ mm. Terminal segment of maxillary palp almost as long as clypeus, dorsal surface with a broad flat sensorium. Antenna with club and shaft subequal in length. Clypeus transverse, evenly rounded in dorsal profile; disc flat, with margins evenly recurved.

Pronotum with sides contracted anterior to obtuse basal angles, disc with a median longitudinal impression, marginal ridges continuous. Scutellum smooth, micropunctate at base. Elytra with epipleural setae darker than those of thorax, and

becoming conspicuously longer anteriorly. Fore tibia without a spur, teeth equidistant; fore tarsus with ventral tufts of fine hairs. Hind tibia bicarinate; spurs short, the smaller about half length of larger, and separated by 3–5 ciliae; hind tarsus with first three segments longitudinally grooved, terminal segment with a ventral notch.

Pygidium flat, subvertical; disc with shallow confluent punctures bearing decumbent pale yellow hairs and, on apical half, erect brown hairs. Abdomen with erect hairs across all segments and with decumbent short paler hairs at sides only. Genitalia similar to those of *bundabergensis* and *tibialis*.

♀. Examination of additional females has not resulted in the need to modify the writer's earlier description of this sex except to note that, as with *simplicitarsus*, two types of female can be recognized: one with coarse heavily-sclerotized fore tibiae (comparable to those of ♀ *cicatricosus*) and stout hind legs, the other with these appendages of similar structure to those of the male. Insufficient specimens are available for this variation to be analysed, but it would appear that robustness of the legs is positively correlated, in both species, with the size of the individual female.

Specimens examined: 1 ♂ "South Isis, H. Tryon" (Queensland Dept. Agriculture & Stock); 1 ♂ (designated as a plesioallotype), 2 ♀♀ "Childers, 19.12.26, at lights, R. W. Mungomery" (South Australian Museum); 1 ♂, 2 ♀♀ of identical label data (British Museum). The type locality of the species is Cleveland, South Queensland.

The British Museum collections contain a single unidentifiable female *Amblyterus* labelled "Western Australia". If this specimen is correctly labelled it represents the first record of the genus from that State.

The only other undescribed species of note is a striking iridescent green ruteline that has affinities with both *Epichrysus* White and *Anoplostethus* Guér. It is represented in the Strasbourg Museum by two males labelled "Austral. Coll. Schwarzenberg". While its morphological affinities strongly suggest that it is of Australian origin, its description must await confirmation of this supposition.

Acknowledgements.

The writer wishes to thank the following, who kindly forwarded specimens for study: Mr. E. B. Britton (British Museum), Mr. G. F. Gross (South Australian Museum), Mr. A. N. Burns (National Museum of Victoria), Dr. W. A. McDougall (Queensland Department of Agriculture and Stock).

Reference.

CARNE, P. B., 1958.—A review of the Australian Rutelinae (Coleoptera : Scarabaeidae). *Aust. J. Zool.*, 6 (2) : 162-240.

OBSERVATIONS ON SOME AUSTRALIAN FOREST INSECTS.

7. The Significance of the *Glycaspis* spp. (Hemiptera: Homoptera, Psyllidae) Associations with their *Eucalyptus* spp. Hosts; Erection of a New Subgenus and Descriptions of Thirty-eight New Species of *Glycaspis*.

By K. M. Moore, Forestry Commission of New South Wales.

(Plates vi-vii; forty-eight Text-figures.)

[Read 26th April, 1961.]

Synopsis.

The genus *Glycaspis* Taylor 1960 is considered, and divided into two subgenera on the basis of morphological divergence among, and host-associations of, the species contained in it.

Those species which breed on *Eucalyptus* spp. hosts contained in Blakely's Renantherae-Renantherae Normales group, constitute the most primitive subgenus *Glycaspis* (*Glycaspis*); the remaining species representing a more recent evolutionary development and placed in the subgenus *Glycaspis* (*Alloglycaspis*) subgen. nov., do not breed on hosts contained in that eucalypt group. The significance of the *Glycaspis* spp.-*Eucalyptus* spp. host-associations is discussed.

Thirty-eight new species of *Glycaspis* are described; previously described species are considered, and the coverings made by nymphs are figured.

Introduction.

Species of the genus *Glycaspis* occur throughout the mainland of Australia and in Tasmania, and it is apparent that numerous species are as yet undescribed.

Large populations of *Glycaspis* spp. have consistently damaged a number of *Eucalyptus* spp. in coastal and highland areas of New South Wales for many years. During investigations in these areas on the cause of mortalities among *Eucalyptus saligna* Smith (Sydney blue gum) (Moore, 1959), it became evident that a complex of *Glycaspis* spp. occurred where damage by these psyllids was severe. Locations of attacked areas were from sea-level to an altitude of about 3,000 feet and numerous collections of specimens were made from these and other areas.

The Genus Glycaspis.

Glycaspis Taylor 1960.

Synonymy: *Psylla* Dobson, 1851, pp. 235–241, Pl. 18, fig. 4; *Spondyliaspis* Schwarz, 1898, p. 68; Froggatt, 1900, p. 288; Tuthill & Taylor, 1955, pp. 230–231, fig. 1; *Glycaspis* Taylor, 1960, p. 384, Pl. 1, figs 2 and 3.

Dobson (1851) described the species on which the genus *Glycaspis* is now based, and placed it in the genus *Psylla*.

Signoret (1879) erected the genus *Spondyliaspis* to which subsequently were assigned by Schwarz (1898), Froggatt (1900, 1903), and Tuthill & Taylor (1955) species now included in the genus *Glycaspis*.

The genus *Spondyliaspis* was re-defined in error by Schwarz (1898), Froggatt (1900) and Tuthill & Taylor (1955).

Taylor (1960) investigated the status of the genus *Spondyliaspis* and erected the genus *Glycaspis* to receive the species described by Dobson, Schwarz, Froggatt and Solomon (1936) which were erroneously assigned to *Spondyliaspis*.

Species of the genus *Glycaspis* are separated into two groups, each of which is given subgeneric status in this paper. The apparent host-specificity of most of the *Glycaspis* spp. occurring on *Eucalyptus* spp. suggested that an examination of both the psyllid and eucalypt taxonomy should be made, and when this was done it was estab-

lished that the two groups of *Glycaspis* spp. could be separated by (*a*) The *Eucalyptus* sp. host-group on which they consistently bred; (*b*) The comparative length of the M + Cu stem in the forewing venation; (*c*) The shape of Cu_1 in the hindwing venation; (*d*) The structure of the male claspers and aedeagus; and (*e*) The presence or absence of a small anterior spine on each meta-coxa.

Subgenus Alloglycaspis, subgen. nov.

(Greek: *allo-* = other, or strange.)

Type Species: *Glycaspis* (*Alloglycaspis*) *baileyi*, sp. nov. (here designated).

Type Locality: Lisarow, New South Wales.

(*a*) Species of *Glycaspis* (*Alloglycaspis*) do not breed on *Eucalyptus* spp. of the Renantherae-Renantherae Normales group (Blakely, 1955), whereas species of *Glycaspis* (*Glycaspis*) breed on host-plants of this group. (*b*) The stem of M + Cu in the venation of the forewing (fig. 1) is longer than that of species in *Glycaspis* (*Glycaspis*) (fig. 5). (*c*) The shape of Cu_1 in the hindwing venation (figs 2, 3 and 4) is distinct from that of *Glycaspis* (*Glycaspis*) (fig. 6). (*d*) Claspers of the males do not bear pads or strongly chitinized pegs on their internal faces as do those of *Glycaspis* (*Glycaspis*), and the claspers and aedeagus are structurally distinct from those of *Glycaspis* (*Glycaspis*) spp. (see figures in descriptions of the species). (*e*) Species of *Glycaspis* (*Alloglycaspis*) do not bear a small anterior spine on each meta-coxa, as do species of *Glycaspis* (*Glycaspis*) (fig. 7).

The morphology and coloration of nymphs and adults in *Glycaspis* (*Alloglycaspis*) are more diverse than those of nymphs and adults in *Glycaspis* (*Glycaspis*).

The Glycaspis-Eucalyptus Association.

The following comments are based on observations made only in New South Wales on the thirty-eight species of *Glycaspis* described in this paper.

Psyllids of the two subgenera are confined to *Eucalyptus* spp. hosts, but the degree of host-specificity within the genus *Eucalyptus* is at present imperfectly understood. It appears that some species of *Glycaspis* are not host-specific, but occur only on eucalypts of close affinity and, although not separated taxonomically in this paper, they may later be given subspecific or specific status.

From an examination of the present classification of the *Eucalyptus* spp. and the morphology of *Glycaspis* spp., it was determined that the evolutionary divergence within the psyllid group is closely associated with a probable evolutionary divergence within the eucalypt group.

(i) No psyllids of either subgenus are known to occur on *Angophora* spp. (at present regarded as close to the ancestral stock from which at least some *Eucalyptus* spp. have evolved) or on any of the *Eucalyptus* "bloodwood" group (included in Blakely's classification as Series iv and v), which contain the species of nearest affinity to *Angophora*. No information has been obtained on any *Glycaspis* spp. associations with the eucalypts in Series i to iii.

(ii) Species of *Glycaspis* (*Glycaspis*) have been reared from *Eucalyptus* spp. contained only in the following Section of Blakely's "Key to the Eucalypts": Section C. Renantherae (Series xxiv and xxv) and Renantherae (Normales) (Series xxvi to xxxiv)

As no eucalypt species contained in Section B occur in New South Wales, the occurrence of *Glycaspis* spp. on them has not been investigated.

(iii) Species of *Glycaspis* (*Alloglycaspis*) have been reared from *Eucalyptus* spp. contained in: Section A—Macrantherae (Series vi to xvi) and Macrantherae (Normales) (Series xvii to xxii); Section D—Porantheroideae (Series xxxv) and Porantheroideae (Normales) (Series xxxvi to xxxviii in part); Section E—Terminales (part Series xxxviii to xl). Froggatt refers to the occurrence of *Glycaspis* sp. on a host in Section F. No species are known to have been reared from hosts in Section G, Micrantherae (Series xlii), containing two eucalypt species only, one of which occurs on Kangaroo Island (South Australia), the other in Western Australia, or from Section H.

To assist with future identifications of *Glycaspis* spp., their host-plant associations are given in Table 1 (p. 131).

Coverings of Nymphs.

Within the genus as a whole, the coverings of the psyllid species are varied in form, and are here placed in five categories: (1) Foliage-galls (Pl. vi, fig. 1). (2) Flat lerps (Pl. vi, figs 2 and 3). These species are of close affinity to the gall-makers. (3) Round, conical lerps (Pl. vi, fig. 4; Pl. vii, figs 5–7) which also may be dome-shaped when reconstructed (Pl. vii, fig. 6). (4) Oval lerps (Pl. vii, fig. 8) which show varying degrees of ovality associated with particular species, intergradation between (3) and (4) thus occurring. (5) Rectangular lerps (Pl. vii, figs 9 and 10).

Species constructing galls are numerous within *Glycaspis* (*Glycaspis*) only, and species constructing flat lerps are confined to this subgenus. Species constructing round lerps appear to be the most numerous and widely distributed and occur in both subgenera (see Table 2). Species constructing oval lerps are numerous within *Glycaspis* (*Alloglycaspis*) only, and those constructing rectangular lerps are confined to this subgenus.

Numerous external filaments (Pl. vii, fig. 7) are usually present on the round lerps in either subgenus, as well as on oval and rectangular lerps in *Glycaspis* (*Alloglycaspis*). The use of characteristics of most lerps or galls for specific determination appears to be of no value.

Galls are variable in shape, size and wall-thickness. They have not been recorded as numerous in any one locality. Flat lerps are usually in the same plane as the leaf-surface, and cover a depression in the leaf-tissues which is caused by the feeding nymphs. They are opaque, dull, and more or less smooth in appearance. The lateral bases of some oval lerps are wider and more firmly attached to the leaf-surface than the bases of the extremities which are indefinitely attached. Rectangular lerps, which may be transparent, translucent or opaque, smooth and glassy or dull in appearance, are attached to the leaf-surface by the lateral bases only, and are arched and open at each extremity. These coverings thus indicate the evolutionary sequence within the genus; i.e., galls, flat lerps (semi-galls), round lerps, oval lerps, rectangular lerps.

The various types of coverings so far correlated with Blakely's eucalypt Series are given in Table 2.

In large populations of *Glycaspis* spp. the various types of lerps and galls may occur, round lerps usually being the most numerous, although occasionally rectangular lerps predominate. The more vigorous and younger foliage of coppice, epicormics or regeneration often appears to provide favourable conditions for a rapid increase in population of psyllids of either subgenus. Large populations of *Glycaspis* spp. have been correlated with young coppice and epicormic growth some months after fire had severely damaged the timber-stand.

Evolution within Glycaspis spp.

According to Eastop (1958), rhinaria occurring on the antennal segments of psyllids resemble those of aphids, and in most psyllids there is a single rhinarium at the apices of segments 4, 6, 8 and 9. He suggests that the presence of a single rhinarium at the apices of segments 4 to 9 inclusive and perhaps a number of rhinaria on segment 3 denotes a primitive condition, and that a similar condition is regarded as primitive in the Aphididae.

From a study of the thirty-eight *Glycaspis* spp. in these investigations it was determined that adults of the three species constructing rectangular lerps and regarded as the more recent and specialized species in the genus bear a rhinarium at the apices of antennal segments 4, 6, 8 and 9 (as is apparently the case with most psyllids); those constructing round, oval or flat lerps bear a rhinarium on segments 4, 5, 6, 8 and 9; and those constructing galls bear a rhinarium on segments 4 to 9 inclusive. The genus *Glycaspis* is thus considered to be a relatively primitive group, with those species constructing galls as the most primitive.

Discussion.

There is apparently some doubt as to the accuracy of Blakely's taxonomic classification of the genus *Eucalyptus* (Gauba & Pryor, 1958, 1959).

The evidence of host-associations of the species of *Glycaspis* (*Glycaspis*) and *Glycaspis* (*Alloglycaspis*) outlined above, agrees with Gauba & Pryor's opinion that the taxonomic arrangement of the *Eucalyptus* spp. should differ from that of Blakely, in that the combined group Renantherae and Renantherae Normales (Section C) might well be constituted a subgenus. The psyllid-eucalypt host-association supports this view, as *Glycaspis* (*Glycaspis*) spp. occurring on hosts contained in that group constitute a clear evolutionary divergence from *Glycaspis* (*Alloglycaspis*) spp. occurring on eucalypts contained in Sections A, D and E. Such a host-sequence therefore is at variance with the eucalypt sequence in Blakely's classification.

Table 1.

Association of Lerps and Galls of *Glycaspis* spp. with *Eucalyptus* spp.

Subgenus *Glycaspis* (*Glycaspis*).

1. Galls:

Series xxvi (*E. pilularis*).
Ser. xxvii (*E. triantha, E. umbra*).
Ser. xxix (*E. agglomerata, E. blaxlandi*).
Ser. xxx (*E. stricta, E. sieberiana*).
Ser. xxxii (*E. piperita*).
Ser. xxxiii (*E. haemastoma*).

2. Flat Lerps:

Ser. xxix (*E. sparsifolia*).
Ser. xxxii (*E. piperita, E. radiata* var. *subplatyphylla*).

3. Round Lerps:

Ser. xxvi (*E. pilularis, E. wardii**).
Ser. xxvii (*E. triantha, E. umbra*).
Ser. xxix (*E. eugenioides*? or *E. wilkinsoniana*?, *E. cameroni, E. caliginosa*).
Ser. xxx (*E. stricta, E. sieberiana*).
Ser. xxxii (*E. piperita, E. campanulata, E. radiata* var. *subplatyphylla*).
Ser. xxxiii (*E. haemastoma*).

Subgenus *Glycaspis* (*Alloglycaspis*).

4. Round Lerps:

Ser. vi (*E. saligna, E. propinqua, E. punctata, E. robusta, E. resinifera*).
Ser. viii (*E. gomphocephala*).
Ser. xi (*E. dumosa*).
Ser. xv (*E. blakelyi*? or *E. dealbata*?, *E. amplifolia, E. umbellata*).
Ser. xviii (*E. dunnii*).
Ser. xxxvii (*E. bosistoana*? or *E. hemiphloia*?, *E. populifolia*).
Ser. xxxviii (*E. paniculata*).

5. Oval Lerps:

Ser. vi (*E. deanei, E. resinifera*).
Ser. xv (*E. camaldulensis, E. blakelyi*).
Ser. xxxvii (*E. populifolia*).
Ser. xxxviii (*E. paniculata*).
Ser. xxxix (*E. melliodora*).

6. Rectangular Lerps:

Ser. vi (*E. grandis, E. saligna, E. botryoides, E. resinifera, E. robusta*).

* The single tree of this species from which *Glycaspis* adults were reared is near the Herbarium, in The Royal Botanic Gardens, Sydney, and is regarded as an F_2 hybrid.

Species of *Glycaspis* (*Glycaspis*) are considered to be the most primitive of the genus, and species of *Glycaspis* (*Alloglycaspis*) the most recent and specialized.

Within Section C, Blakely has placed Series xxvii (white mahoganies) and xxviii (tallow wood) between Series xxvi (blackbutts) and xxix (stringybarks). Should the evolutionary divergence found in *Glycaspis* (*Glycaspis*) spp. occurring on eucalypts contained in Section C be an indication of the evolution of this group of eucalypts, it appears that, from the evidence of morphological divergence in the psyllid species studied, Series xxvii should not separate Series xxvi from Series xxix *et seq.* in Section C.

From numerous inspections no *Glycaspis* spp. were found on *E. microcorys* F. Muell. (tallow wood). Gauba & Pryor suggest that *E. microcorys* is not correctly placed in Blakely's classification. No information on the possible association of *Glycaspis* spp. with *E. muelleriana* Howitt (yellow stringybark) in Series xxvi was obtained.

Further intensive collecting and rearing of *Glycaspis* (*Glycaspis*) and *Glycaspis* (*Alloglycaspis*) spp. from other *Eucalytus* spp. hosts should clarify the general opinions given above.

Species of the psyllid genus *Lasiopsylla* Froggatt (1900), nymphs of which construct broad, flat, white lerps on foliage of ironbarks, and other psyllid genera occurring on the stems of various ironbarks, also occur on *E. populifolia* Hook. (bimble box), *E. behriana* F. Muell. (broad-leaved mallee box), *E. melliodora* A. Cunn. (yellow box), *E. rudderi* Maiden (Rudder's box) and *E. albens* Miq. (white box), thus supporting the currently-recognized close affinity between the eucalypt "ironbarks" and "boxes".

TABLE 2.

Associations of *Glycaspis* spp. Coverings with Hosts in Blakely's Series.

		Subgenus *Glycaspis* (*Glycaspis*).							
1. Galls:	Series	xxvi	xxvii	xxix	xxx	xxxii	xxxiii		
2. Flat Lerps:	Series			xxix		xxxii			
3. Round Lerps:	Series	xxvi	xxvii	xxix	xxx	xxxii	xxxiii		
		Subgenus *Glycaspis* (*Alloglycaspis*).							
4. Round Lerps:	Series	vi	viii	xi	xv	xviii	xxxvii	xxxviii	xxxix
5. Oval Lerps:	Series	vi			xv		xxxvii	xxxviii	
6. Rectangular Lerps:	Series	vi							

PREVIOUSLY DESCRIBED SPECIES.

Specimens of *Glycaspis eucalypti*? (Schwarz) 1898, which have not been examined by the writer, were apparently collected from *E. leucoxylon* F. Muell. (white ironbark). According to the concept presented above, this species would be placed in *Glycaspis* (*Alloglycaspis*), and is unlikely to be identical with that of Dobson's species, *Glycaspis eucalypti* from Hobart, Tasmania, as *E. leucoxylon* occurs only in South Australia, Victoria, and near the town of Barham on the Murray River, in New South Wales. No *Eucalyptus* spp. in Series xxxviii (ironbarks) or in any of the Series xxxiii to xlvii occur in Tasmania.

There is stunted growth of *E. viminalis* Labill. (ribbon-gum) occurring in the Domain at Hobart (Taylor, personal communication, 1959), where Dobson collected his species, and from which Taylor has bred species of *Glycaspis* (*Alloglycaspis*). From Dobson's paper it is reasonable to assume that he collected his material from that host-species. Should his type specimens exist, their location is unknown.

The type of *Glycaspis nigro-cincta* (Froggatt) 1903, which has been examined, was apparently collected from *E. coccifera* Hook. f. (Mount Wellington peppermint). *G. nigro-cincta* and its host agree with the natural morphological division, and host-group association, of the species now placed in *Glycaspis* (*Glycaspis*).

The hosts on which *G. eucalypti* (Froggatt) 1900 is stated to occur are *E. capitellata* Smith (brown stringybark), *E. piperita* Smith (Sydney peppermint), *E. leucoxylon*, *E. gracilis* F. Muell. (yorrell) and several other species. According to the host-association concept presented here, the one species of psyllid would not breed on each of these hosts. Froggatt's specimens from Deniliquin, N.S.W., which have been examined, correspond to species of *Glycaspis* (*Glycaspis*) and would not have been breeding on *E. leucoxylon* or *E. gracilis*. Also, because of host-distribution, they would not have been collected on *E. piperita*.

The lerps attributed to *G. hirsuta* (Froggatt) 1903, which have been examined, do not belong to any species of *Glycaspis* (*Glycaspis*) or *Glycaspis* (*Alloglycaspis*). The adult female type specimen which was examined, and which Froggatt collected on *E. robusta* Smith (swamp mahogany), is placed in *Glycaspis* (*Glycaspis*), which indicates that *G. hirsuta* does not breed on *E. robusta*.

A whole-mount slide of a co-type male of *G. granulata* (Froggatt) 1900 collected on *E. robusta* was examined. The distorted aedeagus of this specimen (fig. 46) was compared with those of specimens constructing rectangular lerps and bred by the writer from *E. robusta* occurring at Mona Vale and Wamberal, N.S.W. The structure of the claspers and aedeagus of the co-type is distinct from that of the species bred from *E. robusta*, but appears to correspond with that of the *Glycaspis* (*Alloglycaspis*) sp. constructing rectangular lerps and reared by the writer from *E. botryoides* Smith

(bangalay) from Kurnell, N.S.W. Hybrids of *E. robusta* and *E. botryoides* often occur and determination of these species and their hybrids is sometimes difficult.

G. occidentalis (Solomon) is placed in *Glycaspis* (*Alloglycaspis*).

G. flavilabris (Froggatt) 1903 is placed in *Glycaspis* (*Glycaspis*), and is now the type species of that subgenus.

G. mannifera (Frogatt) 1900 is placed in *Glycaspis* (*Alloglycaspis*). The type ♂, and a ♂ (not type), which have been examined, were apparently collected at Tumut, N.S.W., and the hosts given as *E. polyanthemos* Schauer (red box), *E. hemiphloia* F. Muell. (grey box) and *E. gracilis*. It appears that more than one species of *Glycaspis* were included in Froggatt's remarks, and it was not determined from which host his specimens were collected. If collected at Tumut, the most probable host among those referred to by him would be *E. polyanthemos*.

Procedure for Descriptions.

New species described in this paper are primarily grouped and arranged according to the number of rhinaria on the antennae, i.e., one on each of antennal segs 4 to 9 (galls); one on segs 4 to 6, 8 and 9 (flat, round and oval lerps); one on segs 4, 6, 8 and 9 (rectangular lerps). The first group is considered to be the most primitive, and the last group the most recent in evolutionary sequence.

The shapes of the coverings of nymphs are also considered of sufficient importance to be used as a basis for separation of the flat, round and oval lerp group, and are arranged in that sequence which is considered to be indicative of their evolutionary development.

Drawings were made with the aid of a graticule and squared paper, and were all drawn to the same magnification. All setae were drawn to scale.

Pinned specimens are usually unsatisfactory for description and the following species-descriptions are based on specimens in alcohol, unless otherwise stated.

Measurements and coloration of adults are apparently an arbitrary means of separating species, so that slides of dissected male claspers and aedeagus were necessary for examination and illustration.

Measurements given of the lengths of the genal processes are from their distal tips to the anterior edges of the antennal foveae.

The technique adopted for the preparation of slide material is explained in a typescript paper of The Ministry of Agriculture, Fisheries and Food, Great Britain; Conference of Advisory Entomologists: Occasional Notes No. 8.

All specimens hereafter referred to in this paper were collected from New South Wales, by the writer, unless otherwise stated.

Type material is distributed to the Institutions referred to by the following abbreviations: AM, The Australian Museum, Sydney; BM, The British Museum, (Natural History), London; CS, The Division of Entomology, C.S.I.R.O., Canberra; FC, The Forestry Commission of New South Wales.

Descriptions.

(A) Subgenus Glycaspis (Glycaspis).

Type Species: *Glycaspis* (*Glycaspis*) *flavilabris* (Froggatt) (designated Taylor 1960) (= *Aphalara flavilabris* Froggatt 1903 = *Spondyliaspis flavilabris* Tuthill & Taylor 1955).

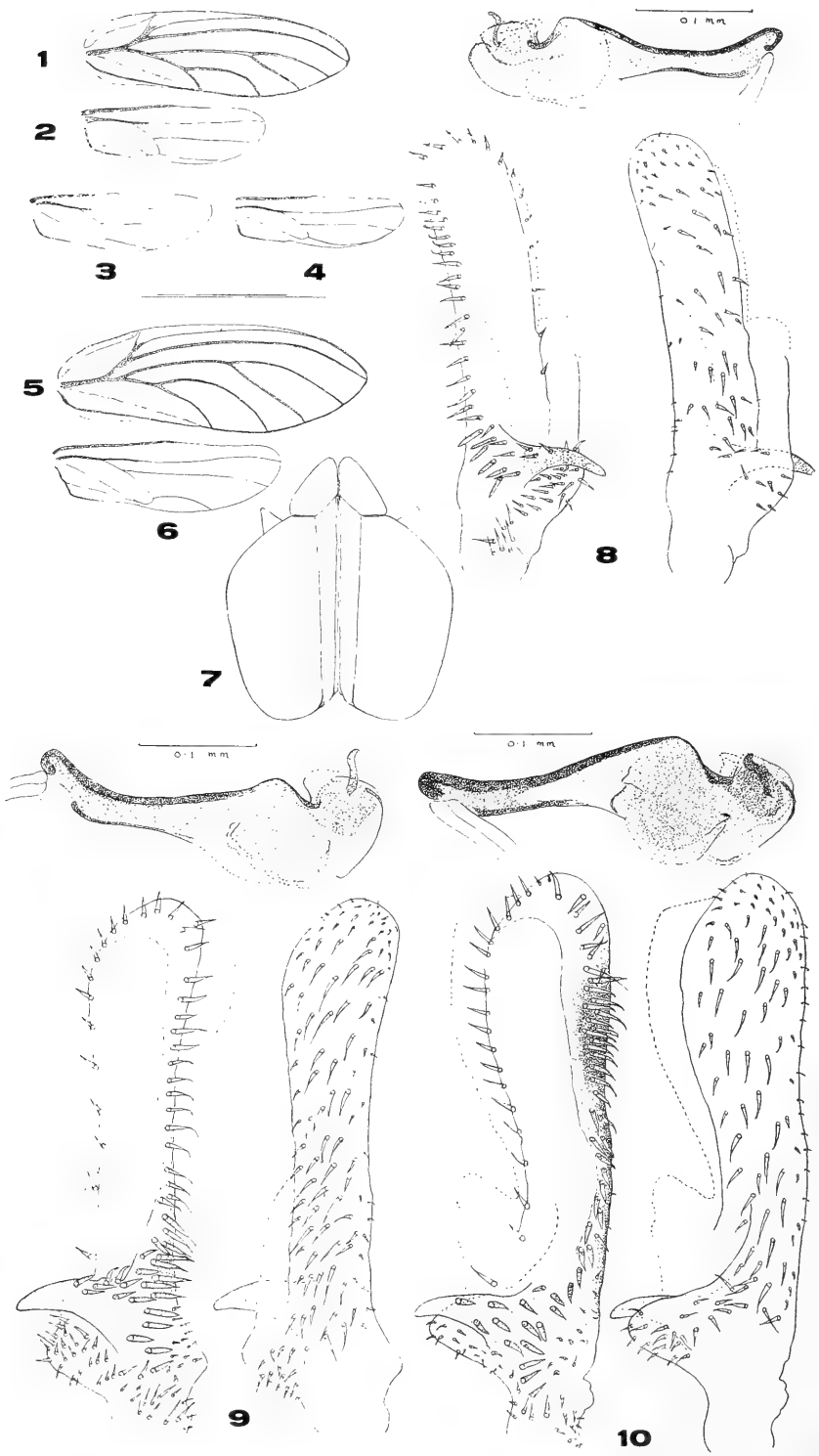
Type Locality: Rylstone, New South Wales.

There is no host-plant recorded for this species, and it is here assumed to be one of the *Eucalyptus* spp. contained in Blakely's Section C.

GALL-FORMERS.

This group is considered to be the most primitive of the genus because of the presence of a single rhinarium at the distal end of antennal segments 4 to 9 inclusive.

General coloration of adults of all the gall-forming species examined is pale to bright green, suffused pale yellow, with the male genitalia orange.


1
2
3
4
5
6
7
8
9
10
0·1 mm
0·1 mm
0·1 mm

GLYCASPIS (GLYCASPIS) AMPLIFICATA, sp. nov.

(L. *amplificatus* = enlarged. Referring to the enlarged leaf-tissues forming the galls.)

General colour: lemon-yellow.

Male: Head: width 0·68 mm.; vertex: along suture 0·24 mm., width 0·42 mm.; genal processes: length 0·27 mm.; antennae: length 1·63 mm., pale brown, darkening to distal end with segs 9 and 10 black. Pronotum: width 0·57 mm. Genitalia: pale orange, with lower plate paler in colour; claspers and aedeagus as in Text-fig. 8. Length of aedeagus: (1 specimen) 0·274 mm. Forewings: length 2·83 mm., pterostigma and base of costa translucent, venation pale to dark brown, darkest towards base of wing, tegulae marked brown. Hindwing: Cu_1 as in Text-fig. 6.

Host-plant: *Eucalyptus triantha* Link. (white mahogany).

Type Locality: Ourimbah State Forest, Section 1, Compartment 17 (Newcastle Forestry District, Wyong sub-district).

Type: Holotype male on slide labelled "Ourimbah S.F. 24 ii 1960, K. M. Moore. From *E. triantha*". Slide deposited with AM.

Notes: Galls: Green, smaller and similar to, but not as elongate as, those occurring on *E. haemastoma* (Pl. vi, fig. 1).

GLYCASPIS (GLYCASPIS) INCLUSA, sp. nov.

(L. *inclusus* = confined, shut in. Referring to the confinement of the nymph within the gall.)

General colour: lemon-yellow.

Male: Head: width 0·93 mm.; vertex: along suture 0·32 mm., width 0·59 mm.; genal processes: length 0·37 mm.; antennae: length 2·34 mm., segs 1 to 8 pale grey-brown, segs 9 and 10 dark brown. Pronotum: width 0·75 mm. Genitalia: orange; claspers and aedeagus as in Text-fig. 9. Length of aedeagus: (1 specimen) 0·311 mm. Forewings: length 3·66 mm., pterostigma and base of costa lightly suffused white. No brown or black on tegulae. Hindwings: Cu_1 as in Text-fig. 6.

Female: Coloration similar to male. Slightly larger.

Host-plant: *Eucalyptus umbra* R. T. Baker (bastard mahogany).

Type Locality: Mangrove Mountain, 7½ miles along Spencer Road, south from Central Mangrove Mountain.

Types: Holotype male, allotype female, on slide labelled "Mangrove Mountain, N.S.W. 3 iv 1960, K. M. Moore. From *E. umbra*". Slide deposited with AM.

Notes: Galls: Green.

GLYCASPIS (GLYCASPIS) CYTOS, sp. nov.

(Gk. *kytos* = a hollow vessel. Referring to the gall.)

General colour: green and yellow.

Male: Head: width 0·88 mm.; vertex: along suture 0·37 mm., width 0·51 mm., strongly concave to foveae and convex along median suture; genal processes: length 0·34 mm.; antennae: missing (see female). Pronotum: width 0·71 mm. Genitalia: colour not apparent; claspers orange distally; claspers and aedeagus as in Text-fig. 10.

Text-fig. 1.—Forewing venation of *Glycaspis* (*Alloglycaspis*) showing length of M + Cu stem.

Text-figs 2, 3 and 4.—Hindwing venation of *Glycaspis* (*Alloglycaspis*) showing variation in shape of Cu_1.

Text-fig. 5.—Forewing venation of *Glycaspis* (*Glycaspis*) showing length of M + Cu stem.

Text-fig. 6.—Hindwing venation of *Glycaspis* (*Glycaspis*) showing shape of Cu_1.

Text-fig. 7.—Ventral aspect of meta-coxae of *Glycaspis* (*Glycaspis*) showing anterior spines.

Text-fig. 8.—Aedeagus and claspers (left, internal face; right, external face) of *Glycaspis amplificata*, sp. nov.

Text-fig. 9.—Aedeagus and claspers of *Glycaspis inclusa*, sp. nov.

Text-fig. 10.—Aedeagus and claspers of *Glycaspis cytos*, sp. nov.

Length of aedeagus: (1 specimen) 0·403 mm. Forewings: length 3·93 mm., suffused yellow below RS. Hindwings: Cu_1 as in Text-fig. 6.

Female: Coloration as for the male, but wings suffused deeper yellow. Antennae: length 2·56 mm., segs 1 to 3 pale brown, segs 4 and 5 dark brown, segs 6 to 10 black.

Host-plant: *Eucalyptus pilularis* Smith (blackbutt).

Type Locality: Kincumber, N.S.W., 1¼ miles along Killcare Road, south from Kincumber.

Types: Holotype male, allotype female, on slide labelled "Kincumber, N.S.W. 22 vii 1958, K. M. Moore. From *E. pilularis*". Slide deposited with AM. Paratypes: Pinned: Kincumber, N.S.W. 22 vii 1958, K. M. Moore; 3 females to AM.

Notes: Galls: Spherical; either red or pink, and partly yellow or green.

Glycaspis (Glycaspis) encystis, sp. nov.

(Gk. *en* = in; *kystis* = a pouch. Referring to the occurrence of the nymph within the gall.)

General colour: bright green, or yellow.

Male: Head: width 0·90 mm.; vertex: along suture 0·39 mm., width 0·49 mm., yellow; genal processes: length 0·34 mm., yellow-green; antennae: length 2·20 mm., brown, with seg. 8 distally and segs 9 and 10 black. Pronotum: width 0·68 mm., yellow-green. Prescutum: yellow-green. Scutum: yellow-green. Abdomen: bright green. Genitalia: orange; claspers and aedeagus as in Text-fig. 11. Length of aedeagus: (3 specimens) 0·295 mm., 0·317 mm., 0·320 mm. Forewings: length 3·71 mm., suffused pale yellow along posterior margin, venation orange-brown. Hindwings: Cu_1 as in Text-fig. 6.

Female: Colour as for the male, but forewings suffused yellow on posterior half.

Host-plant: *Eucalyptus agglomerata* Maiden (blue-leaved stringybark).

Type Locality: Ourimbah S.F., Section 1, Compartment 17.

Types: Holotype male on slide labelled "Ourimbah S.F. 22 xi 1959, K. M. Moore. From *E. agglomerata*". Slide deposited with AM. Paratypes: 2 slides: Ourimbah S.F. 22 xi 1959, K. M. Moore; to AM. In alcohol: Ourimbah S.F. 24 ii 1960, K. M. Moore; 3 adults to AM. Pinned: Yarramalong, N.S.W. 21 ii 1960, K. M. Moore; 2 males to AM.

Notes: Galls: Green, more or less spherical but asymmetrical, glaucous and of similar colour to that of the host-plant foliage; rather brittle and thin-walled. This is the largest of the gall-forming species yet reared.

Glycaspis (Glycaspis) cyrtoma, sp. nov.

(Gr. *kyrtoma* = a swelling. Referring to the gall.)

General colour: yellow, faintly marked with black.

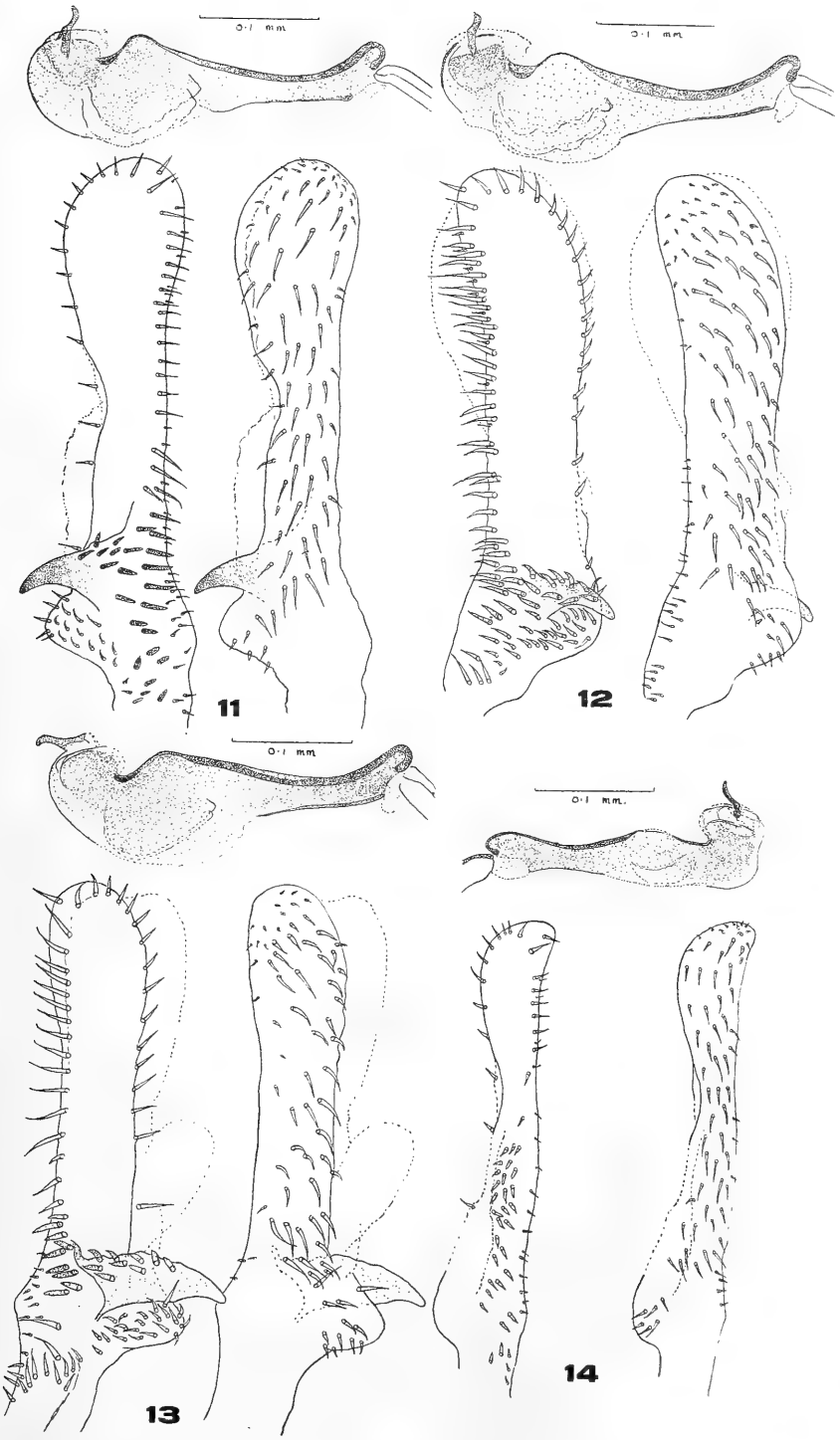
Male: Head: width 0·81 mm.; vertex: along suture 0·27 mm., width 0·44 mm., yellow, median suture and lateral borders faintly brownish; genal processes: length 0·27 mm.; antennae: length 1·83 mm., pale brown, seg. 9 apically and seg. 10 black. Pronotum: width 0·66 mm., dark marks at bases of prominences and indistinctly on posterior border. Prescutum: posterior border narrowly black. Scutum: diffused pale brown longitudinal lines from postero-lateral corners of prescutum to antero-lateral corners of scutellum. Scutellum with antero-lateral corners narrowly marked with black. Metanotum: posterior border narrowly marked with black. Abdomen: very narrow transverse black lines on segs 1 to 5, paler and smaller toward posterior segments, indistinct on seg. 5. Genitalia: upper plate orange, lower plate pale orange; claspers and aedeagus as in Text-fig. 12. Length of aedeagus: (1 specimen) 0·315 mm. Forewings: length 3·66 mm., pterostigma and base of costa slightly opaque, tegulae marked with brown and black. Hindwings: Cu_1 as in Text-fig. 6.

Host-plant: *Eucalyptus piperita* Smith (Sydney peppermint).

Type Locality: Olney East S.F. On boundary of Compartments 13 & 14 McKenzie's Road (Newcastle Forestry District; Wyong Subdistrict).

Type: Holotype male on slide labelled "Olney East S.F. 3 v 1960, K. M. Moore. From *E. piperita*". Slide deposited with AM.

Notes: Galls: Green, or green and red, usually more or less spherical.



Text-fig. 11.—Aedeagus and claspers of *Glycaspis encystis*, sp. nov.
Text-fig. 12.—Aedeagus and claspers of *Glycaspis cyrtoma*, sp. nov.
Text-fig. 13.—Aedeagus and claspers of *Glycaspis perthecata*, sp. nov.
Text-fig. 14.—Aedeagus and claspers of *Glycaspis phreatos*, sp. nov.

GLYCASPIS (GLYCASPIS) PERTHECATA, sp. nov.

(L. *perthecatus* = well-sheathed. Referring to the thick walls of the galls of this species.)

General colour: green to yellow-green; male genitalia orange.

No measurements were made before the specimen was placed on a slide.

Adults of this species are indistinguishable from most of the other gall-formers, unless a slide of the male genitalia is examined. Claspers and aedeagus as in Text-fig. 13. Length of aedeagus (1 specimen) 0·311 mm. Forewings: length 3·56 mm. Hindwings: Cu_1 as in Text-fig. 6.

Host-plant: *Eucalyptus haemastoma* Smith (scribbly gum).

Type Locality: Ourimbah S.F., Section 4, Compartment 4.

Type: Holotype male on slide labelled "Ourimbah S.F. 14 viii 1960, K. M. Moore. From *E. haemastoma*". Slide deposited with AM.

Notes: Galls: (Pl. vi, fig. 1.) Elongate, singly or in a row along surface of leaf; green, often with some red.

FLAT LERPS.

The two species examined, belonging to this group, bear a single rhinarium at the distal end of each of antennal segs 4 to 6, 8 and 9; this, together with their general habits, suggests that their evolutionary position is between the gall-formers and those constructing round lerps.

GLYCASPIS (GLYCASPIS) PHREATOS, sp. nov.

(Gr. *phrear* = a pit. Referring to the depression in the leaf-surface, caused by the nymph.)

General colour: (Pinned specimen) pale yellow, pale green, or lemon.

Adults were not described prior to slides being made, but the species is readily separable from the other known species constructing flat lerps by the structure of the male claspers and aedeagus (Text-fig. 14). Length of aedeagus: (3 specimens) 0·236 mm., 0·239 mm., 0·250 mm. Forewings: length 2·54 mm. Hindwings: Cu_1 as in Text-fig. 6.

Host-plant: *Eucalyptus sparsifolia* Blakely (narrow-leaved stringy-bark).

Type locality: Wentworth Falls, N.S.W. (½ mile north of township).

Types: Holotype male, and nymphs, on slide labelled "Wentworth Falls, N.S.W. 3 i 1959, K. M. Moore. From *E. sparsifolia*". Slide deposited with AM. Paratypes: 5 slides, Wentworth Falls, N.S.W., 3 i 1959; 4 to AM, 1 to CS.

Notes: Lerps usually occur singly, but there may be two or more on a young leaf. Some leaves become curled. Lerps are attached around their perimeters, to the leaf-surface, and are slightly sweet to the taste. No filaments occurred on any of the numerous lerps of this species examined.

When nymphs are parasitized, additional excretion is placed around the enclosed nymph, thus more firmly attaching it to the leaf-surface.

GLYCASPIS (GLYCASPIS) PLANARIA, sp. nov.

(L. *planarius* = flat. Referring to the comparatively flat lerps of this species.)

General colour: (Pinned specimen) yellow, suffused green.

Male: Head: width 0·63 mm.; vertex: along suture 0·22 mm., width 0·34, yellow suffused orange; genal processes: length 0·32 mm., pale green, darker distally; antennae: length 1·22 mm., pale brown with segs 9 and 10 black. Pronotum: width 0·44 mm., yellow. Scutum: yellow. Metanotum: yellow. Genitalia: upper plate pale orange, lower plate yellow suffused green; claspers and aedeagus as in Text-fig. 15. Length of aedeagus: (1 specimen) 0·245 mm. Forewings: length 2·51 mm., venation yellow-brown. Hindwings: Cu_1 as in Text-fig. 6.

Host-plant: *Eucalyptus piperita*.

Type Locality: Wentworth Falls, N.S.W. (¼ mile north of township).

Type: Holotype male on slide labelled "Wentworth Falls, N.S.W. 2 i 1960, K. M. Moore. From *E. piperita*". Slide deposited with AM.

ROUND LERPS.

Species constructing round lerps bear a single rhinarium on each of antennal segments 4 to 6, 8 and 9, as do those species constructing flat lerps, or oval lerps.

GLYCASPIS (GLYCASPIS) MACTANS, sp. nov.

(L. *mactans* = afflicting. Referring to the affliction of trees by this species.)

General colour: pale brown, yellow-brown or dark brown, with red on scutum and abdomen, dorsally. Wings clear, to golden colour.

Male: Head: width 0·59 mm.; vertex: along suture 0·24 mm., width 0·32 mm., pale brown, narrowly edged black; suture black; genal processes: length 0·27 mm., pale brown, upturned distally; antennae: length 1·80 mm., segs 1 to 5 pale brown, 6 to 8 dark brown, 9 and 10 black. Pronotum: width 0·49 mm., pale brown, anterior border and posterior border near prominences, narrowly black. Prescutum: pale brown, narrowly edged black. Scutum: pale yellow-brown, narrowly edged black, two red to brown longitudinal stripes each side of median area. Scutellum and metascutellum yellow-brown, with area between yellow-brown, and paler laterally. Metanotum: yellow-brown, narrowly edged black. Abdomen: yellow-brown with central area red; narrow, black transverse lines on segs 2 to 5. Genitalia: pale brown; upper plate with base narrowly black; claspers and aedeagus as in Text-fig. 16. Length of aedeagus: (25 specimens) Extremes, 0·173 mm. to 0·193 mm., but generally smaller from highlands (extremes, 0·158 mm. to 0·182 mm. from Cloud's Creek S.F.). Forewings: length 2·34 mm., pale honey-colour. Hindwings: Cu_1 as in Text-fig. 6. Whole adult may be suffused red. Ventral: abdominal segments suffused pale to dark grey, and usually a dark area on each metacoxa.

Female: Coloration similar to male, but darker. Abdomen sometimes suffused dark grey or black, ventrally. Wings of deeper honey-colour than on the male. Transverse lines on abdomen often surrounded by an extensive grey to black area.

Host-plants: *E. triantha* and *E. umbra*.

Type Locality: Lisarow, N.S.W., 1¼ miles from level-crossing, along Cut Rock Road.

Types: Holotype male, allotype female, on slide labelled "Lisarow, N.S.W. 31 vii 1958, K. M. Moore. From *E. triantha*". Slide deposited with AM. Paratypes: From *E. triantha*. 10 slides: Lisarow, 31 vii 1958; 6 to AM, 1 to BM, 1 to CS, 2 to FC. 5 slides: Cloud's Creek S.F., 3 v 1959; 4 to AM, 1 to FC. From *E. umbra*. 5 slides: Ourimbah S.F., 6 vii 1960; 4 to AM, 1 to FC. 4 slides: Ourimbah S.F., 21 v 1958; 3 to AM, 1 to FC. 3 slides: Wyong S.F., 17 xii 1958; 2 to AM, 1 to FC. In alcohol: From *E. triantha*. Lisarow, 31 vii 1958; 100 adults to AM. Cloud's Creek S.F., 3 v 1959; 50 adults, and nymphs, to AM. Ourimbah S.F., 20 xi 1958; 100 adults to CS. Kincumber, 23 iii 1959; 15 adults to FC. From *E. umbra*. Ourimbah S.F., 23 viii 1960; 60 adults to AM. Ourimbah S.F., 6 vii 1960; 100 adults to CS. Wyong S.F., 12 viii 1958; 75 adults, and nymphs, to AM. Wyong S.F., 14 v 1959; 50 adults to FC. Pinned: From *E. triantha*. Lisarow, 11 ix 1958; 5 males, 4 females, to AM. Cloud's Creek S.F., 13 x 1958, G. Baur; 2 males, 2 females, to AM. Ourimbah S.F., 23 vii 1957; 5 males, 2 females, to AM. Ourimbah S.F., 14 xi 1958; 7 males, 10 females, to AM. Ourimbah S.F., 14 xi 1958; 8 males, 12 females, to CS. From *E. umbra*. Wyong S.F., 12 viii 1958; 3 males, 4 females to AM. Kincumber, 12 ix 1958; 1 female to AM.

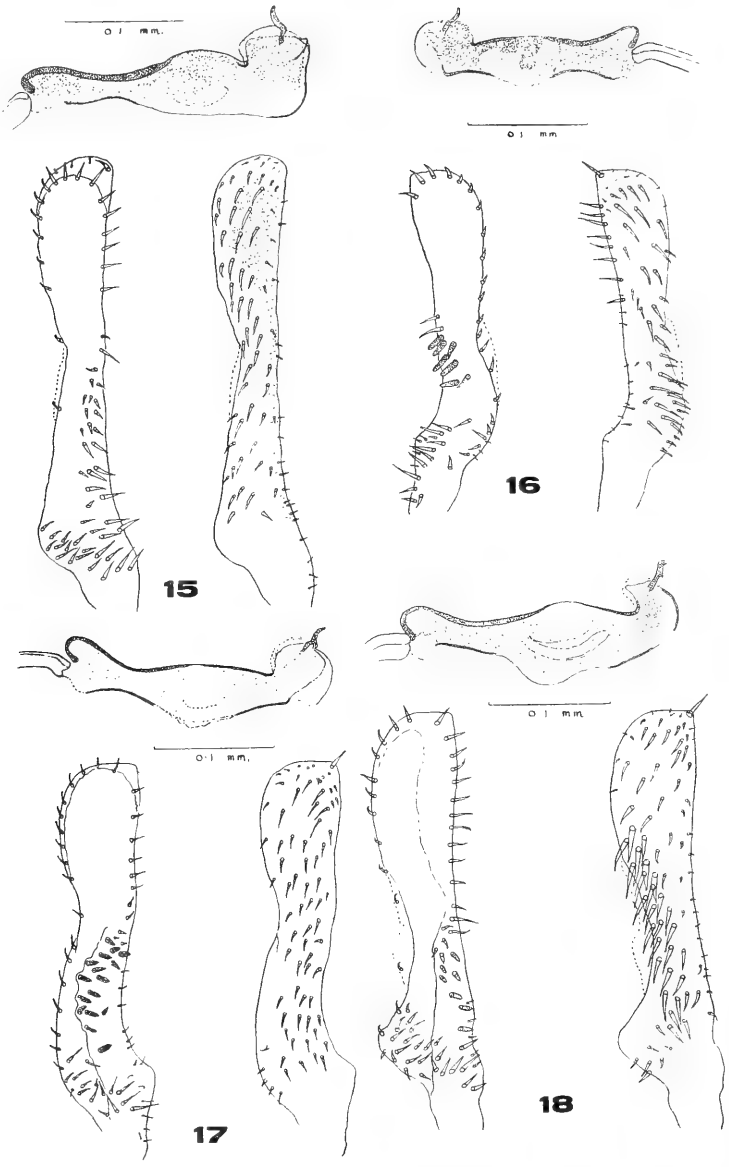
Notes: Specimens which may occur on the above two hosts cannot at present be separated, and are retained as a single species. Eggs: Between 30% and 40% of the eggs occurring on *E. triantha* are oviposited along the edges of the leaves; the remainder may be oviposited anywhere on the leaf-surfaces, usually singly and rarely contiguous. Lerps: Lerps are peaked, and are 3 mm. to 4 mm. in diameter; they may be yellow, but are usually white, and may bear numerous fine filaments on the external surface; they occur on either side of the leaves.

GLYCASPIS (GLYCASPIS) ORIENTALIS, sp. nov.

(L. *oriens* = the east; L. *alis* = pertaining to. Referring to the occurrence of this species in the eastern portion of the continent.)

To reduce confusion with *G. mactans*, because of similarity in the extremes of coloration of the males, a more detailed description of the female is given.

General colour: dark brown or dark red-brown.



Text-fig. 15.—Aedeagus and claspers of *Glycaspis planaria*, sp. nov.
Text-fig. 16.—Aedeagus and claspers of *Glycaspis mactans*, sp. nov.
Text-fig. 17.—Aedeagus and claspers of *Glycaspis orientalis*, sp. nov.
Text-fig. 18.—Aedeagus and claspers of *Glycaspis seriata*, sp. nov.

Male: Paler in coloration, and generally smaller, than female. Head: width 0·63 mm.; vertex: along suture 0·37 mm.; genal processes: length 0·34 mm.; antennae: length 1·80 mm. Pronotum: width 0·51 mm. Genitalia: claspers and aedeagus as in Text-fig. 17. Length of aedeagus: (7 specimens) Extremes, 0·225 mm. to 0·230 mm. Forewings: length 2·49 mm., faintly suffused grey. Hindwings: Cu_1 as in Text-fig. 6.

Female: Head: width 0·66 mm.; vertex: along suture 0·39 mm., creamy brown, sometimes suffused grey, narrowly edged black; suture black; genal processes: length 0·32 mm., red-brown, suffused grey towards distal end, tapering strongly to distal end; antennae: length 2·04 mm., brown, with seg. 7 black apically and segs 8 to 10 black. Pronotum: width 0·59 mm., colour as for vertex, with prominences palest; two depressions, and narrow areas surrounding depressions, grey to black. Prescutum: red-brown, sometimes suffused grey, narrowly edged black. Scutum: as prescutum but sometimes with two dorsal longitudinal red, grey or brown lines each side. Scutellum and metascutellum red-brown, sometimes suffused grey; area between, pale yellow-brown, dark red-brown laterally. Post-metanotum: yellow-brown, with markings and borders grey to black. Abdomen: seg. 1 with anterior and posterior borders narrowly, dark brown, suffused red; remainder red dorsally, with narrow, transverse black lines on grey-brown areas on segs 2 to 5. Forewings: length 3·07 mm., more elongate than those of *G. mactans*; golden-brown to red-brown, suffused light to dark grey posterior to SC or RS, darkest toward apex; venation red on apical half, brown on basal half. Ventral: genal processes edged black posteriorly; area between bases dark brown. Mesosternum dark brown, suffused red. Legs pale cream suffused grey, with posterior femora dark grey. Abdominal segments grey to dark brown.

Host-plant: *E. umbra.*

Type Locality: Somersby, N.S.W., 4¼ miles along Dog Trap Road from the Pacific Highway at Ourimbah.

Types: Holotype male, and nymphs, on slide labelled "Somersby, N.S.W. 18 viii 1958, K. M. Moore. From *E. umbra*". Slide deposited with AM. Paratypes: 8 slides: Somersby, 18 viii 1958; 6 to AM, 1 to BM, 1 to CS. 7 slides: Kincumber, 23 iii 1959; 6 to AM, 1 to FC. In alcohol: Somersby, 18 viii 1958; 8 adults, and nymphs, to AM. Kincumber, 23 iii 1959; 25 adults, and nymphs, to AM. Pinned: Somersby, 18 viii 1958; 5 males, 4 females, to AM, 4 males, 5 females, to CS. Kincumber, 12 ix 1958; 3 females to AM.

Notes: This species is separable from *G. mactans* by the longer and narrower wings, the dark grey suffusion on the wings of the females, and the aedeagus and claspers of the males. Lerps of this species are not as peaked as those of *G. mactans.*

Glycaspis (Glycaspis) seriata, sp. nov.

(L. *seriatus* = arranged in rows. Referring to the tendency of nymphs to be disposed in a row, along the venation of a leaf.)

General colour: yellow to orange, suffused red and lightly marked with black.

Male: Head: width 0·78 mm.; vertex: along suture 0·27 mm., width 0·42 mm., pale yellow, bordered narrowly with black; suture and foveae grey to black; genal processes: length 0·29 mm., cream, sometimes faintly suffused grey; antennae: length 1·66 mm., suffused brown, darkening to distal end with segs 9 and 10 black. Pronotum: width 0·59 mm., lateral prominences cream, with black at bases; medio-dorsal area cream, remainder orange. Small depressions half-way between median line and lateral borders, faintly grey. Prescutum: pale yellow, suffused orange anteriorly, narrowly edged black. Scutum: yellow, faintly edged black on posterior border; two more or less parallel longitudinal red to brown stripes each side of broad median area. Metanotum, scutellum and metascutellum, narrowly marked black, anterior borders and area between, yellow. Area postero-lateral to scutellum, suffused red. Post-metanotum: yellow, narrowly bordered grey to black. Abdomen: medio-dorsal area red, bordered pale brown laterally. A narrow black transverse central line on segs 2 to 5 or 6. Genitalia: upper plate suffused grey-brown, darkest at base; lower plate cream, with upper anterior angle grey; claspers suffused grey; claspers and aedeagus as in Text-fig. 18. Length of aedeagus: (19 specimens) Extremes 0·216 mm. to 0·250 mm. Forewings: Length 2·71 mm., venation pale brown and costal margin black; pterostigma and base of costa suffused white. Hindwings: Cu_1 as in Text-fig. 6. Legs: femora, tibiae and tarsi suffused grey.

Female: Deeper orange, dark marks more intense and extensive than on the male; genal processes tapered to distal end; red on abdomen bordered grey laterally.

Genitalia: prominences of upper plate pale brown. Ventral: May be marked with grey, except longitudinal median area on each segment and genital plate; dark areas variable in extent; sometimes dark lateral area on meta-coxae; mesosternum sometimes suffused grey.

Host-plants: *E. pilularis* and *E. wardii* Blakely (Ward's stringybark). The tree of *E. wardii* from which the adults were reared is near the herbarium, in The Royal Botanic Gardens, Sydney, and is apparently an F_2 hybrid.

Type Locality: Ourimbah S.F., No. 3 extension, near Wyong Creek Road entrance gate.

Types: Holotype male, allotype female, nymphs, on slide labelled "Ourimbah S.F., 29 ix 1958, K. M. Moore. From *E. pilularis*". Slide deposited with AM. Paratypes: From *E. pilularis*. 3 slides: Ourimbah SF., 29 ix 1958; 1 to AM, 1 to BM, 1 to CS. 5 slides: Sylvania, 5 xii 1958; to AM. 5 slides: Kincumber, 27 xi 1958; 4 to AM, 1 to FC. From *E. wardii*. 5 slides: The Royal Botanic Gardens, Sydney, 9 x 1958; 4 to AM, 1 to FC. In alcohol: From *E. pilularis*. Ourimbah S.F., 29 ix 1958; 14 adults to AM. Kincumber, 27 xi 1958; 80 adults to AM. Pennant Hills, 1 viii 1958, K. G. Campbell; 17 adults to CS. Sylvania, 5 xii 1958; 11 adults to FC. Pinned: From *E. pilularis*. Sylvania, 5 xii 1958; 2 males, 2 females, to AM; 2 males, 3 females, to CS. Kincumber, 22 vii 1958; 2 males, 2 females, to AM; 1 male, 3 females, to CS. From *E. wardii*. Roy. Botanic Gdns. Sydney, 9 x 1958; 1 male, 1 female, to AM; 1 male, 1 female, to CS.

Notes: Eggs: Orange in colour. In groups, of up to 100, often near tip or edges of leaves; usually on upper leaf-surface. When there is a large population of adults, eggs may be laid in groups of up to 300. Lerps: White or yellow; up to 200 on a leaf when adults in large numbers; in close proximity within the group when at tips of leaves, but usually scattered along surface of leaf, near edges, or along primary or secondary veins, on either side of leaf; sometimes with filaments.

GLYCASPIS (GLYCASPIS) CONFLECTA, sp. nov.

(N.L. *conflectus* = crowded, thickly clustered. Referring to the disposition of lerps of this species.)

General colour: orange, prominently marked with brown and black.

Male: Head: width 0·73 mm.; vertex: along suture 0·27 mm., width 0·39 mm.. yellow, prominently bordered with black which extends on to post-occipital sclerites; suture and foveae black; genal processes: length 0·32 mm., pale brown, suffused black; antennae: length 1·51 mm., dark brown, darkening distally, with segs 7 to 10 black. Pronotum: width 0·54 mm., orange, with prominences and median area cream; anterior edge prominently marked with black. Bases of prominences and small depressions half-way between median line and lateral borders, black. Prescutum: yellow, sometimes suffused grey, prominently edged with black; posterior edges of lateral ridges, and small adjacent sclerite marked with black. Scutum: yellow, narrowly bordered black, two broad orange-red to brown longitudinal bands each side of median area. Scutellum, metascutellum and area between, pale orange which may be suffused grey. Area postero-lateral to scutellum, orange suffused grey. Post-metanotum orange, marked with black. Abdomen: segs 1 and 2 with anterior edges narrowly brown to black, seg. 1 orange, suffused red. Remainder red dorsally. Narrow black transverse central lines on segs 2 to 5 and sometimes on seg. 6. Genitalia: upper plate brown, suffused grey; lower plate suffused grey; claspers and aedeagus as in Text-fig. 19. Length of aedeagus: (9 specimens) Extremes 0·239 mm. to 0·263 mm. Forewings: length 2·59 mm. Hindwings: Cu_1 as in Text-fig. 6. Ventral: Mesosternum, metacoxae and abdomen brown to black. Metacoxae with dark lateral spot. All femora, coxae, tibiae and tarsi suffused brown to black. Abdomen with pale, narrow median line. All pleurites marked brown to black.

Female: As for the male, but dark markings very pronounced and more extensive, particularly dorsal and ventral aspects of abdomen.

Host-plants: (*a*) *E. eugenioides* Sieb. (white stringybark) or (*b*) *E. wilkinsoniana* R. T. Baker (small-leaved stringybark); *E. cameroni* Blakely and McKie (diehard stringybark). (*a*) and (*b*) are of uncertain identification.

Type Locality: Kurrajong, N.S.W. Bell-bird Corner, on the Bell Road to Kurrajong Heights.

Types: Holotype male, allotype female, on slide labelled "Kurrajong, N.S.W. 31 vii 1959, K. M. Moore". Reared from host-plant (*a*) or (*b*). Slide deposited with AM. Paratypes: From (*a*) or (*b*). 8 slides: Kurrajong, 31 vii 1959; 6 to AM, 1 to BM, 1 to CS. From *E. cameroni*. 7 slides: Cloud's Ck. S.F., 6 v 1959; to AM. In alcohol: From (*a*) or (*b*). Kurrajong, 31 vii 1959; 60 adults, and nymphs to AM. From *E. cameroni*. Cloud's Ck. S.F., 6 v 1959; 30 adults to AM.

Material Examined: From (*a*) or (*b*); 4 slides (6 males, 1 female, and nymphs), Mona Vale, 24 ix 1958. (In collection of FC.)

Notes: Eggs: Contiguous, in groups, often near edges of leaves, on either surface. Occur singly, on edge of leaf, on *E. cameroni*. Nymphs: Bright orange. Lerps: Often situated along veins of leaf, on upper or lower leaf surfaces; contiguous when large.

The specimens from Kurrajong and Cloud's Ck. S.F. are at present considered to be the same species.

Glycaspis (Glycaspis) conserta, sp. nov.

(L. *consertus* = connected, joined. Referring to the disposition of most of the lerps of this species.)

General colour: yellow, often suffused with red, and marked with brown and black.

Male: Head: width 0·73 mm.; vertex: along suture 0·24 mm., width 0·42 mm., pale yellow, narrowly bordered with black, darkest on posterior border of vertex and on post-occipital sclerites; foveae brown, suture black; vertex may be all suffused red; genal processes: length 0·29 mm., cream, and may be suffused pale brown, darkest laterally near apices; antennae: length 1·39 mm., two basal segs suffused dark grey, segs 3 to 6 pale brown, 7 and 8 dark brown, 9 and 10 black. Pronotum: width 0·54 mm., pale cream central area and on prominences, remainder suffused red, with depressions brown, and bases of prominences marked with black. Prescutum: cream, suffused red anteriorly; narrow median line, cream; narrowly bordered black, darker posteriorly, and with apex black. Scutum: cream, suffused red, with two reddish wavy lines each side; black each side of scutellum. Scutellum and metascutellum cream with anterior sutures edged black; area between, suffused red, with a red spot, suffused brown each side and narrowly bordered grey to black. Post-metanotum: cream, narrowly edged brown to black, with central cream square area bordered brown to black; central area palest. Abdomen: reddish-orange; lateral borders cream suffused grey. Seg. 1 with pale to dark grey anterior and posterior borders, segs 2 to 5 with narrow black transverse line on a wide grey to black area. Genitalia: brown suffused grey, darkest at base; lower plate with anterior corner and dorsal edge sometimes grey; claspers and aedeagus as in Text-fig. 20. Length of aedeagus: (12 specimens) Extremes 0·267 mm. to 0·284 mm. Forewings: length 2·83 mm., tinged grey on pinned specimens; tegulae grey-brown. Hindwings: Cu_1 as in Text-fig. 6. Ventral: Gular area and mesosternum pale brown. Femora, tibiae and tarsi suffused pale brown.

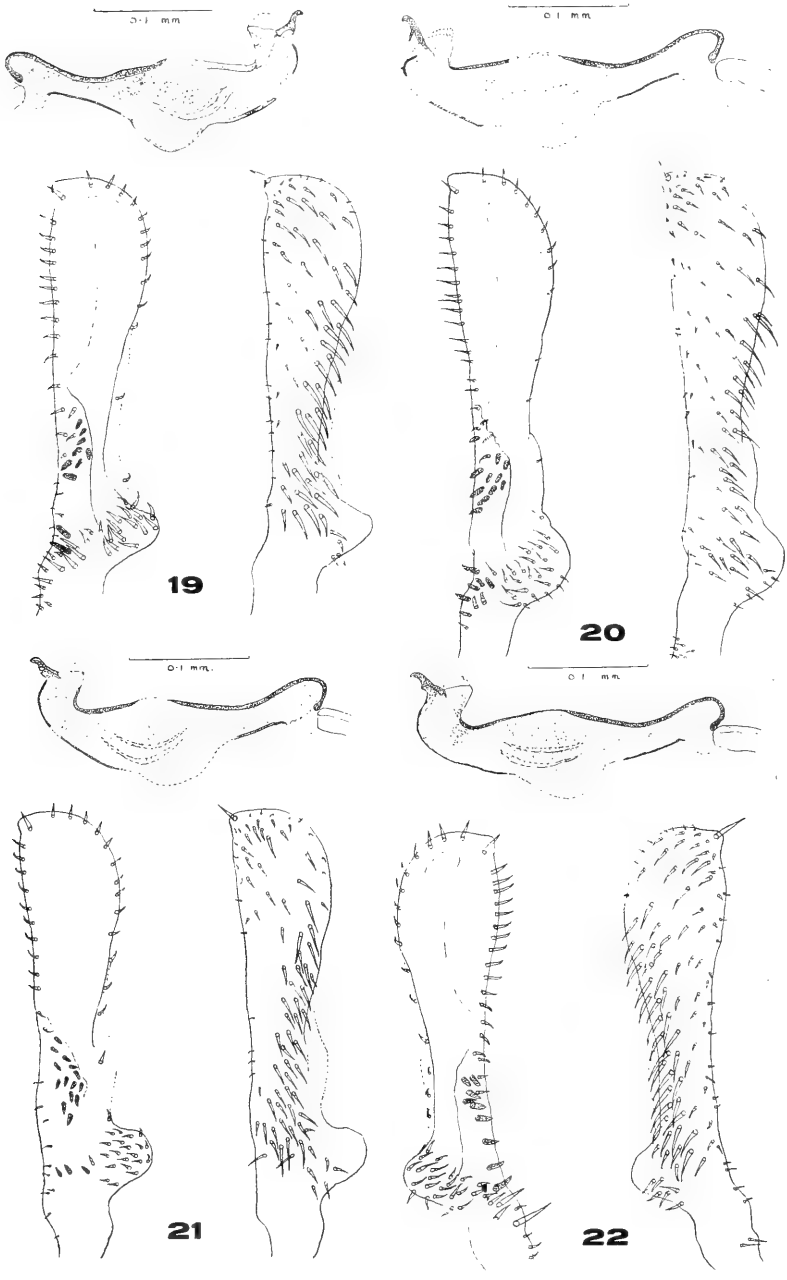
Female: Darker than male. Occipital sclerites posteriorly grey to black. Genal processes cream to pale brown, dark grey distally.

Host-plant: *E. sieberiana* F. Muell. (mountain ash).

Type Locality: Somersby, N.S.W., 5¼ miles along Dog Trap Road from Pacific Highway at Ourimbah. *Types*: Holotype male, allotype female, nymphs, on slide labelled "Somersby, N.S.W. 2 viii 1958, K. M. Moore. From *E. sieberiana*". Slide deposited with AM. Paratypes: 7 slides: Somersby, 2 viii 1958; 4 to AM, 1 to BM, 1 to CS, 1 to FC. 7 slides: Wentworth Falls, 7 i 1959; to AM. In alcohol: Somersby. 2 viii 1958; 30 adults, and nymphs, to AM. Pinned: Somersby, 18 viii 1958; 7 males, 2 females, to AM, 6 males, 3 females, to CS.

Material Examined: 1 tube of 100 adults, and nymphs, Somersby, 2 viii 1958, to FC.

Notes: This species can be separated from that occurring on *E. haemastoma* by the more general and intense red suffusion and paler markings, and the absence of a pale median area on the abdomen. Placement of eggs by the two species at oviposition,



Text-fig. 19.—Aedeagus and claspers of *Glycaspis conflecta*, sp. nov.
Text-fig. 20.—Aedeagus and claspers of *Glycaspis conserta*, sp. nov.
Text-fig. 21.—Aedeagus and claspers of *Glycaspis cyanoreios*, sp. nov.
Text-fig. 22.—Aedeagus and claspers of *Glycaspis salebrosa*, sp. nov.

also differs. Eggs: In groups, near edge of leaf, at tip, near centre, or in a row along edge of leaf. Lerps: White; some may be dark red. Singly or in groups of up to 100; not contiguous until later instars; disposed along veins of leaf on upper or lower leaf-surface. Filaments may be very numerous during the first instar.

GLYCASPIS (GLYCASPIS) CYANOREIOS, sp. nov.

(Gr. *kyanoreios* = of the blue mountain. Referring to the collection-locality of the types.)

General colour: pale green to yellow; paler than *G. seriata.*

Male: Head: width 0·73 mm.; vertex: along suture 0·29 mm., width 0·42 mm., yellow, edged faintly black; suture black; foveae pale grey; genal processes: length 0·29 mm., cream, suffused pale brown near apices; antennae: length 1·46 mm., pale brown except segs 9 and 10 which are black. Pronotum: width 0·59 mm., yellow, with lateral prominences and median area paler; prominences marked black at bases. Prescutum: cream, suffused yellow anteriorly, and edged black, darkest anteriorly. Scutum: cream except for two orange longitudinal stripes each side. Scutellum and metascutellum very pale cream with area between pale cream, and area postero-lateral to scutellum, orange. Metanotum: sometimes very faintly marked brown. Abdomen: orange, with longitudinal median area cream; transverse central black line on segs 2 to 5 or 6. Genitalia: upper plate suffused pale brown, darker at base; claspers and aedeagus as in Text-fig. 21. Length of aedeagus: (4 specimens) Extremes 0·245 mm. to 0·252 mm. Forewings: length 3·07 mm. Hindwings: Cu_1 as in Text-fig. 6. Ventral: Femora, tibiae and tarsi suffused dark brown.

Female: Coloration as for male, but dark markings more intense and extensive. Abdomen sometimes suffused red dorso-laterally. Genitalia: prominences of upper plate brown. Anal aperture surrounded with dark brown to black band.

Host-plant: *E. stricta* Sieb. (Blue Mountain mallee).

Type Locality: Wentworth Falls, N.S.W., ½ mile north of township.

Types: Holotype male, nymphs, on slide labelled "Wentworth Falls, N.S.W. 6 i 1959, K. M. Moore. From *E. stricta*". Slide deposited with AM. Paratypes: 10 slides: Wentworth Falls, 6 i 1959; 8 to AM, 1 to BM, 1 to CS. In alcohol: Wentworth Falls, 6 i 1959; 60 adults to AM. Pinned: Katoomba, 15 i 1959; 3 males, 2 females, to AM; 3 males, 3 females, to CS.

Notes: Eggs: Orange-yellow; in groups of 25 to 100, at tip, near edge, or centre of leaf, but a few sometimes occur on edge of leaf. Lerps: White; situated along venation.

This species can be separated from *G. seriata* by: (1) Oviposition on edge of leaf; (2) Pale medio-dorsal area longitudinally (except vertex); (3) Shape of claspers; (4) Adults yellow or yellow-green, not orange; (5) Length of antennae; (6) Dark border on scutellum and metascutellum absent; (7) No brown marks on scutum; (8) Length of wings.

GLYCASPIS (GLYCASPIS) SALEBROSA, sp. nov.

(L. *salebrosus* = rough, uneven. Referring to the rough outer surface and circumference of lerps of this species.)

General colour: (Pinned specimens) greenish-yellow, lightly marked with black and red-brown; abdomen dark green.

Male: (In alcohol.) Head: width 0·66 mm.; vertex: along suture 0·24 mm., width 0·37 mm., yellow, narrowly edged black; foveae and suture black; genal processes: length 0·27 mm., cream, suffused grey-brown; antennae: length 1·36 mm., brown, darker distally, segs 8 to 10 black. Pronotum: width 0·54 mm., yellow, lightly marked with black on anterior border; prominences cream, marked with black at bases; depression each side at half, grey. Prescutum: yellow, lightly marked red-brown anteriorly, and narrowly edged black. Scutum: yellow, narrowly edged black, more intense near scutellum; two brown or red longitudinal lines each side. Scutellum: cream, sometimes suffused grey. Metascutellum: cream; area between, yellow, suffused red-brown laterally. Post-metanotum: yellow, narrowly edged black, and ridges lightly black. Abdomen:

always red dorsally with anterior and posterior edges of seg. 1 narrowly black; narrow black transverse lines on grey bands on segs 2 to 6. Genitalia: upper plate brown to black; lower plate pale yellow, suffused grey, with anterior and posterior borders dark grey to black; claspers and aedeagus as in Text-fig. 22. Length of aedeagus: (23 specimens) Extremes 0·250 mm. to 0·270 mm. Forewings: length 2·71 mm., venation dark brown to black; base of costa and tornus edged black. Pterostigma and base of costa suffused white. Hindwings: Cu_1 as in Text-fig. 6. Ventral: Gular, mesopleura, lateral spot on metacoxae, and femora, tibiae, tarsi and abdomen, suffused brown.

Female: Larger and darker than male.

Host-plants: *E. piperita* and *E. campanulata* R. T. Baker (stringybark peppermint).

Type Locality: Somersby, N.S.W., 5¼ miles along Dog Trap Road from Pacific Highway at Ourimbah.

Types: Holotype male, allotype female, nymphs, on slide labelled "Somersby, N.S.W., 2 viii 1958, K. M. Moore. From *E. piperita*". Slide deposited with AM. *Paratypes*: From *E. piperita*. 7 slides: Somersby, 2 viii 1958; 4 to AM, 1 to BM, 1 to CS, 1 to FC. 4 slides: Wentworth Falls, 6 i 1958; to AM. 4 slides: Olney S.F. 13 viii 1959; to AM. 3 slides: Killara, 7 viii 1958; to AM. From *E. campanulata*. 7 slides: Cloud's Creek S.F. 6 v 1959; to AM. In alcohol: From *E. piperita*. Somersby, 2 viii 1958; 12 adults, and nymphs, to AM. Killara, 7 viii 1958; 1 adult, eggs and nymphs to AM. Wentworth Falls, 6 i 1958; 12 adults, and nymphs, to AM. Pinned: From *E. piperita*. Somersby, 18 viii 1958; 3 males, 4 females, to AM; 4 males, 4 females, to CS. Olney S.F. 12 xi 1958; 1 male to AM. Killara, 23 iv 1958; 5 females to AM.

Notes: Eggs: Deep yellow to orange; in groups of 20 to 100, nearly always near edge of leaf, but sometimes along mid-vein. Lerps: Cream, yellow or white; some with filaments; contiguous when large, in groups of 25 to 50, sometimes along veins, rarely on upper leaf-surface. Nymphs: Bright orange; slow-moving.

About 20 specimens on one leaf from Wentworth Falls were reared, and all were females, which suggests parthenogenetic reproduction.

No differences could be found between the specimens occurring on *E. piperita* and those on *E. campanulata*, and they are at present considered to be the same species.

Glycaspis (Glycaspis) aggregata, sp. nov.

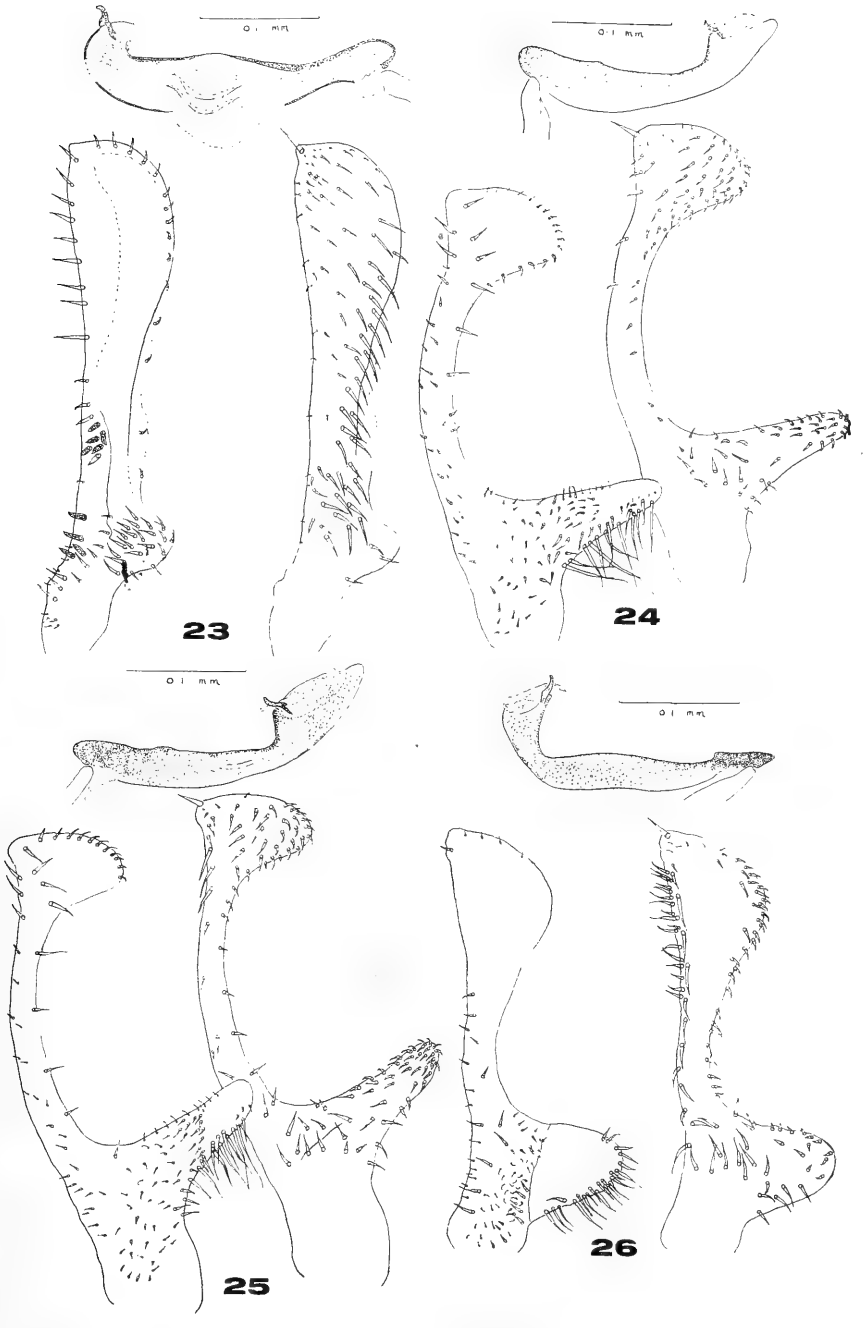
(L. *aggregatus* = herded together. Referring to the disposition of nymphs and lerps of this species.)

General colour: As *Glycaspis conserta*, but with less red suffusion; orange-red on thorax, abdomen and between scutellum and metascutellum.

Male: Head: width 0·83 mm.; vertex: along suture 0·27 mm., width 0·46 mm., coloration as *G. conserta*; genal processes: length 0·29 mm., usually with a black spot laterally, near apex; antennae: length 1·61 mm., colour as for *G. conserta*. Pronotum: width 0·66 mm., prominences with bases narrowly black in the form of an arc which terminates at half the length of prominence. Prescutum: yellow, suffused pale orange anteriorly, with narrow cream median line, remainder as for *G. conserta*. Scutum: cream, with two pale orange to orange-red wavy lines each side; small lateral prominences between scutum and prescutum, pale cream surrounded with grey-brown; area between scutellum and metascutellum sometimes suffused red. Abdomen: longitudinal median line cream, with orange-red area each side. Genitalia: claspers and aedeagus as in Text-fig. 23. Length of aedeagus: (12 specimens) Extremes 0·252 mm. to 0·267 mm. Forewings: length 2·93 mm. Hindwings: Cu_1 as in Text-fig. 6.

Female: Darker than male, and darker than *G. conserta*. Post-occipital sclerites grey to black. Genal processes black. Wavy lines on scutum, brown to grey, and area lateral to scutellum usually red with pronounced red-brown area. Ventral: Legs: Anterior and median femora black; coxae and trochanters suffused grey; tibiae and tarsi pale to dark grey. Posterior coxae with dark lateral mark; posterior femora, tibiae and tarsi paler than anterior and median. Gular area almost black; mesosternum dark brown to black.

Host-plant: *E. haemastoma* Smith (scribbly gum).



Text-fig. 23.—Aedeagus and claspers of *Glycaspis aggregata*, sp. nov.
Text-fig. 24.—Aedeagus and claspers of *Glycaspis baileyi*, sp. nov.
Text-fig. 25.—Aedeagus and claspers of *Glycaspis imponens*, sp. nov.
Text-fig. 26.—Aedeagus and claspers of *Glycaspis australoraria*, sp. nov.

Type Locality: Somersby, N.S.W., 5 miles along Dog Trap Road from Pacific Highway at Ourimbah.

Types: Holotype male, allotype female, on slide labelled "Somersby, N.S.W., 2 viii 1958, K. M. Moore. From *E. haemastoma*". Slide deposited with AM. Paratypes: 9 slides: Somersby, 2 viii 1958; 6 to AM, 1 to BM, 1 to CS, 1 to FC. 2 slides: Cowan, 25 iii 1960; 1 to AM, 1 to FC. 1 slide: St. Ives, 7 viii 1958; to AM. In alcohol: Cowan, 25 iii 1960, 10 adults to AM. Pinned: Somersby, 18 viii 1958; 5 males, 8 females, to AM; 6 males, 8 females, to CS.

Notes: Eggs: Bright orange; in small or large groups up to approximately 300, near edge of leaf; eggs in these groups are oviposited further apart than are those of *G. conserta*; no eggs were found on the edges of leaves, as were those of *G. conserta*. Lerps: White or yellow; large lerps are usually contiguous and situated along veins on upper or lower leaf-surface; dome-shaped, and with or without filaments. On 25 ix 1958, at Mona Vale, 288 occurred on one leaf.

This species can be separated from *G. conserta* by the darker coloration, and less red suffusion.

GLYCASPIS (GLYCASPIS) FLAVILABRIS (Froggatt) and
GLYCASPIS (GLYCASPIS) NIGRO-CINCTA (Froggatt).

The morphology and coloration of these two species are sufficiently distinct from all other known species of *Glycaspis* to obviate the need, at present, for slides of their genitalia.

(B) Subgenus GLYCASPIS (ALLOGLYCASPIS).

Type Species: *Glycaspis* (*Alloglycaspis*) *baileyi* sp. nov.

Type Locality: Lisarow, New South Wales.

Species contained in this subgenus constitute a heterogeneous group, and various indications of evident morphological affinities are discussed after the descriptions.

Apart from the broad classification adopted here, which is based primarily on the number of antennal rhinaria and secondly on the shape of the lerp (knowledge concerning which is at present limited), an attempt to arrange the species in a correct evolutionary sequence seems inadvisable until the majority of existing species have been collected, and biological details studied.

The presumed evolutionary sequence of the groups containing round lerps, then oval lerps and finally rectangular lerps, has been adopted, with species constructing rectangular lerps as the more recent and specialized group. Species within each group have been arranged in the sequence of their host-plant association, and correlated with Blakely's classification of the eucalypts.

ROUND LERPS.

GLYCASPIS (ALLOGLYCASPIS) BAILEYI, sp. nov.

(Named after Mr. F. M. Bailey of the Forestry Commission of N.S.W., who during 1944 officially reported the occurrence of *Glycaspis* sp. on *Eucalyptus saligna* Smith (Sydney blue-gum) on State Forests.)

General colour: red, or yellow, marked prominently with brown or black. Abdomen always with red medio-dorsal area.

Male: Head: width 0·68 mm.; anterior ocular sclerites brown with inner edges black, but may be all black; occipital sclerites cream, edged black posteriorly; vertex: along suture 0·27 mm., width 0·37 mm.; yellow marked brown or black, or all black; suture black; genal processes: length 0·32 mm.; turquoise or orange on recently emerged specimens, and later with variable amounts of red suffusion; antennae: length 1·68 mm.; segs 1 and 2 brown, seg. 3 grey-brown; each segment towards apex darker, with seg. 5 distally and segs 6 to 10 black. Pronotum: width 0·61 mm.; lateral prominences cream, with depression at bases marked brown; small depressions half-way between median line and lateral margins; brown to black except prominences and small areas each side of median line posteriorly; propleura cream, edged black. Prescutum: lateral ridges black, tipped cream distally; central area cream, narrowing anteriorly;

remainder dark brown to black, narrowly on posterior edge. Scutum: laterally bordered black; broad median stripe and small area near tegulae, yellow; mesopleuron rectangular, with raised prominence yellow; anterior half of dorsal and ventral borders, and anterior suture, narrowly edged brown to black. Scutellum and metascutellum cream, with area between, red. Metanotum: red-brown. Post-metanotum: yellow marked with brown or black; metapleura with suture from tegulae to spiracles, black. Abdomen: Always with red medio-dorsal area on segs 1 to 5; a short, narrow black line each side of anterior border on segs 1 and 2, 2nd seg. with central, transverse black line for width of red area; lines on segs 3 to 5 similar to that on seg. 2; seg. 6 yellow. Genitalia: upper genital plate pale yellow with variable brown to black basal area; lower plate cream with black on antero- and dorso-lateral borders continuing to a point near base of upper plate; claspers and aedeagus as in Text-fig. 24. Length of aedeagus: (150 specimens) Extremes 0·203 mm. to 0·250 mm. Forewing: length 3·07 mm.; posterior half may be suffused red; pterostigma and base of costa suffused white or red. Hindwing: venation colourless, except base of RS pale brown; Cu_1 as in Text-fig. 2. Ventral: Cream; dividing suture of genal processes brown, which may continue to occipital sclerites; brown to black area on postero-lateral angle of metacoxae; anterior and median femora grey on outer edges; tibiae and tarsi brown. Any portion of adults may be suffused with variable amounts of red or turquoise.

Female: General colour as for the male, but red suffusion more intense and black more extensive. Head: width 0·71 mm.; vertex: along suture 0·27 mm., width 0·39 mm.; genal processes: length 0·32 mm.; antennae: length 1·61 mm.; segs 3 to 7 pale brown, seg. 8 distally and segs 9 and 10 black. Pronotum: width 0·63 mm. Abdomen: narrow, central transverse black line on segs 2 to 5; anal aperture cream suffused red, surrounded with red and with broad postero-lateral black band. Genitalia: deflexed; distal prominences yellow. Forewings: length 3·34 mm. Other details are as for the male.

Host-plants: *E. saligna*, *E. robusta* Smith (swamp mahogany), *E. resinifera* Smith (red mahogany).

Type Locality: Lisarow, N.S.W., 1¼ miles along Cut Rock Road from level-crossing.

Distribution: Cloud's Creek S.F., Doyle's River S.F., Moonpar S.F., Bulga S.F., Wyong S.F., Ourimbah S.F., and the Gosford-Wyong area generally.

Types: Holotype male, allotype female, on slide labelled "Lisarow, N.S.W. 20 vi 1960, K. M. Moore. From *E. saligna*". Slide deposited with AM. Paratypes: From *E. saligna*. 4 slides: Lisarow, 20 vi 1960; 1 to each of AM, BM, CS, FC. Remainder to AM, from Lisarow, 8 i 1960, (4); Lisarow, 20 x 1959, (34); Lisarow, 25 xi 1959, (4); Lisarow, 27 viii 1958, (1); Lisarow, 11 viii 1959, (1); Cloud's Creek S.F. 6 v 1959, (10); Doyle's River S.F. 8 v 1959, (7); Moonpar S.F. 4 v 1959, (8); Bulga S.F. 12 v 1959, (12); Bulga S.F. 11 v 1959, (7). From *E. resinifera*. 7 slides: Kincumber, 28 viii 1958, to AM. 6 slides: Wamberal, 2 x 1958, to AM. From *E. robusta*. 7 slides: Wamberal, 2 x 1958, to AM. In alcohol: From *E. saligna*. Lisarow, 20 vi 1960, 200 males and 200 females to each of AM, CS and FC. Remainder to AM; from Bulga S.F. 11 v 1959, 100 adults, and nymphs; Doyle's River S.F. 26 viii 1957, K. G. Campbell, 35 adults, and nymphs; Lisarow, 8 i 1960, and 8 iii 1960, 50 adults, and nymphs; Moonpar S.F. 17 ix 1958, G. Baur, 10 adults, and nymphs; Doyle's River S.F. 8 v 1959, 4 adults, and nymphs; Moonpar S.F. 4 v 1959, 100 adults, and nymphs; Lisarow 26 vi 1958, and 14 vii 1958, 50 adults; Lisarow, 7 viii 1960, 100 adults; Lisarow-Ourimbah, 1958-1959, 1 tube each of nymphs of each instar, and eggs. Pinned: From *E. saligna*. Lisarow, 15 vii 1959, 28 males, 31 females, to AM; 13 males, 15 females to CS. Lisarow, 9 xii 1958, 5 males, 4 females, to AM; 2 males, 2 females to CS. Lisarow, 27 viii 1958, 4 males, 4 females, to AM; 3 males, 3 females to CS. 23 specimens from Ourimbah S.F. 18 xi 1956, Lisarow, 6 vi 1959, Moonpar S.F. 17 ix 1958 G. Baur, to AM. From *E. robusta*. Wamberal, 16 x 1958, 8 to AM. From *E. resinifera*. Kincumber, 28 viii 1958, 4 to AM.

Notes: Lerps: 4 mm. to 5 mm. in diameter; white, round and conical.

Considerable biological data for this species will be given in a separate paper.

Two tubes of adults and nymphs, reared on *E. camaldulensis*, are in AM.

GLYCASPIS (ALLOGLYCASPIS) IMPONENS, sp. nov.

(L. *imponens* = deceiving. Referring to the similarity of this species to *G. baileyi* in coloration, morphology and biology.)

General colour: As for *G. baileyi.*

The description given for *G. baileyi* applies equally as well to *G. imponens*, but the two species are readily separable by: (*a*) The constant association of *G. imponens* with *Eucalyptus propinqua* Deane & Maiden (small-fruited grey gum) and not with the host-plants of *G. baileyi*; (*b*) The structure of the aedeagus of the male genitalia, and the claspers (Text-fig. 25).

Length of aedeagus: (44 specimens) Extremes 0·252 mm. to 0·286 mm.

Type Locality: Kincumber, N.S.W., 1¼ miles along Killcare Road, south from Kincumber.

Distribution: Kincumber, Kurrajong, Wyong S.F.

Types: Holotype male, allotype female, on slide labelled "Kincumber, N.S.W. 23 x 1958, K. M. Moore. From *E. propinqua*". Slide deposited with AM. Paratypes: 8 slides: Kincumber, 23 x 1958, 5 to AM, 1 to each of BM, CS, FC. 5 slides: Kincumber, 29 xii 1958, to AM. 13 slides: Kurrajong, 6 xi 1958, to AM. In alcohol: Kincumber, 23 x 1958, 100 adults to each of AM, CS, FC. Pinned: Kincumber, 12 ix 1958, 6 males, 2 females, to AM.

Notes: The biology of *G. imponens* closely resembles that of *G. baileyi*, the species of closest affinity, and no differences between nymphs or lerps of these species were found.

GLYCASPIS (ALLOGLYCASPIS) AUSTRALORARIA, sp. nov.

(L. *australis* = southern; L. *orarius* = belonging to the coast. Referring to the collection-locality of the type.)

General colour: (Dried specimen) bright green, lightly marked with brown and black; centre of vertex and thorax yellow.

Male: Head: width 0·67 mm.; lemon-yellow; vertex: along suture 0·28 mm., width 0·39 mm.; lemon-yellow, suture very pale brown; lateral extremities of posterior border narrowly marked black; genal processes: length 0·31 mm.; cream, lightly suffused pale brown, internal edges suffused red; antennae: length 1·57 mm.; seg. 1 suffused pink, segs 1 to 6 pale brown, 3 to 6 darker distally, 7 and 8 dark brown with seg. 8 distally and segs 9 and 10 black. Pronotum: width 0·54 mm.; lemon-yellow with a small, longitudinal dark mark at base of each lateral prominence. Prescutum: lemon-yellow; brown-black anteriorly beneath pronotum; lateral margins narrowly black. Scutum: lemon-yellow; antero-lateral borders faintly marked brown; postero-lateral borders more prominently marked black. Scutellum: cream. Metascutellum: cream; brown areas on postero-lateral borders of metanotum and antero-lateral borders of post-metanotum. Abdomen: lemon-yellow; segs 2 to 5 each with a narrow, transverse brown line across the centre. Genitalia: lemon-yellow; narrowly marked pale brown at base and suffused red ventrally; lower plate lemon-yellow on antero-dorsal border; claspers and aedeagus as in Text-fig. 26. Length of aedeagus: (1 specimen) 0·234 mm. Forewings: length 2·39 mm.; pterostigma and base of costa suffused white. Hindwings: Cu_1 as in Text-fig. 4. Ventral: Cream to lemon-yellow; anterior and median legs suffused pale brown.

Host-plant: Collected on *Eucalyptus longifolia* Link & Otto (woolly-butt).

Type Locality: Corrimal, N.S.W., at camping-grounds, Corrimal east.

Types: Holotype male, and nymphs, on slide labelled "Corrimal, N.S.W. 9 x 1958, K. M. Moore; on *E. longifolia*". Slide deposited with AM.

GLYCASPIS (ALLOGLYCASPIS) STRUICIS, sp. nov.

(L. *struix* = a mass of things. Referring to the large population found when collecting the types.)

General colour: yellow to green, sometimes suffused red and with little or no black markings.

Male: Head: width 0·63 mm.; vertex: along suture 0·22 mm., width 0·34 mm.; pale orange; genal processes: length 0·27 mm.; orange, grey along inner edges; antennae: length 1·54 mm.; pale brown, darkening distally; segs 9 and 10 black. Pronotum: width 0·49 mm.; yellow. Prescutum: yellow. Scutum: yellow, with paler median longitudinal stripe. Metanotum: yellow. Abdomen: yellow. Genitalia: pale orange; claspers and aedeagus as in Text-fig. 27. Length of aedeagus: (19 specimens) Extremes 0·193 mm. to 0·218 mm. Forewings: length 2·37 mm. Hindwings: Cu_1 as in Text-fig. 4.

Female: Very similar to male. Occasional specimens with central transverse black lines on abdominal segs 2 to 6. Prescutum and scutum narrowly edged grey, and suture of vertex black; black sometimes on posterior border of vertex.

Host-plant: *Eucalyptus umbellata* (Gaertn.) Domin. (forest red-gum).

Type Locality: Merrylands, N.S.W.

Types: Holotype male, allotype female, nymphs, on slide labelled "Merrylands, N.S.W. 7 xi 1958, K. M. Moore. From *E. umbellata*". Slide deposited with AM. Paratypes: 9 slides: Merrylands, 7 xi 1958; 6 to AM, 1 to each of BM, CS, FC. In alcohol: Merrylands, 7 xi 1958, 70 adults, and nymphs, deposited with AM. Pinned: Merrylands, 7 xi 1958; 3 males, 3 females, to each of AM and CS.

Notes: Eggs: Scattered, singly or in groups of up to 50. Lerps: White, round and conical.

Glycaspis (Alloglycaspis) pratensis, sp. nov.

(L. *pratum* = a meadow; L. *-ensis* = belonging to. Type specimens were collected in an open, meadow-like area.)

General colour: (Dried specimen) pale orange, abdomen sometimes pale green with a few dark markings.

Males: (Dried specimen) Head: width 0·71 mm.; vertex: along suture 0·29 mm., width 0·37 mm.; yellow, suffused pink, suture brown to black; posterior border grey; genal processes: length 0·34 mm.; yellow; antennae: length 1·66 mm.; pale brown, with segs 9 and 10 black. Pronotum: width 0·57 mm.; yellow. Prescutum: yellow edged black anteriorly. Scutum: longitudinal, broad cream stripe; lateral areas yellow, suffused pink. Scutellum and metascutellum cream; area between, rose-red, more intense laterally. Abdomen: transverse, narrow central black stripes on segs 2 to 4; pale orange suffused green. Genitalia: claspers and aedeagus as in Text-fig. 28. Length of aedeagus: (3 specimens) Extremes 0·223 mm. to 0·234 mm. Forewings: length 2·73 mm. Hindwings: Cu_1 as in Text-fig. 4.

Female: As for the male, but orange and black coloration more intense and extensive.

Host-plant: *Eucalyptus amplifolia* Naudin (cumbora or cabbage-gum).

Type Locality: Jilliby, N.S.W.

Types: Holotype male, allotype female, nymphs, on slide labelled "Jilliby, N.S.W. 15 x 1958, K. M. Moore. From *E. amplifolia*". Slide deposited with AM. Paratypes: 3 slides: Jilliby, 15 x 1958, to AM. Pinned: Jilliby, 15 x 1958, 2 males, 2 females, to AM; 1 male, 1 female, to CS.

Notes: Lerps: Round; scattered, scarce; singly, on either side of leaf.

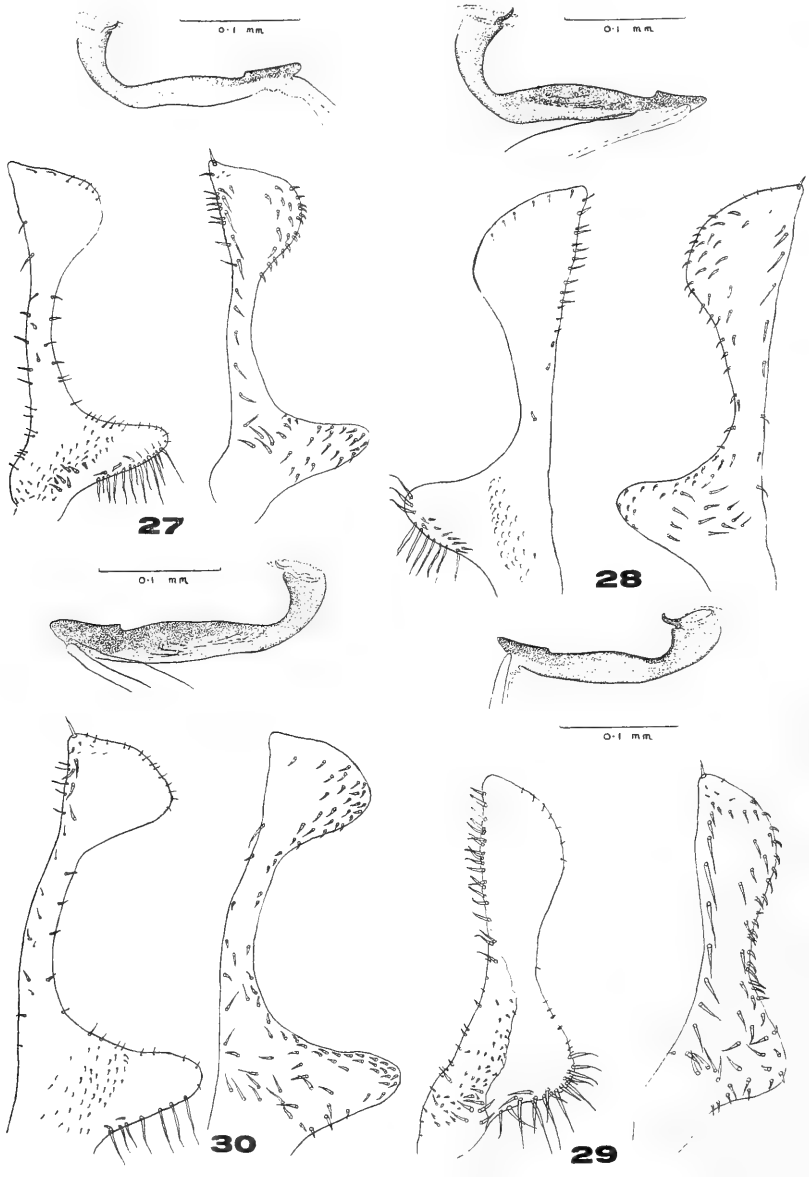
Glycaspis (Alloglycaspis) lactea, sp. nov.

(L. *lacteus* = milky. Referring to the appearance of the lerps.)

General colour: yellow, lightly marked with black and red.

Male: Head: width 0·63 mm.; pale yellow; vertex: along suture 0·24 mm., width 0·37 mm.; pale yellow suffused red anteriorly; median suture pale brown with posterior third black; posterior border black, extending onto post-ocular sclerites; genal processes: length 0·24 mm.; cream suffused pale brown ventrally and on internal edges; antennae: length 1·26 mm.; segs 1 and 2 pale cream, remainder darkening to seg. 8 which is black distally, segs. 9 and 10 black. Pronotum: width 0·51 mm.; pale yellow; anterior edge with small black marks each side, and across bases of prominences. Prescutum: pale yellow; black beneath pronotum, and borders narrowly and faintly black. Scutum: pale yellow; antero-lateral borders faintly and narrowly black; postero-

lateral borders prominently black. Scutellum: pale yellow. Metanotum: pale yellow, suffused pink. Post-metanotum: suffused pink medio-dorsally and small pale brown marks on antero-lateral borders. Abdomen: pale yellow; indistinct, narrow, transverse pale brown lines on segs 3 to 5. Genitalia: upper plate pale yellow with narrow, pale



Text-fig. 27.—Aedeagus and claspers of *Glycaspis struicis*, sp. nov.
Text-fig. 28.—Aedeagus and claspers of *Glycaspis pratensis*, sp. nov.
Text-fig. 29.—Aedeagus and claspers of *Glycaspis lactea*, sp. nov.
Text-fig. 30.—Aedeagus and claspers of *Glycaspis montana*, sp. nov.

brown band around base dorsally; lower plate cream, with narrow black area along anterior border; claspers and aedeagus as in Text-fig. 29. Length of aedeagus: 0·193 mm. Forewings: length 2·29 mm.; suffused white; suffused lightly with brown on apical half. Hindwings: Cu_1 as in Text-fig. 2.

Female: General colour darker than male, with orange on scutum and metascutellum laterally, and abdomen dorsally. Black markings more extensive and intense than on male. Vertex as male but with lateral edges and foveae black. Pronotum with median suture black, and a central brown spot each side, at half. Abdomen with short, narrow transverse black lines surrounded with diffused grey area on segs 2 to 5, and suffused red dorsally. Anal aperture with triangular black area at postero-lateral angles.

Host-plant: Uncertain identification; but either *Eucalyptus blakelyi* Maiden (Blakely's red-gum) or *Eucalytus dealbata* A. Cunn. (tumbledown gum).

Type Locality: Strahorn State Forest (Dubbo Forestry District).

Types: Holotype male, allotype female, on slide labelled "Strahorn S.F. 1 iv 1960, K. M. Moore. From *E. blakelyi* or *E. dealbata*". Slide deposited with AM. Paratypes: In alcohol: Strahorn S.F. 1 iv 1960, 4 males, 1 female, to AM.

Notes: Lerps: Round and more or less dome-shaped.

GLYCASPIS (ALLOGLYCASPIS) MONTANA, sp. nov.

(L. *montanus* = belonging to a mountain. Referring to the collection-locality for this species.)

General colour: As for *G. baileyi* and *G. imponens* except that: there is usually brown suffusion on scutum; claspers are paler in colour and whitish at distal edge; black transverse lines on abdomen are longer and wider; there is less red on dorsal aspect of abdomen, which may be pink, sometimes suffused yellow.

Male: Head: width 0·63 mm.; vertex: along suture 0·22 mm., width 0·37 mm.; genal processes: length 0·27 mm.; antennae: length 1·66 mm.; pale brown proximally, darkening toward distal segs with segs 9 and 10 black. Pronotum: width 0·51 mm. Genitalia: claspers and aedeagus as in Text-fig. 30. Length of aedeagus: (8 specimens) Extremes 0·227 mm. to 0·248 mm. Forewings: length 2·59 mm. Hindwings: Cu_1 as in Text-fig. 2.

Host-plant: *Eucalyptus dunnii* Maiden (Dunn's white-gum).

Type Locality: Along Grafton Road, 10 miles north of Cloud's Creek, N.S.W.

Types: Holotype male, allotype female, nymphs, on slide labelled "Cloud's Creek, N.S.W. 6 v 1959, K. M. Moore. From *E. dunnii*". Slide deposited with AM. Paratypes: 7 slides: Cloud's Ck., 6 v 1959, to AM. 2 slides: Cloud's Ck., October 1958, G. Baur, to AM. In alcohol: Cloud's Ck., 6 v 1959; 20 adults, and nymphs, to AM. Pinned: Cloud's Creek, October 1958, G. Baur; 1 female to AM.

Notes: Lerps, nymphs and general biology similar to *G. baileyi* and *G. imponens*.

GLYCASPIS (ALLOGLYCASPIS) MINUSCULA, sp. nov.

(L. *minusculus* = very small. Referring to the comparatively small size of this species.)

This species was not described prior to being placed on a slide.

The aedeagus cannot be confused with any of the other species examined. Claspers and aedeagus as in Text-fig. 31. Forewings: length 2·17 mm. Hindwings: Cu_1 as in Text-fig. 3.

Host-plant: *Eucalyptus cinerea* F. Muell. (argyle apple).

Type Locality: Along Hume Highway, 26 miles north of Goulburn, N.S.W.

Types: Holotype male, on slide labelled "Goulburn, N.S.W. 23 ii 1959, K. M. Moore. On *E. cinerea*". Slide deposited with AM.

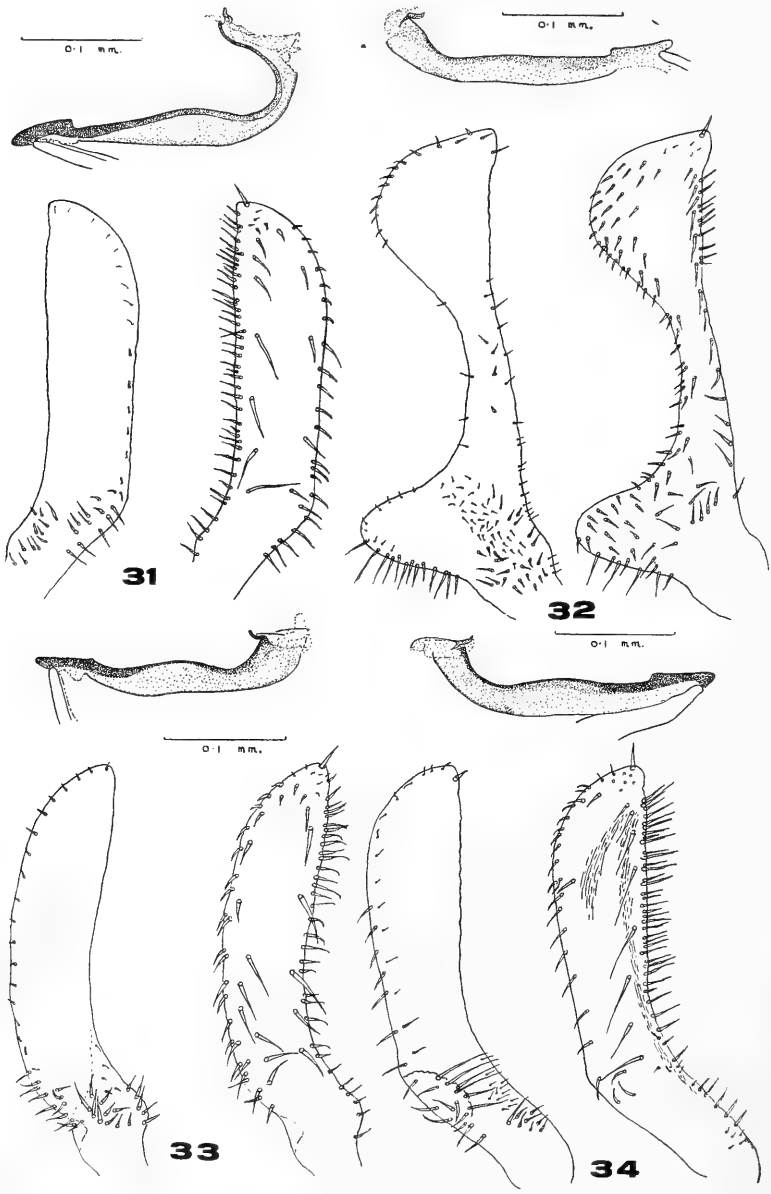
GLYCASPIS (ALLOGLYCASPIS) VELLEROSA, sp. nov.

(N.L. *vellerosus* = woolly, fleecy. Referring to the woolly appearance of the lerps which bear large numbers of filaments on the outer surface.)

General colour: pale green to yellow, suffused reddish-orange.

Male: Head: width 0·73 mm.; vertex: length along suture 0·29 mm., width 0·39 mm.: deep yellow, lightly suffused red; suture black; posterior border prominently marked with black; foveae brown; anterior and lateral borders marked with diffused red-brown; genal processes: length 0·34 mm.; pale yellow, inner edges marked with black;

antennae: length 2·02 mm.; brown, darker distally; segs 9 and 10 black. Pronotum: width 0·59 mm.; yellow, palest medianly; black marks at bases of prominences; anterior edge marked lightly with grey. Prescutum: deep yellow; black apically beneath pronotum, with edges narrowly marked black except posterior border. Scutum: deep



Text-fig. 31.—Aedeagus and claspers of *Glycaspis minuscula*, sp. nov.
Text-fig. 32.—Aedeagus and claspers of *Glycaspis vellerosa*, sp. nov.
Text-fig. 33.—Aedeagus and claspers of *Glycaspis suavis*, sp. nov.
Text-fig. 34.—Aedeagus and claspers of *Glycaspis rivalis*, sp. nov.

yellow suffused red, with pale yellow median longitudinal line; posterior border prominently edged black. Metanotum: Scutellum and metascutellum pale yellow, with area between suffused rose-red which extends laterally and is edged posteriorly with grey. Post-metanotum suffused rose-red, with black antero-laterally. Abdomen: yellow,

with two distal segments suffused red; short grey to black central transverse lines on segs 2 to 6. These marks may be very faint on some specimens. Genitalia: yellow suffused red; anterior border of lower plate edged narrowly with black; claspers and aedeagus as in Text-fig. 32. Length of aedeagus: (5 specimens) Extremes 0·223 mm. to 0·245 mm. Forewings: length 2·88 mm.; venation pale brown, intensifying to base of wings. Hindwings: Cu_1 as in Text-fig. 4.

Female: Red suffusion usually more extensive than on the male. Dark lines on abdomen usually brown, and more extensive, often on a dark red-brown background. Anal aperture with a broad triangular mark at each postero-lateral corner.

Host-plant: Uncertain identification, but either *Eucalyptus bosistoana* F. Muell. (Bosisto's box), or *Eucalyptus hemiphloia* F. Muell. (grey box).

Type Locality: Prospect, N.S.W., ¾ mile west of township.

Types: Holotype male, allotype female, nymphs, on slide labelled "Prospect, N.S.W. 1 ix 1958, K. M. Moore. From *E. bosistoana* or *E. hemiphloia*". Slide deposited with AM. Paratypes: 5 slides: Prospect, 1 ix 1958, 4 to AM, 1 to CS. In alcohol: Prospect, 1 ix 1958, 15 adults, and nymphs, to AM. Pinned: Prospect, 1 ix 1958, 3 males, 3 females, to AM; 2 males, 3 females, to CS.

Notes: Lerps: Round, white, very large, up to 6·5 mm. in diameter and 6 mm. in height; filaments appear fine in comparison to size of lerp.

Glycaspis (Alloglycaspis) suavis, sp. nov.

(L. *suavis* = sweet. Referring to the lerps of this species.)

General colour: yellow, lightly marked with black. Abdomen turquoise or yellow, with black bands. Metanotum always with rose-pink area near each postero-lateral angle of scutellum.

Male: Head: width 0·61 mm.; yellow; vertex: along suture 0·24 mm., width 0·37 mm.; median suture very pale brown; posterior border black, which extends on to post-ocular sclerites; foveae indistinctly black; genal processes: length 0·20 mm.; yellow; antennae: length 0·93 mm.; suffused brown, darkening distally, seg. 9 dark brown, seg. 10 black. Pronotum: width 0·54 mm.; yellow; indistinct dark mark below each prominence; pale brown central spot at half, each side of median line. Prescutum: yellow; black anteriorly beneath pronotum, and anterior half of lateral borders. Scutum: yellow; antero-lateral borders faintly and narrowly black; postero-lateral borders more prominently black. Scutellum: pale yellow. Metanotum: rose-pink area with brown base, posterior to each postero-lateral corner of scutellum. Post-metanotum: faintly suffused pink, and antero-lateral borders lightly and narrowly black. Abdomen: yellow or green; indistinct transverse central grey lines on segs 2 to 4. Genitalia: upper plate cream; lower plate with grey area at antero-dorsal corner near base of upper plate; claspers and aedeagus as in Text-fig. 33. Length of aedeagus: (2 specimens) 0·227 mm. and 0·218 mm. Forewings: length 2·04 mm.; rounded apically. Hindwings: Cu_1 as in Text-fig. 3.

Female: General colour more lemon-yellow than on male, and dark markings more extensive and intense. Suffused grey transverse lines on abdomen are larger, and on segs 2 to 5 are paler and narrower medianly, than on male. Abdomen always bright green.

Host-plant: *Eucalyptus populifolia* Hook. f. (bimble box).

Type Locality: Strahorn State Forest (Dubbo Forestry District), N.S.W.

Types: Holotype male, allotype female, on slide labelled "Strahorn S.F. 1 iv 1960, K. M. Moore. From *E. populifolia*". Slide deposited with AM. Paratypes: 1 slide: Strahorn S.F. 1 iv 1960, to AM. In alcohol: Strahorn S.F. 1 iv 1960, 25 adults to AM.

Notes: Eggs: In groups, anywhere on leaves. Lerps: Round and conical, usually with filaments; found on larger leaves only.

Glycaspis (Alloglycaspis) rivalis, sp. nov.

(L. *rivalis* = a rival. Referring to apparent competition of this species with others of the same genus on the host-plant.)

General colour: pale to dark brown; considerable variation in intensity of coloration on specimens from different areas. Intergradation in coloration with *G. permista.*

Male: (Dark specimen) Head: width 0·66 mm.; vertex, along suture 0·22 mm., width 0·37 mm.; deep cream bordered narrowly brown-black; suture black, edged widely dark brown posteriorly, narrowing anteriorly; foveae brown-black; genal processes: length 0·32 mm.; suffused red; antennae: length 1·56 mm.; pale brown darkening distally; segs 9 and 10 black. Pronotum: width 0·59 mm.; dark brown; suture black; prominences cream. Prescutum: dark brown to black with posterior median area cream. Scutum: narrowly edged black; dark brown lateral areas; wide longitudinal median stripe pale brown, often with a narrow median longitudinal line brown-black. Scutellum: cream, marked dark brown posteriorly. Metascutellum: dark brown; area between, cream medianly, dark brown laterally. Post-metanotum: dark brown to black. Abdomen: cream, suffused red; wide black transverse lines on segs 2 to 6. Genitalia: base of upper plate dark brown; lower plate with dorsal and anterior edges brown-black; claspers with dark area near distal end; claspers and aedeagus as in Text-fig. 34. Length of aedeagus: (19 specimens) Extremes 0·216 mm. to 0·248 mm. Forewings: length 2·66 mm. Hindwings: Cu_1 as in Text-fig. 3. (Pale specimen) Dark brown areas reduced, or may be absent except on edges of vertex, and suture, suture of pronotum, edges of prescutum and scutum, and edges of post-metanotum. Transverse lines on abdominal segments may be greatly reduced. Any part may be suffused red.

Female: Abdomen usually orange before feeding, turning to red. Whole adult often red. Dark marks on dorsal aspect of abdomen usually more extensive than on male.

Host-plant: *Eucalyptus paniculata* Smith (grey ironbark).

Type Locality: Ourimbah State Forest (Section 1, Compartment 3).

Types: Holotype male, allotype female, on slide labelled "Ourimbah S.F., 20 xi 1958, K. M. Moore. From *E. paniculata*". Slide deposited with AM. Paratypes: 7 slides: Ourimbah S.F. 20 xi 1958, 5 to AM, 1 to BM, 1 to CS. 5 slides: Wamberal, 26 xi 1958, to AM. 2 slides: Wamberal, 15 x 1959, to AM. In alcohol: Ourimbah S.F. 20 xi 1958, 150 adults, and nymphs, to AM. Ourimbah S.F. 8 ix 1960, 40 adults to CS. Remainder to AM from Kincumber, 7 ix 1960, (25 adults); Kincumber 15 vii 1960, (10 adults); Kincumber, 27 xi 1958, (120 adults, and nymphs); Wamberal, 16 vi 1960, (30 adults); Wamberal, 15 x 1959, (50 adults, and nymphs); Wamberal, 26 xi 1958, (10 adults, and nymphs); Wyong S.F. 7 xii 1958, (100 adults, and nymphs); Lisarow, 21 iii 1959, (50 adults, and nymphs). Pinned: Ourimbah S.F. 6 viii 1958, 5 males, 2 females, to AM; 4 males, 1 female, to CS; Ourimbah S.F. 10 ix 1958, 7 males, 4 females, to AM; 6 males, 3 females, to CS; Ourimbah S.F. 14 xi 1956, 1 female to AM; Kincumber, 28 viii 1958, 2 males, 6 females, to AM; Wyong S.F. 17 xii 1958, 5 males, 4 females, to AM; 5 males, 3 females, to CS.

Notes: Lerps: Round, white, conical; about 4 mm. in diameter. Nymphs: Dark in last instar; similar to those of *G. baileyi*, but not as dark.

Glycaspis (Alloglycaspis) pilata, sp. nov.

(L. *pilatus* = thick, dense. Referring to large numbers of lerps found on this host.)

General colour: similar in general markings to *G. rivalis*, the description of which is the same as for this species. Coloration variable.

Male: Head: width 0·66 mm.; vertex: along suture 0·22 mm., width 0·37 mm.; cream, prominently edged black; suture, and usually on vertex from suture to foveae and to posterior border, black; genal processes: length 0·27 mm.; suffused red; antennae: length 1·51 mm.; brown, darkening to distal end; segs 7 to 10 black. Pronotum: width 0·57 mm.; brown-black except prominences. Prescutum: as *G. rivalis*. Scutum: as *G. rivalis*; area between scutellum and metascutellum orange-red. Remainder as *G. rivalis*. Genitalia: claspers and aedeagus as in Text-fig. 35. Length of aedeagus: (6 specimens) Extremes 0·236 mm. to 0·263 mm. Forewings: length 2·59 mm. Hindwings: Cu_1 as in Text-fig. 3. Adults may be lightly marked with brown only.

Host-plant: *Eucalyptus paniculata.*

Type Locality: Kurrajong, N.S.W. (Bell-bird Corner, on Bell Road).

Types: Holotype male, on slide labelled "Kurrajong, N.S.W. 25 ix 1959, K. M. Moore. From *E. paniculata*". Slide deposited with AM. Paratypes: 5 slides: Kurrajong, 25 ix 1959, to AM. In alcohol: Kurrajong, 27 viii 1960, 40 adults to AM.

Notes: Lerps: Round and conical.

Glycaspis (Alloglycaspis) mannifera, (Froggatt).

The aedeagus and claspers of a co-type of *Glycaspis mannifera* (Froggatt) are given in Text-fig. 36.

As the lerps of this species are not known and the identity of the host-plant is uncertain, the figures have been given here so that it may be correctly placed when its biology is known.

OVAL LERPS.

Adults of this group bear a single rhinarium on each of antennal segments 4, 5, 6, 8 and 9, as do those constructing flat or round lerps, and are considered to be the most recent of those three groups in evolutionary development. Oval lerps are most similar in shape to the rectangular lerps.

Glycaspis (Alloglycaspis) ignea, sp. nov.

(L. *igneus* = fiery. Referring to the very quick movements of the nymphs.)

General colour: bright turquoise or green on abdomen and thorax; sometimes yellow or orange, lightly marked with black; there is considerable variation in coloration in this species.

Male: Head: width 0·66 mm.; vertex: length 0·27 mm., width 0·34 mm.; yellow, suffused red; suture black, foveae brown-black; posterior border marked with black; genal processes: length 0·29 mm.; suffused red, internal edges darkly marked; antennae: length 1·80 mm.; pale brown proximally, darkening distally; seg. 6 black apically, segs 7 to 10 black. Pronotum: width 0·54 mm.; yellow; anterior edge black; black marks at bases of prominences. Prescutum: yellow; black anteriorly, to beyond pronotum and narrowly edged black, except posterior border. Scutum: width 0·59 mm.; yellow median stripe; suffused red laterally; postero-lateral edges marked with black, most prominently near scutellum. Scutellum and metascutellum yellow, with area between rose-red, which extends laterally and is suffused with black. Post-metanotum: pink to red with a central anterior black spot, and anterior borders black transversely. Abdomen: yellow suffused red, palest medianly; prominent black transverse lines on segs 2 to 5. Genitalia: upper plate red, base indistinctly marked grey; lower plate cream, with anterior border marked with black; claspers suffused pink; claspers and aedeagus as in Text-fig. 37. Length of aedeagus: (16 specimens) Extremes 0·223 mm. to 0·239 mm. Forewings: 2·61 mm.; suffused pale honey-colour, apically. Hindwings: Cu_1 as in Text-fig. 2.

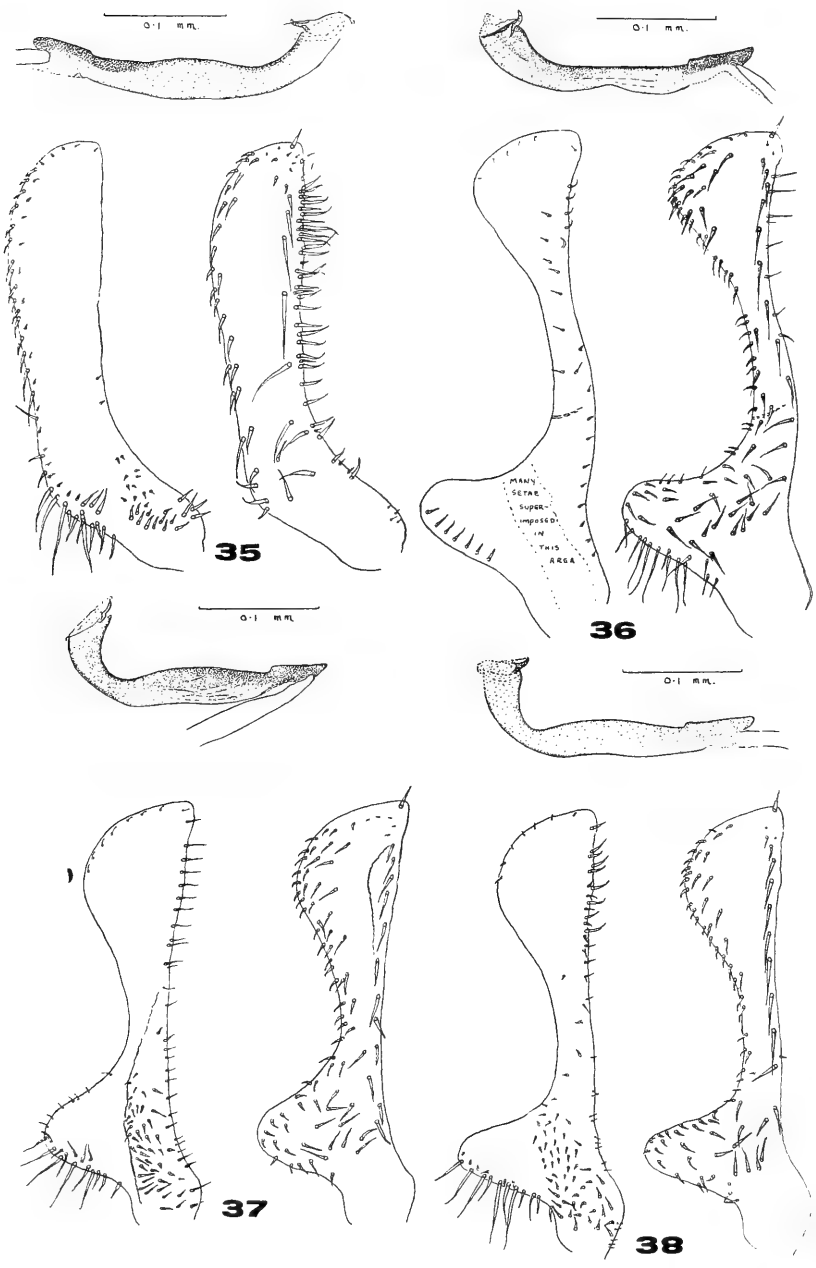
Female: Abdomen often rose-red dorsally, or various amounts of red more extensive than on male. Black more intense and extensive than on the male, except on abdomen. Wings more darkly suffused honey-colour than on the male.

Host-plant: *Eucalyptus deanei* Maiden (Deane's gum).

Type Locality: Ourimbah State Forest, Section 1, Compartment 3.

Types: Holotype male, allotype female, on slide labelled "Ourimbah S.F. 2 ix 1958, K. M. Moore. From *E. deanei*". Slide deposited with AM. Paratypes: 11 slides: Ourimbah S.F. 2 ix 1958, 8 to AM, 1 to each of BM, CS, FC. In alcohol: Ourimbah S.F. 6 vii 1960, 130 adults to CS; Ourimbah S.F. 6 vii 1960, 100 adults to FC. Remainder to AM, all from Ourimbah S.F., 18 iii 1959, (3 adults and nymphs); 20 xi 1958, (2 adults); 21 iv 1959 (30 adults); 19 vi 1959 (20 adults); 6 vii 1960 (100 adults); 2 ix 1958 (30 adults and nymphs). Pinned: Ourimbah S.F. 2 ix 1958, 6 males, 4 females, to each of AM and CS.

Notes: Lerps: Round or oval.



Text-fig. 35.—Aedeagus and claspers of *Glycaspis pilata*, sp. nov.
Text-fig. 36.—Aedeagus and claspers of *Glycaspis mannifera* (Froggatt).
Text-fig. 37.—Aedeagus and claspers of *Glycaspis ignea*, sp. nov.
Text-fig. 38.—Aedeagus and claspers of *Glycaspis oraria*, sp. nov.

GLYCASPIS (ALLOGLYCASPIS) ORARIA, sp. nov.

(L. *orarius* = belonging to the coast. Referring to the collection-locality of the types.)

General colour: (Dried specimen) green, yellow-green or yellow, with faint dark markings.

Male: Head: width 0·68 mm.; vertex: along suture 0·29 mm., width 0·39 mm.: yellow; foveae pale brown, small; suture dark on posterior half only; a small black line in centre of each side of posterior border; genal processes: length 0·37 mm.; cream, suffused brown on inner edges; antennae: length 1·85 mm.; pale brown, darkening distally, with segs 9 and 10 black. Pronotum: width 0·54 mm.; small black line each side on anterior edge opposite to the similar lines on border of vertex; indistinct pale brown marks at bases of prominences. Prescutum: yellow; black at apex beneath pronotum; antero- and postero-lateral edges, narrowly black. Scutum: yellow with cream medio-dorsal area; lateral borders narrowly edged black, prominently black near scutellum; rose-pink areas near posterior corners of scutellum. Scutellum, metascutellum and area between, cream. Metanotum: yellow. Abdomen: yellow, with thin grey transverse central lines, usually on segs 2 to 5. Genitalia: yellow, with base of upper plate suffused grey; lower plate with small black area at corner of anterior and upper edges; claspers and aedeagus as in Text-fig. 38. Length of aedeagus: (5 specimens) Extremes 0·232 mm. to 0·248 mm. Forewings: 2·83 mm.; venation cream, to pale brown at base of wings. Hindwings: Cu_1 as in Text-fig. 4.

Female: Black markings more intense than on male.

Host-plant: Identification uncertain, but probably a hybrid of *Eucalyptus robusta* Smith (swamp mahogany) × *Eucalyptus resinifera* Smith (red mahogany).

Type Locality: Mona Vale, N.S.W., 1 to 2 miles west of Mona Vale, along St. Ives Road.

Types: Holotype male, allotype female, on slide labelled "Mona Vale, N.S.W. 25 ix 1958, K. M. Moore. From *E. robusta* × *E. resinifera*". Slide deposited with AM. Paratypes: 5 slides: Mona Vale, 25 ix 1958, to AM. 5 slides: Kincumber, 29 xii 1958. to AM. In alcohol: Mona Vale, 25 ix 1958, 5 adults, to AM. Pinned: Kincumber, 29 xii 1958, 2 males, 2 females, to AM. Mona Vale, 24 ix 1958, 1 male, 3 females, to AM.

Notes: Lerps: Round, or tend to be oval; white to yellow; occur singly, or contiguous, and with or without filaments.

GLYCASPIS (ALLOGLYCASPIS) CONVALLARIA, sp. nov.

(N.L. *convallarius* = pertaining to a valley. The types were collected in a broad, savannah valley.)

General colour: yellow-green, sometimes lightly marked with black.

Male: Head: width 0·66 mm.; vertex: along suture, 0·29 mm., width 0·34 mm.; genal processes: length 0·34 mm.; dark along inner edges; antennae: length 1·85 mm.; suffused pale brown, darkening distally; segs 9 and 10 black. Pronotum: width 0·63 mm. Abdomen: dark marks absent. Genitalia: claspers and aedeagus as in Text-fig. 39. Length of aedeagus: (3 specimens) Extremes 0·259 mm. to 0·267 mm. Forewings: length 2·68 mm. Hindwings: Cu_1 as in Text-fig. 4.

Female: Larger than the male, sometimes with small dark medio-dorsal marks on abdominal segs 2 to 5; prescutum may be black apically beneath pronotum.

Host-plant: *E. blakelyi*.

Type Locality: 10 miles south-east of Breeza, along Quirindi Road.

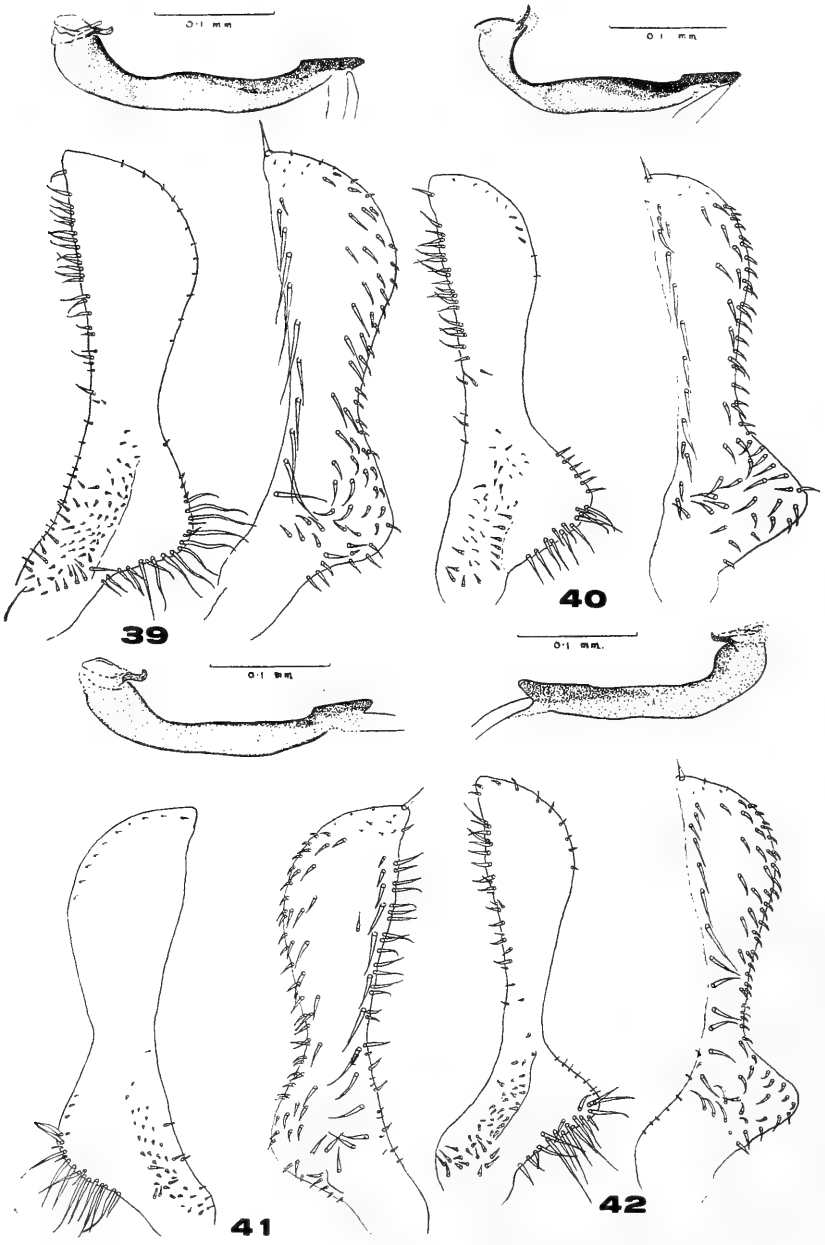
Types: Holotype male, allotype female, nymph, on slide labelled "Breeza, N.S.W. 13 x 1960, K. M. Moore. From *E. blakelyi*". Slide deposited with AM. Paratypes: 2 slides: Breeza, 13 x 1960, to AM.

Notes: Some lerps tend to be oval.

GLYCASPIS (ALLOGLYCASPIS) AMNICOLA, sp. nov.

(L. *amnicola* = one that dwells by a river. Referring to the occurrence of this species along the inland rivers of N.S.W.)

General colour: pale yellow, suffused orange.



Text-fig. 39.—Aedeagus and claspers of *Glycaspis convallaria*, sp. nov.
Text-fig. 40.—Aedeagus and claspers of *Glycaspis amnicola*, sp. nov.
Text-fig. 41.—Aedeagus and claspers of *Glycaspis locaridensis*, sp. nov.
Text-fig. 42.—Aedeagus and claspers of *Glycaspis kurrajongensis*, sp. nov.

Male: Head: width 0·68 mm.; vertex: along suture 0·27 mm., width 0·39 mm.; orange, with suture and the centre of each side of the posterior edge, black; genal processes: length 0·34 mm.; suffused pale orange, with inner edges dark brown; antennae: length 1·61 mm.; pale brown proximally, to dark brown distally, with segs 9 and 10 black. Pronotum: width 0·61 mm.; cream, suffused orange; dark marks at bases of cream prominences; centre of each side of anterior edge black, which is placed opposite to the corresponding black marks on posterior edge of vertex. Prescutum: cream, suffused orange; borders faintly and narrowly black; apex to beyond pronotum, black. Scutum: orange, with broad longitudinal median stripe cream; edged faintly with black, but prominently near scutellum. Scutellum and metascutellum cream; area between, rose-red lightly marked with black on anterior edges. Metanotum: orange, with narrow black lines each side of metascutellum. Abdomen: orange. Genitalia: upper plate suffused orange; lower plate cream with part of anterior border marked with black; claspers and aedeagus as in Text-fig. 40. Length of aedeagus: (1 specimen) 0·227 mm. Forewings: length 3·05 mm. Hindwings: Cu_1 as in Text-fig. 4.

Host-plant: *Eucalyptus camaldulensis* Dehn. (Murray red-gum).

Type Locality: Tocumwal, N.S.W.

Types: Holotype male on slide labelled "Tocumwal, N.S.W. 10 ii 1959, K. G. Campbell. From *E. camaldulensis*". Slide deposited with AM. Paratypes: 2 slides: Tocumwal, 10 ii 1959, K. G. Campbell; to AM. In alcohol: Millewa S.F. v 1959, K. G. Campbell, 1 male and nymphs to AM.

Notes: Eggs: Usually singly, on or near to edge of leaf. Lerps: Round, but larger lerps oval (approx. 4·6 mm. × 3·7 mm.); filaments usually present.

Glycaspis (Alloglycaspis) locaridensis, sp. nov.

(L. *locus* = a place; L. *aridus* = dry; L. *-ensis* = belonging to. The type locality is in a comparatively dry area.)

General colour: (Live specimens) bright green, with vertex, prescutum and scutum suffused yellow; very few dark markings. Pale yellow in alcohol.

Male: Head: width 0·71 mm.; vertex: along suture 0·27 mm., width 0·39 mm.; genal processes: length 0·34 mm.; projecting slightly inwards at tips; suffused dark grey along internal edges; antennae: length 1·59 mm.; suffused pale brown, slightly darker distally, with seg. 9 dark brown and seg. 10 black. Pronotum: width 0·57 mm. Genitalia: claspers and aedeagus as in Text-fig. 41. Length of aedeagus: (2 specimens) 0·256 mm., 0·243 mm. Forewings: length 2·51 mm.; suffused honey-colour; pterostigma and base of costa suffused white. Hindwings: Cu_1 as in Text-fig. 4.

Female: As the male, but slightly deeper in colour.

Host-plant: *E. populifolia.*

Type Locality: Strahorn State Forest (Dubbo Forestry District).

Types: Holotype male, allotype female, on slide labelled "Strahorn S.F. i iv 1960, K. M. Moore. From *E. populifolia*". Slide deposited with AM. Paratypes: 1 slide: Strahorn S.F. 1 iv 1960, to AM. In alcohol: Strahorn S.F. 1 iv 1960, 1 female to AM.

Notes: Eggs: Occur singly; on either side of leaf and in any position on leaf. Lerps: Mainly on young foliage. Small lerps round, but oval during late instars; filaments numerous during all instars.

Glycaspis (Alloglycaspis) kurrajongensis, sp. nov.

(L. *-ensis* = belonging to. Referring to the type locality.)

General colour: cream, lightly marked with black.

Male: Head: width 0·61 mm.; vertex: along suture 0·22 mm., width 0·32 mm.; suffused orange; foveae grey to black, suture black, edges sometimes suffused grey; posterior edge black; genal processes: length 0·29 mm.; suffused red; antennae: length 1·49 mm.; pale brown proximally, darkening towards distal end with segs 7 to 10 black. Pronotum: width 0·49 mm.; cream suffused orange-red medianly; foveae grey which extends to posterior border; prominences cream edged black posteriorly; anterior border prominently black. Prescutum: yellow, suffused orange-red; borders lightly

marked with black. Scutum: orange-red, narrowly edged black, with broad, cream longitudinal median stripe. Scutellum and metascutellum cream, with area between orange-red and laterally brown, suffused red. Abdomen: orange-red, broad transverse black lines on segs 2 to 6. Genitalia: cream; upper plate black at base; lower plate black at antero-dorsal corners; claspers and aedeagus as in Text-fig. 42. Length of aedeagus: (17 specimens) Extremes 0·200 mm. to 0·216 mm. Forewings: length 2·68 mm.; faintly suffused orange-red near apex. Hindwings: Cu_1 as in Text-fig. 4.

Female: Darker than the male.

Host-plant: *E. paniculata.*

Type Locality: Kurrajong, N.S.W. (At Bell-bird Corner, on Bell Road.)

Types: Holotype male, allotype female (taken *in copula*), on slide labelled "Kurrajong, N.S.W. 25 ix 1959, K. M. Moore. From *E. paniculata*". Slide deposited with AM. Paratypes: 8 slides: Kurrajong, 25 ix 1959, 5 to AM, 1 to CS, 1 to BM, 1 to FC. In alcohol: Kurrajong, 27 viii 1960, 35 adults to AM.

Notes: Lerps: Oval.

This species is similar in coloration to *G. permista*, sp. nov.

Glycaspis (Alloglycaspis) permista, sp. nov.

(L. *permistus* = mixed, confused. Referring to the confusing of this with similar species.)

General colour: orange-red marked with black. Intergradation in coloration with that of *G. rivalis* occurs.

Male: Head: width 0·63 mm.; vertex: along suture 0·29 mm., width 0·34 mm.; suffused red; suture, foveae and posterior edge, black; grey suffusion posterior to foveae; antennae: length 1·63 mm.; proximal half, pale brown; distal half, dark brown; segs 8 to 10 black. Pronotum: width 0·54 mm.; suture black; dark grey suffusion except on prominences which are cream; suffused red. Prescutum: darkest anteriorly, and with variable grey suffusion; edged black. Scutum: broad median stripe, yellow; lateral areas orange-red lightly suffused grey; edges narrowly black, prominently black near scutellum. Scutellum and metascutellum cream; area between suffused rose-red with lateral areas brown, suffused red. Post-metanotum: brown to black. Abdomen: rose-red; prominent, wide brown transverse lines on segs 2 to 5, and usually on 6. Genitalia: dark at base of upper plate, and anterior corners of lower plate; claspers and aedeagus as in Text-fig. 43. Length of aedeagus: (5 specimens) Extremes 0·214 mm. to 0·225 mm. Forewings: length 2·73 mm. Hindwings: Cu_1 as in Text-fig. 4.

Female: Similar to male, but with lines on abdomen more intense and extensive.

Host-plant: *E. paniculata.*

Type Locality: Wamberal, N.S.W.

Types: Holotype male, allotype female, on slide labelled "Wamberal, N.S.W. 16 vi 1960, K. M. Moore. From *E. paniculata*". Slide deposited with AM. Paratypes: 2 slides: Wamberal, 16 vi 1960, to AM. In alcohol: All to AM, from Wamberal, 16 vi 1960, (100 adults); Ourimbah S.F. 8 ix 1960, (15 adults); Kincumber, 18 vii 1960, (50 adults); Kincumber, 7 ix 1960, (50 adults). Pinned: Ourimbah S.F. 6 viii 1958, 1 male, 2 females, to AM. Kincumber, 28 viii 1958, 1 male, 4 females, to AM.

Notes: Lerps: There is considerable variation from round to oval, in the shapes of lerps of *G. permista.*

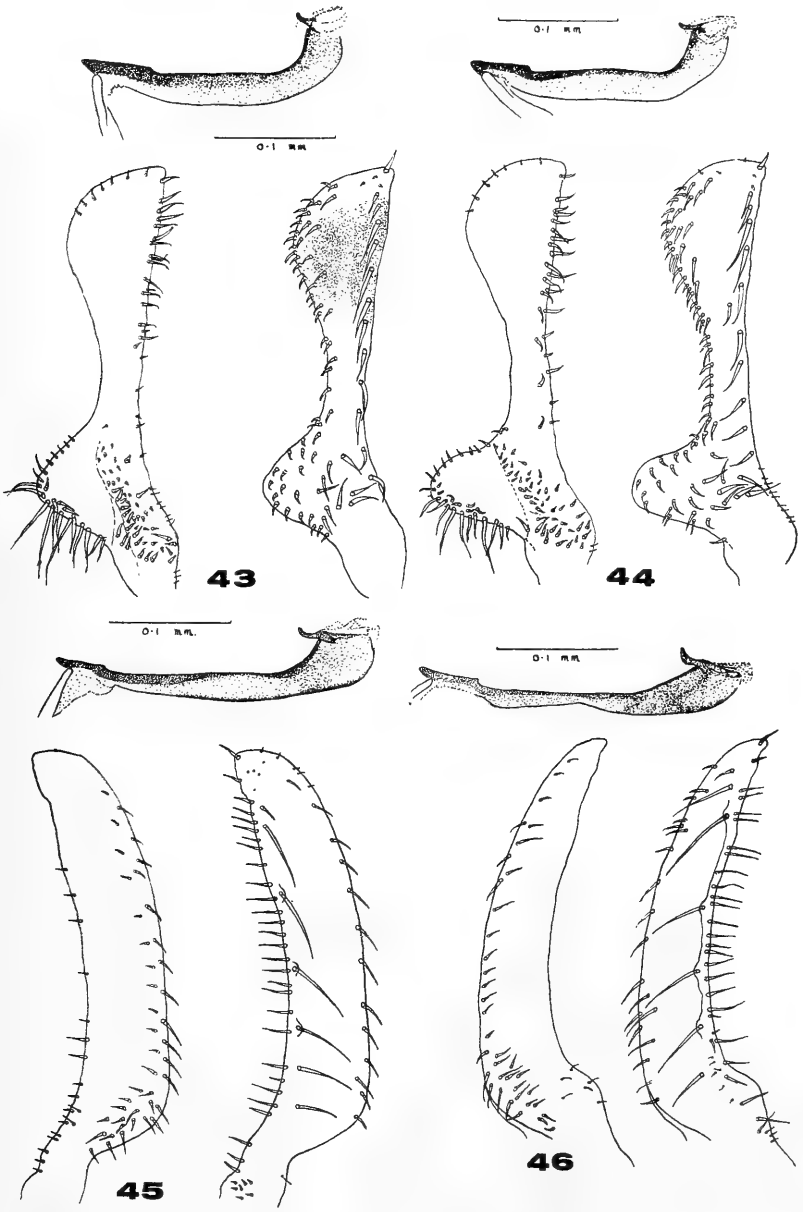
This species can be separated from *G. rivalis* which occurs on the same host, by the absence of brown on scutum, and by the structure of the claspers and aedeagus; and can be separated from *G. mellialata*, sp. nov., which also occurs on the same host, by the paler coloration of the latter species and the structure of the claspers and aedeagus.

Glycaspis (Alloglycaspis) mellialata, sp. nov.

(L. *mel* = honey; L. *alatus* = winged. Referring to the colour of the wings of this species.)

General colour: yellow, lightly marked with grey to black; wings suffused honey-colour.

Male: Head: width 0·61 mm.; vertex, along suture 0·24 mm., width 0·32 mm.; yellow, with foveae pale brown and suture sometimes faintly brown; posterior edge often pale brown; genal processes: length 0·29 mm.; pale yellow, sometimes suffused



Text-fig. 43.—Aedeagus and claspers of *Glycaspis permista*, sp. nov.
Text-fig. 44.—Aedeagus and claspers of *Glycaspis mellialata*, sp. nov.
Text-fig. 45.—Aedeagus and claspers of *Glycaspis mirabilis*, sp. nov.
Text-fig. 46.—Aedeagus and claspers of co-type male of *G. granulata* (Froggatt).

pink; antennae: length 1·80 mm.; pale brown, darkening distally; segs 9 and 10 black. Pronotum: width 0·51 mm.; sometimes lightly marked with brown. Prescutum: apex and anterior edges usually suffused grey. Scutum: longitudinal cream stripe; lateral areas rose-red lightly edged brown. Scutellum and metascutellum cream; area between.

suffused pink and laterally pink suffused pale brown. Abdomen: usually suffused red, with faint brown lines on segs 2 and 3, but often no lines present. Genitalia: pale brown at base of upper plate and anterior corner of lower plate; claspers and aedeagus as in Text-fig. 44. Length of aedeagus: (7 specimens) Extremes 0·203 mm. to 0·225 mm. Forewings: length 2·44 mm.; suffused honey-colour. Hindwings: Cu_1 as in Text-fig. 4.

Female: As male, but with abdomen bright red; lines indistinct on segs 3 to 5.

Host-plant: *E. paniculata.*

Type Locality: Wyong S.F. (Newcastle Forestry District: Wyong subdistrict) near eastern boundary of Compartment 13.

Types: Holotype male, allotype female, on slide labelled "Wyong S.F. 12 viii 1958, K. M. Moore. From *E. paniculata*". Slide deposited with AM. Paratypes: 3 slides: Wyong S.F. 12 viii 1958, to AM. In alcohol: All to AM; from Wyong S.F. 12 viii 1958, (35 adults); Ourimbah S.F. 20 xi 1958, (9 adults); Wamberal, 25 xi 1958, (13 adults, and nymphs); Kincumber, 27 xi 1958, (8 adults, and nymphs). Pinned: Wyong S.F. 17 xii 1958, 1 male, 1 female to AM; Kincumber, 28 viii 1958, 1 male to AM.

Notes: Lerps: Oval.

RECTANGULAR LERPS.

This group at present contains three species only, and adults bear a rhinarium on each of antennal segments 4, 6, 8 and 9, which suggests that these species are of the most recent development within the genus *Glycaspis.*

GLYCASPIS (ALLOGLYCASPIS) MIRABILIS, sp. nov.

(L. *mirabilis* = strange. Referring to the strange shape of lerps of this species.)

General colour: Yellow or turquoise, lightly marked with grey or black; sometimes grey on internal edges of genal processes only.

Male: (Pinned specimens) Head: width 0·68 mm.; vertex: along suture 0·29 mm., width 0·34 mm.; yellow, with foveae and central area along suture, grey to black; genal processes: length 0·34 mm.; yellow; may be green or turquoise distally; antennae: length 1·95 mm.; pale brown with segs 9 and 10 black. Pronotum: width 0·51 mm.; cream, suffused green, with central longitudinal dark area. Prescutum: brown-black. Scutum: broad, median, yellow longitudinal stripe; red lateral areas; posterior border with dark marks contiguous to scutellum. Scutellum, metascutellum and area between, brown-black, red laterally. Abdomen: greenish-yellow; indistinct transverse lines on segs 2 to 5. Genitalia: yellow; claspers and aedeagus as in Text-fig. 45. Length of aedeagus: (14 specimens, Lisarow) Extremes 0·265 mm. to 0·299 mm.; (3 specimens, Cloud's Creek) 0·261 mm. to 0·274 mm. Forewings: length 2·71 mm. Hindwings: Cu_1 as in Text-fig. 3.

Female: Similar to male, but with dark markings more extensive and intense.

Host-plant: *E. saligna.*

Type Locality: Lisarow, N.S.W., 1¼ miles along Cutrock Road from level-crossing.

Types: Holotype male, allotype female, nymphs, on slide labelled "Lisarow, N.S.W. 18 ix 1958, K. M. Moore. From *E. saligna*". Slide deposited with AM. Paratypes: 11 slides: Lisarow, 18 ix 1958, 8 to AM, 1 to BM, 1 to CS, 1 to FC. 2 slides: Lisarow, 3 xii 1958, to AM. 5 slides: Cloud's Creek S.F. 6 v 1959, to AM. Pinned: Lisarow, 18 ix 1958, 2 males, 2 females to AM; 2 males, 3 females to CS.

Notes: Lerps: Rectangular; 5 mm. × 3·5 mm. (last instar). Exuviae often attached to outside of lerp.

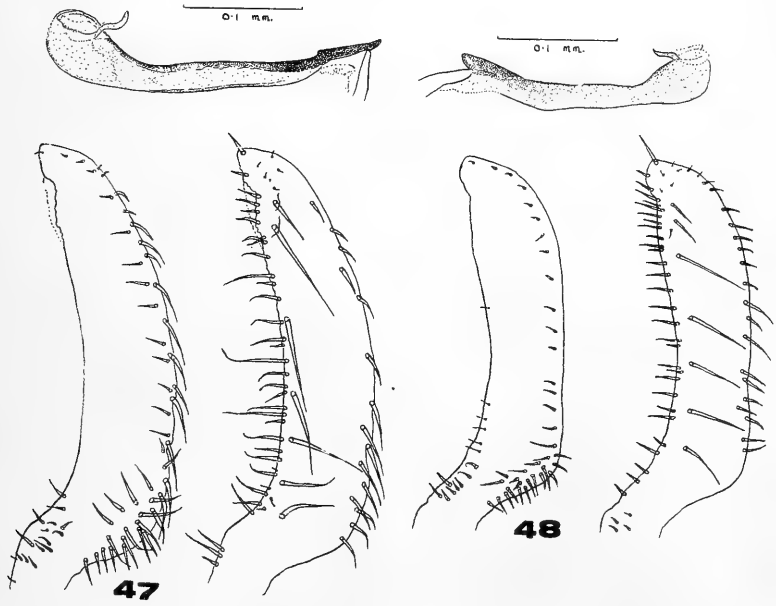
GLYCASPIS (ALLOGLYCASPIS) GRANULATA (Froggatt).

Froggatt's description of this species is inadequate for identification purposes, and it is considered necessary to re-describe the species.

General colour: lemon-yellow or yellow-green, marked with grey to black.

Male: Head: width 0·73 mm.; vertex: along suture 0·24 mm., width 0·39 mm.; suffused pink and lightly marked with black on foveae and posterior border; genal processes: length 0·39 mm.; yellow; dark on inner edges; antennae: length 2·02 mm.;

segs 1 to 4 brown; 5 to 8 dark brown; 9 and 10 black. Pronotum: width 0·59 mm.; suffused pink; central area cream; grey-black areas each side; prominences yellow, with dark mark at bases. Prescutum: edges narrowly black, except posterior border. Scutum: yellow median area, narrowly edged black laterally, most pronounced contiguous to scutellum; orange laterally. Scutellum and metascutellum yellow; never dark as in *G. mirabilis*, but sometimes a small dark central area on scutellum of females; area between, rose-red edged narrowly with black. Post-metanotum: pale yellow edged anteriorly and laterally with black. Abdomen: narrow black transverse line on each of segs 2 to 5. Genitalia: dark area on base of upper plate and at anterior corner of lower plate; claspers on edge, and aedeagus distorted in the drawings of Froggatt's co-type male (Text-fig. 46). Claspers and aedeagus of *G. granulata* reared from *E. botryoides* from Kurnell, N.S.W., are given in Text-fig. 47. Length of aedeagus: (4 specimens from Kurnell and Mona Vale) Extremes 0·284 mm. to 0·290 mm. Forewings: length 2·95 mm. Hindwings: Cu_1 as in Text-fig. 3.



Text-fig. 47.—Aedeagus and claspers of *G. granulata* reared from *Eucalyptus botryoides* from Kurnell, N.S.W.

Text-fig. 48.—Aedeagus and claspers of *Glycaspis siliciflava*, sp. nov.

Female: Similar to male, but with dark markings more extensive; often with red dorsal suffusion.

Host-plant: *E. botryoides* Smith (bangalay).

3 slides: Kurnell, N.S.W. 13 vi 1960 K. M. Moore; bred from *E. botryoides*. Deposited with AM. 3 slides: Mona Vale N.S.W. 7 ix 1958 K. M. Moore; bred from *E. botryoides*. Deposited with AM. In alcohol: Kurnell, N.S.W. 13 vi 1960, K. M. Moore; 9 adults to AM. Pinned: Material, the species of which is not determined, collected from Mona Vale, N.S.W. 24 ix 1958, K. M. Moore, (7 males, 6 females) from hosts either *E. robusta* or *E. botryoides*, are in the collection of AM.

Notes: Lerps: Rectangular; white or yellow; approximately same size as those of *G. mirabilis*, but more peaked, and usually opaque.

Glycaspis (Alloglycaspis) siliciflava, sp. nov.

(L. *siliceus* = of flint; L. *flavus* = yellow. Referring to the appearance of the lerps.)

General colour: There is considerable variation of coloration within the species. Green, yellow, with variable amounts of red, with a dark, longitudinal medio-dorsal

area along centre of vertex, pronotum, all of prescutum, on scutum contiguous to scutellum only, whole of scutellum and metascutellum, and on post-metanotum.

Male: Head: width 0·71 mm.; vertex: along suture 0·22 mm., width 0·34 mm.; genal processes: length 0·37 mm.; suffused red; antennae: length 1·83 mm.; pale brown; segs 9 and 10 black. Pronotum: width 0·59 mm. Abdomen: small, transverse lines usually on segs 2 to 5. Genitalia: black on base of upper plate and anterior corner of lower plate; claspers and aedeagus as in Text-fig. 48. Length of aedeagus: (9 specimens) Extremes 0·216 mm. to 0·236 mm. Forewings: length 2·71 mm.; suffused pale honey-colour on apical half. Hindwings: Cu_1 as in Text-fig. 3.

Female: Longitudinal medio-dorsal area darker than on male; red suffusion often on whole of dorsal area except medio-dorsal area on scutum; black lines on abdomen much larger than on the male, and usually for length of segments laterally, but narrower medianly; wings with honey-colour more intense.

Host-plant: *E. robusta.*

Type Locality: Wamberal, N.S.W.

Types: Holotype male, allotype female, on slide labelled "Wamberal, N.S.W. 25 xi 1958, K. M. Moore. From *E. robusta*". Slide deposited with AM. Paratypes: 6 slides: Wamberal, 25 xi 1958, 3 to AM, 1 to BM, 1 to CS, 1 to FC. 5 slides: Wamberal, 25 xi 1958, (pale adults) to AM. 4 slides: Wamberal, 25 xi 1958, (dark adults) to AM. 1 slide: Lisarow, 9 viii 1958, to AM. 2 slides: Mona Vale, 25 ix 1958, to AM. In alcohol: Wamberal, 25 xi 1958, 40 adults; Wamberal, 2 x 1958, 30 adults; Wamberal, 16 x 1958, 6 adults, and nymphs; all to AM. Pinned: Wamberal, 16 x 1958, 3 males, 3 females, to AM.

Notes: Eggs: Orange-red; singly, or in twos or threes, on either surface of leaf. Lerps: Rectangular; white to deep yellow; up to 5·5 mm. × 4 mm.; often yellow when on lower leaf-surface and white when on upper surface. Nymphs: Coloration variable; last instar may be almost black. Some exuviae are shed outside of the lerp. Adults: Dark areas on the male may be only a pale grey suffusion. Slides of pale and dark specimens, collected on the same day from the same area and host, were made and determined to be the same species.

Discussion on Species of the Subgenus Alloglycaspis.

The coloration and morphology of the last instar nymphs of *G. baileyi*, *G. imponens*, *G. montana*, *G. rivalis* and *G. pilata* suggest that they possess some affinity as a separate group, although the morphological characteristics of the aedeagus and claspers of the adults appear of insufficient homogeneity to warrant such grouping.

There are similarities in the morphology of the aedeagus of *G. montana*, *G. struicis*, *G. pratensis*, *G. australoraria*, *G. amnicola*, *G. oraria* and *G. ignea*, but the grouping of these species is considered to be inadvisable at present.

Similarities in the structure of the aedeagus are evident in *G. suavis*, *G. lactea*, *G. locaridensis*, *G. kurrajongensis*, *G. permista*, *G. mellialata* and *G. siliciflava*, but the shapes of lerps constructed by these species require three different groupings, and their claspers are of variable shapes.

Each of the species *G. suavis*, *G. pilata* and *G. rivalis*, which construct round lerps, and also *G. minuscula*, the lerps of which were not seen, possess scimitar-shaped claspers, as do each of the species *G. mirabilis*, *G. granulata* and *G. siliciflava*, which construct rectangular lerps. The homogeneity in the structure of these claspers suggests some affinity between the two groups, irrespective of the shapes of the lerps constructed by them. The possibility of such affinity is supported by the consistent shape of Cu_1 of the hindwing in each of these species being as that in Text-fig. 3.

Further conjecture on possible evolutionary trends within *Alloglycaspis* appears unwarranted until considerably more material is studied.

Acknowledgements.

Without the continued interest shown in this project, and considerable assistance given, by Mr. L. A. S. Johnson of The Royal Botanic Gardens, Sydney, in identifying

the numerous *Eucalytus* spp. hosts, for which I am greatly indebted to him, the value of the data from these investigations would have been considerably reduced.

Grateful acknowledgement is made to Dr. V. F. Eastop, of The British Museum, London, for much assistance and time willingly given while at C.S.I.R.O., Canberra, in the preparation of a considerable amount of the slide-material used in these investigations.

Advice concerning the taxonomy, given by Dr. K. H. L. Key and Mr. K. L. Taylor, both of the Division of Entomology, C.S.I.R.O., Canberra, and assistance with the nomenclature by Mr. R. M. Moore, is gratefully acknowledged.

Thanks are extended to Mr. J. Schumacher of The Forestry Commission of N.S.W. for the photograph of the galls; and to those who assisted with criticism of the manuscript.

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EXPLANATION OF PLATES VI-VII.

Plate vi.

Coverings of *Glycaspis* (*Glycaspis*) spp. (Psyllidae).

Fig. 1.—Galls on *Eucalyptus haemastoma* (approx. natural size). Figs 2, 3.—Flat lerps (*ca.* 7 ×) covering indentation in leaf-surface. Fig. 4.—Round, conical lerps (*ca.* 10 ×) showing typical grouping. (Note emergence-holes of parasitic Chalcidoidea: Hymenoptera.)

Plate vii.

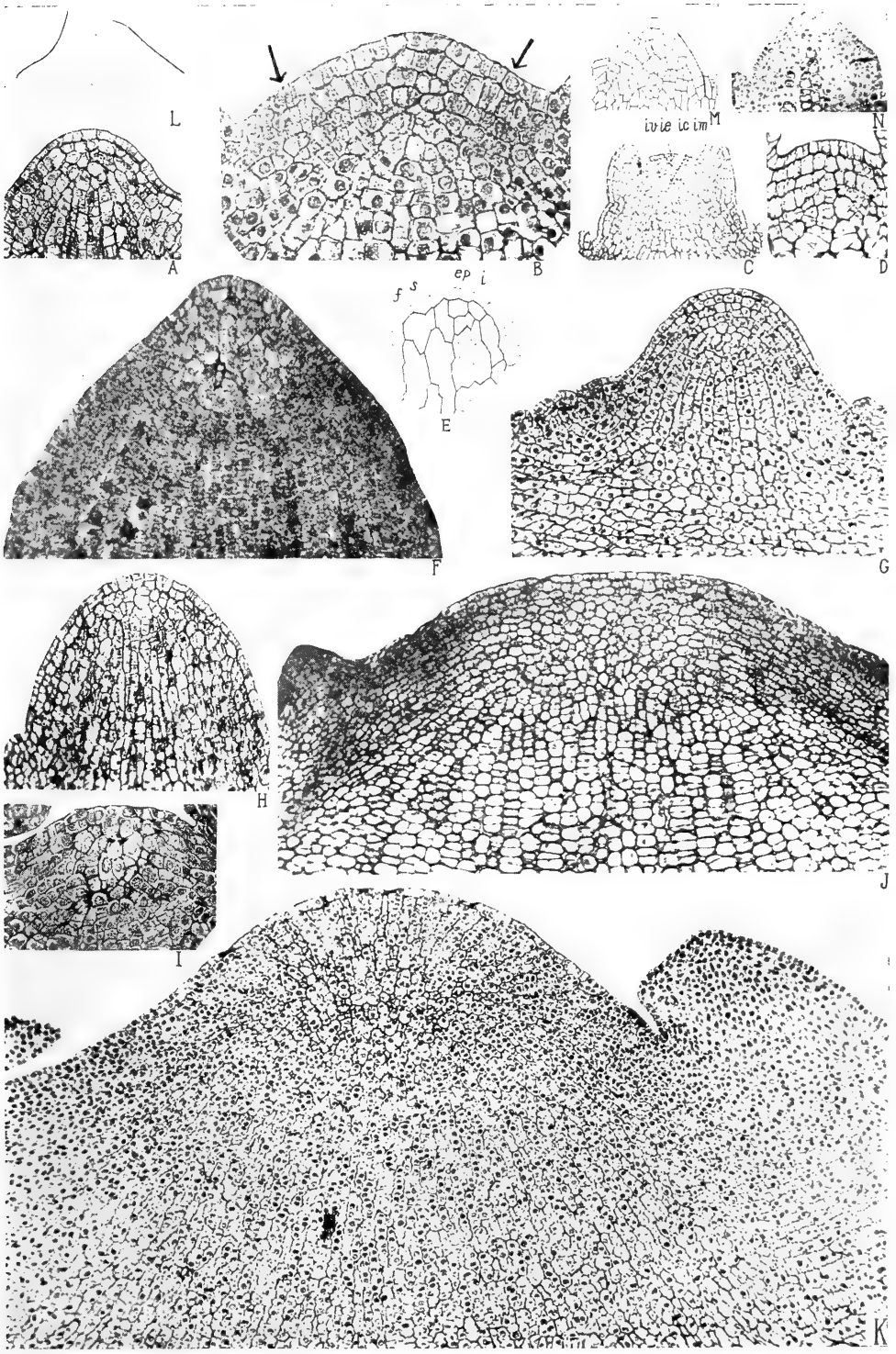
Coverings of *Glycaspis* (*Alloglycaspis*) spp. (Psyllidae).

Fig. 5.—Round, conical lerp (*ca.* 10 ×) on *Eucalyptus saligna*. Fig. 6.—Dome-shaped lerp (*ca.* 10 ×) on *E. saligna*. Fig. 7.—External filaments on round, conical lerp (*ca.* 6 ×). Fig. 8.—Oval lerp (*ca.* 7 ×). Fig. 9.—Rectangular lerp (*ca.* 15 ×). (Side view.) Fig. 10.—Rectangular lerp (*ca.* 10 ×). (From above.)

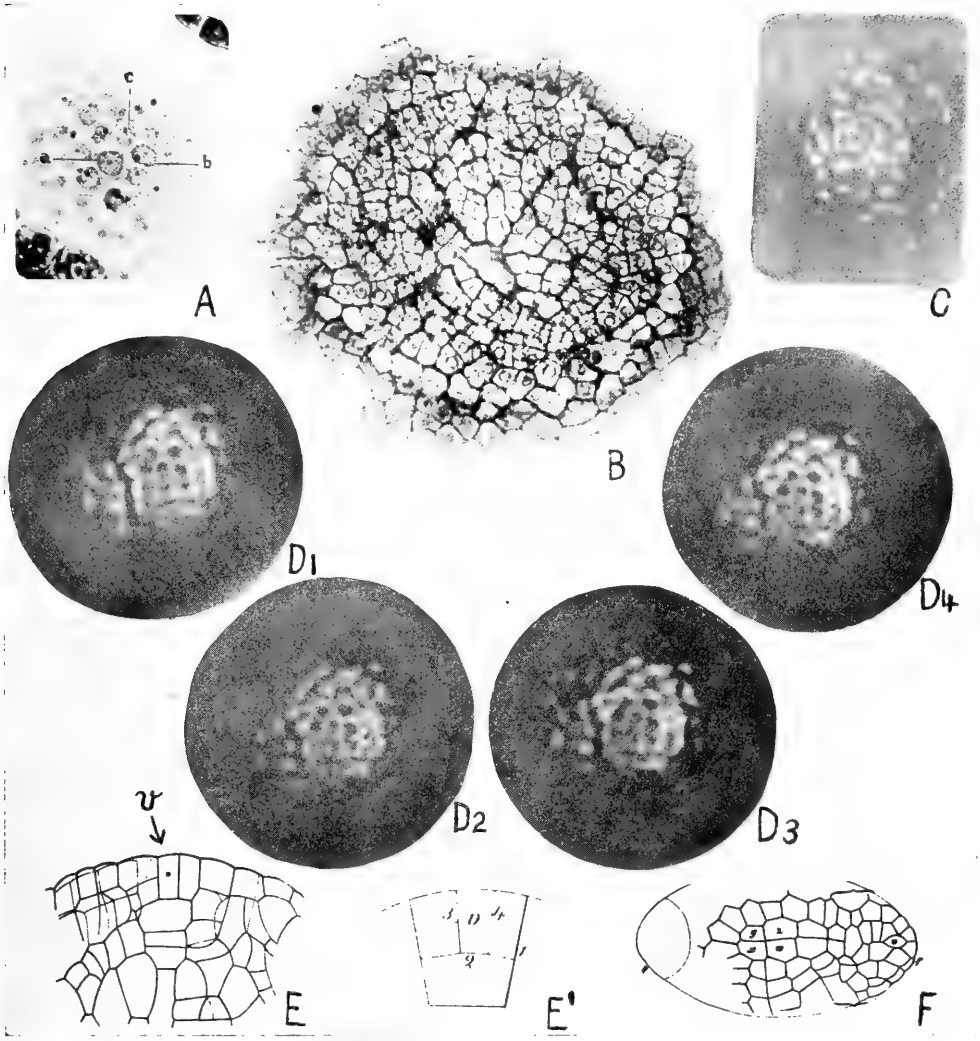
A NEW NAME FOR *HYLA PEARSONI*, PREOCCUPIED. (AMPHIBIA.)

By Stephen J. Copland.

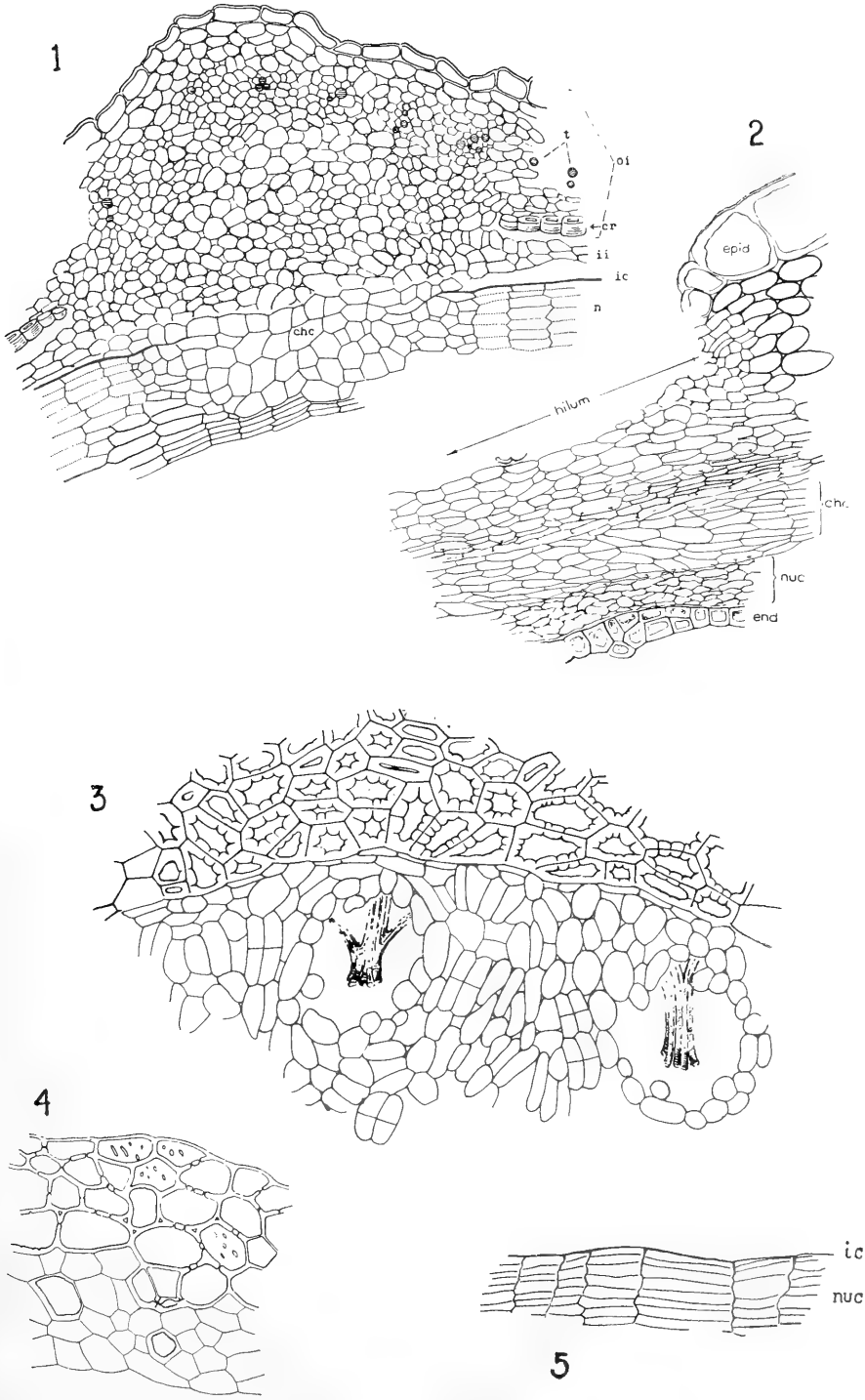
Mr. John Condit has courteously advised me that the name *Hyla pearsoni*, which I used for a new species of frog, 1960, A New Tree-Frog (Genus *Hyla*) from Queensland, Proc. Linn. Soc. N.S.W., 85 (1): 154–6, is preoccupied by *Hyla pearsoni* Gaige, 1929, *Occ. Pap. Mus. Zool. Univ. Michigan*, no. 207: 3, from Bolivia. Accordingly the specific name of the Queensland frog is changed to *pearsoniana*, the genitive substantive being altered to an adjective to agree in gender with the Greek word for wood, not Hylas. The name of the frog is now *Hyla pearsoniana*. I have to thank Mr. Condit, Mr. R. H. Anderson, Dr. Joyce Vickery and Dr. A. B. Walkom for help and advice.



Cellular pattern in apical meristems of selected gymnosperms, angiosperms, and a fern.



The apex in vertical view and in section.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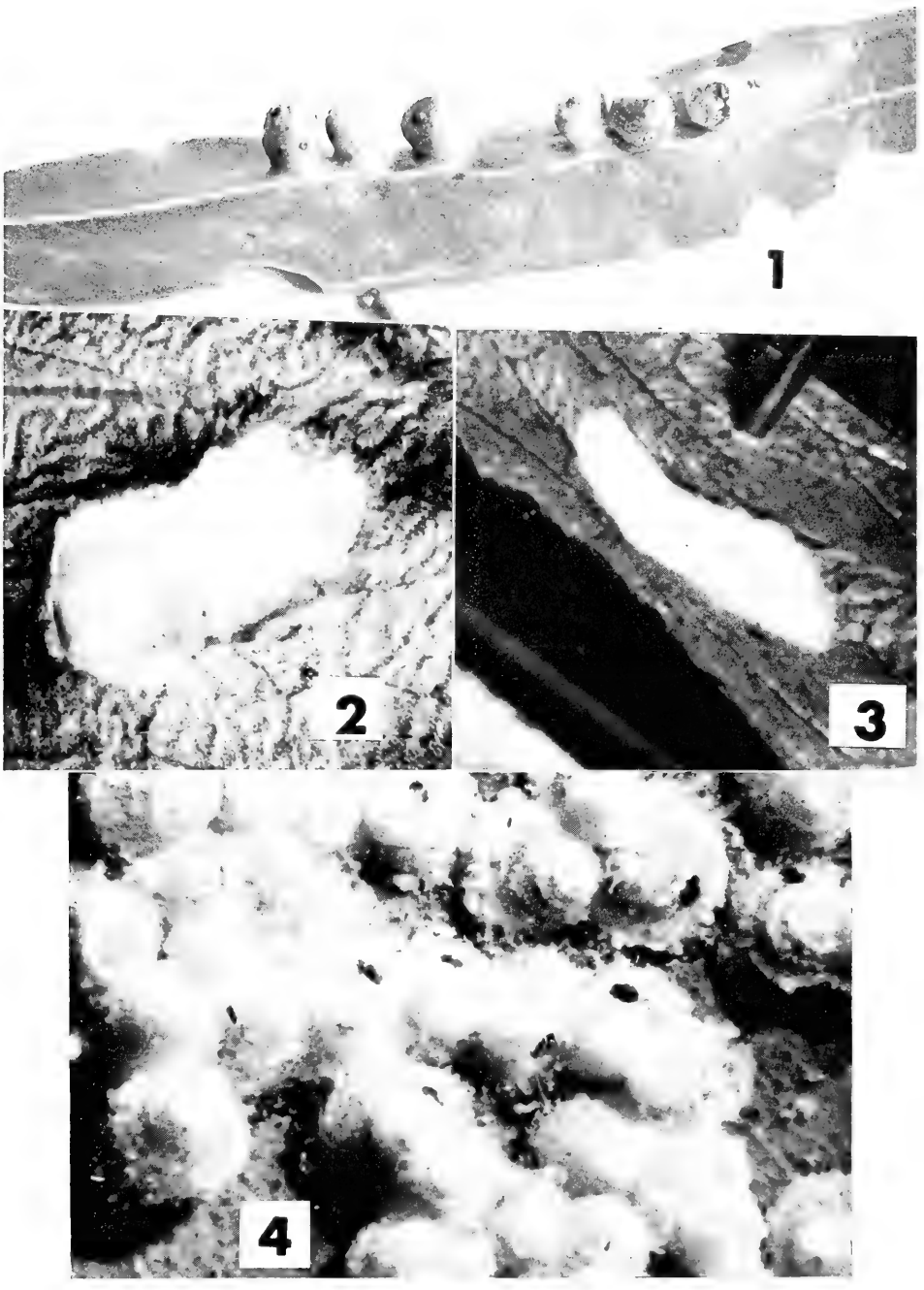
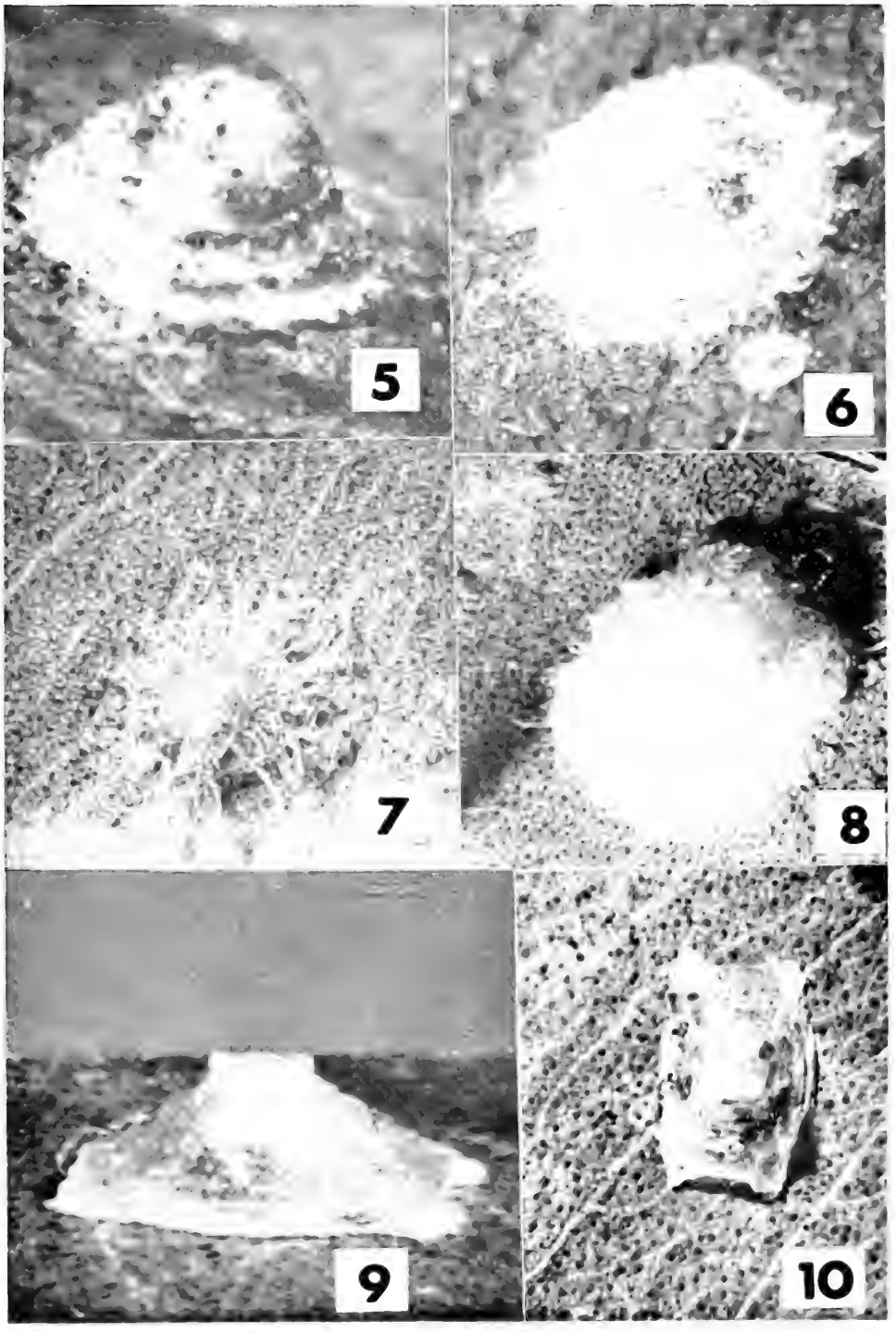
Konangaroo State Forest. 1. Area controlled burned (to left of car). 2, 3. Trees defoliated completely by phasmatids killed outright.

A. Musgrave.



Coverings of *Glycaspis* (*Glycaspis*) spp.



Coverings of *Glycaspis* (*Alloglycaspis*) spp.

NOTES ON THE MORPHOLOGY AND BIOLOGY OF *CAENOPROSOPON TRICHOCERUS* (BIGOT). (DIPTERA, TABANIDAE, PANGONIINAE.)

By Kathleen M. I. English, Department of Zoology, University of Sydney.

(Fifteen Text-figures.)

[Read 28th June, 1961.]

Synopsis.

The larva and pupa of *Caenoprosopon trichocerus*, collected at Epping, N.S.W., are described and figured. Immature stages are known of only one other species, *Ectenopsis angusta* (Macq.), of the Tribe Pangoniini. The larva and pupa of both species have characters which distinguish them from other Tabanidae, but they can also be readily distinguished from one another.

Introduction.

This species was described by Bigot (1892) as *Corizoneura trichocera*, and the genus *Caenoprosopon* was erected by Ricardo (1915). The adults are more fully described by Mackerras (1956). The immature stages of only one other species of the tribe are known, *Ectenopsis* (*Ectenopsis*) *angusta* (Macq.) (English, 1953), and the larva and pupa described in this paper resemble those of *Ectenopsis* in many characters which distinguish them from other Tabanidae.

Occurrence.

A number of larvae and some pupae were found near Epping, New South Wales, at various times between 1919 and 1936 by Mr. Luke Gallard, then Fruit Inspector of the N.S.W. Department of Agriculture, who lived and worked in the district. Mr. A. Musgrave of the Australian Museum, Sydney, in his Bibliography of Ausralian Entomology (1932) says of Mr. Gallard: "He was an economic entomologist who has done good work in investigating the life-histories of insects."

For many years Mr. Gallard kept a detailed diary of his work and his collecting, often with notes on the locality and situation of his finds. After his death in March, 1938, his diary (in several books) was given to the Australian Museum, where I was able to read it in 1960.

He was always on the lookout for insect larvae, and in 1917 he began to search particularly for the larvae of *Ithone* (Tillyard, 1919 and 1922), an unusual neuropteran, in which Tillyard was greatly interested at that time. In 1918 they found the first larva of *Ithone* at Woy Woy, N.S.W., and it was during the search for these larvae in subsequent years, mostly at Epping, that he found the larvae of *Caenoprosopon*, and apparently the two species were often associated.

The locality in which the pupae and most of the larvae were found he calls "Cadell's Creek", evidently a local name for part of Terry's Creek, for in the diary is a small locality sketch with a bridge in Pembroke Street marked "Cadell's Bridge", and heavy timbers of this bridge still remain beside the new concrete bridge over Terry's Creek on the Epping Highway which cuts Pembroke Street just there.

Few people now remember the name, but two residents could tell me that a family named Cadell lived near Pembroke Street, east of the creek, and they had fruit trees on their land near the creek, so Gallard's "Cadell's Creek" is probably part of Terry's Creek south of Epping Highway, where Cadell's land came down; a narrow reserve now follows the creek from the old bridge to Dence Park.

In the diary he refers always to the *Caenoprosopon* larvae as "ribbed fly larvae", presumably because the abdominal pseudopods are quite prominent, and this would distinguish them from other tabanid larvae he knew, species of *Scaptia* and *Dasybasis*, in which the abdominal pseudopods are scarcely noticeable.

The first entries that I found in the diary relating to these larvae were very short. "Sept. 2, 1919. Got three more *Ithone* larvae. Another ribbed fly." "Sept. 3, 1919. Got four more *Ithone* larvae about 15 inches under the surface in yellow sand and one more ribbed fly larva." "Oct. 21, 1919. Got three more ribbed fly larvae from soil about 6 inches deep . . . and *Ithone* larvae about 18 inches deep." Other entries in the diary about this time record finds of the fly larvae, but, except the first, I have only quoted those giving details of situation in the soil.

Some of the later entries are fuller and most larvae found at Epping were "in the gully through which runs Cadell's Creek" usually within about six yards of the creek. "Nov. 15, 1930. At Cadell's Creek got three fair sized ribbed fly larvae . . . they were close to the surface. The three were within one square yard." On September 11, 1934, Miss V. Irwin Smith of Woolwich, N.S.W., went with Mr. Gallard, and she wrote: "About eight feet above the creek bank he cut with a pick into the hard earth of a small embankment . . . and on breaking up the heavy clods of earth taken from a foot or two below the surface of the path found a ribbed larva firmly embedded and encrusted with dirt. The earth was damp following several weeks of heavy rain, but Mr. Gallard says it is usually dry and hard."

Again quoting the diary. "Sept. 23, 1936. I got ten *Ithone* larvae and ten pupae also four ribbed fly larvae. The ground was dry and hard, they were in a place where the top soil had been removed two years ago." He had found some of the fly larvae near Pittwater, N.S.W., where he went to prune fruit trees; he wrote: "July 23, 1934. At Pittwater I dug in the soil just outside the cowyard and secured . . . four large ribbed Tab. larvae like those taken at Epping. The soil is rich black loam with small rubble stones."

A number of larvae were obtained from Mr. Gallard by Miss Irwin Smith between 1919 and 1936, and from her own notes, or from data given her by Mr. Gallard, she had records of 22 larvae. Of these: 1 was injured in collecting; it died, and was preserved; 5 were killed and preserved soon after collecting; 3 escaped; 1 lived for 10 months, and there is no further record; 9 lived for periods varying from 3 to 28 months, then died; 2 pupated after 3 months and 16 months, and died as pupae; 1 began to pupate within two days of collection, but it failed to shed the larval exuvia, and died as a pupa.

Two pupae had been collected in 1932, one in January and one in March, and from these adults emerged. The only other pupa found was in February, 1920, and it died without emerging.

Mr. Gallard kept some larvae and one imago; Miss Irwin Smith kept some larvae and one ♀ imago which Mr. F. H. Taylor identified for her in 1933 as *Demoplatus trichocerus* (Bigot), and in 1958 she gave me her material. In 1959 Dr. I. M. Mackerras confirmed the identification as *Caenoprosopon trichocerus* (Bigot), *Demoplatus* having become a synonym.

The larvae are carnivorous, and apparently fed readily in captivity, but the record above suggests that they are difficult to rear to maturity.

One other record is of a larva collected by the author at Pymble, N.S.W., on January 17, 1948, at the foot of a large gum tree, in loose top soil beneath damp, decaying leaves and bark, where there had once been a fowlyard, about 15–20 feet from a creek. The larva began to pupate within a few days, but failed to shed the larval skin, and was dead and slightly mouldy within ten days with pupation not completed. It was probably injured in collecting.

Material used in the preparation of this paper consists of one pinned imago ♀ with pupal exuvia, and one pupa with larval exuvia and six larvae, in spirit, all received, together with records, from Miss V. Irwin Smith, and also the partly pupated larva

from Pymble. Some of the larvae were in rather poor condition, as they had died and become mouldy before being preserved. Several larvae have been dissected and mounted; so, too, has the last larval exuvia, which was also in bad condition.

Larva (Text-figs 1 to 9).

Measurements of five larvae made soon after collection by Miss Irwin Smith vary from 28 × 3 mm. to 36 × 4 mm.; two of these were killed at once, and the others (two of the larger size) lived for four months or longer, so they were apparently not mature larvae. The Pymble larva, which was mature, was approximately 45 × 5 mm. But size probably has little relation to maturity, for Mackerras (1956) says of the adults: "The series before me shows considerable variation in size. . . ." In her notes on the living larvae Miss Irwin Smith says "they are a dirty browny yellow colour", and "they are thickest in the thoracic region and thinnest at the last three abdominal segments" (Text-figs 1 and 2). This shape is very similar to that of *Ectenopsis*, and in both species the greater thickness of the thorax is not always so noticeable when the larva is killed and preserved.

The larva is circular in cross-section, not flattened at all. The skin is longitudinally striated; the striations can be seen readily with magnification × 20; they are very fine on the first six abdominal segments, slightly coarser on the last two segments and on the thorax; this arrangement is very similar to *Ectenopsis*.

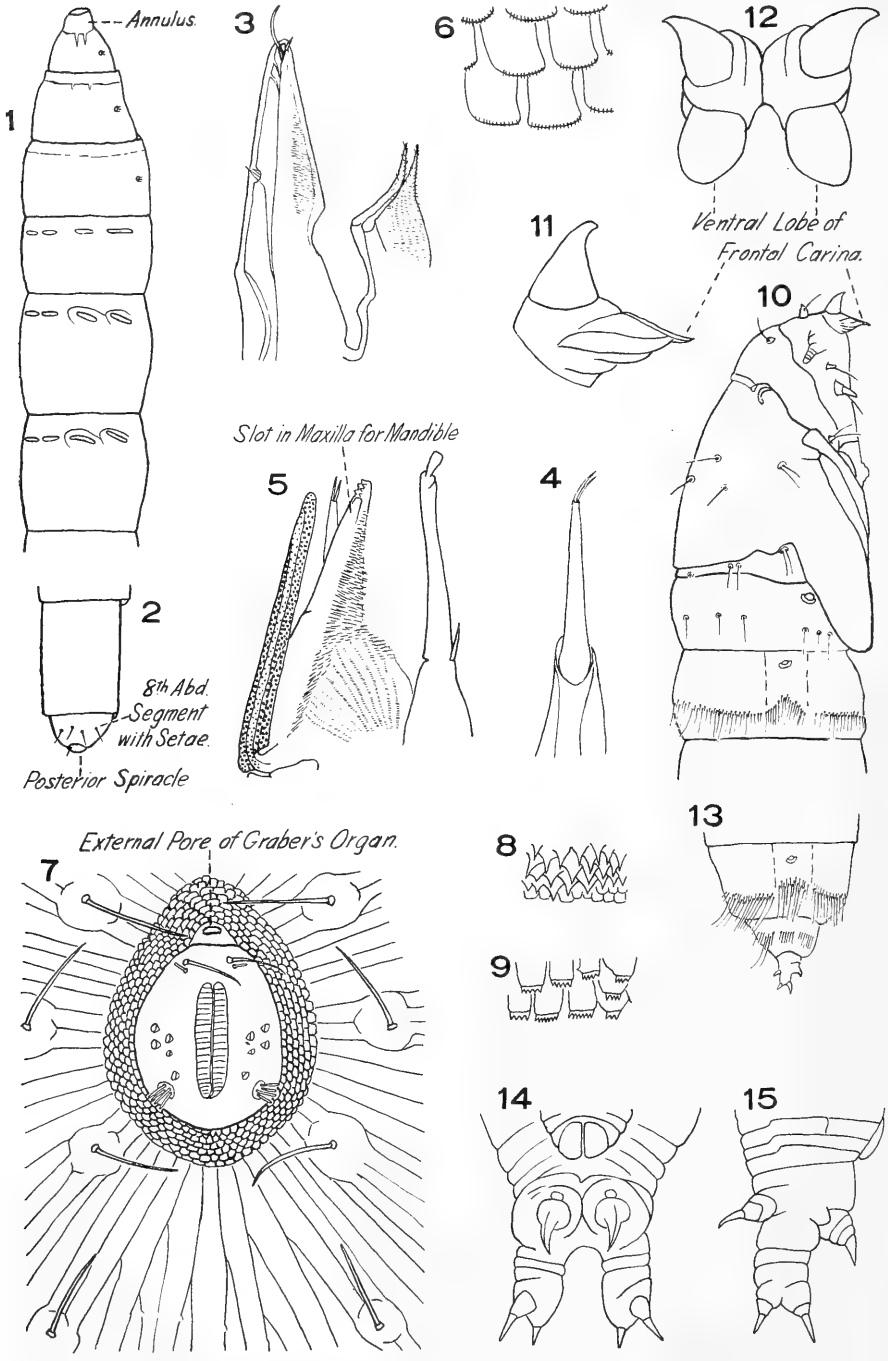
Head. The head capsule is about 4 mm. long; it is slender, and can be completely withdrawn.

The combined clypeus and labrum (Text-fig. 3) is of pale thin chitin. It is long, and tapers to the rounded apex, where there are two long, slender, curved spines set dorsally; other very small processes are present at the apex and on the dorsal edge, and the ventral part is armed with numerous short, fine hairs or spines; the labrum is not differentiated in any way. The labium is much shorter, and terminates in paired, flexible, pointed glossae, which are covered with numerous, closely set, short, fine spines or setae. The labial palps are short and stout.

The antennae (Text-fig. 4) are three-segmented. The basal segment is short, broad at base, and tapering slightly; the middle segment is long, slender, and tapering gradually to the small apical segment which is bifid, the slender branches being more or less equal.

Mandibles and maxillae (Text-fig. 5). The mandibles are long and slender, tapering very slightly to the rounded apex; they are fairly heavily chitinized, brown in colour, with the longitudinal canal opening on the anterior dorsal surface which is characteristic of tabanid larvae, but they lack any serrations on the ventral edge. The maxillae are very lightly chitinized, colourless, transparent and flexible, and they bend back readily when being mounted in balsam. They are broad at base and for part of the length, then narrow sharply and taper to the apex. The upper part is recessed to form a slot for the shorter mandible; the ventral edge is armed with long, slender spines, above which are slightly larger spines extending back; and most of the broad base is covered with numerous rows of very small, closely set setae or spines. The apex (anterior to the slot) is armed with very short, broad-based, pointed spines, with points directed upwards. The maxillary palp is three-segmented; the basal segment short, broad at base, and tapering, with a slender ventral seta; the middle segment long, slender, and tapering to the small apical segment, which is short and rounded at the apex. No piercing spines could be detected.

Thorax. The prothorax (Text-fig. 1) is encircled anteriorly by a wide collar or annulus of small scales, and this is continued back in small points, two on each side; the scales are each armed at the posterior edge with numerous, fine spines visible with low power in slide mounts (Text-fig. 6). At the anterior edge of meso- and metathorax is a narrow band of small scales, some of which are similarly armed. On the dorsal surface of the prothorax, immediately posterior to the annulus, are about ten small, transparent setae; other smaller setae are placed irregularly among the striae on the three thoracic segments; also on each segment are two groups of small setae repre-



Text-figures 1-15. *Caenoprosopon trichocerus* (Bigot). 1-9 Larva: 1, Thorax and abdominal segments 1-3, × 5; 2, Abdominal segments 7 and 8, × 5; 3, Clypeus and labrum with labium, × 50; 4, Antenna, × 50; 5, Mandible, maxilla and maxillary palp, × 50; 6, Scales of annulus of prothorax, × 150; 7, Posterior spiracle and surrounding processes, × 50; 8, Scales of spiracular ring, × 150; 9, Scales of ring round anal papilla, × 150. 10-15, Pupa: 10, Anterior end, × 5; 11, Frontal carina, lateral view, × 25; 12, Frontal carina, end view, × 25; 13, Posterior end, × 5; 14, Aster, ventral view, × 25; 15, Aster, lateral view, × 25.

Note.—The magnifications should be taken as approximate only, because the size of mature larvae and of pupae varies considerably.

senting the prolegs of other larvae. All these setae are visible in slides with low power. At the posterior edge of the prothorax, and near the anterior border of the metathorax, are the small apertures of the thoracic spiracles.

Abdomen (Text-figs 1 and 2). On segments 1 to 5 there is a ring of abdominal pseudopods: two dorsal, long and low; two ventral, short and low; and on each side two higher, more or less rounded mounds, very prominent on segments 3 to 5. On the pseudopods, and at the junction of the segments, the skin has a network pattern; elsewhere it is striated, and among the striae are isolated, single, small setae or hairs as on the thorax. Segment 8 bears the posterior spiracle and anal papilla. The posterior spiracle (Text-fig. 7) is of typical tabanid form. Just dorsal to the aperture, on the spiracular area, are two long and two short hairs; laterally there are very small, mushroom-shaped structures, about five on each side; and near the ventral edge on each side is a group of about four hairs. At the dorsal edge of the area is the aperture of Graber's organ. Surrounding the whole area is a band, more or less uniform in width, of very small scales of variable shapes, some with two points, some with one, and some without points (Text-fig. 8); the shape is visible only in slides, with high power. The anal papilla on the ventral surface is surrounded with an irregular ring of scales, mostly armed with spines (some as in Text-fig. 9). Among the striae on this segment are four pairs of long, slender hairs (Text-figs 2 and 7), readily visible with a hand lens.

PUPA (Text-figs 10 to 15).

This description is based on one ♀ pupal exuvia, length 24 mm., width on first abdominal segment 5 mm., and on one rather shrunken pupa in spirit.

Head and *thorax* (Text-fig. 10). The head bears a large and prominent carinate tubercle (Text-figs 11 and 12) unlike any seen before. It has a pair of large dorsal arms, broad at base, curved, and tapering to a point, and a pair of ventral arms, with apical half more or less flattened, and rounded at the extremity; the four arms are set on a wide rounded base. The anterior orbital seta is long and slender and is set just below the apex of a small triangular tubercle; the posterior orbital seta is very long and slender and is set on the posterior edge of a large, broad based, tapering tubercle, about mid-way between base and apex; the frontal seta is long and slender and is set on the side of a high, tapering tubercle. The vertical seta is long and slender and is set on a small, low mound. The two lateral setae on each side are set together on a small high mound. The antennal sheath reaches almost to the coronal suture, and there is a very small, conical tubercle on the basal segment. The sheath of the proboscis terminates in an almost circular mound topped with a longitudinal ridge.

The thorax bears three pairs of dorsal setae, and on each side there are two alar setae; all are long and slender, and not on tubercles. The thoracic spiracle has a wide rima, almost semi-circular in shape, with the posterior arm extended a little, and the concave side of the rima towards the ventral surface of the pupa. The spiracular pit is separated from the spiracular mound by a small, low mound with a ridged surface. The metathorax bears three pairs of dorsal setae and paired lateral setae; all are long and slender.

Abdomen (Text-figs 10 and 13). The first abdominal segment bears three pairs of tergal setae, not on tubercles, and on each side are three pleural setae, each on a very small tubercle; all setae are long and slender; the spiracular mound is large, with a wide, semi-circular rima. On tergites 2–7 there are strong setae in two, more or less regular rows, with irregularly placed setae between the rows; on tergite 2 the setae are mostly short and very short in the anterior row, mostly long and very long in the posterior row, and between the rows are a few widely spaced long setae; on each succeeding tergite the setae increase slightly in length, they become more closely set in anterior and posterior rows, and more numerous between the rows. On the sternites, the arrangement of setae is very similar. It is similar on the pleurae also, except that the irregularly placed setae between the rows are more numerous. The spiracles on these segments have a wide, semi-circular rima; the spiracular mound and the rima decrease in size gradually from segments 2 to 7.

On the 8th segment, each dorso-lateral comb has about eight setae, two very long, the remainder long and short; each lateral comb has about six short setae; each ventral comb has about six setae, long and short, and these combs are separated in the female by a bare space. The segment terminates in an aster (Text-figs 14 and 15) of unusual shape. It has six arms; the two dorsal and two ventral each have a rounded base with a terminating spine; the two lateral arms are unusual, each consisting of a long column, with more or less parallel sides, terminating in two spines, a larger ventral and a smaller dorsal one.

The material used in the preparation of this paper, i.e., one adult fly with pupal exuvia, one pupa and larvae in spirit, together with slide mounts of dissected larvae and larval exuvia, have been deposited in the Macleay Museum at the University of Sydney.

Discussion.

Besides the larva and pupa of *Caenoprosopon trichocerus* (Bigot), described in this paper, the immature stages of the following species of Pangoniinae have been described: *Goniops chrysocoma* O.S. (Hart, 1895; McAtee, 1911), *Scaptia patula* (Walk.) (Fuller, 1936) (described as *S. auriflua* Don.), *Ectenopsis angusta* (Macq.) (English, 1952), *Scaptia vicina* (Taylor) and *S. muscula* Eng. (English, 1954).

I have been given larvae and pupae of *Goniops chrysocoma*, and loaned larvae and pupae of *Scaptia patula*, and a pupal exuvia of *Scaptia adrel* (Walk.) from New Zealand, so have been able to compare characters in the actual specimens.

The larvae run down to the family Tabanidae in the latest obtainable key of Diptera larvae (Peterson, 1951) and, from descriptions and with the material available, a tentative key has been drawn up for the larvae of the subfamily Pangoniinae, the tribes and the two genera.

Key to Larvae.

1. The eighth abdominal segment bears processes outside the spiracular area and the annulus of the prothorax is covered with small scales armed with spines on the posterior edge ..... Subfamily Pangoniinae 2.
   The eighth abdominal segment does not bear processes outside the spiracular area and the annulus of the prothorax is covered with fine setulae ..... Subfamilies Chrysopinae and Tabaninae.
2. Larva long and slender, white or creamy colour, abdominal segment 7 about twice as long as wide. The body shortens very little when larva contracts ..... Tribe Pangoniini. 3.
   Larva stout, dark in colour or with pigment pattern under skin, abdominal segment 7 about twice as wide as long. The body shortens greatly when larva contracts .. Tribe Scionini.
3. Abdominal segment 8 bears eight stout hairs outside the spiracular area, and on the area dorsal to the spiracular slit are two stout hairs ..... Genus *Caenoprosopon.*
   Abdominal segment 8 bears four slender, tapering, flexible processes outside the spiracular area, and on the area dorsal to the spiracular slit is a single tapering process ..... Genus *Ectenopsis.*

All characters in the key are visible with a hand lens, except the covering of the prothorax which can be seen satisfactorily only in slide mounts with high power. Other differences between the two species can be found in mounted dissections of the head capsule: in *Caenoprosopon trichocerus* the apex of the maxilla is armed with small spines and the second segment of the antenna is almost as long as the second segment of the maxillary palp; in *Ectenopsis vulpecula* the apex of the maxilla is unarmed and the second segment of the antenna is less than half as long as the second segment of the maxillary palp.

The pupae present a much more difficult problem, for there do not appear to be any characters to distinguish the subfamily and only the Pangoniini can be grouped as a tribe on similar characters. One character only, three pairs of setae on the dorsum of the thorax, occurs in all the species listed above, and it is unsatisfactory as a subfamily character for two reasons: (*a*) in *Goniops* and in the three Australian species of *Scaptia* these setae are very fragile and are frequently broken off, leaving no trace, and (*b*) the same character occurs in at least two species of the tribe Rhinomyzini subfamily Chrysopinae.

Pupae of the tribe Pangoniini can be distinguished by paired lateral setae, long and slender, on the metathorax, and paired alar setae, long and slender on the thorax. No other pupae known to me bear paired lateral setae on the metathorax and only in species of *Chrysops* are there paired alar setae, these being very small and fragile. The posterior orbital seta on the characteristic thorn-like tubercle may be another tribal character, but it is not very useful because so often the head shield is lost. For the tribe Scionini distinguishing generic characters may be: for *Scaptia*, a second mound, large or small, between the thoracic spiracular mound and the spiracular pit, and the rima of the spiracle is a very small semi-circle; for *Goniops*, on the dorsal edge of the thoracic spiracular mound, is an excavated channel running down to the spiracular pit almost immediately below.

Except in *Caenoprosopon trichocerus*, where there is a very small secondary thoracic mound, no other tabanid pupae known to me have these characters.

Pupae of the two species of Pangoniini can be distinguished most readily by the frontal carina and by the aster on the eighth abdominal segment, though there are other differences. In *Caenoprosopon trichocerus* the frontal carina has four arms, the thoracic setae are not on tubercles, the abdominal spiracular mounds are wide-based and low and the large wide rima covers about half the surface of the mound, the middle arms of the aster are much larger than the others and each bears two terminal thorns or spines. In *Ectenopsis vulpecula* the frontal carina has two arms, the thoracic setae are set on small tubercles, the abdominal spiracular mounds are small-based and high and the small wide rima covers almost all the apical surface of the mound, the arms of the aster are more or less equal in size and each bears a long seta.

With larvae and pupae of so few species available the characters for determining the subfamily and the tribes are suggested tentatively; they may not hold when other specimens are found.

A striking result of these investigations was the finding that there are such definite characters for grouping the larvae in the subfamily and the tribes, and such a lack of distinguishing characters for grouping the pupae.

Does this mean that the larvae have retained their primitive characters in spite of changes in environment whilst the pupae, or some of them at any rate, have made structural changes in adapting themselves to different environments?

This is quite possible, for the larvae are mainly carnivorous and would not be much affected by changed conditions, they would live on other creatures whatever the environment, whilst the pupae must adapt themselves to survive in and to emerge from the very varied media in different environments.

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The opportunity to compare the larva and pupa of this species with the immature stages of so many others has been made possible by gifts or by material on loan. For specimens of the American species *Goniops chrysocoma* O.S. I wish to thank Dr. C. B. Philip, Rocky Mountain Laboratory, Montana, and Professor J. L. Lancaster, University of Arkansas, for larvae and pupae; Dr. A. Stone, U.S. National Museum, for adult flies and pupal exuviae; and Professor H. H. Schwardt, Cornell University Agricultural Experimental Station, who sent me specimens on loan. I wish to thank Dr. A. J. Nicholson, Division of Entomology, C.S.I.R.O., Canberra, for the loan of material of *Scaptia patula* collected by the late Mary Fuller, who described the larva and pupa as *S. auriflua* Don. I wish to thank Dr. I. M. Mackerras, Queensland Institute of Medical Research, for the loan of the pupal exuvia of *S. adrel* (Walk.), and I am indebted to him also for the opportunity to examine pupal exuviae of Rhinomyzini whilst they were on loan to him; these were: one exuvia of *Specodemyia lamborni* (Aust.) and two labelled *Hinea* or *Specodemyia*, from the British Museum; and one exuvia of *Thriambeutes v-album* Surc. from Dr. C. B. Philip.

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THE GENERIC POSITION OF THE AUSTRALIAN LIGHT-BROWN APPLE MOTH (LEPIDOPTERA: TORTRICIDAE).

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(Sixteen Text-figures.)

[Read 28th June, 1961.]

Synopsis.

The Light-brown Apple Moth *Teras postvittana* Walker, usually known in the literature as *Tortrix postvittana*, is here assigned to *Epiphyas* Turner, of which *Austrotortrix* Bradley is a synonym. The genitalia of the type species *E. eucyrta* Turn. and three species known to be of economic importance, *E. postvittana* (Walk.), *E. xylodes* (Meyr.) and *E. liadelpha* (Meyr.), are figured. Altogether 32 Australian species are now referred to *Epiphyas* and their synonymy is given.

Introduction.

The important Australian tortricid pest, the Light-brown Apple Moth *Teras postvittana* Walker, has for long been referred to the genus *Tortrix* Linnaeus. Recent systematic studies of the Tortricidae have shown that the structure of the genitalia is of the greatest value in differentiating genera and most of the species. On the basis of these characters, the genus *Tortrix* must be restricted to the single European type species *Phalaena Tortrix viridana* L., while some 200 species included by Meyrick (1913) in this genus must be assigned elsewhere.

Having concluded that *T. postvittana* and certain related species could not be referred to *Tortrix*, or any of the genera formerly placed in its synonymy, Bradley (1956) based a new genus *Austrotortrix* on this species and added nine species from Australia and New Zealand. Differences in venation, shown here not to be of generic significance, no doubt caused Bradley (1956) to overlook the genus *Epiphyas* Turner when describing his new genus. The present paper assigns *postvittana* and 31 related species to *Epiphyas*, redefines the genus and states the synonymy of the species included. In addition to *E. postvittana*, the two species *E. xylodes* (Meyr.) and *E. liadelpha* (Meyr.) are known to attack plants of economic importance.

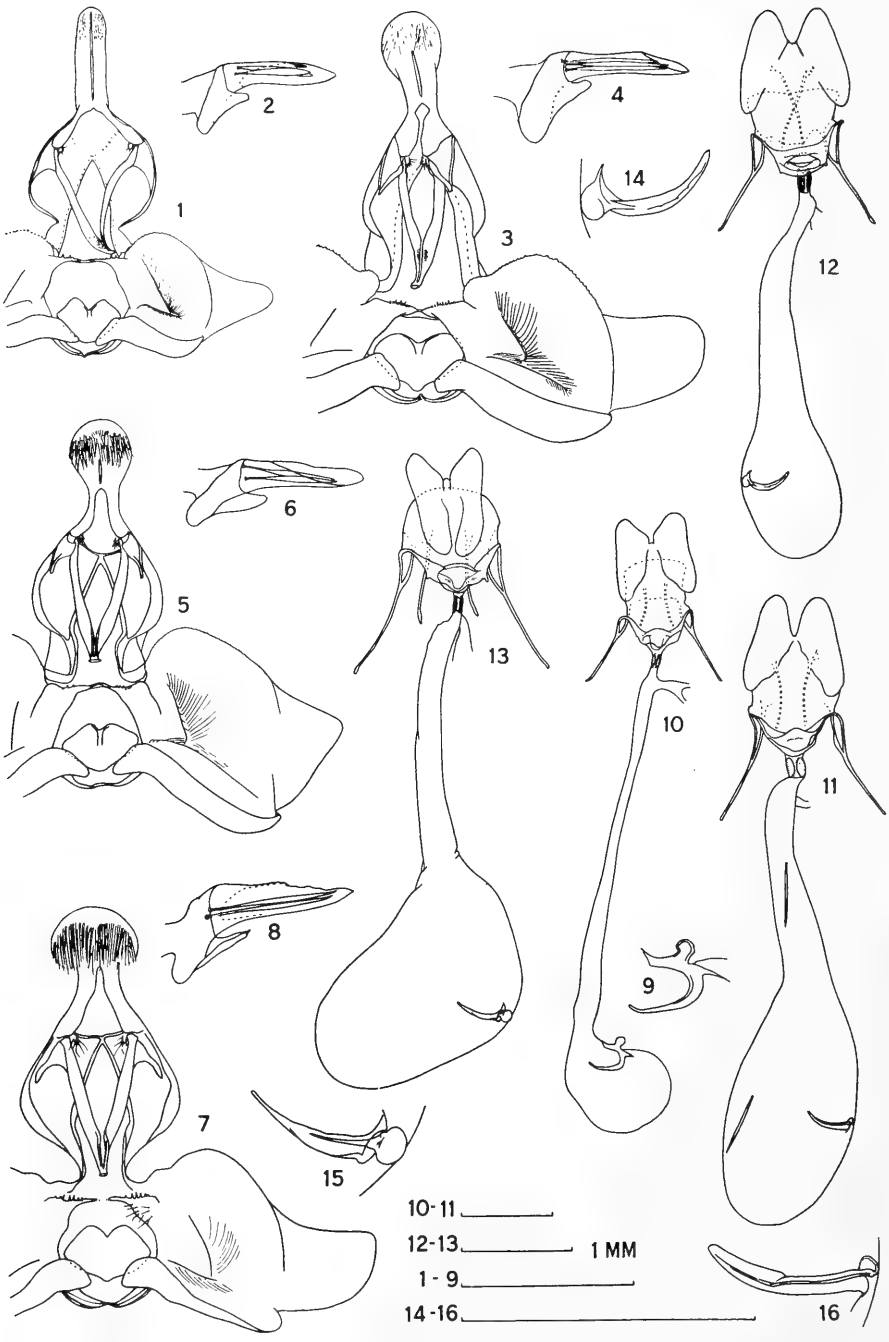
Genus Epiphyas Turner.

Epiphyas Turner, 1927, *Pap. roy. Soc. Tasm.* (1926): 125. *Austrotortrix* Bradley, 1956, *Bull. ent. Res.*, 47: 101. (Type species *Teras postvittana* Walk., 1863, by original designation.) (New synonymy.)

Type species *Epiphyas eucyrta* Turner, 1927, by original designation.

Antenna in male finely serrate and ciliated; labial palpus about twice diameter of eye, second segment curved slightly upwards, expanded above with appressed scales, apical segment smooth-scaled, porrect. Thorax without posterior crest. Forewing smooth, R_1 from one-half cell, R_2 from three-quarters, R_4 from upper angle to costa, R_5 separate to termen, M_2, M_3 and Cu_1 more or less equidistant at base, M_3 and Cu_1 often strongly curved and nearly parallel, M_3 absent in some specimens. Hindwing with Rs and M_1 closely approximated at base, connate or short-stalked, M_2 approximated at base to M_3 or Cu_1, M_3 connate or stalked with Cu_1 from lower angle of cell, or M_3 absent. Abdomen in male with well differentiated mensis ventralis, clothed with long scales, on eighth sternum.

Male genitalia (Text-figs 1–2): Uncus long, strongly spatulate, with slender base or with parallel sides, apex rounded, truncate or slightly concave; socii small; gnathos arms long, slender, curved, united medially to form a slight hook; transtilla absent; valva broadly rounded with a differentiated distal lobe or cucullus, often large, sacculus



Text-figs 1-8.—Ventral view of male genitalia, and lateral view of aedoeagus, of *Epiphyas*: 1, 2, *E. eucyrta* Turn., holotype; 3, 4, *E. postvittana* (Walk.); 5, 6, *E. liadelpha* (Meyr.); 7, 8, *E. xylodes* (Meyr.).

Text-figs 9-16.—Ventral view of female genitalia, and enlarged signum, of *Epiphyas*: 9, 10, *E. postvittana* (Walk.), holotype; 11, 16, *E. xylodes* (Meyr.), holotype of *Tortrix paraplesia* Turn.; 12, 14, *E. eucyrta* Turn., allotype; 13, 15, *E. liadelpha* (Meyr.).

well developed, smooth, sclerotized, extending from base of valva to end of valvula, costa strongly arched, valvula membranous with a longitudinal and an oblique fold, and clothed with long scales; basal processes of valvae broad at base, slender apically, straight above with small irregular marginal spines, apices joined medially by membranous band. Aedoeagus pistol-shaped, without external ornamentation, or with a single short thick projection above orifice; cornuti two to four, flattened, elliptical, deciduous but with basal point of articulation of each clearly visible when cornuti shed.

Female genitalia (Text-figs 13, 15): Ostium a membranous shallow cup, sterigma moderately sclerotized, colliculum a sclerotized plate, longitudinally curved, the free ventral edges rounded and sometimes overlapping; ductus bursae constricted at colliculum, gradually broadening to junction of corpus bursae, cestum absent; corpus bursae rounded, signum a sclerotized plate, blade-like, hook-like or in the form of a short tapering dagger, often with capitulum.

Turner (1927) considered that *Epiphyas* was derived from *Tortrix*, from which it differed only in the stalking or coincidence of M_3 and Cu_1 of the hindwing. In the type species, these two veins were coincident, although in one specimen which Turner believed to be conspecific these two veins were stalked. In a second species *chlidana* Turn., which he also referred to *Epiphyas*, Turner stated that M_3 and Cu_1 of the hindwing were stalked.

An examination of the type series of *E. eucyrta* and *E. chlidana* has revealed an extraordinary confusion. The latter species clearly does not belong to the Tortricidae at all, but to the Olethreutidae, the genitalia being quite characteristic of that family, while there is also a well developed cubital pecten of the hindwing, apparently overlooked by Turner.

Two of Turner's type series of *E. eucyrta*, including the holotype, came from Rosebery, Tasmania, and three from Strahan, Tasmania. The genitalia in both sexes are so closely similar to those of *Tortrix leuropa* Turner (1939) from Scottsdale, Tasmania, in which both M_3 and Cu_1 of the hindwing are present, that there seems little doubt that the two are conspecific. In general facies also these two species are almost identical. In other specimens from Victoria, with genitalia and facies similar to *E. eucyrta*, these two veins are either stalked or connate. It must be concluded, therefore, that the loss or stalking of M_3 in the hindwing is not of generic significance in this group of the Archipinae.

Although Turner stated that all the veins of the forewing were present in *Epiphyas*, he apparently overlooked the fact that M_3 is absent in both forewings of the type series of *E. eucyrta*. However, once again the specimens of *Tortrix leuropa* have all the veins present in the forewing, while in the series from Victoria M_3 is either present or absent. The loss of M_3 in the forewing therefore is likewise not of generic significance in the group.

The genitalia of both sexes of *E. eucyrta* are quite typical of many Australian species, including *postvittana*, formerly referred to *Tortrix* and more recently to *Austrotortrix*. The genus *Epiphyas* Turner is therefore sustained, not on the grounds proposed by Turner, but chiefly on the genitalic characters. Thus the name of the Light-brown Apple Moth becomes *Epiphyas postvittana* (Walker).

Epiphyas is one of the more specialized genera of the subfamily Archipinae, a group which has reached a remarkable degree of development in Australia and New Zealand (Common, 1958). Of special importance in separating it from related genera is the form of the colliculum, ostium and sterigma in the female and the form of the valva, with its basal processes, and of the aedoeagus in the male. The colliculum is short, almost cylindrical, with approximated or overlapping rounded ventral edges. In *Adoxophyes* Meyrick this structure is similar or is reduced to two small sclerotized plates. In *Isotenes* Meyrick it is also small and often similar to *Epiphyas*. The cestum, a ribbon-like thickening of the ductus bursae, common in many related genera of the Archipinae, is entirely lacking in *Epiphyas*. In the male, the large rounded membranous valva, with longitudinal and oblique folds, and usually with a large membranous

cucullus, is characteristic. In some species, however, the cucullus is quite small. The sclerotized sacculus is smooth, without the terminal spine-like projection present in *Homona* Walker and such Holarctic genera as *Archips* Hübner. The aedoeagus is usually without any external projections.

To the genus *Epiphyas* should be referred the following Australian species. The author has examined the genitalia of the holotypes or lectotypes of all the species and their synonyms, with the exception of *T. cerussata* Meyr. and *T. eugramma* Low. The genitalia of specimens from the original series or from the type locality of these two species have been studied. With the exception of *E. eucyrta*, each of the following assignments is a new combination.

Epiphyas postvittana (Walk.) (Text-figs 3, 4, 9, 10). *Teras postvittana* Walk., 1863, *List Lep. Ins. Brit. Mus.*, 28: 297 (Type locality: Sydney, N.S.W.; holotype ♀ Brit. Mus., genitalia slide No. BM1815). *Dichelia vicariana* Walk., 1869, Characters undescr. Lep. Het., p. 82 (Holotype ♂ "Dichelia vicariana, Det. by Walker, Type 372", without locality data, without abdomen, Nat. Mus. Vict.). *Tortrix stipularis* Meyr., 1910, Proc. Linn. Soc. N.S.W., 35: 226 (Type locality: Murtoa, V.; holotype ♂ No. 837, Nat. Mus. Vict.) (New synonymy). *Tortrix oenopa* Meyr., 1910, Proc. Linn. Soc. N.S.W., 35: 230 (Type locality: Gisborne, V.; holotype ♂ Nat. Mus. Vict.) (New synonymy). *Tortrix phaeosticha* Turn., 1939, *Pap. roy. Soc. Tasm.* (1938): 76 (Type locality: Strahan, Tas.; holotype ♂ C.S.I.R.O., genitalia slide No. T289) (New synonymy). The holotypes of the other synonyms listed by Bradley (1956) have also been examined, but the references are omitted here for brevity.

Epiphyas dotatana (Walk.). *Teras dotatana* Walk., 1863, *List Lep. Ins. Brit. Mus.*, 28: 298 (Type locality: Tasmania; holotype ♀ Brit. Mus., genitalia slide No. BM1814). *Tortrix tanyptera* Meyr., 1910, Proc. Linn. Soc. N.S.W., 35: 228 (Lectotype ♀ "Gisborne, 30.3.97", hereby designated, Nat. Mus. Vict.) (New synonymy).

Epiphyas cetrata (Meyr.). *Tortrix cetrata* Meyr., 1910, Proc. Linn. Soc. N.S.W., 35: 230 (Type locality: Deloraine, Tas.; holotype ♂ Brit. Mus., genitalia slide No. BM3398).

Epiphyas xylodes (Meyr.) (Text-figs 7, 8, 11, 16). *Tortrix xylodes* Meyr., 1910, Proc. Linn. Soc. N.S.W., 35: 224 (Type locality: Mt. Victoria, N.S.W.; lectotype ♂ Brit. Mus., designated by Bradley (1956), genitalia slide No. BM2000). *Tortrix eurystropha* Turner, 1926, *Trans. roy. Soc. S. Aust.*, 50: 135 (Type locality: Lamington National Park, Q.; holotype ♂ C.S.I.R.O., genitalia slide No. T249) (New synonymy). *Tortrix paraplesia* Turner, 1914, Proc. Linn. Soc. N.S.W., 39: 553 (Type locality: Ebor, N.S.W.; holotype ♀ C.S.I.R.O., genitalia slide No. T303) (New synonymy).

Epiphyas lycodes (Meyr.). *Tortrix lycodes* Meyr., 1910, Proc. Linn. Soc. N.S.W., 35: 232 (Type locality: Mt. Wellington, Tas.; holotype ♂ Brit. Mus., genitalia slide No. BM1811).

Epiphyas hemiphoena (Turn.). *Tortrix hemiphoena* Turn., 1927, *Pap. roy. Soc. Tasm.* (1926): 126 (Type locality: Russell Falls, Tas.; holotype ♂ C.S.I.R.O., genitalia slide No. T288).

Epiphyas lypra (Turn.). *Tortrix lypra* Turn., 1945, *Trans. roy. Soc. S. Aust.*, 69: 65 (Type locality: Margaret River, W.A., holotype ♂ C.S.I.R.O., genitalia slide No. T344).

Epiphyas sobrina (Turn.). *Tortrix sobrina* Turn., 1945, *Trans. roy. Soc. S. Aust.*, 69: 62 (Type locality: Brisbane, Q., holotype ♂ C.S.I.R.O., genitalia slide No. T258).

Epiphyas eucyrta Turn., 1927 (Text-figs 1, 2, 12, 14). *Pap. roy. Soc. Tasm.* (1926): 125 (Type locality: Rosebery, Tas.; holotype ♂ C.S.I.R.O., genitalia slide No. T762). *Tortrix leuropa* Turn., 1939, *Pap. roy. Soc. Tasm.* (1938): 79 (Type locality: Scottsdale, Tas., holotype ♀ C.S.I.R.O., genitalia slide No. T760) (New synonymy).

Epiphyas liadelpha (Meyr.) (Text-figs 5, 6, 13, 15). *Tortrix liadelpha* Meyr., 1910, Proc. Linn. Soc. N.S.W., 35: 227 (Type locality: Albany, W.A.; lectotype ♂ Brit. Mus., designated by Bradley (1956), genitalia slide No. BM1810).

EPIPHYAS FABRICATA (Meyr.). *Tortrix fabricata* Meyr., 1910, PROC. LINN. SOC. N.S.W., 35: 233 (Type locality: Lorne, V.; lectotype ♂ Brit. Mus., designated by Bradley (1956), genitalia slide No. BM2424).

EPIPHYAS CARYOTIS (Meyr.). *Tortrix caryotis* Meyr., 1910, PROC. LINN. SOC. N.S.W., 35: 227 (Lectotype ♂ "Mt. St. Bernard, Victoria, 5000′, G.L., 2.08", selected by J. D. Bradley and hereby designated, Brit. Mus., genitalia slide No. BM1954).

EPIPHYAS SCLEROPA (Meyr.). *Tortrix scleropa* Meyr., 1910, PROC. LINN. SOC. N.S.W., 35: 236 (Lectotype ♂ "Mt. St. Bernard, Victoria, 5000′, G.L., 2.08", selected by J. D. Bradley and hereby designated, Brit. Mus., genitalia slide No. BM1975).

EPIPHYAS BALIOPTERA (Turn.). *Tortrix balioptera* Turn., 1916, *Trans. roy. Soc. S. Aust.*, 40: 513 (Type locality: Brisbane, Q., holotype ♂ C.S.I.R.O., genitalia slide No. T246).

EPIPHYAS ERYSIBODES (Turn.). *Tortrix erysibodes* Turn., 1916, *Trans. roy. Soc. S. Aust.*, 40: 512 (Type locality: Mt. Kosciusko, N.S.W.; holotype ♂ C.S.I.R.O., genitalia slide No. T947).

EPIPHYAS HAEMATEPHORA (Turn.). *Tortrix haematephora* Turn., 1916, *Trans. roy. Soc. S. Aust.*, 40: 511 (Type locality: Mt. Kosciusko, N.S.W.; holotype ♂ C.S.I.R.O., genitalia slide No. T325).

EPIPHYAS HAEMATODES (Turn.). *Tortrix haematodes* Turn., 1916, *Trans. roy. Soc. S. Aust.*, 40: 513 (Type locality: Mt. Kosciusko, N.S.W.; holotype ♂ C.S.I.R.O., genitalia slide No. T672).

EPIPHYAS ORESIGONA (Turn.). *Tortrix oresigona* Turn., 1939, *Pap. roy. Soc. Tasm.* (1938): 77 (Type locality: Mt. Wellington, Tas.; holotype ♂ C.S.I.R.O., genitalia slide No. T336).

EPIPHYAS EPICHORDA (Meyr.). *Tortrix epichorda* Meyr., 1910, PROC. LINN. SOC. N.S.W., 35: 249 (Lectotype ♂ "Melbourne, Victoria, /92", selected by J. D. Bradley and hereby designated, Brit. Mus., genitalia slide No. BM1812).

EPIPHYAS PLASTICA (Meyr.). *Tortrix plastica* Meyr., 1910, PROC. LINN. SOC. N.S.W., 35: 234 (Type locality: Mt. Wellington, Tas.; holotype ♂ Brit. Mus., genitalia slide No. BM2300).

EPIPHYAS AULACANA (Meyr.). *Tortrix aulacana* Meyr., 1881, PROC. LINN. SOC. N.S.W., 6: 513 (Lectotype ♂ "Sydney, N.S. Wales, 28.9.78", hereby designated, Brit. Mus., genitalia slide No. BM3410). *Tortrix echinitis* Meyr., 1910, PROC. LINN. SOC. N.S.W., 35: 249 (Lectotype ♂ "Port Lincoln, S. Australia, 8.11.82", hereby designated, Brit. Mus., genitalia slide No. BM3401) (New synonymy).

EPIPHYAS PELOXYTHANA (Meyr.). *Tortrix peloxythana* Meyr., 1881, PROC. LINN. SOC. N.S.W., 6: 514 (Type locality: Murrurundi, N.S.W.; holotype ♂ Brit. Mus., genitalia slide No. BM3331).

EPIPHYAS IODES (Meyr.). *Epichorista iodes* Meyr., 1910, PROC. LINN. SOC. N.S.W., 35: 258 (Lectotype ♂ "Wallaroo, S. Australia, 2.11.82", hereby designated, Brit. Mus., genitalia slide No. BM3425).

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Thanks are due to the authorities of the various institutions who have made material available for study, either on loan or during visits. The author is especially indebted to Mr. J. D. Bradley, British Museum (Natural History), to Mr. A. N. Burns and Mr. A. Neboiss, National Museum of Victoria, and to Mr. N. B. Tindale and Mr. G. F. Gross, South Australian Museum, Adelaide.

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LARVAL DEVELOPMENT OF *VELACUMANTUS AUSTRALIS*.

By R. J. MacIntyre, C.S.I.R.O. Division of Fisheries and Oceanography, Cronulla.

(*Communicated by Dr. G. F. Humphrey.*)

(Seven Text-figures.)

[Read 26th July, 1961.]

Synopsis.

Eggs, 0·1 mm. in diameter, were laid in capsules in aquaria at 23·8° C. during February. They developed to produce trochophores in 24 hours and veligers in 48 hours; the veligers hatched out in 60 hours. Normal twin embryos as well as fragmentary exogastrulae were observed.

Velacumantus australis (Quoy and Gaimard) (*Pyrazus*) is one of the commonest molluscs on the shores of sheltered bays and estuaries from Queensland to Tasmania and south-west Australia. It is one of many organisms which constitute the association known as the Zosteretum (Hedley, 1915) based on dense beds of the marine grass *Zostera*. It is also well known as the carrier of the parasite responsible for schistosome dermatitis in humans (Pope, 1955). So far the eggs and early development of *V. australis* have not been described: in fact, Anderson (1960) cites only three descriptions within the entire family Cerithiidae (Lebour, 1945; Ostergaard, 1950; Thorson, 1946).

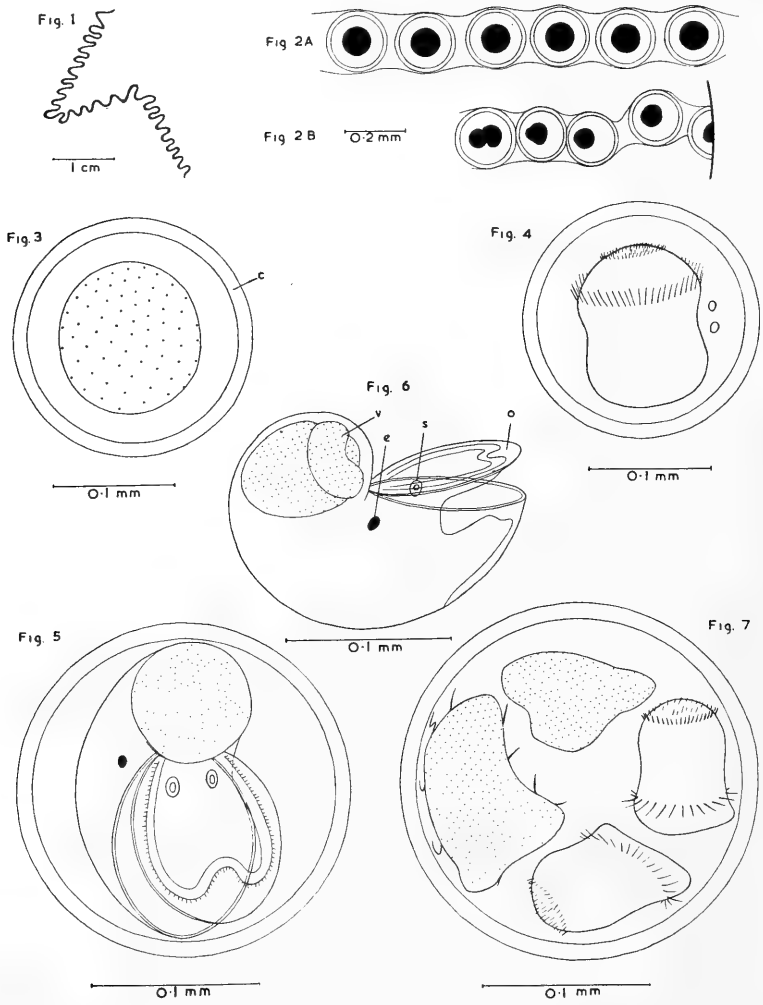
For two years a group of these snails was kept at this laboratory in glass aquaria with running sea-water; the abundant algal films on the aquarium walls served as food. In late February at a water temperature of 23·8° C. a group of adults averaging 3·4 cm. in length commenced laying egg strings on the glass walls of the tanks. The opaque white eggs had presumably been fertilized prior to laying, though the process of copulation was not observed. The eggs were enclosed in transparent gelatinous capsules within which larval development took place; they were arranged in a single series in a thin-walled, colourless tube and, in this respect, differed from the condition in other cerithiids where the eggs lie several deep across the width of the tube. The tube itself was cemented to the walls of the aquarium in the form of a wavy line, and it was noticed that although there was no shortage of space, the egg strings were always laid down in the same pattern of tight waves about 2 mm. wide (Fig. 1). This string would easily fit along a *Zostera* leaf which is assumed to be the normal site for egg laying.

Seven hours after laying, cleavages had developed in the eggs to produce an eight-celled blastula. Subsequently the smaller micromeres began to divide more rapidly and spread so that after eleven hours the few large macromeres were almost completely enveloped. The first larval phase, the trochophore, was complete in twenty-four hours: it had a crown of long cilia and an apical patch of smaller ones (Fig. 4). The polar bodies which had been extruded at first cleavage remained up to this stage, and adhered to the trochophore as it slowly rotated in its capsule. At forty-eight hours the final larva, the veliger, with its shell, operculum, eyes, and statocysts complete, was swimming rapidly round and round, but still within the confined space of the capsule (Fig. 5). The veligers hatched out sixty hours after laying (Fig. 6), whereupon they swam rapidly round the dish and crawled on the bottom, though it appeared that some time would elapse before they would cease to swim and finally settle.

Twin embryos were frequently observed developing within a single capsule. While it is not known how commonly this occurs in natural conditions, it was noted that the course of development was very plastic and could be altered by rough treatment and mechanical shocks or contamination with traces of alcohol. Mechanical disturbances could easily have caused separation of the first pair of cells which would then develop independently into twin larvae. Traces of ethyl alcohol profoundly affected the process of gastrulation to produce fragmentary exogastrulae which, being composed of more or less differentiated tissues, followed an erratic and incomplete development. Figure 7 shows the result when an egg first produced twin embryos, both of which subsequently

underwent exogastrulation and fragmentation to produce masses of densely yolked endodermal cells as well as ectodermal tissue fragments; these produced partial trochophore larvae in which the crown of larger cilia had slipped to become a belt.

The hardiness, abundance, and wide distribution of this species, together with the plasticity of its development, make it a useful animal for laboratory studies in cytology and embryology.



Figs 1-7.—1. Egg-string of *Velacumantus australis*. 2A. Eggs in capsules within egg-string. 2B. Embryos in capsules within egg-string. 3. Egg in capsule, *c*. gelatinous capsule. 4. Trochophore stage in capsule at 24 hours. 5. Veliger stage in capsule at 48 hours. 6. Hatched veliger partially open at 60 hours, *e*. eye, *o*. operculum, *s*. statocyst, *v*. visceral mass. 7. Fragmentary larvae.

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OBSERVATIONS ON SOME AUSTRALIAN FOREST INSECTS.

8. The Biology and Occurrence of Glycaspis baileyi Moore in New South Wales.

By K. M. Moore, Forestry Commission of New South Wales.

(Plate ix; seventeen Text-figures.)

[Read 26th July, 1961.]

Synopsis.

The occurrence of large populations of *Glycaspis baileyi* Moore 1961 on *Eucalyptus saligna* Smith in coastal areas of New South Wales, and the severe debilitation and deaths of trees associated with these infestations, were investigated. The biology of this insect and its association with the affected trees were studied and parasites and predators recorded. Damage to *E. saligna* is described and reports of recent attack are reviewed. Results of trial rearings made on host-plants other than those on which *G. baileyi* normally occurs in the field, and of laboratory experiments to determine possible effects of temperature and relative humidity on embryonic development, are recorded. Some effects of weather, site-favourability of hosts, and other factors apparently influencing population fluctuations of this species, are discussed.

Introduction.

Species of the Psyllidae feed on the sap of many species of plants and construct "lerps" or coverings on the surfaces of leaves and twigs, feed openly among the tender growth of new shoots, or form galls in the leaf-tissues. They are known by the common names of "jumping plant lice" or lerp insects. Dobson (1851) states that the word "lerp" was used by some Australian aboriginal tribes to denote the sweet coverings which some psyllid nymphs (probably those of the genus *Glycaspis*) construct over and around themselves from their body-excretions, and which were apparently utilized by the aboriginals as part of their food. The word "psyllid" will be used here to refer to the various stages of the insects of the family Psyllidae, and the word "lerp" used to denote the coverings made by certain species of these insects during their immature stages.

The psyllids previously reported as being of economic significance in New South Wales are *Aconopsylla sterculiae* (Froggatt) (the kurrajong psyllid) and *Protyora sterculiae* (Froggatt) (the kurrajong star psyllid), both of which occur in areas west of the Great Dividing Range; *Cardiaspina artifex* (Schwarz) (the brown lace-lerp) and *C. vittaformis* (Froggatt) (the lace-lerp), the latter severely affecting ironbarks on State Forests, and the former periodically attaining plague proportions on *Eucalyptus* spp. in many areas.

Glycaspis spp. have been recorded as breeding on certain species of the genus *Eucalyptus* only, some species of which are apparently unsuitable as hosts. They occur on coppice growth, epicormics, regeneration, or on crown-foliage, and exist under diverse climatic conditions, occurring as limited populations in the drier inland areas where rainfall may be only about 11 inches per annum; or at times as large populations in coastal areas, where an annual rainfall of 90 inches may occur. They are found from sea-level to an altitude of about 4,000 feet.

During 1953 a number of trees of *Eucalyptus* spp. on Ourimbah State Forest No. 290 (Newcastle Forestry District: Wyong Subdistrict) were reported to be dying, and during the years 1956–1960 the cause of these deaths was investigated. Mortalities at first appeared to be the result of persistent attack by *Glycaspis* spp. during a number of years, and although apparently not the direct cause of the deaths, the debilitation due to continual defoliation caused by them was a contributing factor. Weakened trees appeared to induce attack by *Xyleborus truncatus* Er. (Coleoptera: Scolytidae) which

was associated with brown staining in the timber, and deaths of trees (Moore, 1959). A complex of species of the genus *Glycaspis* was studied and many new species described (Moore, 1961).

E. saligna, *E. paniculata* J. E. Smith (grey ironbark), *E. triantha* Link. (white mahogany), *E. deanei* Maiden (Deane's gum) and *E. umbra* R. T. Baker (bastard white mahogany) grew intermingled on an attacked area on Ourimbah S.F., and most of the species of *Glycaspis* found there fed and bred only on their respective host-species. From an examination of *Glycaspis* spp. populations some 300 miles further north it was verified that considerable host-specificity occurred. Collections of adults, nymphs and lerps were made in many areas, as the tree-species collectively constituting some of the timber-stands differed considerably from the timber-stand composition on Ourimbah S.F.

The biology of *Glycaspis baileyi* Moore occurring from sea-level to over 3,000 feet in New South Wales was studied.

When investigations were commenced by the writer during 1956, current deaths of trees were apparently confined to *E. saligna*, but large populations of psyllids also persisted on the other tree-species. Variable degrees of attack, from very slight to heavy, with numerous trees apparently killed by constant infestation over many years in the one locality, were occurring in approximately 150 separate areas throughout the Gosford-Wyong district.

The most extensive single area of severe attack, on Ourimbah S.F., extended for about 1½ miles at a more or less constant width of about 9 chains, along the approximate centre of a slope with a general north-easterly aspect, the continuous area of attack crossing many small intersecting gullies and occasionally encroaching on the flats of the open valley where *E. saligna* grew. All of the *Eucalyptus* spp. were attacked by large, discrete populations of psyllids, principally of the genus *Glycaspis*.

The distribution of *E. saligna*, the principal host of *G. baileyi*, is from the south-east corner of Queensland, to Bateman's Bay on the south coast of New South Wales, and it occurs only within 100 miles of the coast, between sea-level and 1,000 feet altitude in the south to about 4,000 feet altitude at the northern extremity of its range (Anon., 1957).

Damage.

During the early stages of an incipient large population of *Glycaspis* spp. damage is not readily discernible from the ground. The first indication of psyllid attack may be the presence of bell-birds. Damage is often characteristic of the particular psyllid species concerned.

Foliage of *E. saligna* heavily attacked by *G. baileyi* gradually becomes reddish-purple, and deepens in colour. This coloration is evident from a considerable distance when the attack has persisted for some months, and is most evident during the late winter. Foliage may remain in this condition for some months during the colder months of the year, and during early spring the trees shed most of the affected leaves. New crown foliage or epicormic growth on the trunks and branches may then appear and the trees seem to be recovering. This regrowth may be again heavily attacked, the trees thus being weakened further by recurring attempts to produce new foliage. Trees almost defoliated many times over a number of years are thus conditioned for attack by other insect pests.

A tree of approximately 12″ diameter-at-breast-height, with about half of its normal crown-foliage, and attacked by a large population of *G. baileyi*, may carry approximately 15,000 last instar nymphs at the one time.

Recent Infestations.

(*a*) Wauchope and Glen Innes Forestry Districts.

The first known official report of *G. baileyi* occurring in large numbers on *E. saligna* was made during 1944 by Mr. F. M. Bailey (Forestry Commission records). Attack occurred beside the Oxley Highway between Yarras and Yarrowitch, on Doyle's River State Forest No. 911 (Wauchope Forestry District) and Enfield S.F. No. 337 (Glen Innes

District). *E. saligna* had been severely attacked in the vicinity of Myrtle Scrub, Tobin's Camp and Stockyard Creek, where the infested areas were at an altitude of about 3,000 ft.

During 1957 and 1958 attack by *G. baileyi* was reported on three small areas on Doyle's River S.F., causing severe defoliation and death of young *E. saligna* trees of 6″ to 8″ diameter-at-breast-height. *Xyleborus truncatus* was present in all stages of its life-cycle, in association with brown staining of the timber.

(*b*) Coff's Harbour Forestry District.

During 1949 and 1952 severe infestations of *G. baileyi* occurred on *E. saligna* on Cloud's Creek S.F. No. 111, and on Moonpar S.F. No. 489. The psyllids persisted for many years and the total area affected was assessed as more than 100 acres.

The areas of attack by large numbers of *Glycaspis* spp. were inspected by the writer during May, 1959, and heavy attack persisted on crowns and epicormics of *E. triantha* on Cloud's Creek S.F. *E. dunnii* Maiden (white-gum) was attacked in an area 10 miles north, and *E. saligna* in an area 1 mile north of Cloud's Ck.

(*c*) Taree Forestry District.

At Craven Plateau Mill Road in the Barrington area during 1952, severe attack by *G. baileyi* had occurred on young regeneration of *E. saligna* for more than three consecutive years.

During 1952, 1953 and 1957, 30 to 40 acres of *E. saligna* were severely attacked on Bulga S.F.

From the inspections of each of the above Districts it was determined that the severity and extent of attack were much less than that occurring in the Newcastle Forestry District at the same time.

(*d*) Newcastle Forestry District.

The first known report of *G. baileyi* on *E. saligna* in the Gosford-Wyong area was made during 1950 by Mr. P. C. Hely (N.S.W. Dept. of Agriculture records). Large trees and saplings were affected in a manner similar to those in the previously mentioned Forestry Districts, and attack had been apparent during the two previous seasons.

Large numbers of *Glycaspis* spp. were reported on *E. paniculata* on Ourimbah S.F. during 1952 and 1953 when a small percentage of the trees was dying. Beetles of the Scolytidae, particularly the species *Xyleborus pseudoangustatus* Schedl, were associated with the dying and dead trees. By 1954 numerous *E. saligna* and *E. deanei* had died and damage by the psyllids was reported to have been evident for some years. *E. triantha*, *E. umbra*, *E. paniculata*, *E. deanei* and *E. saligna* were all affected during October, 1956.

In all areas of infestation bell-birds occurred in variable numbers.

Biology.

So that biological observations could be made under conditions as near natural as possible, coppice growth and regeneration of *E. saligna* were enclosed in separate cages of mosquito netting (Plate ix, figs 1 and 2), the netting forming the base of each cage being tied around the plant stem. These cages, approximately 3 ft. × 3 ft. × 4 ft., were erected during 1957 in the heavily attacked area on Ourimbah S.F. All adults and nymphs of *G. baileyi* were removed from the cages, leaving only the eggs on the leaves. The netting excluded small parasitic wasps of the Chalcidoidea, and during these observations parasitism of nymphs on foliage of coppice near the cages varied from 23% to 50%. External shade-temperatures during these observations were: highest maximum 65° F., lowest maximum 53° F., and the lowest minimum 38° F.

Eggs (Plate ix, figs 3 and 4).

Length 0·41 mm.; width 0·15 mm. Eggs are firmly attached to the leaf-surface by a narrow, curved pedicle, the length of which is 0·10 mm., and their long axes form an angle of about 35° with the leaf-surface. The translucent eggs are at first cream to pale yellow, later deepening in colour, and with a reddish-orange proximal area; the chorion is hard, smooth, shiny and transparent. Oviposition occurs on either the upper or the

lower leaf-surface, the greatest number of eggs usually occurring on the former during the cooler months of the year. They may be found singly, or in groups of from two to about 100. The larger groups, usually oviposited when a female feeds beside the mid-vein of a leaf, are formed of eggs arranged side by side in a line describing an arc, or a complete circle composed of 80 to 100 eggs. This suggests a feeding-site favourability for this species of psyllid, and may be associated with a more copious supply of sap in the larger veins. It appears that the circles of eggs (i.e., up to about 100 eggs) are oviposited by the one female. Eclosion is effected from the distal end of the egg.

The number of eggs occurring on *E. saligna* leaves randomly collected from coppice, and epicormics at a height of 20 ft. and 50 ft. during June, 1958, is: Number of leaves examined, 225; average number of eggs per leaf, 36·8; greatest number on one leaf, 225; on seventeen leaves there were no eggs. There was a large population of psyllids in the area from which the foliage was collected.

The average number of fully formed eggs dissected from 10 females collected in the field on the same day was 37·1, the greatest number from one specimen being 53.

No parasitism, predation or disease of psyllid eggs was observed during these investigations.

Nymphs.

G. baileyi passes through five nymphal instars, each of which may be distinguished by the morphology of the antennae (Text-figs 1 to 5).

Within a few minutes after emergence, the first instar nymph commences to feed, and to construct its lerp. The proboscis is inserted adjacent to main veins, to approximately half of the thickness of a more mature leaf; thus the oil-glands of the leaf are always avoided. Prior to feeding, nymphs may move from the leaf where they have emerged to another leaf usually nearer the growing tip of the branchlet where the younger leaves appear to be preferred.

The dark coloration (Text-fig. 6) on nymphs of all instars is variable, and this, together with the orange coloration, is always more intense on those feeding on the upper leaf-surface.

During the third, fourth and fifth instars, a fine, filamentous excretion, waxy in appearance, issues from the edges of the three posterior abdominal segments. During ecdysis the nymph expands and contracts the abdomen, and arches the thorax so that the exoskeleton fractures longitudinally along the medio-dorsal line. The final instar nymph moves out from under the lerp before ecdysis.

Growth during each instar is more or less continuous and measurements are considered arbitrary. Antennal sensoria are shown in the figures.

First instar: Pale yellow to orange; dark grey marks absent; eyes red. Antennae 3-segmented (Text-fig. 1), pale or dark grey, darker distally; distal seta 1½ to 2 times length of distal segment.

Second instar: General colour as for first instar; dark marks may be absent, or present as in Text-fig. 6. Antennae 3-segmented (Text-fig. 2); distal seta one-half to two-thirds length of distal segment.

Third instar: General colour as for first instar, with eyes deeper red. Antennae 5-segmented (Text-fig. 3).

Fourth instar (Text-fig. 6): General colour as for the first instar, but eyes darker, sometimes purplish-red; antennae and legs darker. Abdominal segments sometimes suffused grey or red laterally. Antennae 7-segmented (Text-fig. 4).

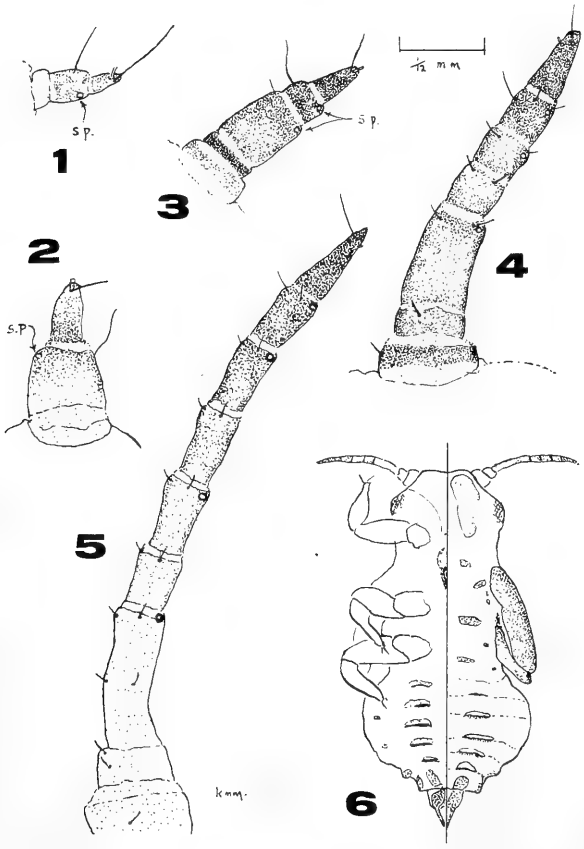
Fifth instar: The colouring of nymphs is variable, denoting an early stage and a late stage in this instar. Antennae 9-segmented (Text-fig. 5); grey to black, darker distally.

(*a*) Early stage: 5th instar.

Head: Yellow to orange with variable amounts of red suffusion; eyes pale violet, pale grey or pale green. Dark, longitudinal marks on head sometimes present, and the head may be suffused red. Some nymphs have a dark grey crescentic mark which may

be suffused red, on each side of median area on posterior border; marks may be joined by a dark line. Wing-pads grey to black.

Thorax and abdomen with dark markings as described for previous instars, but generally indistinct because of surrounding grey to black suffusion. Broad, longitudinal median stripe on thorax, yellowish. Abdominal segments suffused grey to black laterally; yellow to orange median area, narrowing on each segment posteriorly to distal extremity of abdomen.



Text-figures 1-6. 1, Antenna of first instar nymph of *Glycaspis baileyi*. 2, Antenna of second instar nymph of *Glycaspis baileyi*. 3, Antenna of third instar nymph of *Glycaspis baileyi*. 4, Antenna of fourth instar nymph of *Glycaspis baileyi*. 5, Antenna of fifth instar nymph of *Glycaspis baileyi* (sp., sensory pit). 6, Penultimate instar nymph of *G. baileyi*: left, ventral aspect; right, dorsal aspect.

Ventral: Head pale yellow or cream, with anterior border darker; thorax and wing-pads pale grey; abdomen pale grey or suffused pale turquoise-blue; abdominal segments with a series of dark lines and lateral spots; lateral areas may be suffused grey; legs grey, darker distally.

(*b*) Late stage: 5th instar.

Colouring of head as for early stage, but dark longitudinal marks may be absent; eyes grey, green, violet or suffused with red.

Dark markings on thorax and abdomen paler, and thorax suffused with pale to deep greenish-yellow; red area each side of broad, yellow to green, median longitudinal stripe.

Abdomen: First segment yellow, orange, greenish-yellow or green, with variable amounts of red suffusion; median area, yellow or orange, sometimes turquoise or green laterally, with contiguous longitudinal areas red suffused grey, and with yellow or orange median area of variable widths, narrowing posteriorly, on abdominal segments 2 to 6; dark lines on posterior edges of segments.

Ventral: Pale to bright turquoise; dark markings as for second instar, with lateral greyish suffusion.

Some specimens show little or no darkening during this or earlier instars, remaining yellow to orange in colour, with variable amounts of red suffusion. This is associated with parasitism by wasps of the Chalcidoidea.

Adults.

Adults feed on the sap of the host-plant in a manner similar to the nymphs. They appear to prefer the younger foliage when it is available. While they feed, they move in a circle around the point of insertion of the proboscis. Female adults may feed for several days before commencing oviposition. Globules of a clear liquid coated with a fine, white powdery substance are exuded from the anal aperture.

A short time elapses after the emergence of the adults before their complement of dark colouring has attained maximum intensity, and as they feed, the turquoise colouring of recently emerged adults turns to red.

Life Cycle.

Six or seven generations of *G. baileyi* may occur during the one year. The period from oviposition to eclosion of the winter generation reared at Lisarow is 32 to 40 days, and about 8 to 10 days for the summer generation. Nymphal development of the winter generation occupies 42 to 53 days, so that the total period from oviposition to the adult stage is 80 to 93 days. The second or spring generation occupies about 53 to 63 days and the early autumn generation is approximately of the same duration.

There is a considerable overlap of generations in the field throughout the year, with no evidence of a seasonal colour-variation within the species.

Lerps (Pl. ix, figs 5 to 7).

Lerps of *G. baileyi* are round and conical, with the smallest section constructed by the first instar nymph, at the apex. They vary in size according to the instar of the nymph which they cover, and may be almost 5 mm. in diameter. The exudation of which they are composed is at first transparent and soft, but soon becomes opaque, harder, and crystalline in appearance. They are usually white, but a few may be grey, brown or pink in colour. Lerps of the many species of *Glycaspis* are known to be sweet to the taste.

Lerps are attached to either the upper or the lower leaf-surfaces; they are rarely contiguous, usually more than 1 mm. apart when nymphs are in the last instar. When rearing *G. baileyi* on *E. camaldulensis* some third instar nymphs constructed their lerps on young stems of the plant. This does not occur on *E. saligna.*

The method of construction of a lerp is variable. A nymph, with its proboscis inserted for feeding, exudes from the posterior abdominal segment a colourless, transparent, sticky fluid which adheres to the leaf-surface. On contact with the atmosphere the exudation appears to solidify partially, thus allowing the nymph to construct narrow ribs upward and over itself as the abdomen is raised with short, quick rubbing movements, backward and forward along and beyond these ribs. The number of supports may vary from five to fifteen, and when the lerps are partly constructed with the supports joined more or less at the apex, the sides are filled in as the nymph attaches an almost continuous stream of exudation from one rib to the other, and to the base of the lerp.

After each nymphal ecdysis additions are made to the wall of the lerp, increasing its height and diameter. The additional excretion is first attached to the internal surface of the existing lerp, close to the base. A ledge, represented by the previous area of attachment to the leaf-surface, projects beyond the new portion until this is eventually

produced to a greater diameter than the ledge, as it is forced upward. The relevant portions constructed by the various nymphal instars are distinguished by ridges around the outer surface of the lerp.

Loosening of the lerp may be caused by humid or showery weather, heavy dews, birds, the rubbing together of the leaves, larvae of syrphid predators, or when there is copious excretion by the nymph. Large numbers of lerps covering late-instar nymphs, when detached from the foliage, almost cover the ground beneath trees carrying a large population. After a lerp is displaced, and another is being constructed by a late-instar nymph, a variable number of struts is raised toward the apex before the circumference of the base is commenced. The reconstruction of more or less transparent, thin-walled lerps is comparatively common, and the opaque struts in the translucent or transparent walls are readily visible. The reconstructed portion (Pl. ix, fig. 7) is dome-shaped, and not conical as is the original lerp (Pl. ix, fig. 6). The exuviae shed at the completion of the first four nymphal ecdyses may be attached to, or incorporated in, the internal surface of the lerp, usually toward the apex.

When dry, lerps apparently afford little or no protection from parasites or predators, so that their main function may be to reduce desiccation of the nymphs, or act as a fortuitous method of disposal of their excess exudation.

Parasitized nymphs deposit an additional layer of excretion on the leaf-surface, inwards from the circumference of the lerp, which becomes hard and dry, thus more firmly attaching the lerp to the leaf.

Nymphs of *G. baileyi* at times exude large quantities of honeydew which flows from beneath the lerps. Sooty mould, developing on the honeydew, may cover the surface of the foliage.

Numerous straight, or curled, hair-like filaments are sometimes present on the outer surface of lerps, and are composed of the same type of exudation as that constituting the lerps.

Excessive humidity present in the air in artificial containers or in the field condenses on, and covers, lerps, but they retain their normal shape when drying. They may become partly or wholly covered externally with a greenish-black fungus which spreads downwards from the apex, but which does not appear to affect the nymphs adversely beneath.

Lerps of *G. baileyi* are occasionally constructed beneath those of species belonging to other psyllid genera.

Some idea of the population density on foliage, collected at random from various heights during June, 1958, may be gained from the following: Number of leaves inspected, 50; total number of lerps, 2,807; average number of lerps per leaf, 56; greatest number on one leaf, 166.

Distribution.

The known distribution of *G. baileyi* in New South Wales is: Cloud's Creek State Forest; Moonpar S.F.; Doyle's River S.F.; Bulga S.F.; Wyong S.F.; Ourimbah S.F.; and in more than 150 separate localities in the Gosford-Wyong area generally.

G. baileyi probably occurs wherever its host-plants are distributed naturally.

Dispersal.

Populations of *G. baileyi* generally showed a relatively sudden increase in numbers during March-April, increasing to plague proportions during the winter months and persisting in large numbers to September, October or even to January, depending on the weather conditions. The population then usually decreased and remained in low numbers until the following March or April, although, again, weather conditions influenced variations in this generalized pattern of fluctuations in numbers.

Adults of the genus *Glycaspis* are capable only of limited flight. After the initial jump from a leaf they have not been observed to fly beyond about 10 feet in still air.

During five years of observations on one valley at Lisarow where *G. baileyi* periodically occurred in plague numbers, the rate of movement was recorded. The centre of infestation proceeded about 1,000 yards in an easterly direction along the slope, thus

representing an average annual lineal dispersal of 200 yards during that time. The original area of infestation was then apparently free from attack, numerous trees of *E. saligna* had died, and regeneration appeared to be vigorous and healthy. During the fifth year (1958–1959) the extension of attack equalled that of the previous four years. Such movement did not occur in all areas, for some populations observed during those same years remained static.

Dispersal of large numbers of some small insects over great distances by air-currents occurs, and adults of this species may be carried from one locality to another by this means, although they are not readily detached from the leaves when feeding.

Parasites and Hyperparasites.

In the nymphal stages *Glycaspis baileyi* is attacked by a complex of species of the Chalcidoidea during all months of the year.

After consuming the contents of the nymphal skins the larvae of the parasites and hyperparasites pupate within them, the adults later emerging by cutting a round hole with their mandibles through the skin and the lerp, close to the leaf-surface.

The early stage of parasitism of psyllid nymphs by chalcidoid wasps may be determined from the swelling of the thoracic region, and later by distension of the abdomen. Oviposition by parasites and hyperparasites occurs through the lerp, and penetration by the ovipositor of a single wasp may occur several times, and in different places, through the one lerp.

Adult wasps of most species reared usually emerged in about 6 to 10 days after pupation during summer, or about 15 to 20 days during winter. Lerps covering nymphs showing a late stage of parasitism are more firmly attached to the leaf-surface than lerps covering unparasitized nymphs. Parasitism of first instar nymphs was not observed.

Small, black chalcid eggs were often found in nymphs. The black eggs, from which an attached "stalk" protrudes through the integument of the nymph, were found inserted in the ventral area of the abdominal segments, in and beneath the wing-pads, below the thorax, in the legs, eyes or other parts of the head, ventrally or laterally. As many as four black eggs were found in the one nymph, and psyllids of other genera occurring with *G. baileyi* were also attacked. Larvae of wasp-parasites in the skins of psyllid nymphs also contained these black eggs and it was assumed that they had been attacked by hyperparasites. Black eggs have been found in nymphs of instars 3 to 5. When parasitized, a psyllid nymph is gradually immobilized, becomes swollen by the parasite larva within, and is ventrally attached firmly to the leaf-surface.

For assessments of parasitism and hyperparasitism, nymphs of penultimate and last instars only were utilized. They were collected each month from the same area of heavy attack at Lisarow. After selection of a tree of *E. saligna* with a diameter-at-breast-height of no more than 15″, it was felled, and large twigs with foliage attached were removed from different areas of the crown, and epicormics when present, from the branches and varying areas of the stem.

As much material as possible was carried to the laboratory where leaves bearing the largest lerps were randomly taken and placed in a large container. From this container leaves were taken at random and all nymphs of instars 4 and 5 assessed as being parasitized or not parasitized. No more than 200 nymphs were examined at any one assessment and, when possible, at least 100 nymphs were examined at each assessment. When the population in the field was low, as many as five trees were felled to obtain a sufficient number of nymphs for an assessment. Results are expressed as percentage parasitism in the graph showing the association of high parasitism with drier weather conditions (Text-fig. 17).

In the attacked area on Ourimbah S.F., certain chalcid species were found to attack *G. baileyi* consistently, but not the species of *Glycaspis* which occurred on *E. triantha*, although these host-tree species grew intermingled. Some of the Chalcidoidea reared from *G. baileyi* from Cloud's Creek, Moonpar and Bulga S.F's appear to be other species than those reared from *G. baileyi* collected in the Gosford-Wyong area.

It was not possible to obtain identifications of these parasites and hyperparasites, and as a basis for reference, figures of the antennae of those occurring on *E. saligna* are given. The reference-letters are attached to specimens in the collection of the Forestry Commission.

From nymphs on *E. saligna*: From Cloud's Creek and Moonpar S.Fs. (highlands): C, D^1, G, J^1. From Gosford-Wyong area (coastal): A, B, C, D^1, F^2, G, H, J^1, J^2, M^1, P, R, T, W.

From nymphs on *E. triantha*: From Cloud's Ck. S.F.: D, E, F^1, F^2, H, J, J^1, K, M, M^1. From Gosford-Wyong area: D, E, F^1, F^2, H, M, M^1.

Those bred from a common host-plant association in both areas may thus be summarized as: From *E. saligna*: C, D^1, G, J^1. From *E. triantha*: D, E, F^1, F^2, H, M, M^1; and those bred from both hosts in a common area as: Cloud's Ck. S.F.: J^1. Gosford-Wyong area: F^2, H, M^1.

Specific host-association is thus indicated by the following chalcids occurring only on: *E. saligna*: A, B, C, D^1, G, P, R, T, W; *E. triantha*: D, E, F^1, J, K, M.

Some Details of Parasites and Hyperparasites.

Species (A). Hyperparasite (?). These adults are the smallest of the species reared from *G. baileyi*, and are approximately 0·88 mm. to 1·07 mm. in length, the female being slightly larger than the male. They are black, indistinctly suffused dull green or purplish, with the frons metallic-green. The scape of the antenna of the male is mainly yellowish-brown and that of the female is black. Antennae are creamy-brown, moderately hairy on the male, but less so on the female (Text-fig. 7).

Species (B). Parasite (?). Adults suffused metallic-green or -blue. They have been bred from last instar psyllid nymphs. The broad antennal scape is cream, the small proximal segment with a black mark (Text-fig. 8), and remaining segments suffused pale brown. It has been reared only from the Gosford-Wyong area.

Species (C). Parasite (?). This species is suffused purplish-black with frons metallic-green. Antennal scape mainly yellow, grey distally; proximal antennal segment marked with black, other segments suffused pale brown (Text-fig. 9).

Species (D^1). Parasite (?). Metallic-green. Antennae similar to (C).

Species (G). Parasite (?). Dull purplish-black, with frons metallic-green. Scape of antenna yellow; other antennal segments pale brown (Text-fig. 10).

Species (H). Hyperparasite. Metallic-green with antennal scape bordered black ventrally (Text-fig. 11).

Species (J^1). Hyperparasite. Adults black, with frons and ventral area dull purple or green. Antennal scape and antennae shiny black (Text-fig. 12). This species appears to be the female of J^2. They have also been reared from the species of *Glycaspis* occurring on *E. cameroni* Blakely & McKie (diehard stringybark).

Species (J^2). Hyperparasite. Adults as J^1, but with antennae hairy.

Species (M^1). Hyperparasite (?). Adults black, with scutellum faintly suffused green. Antennae similar to J^1, but less hairy. Antennal scape black; proximal segment black, remainder dark brown.

Species (P). Dull bronze-green with frons bright metallic-green. Antennal scape black at distal two-thirds on internal face and on posterior edge, yellow on external face (Text-fig. 13).

Species (R). Parasite. Bright metallic-green, bronze-green or metallic-blue-green. Antennal scape black, sometimes suffused brown or cream distally; shape similar to (C); segments grey-brown, with the club darkest.

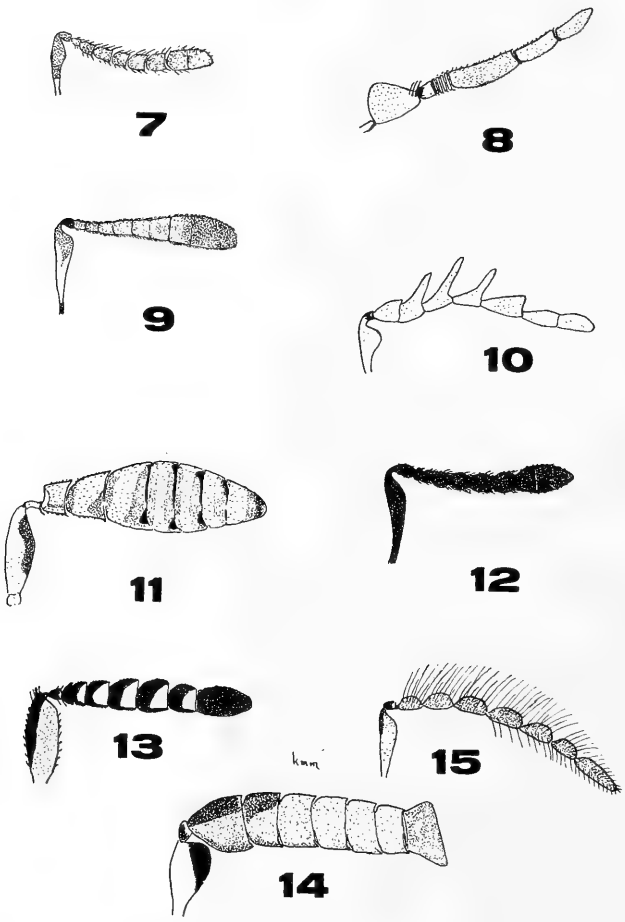
Species (T). Hyperparasite. Metallic-green. Broad antennal scape yellow, marked with black ventrally; antennal segments brownish-yellow to grey, small basal segment and following two or more segments marked with black dorsally; apical segment truncate (Text-fig. 14).

Species (W). Bright metallic-green. Antennal scape cream, tipped black distally; antennal joints hairy (Text-fig. 15).

Predators.

Syrphidae.

Many larvae of *Syrphus viridiceps* Macq. (Diptera: Syrphidae), predatory on nymphs of *G. baileyi*, were reared to the adult stage. Their life cycle occupies about 11 weeks during winter, 5 weeks during spring and 4 weeks during summer. The opaque, white eggs, approximately 0·88 mm. in length, and with flattened tubercles on the chorion, are laid on the leaf-surfaces, usually near large groups of lerps.



Text-figures 7-15. Antennae of parasites (Chalcidoidea): 7, Species A. 8, Species B. 9, Species C. 10, Species G. 11, Species H. 12, Species J1. 13, Species P. 14, Species T. 15, Species W.

Fully grown larvae may be 8 mm. to 10 mm. in length and are variable in colour from pale yellow in the early instars to yellow, yellow and orange, orange, orange and green, green, green and grey or black, and various combinations of some or all of these colours. Larvae are mottled with variable amounts of grey or black.

The puparia, about 6 mm. in length, are at first light brown with wavy, light grey lateral markings and medio-dorsal spots, which darken to almost black.

During 1957 a larva of *S. viridiceps* destroyed 67 penultimate and last instar nymphs of *G. baileyi* during its larval life of about 15 days. The adult syrphid emerged ten days after pupation.

Occurrence of the various stages of *S. viridiceps* during these investigations were: Eggs: April to July, September, November to January; Larvae: April to January, and most numerous during June and July.

S. viridiceps was abundant during most of the year when psyllid nymphs were plentiful, and usually absent from about January to March when psyllids were few in number.

Hemerobiidae.

A larva of the brown lace-wing, *Drepanacra* sp., attacking nymphs during July, 1957, pupated by 23 August, the adult insect emerging on 1 September, 1957.

Chrysopidae.

Larvae of the green lace-wing, *Notochrysa ramburi* Schneider, are predatory on nymphs of *G. baileyi.* Larvae place pieces of lerp, sooty mould, skins of destroyed psyllid nymphs and other debris on their backs. When about to pupate, they spin thin, silken cocoons to which they attach externally the debris and cast skins. Two larvae pupated during November, and adults emerged two weeks later.

Coccinellidae.

Larvae of *Rhizobius evansi* Mulsant were reared during November and April. Adults emerged about six weeks after pupation during autumn.

Adults of the black, yellow-banded larvae of *Leis conformis* (Boisd.), predatory on *Glycaspis* spp., were also reared.

Acarina.

The red mites, *Erythraeus urrbrae* Womersley (Erythraeidae), were numerous during the winter and spring of 1958, principally on adults of *G. baileyi*, but they did not appear to affect either adults or nymphs adversely. They were usually found attached to the abdominal intersegmental membranes, or sutures of the head and thorax. Nymphs beneath lerps were also attacked.

Arachnida.

Numerous spiders, in leaves which they had curled and spun together with their webs, were predatory on the psyllids. Their webs covered groups of lerps, so that when psyllid adults emerged, some became entangled in the web. Species were identified as *Theridion pyramidale* L. Koch (Thoridiidae), *Deliochus zelivira* (Keyserling) and *Arcys clavatus* Keys. *Diaea* sp. is predatory on *D. zelivira.*

During April and May, 1958, practically the entire crowns of trees showing severe damage by *G. baileyi* were shiny with the webbing of *T. pyramidale.*

Birds.

Manorina melanophrys Latham (the bell-bird) was present wherever *Glycaspis* spp. were most numerous throughout the coastal and highland areas of N.S.W. This bird belongs to the family of honey-eaters, and appears to prefer lerps of *Glycaspis* spp. although it is also insectivorous (Campbell and Moore, 1956).

From general observations covering the period of investigations, the population of bell-birds in each area studied did not noticeably fluctuate, irrespective of the considerable fluctuations in psyllid population.

Experimental Work.

Effects of Various Temperatures and Humidities on Emergences of Nymphs.

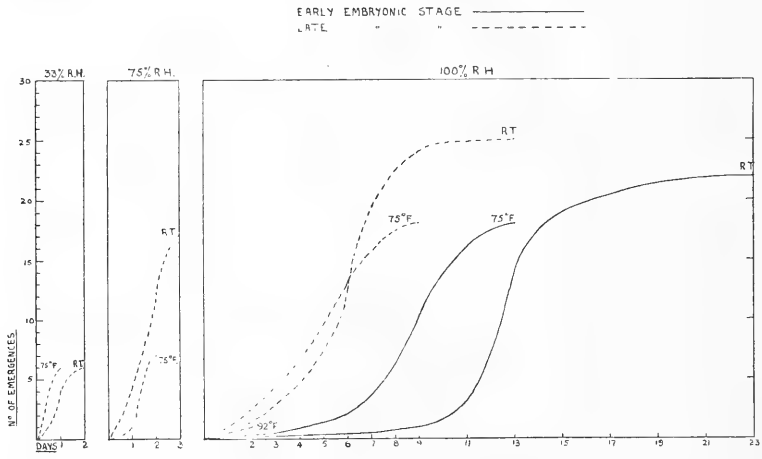
The embryonic development in eggs was regarded as of two stages, the early stage considered as terminating when the eyes of the future nymph occurred near the distal end of the egg, approximately 15 to 20 days after oviposition in the winter generation, or 5 days in the late spring generation. The late stage was considered to occupy the remainder of the time to eclosion of the nymph and was represented by a period of from 17 to 20 days during winter, or about 3 days during November-December.

A total of 360 eggs of the winter generation, in half of which the embryos were in the early stage, were selected at random from the one tree of *E. saligna* in the severely attacked area on Ourimbah S.F. The two stages of embryonic development were separated, and portions of leaves with 30 eggs attached were placed in open Petri dishes. Six dishes each containing eggs in the early stage, and six in the late stage were used

in various combinations of temperature and relative humidity. Eggs were examined on the fifth day. A longitudinal indentation in the ventral surface of the chorion was interpreted as indicating desiccation of the egg-contents.

Because of the large number of eggs desiccated by the fifth day, a further experiment was carried out, with the same procedure and treatment as previously, with additional treatments at 100% r.h. for each temperature. Desiccation accounted for 99% of the mortalities.

Results indicate that the most favourable conditions for embryonic development and emergence of the nymphs were obtained with a combination of the higher r.h. and lower temperatures.



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Text-figure 16. Emergences of nymphs of *G. baileyi* from eggs held at various temperatures and humidities.

Rearing of Nymphs.

In an attempt to determine whether *G. baileyi* could survive on alternative host-species, cages were erected at Lisarow, over coppice about 3 feet in height, of *E. triantha*, *Angophora floribunda* (Sm.) Sweet (rough-barked apple) and young trees of *E. camaldulensis* Dehn. (Murray River red-gum). Five hundred eggs of *G. baileyi* were placed on the foliage of each of two bushes of each of these species. The nymphs apparently could not survive on the two former species, although they attempted to feed on their foliage. This experiment was repeated three times on *E. triantha*, with the same results.

Twenty early instar nymphs covered by their lerps were observed on the *E. camaldulensis*, and six were reared to the adult stage. A further attempt to rear *G. baileyi* on this host-plant was made, and although numerous first instar nymphs were observed to construct lerps, only 40 specimens survived to the adult stage from approximately 800 eggs placed on the plant. Again, about 500 eggs were placed on the same plant, and 48 adults and 11 last instar nymphs were reared.

Blakely (1955) places *E. camaldulensis* in Series 15 (Exsertae) and, as far as is known, the natural ranges of *E. saligna* and *E. camaldulensis* are not contiguous, nor do they overlap at any point.

Some hundreds of nymphs of the species occurring on *E. paniculata* in the attacked area on Ourimbah S.F. were placed on *E. saligna*, but no adults were reared, although most nymphs had transferred to the *E. saligna* coppice as the branches and leaves of *E. paniculata* became desiccated. Large populations of *G. baileyi* were present in all infested areas during these rearing experiments.

Results of these experimental rearings assisted in determining a degree of host-specificity (Moore, 1961).

Discussion.

Information was sought from property-owners, timber cutters, bush-workers and the older residents able to assist with details of the occurrence and movements of bell-birds, or other relevant observations on the areas examined. Such information concerning felling and logging operations, with the consequent opening up of the undergrowth and thinning of the timber-stand, and occurrence of fires, etc., could not be correlated consistently with the increases or decreases in large psyllid populations.

Apparently reliable verbal reports by residents of some of the areas for 30 to 40 years indicated that populations of psyllids and bell-birds have persisted in certain localities on the poor-quality *E. saligna* along the creeks and watercourses of the more open valleys in the Matcham and Holgate areas for more than 50 years.

Possible Causes of Incidence of Attack.

Many areas where no plague population had been observed over a period of eight years previously, and where bell-birds were not then occurring, carried a large psyllid population during the years 1948 to 1959. Thus trees previously not carrying a large population of psyllids had apparently become suitable hosts during these years.

Plagues occurred on slopes of all aspects and with variable degrees of timber- or undergrowth-cover, in very sheltered situations, or in those open to strong, cold south-westerly winds or hot north-westerly winds, typical of winter or summer conditions respectively, occurring on the central coast of New South Wales. In some gullies, *E. saligna* on one of the slopes was sometimes attacked, while little or no attack occurred on the opposite slope. *E. saligna* of diverse ages and heights was plentiful in many gullies where no attack occurred. No consistent correlation of incidence of attack with age, aspect, or apparent general health of trees could be made.

Because of the general increases and decreases over many years in the populations of all the different species of *Glycaspis* found in the same locality at the one time and occurring on various host-tree species, it appears that some local influence common to all these psyllid species has acted as one of the predominating factors affecting their population numbers.

At times, but not consistently, incidence of new foliage on *E. saligna* appeared to be associated with an increase in population, and when available, new foliage appeared to be favoured for oviposition.

Should there be a feeding-site favourability on the leaves for adults to oviposit a maximum number of eggs, and an association with a stronger sap-flow, then a reduced flow of sap during drier years may be expected to influence the occurrence of large populations.

The regrowth of *E. saligna* on all of the areas investigated may be classed as relatively immature in comparison with that which occurred in those areas when undisturbed for long periods, as was probably the case prior to settlement by white people. Timber on these areas has been cut over many times, so that virgin stands are found only in the less accessible areas. Because of the intensified disturbances to the general equilibrium of the *Eucalyptus* spp. and other flora, which was presumably more or less stabilized over the preceding centuries, it appears that certain of these tree-species have regenerated in unfavourable situations for which previously they could not compete. Their present distribution may thus tend to induce attack on the species in less favourable situations, and so exert an important influence on the persistent large populations of *Glycaspis* spp. This appears to be paralleled in many localities in the Gosford-Wyong area where attack by longicorns (Coleoptera: Cerambycidae) is often more concentrated in *E. saligna* now occurring on or near the tops of ridges, where this species does not appear to flourish, but where the slower-growing and naturally occurring species such as *E. triantha* have been suppressed.

The only constant factor correlated with the large populations of the various *Glycaspis* spp. throughout the Gosford-Wyong area was that they were not in large numbers on the tops of ridges, even though their host-trees, occurring as a mixed stand, persisted to the ridges above the areas of attack. In many instances there was a

definite demarcation of the upper limit or lateral dispersal of heavy attack, which did not extend to the limits of host-distribution. This was sometimes denoted by the presence of a road, an abrupt rock-face, or a steep incline, beyond which the psyllids did not persist in large numbers. This suggests a definite local condition affecting the incidence of plagues, such as a soil-drainage effect unfavourable to the trees during seasons of high rainfall. To investigate this aspect, a 2½″ soil-auger was used to a depth of 6′ 4″ to examine occurrence and distribution of the various soil-types in attacked and adjoining areas. Although information from these investigations was inconclusive, it was found that the attacked areas examined were situated in areas of shallow top-soil (11″ to 18″) over deep, heavy clay, the consistency of the various clay layers varying considerably.

An association of the fungus *Armillaria mellea* (Vahl.) Quel. with *E. saligna* was noticed during November, 1959. Although the tree had recently died and the dead leaves were retained on the crown, no apparent cause of mortality apart from the fungal attack could be found. This fungus, also recorded from several other *Eucalyptus* spp., may be involved in the deaths of *E. saligna* in areas of large psyllid populations.

The discrete populations of *Glycaspis* spp. which occurred on *E. triantha*, *E. umbra*, *E. deanei*, *E. saligna* and *E. paniculata* on the one area at the same time, fluctuated considerably in relation to each other.

Some Influences Exerted by Weather.

De Bach (1958) presents evidence of the natural control of insect populations by weather-influences, and it appears that the general weather conditions have exerted considerable influence on the *Glycaspis* spp. populations in the areas studied. During seasons approaching the normal in New South Wales, the paths of anti-cyclones bringing drier air with consequent heavy frosts in winter, and higher temperatures with lower relative humidities in summer, is from west to east across the approximate centre of the State.

For about 15 years prior to 1957 the cyclonic centres had gradually moved in a southerly direction, and conditions of moist air with above-average ranfall and relative humidity had increased to a maximum during 1949–1950, when more than 86 inches of rain was recorded for each of these years. From 1942 a cycle of 15 years of comparatively higher rainfall occurred.

During the 6-year period 1917 to 1923 the yearly average rainfall exceeded the mean average for all recorded years on only one occasion, the same situation recurring during the 6-year period 1935 to 1941. These years may be considered as comparatively dry.

During the ten-year period 1924 to 1934 the mean was exceeded on all but two of these years, and for the 15-year period 1942 to 1957 the mean was exceeded on all but three occasions. The average annual precipitation for the latter period exceeded that of any of the other periods. These periods may be considered as years of comparatively high rainfall.

Records of the occurrence of *G. baileyi* prior to 1944 on the north coast, or prior to 1948 in the Gosford area, are not available. Lack of records thus limits the possibility of an accurate estimate of previous plagues. The earliest reports coincide with the cycle of years of higher rainfall, and the future influence of weather on the incidence of psyllid plagues will continue to be investigated in the latter district.

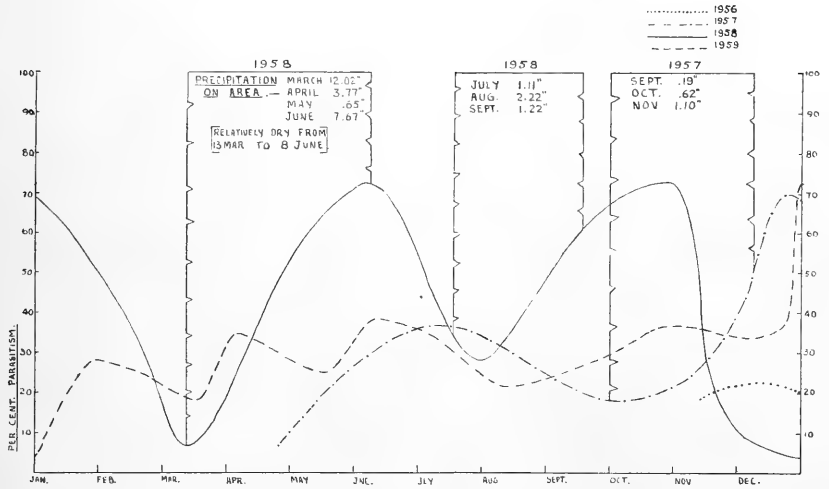
During the spring and summer of 1959–1960 general weather conditions remained comparatively humid until 24 January, 1960. In all of the areas examined large psyllid populations persisted from the previous winter until that time. Parasitism had risen to 72·2% by 21 January, the increase coinciding with a fine, dry period during the previous six weeks.

From 25 January to 29 January, 1960, the daily maximum shade-temperatures recorded near the area utilized for assessments of parasitism were 99°, 104°, 104°, 104° and 97° F.

These temperatures apparently exerted sufficient influence on the psyllid population to reduce it to such an extent that great difficulty was experienced in obtaining sufficient material (i.e., about 100 penultimate and last instar nymphs) for parasitism assessments during the following three months. Many other areas previously carrying large populations of *Glycaspis* spp. were then examined, and it was determined that they were almost, if not entirely, absent from each area.

Influence of Weather on Parasitism.

Lerps become covered with moisture during wet or humid weather, and after considering the method of oviposition by the chalcidoid wasps, it appears that they are able to operate at a high level of efficiency only when the lerps are more or less dry, and this is associated with periods of relatively dry weather conditions. Such conditions, occurring from September to December, 1957, March to June, 1958, August to October, 1958, and November, 1959, to February, 1960, were in each instance associated with significant increases in the incidence of parasitism by the chalcidoid wasps, which increased on each occasion until parasites reached the maximum numbers within the period of these investigations. This association of increase in parasitism with drier weather conditions is expressed in Text-figure 17.



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Text-figure 17. Percentage parasitism of nymphs of *G. baileyi* associated with periods of dry weather.

Influences exerted by dry weather conditions on the ability of the parasites to operate effectively and the apparent favourability of moist conditions with moderate temperatures for the increases of *G. baileyi* thus may have been the most important factors in the incidence of plague numbers of *Glycaspis* spp. in the areas studied.

Influence of Predators.

Bell-birds did not apparently diminish in numbers in the areas studied. Limited reductions in the psyllid populations at times coincided with various factors such as an increase in the population of *Syrphus viridiceps*, of chalcidoid wasps, or the various species of spiders. Parasites and predators were capable of exerting only temporary and limited control during the investigations. No reducing factor from which the psyllid population was unable to recover rapidly during the autumn and winter generations was observed.

Acknowledgements.

The author is grateful to his colleagues, Messrs. K. G. Campbell and P. Hadlington, for their assistance during the investigations; to Mr. P. C. Hely for assistance with

references on files of the N.S.W. Department of Agriculture; to Mr. F. R. Humphreys of the Chemistry Section, Forestry Commission of N.S.W., for advice and assistance with the laboratory experiments; and to Mr. L. A. S. Johnson of The Royal Botanic Gardens, Sydney, for identifications of the *Eucalyptus* spp.

For identifications of specimens, acknowledgements are made to Professor V. V. Hickman, Ralston Professor of Biology, University of Tasmania (Arachnida); Mr. D. K. McAlpine of The Australian Museum, Sydney (Coccinellidae, Syrphidae, Hemerobiidae and Chrysopidae); Mr. W. Stahl of the Forestry and Timber Bureau, Canberra (fungus); and to Mr. A. Womersley of the South Australian Museum (Acarina).

Appreciation is expressed to many owners of private property who offered helpful information, and to Messrs. J. Catt, R. E. Jackson, and W. Mann of Lisarow, who willingly granted permission to utilize trees on their properties during these investigations; to Messrs. K. D. Fairey and R. Moulton of the Forestry Commission for the photographs; to all who assisted with criticism of the manuscript; and to my wife for considerable assistance with its preparation.

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EXPLANATION OF PLATE IX.

Figs 1, 2. Cages erected at Ourimbah State Forest for biological observations on *Glycaspis baileyi.*

Figs 3, 4. Disposition of eggs of *G. baileyi* on leaf-surfaces.

Fig. 5. Partly constructed lerp of *G. baileyi.*

Fig. 6. Conical lerp of last instar nymph of *G. baileyi.*

Fig. 7. Dome-shaped lerp of last instar nymph of *G. baileyi.*

(Figs 3 to 5, photos by R. Moulton; Figs 6, 7, photos by K. Fairey.)

OBSERVATIONS ON SOME AUSTRALIAN FOREST INSECTS.

9. A New Species of Glycaspis (Glycaspis), (Homoptera: Psyllidae).

By K. M. Moore, Forestry Commission of New South Wales.

(One Text-figure.)

[Read 30th August, 1961.]

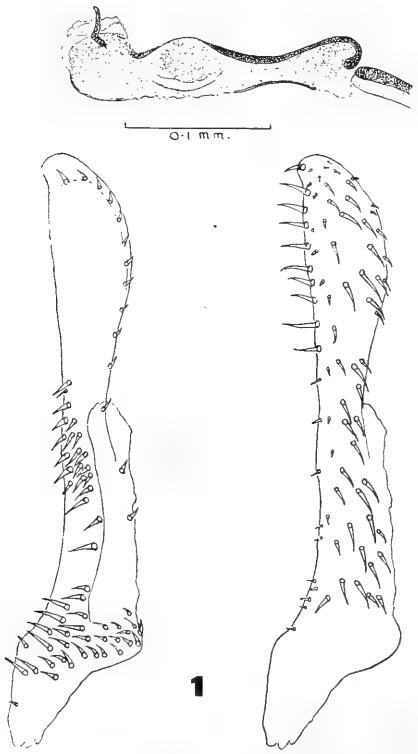
Thirty-eight species of *Glycaspis* (*Glycaspis*) and *Glycaspis* (*Alloglycaspis*) were previously described (Moore, 1961).

The host-association of the species described in this paper supports the remarks made concerning the *Eucalyptus* spp., and agrees with the placement of species constructing flat lerps in the subgenus *Glycaspis* (*Glycaspis*) in the earlier paper.

Glycaspis (Glycaspis) nundlensis, sp. nov.

(The name refers to the type locality of this species, Nundle State Forest).

General colour: (specimens preserved in alcohol) Yellow, with abdomen sometimes orange; black markings of pale to moderate intensity.



Male: Head: width 0·63 mm.; vertex, along suture, 0·22 mm., width 0·39 mm.; pale yellow with lateral borders pale grey narrowly from anterior prominences along anterior edge of ocelli and connecting with black areas on posterior of head; suture black; foveae small, pale grey; vertex deeply indented between suture and grey lines on lateral borders; genal processes, 0·29 mm. in length, cream suffused grey across

centres dorsally and with inner edges darker; antennae 1·41 mm. in length, dark brown to black, darkening distally, with segments 6 to 10 black. Pronotum: width 0·54 mm., lateral prominences cream, bordered black at bases posteriorly; anterior border narrowly grey; a small grey-brown depression between median line and each lateral border. Prescutum: pale yellow, narrowly edged black and with apical area black. Scutum: pale yellow, narrowly edged black on posterior border; two longitudinal lines pale grey, each side of median area. Metanotum: scutellum and meta-scutellum cream, the former indistinctly edged grey anteriorly and the latter posteriorly; a broad area each side lateral to the area between scutellum and meta-scutellum, grey lightly suffused rose-pink. Post-metanotum: yellow, narrowly edged pale grey, and a longitudinal stripe at centre of each side, dark grey to black. Abdomen: yellow with indistinct grey line on anterior and posterior border of segment 1 each side; a narrow black transverse central line on segments 2 to 6 with narrow grey area posterior to each on segments 2 and 3, and both anterior and posterior to each on segments 4 to 6. Genitalia: upper plate yellow, with black at base extending along medio-dorsal area to about half; distal projection tipped grey; claspers suffused pale grey, darker distally. Claspers and aedeagus as in Text-figure 1. Length of aedeagus (2 specimens) each 0·214 mm. Forewings: length 2·78 mm., venation pale brown. Legs: femora, tibiae and tarsi suffused grey, with posterior legs palest.

Female: Similar to male, but genal processes and lines on scutum darker; the antennae and dark marks on abdomen are paler. Ventral aspect, cream with a small black distal line each side of ovipositor.

Host-plant: *Eucalyptus radiata subplatyphylla* Blakely and McKie (almond-leaved peppermint).

Type Locality: Nundle S.F., five miles east of Foreman's house.

Types: Holotype ♂ on slide labelled "Nundle S.F. 20 xii 1960 K. M. Moore. *E. radiata subplatyphylla*". Paratypes: 1 ♂, 1 ♀, nymphs, on slide, and 1 ♀ and nymphs on slide, both labelled as above. Type material is deposited with The Australian Museum, Sydney.

Acknowledgement.

Acknowledgement is made to Mr. L. A. S. Johnson, of The Royal Botanic Gardens, Sydney, for identification of the host-plant.

Reference.

Moore, K. M., 1961.—Proc. Linn. Soc. N.S.W., 86 (1): 128-167.

THE REPRODUCTION AND EARLY LIFE HISTORY OF THE GASTROPOD *BEMBICIUM NANUM* (LAMARCK, 1822) (FAM. LITTORINIDAE).

By D. T. Anderson, University of Sydney.

(Plate viii; five Text-figures.)

[Read 26th July, 1961.]

Synopsis.

Spawning in *B. nanum* takes place during the spring and summer. Eggs are laid in gelatinous egg masses attached to the rock surface and hatch after about 12 days as pelagic planktotrophic veligers. The relationship between habitat and breeding in New South Wales littorinids is similar to that of littorinid species in other parts of the world.

Introduction.

It is well known (Anderson, 1960) that the littorinids present an intriguing problem of development, some species of the mid- and upper reaches of the shore lacking a free-swimming stage (e.g., *Littorina obtusata*, *L. saxatilis*, Pelseneer, 1911; Delsman, 1914; Linke, 1934; Thorson, 1946), others of similar habitat retaining planktotrophic veligers (e.g., *L. neritoides*, Lebour, 1935; *L. angulifera*, Lebour, 1945). The marked zonation of the New South Wales rock-platform littorinids *Bembicium nanum* (Lamarck), *Melaraphe unifasciata* (Gray) and *Nodilittorina pyramidalis* (Quoy and Gaimard) raises the question, whether corresponding anomalies exist among these species. A partial answer can now be given on the basis of the present study of the reproduction and life history of *B. nanum*.

Spawning.

Observations during 1960 and 1961 on the breeding season and spawning of a population of *B. nanum* inhabiting the rock platform at Harbord, north of Sydney, showed that both males and females contained ripening gametes by the beginning of September, but the first egg masses were not found in this locality until the end of October. Thereafter, however, they were commonly found until the end of April. No female of *B. nanum* was observed in the act of spawning, but the egg masses of the species were identifiable on the more indirect criteria of correlation between the onset of seasonal sexual ripening and the occurrence of egg masses in the habitat, and of exact correspondence of dimensions and colour of ovarian eggs transferred to seawater and eggs in the egg masses. The occasionally observed close association of females with newly deposited egg masses also supported the identification.

Egg masses of various ages were maintained in dishes of aerated seawater and observed at frequent intervals and drawings of living embryos made using a camera lucida.

The photographs of Plate viii were taken by the Department of Medical Artistry, University of Sydney.

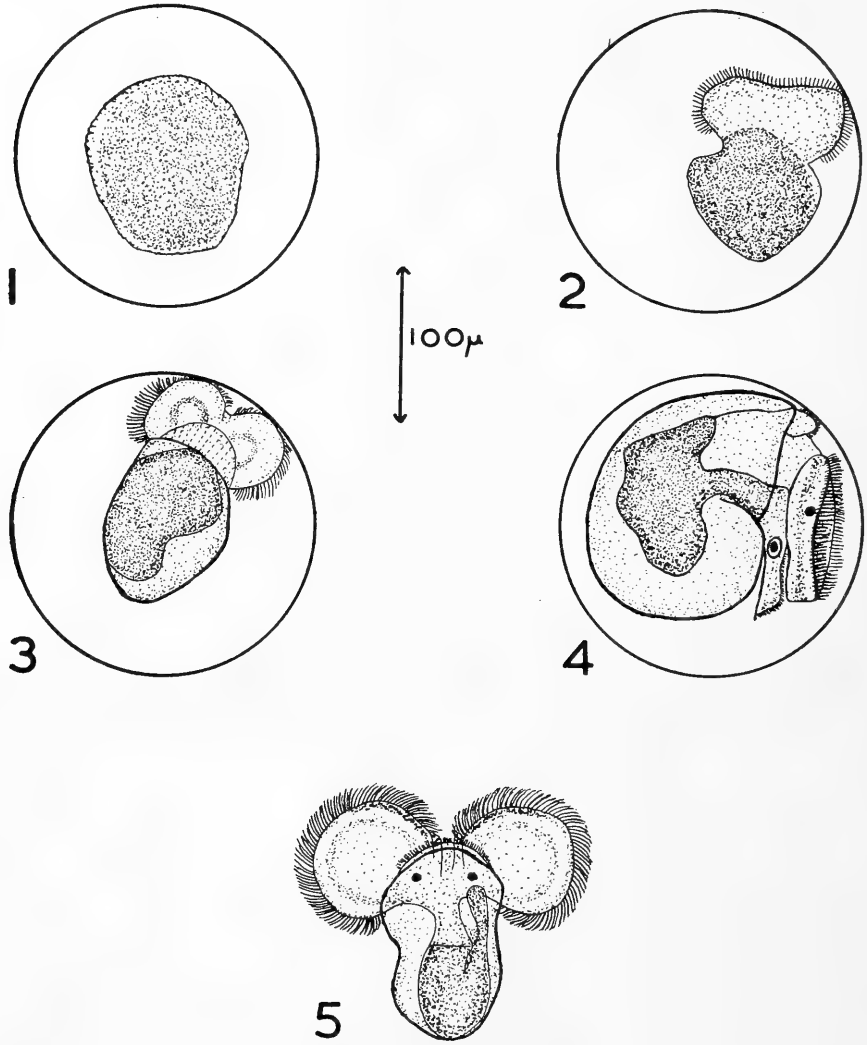
Development.

The spawn (Pl. viii) consists of an irregularly distributed, closely packed series of oval transparent jelly masses each containing about 100–200 creamy-white eggs 100μ in diameter, surrounded by ovoid transparent envelopes 200–220μ in length and 190–210μ in width. The group of jelly masses is firmly attached to the rock surface, generally in a sheltered position either in a fissure or under weed, in the habitat occupied by the adults.

The eggs develop rapidly, passing in about two days through a simple yolky trochophore stage (Text-fig. 1), then gaining in the succeeding two days the apical

tuft, blunt transverse foot and lateral velar lobes of the young veliger (Text-fig. 2). Rotation within the envelope begins at about this time.

During the next five days, the veliger enlarges and becomes more elaborate, with a well-developed bilobed velum and a pair of black eyespots, a ciliated foot with paired otocysts and thin operculum and a visceral hump covered by a shell in which the



Text-figs 1-5.—*B. nanum*. 1. Trochophore, 2 days. 2. Early veliger, 4 days, dorsal view. 3. Veliger, 7 days, ventral view. 4. Veliger, 12 days, lateral view. 5. Veliger, newly hatched.

beginnings of coiling are visible (Text-fig. 3). Growth and development, however, continue for a further five days before hatching, the shell becoming brown-pigmented and distinctly coiled, with a widely flared aperture, the larval heart conspicuous and active and the yolk reserves of the embryo almost completely resorbed (Text-fig. 4). Withdrawal into the shell also becomes possible during this time.

On hatching from its envelope, the veliger makes its way to the surface of the jelly and escapes into the surrounding water. The velar lobes, each of which has a black-pigmented dorso-lateral margin, spread out, the velar cilia begin to beat rapidly and the veliger swims immediately to the water surface (Text-fig. 5). Pelagic plankto-

trophic life is maintained for at least four days. Attempts to keep the veligers alive beyond this time and follow their metamorphosis have so far proved unsuccessful, but it seems likely that pelagic life is of several weeks' duration.

The rate of development outlined above is typical of eggs at the periphery of the jelly mass. Eggs in the interior of the mass develop more slowly, so that veligers continue to escape from the jelly for several days.

Discussion.

B. nanum thus follows early development within the protection of a gelatinous spawn by escape as a pelagic planktotrophic veliger. In this it resembles the Atlantic species of similar habitat, *Lacuna divaricata* (Hertling and Ankel, 1927; Hertling, 1928; Lebour, 1937; Thorson, 1946) and *Littorina littorea* (Hayes, 1929; Linke, 1934; Lebour, 1937; Moore, 1937; Thorson, 1946), save that the latter lays its eggs in floating capsules.

Of the species which replaces *B. nanum* in the upper littoral, *Melaraphe unifasciata*, we have at present no direct knowledge of the life history. The corresponding Atlantic species, *Littorina obtusa*, which has a gelatinous spawn, and *L. saxatilis*, which is ovoviviparous, hatch at the crawling stage (Pelseneer, 1911; Delsman, 1914; Linke, 1934; Thorson, 1946). Intensive searching of the habitat of the Harbord population of *M. unifasciata* at a time (November-January) when the females contain ripe yellow ova has failed to yield corresponding egg masses, and no animals have yet been found to contain developing embryos. It seems probable that *M. unifasciata* resembles the supra-littoral Atlantic species *Littorina neritoides* (Lebour, 1935), laying its eggs in floating capsules and hatching as a planktotrophic veliger, especially as recent work by Habe (1956) and Kojima (1958) has revealed an identical mode of spawning for *Nodilittorina pyramidalis*, whose supra-littoral distribution overlaps that of *M. unifasciata*. The curious anomaly of adaptation to extreme exposure and retention of planktotrophic early development thus appears to be especially marked in New South Wales rock-platform littorinids.

The present study of *B. nanum* also supplements the work of H. Anderson (1958) on spawning and development in *B. melanostoma* and *B. auratum*. The former, in contrast to *B. nanum*, shows adaptation to prolonged exposure by spawning fewer and larger eggs in jelly masses from which the young hatch at the crawling stage (compare *Littorina obtusata*). In *B. auratum*, however, although the habitat extends to the supra-littoral of mangrove swamps, the egg masses resemble those of *B. nanum* and the embryos probably hatch as planktotrophic veligers. This further example of retention of planktotrophic development in a supra-littoral species finds a parallel in the ovoviviparous supra-littoral mangrove species of Bermuda and Florida, *Littorina angulifera*, in which the young are released either as free eggs or as planktotrophic veligers (Lebour, 1945; Lenderking, 1954).

Acknowledgements.

I should like to thank Miss I. Bennett for discussion of this paper and for allowing me to use as illustrations the photographs of Plate viii, and Dr. G. Thorson for bringing to my notice certain papers on littorinid reproduction.

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EXPLANATION OF PLATE VIII.

1. *B. nanum*: Female and spawn. × 3.
2. *B. nanum*: Jelly masses containing eggs at a late cleavage stage. × 40.

THE STATUS OF NITROGEN IN THE HAWKESBURY SANDSTONE SOILS AND THEIR PLANT COMMUNITIES IN THE SYDNEY DISTRICT. III.

The Sources of Loss of Nitrogen.

By Nola J. Hannon, School of Biological Sciences, University of New South Wales.*

[Read 26th July, 1961.]

Synopsis.

All available data relevant to the loss of nitrogen from climax communities developed on Hawkesbury Sandstone are presented. The sources of loss are erosion, drainage water, denitrification and fire. Erosion losses resulting from the natural geologic erosion cycle and fire are estimated at approximately 0·15 lb N per acre per year and are based on data of a siltation survey of a water storage dam. A lysimeter study and analysis of dam water indicate that the nitrogen content of rainwater is not completely absorbed during its passage through these communities, but that losses in drainage water are small. The results of laboratory incubation of soil suggest that denitrification occurs only in local areas of swamp where nitrate-nitrogen may frequently be detected in the surface layers of the soil. Losses due to fire are erratic, being dependent on the occurrence and severity of the fire as well as the nature of climatic conditions immediately after the fire.

The losses of nitrogen are assessed in relation to the losses of phosphorus and calcium which have occurred in the development of the sandstone communities. A comparison of the initial level of phosphorus and calcium, determined by the amounts present in the parent material, and the existing levels in the communities developed on this parent material, indicates that phosphorus has been retained to a far greater extent than has calcium. At the present time, phosphorus is the chief nutrient deficiency of these soils and it is suggested that phosphorus levels have always controlled the economy of other nutrient elements, including nitrogen, in these communities.

Introduction.

The nutrient capital of an ecosystem is a resultant due to the operation of factors which are contributing to and removing from it. The capital of nitrogen in Hawkesbury Sandstone communities has been calculated in earlier papers (Hannon, 1956, 1958) and the factors concerned in the removal of fixed nitrogen in these communities will now be discussed.

A loss of nitrogen from a plant community may occur by any of several possible routes. These may involve factors resulting in the loss of nitrogen from one stand and its redistribution in other areas, or an absolute loss of nitrogen from the earth's surface to either the ocean or the atmosphere. Either mechanism causes a loss from any particular stand. They may involve the removal of nitrogen-containing soil particles by wind or water erosive forces; the solution and removal of nitrogen in drainage waters; or the mechanism of absolute loss—the change from a combined state of nitrogen to a free gaseous form and its release to the earth's atmosphere. It is obvious that a certain loss is of probable occurrence in the majority of ecosystems, but the magnitude of losses will depend on the nature of the ecosystem. The factors operating to allow loss of nitrogen from the Hawkesbury Sandstone ecosystem are erosion, drainage water, denitrification and fire.

1. Erosion.

Presentation and Discussion of Data.

No direct measurements of the removal of soil particles have been made, but field observations allow at least a qualitative assessment of this source of loss. On the plateau, soil and weathered particles from rock outcrops are exposed to wind action on

* This investigation was made during the tenure of a Linnean Macleay Fellowship of the Linnean Society of N.S.W.

the flat-topped dividing sectors between the valleys. Nevertheless, where plant cover occurs, it is quite dense and shows marked reduction in height and increase in density in increasingly exposed situations, and thus protects the soil.

It therefore is probable that a far greater source of erosion is the water run-off down the sides of the steep valley slopes. The general physiography of the Hawkesbury Sandstone region—the narrow, flat-topped ridges and the youthful steep gullies—indicates that a natural loss of soil particles by water erosion must be occurring to allow for the normal geological erosion cycle. Since natural erosion on a geological time scale is a very slow process, the lack of exposure of plant root systems is of no significance in assessing the extent of erosion. Soil depth is shallow on the ridges and especially on the upper slopes of the gullies; there is a marked improvement in comparison to these sites in the lower portions of the gullies which benefit by the accumulation of soil, water and nutrients from the surrounding uplands.

The only quantitative information that exists on the rate of erosion in these areas is a few data obtained by the Metropolitan Water, Sewerage and Drainage Board on the amount of sedimentation occurring in the water reservoirs. This constitutes a

TABLE 1.
Data Relevant to Silt Accumulation in the Bargo Weir in 1956.
(Taken from records of Metropolitan Water, Sewerage and Drainage Board.)

Age. (year.)	Catchment Area. (sq. mile.)	Surface Area. (acre.)	Original Capacity. (gal.)	Present Capacity. (gal.)
67	29	17	67,246,093	52,764,062

Note.—The height of the outlet pipe above the foundation level is five feet, but this has never been used. Water is drawn from near the surface by means of a trunnion pipe.

certain measure of the erosion that is occurring, but sets only a minimum value. It represents the resultant loss from a large area within which several plant formations occur. Differing amounts of soil will have been lost from different formations and, in certain of them, some re-deposition of soil particles may have occurred. Nevertheless this over-all average value of the loss of soil particles from large areas is admirably suitable for inclusion in this general survey.

The storage system providing for the Sydney water supply consists of a series of dams built on the rivers in the areas where Hawkesbury Sandstone outcrops. The construction of the dams has necessitated the building of access roads, but in order to maintain the purity of the natural precipitation, a minimum of disturbance has occurred in the catchment areas. Virgin forest covers these areas which are the private property of the Water Board. Erosion of soil particles will thus be occurring within these areas at a rate which is very similar to the natural rate. The dams, however, are of relatively recent construction (ranging in age from 1 to 55 years), and since silt accumulation has as yet provided no inconvenience, no investigation has been made of this factor. This, however, does not necessarily imply that the rate of silting is negligible, since calculations from information supplied by the Water Board show that very large quantities of soil would need to accumulate before causing difficulty.

The only survey that has been made is in the Bargo Weir situated on the Nepean Ramp about sixty miles south of Sydney. The Metropolitan Water, Sewerage and Drainage Board took control of this weir only in 1956 and the catchment area had been subject to greater biotic influences than are allowed on their other properties. Examination of aerial photographs of the catchment area reveals that 13% of the total area has been cleared; of this area, 4% is used for mixed farming. This is entirely confined to the ridges on the extreme edge of the catchment area and therefore will not have influenced the quantity of silt accumulated in the weir to a very great extent. The data supplied by the Water Board are shown in Table 1.

The loss of 14,482,031 gallons' storage capacity (Table 1) is equivalent to a volume of 2,323,780 cubic feet of silt. On the basis of an apparent density of 81 lb per cubic foot (since only surface soil will have been eroded and formed the silt), it may be calculated that this volume of soil has a mass of 188,226,180 lb. Since only the shallow uppermost layer of soil which has the highest nitrogen content would be removed by natural erosion, an apparently high value of 1,000 p.p.m. nitrogen (Hannon, 1956) will be assumed as the nitrogen content of this layer. On this basis, 188,226 lb of nitrogen has been lost over a period of 67 years from an area of 29 square miles. It is thus readily calculated that this loss corresponds to 0·151 lb of nitrogen per acre per year.

Brown (1943) and Kittredge (1948) provide figures of the quantity of soil eroded from virgin areas. Apart from one value of 1·38 cubic feet per acre per annum in mature oak forest, their values are very much less than the calculated value of 1·87 cubic feet per acre per annum for the sandstone forest.

Since many factors—such as climate, nature of the soil slope and vegetative cover—are known to influence erosion, widespread values are to be expected in different areas. In particular, the coarse texture and single grained structure of the sandstone soils and the steep slopes of the valley sides would favour erosive action. It is also worthy of note that fires are of common occurrence in the sandstone areas. Brown (1943) has shown that yearly erosion from burned areas ranged from 22 to 239 times that of unburned. The remarkable adaptations exhibited by the native species to withstand fire would indicate, however, that it is a natural occurrence in these communities.

2. Drainage.

Introduction.

The nitrogen content of drainage water is frequently investigated and stressed as a serious source of loss from cultivated fields. Where readily available forms of mineral nutrients are added to the soil in fertilizer treatment, considerable losses by this means are to be anticipated. In natural communities, similar losses would not be encountered, especially in Hawkesbury Sandstone areas where nitrogen—especially available nitrogen—is at low levels. In addition, in natural communities, drainage water can originate only from precipitation of which a certain fraction is absorbed by the soil and plant cover. Natural precipitation is a well-recognized source of fixed nitrogen; the question of greatest significance for the present purpose, therefore, becomes whether or not the drainage water, after passage through the soil, has a higher nitrogen content than the precipitation.

Lysimeters—arrangements whereby drainage waters which have percolated through a soil column are collected—are of various designs, but may be classified according to the principle of their construction into three main types—monolith, Ebermayer and filled-in varieties. Difficulties, such as (*a*) artificiality of the base, (*b*) failure to delimit the drainage area, and (*c*) disturbance of the soil block, apply to one or other of these designs and hence none is entirely satisfactory. The use of an abnormal lower surface is a serious criticism of all types of lysimeters, since gravitational water at this point has to overcome the resistance caused by surface tension at the soil/air interface before it can drain away. A waterlogged condition in this position causes many changes in the soil and influences the chemical composition of the percolate.

Method.

The least departure from natural conditions was considered an essential requirement in the present study. The principle of the Ebermayer lysimeter, where the soil is left *in situ*, was therefore followed. In this type of lysimeter, no side walls separate a definite soil block from the adjoining soil. However, by selecting areas of appropriate position and slope, it is possible, in the sandstone communities, to delimit by eye the area from which drainage waters would be collecting and in which lateral movement would be most improbable. In such areas, the naturally occurring sandstone underlying the soil mass can be used for the base of the lysimeter block, since it is less pervious to water than is the soil derived from it.

The edge of a narrow plateau region, adjacent to a steep gully, was selected for this study; this area, including the highest point of the ridge, was of gentle slope (1/12) and of 74 feet length, 10 feet width and averaged approximately 1 foot in depth (ranging from 0 to 2 feet). No waters from higher land fell onto this area which supported low scrub forest.

Soil was cut away at the lowermost edge of the selected area to uncover the underlying sandstone. A graded groove was cut in the stone to direct the flow of the water which would accumulate from the higher level. A metal sheet covered the groove and the earth was replaced over it. Thus the only disturbance was made at the point where the water was collected. The area through which the drainage water percolated remained completely undisturbed. The water flowed from the groove in the rock via a length of pipe into a funnel where it was filtered, passing thence through cationic and anionic exchange resin columns and thence into a collecting drum which contained

TABLE 2.
The Adsorption of Ammonia from Rainwater by Hawkesbury Sandstone Soil.

Ammonia Content (p.p.m.).		Ammonia Adsorbed by Soil. (%)
Rainwater.	Drainage Water.	
0·29	0·20	31
0·27	0·20	26
0·05	0·04	20
0·20	0·16	20

1½″ depth of paraffin. This arrangement for the collection of drainage waters fulfilled its purpose very satisfactorily. The ammonia and nitrate and nitrite content of the percolate was concentrated on the resin columns which were renewed at intervals. On these occasions, the volume of water collected in the drum, which had been shielded to prevent evaporation, was measured and discarded.

Presentation and Discussion of Data.

There is no certainty that the total amount of drainage water from this area was collected. Some of the drainage water may have been absorbed by the sandstone, some may even have been lost through cracks in the underlying rock, but the aim of the present study, unlike many lysimeter studies, was not concerned with the quantity of drainage waters. A measure of the relative nitrogen content of precipitation and drainage water was the information required. This information would indicate whether a positive or negative nitrogen balance results from these two opposing factors in the sandstone communities.

A parallel study was therefore made of the rainwater and drainage water nitrogen content, and the results for the ammonia content of each are shown in Table 2.

A survey of the literature concerned with the nitrogen content of drainage waters shows that nitrate is the most common form—in fact, some investigators analyse only for nitrate. Ammonia, where present, is usually in only small amounts. However, lysimeter investigations are most frequently made in cropped soils where fertilizer additions are applied. Neither nitrite nor nitrate was detected in drainage water on any occasion. During this period, a similar condition applied to the rainfall and will be discussed in that connection in a later paper.

The quantity of nutrients in drainage water will depend on such a complex of factors—nature of the soil, vegetation cover and climatic conditions—that comparison with unrelated circumstances serves little useful purpose. However, in virgin bunchgrass on silty clay loam, where nitrogen is regarded as the principal limiting nutrient, Kardos (1948) records that the concentration of total nitrogen over a period of three years was consistently of the order of 2–3 p.p.m.

Table 2 shows that appreciable quantities of the ammonia content of the rainwater had been absorbed by passage through a relatively small soil block. In addition, it is most improbable that all of the drainage water had passed through all of the soil—rain falling on the lower edge would have passed through only a small fraction of the soil block.

The water stored in the dams of the Metropolitan Water, Sewerage and Drainage Board consists of surface run-off and drainage from large tracts of sandstone country. The analytical data of the composition of dam water sampled at one foot depth at monthly intervals were therefore consulted. This showed that free ammonia, albuminoid ammonia and nitrate are consistently present in these samples and nitrite very occasionally.

As is to be expected, variation is marked between dams with respect to the absolute amount of each fraction at any given sampling time; variation is also great at different sampling times; nevertheless, the values are consistently low for all nitrogenous fractions. 0·1–0·2 p.p.m. nitrogen are usual values for albuminoid ammonia and both free ammonia and nitrate usually vary between 0 and 0·088 p.p.m. nitrogen.* These values will not necessarily represent accurate values for soil leachate water nitrogen content, since dam water consists of drainage water and a small percentage of rainwater, together with surface run-off, which introduces soil particles (see silt accumulation above) as well as organic material from the litter layer. In view of the data in Table 2 and the low nitrogen content of the dam water, it appears that losses of nitrogen in drainage water reduce the nitrogen contribution made by rainfall to only a small extent.

3. Denitrification.

Method.

A typical stand of low scrub forest dominated by *Eucalyptus haemastoma – E. gummifera* and the edge of a shrub swamp dominated by *Hakea teretifolia* were selected as soil-sampling sites for investigations of microbial activity with respect to nitrogen transformations. Soil bags, containers and sieves had been sterilized and the spades thoroughly disinfected. A composite soil sample of about 10 kilograms was taken to a depth of 8″ in approximately 1 kilogram portions from ten sites within each stand. To avoid undue exposure of the soil to the foreign atmosphere of the laboratory, both samples were sieved and thoroughly mixed in the field before being placed into sterile containers for transport to the laboratory. Only three days elapsed from the time of sampling to the time of commencement of incubation.

100-gram portions of soil were weighed into sterile 250 ml. conical flasks for aerobic and 150 ml. flasks for anaerobic treatment. The flasks contained either (i) distilled water or (ii) a nitrogen-free mineral solution (Hannon, 1956) or (iii) 1% glucose solution or (iv) 1% glucose in the nitrogen-free mineral solution, to provide a 25% moisture level.

Each treatment was set up in duplicate and under aerobic and anaerobic conditions. In the case of the aerobic treatment, the flasks were plugged with rubber bungs fitted with both a stopcock tap and also glass tubing bent to form a double trap which contained 2N sulphuric acid and methyl red indicator. Acid in this concentration does not cause desiccation of the internal atmosphere. Any ammonia contained in air moving inwards from the external atmosphere would be fixed in the outer trap and ammonia diffusing outwards from the incubation vessel would be fixed in the inner trap. The stopcock was inserted to allow air to be drawn out of the flasks through the acid traps at the conclusion of the experiment.

The anaerobic flasks were plugged with bungs fitted with an inlet and an outlet glass tube, both of which were drawn out to narrow diameter towards their outer extremities. Within these flasks were placed: (i) a tube containing sulphuric acid and methyl red

* Visual methods of comparison of the colours of standard and unknown solutions are employed in the Water Board laboratories. The accuracy of the absolute values is therefore open to question, since visual methods are not so reliable as those employing a photo-electric cell. Undoubtedly, however, the low order of the values is correct.

suspended by enamelized wire from the bung, (ii) a bottle of steel wool which had been dipped in copper sulphate solution. As the steel wool rusted, it used any remaining traces of oxygen in the flask (Parker, 1955), (iii) a bottle of an alkaline solution of glucose and methylene blue to indicate when anaerobic conditions had been attained.

Each flask was evacuated and filled with nitrogen free of carbon monoxide, oxygen and ammonia. The nitrogen passed through a cotton plug which acted as a filter. This procedure was repeated until the methylene blue decolorized. The outlet tube was then sealed with a hand torch. The pressure within the flask was then reduced. Carbon dioxide was produced externally with a measured volume of sulphuric acid reacting with sodium carbonate to provide 5% of the volume of the flask atmosphere. By

TABLE 3.

The Total Nitrogen Content of Hawkesbury Sandstone Soils before and after Incubation under Conditions of Darkness.

Soils were incubated for 12 weeks, with various nutrient additions at 25 °C. and with an initial moisture level equivalent to field capacity.

Soil Sample.	Gaseous Treatment.	Nutrient Treatment.	Total Nitrogen Content (p.p.m.).	Change in Nitrogen Content.
Forest.	Aerobic.	Non-incubated.	580	Initial value.
		Control (+water).	560	Not significant.
		N-free minerals.	570	Not significant.
		1% glucose.	565	Not significant.
		Glucose+N-free minerals.	560	Not significant.
	Anaerobic.	Control.	580	Not significant.
		N-free minerals.	585	Not significant.
		1% glucose.	600	Not significant.
		Glucose+N-free minerals.	600	Not significant.
Swamp.	Aerobic.	Non-incubated.	690	Initial value.
		Control.	590	16% loss.
		N-free minerals.	590	16% loss.
		1% glucose.	610	12% loss.
		Glucose+N-free minerals.	600	14% loss.
	Anaerobic.	Control.	620	11% loss.
		N-free minerals.	600	14% loss.
		1% glucose.	580	17% loss.
		Glucose+N-free minerals.	570	19% loss.

opening the evacuated flask to the chamber where the carbon dioxide had been produced, the gas was drawn into the flask, nitrogen was flushed through to restore atmospheric pressure and the inlet tube also sealed.

Both aerobic and anaerobic treatments were incubated in darkness for twelve weeks. Analyses were made by the Kjeldahl method (Hannon, 1956) to determine differences in the initial and final total nitrogen content of the soil samples.

Presentation and Discussion of Data.

The results in Table 3 show that no fixation of nitrogen occurred in either sample under these experimental conditions. In addition, although no loss occurred in the forest sample, significant losses of nitrogen occurred in all treatments of the shrub swamp soil. Apparently the aerobic treatment contained local patches of anaerobic conditions which prevented distinction between the aerobic and anaerobic conditions employed. The losses of nitrogen in the swamp soil are of interest, since it has already been shown (Hannon, 1956) that the swamps generally have a higher total nitrogen content than the forest soils; in addition, in a bio-assay trial, more nitrogen became available in the swamp samples.

At the conclusion of the incubation, in no instance was ammonia detected in the acid traps in quantities of even 10 micrograms. The observed losses were of the order of 10,000 micrograms and apparently occurred in the form of elemental nitrogen or as an oxide of nitrogen.

Wijler and Delwiche (1954) have shown that nitrous oxide is the usual form of nitrogen loss under most soil conditions, but where the environment is strictly anaerobic, only molecular nitrogen is lost (Jones, 1951). Except in instances where ammonium and nitrite have been added at levels which probably never occur in natural soils (Ingham, 1938; Fraps and Sterges, 1939; Wahhab and Fazal-Uddin, 1954) denitrification has been shown to be due to bacterial activity. Denitrification occurs only in the presence of nitrogen in an available form and in the absence of oxygen from the soil solution (Jones, 1951; Skerman, 1953; Arnold, 1954).

It therefore appears that the losses occurring under incubation conditions in swamp soils may very probably occur in these habitats in the field. Available nitrogen is at very low levels in sandstone soils, but in swamp areas nitrate is frequently detected in the surface layers. The presence of free water would assist in the development of anaerobic conditions. Nothing is known of the availability or of the carbon-nitrogen ratio of the oxidizable water soluble substances which provide the necessary substrate for the activity of the appropriate bacteria. However, since nitrogen losses occurred in the control treatment of the incubation series, the naturally occurring organic matter apparently furnishes a suitable substrate. Some character of the soil from the sclerophyll forest areas must prevent the occurrence of denitrification—lower levels of nitrate and naturally occurring organic matter may be suggested.

4. Fire.

Discussion.

The destruction of organic matter as a result of fire causes a potential loss of nitrogen and mineral constituents from the nutrient capital of the ecosystem—from the vegetative cover, the litter and in some instances from the surface layers of the soil. The charred remnants and ash are left exposed to the erosive forces of the environment.

In the sandstone communities, while all but the heaviest of the woody material is burnt, most of it is only charred and allows for the early commencement of regeneration. A fine deposit of ash is left covering the ground surface and floating in the atmosphere in the wake of the fire. In local patches where fallen logs have smouldered, distinct areas of ash deposits are to be found. The ash is very readily disturbed and usually is completely removed soon after the fire. The extent of loss depends on the nature of the environmental conditions immediately after the fire. The ash is largely derived from the foliage of the shrub layer. In forest areas, the leaves of the trees often are only scorched and drop soon after the fire. This litter layer often assists in the protection of the ash lying on the bared ground surface. Regeneration by way of seed, lignotubers and epicormic buds probably draws largely on stored food reserves, but in such periods of active growth, nutrient absorption by the root systems from the temporarily enriched soil could well occur and incorporate the ash components once again into living tissue.

Certain losses of nutrient capital undoubtedly occur as a result of fire and the cumulative effect of the countless fires that must have occurred since the establishment of plant communities on Hawkesbury Sandstone could well be considerable. It is probable that no stand occurring on Hawkesbury Sandstone can be regarded as "fire-free". The remarkable protective adaptations of the flora against fire suggest that fire occurrence predated and may possibly have contributed to the selection of the present flora. Fire cannot therefore be regarded as a completely unnatural phenomenon in these communities. It may be that the present-day communities are not equivalent to the original cover because, amongst other factors, the nutrient capital has been depleted. However, as far as can be judged in the absence of fire history records, the marked differences that often occur between various stands of the same formation could well be related to local environmental differences, such as wind exposure, moisture level or the stage of regeneration from fire, rather than the past history of firing. Field observations of fully regenerated stands indicate either that the losses are made up or that the loss as a result of fire is insignificant.

Hatch (1959) has found that in fire-breaks within *Eucalyptus marginata* forest in Western Australia, controlled burning at 1–3 year intervals has not significantly

influenced the properties, including total nitrogen content, of surface (0–3½″) soils by comparison with adjacent forested soil protected from fire for 15–25 years.

Reports regarding the effect of fire on soil nitrogen are contradictory (Ahlgren and Ahlgren, 1960). Increased nitrification rate has often been reported due to the effect of the changed pH on bacterial growth. Such changes represent only a redistribution of the total capital of nitrogen in the soil. Absolute losses of nitrogen as in a stimulated rate of denitrification have also been reported, but further investigation of these aspects is required.

Certain compensation for the losses caused by fire will result from the slow but continual weathering of the outcropping parent material. In addition, the heat of the fire frequently causes fretting of superficial layers of the sandstone, thus releasing ash components and making further nitrogen fixation possible.

TABLE 4.

A Comparison of the Phosphorus and Calcium Content of Hawkesbury Sandstone and Sandstone-Derived Soil.

	Total P Content.*			Total Ca Content.*		
		Soil.			Soil.	
	Hawkesbury Sandstone. (p.p.m. P.)	0–6″ (p.p.m. P.)	6–40″ (p.p.m. P.)	Hawkesbury Sandstone. (p.p.m. Ca.)	0–6″ (p.p.m. Ca.)	6–40″ (p.p.m. Ca.)
Average	29	30	24	307	33	18
Range	15–38	22–34	16–37	215–430	9–48	9–27

* P analyses are based on 8 samples, Ca analyses on 5 samples. Calcium analyses of the sandstone were made at the School of Mining Engineering and Applied Geology, University of New South Wales, and calcium analyses of the soil are from Storrier (1951).

Losses of nitrogen due to fire cannot be denied and their significance is difficult to assess. However, the fractionation of nitrogen in the Hawkesbury Sandstone ecosystem (Hannon, 1958) shows that the main bulk of nitrogen is contained in the soil and woody tissue of the plant cover and this will be practically unaffected by fire.

An Assessment of the Losses of Nitrogen.

The nitrogen content of the Hawkesbury Sandstone ecosystem has obviously been derived from external sources rather than the parent material (Hannon, 1956). Many factors may have contributed and caused losses in the development of the nitrogen capital of the present-day community. Consequently, it is impossible to estimate quantitatively or with accuracy the extent of the contribution or of the removal caused by each factor since the first plant colonization of Hawkesbury Sandstone. A statement concerning the absolute losses of nitrogen from the combination of all possible sources of loss is therefore not possible.

However, by the time the ecosystem attains maturity, an equilibrium value has been reached for the content of each nutrient element in organic form. This is the amount which can be actively used under the conditions of the existing environmental complex. Instances of luxury consumption of certain elements would prove exceptions to this statement, but are unlikely to be relevant in the case of most nutrient elements in Hawkesbury Sandstone communities, where the parent material contains only very low concentrations of the elements required for the growth of living organisms.

Since the incorporation of nitrogen into an ecosystem, at least by biological means, is dependent on the supply of other mineral elements to allow the development of the appropriate organisms, a consideration of the losses of other nutrients, whose amount in the ecosystem is determined initially by the amount in the parent material, will be of relevance to the assessment of the losses of nitrogen.

Phosphorus and calcium have therefore been selected, since it has already been shown that phosphorus is the primary nutrient deficiency of these communities (Beadle. 1953, 1954; Hannon, 1956) and calcium levels in the sandstone soils are very low. The

significance of calcium to biological nitrogen-fixing agencies is well known. Analytical data of Hawkesbury Sandstone, sandstone-derived soils, plant tissue and litter of the sandstone species are relatively few in number and have frequently been made by different workers on samples collected in different areas.

Hawkesbury sandstone and soil derived from sandstone taken from the same area are compared with respect to their phosphorus and calcium contents in Table 4. Where comparison is to be made between the nutrient contents of the solid parent material and of the porous soil derived from it, a concentration or mass basis must be used rather than a volume basis. It appears that the mineral content of the parent material has been retained in the soil to a greater extent in the case of phosphorus than of calcium. Even without the addition of the phosphorus content of living plant tissue and litter, it is obvious that the initial phosphorus content has been largely retained in the present-day communities. However, on the basis of measurements and observations recorded previously (Hannon, 1958) and unpublished analytical data of Beadle, Winterholder, Fraser (1948) and Turner (1954), a calculation relating the calcium content of the Hawkesbury Sandstone to that of soil, plant tissue and litter indicates that only 20% of the calcium contributed from decomposition of the sandstone can still be accounted for.

Presumably the leaching action of drainage waters over long periods of time has caused the losses of calcium during the development of the present-day sandstone communities. Erosion losses cannot be considered as contributing to this loss to the same extent, since a given quantity of soil is compared with a similar quantity of parent material.

It may be suggested that a severe limitation to plant growth set by the phosphorus level may have prevented the uptake and utilization of calcium. Similarly, it may be suggested that the accretion of nitrogen by biological agencies would also have been limited by the phosphorus level, and that nitrogen fixation has proceeded at a rate in pace with the rate of phosphorus liberation from the parent material. Under these circumstances, excess quantities of nitrogen would never have occurred and consequently never provided a source for loss. If denitrification has occurred, loss of nitrogen by this means is not accompanied by a loss of phosphorus and therefore a counterbalancing gain of nitrogen by fixation could occur. Because of the necessity for particular environmental conditions for its occurrence, denitrification probably has always been confined to swamp areas, which may have been more extensive in the past.

In fires, where the loss of nitrogen will be relatively greater than that of phosphorus, a similar counterbalancing gain of nitrogen by fixation might be anticipated.

Losses of nitrogen due to losses of soil by natural erosion in these communities must also be accompanied by losses of phosphorus and other nutrient elements. Such losses therefore do not result in the relative depletion of the remaining soil in the same manner as does, for example, denitrification, where nitrogen alone is lost. It is well recognized, however, that the upper layers of the soil which are removed by erosion are the most fertile, especially with respect to nitrogen (Ensminger and Pearson, 1950). Of all sources, erosion probably has caused the greatest loss of fixed nitrogen from these communities.

On these grounds, it appears that the nitrogen economy of these communities is controlled by an efficient phosphorus regime. Erosion, leaching, denitrification and fire all play a role in some phase of the sandstone communities. Unless factors are operating to counterbalance these losses, deterioration of the communities must ensue. Studies reporting the occurrence and activity of agencies capable of contributing nitrogen to these ecosystems will be reported later.

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A STUDY OF INHERITANCE OF PATHOGENICITY IN *PUCCINIA GRAMINIS* VAR. *TRITICI*.

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Synopsis.

The inheritance of pathogenicity in *P. graminis* var. *tritici* was studied by selfing strain 21 Anz-2 on *Berberis vulgaris* and determining the reactions of 285 isolates on 23 differential varieties. The three varieties Little Club, Marquis and Kota were susceptible to all progeny strains except one. Two varieties, Kenya 117A and Khapstein, were resistant to all strains. On the remaining varieties the segregation of the 37 strains showed the parent strain to be heterozygous for pathogenicity. On Kanred, Einkorn, Vernal Emmer and Mentana avirulence was inherited as a dominant character and conditioned by a single major factor in each instance. On Acme and Kubanka virulence was dominant and one of the factors for pathogenicity seemed to operate against both varieties. Virulence on Arnautka, Mindum and Spelmar was inherited as a unit with a single dominant factor involved. On Celebration which carries Marquillo-type resistance avirulence was recessive and due to a single factor. The same resistance operated in Thatcher which possesses also the immunity factor of Kanred. On Yalta virulence was dominant, while avirulence was dominant on Eureka, Bowie, Bokveld and W1656. There was evidence of association of certain of the genes for virulence and several strains showed abnormal characteristics. Abnormal uredosorus colour was associated with homozygous recessive genes for pathogenicity.

Introduction.

During the last fifteen years, new, virulent strains of wheat stem rust, *Puccinia graminis* var. *tritici* Eriks. and Henn., have appeared in the eastern Australian wheat belt and have rendered ineffective many sources of resistance. It was thought (Watson and Singh, 1952) that the main source of new strains in this country was mutation. These workers suggested the incorporation of two different genes for resistance into varieties to be released on the assumption that a combined resistance would remain effective for a longer period as it could be overcome only by a double mutation in the fungus. Later research, however, produced evidence of sexual hybridization of the pathogen on the alternate host, *Berberis vulgaris*, which is widespread in Tasmania, and also of somatic hybridization which was shown to occur readily between field strains (Watson and Luig, 1958*a*, 1958*b*). It could therefore be expected that two strains, both heterozygous for two recessive genes for virulence, by somatic hybridization would produce a strain pathogenic on a variety carrying combined resistances. The present study was undertaken to determine the genotype of the most prevalent Australian strain of wheat stem rust in order to evaluate individual sources of resistance. Those genes for resistance which remain effective to the progeny of existing strains of rust would be the most valuable for breeding.

Review of Literature.

In *Melampsora lini* (Pers.) Lév. extensive studies of a fundamental nature conducted by Flor have suggested a relationship between the genes for pathogenicity in the fungus and the genes for resistance in the host. In *Puccinia graminis*, apart from the Canadian work, little has been reported on the genetics of pathogenicity.

Waterhouse (1929) was the first to obtain experimental proof that new forms of stem rust had their origin on barberry. In 1930 Newton, Johnson and Brown reported that most races of wheat stem rust studied by them, including race 21, were heterozygous. By selfing race 21 six different races were isolated, viz., 11, 17, 21, 34, 49 and 56, indicating heterozygosity of genes for pathogenicity on Kanred, Einkorn,

Arnautka, Mindum, Spelmar and Kubanka. Five per cent. of the aecial cups gave rise to more than one physiologic form. In another study (1930*b*) the same investigators found the inheritance of normal red uredospore colour to have a Mendelian basis and to depend upon the interaction of two dominant complementary factors. Orange and greyish-brown were both conditioned by one or other of the complementary factors and white colour was explained by the presence of the two recessive alleles. Avirulence ("3-c" reaction) on Marquis and Kota was found to be due to maternal influences. In second generation hybrids there was evidence of an association of orange spore colour with avirulence on Marquis and Kota, and of an association of greyish-brown spore colour with the occurrence of races 36 and 85. These findings were confirmed in a later publication (Johnson, Newton and Brown, 1934). In a more recent study with *Puccinia graminis* var. *avenae* (Johnson, 1949), parallel results were obtained. Pathogenicity on the oat varieties Sevnothree and Joanette was found to be cytoplasmic with possible nuclear influences, and red spore colour was dominant over orange.

Mendelian inheritance of pathogenic characters in *P. graminis* var. *tritici* has been reported in two papers (Johnson and Newton, 1940; Johnson, 1954). In the first study, avirulence ("0" reaction) on the variety Kanred was found to be dominant and governed by a single factor pair. Virulence on Mindum ("4" type reaction) was dominant over avirulence ("1" type reaction) and was also due to a single factor. Virulence on Vernal Emmer, on the other hand, was governed by two recessive factors. Independence of all factors was indicated. Johnson and Newton concluded that despite the binucleate condition of the rust organism, genes for pathogenicity are inherited as if they were present in a single diploid nucleus. In the second study, the mode of inheritance of pathogenicity on the varieties Kanred, Mindum, Vernal Emmer, Einkorn, Marquis and Kota was studied by selfing 34 physiologic races of rust. The previous findings were confirmed and additional evidence indicated that avirulence on Einkorn was dominant. Johnson thought that apart from the "0" and "4" types of infection on the *durums* Arnautka, Mindum and Spelmar, which seemed to be inherited as a unit, there was no indication of linkage between genes for virulence. Fourteen additional differential hosts including Gabo, McMurachy, *Triticum timopheevi* and Kenya 117A were inoculated with mass cultures derived from 12 races (among them race 21), but only on the *durum* Carleton did segregation for susceptibility occur.

More recently Wilcoxson and Paharia (1958) isolated 15 different races by selfing race 111 to which the standard hosts, except Little Club, are resistant. It was suggested that race 111 arose as a hybrid of *P. graminis* var. *tritici* and *P. graminis* var. *secalis* and that the unusual behaviour of its progeny was due to the segregation of inhibitors suppressing pathogenicity in the parent race.

Materials and Methods.

The studies reported herein were carried out at the University of Sydney during the years 1957 and 1959. In 1957 teleutospore material from a summer crop of the variety Celebration was collected at Castle Hill. Uredospore samples from the same field were identified, the majority were of strain 21 Anz-2* and there were a few isolates of 21 Anz-1. At this time these two strains were the only Australian stem rusts attacking Celebration which carries Marquillo-type of resistance. Half the telia-bearing material was sent to Glen Innes Experimental Farm, N.S.W., and left in the open over the winter months to induce germination. The remainder was put into a deep-freeze chamber and at weekly intervals removed, wetted and allowed to thaw. Better infection was obtained with the material that had been allowed to overwinter at Glen Innes.

For the 1959 study teleutospore material was collected at Parkes, N.S.W., from a heavily rusted, self-sown crop of an unknown variety. This material had become infected in the autumn of 1959 and the teleutospores had overwintered under natural conditions. No artificial treatment was necessary to induce germination. From uredospores collected in the autumn strain 21 Anz-2 was found to make up almost all the inoculum. In addition, however, a few pustules of the resistant type were noticed

* Anz stands for the geographical area of Australia and New Zealand.

on the differential variety Yalta, and they subsequently proved to belong to a strain which resembled 34 Anz-1 except for the reaction types on Federation and C.I.12632. The mode of origin of this strain is not known, it has not been found previously in this country and, during the foregoing rust survey, all the samples collected in this part of New South Wales proved to be 21 Anz-2.

The following procedure was used in inoculating the barberry: Young shoots were sprayed with water and the leaves rubbed between the fingers to break down surface tension. An inoculating needle was then used to transfer the spores to the leaf surfaces. In addition, straw-bearing telia were suspended above the barberry plants which were set in an incubator for a period of two or more days.

Several attempts to obtain infection on barberry were entirely unsuccessful or produced only a few pycnia which were often sterile despite mixing of pycnial fluids. The complete sexual cycle finally developed mostly on young leaves, but also on older leaves, spines and stems. Rye stem rust inoculated by the same method onto barberry gave abundant infection.

After formation of the pycnia the nectar was intermixed by means of a blunt needle. When single aecial cups from different aecial clusters were inoculated onto seedlings of Little Club striking differences in the ability to infect were noted. Mass inoculation with subsequent random selection of pustules would have obscured this difference, and for this reason the mass-inoculation method was not employed. In each case a single aecial cup was carefully cut off by means of a sharpened needle, lifted onto seedlings of Little Club in a separate pot and smeared and crushed thereon. After infection occurred plastic covers were placed round the pots to prevent contamination. The cultures were built up and inoculated onto differential sets, and the reaction types recorded in the usual way.

Experimental Results.

(i) *Inheritance of Pathogenicity.*

Strain 21 Anz-2 was heterozygous for most of the genes for virulence under study. In 1957, 14 different strains were obtained from 180 isolates. In 1959, from the study of a second lot of material, 23 strains were obtained from 105 isolates (Table 1). Although different strains were found in the two studies, the results were not contradictory, as similar segregation patterns were observed for individual virulence genes. Most of these strains are new records for Australia.

Four of Stakman's twelve standard hosts, viz., Little Club, Marquis, Kota and Khapli, did not give a differentiating reaction to any of the isolates except strain 104 Anz-1. The first three varieties were susceptible and Khapli highly resistant.

The results of testing the isolates on Kanred agreed with those of Johnson and Newton (1940) and Johnson (1954), who reported a single recessive gene for pathogenicity in the fungus. Twenty-five strains were avirulent on Kanred and 12 were virulent (χ^2 for a 3:1 ratio = 1·090; P-value = 0·30–0·20).

The present studies also have shown that virulence on Einkorn is recessive and controlled by a single factor. Only 7 strains gave a susceptible reaction ("3" to "3+" type), while 30 strains produced a variation from ";" to "2=" (χ^2 for a 3:1 ratio = 0·730; P-value = 0·50–0·30).

Further it was observed that the majority of strains were avirulent on Vernal Emmer. Isolates from 28 strains produced a ";" to "2=" resistant reaction, 4 strains gave a semi-susceptible reaction ("2" to "3c") and to 5 strains Vernal Emmer was fully susceptible. Grouping the semi-virulent and virulent strains together would give a ratio of avirulent to virulent of approximately 3 to 1 (χ^2 for a 3:1 ratio = 0·009; P-value = 0·95–0·90). If the semi-virulent are grouped with the avirulent, however, a ratio in the vicinity of 15 to 1 is obtained (χ^2 for a 15:1 ratio = 3·332; P-value = 0·10–0·05). The latter ratio would be in agreement with the findings of Johnson and Newton (1940) and Johnson (1954). A two-factor segregation involving two genes unequal in their pathogenic effects could satisfactorily explain the present results and account for the semi-virulent strains.

TABLE 1.

Reactions of Strain 21 Anz-2 and of 35 Products of Selfing on 22 Wheat Varieties.

Strain.	Differentiating Variety.																					Uredosorus Colour.
	Little Club.	Marquis.	Kanred.	Kota.	Arn., Min., Spm.*	Kubanka.	Acme.	Einkorn.	Emmer.	Khapli Emmer.	Eureka.†	Bowie.‡	Bokveld.‡	Yalta.	W1656.	Mentana.	Celebration.	Thatcher.	Khapstein.	Kenya 117A.	Federation.	Culture Number.	
21 Anz-2 ..	4	4	0	3	4	3+	3+	;	;	;	;	2−	;	4	;1	2−	3+	0	;1+	;2=	4		Argus Brown
1957																							
NR 10§ ..	4	4	0	3	;	X	X+	;	;	;	;	2−	;	;2=	;1	2−	3+	0	;1+	;2=	4	2P	Amber Brown
NR 11 ..	4	4	0	3	3+	X	X	;	;	;	;	2−	;	;2=	;1	2−	3+	0	;1+	;2=	4	3C	Amber Brown
NR 12 ..	4	4	0	3	3+	X	X+	;	;	;	;	2−	;	3	;1	2−	3	0	;1+	;2=	4	3L	Amber Brown
NR 13 ..	4	4	0	3	3+	X+	X+	;	;	;	;	2−	;	3	;1	2=	X	0	;1+	;2=	4	5X	Amber Brown
NR 14 ..	4	4	0	3	;	X	X	;	;	;	;	2−	3−c	;2=	;1	2−	3+	0	;1+	;2=	4	2W	Amber Brown
21 Anz-1 ..	4	4	0	3	4	3+	3+	;	;	;	;1++	2−	;	;2=	;1	2−	3+	0	;1+	;2=	4	2E	Amber Brown
21 Anz-2 ..	4	4	0	3	4	3+	3+	;	;	;	;1++	2−	;	4	;1	2−	3+	0	;1+	;2=	4	2X	Amber Brown
9 Anz-1 ..	4	4	0	3	3	X++	3	3	3	;	;	2−	;	;2=	;1	3+	3	0	;1+	;2=	4	6V	Orange Rufous
17 Anz-1 ..	4	4	0	3	3+	3	3	3	;	;	;	2−	;	;2=	;1	3+	3	0	;1+	;2=	4	3D	Sudan Brown
222 Anz-6 ..	4	4	3	3	X+	;1	X=	;	;	;	;	2−	;	3+	;1	3+	;1+	;1+	;1+	;1	4	5D	Amber Brown
222 Anz-7 ..	4	4	3	3	X+	;1	2=	;	;	;	;	2−	2c	3+	;1	3+	;1+	;1+	;1+	;1−	4	6L	Amber Brown
222 Anz-3 ..	3	3	3	3	X+	;1−	;1	;	;	;	3	3−	3c	3	;1	3	;1+	;1+	;1−	;1−	3	2ye	Mars Yellow
222 Anz-4 ..	3+	3+	3	3	X+	;1=	;1=	;	;	;	3	3	3c	3+	3	3+	;1+	;1+	;1−	;1−	3+	2K	Orange Rufous
176 Anz-1 ..	4	4	0	3	;	3	3+	;	;	;	;	2−	;	;2=	;1	2−	3+	0	;1+	;2=	4	2Y	Amber Brown

NR 15	..	4	4	3	3	3+	X−	3+	;	;	;	;	X	3−c	;2=	X++	3+	X−	1+	;1+	3−c	4	B20	Sudan Brown
NR 16	..	4	4	0	3	3+	X	X+	;	;	;	;	2−	;1	3+	;1	2−	3	0	;1+	;2=	4	E9	Sanfords Brown
NR 17	..	4	4	3	3	3+	3−c	3+	;	;	;	;	3+c	;	3+	;1	3+	3−	X++	;1	3=c	4	E3	Amber Brown
NR 18	..	4	4	3	3	3+	3c	X+	;	3	;	;1++	3+c	;	3+	;1+	3+	3	3	;1+	3−c	4	D3	Bay
NR 19	..	4	4	3	3	3+	X	X	;1	2	;	;	2+	;1	3+	;1+	3+	3	3	;1=	3=c	4	F2	Argus Brown
NR 20	..	4	4	0	3	3+	3+	X	;1−	;1	;	;	2−	;1	3+	X−	2	3+	0	;	3−c	4	Q3	Amber Brown
NR 21	..	4	4	0	3	3	X+	X+	;	;	;	;1++	2	;	;2	;	2	3+	0	;2=	3=c	4	R1	Amber Brown
NR 22	..	4	4	0	3	3+	3+	3+	2=	2+	;	;	2−	;	3+	;	2−	3+	0	;1=	2≡	4	A1	Amber Brown
NR 23	..	4	4	0	3	3	;1	;1	;	3c	;	;	3−c	;	3+	;1−	3+	3	0	;1	;	4	C13	Bay
NR 24	..	4	4	0	3	;	3+	1++	3	;	;	;	2=	;	3+	;1=	;2=	3	0	;1=	;2=	4	O3	Amber Brown
NR 25	..	4	4	0	3	3+	X+	X+	3	3	;	;	2−	;	3+	;1	2−	3+	0	;1	;1	4	D14	Amber Brown
NR 26	..	4	4	0	3	3	X	1+	;	;	;	;	2−	;	;1	;1	2−	3	0	;1	;2=	4	S3	Amber Brown
21 Anz-1	..	4	4	0	3	3+	3+	3+	;	;1	;	;	2−	;	;2	;1+	2	3+	0	;1	2−	4	K2	Mars Yellow
21 Anz-2	..	4	4	0	3	3+	3+	3+	;1−	;1−	;	;	2−	;	3+	;1	2−	3+	0	;	;2=	4	Q2	Amber Brown
57 Anz-1	..	4	4	0	3	;1−	X++	3+	3	3	;	;	2=	;	3+	;1+	2=	3+	0	;1	2=	4	F1	Argus Brown
100 Anz-1	..	4	4	3	3	3+	3	;X=	3	;	;	;	2−	2=	;2=	;1	2	3+	3+	1+	3−c	4	H8	Orange Rufous
104 Anz-1	..	3	1	0	;	;	;	;	3	3c	;	;	;	;	1+	;	;	X=	0	;1	;1=	3	N2	Amber Brown
116 Anz-1	..	4	4	0	3	3	X++	X++	;	3	;	;	3=c	;	3+	;1	3+	3	0	1++	3−c	4	C3	Tawny
213 Anz-1	..	4	4	3	3	3+	X	X	;1−	;	;	3c	2	;	;2−	X++	2	3	3	;	2=	4	B25	Sudan Brown
213 Anz-2	..	4	4	3	3	3+	3c	3c	;	;	;	3	3+	2	;1	;1+	3+	X	X	;	2=	4	A5	Amber Brown
194 Anz-1	..	4	4	0	3	3+	X	1++	;1−	;1=	;	;	2−	;1	3+	X=	2	3	0	;1+	3−c	4	P4	Amber Brown
176 Anz-2	..	4	4	0	3	;1	X++	3	;1	;	;	;	2=	;	3+	;1	2−	3+	0	;1	2−	4	S16	Amber Brown
213 Anz-3	..	4	4	3	3	3+	X	X	;	;	;	;	1,2=	;	3+	;1	2−	X=	X=	;1	2=	4	S1	Sudan Brown

* Denotes Arnautka, Mindum and Spelmar.

† Reaction types in winter; Eureka gave a "3+" reaction with all isolates in summer.

‡ Reaction types at temperatures of 81° to 85° F.

§ Designations NR1–NR9 were used in a previous publication (Watson and Luig, 1958*b*).

On Mentana W1124* a single recessive gene for virulence was indicated. Of the 37 strains 13 were fully virulent, while the remainder produced a semi-resistant reaction varying from a "2=" to a "3–c" (χ^2 for a 3:1 ratio = 2·027; P-value = 0·20–0·10). These degrees of semi-resistance are typical of Mentana when tested in the seedling stage with the 21 and 34 race complexes of Australian field strains. The ";" reaction on Mentana to strain 104 Anz-1 is highly correlated with the ";" reaction on Acme to strains such as 111, 196, NR-2 and NR-4 (Watson, 1957) and is almost certainly due to the segregation of a second gene (Luig, unpublished).

On Acme, susceptible and semi-susceptible reaction types ("4" and "x") were clearly predominant. Many strains gave an intermediate reaction and the data for resistant, intermediate and susceptible classes could fit a 1:2:1 ratio. As the parent strain 21 Anz-2 produces a fully susceptible reaction on Acme, however, these results cannot be explained on the basis of a single incompletely dominant gene. If it is assumed that the intermediate class is the result of segregation of a second minor gene for virulence, the presence of a major dominant gene is indicated (χ^2 for a 3:1 ratio = 0·081; P-value = 0·80–0·70). The ";" reaction of strain 104 Anz-1 is discussed above.

The segregation pattern on Kubanka resembled closely that on Acme. This might be due to the presence of a common factor for resistance in these two *durum* varieties, and segregation of the same major dominant gene in the pathogen would account for the similarity. Several of the strains, however, produced different reactions on Acme and Kubanka, indicating that each variety possesses at least one additional factor for resistance not present in the other.

At high temperatures (80°–90° F. during daylight) the inheritance of pathogenicity on the three *durums* Arnautka, Mindum and Spelmar was less complex than on Acme or Kubanka. Dominance of virulence was also evident: only 7 of the 37 strains were avirulent (";" to ";x=" reaction type) and statistically a single dominant gene for virulence was indicated (χ^2 for a 3:1 ratio = 0·730; P-value = 0·5–0·30).

The reactions of Celebration to the progeny suggested the segregation of a single dominant factor for virulence (χ^2 for a 3:1 ratio = 0·009; P-value = 0·95–0·90). Celebration carries the Marquillo-type of resistance derived from its Double Cross parent. This resistance is lower at high temperatures, but no difficulty was experienced in classifying virulent and avirulent strains.

Thatcher possesses at least two types of physiological resistance, one an immunity derived from Kanred, the other resistance as in Celebration derived from Marquillo. The immunity factor was epistatic to the Marquillo-type resistance, all strains showing a "0" reaction on Kanred showed a "0" reaction on Thatcher. Strains NR17, NR18, NR19, 100 Anz-1 and 213 Anz-1—virulent on both Kanred and Celebration—were the only strains capable of attacking Thatcher.

On the variety Yalta, which carries a resistance identical with that of Gabo against certain Australian field strains, the segregation of strains in the progeny could not be satisfactorily explained on the basis of a single gene, but dominance of virulence was indicated. The significance of this will be discussed later.

On the variety W1656 (C.I.12632) the progeny behaved as though virulence ("x++" and "4" type reaction) was due to the action of two independent, recessive, complementary genes (χ^2 for a 15:1 ratio = 0·218; P-value = 0·70–0·50).

Inheritance of pathogenicity on the varieties Eureka, McMurachy, Bowie and Bokveld was more complicated. Pathogenicity tests suggest that each of these varieties has the gene Sr6 on chromosome XX, a gene which is ineffective at temperatures over 75° F. McMurachy was used in the 1957 study and the reactions were similar to those of Eureka. At low temperatures (60–65° F.) Eureka was fully susceptible to only three strains: virulence in the pathogen was apparently conditioned by two independent, recessive factors (χ^2 for a 15:1 ratio = 0·218; P-value = 0·70–0·50). This result was not expected, as it is known that only a single factor for resistance, Sr6, is operative against certain Australian strains, this factor giving a very distinct necrotic reaction at low temperatures. If a gene-to-gene host-pathogen relationship exists with Sr6, then

* Refers to the University of Sydney Wheat Accession Register.

many more strains virulent on Eureka would have been expected (χ^2 for a 3:1 ratio = 5·630; P-value = 0·02–0·01). At temperatures of 65° to 75° F. Eureka gave a higher reaction with parent strain 21 Anz-2 than with some other strains obtained from selfing. Strain 213 Anz-1 was the only one to which Eureka gave an intermediate reaction at these temperatures; this could be due to strain 213 Anz-1 being recessive for a gene pair for virulence. Eureka was fully susceptible at high temperatures to all isolates.

Bowie gave a full range of reactions to the progeny at high temperatures. To most strains the reaction was "2–", "2", or "2+". Several strains produced necrotic reactions in the range of "1–" to "x+". In addition, Bowie was semi-susceptible or susceptible ("3+c" and "3" type reactions) to five strains, and produced a ";" reaction when tested with strain 104 Anz-1. Segregation of a single major factor could account for most of the reaction types observed on Bowie (χ^2 for a 3:1 ratio of resistant vs. semi-susceptible and susceptible = 2·604; P-value = 0·20–0·10).

A somewhat similar segregation pattern was apparent when Bokveld was used as a differential. In most instances, however, Bokveld was highly resistant (";" to "1" reaction) and in no case fully susceptible. It is evident that genes in Bowie and Bokveld differ. Again, a one-gene segregation could explain the behaviour of the progeny on Bokveld at high temperatures (χ^2 for a 3:1 ratio of resistant vs. semi-susceptible is 1·523; P-value = 0·30–0·20).

When tested with the 37 strains, Khapstein W1451, a *vulgare* derivative from Khapli, showed minor variations from a highly resistant ";" reaction to a semi-resistant "1++, 2–" reaction. These variations might have been due to one of the two independent factors, previously found in this variety (Athwal and Watson, 1956), being ineffective against some strains, or to the segregation of minor genes in the fungus.

Besides Khapli and Khapstein, another variety, Kenya 117A, remained resistant to all strains.

Thirty entries from the 1959 International Wheat Rust Nursery were tested with seven of the progeny strains. All these entries had been selected for their comprehensive resistance to Australian field strains. The aim was to determine whether such resistance could possibly be due to the operation of a single factor rather than to multiple factors. In addition two wheat accessions, W2538, W2539, carrying *Agropyron elongatum* resistance, kindly sent by Dr. D. R. Knott, were also tested with the seven strains. The results indicated that many of these "I.W.R.N." lines are resistant to all the strains and the accessions W2538 and W2539 also showed a high degree of resistance to all seven strains.

(ii) *The Occurrence of Abnormal Characters.*

During the separation and study of the strains obtained from the barberry many abnormalities were noted. Differences were shown between strains in their incubation periods which varied from 9 days in some to 15 days in others. Marked colour variations also occurred, some strains being very dark brown and others almost yellow, the differences being observed in the uredospores. No strains with grey-brown spores were obtained and spores from an aecium suspected of being white failed to give infection on Little Club. It was evident that strains having certain characters such as an inability to break the epidermis and a tendency to be associated with browning and necrotic areas of the host would have less chance of survival in the field.

(iii) *Studies of Association between Factors for Virulence.*

Possible association of factors for virulence was also studied in all combinations. In Table 2 the χ^2 and P-values are tabulated for independent assortment of avirulence or virulence on 13 varieties.

It will be seen from Table 2 that virulence on Yalta was not associated with virulence or avirulence on the other 12 varieties. On two other varieties, Vernal Emmer and Einkorn, factors for pathogenicity seemed to be loosely associated, but this was not apparent between the factors in these varieties and those on the remaining 11 varieties.

TABLE 2.

Linkage between Factors for Pathogenicity in P. graminis *var.* tritici.

χ^2-values and *P*-values for Independent Assortment of Factors for Pathogenicity.

Pathogenic on	Pathogenic on.											
Kanred.	Kanred.	Einkorn.	Vernal Emmer.	Mentana.	Celebration.	Mindum.	Kubanka.	Acme.	Yalta.	Eureka.	Bowie.	Bokveld.	W1656.
Kanred..	—												
Einkorn	1·297 0·30–0·20	—											
Vernal Emmer ..	0·566 0·50–0·30	5·051 0·05–0·02	—										
Mentana	12·384 <0·001	0·163 0·70–0·50	2·176 0·20–0·10	—									
Celebration	11·159 <0·001	0·473 0·50–0·30	1·128 0·30–0·20	5·188 0·05–0·02	—								
Mindum	4·144 0·05–0·02	3·225 0·10–0·05	0·085 0·80–0·70	4·676 0·05–0·02	0·473 0·50–0·30	—							
Kubanka	3·830 0·10–0·05	0·024 0·90–0·80	0·316 0·70–0·50	7·300 0·01–0·001	13·541 <0·001	0·024 0·90–0·80	—						
Acme	1·930 0·20–0·10	1·097 0·30–0·20	0·139 0·80–0·70	1·329 0·30–0·20	4·908 0·05–0·02	0·010 0·95–0·90	19·335 <0·001	—					
Yalta	0·765 0·50–0·30	0·987 0·50–0·30	1·656 0·20–0·10	0·794 0·50–0·30	0·253 0·70–0·50	0·987 0·50–0·30	1·693 0·20–0·10	0·632 0·50–0·30	—				
Eureka	6·801 0·01–0·001	0·741 0·50–0·30	1·049 0·50–0·30	6·027 0·02–0·01	10·157 0·01–0·001	0·741 0·50–0·30	6·116 0·02–0·01	2·601 0·20–0·10	0·001 0·98–0·95	—			
Bowie	12·044 0·001	1·349 0·30–0·20	0·059 0·90–0·80	10·673 0·01–0·001	3·997 0·05–0·02	1·349 0·30–0·20	2·407 0·20–0·10	0·493 0·50–0·30	1·012 0·50–0·30	20·894 <0·001	—		
Bokveld	8·467 0·01–0·001	1·671 0·20–0·10	2·302 0·20–0·10	7·300 0·01–0·001	13·541 <0·001	0·024 0·90–0·80	5·536 0·02–0·01	1·916 0·20–0·10	0·266 0·70–0·50	16·868 <0·001	8·360 0·01–0·001	—	
W1656	6·801 0·01–0·001	0·762 0·50–0·30	1·049 0·50–0·30	1·424 0·30–0·20	3·180 0·10–0·05	0·762 0·50–0·30	0·704 0·50–0·30	0·066 0·80–0·70	0·924 0·50–0·30	2·788 0·10–0·05	1·097 0·30–0·20	6·116 0·02–0·01	—

The factors for virulence on the varieties Kanred, Mentana, Celebration, Eureka, Bowie and Bokveld were associated. The genes for virulence on Kanred and Bokveld, however, also appeared associated with those for virulence on W1656.

Some of these associations could be explained by assuming that certain of these varieties carry one or more of the same genes for resistance in common. This would most likely be the situation with Bokveld, Bowie and Eureka on the one hand and with Kubanka and Acme on the other. Additional genes in these varieties, or alleles, must be assumed present to account for differences in the reaction to different strains.

The possibility of association of genes for abnormal uredosorus colour with genes for pathogenicity was also investigated. It was thought that, if abnormal uredosorus colour was due to homozygosity of recessive genes, a relationship might be established between abnormal uredosorus colour and homozygosity of genes for pathogenicity. The 37 strains obtained from selfing were classed according to their uredosorus colour as normal (group I), comprising "Amber Brown", "Sanford's Brown" and "Argus Brown", or abnormal (group II), comprising all other colours, viz., the very dark "Bay" and the light colours "Sudan Brown", "Tawny", "Orange Rufous" and "Mars Yellow". For each strain the number of homozygous recessive gene pairs for pathogenicity in respect of the 13 above-mentioned varieties was counted. In the case of a strain being fully virulent on Eureka or W1656 the count was increased by two. In all other instances only one gene pair was counted in order to avoid over-estimation of the number of recessive gene pairs. No single recessive gene pair for pathogenicity was present in all strains abnormal for colour. Mean numbers of 2·12 and 4·416 recessive gene pairs were calculated for group I and group II respectively. The significance of the difference between these two means was tested by the t test. The value of t was found to be 2·90, and for 35 degrees of freedom is highly significant. It is therefore concluded that the genes for abnormal uredosorus colour show association with genes for virulence in the cultures that were studied here.

It was also noticed that some strains (NR15 and 213 Anz-1) were more aggressive than others, and that this was expressed by a shorter incubation period, more abundant infection and sporulation and better survival under storage conditions. As these strains also have a number of recessive genes for virulence, it would appear that these latter would not necessarily place these strains at a disadvantage when in competition with strains having dominant genes for avirulence.

Discussion.

The methods employed in this study did not exclude the possibility of some experimental error. Contamination of cultures, environmental effects on rust reaction and possible impurity of the teleutospore material used, make it necessary to consider some results with caution. The linkage of certain genes for pathogenicity with genes causing the loss of ability to produce the complete sexual cycle on the barberry could have been a further source of error. Such abnormalities have been reported by Johnson and Newton (1938). Anomalies due to differential survival of strains were largely eliminated by the technique of initiating each culture from a single aecidial horn. Mass inoculations would probably have favoured the more aggressive cultures and so discriminated against those with virulence genes associated with genes for abnormal characters. Data from which genetic ratios and association of characters were calculated were obtained from the 37 different strains and no statistical use was made of the frequency of appearance of the same strain.

The selfing studies presented were mainly concerned with the inheritance of pathogenicity on 23 differential hosts, but any association of genes for virulence on 13 varieties was also noted.

On eight differential varieties, viz., Kanred, Einkorn, Emmer, Mentana, Celebration, Kubanka, Acme and Mindum, virulence seemed to be inherited according to Mendelian laws and to be governed by a single major factor in each instance. Four of these factors, viz., those concerned in the reactions of Kubanka, Acme, Celebration and Mindum, could, when heterozygous, enable the parasite to overcome the corresponding

resistance. The four remaining factors were recessive. The mode of inheritance of pathogenicity on the five varieties Yalta, W1656, Eureka, Bowie and Bokveld was more difficult to ascertain.

It would appear from the results of this study that in certain instances there operates a system of specific relationships between factors for pathogenicity in the fungus and factors for resistance in the host as established for *Melampsora lini* by Flor.

In Kanred, for example, we suggest that, provided the corresponding dominant genes are present both in the fungus and the host, an interaction results following infection, and this becomes evident in the immunity or hypersensitivity characteristic of this variety. The absence of the appropriate dominant gene either in the fungus or the host or both fails to produce an interaction following infection, and susceptibility is evident. Similar complementary relationships are suggested for Einkorn, Emmer and Mentana.

The relationships, however, are not always simple. It is known that Mentana possesses two or more major factors for resistance to strains such as 104 Anz-1 which produce a ";" reaction (Luig, unpublished), and from the present studies it has not been possible to determine the number of genes in the fungus responsible for this interaction.

There was good evidence that virulence on the five *durum* varieties Acme, Kubanka, Arnautka, Mindum and Spelmar, and on Celebration, was conditioned in each case by a major dominant factor in the pathogen. Virulence or avirulence on Arnautka, Mindum and Spelmar was inherited as a unit. This was probably due to the presence of the same gene for resistance in all three varieties, this gene being the only one conferring high resistance to the progeny from selfing.

Acme and Kubanka, although alike in their reactions to all Australian field strains, reacted dissimilarly when tested with some of the segregates from selfing. Apparently these two varieties share a major factor for resistance, but they differ in their other genes for resistance. The parent strain 21 Anz-2 was heterozygous for genes for virulence on both varieties, and the data suggest a single major factor segregation in each case. The occurrence of strains avirulent on both Acme and Kubanka precludes the possibility of two different alleles controlling pathogenicity on these two varieties.

Celebration, which derived the Marquillo-type resistance from its Double Cross parent, reacted to the progeny as if segregation of a single dominant factor in the parasite were involved. Resistance of Celebration to a non-virulent strain at low temperatures was a ";1" type, which developed into an "x" type at higher temperatures. The reactions on Celebration and Thatcher to strains capable of rendering ineffective the immunity factor in Thatcher were almost identical. It is concluded that the same Marquillo-type resistance is present in both Celebration and Thatcher.

The majority of segregates were fully virulent on Yalta, indicating dominance of virulence. The data, however, fitted not a three to one, but a nine to seven ratio. Yalta possesses the same resistance to many strains of stem rust as Gabo, Charter, Lee and Timstein. Although overseas work reported the presence of two linked, dominant, complementary factors in varieties carrying this resistance (Knott and Anderson, 1956), recent work by one of us (N.H.L.) has shown that probably only a single dominant factor is involved and that differential transmission of gametes could account for the results obtained (Luig, 1960). A gene-to-gene host-pathogen relationship would require in the fungus the segregation of a single factor for virulence on Yalta.*

The origin of the parental strain 21 Anz-2 may have some bearing on the genetical basis of the host parasite relationship. Strain 21 Anz-1, unlike previous Australian field strains in its behaviour on several differential varieties, was first recorded in 1954 from southern New South Wales, and increased rapidly during the following years. In spite of its excellent competitive ability, the extensive cultivation of varieties carrying the Gabo-type resistance limited its spread. In 1956 strain 21 Anz-2 was first isolated from Woodburn, in northern New South Wales. This strain was identical

* In the 1960 study 16 different strains were obtained from selfing strain 21 Anz-2. Thirteen were virulent on Yalta and three were avirulent.

with 21 Anz-1 on all standard differentials and on other hosts except for its virulence on Gabo. Since only one type of resistance differentiates strain 21 Anz-1 from 21 Anz-2, the latter could be considered as a likely mutation from 21 Anz-1. Studies of somatic hybridization in field strains, however, suggested that strain 21 Anz-2 could have arisen by somatic hybridization between strain 21 Anz-1 and a strain capable of attacking Gabo (222 Anz-2). No variants virulent on Gabo were obtained by mixing 21 Anz-1 and 126 Anz-1, nor from extensive selection experiments from pure cultures of 21 Anz-1 (Watson and Luig, 1958*b*; and unpublished data). These studies, as well as that reported herein, suggest that the gene for virulence on Gabo is not present in the heterozygous condition in strain 21 Anz-1, and that somatic hybridization could be an important mechanism for the origin of new strains where the appropriate cultures are mixed in the field.

Virulence on W1656 was apparently controlled by two independent, recessive factors in the fungus. Allard and Shands (1954) and Nyquist (1957) found that crosses between C.I.12633 (a sister selection of W1656 C.I.12632) and susceptible varieties gave more resistant F_2 plants than could be expected if only a single factor was involved. They advanced the hypothesis that resistance depended on the action of two dominant factors linked with a recombination value of approximately 15 per cent. However, Allard and Shands (1954) also found resistance to stem rust and resistance to powdery mildew (*Erysiphe graminis tritici* El. Marchal) to be so closely linked that no recombinants were obtained from 762 F_3 progeny. Nyquist (1957*b*), when studying the mode of inheritance of resistance to leaf rust—located on the same chromosome—obtained a two-factor segregation in a cross between C.I.12633 and Ramona, but a single-factor segregation in a cross with White Federation. These findings taken in relation to recent work (Luig, 1960) suggest that chromosome XIII, on which all these resistances are located, could be differentially transmitted. If this is so, resistance to stem rust is provided by a single factor, and it can be assumed that the two factors in the pathogen are needed to overcome this one factor in the host.

The inheritance of pathogenicity on Eureka, Bowie and Bokveld suggested the segregation of two or more factors. All three varieties appear to carry the Sr6 gene (or an allele of it). In Eureka this was the only gene which operated against the progeny. The behaviour of Bowie to field strain 126 Anz-1 at low and high temperatures could be due either to an allele of Sr6 which confers a resistance less sensitive to temperature, or to the presence of two closely linked genes, one of them being Sr6, the other not affected by higher temperatures (Luig, unpublished data). The resistance of Bokveld can be explained in similar terms, but it should be noted that in no case was this variety fully susceptible. It is not possible to interpret these results in terms of a gene-to-gene relationship, and further studies of the nature of the Sr6 locus are required.

In certain respects these findings may be compared with those of Johnson and Newton (1940) and Johnson (1954). The present conclusions concerning the inheritance of pathogenicity on Kanred and Mindum are in agreement with theirs. Johnson (1954) found that avirulence on Einkorn was dominant, but he did not state the number of factors involved. Upon selfing race 21 he obtained seven forms, two avirulent and five virulent, on this variety. The selfing of race 125 gave a ratio almost the reverse of this. The present work indicates that a single recessive factor is involved.*

Furthermore, Newton, Johnson and Brown (1930) and Johnson (1954), when selfing race 21, did not obtain progeny virulent on Vernal Emmer or avirulent on Acme. This is clear evidence that North American race 21 differs genotypically from the Australian race 21 in respect to genes for pathogenicity on Stakman's twelve standard varieties. It is a well-known fact that, owing to the heterozygous nature of the rust organism, races which are phenotypically similar may nevertheless be quite different in their genotypes. Again, Johnson (1954) did not obtain susceptible infection types on varieties carrying Sr6 and Sr11 Sr12 when inoculating with mass progeny cultures

* In the 1960 study 19 different strains were isolated from selfing strains 21 Anz-1 and 21 Anz-2, nine were avirulent and 10 virulent on Einkorn.

derived from selfing race 21. The progeny from selfing strain 21 Anz-2 segregated on varieties with one or other of these two resistances.

It appears from this work that there is association between certain of the genes for virulence on the differential varieties. Vakili (1959) has reported such association in his studies of the leaf rust organism. He found that nine of the twelve genes conditioning pathogenicity fell into two linkage groups. Four of the twelve genes were dominant for virulence and others were complementary recessives. The gene M2 appeared to operate against two completely different genes for resistance.

Regarding reports of linkage, it should be borne in mind that very little is known about the mechanism of sexual recombination in rusts, and that linkage of semi-lethal genes with genes for pathogenicity could mimic linkage between the latter.

Disturbed ratios and pseudo-linkage can result in cases where the teleutospore material did not consist of only one strain. As mentioned above, a new strain resembling race 34 on Stakman's differentials was found when the inoculum which provided the teleutospore material in 1959 was tested. If preferential germination of basidiospores on barberry had occurred, a high proportion of the pycnia might have been formed by the new strain. This strain differed from strain 21 Anz-2 by its reactions on Kanred and Yalta. If pycnia were formed by the new strain an association between reaction types on Kanred and Yalta in the resulting strains would be expected. No such association, however, was found.

The inbreeding of strain 21 Anz-2 gave rise to several strains manifesting abnormal characteristics. The fact that the same abnormality was observed with isolates from different aecial clusters suggests that the changes from the normal condition were not due to mutations occurring during the passage of the rust organism through the sexual cycle, but to recombinations of recessive genes. The majority of changes seemed to be detrimental to the fungus, but in some instances progeny from selfing showed greater vigour under glasshouse conditions.

The studies on inheritance of and association of genes for virulence was one aspect of this investigation. Equally important was that part which dealt with the potential virulence that could be released on selfing. Selections from the International Rust Nursery and two varieties which are used for breeding, Khapstein and Kenya 117A, remained resistant when tested with all progenies. In each variety at least one gene for resistance was effective against all strains. The gene Sr9 of Kenya 117A has been incorporated into several Australian commercial varieties, and it appears that the genes for rendering Sr9 ineffective are not present in strain 21 Anz-2. The variety Festival, carrying Sr9 and extensively grown in Queensland and in the northern wheat belt of New South Wales, has retained its resistance to stem rust for several years now. An advanced backcross breeding programme at the University of Sydney is aiming at incorporating the resistance of Khapstein into agronomically desirable types. The genes of Kenya 117A and Khapstein may prove to be valuable sources of resistance to present and future strains of stem rust in Australia.

Addenda.

Since this report has been written, further selfing studies with strain 21 Anz-2 and with strain 21 Anz-1 have been carried out. Sixteen different strains were isolated from selfing strain 21 Anz-2 and three from selfing strain 21 Anz-1. The latter strains resembled the parental 21 Anz-1 in their inability to attack Yalta. On Kanred, Vernal Emmer and Mentana avirulence was again inherited as a dominant character with ratios of 15:4, 17:2 and 14:5 respectively. On Arnautka, Yalta and Celebration virulence was dominant and here the ratios were 15:4, 13:3 and 14:5. Only one of the 19 progeny strains was virulent on W1656. On Einkorn nine strains were avirulent and ten virulent, a somewhat different result from that obtained in the 1957 and 1959 studies. The 19 strains showed variations from a "2,3–" to a "3" reaction when tested on Kota, and also segregated for pathogenicity on Renown, Glenwari and Spica which are believed to carry Hope-type resistance. Kenya 117A and Khapstein were again resistant to all isolates from selfing, while Little Club, Marquis and Federation were

susceptible. At temperatures over 75° F. Eureka was susceptible to all isolates. Acme and Kubanka for the most part reacted similarly, but to some isolates they were unlike in their reaction.

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AN INVESTIGATION OF THE POSSIBLE ROLE OF BITING MIDGES (DIPTERA, CERATOPOGONIDAE) IN THE TRANSMISSION OF ARTHROPOD-BORNE VIRUS DISEASES AT TOWNSVILLE.

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(One Text-figure.)

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Synopsis.

At Townsville, North Queensland, in November, 1955, the host preferences of local species of biting midges were investigated. *Culicoides austropalpalis, C. mackayensis* and *C. magnesianus* were shown to feed on bird; *C. molestus* on bird, flying fox and man impartially; and *C. ornatus* together with *C. subimmaculatus* on flying fox and man with a distinct possibility of bird feeding as well. The three species *C. molestus, C. ornatus* and *C. subimmaculatus* must be considered potential vectors of disease between flying fox, bird and man.

Introduction.

The City of Townsville, North Queensland, has long been known as a centre of periodic outbreaks of dengue fever. The possibility of other viruses being involved has been discussed by Rowan and O'Connor (1957) and Rowan (1957). It has also been suggested that flying foxes (*Pteropus* spp.) and certain migratory birds might be implicated as wild reservoirs for dengue or other related viruses, and evidence suggestive of this is recorded by O'Connor *et alii* (1955), Rowan and O'Connor (1957) and Rowan (1957).

If dengue or other related viruses are found in flying foxes or wild birds, then vectors for these must be sought other than the urban and domestic vector, *Aëdes aegypti*, responsible for man to man transmission in human epidemics. The investigation of other possible vectors has been undertaken by Mackerras *et alii* (1955) and on several occasions by members of the staff of the Department of Entomology, School of Public Health and Tropical Medicine, University of Sydney. In the opinion of this Department, based on some years of investigation of the blood feeding habits of blood-sucking flies, concentration solely on mosquitoes as possible vectors would be unwise. In view of the typically coastal incidence of dengue fever outbreaks and sporadically accumulated evidence of the feeding on birds by biting midges, it was thought that any investigation of possible vectors should include a study of these insects.

Because of their small size, cryptic behaviour, and possibly because of a general belief that their life span was very brief, biting midges have received almost no attention as possible disease vectors as compared with the more conspicuous mosquitoes. A review of their known role as vectors of disease appeared in Australian literature in Lee (1948). Since that time biting midges of the genus *Culicoides* have been shown to be vectors of a virus disease, blue-tongue of sheep (Du Toit, 1944), intermediate hosts of *Haemoproteus nettionis* of ducks (Fallis and Wood, 1957), as well as the cause of an allergic dermatitis in horses (Riek, 1954), all previous records having been as intermediate hosts of various nematode parasites of man or cattle.

Feeding by *Culicoides* on birds has been proven occasionally in Australia (unpublished information), but perhaps the earliest pertinent record is that of Jellison and Philip (1933), who found abundant *Culicoides* in birds' nests built close to a stream, and of these many were engorged with blood.

Hence, in the work undertaken by the School of Public Health and Tropical Medicine, evidence of blood-feeding on birds and flying foxes was sought amongst both

mosquitoes and biting midges in selected habitats in the vicinity of Townsville. The results of the mosquito studies have been reported by O'Gower (1960).

The task of proving blood-feeding by biting midges on hosts other than man is not an easy one. Direct observation of diurnal feeding is possible only on quiet and co-operative domestic animals; with nocturnal feeders and wild bird or animal hosts only precipitin testing of the stomach contents of engorged specimens is likely to yield positive data. Even this technique is not as flexible as it is with mosquitoes, since the limited amount of blood taken precludes a wide range of tests and also makes it necessary to smear such specimens within a few hours of actual feeding. In order to effect the capture of significant material, not only must special techniques be used, but the investigator must have an intimate knowledge of the microhabitats worthy of exploitation. Hence in the following account of the Townsville work some stress is laid on both the techniques employed and the habitats investigated.

The study was undertaken in November, 1955, this being the end of the dry season at Townsville. Hence the species caught were predominantly associated with salt-water habitats and little light is thrown on the potentialities of those associated with fresh or brackish water. Observations during the wet season would be required in order to gain a fully representative coverage of the populations and host preferences of all species known to occur in the area.

Technique.

Biting midges were taken by electric suction light trap (modified Du Toit type), acetylene light trap, tent trap, sweep net, and by aspirator. From time to time the light traps were baited with flying foxes in cages, or set in trees visited by flying foxes, or placed in the vicinity of domestic poultry. The tent trap was always baited with flying fox. Unfortunately no wild birds were available as trap bait. On a number of occasions the electric light trap was run throughout the night and cleared every three hours so that freshly fed specimens could be taken out and some idea of preferred feeding times obtained.

Catches were killed with chloroform vapour and sorted forthwith (light traps catch a vast variety of insects other than mosquitoes and biting midges). Engorged specimens were pinned and the blood smeared onto filter paper for source identification by the precipitin technique (Lee *et al.*, 1954). These smears were stored over silica gel in a refrigerator pending transfer to Sydney where the actual precipitin tests were performed by K. J. Clinton at the School of Public Health and Tropical Medicine. The pinned specimens were identified as far as possible while fresh, checked when dry, and further checks made by clearing and mounting any doubtful specimens. Other specimens from the traps were preserved in 70% alcohol, or on pins for later identification.

Results (*Relating to Habitats*).

Of more than 60 collections, engorged material was taken in 24. These 24, yielding significant information, came from six localities which are discussed below in order of recession from the mouth of the Ross R. (see Map, Text-fig. 1).

1. *Townsville Regional Electricity Board Powerhouse (T.R.E.B.).*

The mangrove swamp near the outfall of the condenser cooling water. Of a total of 13 collections, engorged material was taken in 6 and the hosts identified in 5 of these.

2. *Boundary Road.*

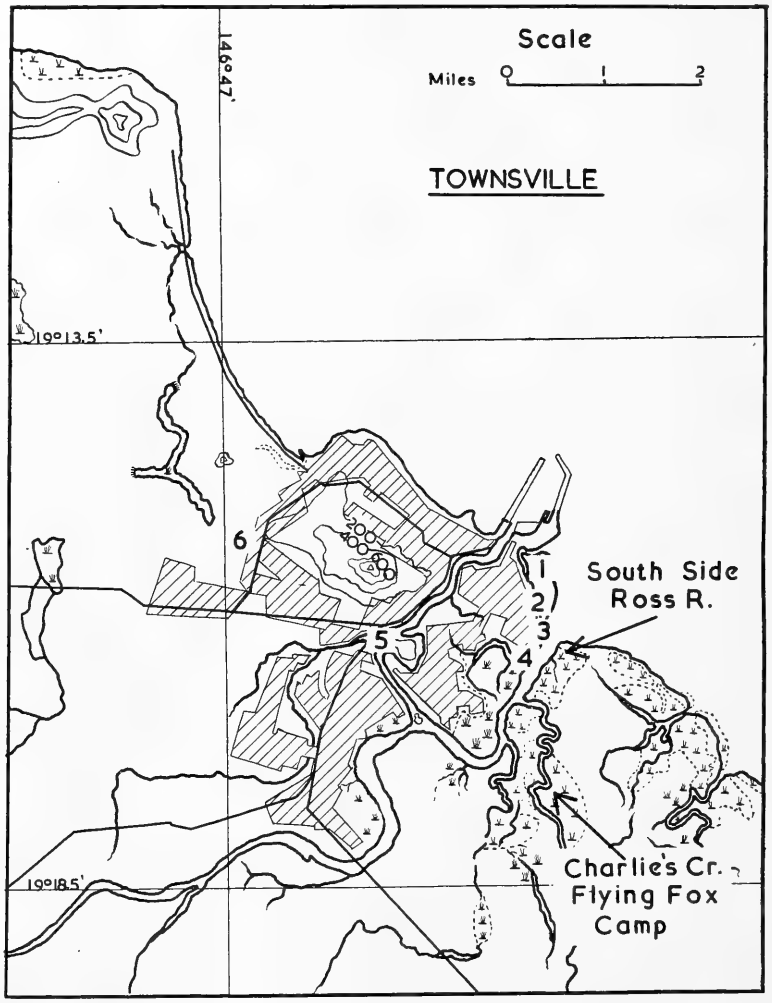
Some 400 yards upstream from 1, an unbaited electric suction trap was used for one night only set among mangroves 200 feet from high water mark towards the stream. In 4 collections only 2 engorged specimens of *Culicoides molestus* were taken for which no host identification could be made.

3. *Ross River Bank.*

At a house a little upstream from 2, on the shore above high water mark. Seven collections were made, all of which contained engorged material and in all cases the host was identified. The electric suction trap was used in a mango tree over flying-fox bait and the acetylene trap was set among poultry.

4. *Bundy Creek.*

A location further up the river where the channel is closer to the bank and there is relatively less mangrove growth on the town side of the river. The unbaited electric suction trap was set in a mango tree at 20 feet above ground level for one night. Four collections were made, each yielding engorged *Culicoides molestus*, and the hosts were identified. One collection aspirated from human bait yielded *Culicoides ornatus*.



Text-fig. 1. Map of Townsville with collection sites referred to in text.

5. *Lowth's Bridge.*

An area of mangrove swamp and salt pan intersected by deep tidal creeks adjacent to the railway yards. Of six collections, three yielded engorged material from which identification of the host also resulted. A sweep net, aspirator and flying-fox baited tent trap were also used here. The baited tent trap proved most effective when used with closed end towards maximum light, in this case sunrise.

6. *Belgian Gardens.*

In this suburb on the northern side of the city the electric suction trap was set unbaited in a mango tree 12 feet above ground. The tree was visited by flying foxes,

but in ten collections only one engorged specimen of *Culicoides austropalpalis* was taken. This gave a positive reaction for flying fox (but see under that species below).

Further small collections were made on the south side of Ross River. *Styloconops* sp. was taken among shoreline dunes near the mouth of the river. This species attacked man in numbers in the late afternoon. At a flying fox camp in the mangrove swamp along the upper part of Charlie's Creek *Culicoides ornatus* was taken attacking flying fox on the ground, and man, at about noon.

Results (*Relating to Species of Biting Midge*).

Species Associated with a Freshwater Habitat.

1. *Culicoides austropalpalis* Lee & Reye.

This was present in all heavily collected localities and was the dominant species at Belgian Gardens and Ross River bank. As this species is believed to breed in freshwater pond margins its activity within and near mangrove foreshores was surprising. Since the proportion of males caught was obviously less in these areas, the possibility of a reasonably wide flight range is suggested. Under favourable conditions this species seemed to be active throughout the night, although with a fall in temperature the numbers fell off after midnight. Host identification showed a marked preference for bird, presumably fowl, for when poultry baited traps were used, up to 45% of the females captured were engorged. The finding of flying fox blood in a single specimen taken in an unbaited trap at Belgian Gardens must be considered atypical in the absence of further confirmation of feeding on this host.

2. *Culicoides dycei* Lee & Reye.

This was relatively rare and only females were taken. None were engorged, but at Belgian Gardens most were taken with the flying fox baited trap (midnight to 0300 hours) and one specimen was taken coming to man at Lowth's Bridge.

3. *Culicoides magnimaculatus* Lee & Reye.

Taken only at Belgian Gardens, this species was not common, nor was engorged material collected, although the best catches were with flying fox baited traps. *C. magnimaculatus* is known to be a diurnally active mammal-biting species in other localities.

4. *Culicoides marksi* Lee & Reye.

This was less common than *C. magnimaculatus*, but again the largest catch was with flying fox baited trap. No engorged material was taken of this known mammal-biting species. Apart from single specimens from Lowth's Bridge and Bundy Creek it was also confined to Belgian Gardens.

Species Associated with a Saltwater Habitat.

5. *Culicoides mackayensis* Lee & Reye.

Although uncommon, this species seemed to favour the mangrove flat area well inside the mouth of the Ross River where its activity was spread evenly throughout the night. Small numbers (including males) taken at Belgian Gardens probably came from the creek north of Kissing Point. Engorged material was taken only from the poultry baited trap at Ross River bank and this showed the host to be bird.

6. *Culicoides magnesianus* Lee & Reye.

Although taken in all localities, this species dominated the electric suction trap catches on the south bank of the Ross River near its mouth. Maximum nocturnal activity appeared to be between 2100 and 0300 hours. The few engorged specimens taken (one from a trap baited with flying fox) had fed on birds.

7. *Culicoides molestus* (Skuse).

This species was widely distributed in the lower part of Ross River, its proportion in catches increasing up the river to Bundy Creek where it became the dominant species. Its nocturnal activity seemed to be at a peak towards midnight and least before dawn. In this series the proportions of engorged to total females in collections of this species

were of the same order whether taken by trap baited with flying fox, or with poultry, or taken attacking man. Despite the proximity of all three baits at times, the engorged specimens had invariably fed on the bait of the particular trap. This is the only species so far proven to feed on man, flying fox and bird. *C. molestus* did not seem to range far from mangroves and the few taken at any distance from this habitat were not engorged.

8. *Culicoides ornatus* Taylor.

Although widely distributed, this species was found most abundantly in mangrove swamps penetrated by narrow creeks. This species presents taxonomic difficulties which will be discussed elsewhere, and may well resolve into a complex of species with diagnostic characters only in the male sex. For the time being the name *ornatus* will be applied to all females in this complex. Baited light traps were not used in the area of maximum abundance (Lowth's Bridge) and the only index of activity is attack on man. This seems to be at its peak just after sundown and just before sunrise. However, they were taken feeding on flying fox and man at noon in the flying fox camp on Charlie's Creek in the still shade of the mangrove swamp. Some idea of the attack rate is given from the results of a flying fox baited tent trap at ground level between 0500 and 0530 hours at Lowth's Bridge. Using a mouth operated aspirator, 380 females were taken, and of these 236 had fed, and the method of capture proved inadequate to cope with the numbers present. Some engorged specimens were taken in a poultry baited light trap, but, as the host was not identified, bird feeding by this species remains an unproven possibility.

9. *Culicoides subimmaculatus* Lee & Reye.

With a wide distribution within the river mouth this species appeared to dominate where the foreshore consisted of mangroves or sandy mud flats, e.g., T.R.E.B. to Boundary Road. Like *C. molestus*, it was not taken at any distance from the river. In traps the peak activity seemed to be about midnight. Like *C. ornatus*, it readily feeds on man and flying fox, and though no proof was obtained that it feeds on bird, the high proportion of fed material in bird-baited traps is suggestive that it does so.

10. *Culicoides marmoratus* (Skuse).

This intertidal zone species was less numerous than expected for this area, only 12 males and 35 females being taken in all, spread over 11 light trap collections. Most were taken in unbaited light traps at Bundy Creek and Belgian Gardens with a few at T.R.E.B. Traps baited with fowl and flying fox at Ross River bank produced single specimens only. No engorged material was taken nor any preferred time of activity shown. From other areas this species is known as a mammal biter often ranging widely from its habitat, being captured inland with the salt-marsh mosquito, *Aëdes vigilax*.

11. *Styloconops* sp.

This was encountered in large numbers attacking man in the late afternoon among shore-line dunes on the southern side of Ross River. As far as is known, this is a diurnal and/or crepuscular species associated with certain types of sandy foreshore. What its natural hosts are in this terrain is in considerable doubt, and the presence of one specimen in a flying fox baited trap at T.R.E.B. is of doubtful significance.

Table 1 summarized the findings relative to hosts and habits.

Discussion.

Within the limits of season and technique it appears that the three common species of *Culicoides* (*molestus*, *ornatus*, *subimmaculatus*) associated with mangroves may be considered as potential vectors of disease among the three hosts used in this survey (man, flying fox, bird). At present *C. molestus* seems the most likely as it attacks all three equally; *C. ornatus* and *C. subimmaculatus* readily attack man and flying fox and there is a distinct possibility that they may also attack birds. All three are possibly active in these mangrove swamps when flying foxes are in camp and birds are roosting.

Since this field work was done other surveys (unpublished) have indicated that the population at least of *C. subimmaculatus* and *C. ornatus*, and probably that of *C. molestus* also, waxes and wanes in relation to the lunar tide cycle. A prior knowledge of this phenomenon could have led to more appropriate timing of trapping at Townsville and to negative results being seen in a different perspective. It is expected that the *Styloconops* sp. taken will also have a similar relationship.

The remaining species associated with the intertidal zone (*C. mackayensis* and *C. magnesianus*) remain as bird-biting species, although there are occasional records from other localities of solitary specimens of *C. magnesianus* apparently attracted to man.

TABLE 1.

SPECIES OF BITING MIDGE.	HOST. Flying Fox.	Bird.	Man.	BITING ACTIVITY.
Culicoides austropalpalis ..	(1) +[1]	(36) + D, B	—	Nocturnal, 1800–0600
Culicoides dycei	?[2]	—	?[3]	Nocturnal, 0–0300
Culicoides magnimaculatus	?[2]	—	—	Diurnal and crepuscular
Culicoides marksi	?[2]	—	—	Probably crepuscular.
Culicoides mackayensis ..	—	(1) + D	—	Nocturnal, 1800–0600
Culicoides magnesianus ..	—	(2) + B	—	Nocturnal, 2100–0300
Culicoides marmoratus ..	—			
Culicoides molestus	(7) +	(23) + D, B	+	Nocturnal, 1800–0600 and crepuscular
Culicoides ornatus	(84) +	?[4]	(6) +	Crepuscular and diurnal
Culicoides subimmaculatus	(44) +	?[4]	(1) +	Nocturnal and crepuscular
Styloconops sp.	?[5]	—	+	Diurnal.

Notes.—Figures in brackets indicate numbers of positive precipitin reactions obtained; + indicates feeding on host demonstrated by observation or precipitin tests; D indicates feeding on domestic poultry and B indicates that the avian blood source was possibly other than a domestic one.

[1] Feeds predominantly on birds, this single positive is somewhat dubious.

[2] Females taken in baited light trap.

[3] One specimen coming to man.

[4] Fed specimens in poultry-baited light trap but host not identified.

[5] Unfed specimen in flying fox baited light trap, doubtful as usually diurnal.

With the exception of the bird-biting *C. austropalpalis*, the species associated with fresh-water were present in such small numbers that little can be said of them from this survey. *C. magnimaculatus*, *C. marksi* and *C. dycei* are known to bite mammals elsewhere, but knowledge of other possible hosts or preferences among mammals must await further study; their presence in the seasonal conditions encountered suggests that they may be important after sufficient rain has fallen to expand the larval habitats.

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THE DISTRIBUTION AND INTER-RELATIONSHIPS OF *PERGA AFFINIS* KIRBY AND *PERGA DORSALIS* LEACH (HYMENOPTERA, SYMPHYTA).

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[Read 30th August, 1961.]

Synopsis.

New characters for the separation of the two closely related species of the sawflies, *Perga affinis* Kirby and *Perga dorsalis* Leach, are recognized. The distribution of each species is discussed, and on the basis of the newly recognized characters each species is divided into geographical subspecies.

In the past considerable difficulty has been experienced in the specific separation of the two sawflies *Perga affinis* Kirby and *Perga dorsalis* Leach. The types of both species are males, and authors in the past have experienced some difficulty in distinguishing between them. In the case of the females there has been less difficulty in distinguishing two forms, though the two were considered to be closely related. Characters are now recognized in the males which make separation of the two species very easy. As these characters are also present in the females there is now no difficulty in associating the sexes and correctly assigning specific names to the two species.

Perga affinis has an extensive range and can itself be separated into three subspecies. The typical form occurs from the southern coast of Victoria around Melbourne, through inland Victoria and New South Wales to at least as far north as Moreton Bay, Queensland. The typical subspecies occurs also in western Victoria and is known from the Adelaide region of South Australia. Throughout this range the legs, except the coxae, are all pale, though in most cases the middle and hind trochanters are somewhat darkened and the femora, especially the hind femur, though pale, are darker than the tibiae. The gaster has a greenish-black iridescence. One female from Hazlewood, Victoria, has the base, apex and caudal margin of the hind femur darkened but not black. In the other two females examined from this locality the hind femur is entirely pale. In the vicinity of Canberra, and possibly at all localities to the north of it, the mesepimeron is generally all black. In southern Victoria the mesepimeron usually has a large pale area. At localities around the New South Wales–Victorian border there is considerable variation in the colour of this structure. Some populations fall clearly into one or other of the above two categories, while other populations are quite variable. Insufficient material has been examined from South Australia to ascertain the position regarding the colour of this structure, but in all specimens examined there was a pale spot, sometimes small.

On Flinders Island and in Tasmania (south at least as far as Hobart) there is a pale subspecies in which the gaster has a distinct brownish hue and the coxae are paler than normal. There are also some small structural differences.

In the western part of the species range, in western Victoria (Horsham, Wilkur) and in South Australia (Sleaford Bay), there is a subspecies with comparatively dark legs, and the gaster has a bluish-black iridescence with less of the underlying brown colour.

It is difficult to account for the presence of the typical form of *affinis* in the region of Adelaide except as an introduction, for both to the west of Adelaide (at Sleaford Bay) and to the east (in western Victoria) there is a quite distinct subspecies common to these two areas.

Perga dorsalis is more of a coastal species. It, too, can be divided into subspecies. In the typical form the gaster has a green-black iridescence and the hind femur is dark

in part. This form occurs in coastal New South Wales, extends south into Victoria and possibly north into Queensland. It occurs inland as far as Canberra, but not commonly so.

In central southern Victoria (Ballarat) there is a pale subspecies in which the gaster is entirely brownish except for the basal segment, and the hind femur is all pale.

In western Victoria (Grampians and Little Desert) there is a third subspecies which does not differ in colouring from the typical form, but which has distinctive ornamentation of head and pronotum.

Key to Species and Subspecies.

Females.

Hairs of ovipositor valves very dense and fine, almost touching one another, tips of hairs not spooned; flattened "saw-bench" on lower margin of saw-sheath very long and thin, without obvious longitudinal striae.

i. Lower jena with only scattered fine hairs (punctures large and usually spaced); all coxae black at least in part.

(*a*) Legs (except coxae) all pale (middle and hind trochanters often partly darkened); abdomen green-black ..... *affinis affinis* Kirby.

1. Mesepimeron with a pale spot, spot rarely indistinct ..... Victorian form.
2. Mesepimeron black, rarely with a pale spot ..... Canberra form.

(*b*) Trochanters mostly dark; bases of middle and hind femora black except narrowly anteriorly, caudal margin and apex of hind femur dark; abdomen blue-black .... *affinis atrata*, subsp. nov.

ii. Lower jena with dense short hairs; coxae with only very small brownish-black areas (legs, except coxae, all pale; mesepimeron with a large pale area; abdomen rather pale, with a brownish tinge) ..... *affinis insularis*, subsp. nov.

Hairs of ovipositor valves not dense, with a considerable space between each hair, tips of hairs spooned; flattened "saw-bench" on lower margin of saw-sheath relatively short and broad, with seven or eight obvious longitudinal striae (lower jena with dense short hairs; coxae black in part; mesepimeron with a pale spot).

i. Hind femur partly dark; abdomen with green-black iridescence.

(*a*) Vertex of head without a small glabrous area at meson above; pronotal lobe with the oblique sulcus ill-defined or absent; spooning of hairs on saw-sheath pronounced .... *dorsalis dorsalis* Leach.

(*b*) Vertex of head with a small glabrous area at meson above; pronotal lobe with the oblique sulcus deep and clearly defined; spooning of hairs on saw-sheath limited to apices ..... *dorsalis nitida*, subsp. nov.

ii. Hind femur all pale; abdomen rather pale, entirely brownish except for basal segment, (vertex of head with a small glabrous area at meson above; pronotal lobe with the oblique sulcus ill-defined or absent; spooning of hairs on saw-sheath limited to apices) .. .. *dorsalis castanea*, subsp. nov.

Males.

Lower jena with only scattered fine hairs (punctures large and usually spaced); first segment of abdomen generally obviously pale except at base; coxae generally mostly pale (dark in Canberra form) ..... *affinis*.

Lower jena with dense short hairs; first segment of abdomen generally only narrowly pale at apex or all dark; coxae generally mostly black ..... *dorsalis*.

Lower jena with dense short hairs; first segment of abdomen obviously pale except at base; coxae mostly pale ..... *affinis insularis*.

Perga dorsalis Leach.

Perga dorsalis Leach, 1817; Benson, 1939: 334.

Benson (1939) has given a key for the separation of this species from others of the genus so that only those characters used in the separation of this species from *affinis* are listed below.

Perga dorsalis dorsalis Leach.

Female. Coxae black in part; hind femur partly dark; trochanters pale; abdomen with green-black iridescence; mesepimeron with the punctate area pale in part. Hairs of ovipositor valves not dense, with a considerable space between each hair, tips of hairs incurved and spooned; flattened "saw-bench" on lower margin of saw-sheath relatively short and broad, with seven or eight obvious longitudinal striae; lower jena with dense short hairs.

Male. Similar to the female, but legs, except coxae, all pale; coxae mostly dark as in the female.

Type. Holotype ♂ in the British Museum (Natural History).

Type Locality. New South Wales.

Distribution. Coastal New South Wales, extending south into Victoria and north possibly into Queensland. The species extends inland to Canberra, but is not common there.

PERGA DORSALIS CASTANEA, subsp. nov.

Female. Similar to the typical form, but the abdomen rather pale, entirely brownish except for the basal segment; hind femur all pale. Spooning of hairs on saw-sheath not as pronounced as in the typical form; vertex of head with a small glabrous area at meson.

Male. Similar to typical form except for small glabrous area at meson of vertex.

Type. Holotype ♀, allotype ♂ and 1 ♂, 16 ♀ paratypes in the C.S.I.R.O. Division of Entomology Museum, Canberra; 2 ♀ paratypes in each of the National Museum of Victoria, Burns Collection and the British Museum (Natural History).

Type Locality. Ballarat, Victoria (Dec. 1958 and Jan. 1959, F. M. Leask).

Specimens from Belgrave, Victoria, tentatively referred to this subspecies, have the abdomen all brownish.

PERGA DORSALIS NITIDA, subsp. nov.

Female. Similar to the typical form in colouring; vertex of head with a small glabrous area at meson; pronotal lobe with the oblique sulcus deep and clearly defined; hairs of lower jena not as dense as in the typical form.

Male. Not known definitely.

Type. Holotype ♀ and 3 ♀ paratypes in the National Museum of Victoria; 1 ♀ paratype in C.S.I.R.O. Division of Entomology Museum, Canberra; 1 ♀ paratype in Burns Collection; 1 ♀ paratype in British Museum (Natural History).

Type Locality. Little Desert, Victoria (22 Jan. 1947 and 27 Mar. 1947, A. N. Burns).

There are also one female and one male from Blackburn, Victoria, in the Burns Collection, which are tentatively referred to this subspecies.

PERGA AFFINIS Kirby.

Perga affinis Kirby, 1882; Benson, 1939: 335.

Benson (1939) has given many of the characters of this species in his key to species.

PERGA AFFINIS AFFINIS Kirby.

Female. Legs, except coxae, all pale; all coxae black in part; mesepimeron with the punctate area often pale in part but sometimes all dark; abdomen with a green-black iridescence. Hairs of ovipositor valves very dense and fine, almost touching one another, tips of hairs not spooned but slightly bent inwards; flattened "saw-bench" on lower margin of saw-sheath very long and thin, without obvious longitudinal striae; lower jena with only scattered fine hairs, punctures large and usually spaced.

Male. Similar to the female, with only scattered hairs on the lower jena; coxae mostly pale, otherwise coloured as in the female. The coxae are mostly dark in the Canberra form.

Type. Holotype ♂ in the British Museum (Natural History).

Type Locality. Victoria.

Distribution. The species ranges from the central southern coast of Victoria north through inland New South Wales to southern Queensland and west to the Adelaide region in South Australia.

In specimens from southern Victoria there is occasionally some darkening of the hind femur.

The holotype of *intricans* Morice from Moreton Bay, Queensland, is placed in *affinis* by Benson (in litt., 1960). It could possibly represent a northern subspecies. The other two specimens in the type series of *intricans* from Adelaide, South Australia, belong in

dorsalis. This is the only record of *dorsalis* from South Australia, and some doubt is expressed as to the correctness of the locality.

PERGA AFFINIS INSULARIS, subsp. nov.

Female. Similar to the typical form, but abdomen with more brownish hues, though with a slight metallic iridescence; first tergite of the abdomen nearly all pale; coxae nearly all pale, with only small brownish-black areas, fore coxa virtually all pale, hind coxa with a narrow dark line laterally, area somewhat expanded at base; mesepimeron with a large pale area usually covering the punctate zone. Structurally differing only in having dense short hairs on the lower jena and with the punctures there confluent.

Type. Holotype ♀ and 4 ♀ paratypes in the National Museum of Victoria; 1 ♀ paratype in each of C.S.I.R.O. Division of Entomology Museum, Canberra, and British Museum (Natural History).

Type Locality. Flinders Island, Tasmania (28 Feb. 1946, B. A. Fisher).

Distribution. The subspecies is known also from Tasmania. 2 ♀♀, Hobart, 18 Mar. 1916, C. Cole, in the Australian Museum; 1 ♀, Hobart, 26 Mar. 1958, L. W. Miller, and 8 ♀♀, 3 ♂♂, Ouse, 8 Feb. 1956, W. J. Newport, in the collection of the Tasmanian Department of Agriculture (2 ♀♀, 1 ♂ retained in the C.S.I.R.O. Division of Entomology Museum, Canberra).

This subspecies of *affinis* approaches *dorsalis* in the density of the hairs on the lower jena, but in the characters of the genitalia it is allied to typical *affinis*.

PERGA AFFINIS ATRATA, subsp. nov.

Female. Similar to the typical form except in colouring; trochanters mostly dark, at least bases of middle and hind femora dark, hind femur often mostly dark.

Type. Holotype ♀ in the C.S.I.R.O. Division of Entomology Museum, Canberra; 2 ♀ paratypes (from Horsham) in the Burns Collection; 1 ♀ paratype (Wilkur) in the National Museum of Victoria.

Type Locality. Sleaford Bay, South Australia (31 Mar. 1959, J. Casanova). Paratypes from Wilkur, Victoria (Apr. 1956, Spurrell), and Horsham, Victoria (18 Mar. 1932, A. N. Burns).

This is a very dark form of *affinis*.

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LEAF RUST ON WHEAT IN AUSTRALIA: A SYSTEMATIC SCHEME FOR THE CLASSIFICATION OF STRAINS.

By I. A. Watson and N. H. Luig, Faculty of Agriculture, The University of Sydney.

[Read 30th August, 1961.]

Synopsis.

The complications arising from the variability of the wheat leaf rust organism are reviewed and an attempt is made to systematize the nomenclature of strains. Use is made of reactions of the wheat varieties which are universally accepted as leaf rust differentials, but the supplemental varieties Thew, Gaza, Spica, Kenya W1483 and Klein Titan are added for further differentiation. The scheme is based on one now accepted by potato workers for use with the organism causing potato blight.

Leaf rust of wheat (*Puccinia recondita* Rob. ex Desm.) has been a disease of wheat known since the first work on the Australian cereal rusts was done (McAlpine, 1906). No extensive tests have been made to determine the importance of this organism in reducing yield in Australia, although a loss in yield of 14·5 per cent. has been suggested from the work of Phipps (1938). In North America the nature of the damage done by this organism is well known and it is generally considered that yield reductions result from fewer grains per head rather than reduced grain weight (Chester, 1946). Chester also figures a graph showing that extensive losses can occur if infection of a crop proceeds at an early stage and is followed by a defoliation of the plant. In Australia, frequently under nursery conditions and occasionally in commercial crops in northern New South Wales, the varieties Spica and Gabo are defoliated by leaf rust. Using the graph presented by Chester, one of us (I.A.W.) has estimated that approximately 10 per cent. of the yield may be lost due to this disease when the infection is severe.

The recent interest in and the cultivation of winter wheats have underlined further the importance of leaf rust. All varieties of winter wheat are at present susceptible and heavy infection follows an early autumn seeding. Defoliation of the plants at the tillering stage greatly reduces their attractiveness for grazing and builds up inoculum for dispersal to other crops during winter and spring.

The damage done by this disease has been recognized by several wheat breeders and efforts have been made to control it by developing resistant varieties. The fate of these latter and the strains that have been responsible for their susceptibility have recently been given by Watson *et al.* (1960).

During the course of the breeding programmes, extensive field surveys have been made to assess the variability of the organism. These surveys were conducted by Waterhouse from 1920 to 1952 and have been summarized (Waterhouse, 1952). He found in the very early stages of this work that the wheat varieties used in variability studies in North America gave an incomplete differentiation of the leaf rust strains present in this area. Thew and Gaza (a parent of Gabo) were added as supplemental varieties to the standard group. In order to catalogue the different rusts he used the letters A and B to designate resistance and susceptibility, respectively. A designation 135AB indicated the race number on the standard set of varieties and a resistant reaction on Thew but susceptibility on Gaza. Race 135BB was virulent on both Thew and Gaza. Many races were found by Waterhouse, but not all were incorporated into this system of nomenclature.

As the breeding programme expanded and the pathogenicity pattern of isolates of the leaf rust population became more complex, there has arisen a need for further modifications to the system of designating strains. With the widespread cultivation of

Spica (a variety believed to have the Hope type of resistance to leaf rust and stem rust), strains arose which were virulent on this variety as well as on Hope, H-44, Renown and other varieties related to them. The necessity for Spica or Renown as a supplemental variety additional to Thew and Gaza became evident and the separation of strains using all three varieties has already been given (Watson, 1958).

In a search for additional genes for resistance to leaf rust which may add genetic diversity to the parents used in breeding, extensive collections of species of *Triticum* have been tested with all known strains of leaf rust in this geographical area. Varieties resistant to all are regularly grown at several centres in New South Wales. Kenya W1483 was among several parents selected for its comprehensive resistance, but the breeding programme in which it figured had barely got under way when leaf rust was found in north Queensland to which this new parent is susceptible. Since 1959, when the first of the strains virulent on Kenya 1483 was found, there have been isolations in northern New South Wales, and it has become necessary to augment the supplementals still further by adding this variety. During the 1960–61 survey period a strain with some virulence on Klein Titan W2553 has been found, and this latter must also be added as a useful supplemental variety.

Procedure in Strain Identification.

As collections come from the field and at least 500 comprising leaf rust are dealt with in a normal season, they are first cultured on W1656 (C.I. 12632), a variety resistant to powdery mildew but with seedling susceptibility to all known local strains. From the resulting inoculum two isolated pustules are each separately increased on the same variety. Each collection is thus divided into two cultures which are expected to be relatively pure but could be dissimilar. The inoculum that develops from each single pustule isolate is used to infect seedlings of the following varieties: Webster, Mentana (representing Mediterranean) and Malakof from the standard group and Thew, Gaza, Spica and Kenya 1483 from the supplemental set. These seven varieties have in the past been adequate to describe the strain making up the original collection, but, as mentioned above, it has now become necessary to add Klein Titan.

From the results of these inoculations it is possible to classify the strain or strains present in the material. Where several strains were present in the collection some will be overlooked by this procedure. Two strains are frequently isolated from the one collection and the technique is considered more convenient than separating the original components by other means.

The spores remaining from the original inoculation of W1656 after the two single pustules have been taken are used to infect seedlings of varieties known to have a resistance effective against all local strains. Included with this group are varieties which, by virtue of a particular combination of genes for resistance, are specific for detecting strains which have the corresponding genes for pathogenicity. The known sources of resistance at present being used are Transfer W2382, La Prevision W1636, Rio Negro W2556, Colotana (266/51) W2555, Exchange W2554 and Timvera W1308. When seed is available this group will be increased by the addition of Aniversario W2097, Agrus W2502, Cornell Selection C.I. 13278, W2503, Dular W2500 C.I. 13373 and possibly some varieties of *T. durum*. At present it is not known whether certain genes for resistance are duplicated among this group, but until that information is available each will be treated as different.

La Prevision is highly resistant to all strains with which it has been tested and, while there is some variation in different environments in the reaction of Timvera seedlings, adult plants have remained very resistant. South Africa 43, originating from the same source, is also resistant to all strains.

The reactions of certain other varieties under trial as supplementals in North America to the Australian strains recently collected in the field are presented in Table 3. It will be apparent that these are not satisfactory as supplementary differentials for the leaf rust strains of Australia since several are resistant to all. These varieties

represent a wide range of factors for resistance as shown by the following pedigrees, some of which were kindly supplied by Dr. R. M. Caldwell.

Agrus W2502 C.I. 13228 (Trumbull-*Agropyron elongatum*) × (Trumbull[3]-Hope-Hussar × Fultz Selection 11845).

Newsar W2497 C.I. 12530 Trumbull × 3616 Al–1–1 = W38 × Fultz 11512 × Hungarian 4830–1.

Waban W2495 C.I. 12990 Wabash × American Banner.

Cornell 82 al–2–4–7C W2503 C.I. 13278 (Honor[2]-Rosen Rye) × (Yorkwin × Cornell 595).

Wardal W2496 Wabash-American Banner × Warden-Leap.

Exchange W2554 C.I. 12635 Warden × Hybrid English.

Rio Negro W2556 C.I. 12469 Centenario × Supresa.

Lee W2084 C.I. 12488 Hope × Timstein.

Aniversario W2097 C.I. 12578 Reliance × Klein 75.

Transfer W2382 C.I. 13296 Chinese × *Aegilops umbellulata.*

Sinvalocho W2013 D.I.V. 4790 Sin Rival × 38 M.A. No. 32. Rafaela.

Klein Lucero W2012 D.I.V. 4094 Klein Progreso × Apulia.

W2518, a genetic stock which combines the genes from Mentana and from Malakof, is only susceptible to strain 122-Anz-1,2 which is virulent on both Mediterranean and Malakof. It serves to distinguish between collections of this strain from those which are mixtures of strains in which some components attack Malakof, others attack Mediterranean, but none is virulent on both. Other combinations of genes are being developed as testers to serve in the same way as W2518 but for other virulence genes, and it is expected they will increase the efficiency of the survey procedure.

The Difficulties of a Standardized Procedure.

Such complexity in the pathogenicity pattern has necessitated a simplification and standardization of nomenclature for the strains of the Australia-New Zealand area. It is desirable that plant breeders recognize the host range by the designation given to the strain and thus ensure that the appropriate strains are responsible for the epiphytotics developed in their nurseries.

North American workers have been confronted with similar problems of differentiation and designation of strains and at present are studying the most suitable varieties that will serve in that geographical area (Loegering *et al.*, 1960). Extensive acreages of wheat, the aerial movement of spores through several countries and the difficulties of co-ordination have not helped to simplify the problem for them.

It has become apparent over the years that the standard group of differential varieties given by Johnston and Levine (1955) is still useful where leaf rust is important. It is equally clear that these varieties are inadequate for an ultimate description sufficiently accurate to be of use to plant breeders in any area. Attempts to reach agreement on a group of varieties that would meet the requirements throughout the world are scarcely worth while, as the predominant genes and combinations of genes for pathogenicity differ very much from one geographical area to another. For each area the most effective group of genes for separating strains at any one time can be readily selected. Such a group must be augmented from time to time as man's efforts in breeding change the frequency of pathogenicity genes in the leaf rust population. Possibly, as breeders resort to the same sources of resistance throughout the world, a common group of host differential genes may become universally acceptable. For example, Renown and Lee may serve as differentials in North America; their counterparts of related origin in Australia and New Zealand are Spica and Gaza. Such a convergence is being hastened by the ready exchange of material now taking place through the medium of the International Rust Nurseries. These interchanges of material may bring uniformity in the differentials sooner than we expect.

Differentiation of Strains in the Australia-New Zealand Area.

The multiplicity of strains of leaf rust that have developed as the breeding programmes advanced would never have been predicted when the early studies were initiated by Waterhouse. From 1920 to 1945, when no leaf rust resistant varieties of

any consequence were grown commercially, only two important races of leaf rust occurred in the field, although others were known. With the cultivation of Gabo, Waterhouse records the finding of four additional races (Waterhouse, 1952). There have been some shifts in the varieties cultivated in Australia since then. Festival and Spica have increased in popularity, but Gabo is still a very prominent variety.

As a result of increases in the acreages sown to varieties with some resistance to leaf rust and possibly as a result of a more detailed survey of the field, much greater variation is now known to occur. At least 21 strains, all markedly different, can be readily found either in the field or in nurseries when the glasshouse tests are made on the appropriate varieties. The complete picture of the area can only be obtained by a study of the strains in New Zealand, and this has been possible through the courtesy of Dr. H. C. Smith, who has submitted samples for several years.

TABLE 1.

Reactions of the Standard Differentials to Leaf Rust Strains in the Australia-New Zealand Area.

	Malakof.	Webster.	Carina.	Loros.	Brevit.	Mediterranean.	Democrat.	Hussar.
10	4	4	4	4	4	;	;	x+
15	;	;	;	;	;	4	4	x+
26	;	x	4	4	4	;	;	4
64	4	x	x	4	4	;	;	x^{+}_{+}
68	;	4	4	4	4	;	;	x^{+}_{+}
76	;	x	x	4	4	4	4	x^{+}_{+}
122	4	4	4	4	4	4	4	x^{+}_{+}
135	;	x	x	x	x	;	;	x^{+}_{+}
162	;	4	4	4	4	4	4	x^{+}_{+}

In contrast to Australia there has been no breeding for leaf rust resistance in New Zealand, and the prevalent strains there are identical with the ones found in Australia during the 1920–1945 period. These strains are now extremely rare in Australia since they are unable to attack Gabo. The other strains present in New Zealand are identical with the prevalent strains of eastern Australia, and it is presumed that they have been transported aerially across the Tasman Sea. Apparently they have been unable to build up sufficiently to be predominant among the leaf rust population and, since Gabo is not widely grown in that country, they have had no advantages over the strains present earlier.

In arriving at a satisfactory system of nomenclature for leaf rust strains in the Australia-New Zealand geographical area, use has been made of the differential varieties and the key given by Johnston and Levine (1955), and to that extent some international co-ordination has been maintained. It is not difficult to obtain from that table a description that adequately fits the strains of Australia and New Zealand, and those given by Johnston and Levine as races 10, 15, 26, 64, 68, 76, 122, 135 and 162 meet the requirement. Within each group, however, further subdivision is necessary.

The system of designation differs from that proposed for North America in that use is made of a very satisfactory scheme that has been adopted for the races of *Phytophthora infestans* (Black *et al.*, 1953).

The North American system incorporates the reaction on the standard differentials, the supplementals and, as well, specifies the year in which these latter were in use. A designation 15–NA59–1 would indicate race 15 on the standard differentials and race 1

on the supplementals in use in 1959. It is proposed that the same combinations of reactions on the supplementals will have the same race number. Thus 5–NA59–1 will differ from 15–NA59–1 on the standard varieties, but will be identical with it on the supplementals in use in 1959.

In the scheme suggested for this area a determination is first made on the standard set of varieties. From this the broad classification results by reference to the table of Johnston and Levine. This is followed by the geographical area Anz and the classification as determined on the supplemental varieties. These are numbered in a standardized way Thew-1, Gaza-2, Spica-3, Kenya 1483-4 and Klein Titan-5. If an isolate which on the standard set is 26 is avirulent on the 4 supplementals the designation is strain 26-Anz-0. An isolate which conforms to 26 and attacks Thew alone among the supplementals would be called strain 26-Anz-1; strain 26-Anz-2 and 26-Anz-3 are virulent on Gaza and Spica respectively, but on no other variety of the supplemental set. Strain 26-Anz-1,2 attacks Thew and Gaza, while strain 26-Anz-1,2,3,4 attacks all the supplementals except Klein Titan. Strain 162-Anz-1,2,3,4 would be indistinguishable from 26-Anz-1,2,3,4 on the supplementals, but would be very different from it on the standard set. As further supplemental differentials become useful they will be added as necessary.

The North American system provides for additions to or deletions from the group of supplementals by specifying a particular year. As no deletions are envisaged at present from the set of 5 varieties given above, the scheme will only accommodate additions to it. As many varieties of potential value as differentials or as parents are constantly under test, their reactions to the existing strains are almost certainly known. For example, Klein Titan, which has been highly resistant to all Australian strains for many years, was attacked by one isolate in the 1960–61 survey. It has only recently been added to the list of supplemental varieties, although as a source of resistance to all strains it has been tested with all field collections.

The Supplemental Varieties.

The varieties Thew, Spica and Kenya W1483 each have a single gene controlling the resistance they possess. The gene from Thew which has been so effective in Australia in differentiation of strains has been of no value in North America where Thew has been found susceptible. This gene is present in many varieties other than Thew. It occurs alone or in combination with some other gene for resistance. Certain Kenya varieties possess the same resistance as Thew and, from the pedigrees given by Dixon (1960), it is clear that it was used as a parent in breeding in that country. This gene is also known to be present in Norka from the work of Pugsley and Carter (1953), and apparently in that variety it is combined with the gene from Malakof. Consequently to Australian strains of leaf rust Norka may be susceptible or have one or two genes for resistance, depending on the strain that is used. Against strains such as 26-Anz-0 (see Table 2), both the Thew and the Malakof components will operate. The Thew gene is extremely closely linked with a gene controlling resistance to powdery mildew and presumably in the study of Norka reported by Mains (1934), where independence was found, he worked with Malakof resistance to leaf rust and the Thew resistance to powdery mildew.

The Thew gene for leaf rust resistance has never been satisfactory as a source of resistance in breeding. Selection experiments show there is a high mutation rate in the organism for virulence on Thew. Strains virulent on it can be readily selected from single spore cultures of avirulent strains. Consequently for most strains avirulent on Thew there is a virulent counterpart. Cytogenetical work on this resistance suggests that the gene concerned is on chromosome XI (Longwell and Shirky, 1951).

The resistance of Gaza (*T. durum*) has been used in the breeding of the varieties Gabo and Koda and for many years was highly effective against the strains of leaf rust found in Australia and New Zealand. This resistance has also figured in the pedigree of the Kenya wheats as shown by Dixon (1960). Kenya Farmer, which is resistant to the local strains avirulent on Gaza, but susceptible to the others, appears to have inherited the resistance from the Bobin^2 × Gaza line used in its pedigree.

Timstein also possesses the resistance of Gaza and this has been passed on to the variety Lee, a variety important in North America and possibly a useful supplemental variety in that geographical area.

Two varieties recently released in Australia, Gamenya and Mengavi (Watson *et al.*, 1960) have been selected for their leaf rust resistance and combine the resistance of Mentana W1124 with that of Gabo. The combination becomes evident when tests with strain 76-Anz-0 are made. The resistance of Mentana is ineffective, but that of Gabo protects them. The single gene of Gabo for resistance to *P. graminis* var. *tritici* is linked in repulsion with the leaf rust resistance of Mentana on chromosome X (Luig, 1960). During the course of selection the linkage was not broken in the case of Gamenya and consequently this variety has the resistance of Mentana to leaf rust but lacks the resistance of Gabo to stem rust. Mengavi, on the other hand, is a recombination type possessing the two genes for resistance, one from Gabo to stem rust, the other from Mentana to leaf rust. Gabo, Gamenya and Mengavi do not have the full resistance of Gaza to leaf rust as apparently all the genes concerned in resistance have not been transferred from the *T. durum* parent. Such a result is found frequently in many interspecific crosses. The genetic nature of the leaf rust resistance of Gaza has not been fully worked out and the gene present in Gabo has not been definitely located on any particular chromosome.

Since no 42 chromosome derivatives are available which give the very sharp hypersensitive reaction of Gaza to strains such as 26-Anz-0, use is made of the latter rather than of Gabo in strain identification.

Pathological tests suggest that a number of varieties received from Egypt as *T. durum* would be interchangeable with Gaza as a suitable supplemental differential.

The third variety Spica W2341 is reported to have originated from a cross between an unfixed hybrid (Three Seas × Kamburico *T. durum*) and an unnamed selection (Pusa × Flora 3202), (Rosser, 1952). It is now a valuable commercial variety having resistance to the important strains of stem rust. When it was first made available for cultivation it was resistant to many of the strains of leaf rust, but susceptibility became evident at a time when leaf rust was also found on the varieties Hofed, Hope, H-44 and Renown. Subsequent tests have established that Spica can be used to differentiate those strains virulent on Hope and derivatives of it. The reactions of Spica are not entirely satisfactory for seedling work as resistance is indicated by a mixture of ";", "2" and "4" type reactions on the one leaf. To some strains such as 122-Anz-1,2 the reactions of Spica and Renown are very definite, with much hypersensitivity, but to others the 4 type reactions predominate although the seedlings are still classed as resistant. There has not been complete correlation between the reactions of Spica and Renown on the one hand, and those of any of the supplementals listed for trial in North America on the other. The variety La Porte received from Dr. R. M. Caldwell has shown the closest agreement with Spica in reaction type and Hope figures in the pedigree.

There has, however, been some correlation between the reactions of Spica and Lee, although impure seed has presented difficulties in this latter variety. Lee is resistant to strains avirulent on Gaza and strains virulent on Spica cannot always attack Lee on account of this protection. Strains virulent on Gaza but unable to attack Spica cannot attack Lee, although the latter shows some variation to this group of strains. Lee has been derived from the cross (Hope × Timstein) and it appears to combine the resistance of Gaza and of Hope to the Australian strains of leaf rust. For this reason it has not been considered a suitable supplemental variety, but rather a variety for detecting those strains virulent on both Gaza and Spica. The cytogenetical work on the locations of this resistance is not yet complete.

The fourth variety among the supplementals is Kenya 112–E–19–J(L) W1483 R.L. 1873, and although the resistance has been found to be simply inherited, its origin has not yet been determined. The resistance is marked by very sharp hypersensitivity to 23 of the 27 strains listed, but to the other four it shows complete susceptibility as seedings. Studies are in progress to combine the gene from Kenya 1483 with other

genes for resistance to assist the survey work, but otherwise the gene has been dropped from the breeding programme. The location of this gene in the chromosomes is still unknown, but it appears to be associated with distorted F_2 ratios (unpublished work).

Klein Titan W2553 D.1.V. 396 (Barleta 7d × Americano 44d) is the fifth of the supplemental varieties and the latest to be added to this group. From field surveys only one collection has been found to comprise a strain virulent on this variety. During the course of this work it has been inoculated with more than 1,000 field accessions and it has normally shown a very high resistance. In Table 2 the strain taken in the field from

TABLE 2.

Reactions of Five Supplemental Differentials to Leaf Rust Strains in the Australia-New Zealand Area.

——	Thew—1.	Gaza—2.	Spica—3.	Kenya 1483—4.	Klein Titan—5.	Previous Designations. Waterhouse (1952).	Watson 1958.	Watson *et al.* (1960).
10-Anz—1, 2, 3	S	S	S	R	R			
15-Anz-0	R	R	R	R	R			
15-Anz-1	S	R	R	R	R			
26-Anz-0	R	R	R	R	R	95	95-Anz-1	
26-Anz-1	S	R	R	R	R	26	26-Anz-1	
26-Anz-3	R	R	S	R	R		95-Anz-2	
26-Anz-1, 3	S	R	S	R	R		26-Anz-2	
64-Anz-1, 2	S	S	R	R	R		64-Anz-1	
68-Anz-2	R	S	R	R	R	138 AB	68-Anz-1	
68-Anz-2, 3	R	S	S	R	R		68-Anz-2	
68-Anz-1, 2, 3	S	S	S	R	R	138 BB	68-Anz-3	
68-Anz-1, 2, 3, 4 ..	S	S	S	S	R			
68-Anz-1, 2, 3, 5 ..	S	S	S	R	S			
76-Anz-0	R	R	R	R	R			
76-Anz-2, 3	R	S	S	R	R			
76-Anz-1, 2, 3	S	S	S	R	R			
122-Anz-1, 2	S	S	R	R	R			
135-Anz-2	R	S	R	R	R	135 AB	135-Anz-1	
135-Anz-1, 2	S	S	R	R	R	135 BB	135-Anz-2	
135-Anz-2, 3	R	S	S	R	R		135-Anz-3	
135-Anz-1, 2, 3	S	S	S	R	R		135-Anz-4	
135-Anz-2, 3, 4	R	S	S	S	R			
135-Anz-2, 3, 4, 5 ..	R	S	S	S	S			
162-Anz-2	R	S	R	R	R		163-Anz-1	163-Anz-1
162-Anz-1, 2	S	S	R	R	R			163-Anz-2
162-Anz-1, 2, 3	S	S	S	R	R			
162-Anz-1, 2, 3, 4 ..	S	S	S	S	R			

R = resistant; S = susceptible.

Bongeen, Queensland, and sent in by Mr. D. Rosser, appears as race 68 on the standard set of differential varieties and has been classified as strain 68-Anz-1,2,3,5. A number of South American wheats which bear the name of Klein have been tested with this strain of rust, but none differentiates it in the same way as Klein Titan. Klein Lucero W2012 shows the same resistant reaction when inoculated with strains either avirulent or virulent on Klein Titan. Apparently it represents a very different genotype.

A second strain attacking Klein Titan was found among the progeny from aecidial infections on *Thalictrum flavum*. This strain attacks Kenya 1483 and has been designated 135-Anz-2,3,4,5.

The Search for Increased Virulence.

By means of systematic field surveys and careful observations on the rust reactions of genetical material in plant breeders' nurseries it has been possible, as shown above, to collect and classify strains representing a wide range of virulence. These strains between them have the ability to attack all members of the standard differential series, strain 122-Anz-1,2 having the widest host range on this latter group. It is now well

known that the strains with the widest host range are not necessarily the most prevalent in the field and consequently in the breeding work little attention has been given to many of the prevalent but relatively avirulent strains of the commercial wheat districts.

All breeding material, especially that in the early generations, is grown at Castle Hill approximately 200 miles east of the fringe of the wheat belt. At this centre all local leaf rust strains are maintained under controlled conditions and, provided they have been collected in the field, any of them may be used in creating epidemics. Under wheat belt conditions in New South Wales, by way of contrast, naturally occurring leaf rust epidemics would be caused mainly by strains 135-Anz-2,3, 135-Anz-1,2,3 and 68-Anz-1,2,3. On the Darling Downs in Queensland the same strains would be prevalent in the nurseries, but an important component would be 68-Anz-1,2,3,4. In these districts, provided their dissemination was assisted by interspersing Gamenya or Mengavi among the rows, strains 76-Anz-2,3, 76-Anz-1,2,3, 162-Anz-1,2,3 and 162-Anz-1,2,3,4 would also be common. Strains such as 10-Anz-1,2,3, 64-Anz-1,2 and 122-Anz-1,2 would be unlikely in the nurseries as they have not yet been found in the wheat districts.

At Castle Hill selections are made using relatively few strains in planned epidemics although spores of common strains are wind borne from other areas within the County of Cumberland to the nursery. Seedlings of hybrid material are tested in the glasshouse with strains 10-Anz-1,2,3, 122-Anz-1,2 and 162-Anz-1,2,3,4. Nursery epidemics are developed in which survival of these strains is assisted by planting the appropriate border rows. With the exception of pathogenicity on Klein Titan these three strains represent all special pathogenic abilities present in the other strains naturally occurring. The aim is to select for resistance to those strains having the widest host range and to examine critically all new resistant hybrids which may serve to screen out virulent mutants or somatic recombinants from them. The effectiveness of this approach has been shown by the isolation of many new strains from the breeding nursery and the incorporation of resistance to them before they have become prevalent in the recognized wheat growing districts.

Strains 10-Anz-1,2,3 and 122-Anz-1,2 were selected in this way at Castle Hill and strain 162-Anz-1,2,3,4 was selected from a nursery at Brookstead, Queensland. Each has been used for a specific purpose in the breeding programme to combine in a genetic background of Gamenya the genes for physiologic resistance from Norka and Mentana with the adult plant resistance of Chinese. In deriving this combination, seedlings of the appropriate hybrids that were resistant to a combination of strains 10-Anz-1,2,3 and 162-Anz-1,2,3,4 were tested as adult plants for their resistance to strain 122-Anz-1,2. In this way it has been possible to get the physiologic resistance of Norka to all strains except 10-Anz-1,2,3, 64-Anz-1,2 and 122-Anz-1,2 combined with the physiologic resistance of Mentana to all strains to which the latter is resistant. Resistant seedlings having this combination and developing resistance to strain 122-Anz-1,2 as adult plants were found to have the three sources of resistance combined, the gene for adult plant resistance being effective against all local strains. This and similar procedures have been found essential to broaden the base on which resistance to leaf rust depends.

The search for new combinations of genes for pathogenicity goes on hand in hand with efforts to combine genes for resistance. In addition, teleutospores of the most virulent strains are collected each year and used to infect the alternate host *Thalictrum flavum*. The aecidial material is increased on a susceptible variety of wheat and the resulting uredospores used to inoculate seedlings of all sources of resistance. Among the strains listed in Table 2 are two, viz.: strain 135-Anz-2,3,4 and strain 135-Anz-2,3,4,5 that have arisen from sexual progeny in this way. Neither of them has been isolated in the field. One of them, 135-Anz-2,3,4,5, is of some significance in that it attacks Klein Titan.

Acknowledgements.

During the course of this work much of the inoculation was done by Mr. D. J. S. Gow. His assistance is much appreciated. We acknowledge financial help from the Wheat Industry Research Council and the University of Sydney Research Grant.

TABLE 3.

Reactions of Supplemental Varieties under Test in North America when Inoculated with Leaf Rust Strains Present in the Australia-New Zealand Area.

		10-Anz.	26-Anz.				64-Anz.	68-Anz.					76-Anz.			122-Anz.	135-Anz.				162-Anz.			
		1, 2, 3	0	1	3	1, 3	1, 2	2, 3	1, 2, 3	1, 2, 3, 4	1, 2, 3, 5	0	2, 3	1, 2, 3	1, 2	2	1, 2	2, 3	1, 2, 3	2	1, 2	1, 2, 3	1, 2, 3, 4
Agrus	W2502	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;
Newsar	W2497	x	x++	4	4	4	x	x+	x+	x	x	x++	x	x	x	x++	x++	x	x++	x	x	x=	x=
Waban	W2495	Seg.	Seg.	Seg.	Seg.	Seg.	x=	Seg.	Seg.	4	Seg.	;1	;	;	4	Seg.	Seg.	Seg.	Seg.	4	4	4	4
C.I. 13278 ..	W2503	Seg.	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;
Wardal	W2496	x+	;	;	;	;	x	4	4	4	4	;	;	;	4	;	;	;	x−	4	4	4	4
Sinvalocho ..	W2013	;	;	;	;	;	;	;	;	;	;	4	4	4	4	;	;	;	;	4	4	4	4
Klein Lucero ..	W2012	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;
Westar	W2498	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Wesel	W2499	x+	4	4	4	4	x	x	x	x	x	x	x=	;	x=	x	x	x	x	x	x	x	;
Exchange.. ..	W2554	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn	3cn
Rio Negro ..	W2556	;	;	;	;	;	;	x=	x=	x=	x	;	;	;	;	;	;	;	;	;	;	;	;
Colotana 266/51	W2555	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Lee	W2084	4	Seg.	Seg.	Seg.	Seg.	;4	4	4	4	4	Seg.	4	4	;4	;4	;4	Seg.	4	Seg.	;4	4	4
Aniversario ..	W2097	;	;	;	;	;	x	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;
Transfer	W2382	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;

Seg. = Segregating.

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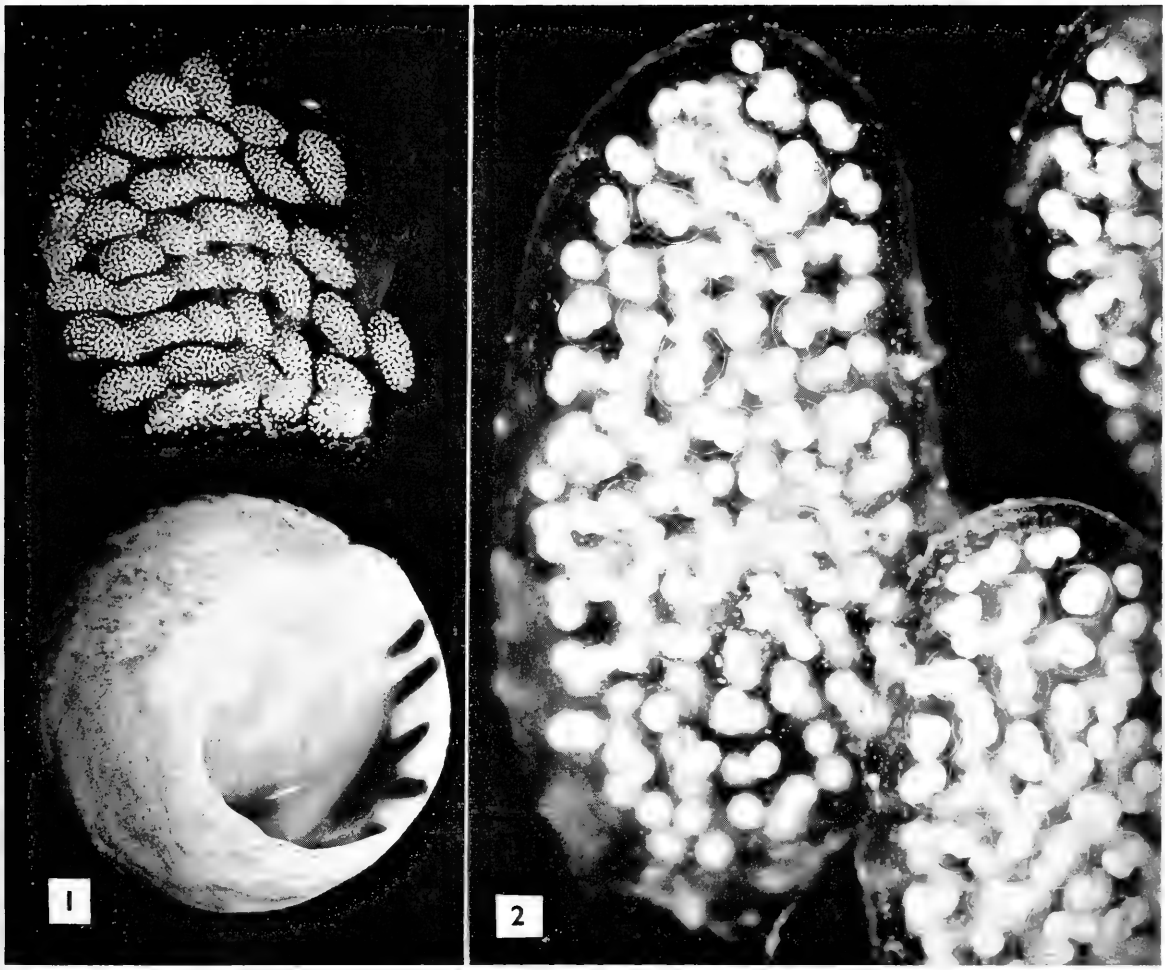
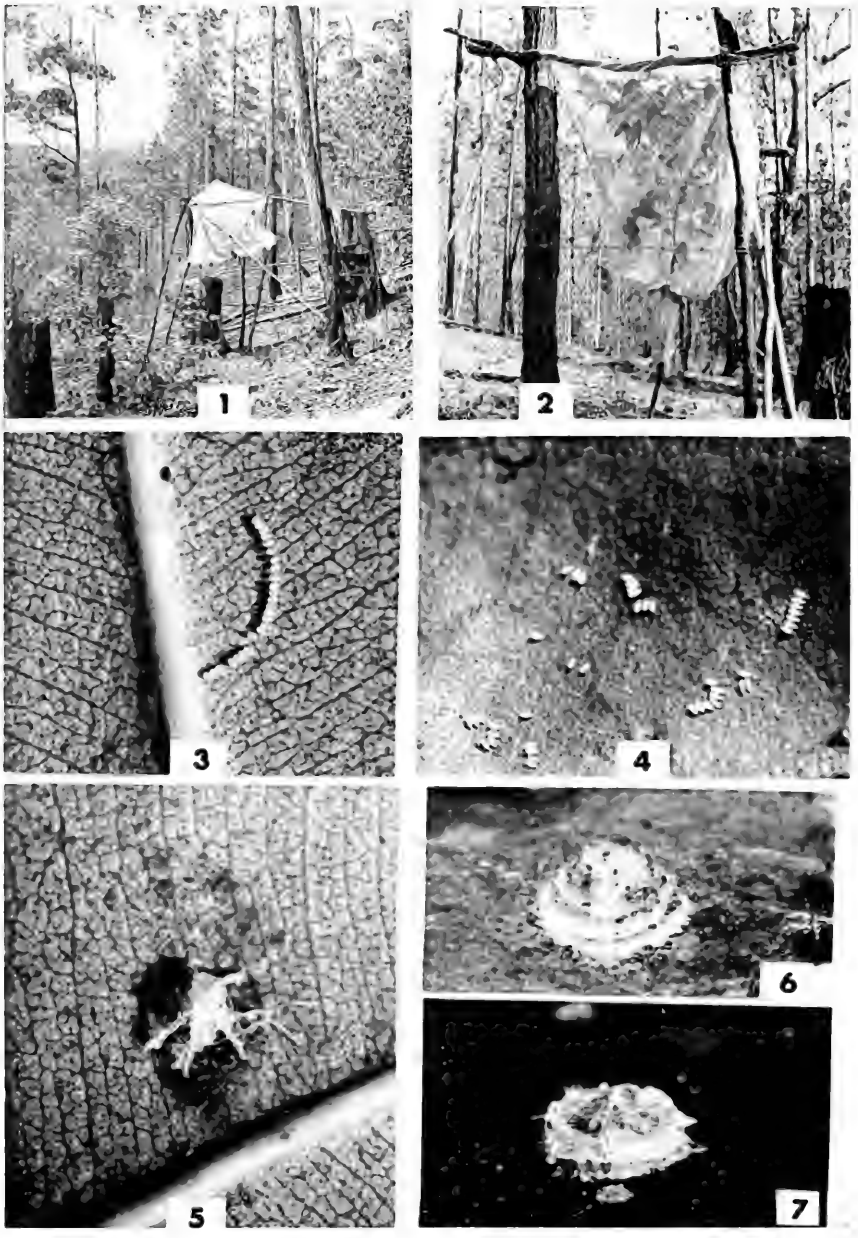


Bembicium nanum. 1, Female and spawn (× 3). 2, Jelly masses containing eggs (× 40).



Glycaspis baileyi. 1, 2, Cages for observations; 3-7, Eggs and lerps.

OBSERVATIONS ON THE LIFE CYCLE OF *STICTODORA LARI* (TREMATODA: HETEROPHYIDAE).

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(Fifteen Text-figures.)

[Read 27th September, 1961.]

Synopsis.

1. The life cycle of *Stictodora lari* includes passage through an operculate gastropod, *Velacumantus australis*, as first intermediate host and through several species of fish as second intermediate hosts. The latter include mullet, gobies and other small fish living in weeds growing in shallow brackish water, the habitat preferred by *V. australis*.

2. Mature parasites occur naturally in *Larus novae-hollandiae* and other fish-eating birds. They can also be reared in cats.

The present paper is one of several dealing with cercariae of estuarine molluscs in Sydney District; titles of these papers are given in the bibliography (Bearup, 1956, 1958, 1960).

The main collecting sites for vectors have been shallow sandflats in Narrabeen Lagoon, a few miles north of Sydney. This brackish lagoon receives several small freshwater streams and empties into the sea through a narrow channel often blocked by sand during rough weather. Estimations of the percentage of chloride in the water over the chief collecting area varied between 1·84 in dry weather and 0·89 after heavy rain. Some sandflats have heavy growths of *Zostera* weed which is the favoured habitat of *Velacumantus australis* (= *Pyrazus australis*), the main vector of *Stictodora* cercariae.

Materials and Methods.

Collections of *V. australis* were made at about monthly intervals and the incidence was calculated by crushing 100–200 of them. Living cercariae were collected from single snails isolated in brackish water in small glass tubes. The cercariae are easily distinguished from other cercariae in *V. australis* by their rapid swimming movements and by the fin-fold on the tail.

Fish were infected by exposing them to naturally emerged cercariae in Petri dishes. The guppies, *Lebistes* ? *reticulatus*, were aquarium bred, the *Gambusia* were taken from freshwater ponds but showed no natural infections with trematodes. Both types were conditioned to brackish water by several additions of sea-water, over several hours. Infections were only successful in brackish water; in fresh water the cercariae lost motility and were soon dead.

Adults were recovered from young seagulls (*Larus novae-hollandiae*) which had been fed on beef heart since they were fledgelings. Kittens, also, were easily infected.

Observations.

Details of the life cycle are incomplete because free miracidia have not been obtained, nor has an experimental infection of the snail been studied. The youngest larvae found, in natural infections, were small colourless rediae in squash preparations of the mantle and digestive gland and no clear evidence of two generations of rediae was found.

Ova (Fig. 1).

Mature ova were thick-shelled, brown, elliptical to oval, with the operculum poorly defined. Ova in the lower uterus or in faeces measured 0·033–0·035 by 0·014–0·020 mm. (average 0·034 × 0·019 mm.) and contained a miracidium, probably mature, although no ciliary movement was seen. Details of the larva were obscured by the thick brown shell.

Rediae (Figs 2, 3).

The youngest larvae found were colourless rediae in the mantle and digestive gland (0·148 by 0·022 mm.) with a gut extending nearly the full length, a pharynx as wide as the body, and germinal tissue filling the posterior end (Fig. 2). The pharynx was mobile and when retracted the anterior body wall formed an outwardly-directed lip. Infections which had mature cercariae also had all stages of developing rediae, the latter varying in size up to 1·1 mm. The large ones contained many germ balls, developing cercariae and usually several advanced cercariae with eyespots but of smaller size than mature ones, and lacking fin-folds on the tail (Fig. 3). No collar or posterior projections were found in young or old rediae. Older rediae were lightly coloured with patches of yellowish-brown pigment in the body wall and in the gut. The gut becomes relatively smaller in large rediae and is eventually confined to a small space behind the pharynx. No birth pore was found.

Neither rediae nor the oldest cercariae within them show more than occasional sluggish movements. The cercariae apparently mature in the digestive gland and, when the surface of this organ is broken, very active cercariae escape in large numbers.

Cercariae (Figs 4, 9).

Small, monostome cercariae of the pleurolophocerca type. Average dimensions (in millimetres) of 10 cercariae killed in hot water: body, 0·219 long by 0·087 wide; tail, 0·429 long by 0·031 wide at base; eyespots 0·061 from anterior end; oral sucker, 0·034 long by 0·031 wide. Cercariae recently killed in hot formalin are smaller; body 0·202 by 0·071; tail, 0·415 by 0·027. Body shape roughly pyriform when at rest. Cuticle thin, covered with rows of extremely fine spines. No sensory bristles found. Oral sucker modified to a rounded protrusible penetrating organ ("anterior organ") with a subterminal mouth on it.

Anterior to the mouth opening is a small pit containing a group of spines with fine lanceolate tips. They are hard to find and in the cercaria are usually seen as a double row of 7 or 8 tips supported by parallel rods. A better view of them in a young metacercaria (2 hours after exposure) showed 16 spines in a circle projecting from the pit, like stamens from a flower (Fig. 9).

Paired eyespots large, at about one-fourth of body length from anterior end; scattered pigment granules around the eyespots and along the lateral borders of the cercaria.

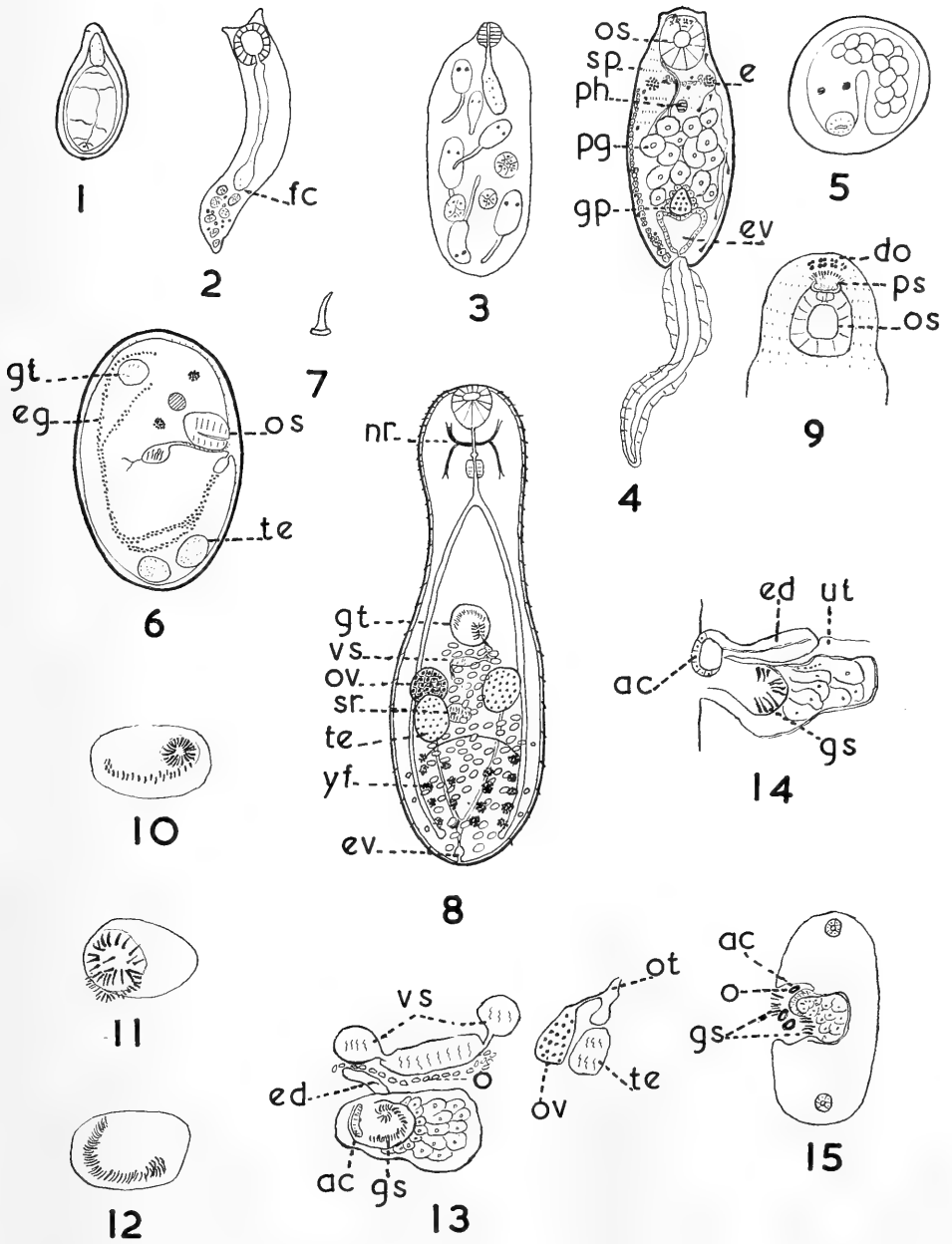
Tail is a powerful swimming organ with two sets of delicate, cuticular fins. Lateral fins extend about 40% of tail length from body and the dorso-ventral fin passes around the tip and extends to about 60% of the tail length. The fins are thrown into small convolutions by the contraction of the tail. Tip of tail bent laterally.

Centre of body occupied by 14 large penetration gland cells with smooth or slightly wavy outlines, large conspicuous nuclei, and finely granular protoplasm staining red with neutral red.

From these cells, lateral ducts go forward in two groups between the eyespots and then diverge; they pass around the dorsal side of anterior organ to open at its anterior border. The inner group consists of four and the outer group of three ducts on each side. Small cells, probably cystogenous cells, line the body just below the cuticle. Pharynx poorly defined; oesophagus and gut not found.

Genital primordium a compact triangular cell mass in front of the bladder.

Excretory system of mesostomate type; consists of large thick-walled vesicle of variable shape but Y-shaped when cercaria at rest; walls of cuboid epithelium. Posterior canal runs into tail; in immature cercariae it divides near the base into two vessels which open laterally. In the body the main canals leave the vesicle antero-laterally and branch into two secondary ones each draining three flame cells. Total number of flame cells in young cercariae is 12 with a formula of $2(3+3)$. The excretory system of mature cercariae is obscured by granules of the penetration gland cells and methods which are often useful (coverslip pressure, examination in neutral red, serum or urine or in young metacercariae) do not make it visible.



Figures 1-15.—Stages in life cycle of *Stictodora lari*. 1, ovum; 2, young redia, from mantle of *V. australis*; 3, older redia, from digestive gland, *V. australis*; 4, cercaria, naturally emerged from *V. australis* (excretory system, drawn from immature cercaria, is superimposed); 5, young metacercaria, 18 hours after penetration, *Gambusia*; 6, metacercaria, 26 days after penetration, *Gambusia*; 7, gonotyl spine; 8, adult, from experimental feeding, *Larus*; 9, cercaria, anterior end, showing penetration spines; 10, 11, 12, gonotyl spines of 3 adults from one experimental infection of *Larus*; 13, adult, genital sac and other genitalia, flattened under coverslip; 14, 15, T/S through genital sac. AC, acetabulam; DO, openings of ducts—penetration glands; E, eyespots; ED, ejaculatory duct; EG, excretory granules; EV, excretory vesicle; FC, flame cells; GP, genital primordium; GT, gonotyl; GS, gonotyl spines; NR, nerve ring; O, ova; OT, ootype; OS, oral sucker; OV, ovary; PG, penetration gland cells; PH, pharynx, PS, penetration spines; SR, receptaculam seminis; TE, testis; UT, uterus; VS, vesicula seminis; YF, yolk follicles.

Nerve ring indistinct, about half-way between pharynx and anterior organ.

The cercariae are active swimmers; two or three seconds of vigorous swimming alternate with longer periods of rest, which vary up to about 10 seconds. While swimming they rise slightly in the water but fall slowly to the bottom during rest. The cercariae are not adapted to creeping and they have difficulty in moving on a glass surface because the "anterior organ" does not seem to act as a sucker and there are no other organs of adhesion. They were attracted to the lighted side of the vessel but not to the surface of the water.

Cercariae lived for 18–24 hours in brackish waters of salinities varying from 3% down to 0·5% sodium chloride. In pond water (0·01% sodium chloride) they stopped swimming immediately and died within an hour. Low temperatures (5° C.) prolong their life and infected snails can be stored for a month in the refrigerator.

Cercariae of this type are common throughout the year in *V. australis* in Narrabeen Lagoon, where the incidence sometimes rose above 30% and would average about 18% (645 in 3,565 *V. a.*), but with no clear seasonal variation. The percentages of infections at intervals over three years are given in brackets: August 1956 (12); x.1956 (15); xii.1956 (7); i.1957 (16); v.1957 (17); ix.1957 (33); xi.1957 (34); i.1958 (43); v.1958 (8); ix.1958 (12); xi.1958 (15); iii.1959 (38). Infection rates were low in young *V. australis* under 25 mm. long and were highest in the 30–34 mm. group; they were also higher in weedbeds not swept by the tide than in those bordering the channels. Double infections were common with the forked-tail cercariae of *Austrobilharzia terrigalensis*, occasionally with *Echinostoma* cercariae, and once a triple infection was found.

V. australis is common on *Zostera* flats in estuaries from about 500 miles south to 500 miles north of Sydney and *Stictodora* cercariae are present throughout the range. Other snails sharing the habitat were usually free of these cercariae, but one infection was found in each of two species, *Pyrazus ebeninus* and *Parcanassa ellani*. The names and numbers of molluscs examined included *Pyrazus ebeninus* Bruguière (73); *Parcanassa ellana* Iredale (326); *Salinator fragilis* Lamarck (339); *Austropyrgus ruppiae* Hedley (1,023); *Austrocochlea obtusa* Dillwyn (143); *Bembicium auratum* (Quoy & Gaimard) (84); *Thalotia comtessei* Iredale (35); *Eumarcia* ? *fumigata* (64).

Cysts and Metacercariae (Figs 5, 6).

Metacercarial cysts containing *Stictodora* metacercariae were found as natural infections in several kinds of small fish that frequent the weedbeds, including species of mullet, gobies, leather-jackets, pipefish, toadfish and hardyheads. Those identified were: *Favingobius lateralis obliquus* McCulloch and Ogilby; *Atherinosoma microstoma* (Gunther); *Urocampus carinorostris* (Castelnau); *Waiteopsis paludis* Whitley; *Mugil* sp. and *Gambusia affinis* Baird and Girard. *Gambusia* sometimes migrates into brackish water and shelters in the weedbeds; of 24 collected from this habitat, 8 had *Stictodora* metacercariae. The same species from a suburban freshwater pool was found to be free of trematode metacercariae.

Freshwater *Gambusia* and *Lebistes* were infected in the laboratory by exposing them in brackish water in small glass Petri dishes to large numbers of naturally emerged cercariae. The penetration of cercariae into the fish could then be watched under a dissecting microscope. The cercariae do not seem to be attracted by the proximity of the fish, but once they make contact the anterior organ is directed towards the skin and is kept closely applied by vigorous lashing of the tail. The cercarial body then bends through 90° to become parallel to the side of the fish and moves to and fro through a quarter-circle, apparently using the spines of the anterior end to bore a hole through the skin. Once penetration is effected the tail falls off.

In ten minutes penetration of the body of the fish was complete. Those cercariae which entered the fins did not remain there but moved towards the body and came to rest in the nearby muscles. Two hours after exposure many cercariae were enclosed in a thin transparent cyst wall and were bent in a semicircle within it; the cyst at this stage measured 0·18 mm. across. The most prominent feature of the young larva was the dark mass of granules in the excretory bladder.

The eyespots and gland cells of the cercaria gradually disappeared and were replaced by adult characters. At 26 days the rounded cysts had diameters up to 0·4 mm. and enclosed metacercariae 0·9–1·0 mm. long by 0·18–0·20 mm. wide with an ovary, testes, gonotyl with rudimentary spines and a complete digestive system with caeca reaching almost to the posterior end. Rows of fine backwardly-directed spines surrounded the body as far back as the gonotyl; posteriorly they got fewer and finally disappeared. At this stage, perhaps earlier, they were infective for seagulls and kittens.

Stictodora cysts in naturally acquired infections were scattered through the body muscles with an odd one in the abdominal viscera, especially in the liver. Cysts were also found free in the body cavity of pipefish, but they were always small and immature. Heavily infected pipefish with dark skin (*Urocampus*) show many small, round, depigmented patches, probably each representing the point of entry of a cercaria.

Feeding experiments to experimental hosts and the results at postmortem follow. Naturally infected fish were all netted from Narrabeen Lagoon, from weedbeds sheltering infected *Velacumantus*. The dates of multiple feedings and of postmortem are given.

A.—Young gull, fed cysts from experimentally infected *Gambusia* after 26 days' development in the fish. Seventeen fish had 22 cysts, the largest measuring 0·45 × 0·49 mm. Thirteen days later, four *Stictodora* recovered.

B.—Young gull, fed cysts from naturally infected *Gambusia*; twenty-three days later, 46 *Stictodora* recovered.

C.—Kitten, fed *Favingobius*, natural infections, 25.xi and 26.xi; forty *Stictodora*, 8.xii.

D.—Kitten, fed small mullet and *Atherinosoma*, natural infections, 7.x, 10.x; seven *Stictodora*, 28.x.

E.—Kitten, fed cysts dissected from toadfish and *Atherinosoma*, natural infections, 11.v, 23.v; five *Stictodora*, 2.vi.

F.—Kitten, fed *Atherinosoma*, natural infection, 4.xi, 12.xi; two *Stictodora*, 14.xi.

Young (2 days) chickens and pigeons were also fed with cysts, but no adults were recovered.

No trematode other than *Stictodora* was present in any of the experimental hosts and a careful examination of the specimens showed no specific differences. The name of the species is discussed later.

Adult (Fig. 8).

The description which follows is based on the examination of many living worms as well as fixed preparations stained with carmine and mounted in balsam. Measurements of anatomical structures in the fixed specimens were about 10% lower than in living worms under slight coverslip pressure.

Body flattened dorso-ventrally, constricted about the middle, 1·15–1·33 × 0·26–0·44 mm. at the level of the testes (average of 10 living worms, 1·135 × 0·342 mm.). Cuticle set with rows of minute backwardly-directed spines as far back as the acetabulum ("gonotyl" of Witenberg); behind this the spines are fewer and gradually disappear.

Oral sucker subterminal, 0·059–0·081 by 0·074–0·092 mm. (av. 0·069 by 0·071). Prepharynx, 0·055–0·074 mm. Pharynx barrel-shaped, 0·055–0·074 by 0·037–0·055 mm. Oesophagus 0·044–0·055 mm. long. Caeca terminating near posterior end of body. Nerve ring 0·09 mm. from head end.

Genital sac at about middle of body, oval, 0·074–0·137 long by 0·082–0·155 mm. wide (av. 0·097–0·103 mm.). Gonotyl spines in a comma-shaped group with about 40 narrow, slightly curved spines, 0·015 mm. long, in a circular group from which extends a semicircle containing 20–30 spines in an irregular row, gradually shortening to 0·008 mm. at the distal end (Figs 10–12). Ventral sucker vestigial, at anterior edge of genital sac.

Testes ovoid, parallel or slightly oblique, smooth outline, 0·078 × 0·092 mm., just inside caeca, at posterior part of middle third of body. Vesicula seminalis voluminous, constricted into three parts between ovary and gonotyl. Walls of ejaculatory duct thickened. Male and female ducts open into genital sinus (Figs 13, 14).

Ovary transversely elongated, oval, sometimes slightly lobed, 0·055–0·070 × 0·074–0·081 mm., just in front of right testes; oviduct originates from median posterior edge and passes through ootype to descending uterus. Uterine loops fill whole of body behind ovary extending laterally beyond the intestinal caeca. Ascending uterus makes a transverse loop in front of testes and continues to the genital pore. Eggs elliptical to oval, brown, average 0·034 × 0·019 mm., embryonated, some with prominent abopercular knob. Vitellaria acinous, in posterior third of body, mostly inside post-testicular intestinal caeca. Seminal receptacle between testes.

Stictodora specimens from feeding experiments A to F were compared and were all regarded as belonging to one species. The same species was also found as a natural infection in 3 of 7 mature *Larus novae-hollandiae* collected from Five Islands, near Sydney. This is a breeding site for gulls which normally live and feed at Narrabeen and other coastal lagoons where they would be exposed to infection by cercariae from *Velacumantus*.

Discussion.

Species of *Stictodora* previously reported from Australia are *S. diplacantha* Johnston, 1942, from a cormorant, *Phalacrocorax varius*, and *S. lari* Yamaguti, 1939, from *Pelecanus conspicillatus* and the domestic cat (Pearson, 1960).* Pearson and the writer have compared the last-named specimens with those recovered from experimental gulls and cats in Sydney and agree that they are the same species.

The genus was named and defined by Looss (1899) with the type species *S. sawakinensis*; revisions of the generic description have been made by Witenberg (1929, 1953) and Yamaguti (1939). Chen (1951) tabulates the characters of eight species, Witenberg (1953) has a key to 10 species, and Yamaguti (1958) lists 14 species. The type host of *S. lari* is *Larus crassirostris* Vieillot from Japan.

The most important features defining species of *Stictodora* are those of the genital sac and gonotyl, especially the number, arrangement and shape of the gonotyl spines. In the present study, some variation in the arrangement of spines was noted even in specimens from one experimental host (Figs 10, 11, 12 from gull A). The variations may be due to coverslip pressure during fixation; living specimens under light pressure generally appear as in Figure 10.

Witenberg's (1953) drawing of the gonotyl spines of *S. guerreroi* Garcia and Refuerzo, 1936, resembles Figure 12 except that he shows twice as many spines. This also applies to *S. japonica* Yamaguti, 1939. Exact counts of the gonotyl spines are usually difficult, but can be estimated closely, and the numbers lie between 50 and 80 in my own material.

Members of the family Heterophyidae use fish-eating birds as main hosts, but can maintain themselves in a variety of mammals which eat raw fish, notably cats, dogs and other carnivores, and man. Cercariae develop in operculate snails and encyst as metacercariae in several species of fish, perhaps belonging to different families. *Stictodora lari* shows no exceptional features from this general pattern of development.

Little is known of specific or generic differences in the cercariae of Heterophyidae and it is possible that more than one species are present in *V. australis*. Evidence against this is provided by the absence of other trematodes in cats and gulls fed with several kinds of small fish from the weedbeds.

Birds other than the silver gull have not been examined for *Stictodora* in Sydney area, but in Brisbane Pearson (1960) found them in pelicans and reared them in cats. The wide host ranges of heterophyids suggest that other species of aquatic birds would be infected. Migrating species coming from north-east Asia are common during summer on littoral Australia and bring many parasite species with them. A small number of them were examined at Townsville, North Queensland, but no species of Heterophyidae was found. Migrant species available and their numbers were: *Limosa lapponica*, 7;

* Dr. Pearson reported these parasites as *S. caballeroi* Martin, 1955. He has recently compared type material of this species and of *S. lari* Yamaguti, 1939, and now regards them as synonymous (personal communication, 1961).

Charadrius leschenaultii, 3; *C. alexandrinus*, 1; *Calidris tenuirostris*, 3; *C. canuta*, 2; *Tringa hypoleuca*, 1. The diets of these birds are probably small insects and crustaceans, and not fish. Eight silver gulls and four terns (*Sterna bergii*) from the same locality had Heterophyidae, but none of the genus *Stictodora*. In this latitude (19° 5′ south) estuarine flats are covered with mud and mangroves, and *Velacumantus* does not occur.

Slides of adult *S. lari* from this investigation are stored in the parasite collection of this School numbered Mn 1380, 1381, 1385, 1488, 1489; metacercariae and cercariae are in formalin, numbered Mn 1386.

Acknowledgement.

My grateful thanks are tendered to the following persons who were of great help during this investigation:

Miss Joyce Allan, Mr. T. Iredale and Dr. D. McMichael who identified the Mollusca, and Mr. G. Whitley who named the fish. All are staff members of the Australian Museum. Mr. Kent Keith of the Wild Life Survey Section, Commonwealth Scientific and Industrial Research Organization, identified the birds collected in Townsville.

Professor G. Witenberg, the Hebrew University, Jerusalem, and Dr. J. Pearson, Parasitology Department, Queensland University, gave advice on the identification of species of *Stictodora*; Miss M. Angel, Zoology Department, Adelaide University, lent a cotype slide of *S. diplacantha* for examination.

Mrs. V. Klavins, Lorna Chambers and Misses Judy Ransley and Beverley Nicholls of the staff of this School helped to gather and to examine the living materials needed for study.

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RE-DISCOVERY OF A LITTLE KNOWN VICTORIAN FROG.

By Stephen J. Copland.

(One Map.)

[Read 25th October, 1961.]

Synopsis.

The little known Victorian frog *Hyla maculata*, which was described in 1901 by Spencer from a single specimen and which had apparently not been collected since, is now established as valid by the examination of three further specimens. Its range is extended by 150 miles and additional information is adduced. A standard description is also given to facilitate comparison with other members of the genus *Hyla* as presented in the author's 1957 paper. A neotype of *Hyla irrorata* De Vis is designated.

On December 29, 1958, my daughters Janet and Christina collected two frogs at Lightning Creek, on the Omeo Highway, in Eastern Gippsland, Victoria. These both turned out to be males of the tree-frog *Hyla maculata*, described by Spencer in 1901 from a single specimen from Powong, now spelt Poowong, about 150 miles south-west of Lightning Creek. The 1958 frogs appear to be the second and third individuals collected in 57 years. They extend the range of the species 150 miles. On January 4, 1959, I collected a further specimen near Glenrowan, about 70 miles west of Lightning Creek. These three frogs completely establish the validity of *maculata*, which had been in doubt.

Map of eastern Victoria. Localities at which *Hyla maculata* has been collected are underlined. Several large towns are shown for reference.

Spencer's short original description (1901: 177) reads: *Hyla maculata*, sp. n. Tongue subcircular, free and slightly nicked behind. Vomerine teeth in two small groups close to the middle line behind the level of the choanae. Head decidedly broader than long. Snout as long as broad; truncate and slanting downwards so that the nares are vertically on a level with the margin of the upper jaw. Canthus rostralis distinct; the loreal region oblique and slightly concave; interorbital space nearly twice as broad as the upper eyelid. Tympanum not visible. Fingers very slightly webbed; toes completely webbed. Discs on the fingers slightly larger than those on the toes. Subarticular tubercle present, no outer metatarsal tubercle. A distinct fold extending over

the tympanic region to the shoulder. The hind limb being carried forwards, the tibio-tarsal articulation reaches the anterior canthus of the eye. Upper surface of the body covered with minute pits, the closely opposed margins of which present a finely reticulate appearance; lower surface granulate. A distinct fold along the inner edge of the tarsus. Colour, olive grey above, blotched with darker markings; the same on the upper surfaces of the limbs. Length from snout to vent, 50 mm. Habitat, Poowong, Victoria. Collected by Mr. R. Hall.

Description of No. A.C.6877, a male, Lightning Creek, Victoria, 29.xii.1958.

Habitus moderately slender with fairly long limbs, length of head and body 29 mm.; head smoothly triangular, very slightly broader than long (11 × 10·5 mm.); snout blunt and short (4·5 mm.), but the strongly incurved canthus rostralis makes it appear prominent, one and a half times diameter of eye (3 mm.), rounded when seen from above, in profile curved and receding, strongly overhanging lower lip; canthus rostralis curved, distinct and angular; lores distinctly concave, sloping inwards from jaw to canthus rostralis; interorbital width about 1·6 times that of an upper eyelid (4 to 2·5 mm.), top of head flat between prominent eye bulges; internasal space 3 mm.; diameter of eye equals its distance from nostril; tympanum very indistinct, surface practically the same as surrounding skin, but portion of the anterior border can be distinguished in a certain light and position, it appears to be elliptical with longer axis directed forward and upward, contained in diameter of eye about three times, distance from eye 1 mm.; a strongly marked supratympanic ridge runs from eye to above shoulder.

Skin on the back and limbs at first glance smooth, but in detail uniformly and minutely pitted; a very few low, rounded but quite distinct warts dorsally, becoming more plentiful dorso-laterally; chin, throat and particularly abdomen coarsely granulate; postero-ventral surfaces of thighs granulate and area about anus extremely so; no or obscure pectoral fold; small flaps at knees; small anal flap, narrow, not very pronounced, tarsal fold.

Forelimb moderately strong and long (16 mm.), 55% of length of head and body; hand 8 mm.; finger discs distinct though not large, about half diameter of eye (1·5 mm), rounded with concave, cup-like undersurfaces; fingers in order of length, 1, 2, 4, 3; fingers only slightly webbed at base, extent of webbing, 10, 18 and 12%; subarticular tubercles small but distinct; large tubercle along thumb and three large tubercles at outer side of palm, arranged in shape of a U.

Hindlimb moderately long and robust, length (46 mm.) 160% of head and body; femur 13 mm., tibia 16 mm., foot 18 mm.; heel reaches just short of snout; toe discs elongated, small, hardly wider than toes and only about half size of finger discs, the discs are blackish, as are the subarticular tubercles and inner metatarsal tubercle, and very conspicuous; toes in order of length, 1, 2, 3, 5, 4; all toes nearly completely webbed, web extending to all discs except outer sides of 2nd, 3rd and 4th, extent of webbing, 90, 92, 93 and 100%; very narrow fringes on the short unwebbed sections of toes; subarticular tubercles small but distinct; sole with very small, low tubercles in lines; inner metatarsal tubercle elongated, not large but prominent, no outer one.

Vomerine elevations paired, quite small, rounded, distinctly separated from each other and widely separated from the choanae, each smaller than one of the choanae, which are themseves small and rounded, elevations completely behind choanae; tongue almost round, free and slightly indented behind, at least half width of mouth at angle of jaws; no external vocal sac.

Dorsal colour of body and limbs rather dark bluish grey with obscure blackish mottling and markings; posterior and dorsal surfaces of thighs with a good deal of yellow; warts and shagreening on sides and tympanic area whitish; chin, throat and anterior part of abdomen nearly white, remainder of abdomen and ventral surfaces of limbs yellow. These colours were noted in life and have changed little in three years of preservation.

Variation.—Another male, A.C.6876, was collected with A.C.6877. The two specimens resemble each other almost exactly. A.C.6876 has a head and body length of 26 mm. The tympanum can fairly be described as "not visible", although as in A.C.6877 a

relatively flattened area of the rough skin can be recognized with a hand lens if carefully sought. A narrow and not very prominent black line, which is very inconspicuous in A.C.6877, runs from the nostril through the eye to over the shoulder. A.C.6924, an almost completely metamorphosed frog with head and body length 26 mm. and unabsorbed tail 4 mm., was found under a plank beside a pond near the Hume Highway 2·5 miles south of Glenrowan. It was much paler than adults, and dotted and flecked sharply with black rather than mottled. Toes were all completely webbed to the discs, even more so than in adults, and the fingers were slightly more webbed. The tympanum was not visible. A recently occluded gill cleft slants downwards and backwards at an angle of about 45 degrees to the horizontal from just behind the eye to the base of the forelimb on each side. The tongue, which is only a late larval development, is only about half the size of that of A.C.6876, a young adult with identical head and body length. The vomerine elevations in both A.C.6876 and 6924 are slightly more anterior than in A.C.6877, being partly between the choanae.

Discussion.—Spencer's original description is so good that any modifications based on the two new Lightning Creek specimens are only minor. It may be mentioned here that the position of the species in the key given by Copland (1957: 12) still stands, but can be made more strictly accurate by changing "tympanum not visible" to tympanum covered by rough skin and practically invisible, and for "olive grey back" olive or bluish grey back. The head is quite broad and the difficulty of measuring to the posterior border of the tympanum probably accounts for Spencer's "head decidedly broader than long". The situation as regards the tympanum is discussed above with A.C.6876 and 6877. The colour of these two specimens is more bluish than olive grey. The difference in size is probably due to sexual dimorphism, the Poowong type being a female while the Lightning Creek specimens are definitely males. There is no doubt that the Lightning Creek frogs are *maculata*. The present author's discussion (1957: 55) was based entirely on the type description. In the previous 56 years apparently nothing had been published which added to our knowledge of the species. Fry (1912: 97) merely noted that he had not seen it, and Nieden (1923: 236) simply repeated the type description. My discussion dealt with the salient characters which separate *maculata* from allied species, and noted that "It seems remarkable that this distinctive frog has not been collected again . . . especially as Poowong in Gippsland is only about 60 miles from Melbourne". It appeared to me then that the species was valid. Since 1957 sole comment seems to have been by Moore (1961), who did not study a specimen. He excludes *maculata* in his synoptic list of Australian amphibians as a valid species, but includes it as a doubtful one (p. 331). He mentions it again: "Status uncertain; possibly *Hyla citropa*" (p. 344), and excludes it from his list of 19 frogs, including five *Hylas*, from Victoria (p. 357). It is an interesting fact that Aberfeldy, the only locality I know where *citropa* has been reported from Victoria, is only about 50 miles from Poowong and in much the same type of country. However, *citropa* differs strikingly from *maculata* in many characters. A few are the distinct tympanum, less webbing between the fingers, much less webbing between the toes (average 42% against 94%), stronger vomerine elevations, and presence of a well-marked colour pattern. In spite of these well-marked differences there is no specialized feature which would preclude a common origin; but there are general morphological similarities which indicate that *citropa* and *maculata* share a remote derivation from a, probably long extinct, ancestral species. I am able to remove any doubt as to identification by examining the type of *maculata*, which Mr. Charles W. Brāzenor, Director of the National Museum of Victoria, kindly made possible by forwarding the specimen to the Australian Museum. He said in reply to my inquiry: "We have the type specimen in the museum (No. D.8498), though, like many frogs, it has not preserved well. It is simply labelled 'Powong'." The type is somewhat hardened and distorted, but, allowing for the fact that it has been preserved for 60 years and that even living specimens are drab in colour, it is still in a very fair state. Although the type was available it was thought better to use A.C.6877 as the basis of the standard description because more and clearer detail could be made out. There are no diagnostic breaks between D.8498 and A.C.6877, differences being

only of degree and mainly due to the big contrast in size. The tympanic area can fairly be described as "not visible" at first glance, but with careful inspection it can be distinguished as a rounded, rough, skin-covered area in certain lights. It is slightly more distinct than in the Lightning Creek frogs. The head is wider than long (18 to 15 mm.). The canthus rostralis is distinctly angular. The snout measures 7·5 mm., the eye and internasal space each 5 mm. Webbing of the toes is practically complete, and of fingers scanty but quite noticeable, especially between 3rd and 4th. The vomerine elevations are just behind the posterior level of the choanae. There is a mere suggestion of a pectoral fold. Details of the skin, with its small but very distinct dorsal pitting, coarsely granulate venter, limbs which are as identical as may be even to the concave, cup-like discs, body proportions which are difficult to measure, and other remarks hold good for both A.C.6877 and D.8498. The Lightning Creek specimens were collected on snags partly submerged in the shallow water of fast-flowing Snowy Creek. Lightning Creek is a locality marked on the map near the junction of Lightning Creek itself and Snowy Creek. The elevation is about 1,500 feet. Much the same type of well-timbered country extends to Poowong, which is, however, at a somewhat lower elevation (600 ft.). So *maculata* probably occurs in suitable habitats throughout the 150 miles between Lightning Creek and Poowong and also in the triangle whose third point is Glenrowan. It could quite easily extend its range into New South Wales, both Lightning Creek and Glenrowan being only 30 miles or so from the border. *Maculata* affords an illustration of valid basing of a species on a single specimen; which must normally be accepted as poor modern taxonomic practice. However, this procedure must have justification under circumstances when the possibility of the presence of an abnormal or pathological specimen has been examined and ruled out and the individual still does not fit any specific category. I am certain that the same position which applies to *Hyla maculata* also holds for *Hyla irrorata** De Vis (1884: 128) and *Hyla jenolanensis* Copland (1957: 97). I have seen a specimen of each species. Examination of the three further specimens and re-examination of the type not only firmly establishes *maculata* as a member of the Victorian fauna and provides additional information, but gives reason for hope that this interesting *Hyla* will become better known.

Acknowledgements.—I wish to thank Dr. J. W. Evans and Professor L. C. Birch for affording me facilities at the Australian Museum and the Zoology Department in the University of Sydney. Mr. Charles W. Brazenor kindly supplied information and enabled me to examine the type of *maculata* in his charge at the National Museum, Melbourne. I am obliged to the Department of Crown Lands and Survey, Melbourne, for details concerning localities and their elevations.

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* The position of *irrorata* has been complicated by the fact that the type has been lost, vide Fry (1912: 100), also Copland (1957: 34). The only other known specimen, J.9255 in the Queensland Museum, from Dalby, Queensland, is here designated the neotype.

NOTES ON AUSTRALIAN MOSQUITOES (DIPTERA, CULICIDAE).

1. The Life History of Aedomyia venustipes (Skuse).

By G. W. Douglas, Vermin and Noxious Weeds Destruction Board, Department of Crown Lands and Survey, Melbourne, Victoria.

(One Text-figure.)

[Read 29th November, 1961.]

Synopsis.

The male, larva and pupa of *Aedomyia venustipes* (Skuse) are described and the female re-described, from specimens collected at Woodside, near Yarram, Victoria.

The larvae and pupae are found chiefly in open, permanent, well-vegetated pools during spring and summer. The larvae are pale green and remain submerged amongst vegetation, and they can spend long periods on the bottom of collecting jars free of vegetation without rising to the surface. The larvae do not appear to have special structures for obtaining oxygen from plants. The pupae are brown in colour and frequently rest amongst surface vegetation and move rapidly through the water like a tadpole with their tails out behind them. Adults have not been collected in the field although numerous attempts have been made to attract them to man and rabbit. Laboratory bred adults feed readily on sugar solution and raisins after emergence. The eggs are unknown.

This species is recorded from the Gippsland and Mallee regions of Victoria, and from the Elizabeth Bay and National Park districts of New South Wales.

Adults of *A. venustipes* can be distinguished from *Aedomyia catasticta* Knab by the scales forming the prominent scutal pattern being short and broad in *venustipes* and long and narrow in *catasticta*; the third hind tarsal segment all white and fifth all dark in *venustipes*, whilst the third white at base and apex, dark in between, and the fifth mostly white in *catasticta*.

Aedomyia venustipes (Skuse).

Aëdes venustipes Skuse 1889, Proc. Linn. Soc. N.S.W., (2) 3: 1761. *Aëdes* (*Aedomyia*?) *venustipes* Skuse, Theobald, 1901, *Mon. Cul.*, II: 223; *Aedomyia catasticta*, Knab, 1909, *Ent. News*, 20: 387; *Aedomyia squamipennis* Leicester (nec. L–A), 1908, *Cul. Malaya*, p. 182; *Aedomyia venustipes* Edwards, 1924, *Bull. Ent. Res.*, 14: 364.

As can be seen from some of the early publications, Taylor (1914), Edwards (1924, 1929), Mackerras (1937) and Baisas (1938), there has been confusion over the distribution (and specific determination) of *A. venustipes* and *A. catasticta*. It appears, however, that *A. venustipes* is the species found chiefly in southern Australia.

Types: Holotype female, collected by Skuse at Elizabeth Bay, Sydney, in 1886, is in the Macleay Museum, Sydney. The allotype male, 3 males and 3 females of this series, 3 morphotype larvae and 3 morphotype pupae from Woodside, are in the collection of the National Museum of Victoria, Melbourne. One male and one female are in each of the following collections: C.S.I.R.O. Division of Entomology, Canberra; School of Public Health and Tropical Medicine, Sydney; Macleay Museum, Sydney; University of Queensland, Brisbane; Queensland Institute of Medical Research, Brisbane; British Museum (Natural History), London, and U.S. National Museum. Washington. The holotype and another female in the National Museum, Melbourne, which bears two labels, 1—"18.11.25 Melbourne, Victoria. G. F. Hill" and 2—"*Aedomyia venustipes* (Skuse) Id. by G. F. Hill, Nov. '25", were the only adults known prior to the series described in this paper.

The holotype female was examined in November, 1956, and was found to be faded and with many scales and some legs missing. In addition, it was mounted on cardboard and only one side was examined. The Woodside specimens agree with it in the following details: third hind tarsal segment pure white, fifth segment dark; scutal scale patterns and scale types similar; wing scaling apparently similar; and proboscis with bands of white scales medially and at the apex.

Distinctive Features.

Adult: A medium sized, ornate species, with banded proboscis and tarsi, third hind tarsal segment entirely white, and broad, dark, cream and white scales on wings. To be distinguished from *A. catasticta* Knab by: scales forming the prominent scutal pattern short and broad, in *venustipes*, long and narrow in *catasticta*; third hind tarsal segment all white and fifth all dark in *venustipes*, third white at base and apex, dark in between, and fifth mostly white in *catasticta*.

Larva: General coloration is pale green with light brown head siphon and saddle. Hair tufts generally enlarged, giving a hairy appearance. In *venustipes* head hair B consists of 8–9 plumose hairs about three-quarters the length of A, whilst in *catasticta* head hair B is a tuft of 6–7 plumose hairs about half the length of A. In *venustipes* head hair C is a tuft of at least 6 plumose hairs nearly as long as A, whilst in *catasticta* head hair C is a tuft of only 3 plumose hairs. Siphonal index of *venustipes* is at least 3·6, whilst that of *catasticta* is about 3.

Pupa: General coloration brown with pigmented areas on trumpet paddles. No Australian pupae of *catasticta* have been described, so comparison with that species cannot be made.

Allotype Male: *Head*: Vertex with broad black and white flat and upright scales; a prominent patch of erect, cream and few dark scales medially. Border scales of eyes mostly black and flat, with some white scales. A pair of strong black vertical setae, and a row of fine golden ocular setae. Palpi about one-eighth length of proboscis, black-scaled, with white scales at apex of each segment. Proboscis black-scaled, about one and a quarter times length of hind femur, mottled with white scales dorsally near base; a band of white scales forming a conspicuous ring at middle, and another band near apex. Labella dark. Antennae about two-thirds length of proboscis, the last two segments clothed with short fine hairs; terminal segments about half length of penultimate. Clypeus dark, with patch of white scales dorsally. Torus dark, with some small white scales. *Thorax*: Integument black. Anterior pronotum with broad white scales and a few black scales and numerous hairs. Posterior pronotum with broad black and white scales; lower scales mostly white. Patches of broad white scales on prosternum, upper and lower sterno-pleuron, upper and lower mesepimeron, pre-alar and post-spiracular areas. Pleural bristles dark and pale; 4 dark upper and 4 pale lower sterno-pleurals near posterior margin; 14 pale pre-alar; 8 pale upper and 4 lower mesepimerals; no spiracular or post-spiracular bristles. Scutum black, covered with dark, white and cream scales. On anterior half and dorsally, a broad band of cream scales extends posteriorly to about half length of scutum, with two smaller patches of similar scales continuous with the large patch extending laterally on either side of middle line. Numerous dark acrostichal and dorsocentral bristles, and 8 dark pre-scutellar bristles. Scutellum black, with broad black and white scales, and black scales over apex of each lobe; bristles dark and strong, 6 on inner lobe and 10 on lateral lobes. Metapostnotum dark. *Wings*: Densely covered with broad dark and cream scales, with patches of broad white scales. Costa with three patches of white scales, one near base, one about one-quarter length of wing from base, and one extending posteriorly from tip of SC to form the largest area of white scales on the wing. Cell R_2 about twice length of its stem; cell M_1 about one and a half times length of its stem, the base of M_1 proximal to that of R_2. R_1 with subcostal and pre-apical areas of white scales; R_2, R_3, M_1 and M_2 with patches of white scales over bases; small patches of white scales at apices of all veins, and at all forks and crossveins; small pre-apical patch on R_{4+5} and M_{3+4}, the latter extending to about half length towards base. Fringe with white scales opposite all veins. Halteres with pale stems and small flat white scales on knobs. Wing length 3·8 mm. *Legs*: Mottled with black and white scales, and with banded tarsi. Coxae of all legs with patches of broad white scales; fore and mid with dark bristles and some fine hairs, hind with fine hairs only. Trochanters white-scaled. Femora with black and white scales, white scales basally and anteriorly, and erect tufts of black and cream scales at apex of mid and hind femora; tibiae mottled with black and

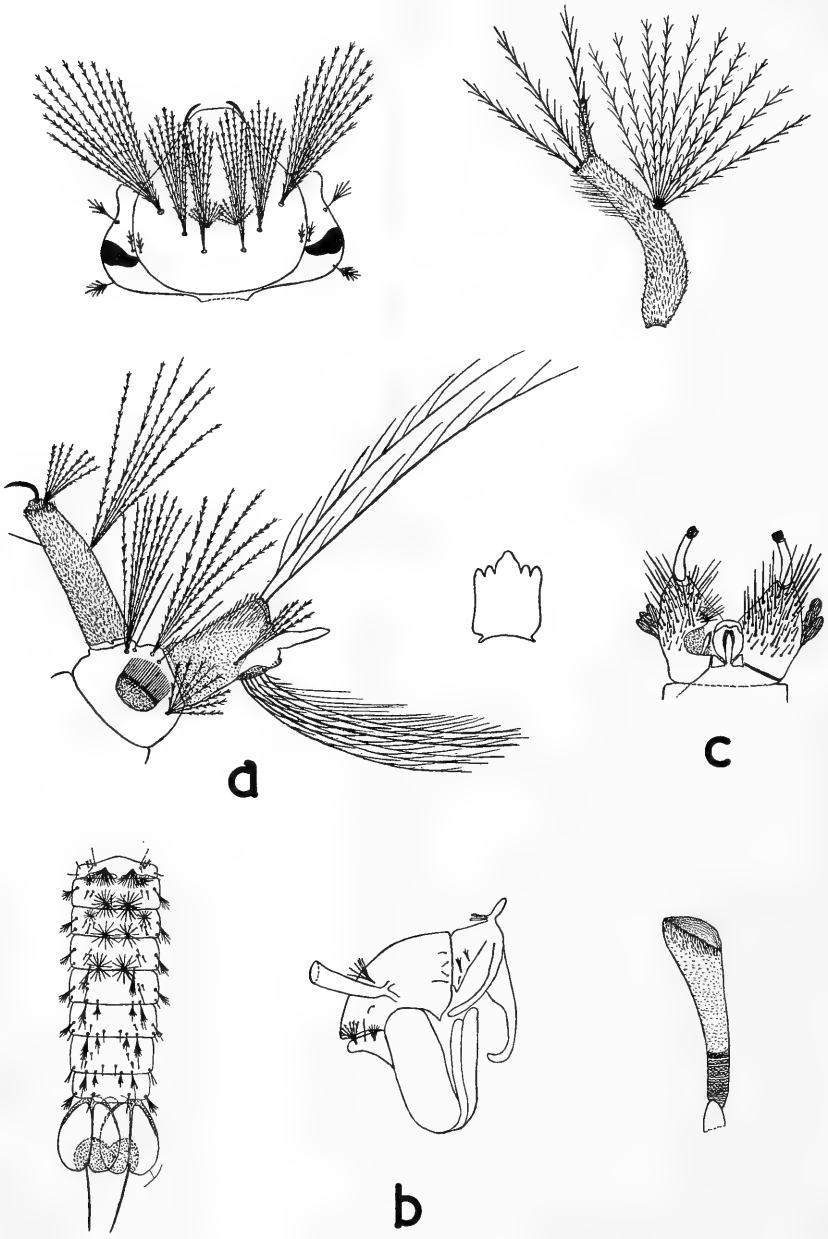

Fig. 1. *Aedomyia venustipes* (Skuse). *a*, head, mentum, antenna and terminal segments of larva; *b*, pupal abdomen (dorsal view), cephalothorax and trumpet; *c*, male terminalia.

white scales, with narrow rings of white scales near apex in fore and mid legs; on hind leg the narrow rings of white scales are about one-third of length of tibia from base. Tarsal segments with white and black scales, except fifth segments which are black-scaled, and third segment of hind tarsus which is white-scaled. Claws of fore and mid legs large and slightly unequal, the larger with a median tooth, the smaller simple; hind claws small, simple. *Abdomen*: Integument black. First tergite sparsely covered with cream, white and black scales; second to eighth predominantly black scaled; second with patch of white scales medially and apically; third and fourth with sub-apical patches of cream scales; third to seventh with few white scales on apical borders and laterally; seventh with three small patches of cream scales on apical border; eighth with scattered white scales and a dense patch of cream scales on apical border. Sixth and seventh tergites wider at apex than at base. Numerous hairs on all segments on apical border and laterally. Sternites black-scaled, with extensive mottling of white scales, particularly on second to sixth. *Terminalia* (Text-fig. 1, *c*): Coxite stout, about one and a half times as long as width at base; fine setae on coxite smallest near base, with longer setae laterally and ventrally; broad scales, longitudinlly striated, laterally on coxites. Style about half length of coxite, expanded just above base, curved and tapering on apical half; terminal appendage about one-fifth length of style, comb-like and chitinized. Tenth sternite chitinized. Phallosome simple. Basal lobe small, well separated, with stout setae.

Males: The series of six males does not show much variation. In some specimens there are sub-erect white scales on vertex between the eyes, and the white scaling anteriorly and basally on femora is more extensive. Some specimens have paired pre-apical patches of white scales on third, fourth and fifth tergites. Bristles on lateral lobes of scutellum reduced to seven. Wing length 3·6–3·9 mm.

Re-described Female.

Differs from allotype male as follows: Palpi about one-fifth the length of the proboscis. Antennae about two-thirds length of the proboscis. Some erect white scales in front of erect cream scales on vertex. White scales dorsally on anterior margin of scutum prominent. Pre-alar bristles reduced to about 10; 10–12 upper and 8–9 lower mesepimerals. Wing length 3·5–4·0 mm. Tarsal claws of all legs small and simple. Second to seventh abdominal tergites with white scales laterally; fourth to eighth with cream scales laterally on apical border; eighth smaller than other tergites, and with dense patch of cream scales on apical border. Second to seventh sternites chiefly white-scaled, eighth mottled with black and white scales. Ninth tergite not well developed; cerci small.

Females: The series of six other females does not show much variation. In one specimen, the band of white scales on apex of proboscis is absent, and the area from which they are absent is lighter than any other parts of proboscis.

Larva (Text-fig. 1, *a*). Length 6·2–6·8 mm.; pale green, except for the light brown head, siphon and saddle. *Head*: About three-fourths as long as broad. Antenna long, curved, about as long as head, clothed with fine hairs; tuft well developed, with 10–14 branched plumose hairs about length of the head; three very long apical plumose hairs of approximately equal length, and one stout terminal spine. Clypeal spines curved slightly inwards, strong and pointed. Head hairs A, B and C in an oblique row, with D a stellate tuft lying anterior and slightly medial to C. A consists of 9–11 long, dark, heavily plumose hairs about the length of the head; B of 8–9 plumose hairs about three-quarters length of A; C 6–8 plumose, nearly as long as A; D is a stellate tuft of nine finely frayed hairs; *e* short and 4-branched; *f* short, 5-branched. There is a short 4-branched hair just below base of antennae as conspicuous as *e* and *f*. Ocular hair single and simple. Mentum with one large median tooth and two lateral teeth. *Thorax*: Prothoracic hairs 1–3 dark, plumose, about twice length of thorax; 4 and 6 about 3 times length of thorax; 5 and 7 greatly enlarged to about 5 times length of thorax; 8 very short, with about 4 branches. Meso- and meta-thoracic dorsal and dorso-lateral hairs dark, plumose, and about 5 times length of thorax. *Abdomen*: Lateral hairs on all

segments dark and plumose. On first and second segments they are about 3 times length of segment; on third to seventh segments about twice length of segment. Lateral comb arises as a single row of 20 long, slender, pointed spines from the posterior margin of a chitinized plate. Pentad hair 1 with 5–8 branches, heavily plumose; 2 single and simple; 3 with 5–6 branches, heavily plumose; 4 single, with 4–5 fine branches near apex; 5 with 8 finely plumose hairs. Siphon of medium length, somewhat curved and tapering; index from 3·6 to 4·8, mean 4·2; covered with short, soft hairs, not enlarged on any part. Tracheae very narrow. Ventrolateral tuft of 6 long, plumose hairs arising about two-thirds of length from base; dorsolateral hair single, simple; a pair of strong curved terminal hooks, and tufts of 6 plumose hairs on siphonal valves. No pecten. Saddle complete, covered with short, soft hairs, with a patch of longer hairs dorsally. Saddle hair tuft of 4 plumose hairs almost as long as the saddle. Dorsal sub-caudal hairs very long, branching dorsally from about one-quarter of length from base. Anal papillae short, about half length of saddle, moderately pointed. Ventral brush of 6 multiple tufts, arising from a grid, each single, with branches on one side only.

Description based on 6 larvae from Woodside, Victoria.

Pupa (Text-fig. 1, *b*).—General coloration brown. Length 7–8 mm. *Cephalothorax*: Darker pigmented areas around base of trumpet and medially on metapostnotum. Trumpet about four times as long as greatest width, narrow at base; opening oblique, fringed with small hairs near apex; base dark, with toothed area extending to about one-third of length of trumpet. *Abdomen*: Pigmentation darker on segments 1 and 8. Float hairs dendritic, with about 15 branches. Lateral hairs of segments 8 with 5 branches, short and simple. Paddles oval, with conspicuous midribs, and pigmented areas near apices; margins smooth; paddle hairs long, about width of paddle, single and simple.

Description based on three pupae from Woodside, Victoria.

Eggs: The eggs are unknown. None have been collected in the field, and no females in captivity have laid eggs.

Distribution: New South Wales: Elizabeth Bay, Sydney (Skuse, 1889); National Park (Mackerras, 1937); probably Narrabeen, according to Lee (1944). Victoria: Bairnsdale (29.iv.1954); Box Ridge (17.iii.1954); Darriman (14.ix.1953, 16.ix.1953, 5.xi.1953, 10.xii.1953); Giffard (30.iv.1953, 8.xii.1955); Won Wron (26.vi.1953, 10.xii.1953, 14.xii.1953, 5.xi.1953); Woodside (23.xii.1952, 8.i.1953, 10.i.1953, 3.ii.1953); Yarram (12.ix.1954, 19.x.1954, 10.iii.1955, 8.xii.1955); Ouyen (1.v.1955); all collected by G. W. Douglas; Melbourne (18.xi.1925), G. F. Hill.

Biology.

This species is not common. It was first collected from a temporary roadside pool at Woodside, in January, 1953, but has not been found in temporary pools since. The high rainfall of late 1952 in Gippsland filled many roadside depressions, and these contained water until late in the summer of 1953.

The larvae and pupae are found chiefly in permanent water swamps, stock dams in the open, and forest dams and pools in the Gippsland region. Forest dams, sunk to provide water for fire-fighting, and now well vegetated, are common breeding places in late spring and summer. The Gippsland Plains, where most specimens were collected, have an annual rainfall of about 25 inches; but larvae were also collected on 1.v.1955 from Lake Timberoo, a channel-fed lake about 15 miles south west of Ouyen in the Victorian Mallee, where the annual rainfall is about 12 inches.

The larvae are usually difficult to find, on account of their pale green coloration and their habit of remaining amongst vegetation below the water surface. They can frequently be collected with a net placed deep in the water and drawn up slowly through the vegetation, particularly through water milfoil (*Myriophyllum* sp.). They frequently wriggle backwards on the collecting net. When placed in collecting jars, most larvae drop to the bottom of the jar and rest on their backs. Occasionally some rise to the surface, whilst others can spend long periods amongst the suspended vegetation without rising. Some larvae were held for about three months in jars without vegetation, and

frequently stayed below the surface for long periods. This species does not appear to have special structures to obtain oxygen from plants.

The pupae are usually collected amongst surface vegetation, often in the deepest parts of the water body. They invariably come to the surface, and are often difficult to disturb when on the surface. They move through the water rapidly, like a tadpole, with their tails out behind them. The paddles have pigmented areas which are very conspicuous whilst the pupae are in the water.

Larvae and pupae have been collected throughout the year, but appear to have breeding peaks in spring and summer. The occurrence of small numbers of larvae in many places, often in association with *Anopheles annulipes* Walk., suggests that single eggs are laid rather than egg rafts.

Adults have not been collected in the field, although numerous attempts have been made to attract them to man and animal bait during field studies on myxomatosis. Caged adults feed readily on sugar solution and raisins after emerging. On one occasion females attempted to pierce the skin of the forearm, but the proboscis bent every time, and the skin was never pierced. The resting adults lie close to the surface they are on, and the legs are placed close to the body, giving a very streamlined appearance. When released in a large room, the adults are capable of very fast flight.

Acknowledgements.

The author is grateful to Dr. I. M. Mackerras, The Queensland Institute of Medical Research, Brisbane, and Mr. F. N. Ratcliffe, Wildlife Survey Section, C.S.I.R.O., Canberra, for their helpful advice; to Dr. E. N. Marks, University of Queensland, for the loan of material of *A. catasticta* Knab from Queensland; to Mr. N. V. Dobrotworsky, University of Melbourne, for his advice and assistance; to Mr. A. L. Dyce, Wildlife Survey Section, C.S.I.R.O., Canberra, for criticism of the manuscript; Professor P. D. F. Murray and Mr. J. R. Henry, for permission to examine the type of *A. venustipes* in the Macleay Museum, Sydney, N.S.W.

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DIAPAUSE AND PARTHENOGENESIS IN THE EGGS OF THREE SPECIES OF PHASMATODEA.

By P. Hadlington, Forestry Commission of New South Wales, and E. Shipp, University of New South Wales.

(Plate x, B; one Text-figure.)

[Read 29th November, 1961.]

Synopsis.

Podacanthus wilkinsoni Macl., *Didymuria violescens* (Leach) and *Ctenomorphodes tessulatus* (Gray) are stick insects (Phasmatodea) which have occurred recently in plague numbers in some eucalypt forests in south-eastern Australia.

These three species have been recorded as having both a one-year and two-year life cycle in the field, and experiments were designed to study their embryogenesis, and the occurrence of embryonic diapauses indicated by field observations. The eggs of each species may have one or two diapauses. Where there is one diapause in eggs of *P. wilkinsoni* and *D. violescens* it is post-embryonic and either pre-embryonic or post-embryonic in eggs of *C. tessulatus*. In those eggs which have two diapauses, the first diapause is pre-embryonic, variable in duration, and determines the length of the life cycle. The second diapause is post-embryonic.

It appears that eggs of the two highland species, *P. wilkinsoni* and *D. violescens*, require preliminary exposure to periods of cold for morphogenesis and hatching to occur. *C. tessulatus* occupies a warmer climatic region than the other two species and its eggs do not require the same intensity of cold during diapause for morphogenesis and emergences to occur.

P. wilkinsoni and *D. violescens* in the Jenolan area have predominantly a two-year life cycle when the eggs are kept in an environment normally occupied by the species and also when kept in a coastal environment. *C. tessulatus* in the Kempsey area has predominantly a one-year life cycle. Thelytokous parthenogenesis was observed in *P. wilkinsoni* and *D. violescens*, whereas deuterotokous parthenogenesis occurred in *C. tessulatus*. Females of *C. tessulatus* may retain viable sperms for at least ten weeks and those of *P. wilkinsoni* and *D. violescens* for at least one week.

Introduction.

Podacanthus wilkinsoni Macl., *Didymuria violescens* (Leach) and *Ctenomorphodes tessulatus** (Gray) are stick insects which have occurred recently in plague numbers in some eucalypt forests in south-eastern Australia. The general biology of *P. wilkinsoni* and *D. violescens*, the two species which occur mainly in the highland areas, has been described by Richards (1952) and Campbell (1960). The ecology of *C. tessulatus*, a pest in north-eastern New South Wales, was studied by Hadlington and Hoschke (1959).

The life histories of the three species are similar, although the duration of the life cycles is variable. Oviposition occurs during the late summer and autumn and the eggs hatch either during the spring of the same year or that of the year following oviposition. Individuals reach the adult stage and begin reproduction in mid-summer. A predominantly one-year life cycle for *C. tessulatus* was established by Hadlington and Hoschke (1959), while Richards (1952) and Campbell (1960) recorded a predominantly two-year life cycle for *P. wilkinsoni* and *D. violescens*. Campbell (1960) found that, by sampling egg populations in the field, a reliable assessment could be obtained of the numbers of nymphs which hatched from these in the following seasons. From his work, it is apparent that the results would be more accurate after embryonic development in the eggs was complete. Observations made during his work suggested that an embryonic diapause was occurring in the eggs of these phasmatids and that a knowledge of the occurrence, intensity and duration of the diapause would be an essential preliminary to any studies of egg parasitism and other aspects of the ecology which involved the egg stage. The investigations recorded in this paper are intended to form a basis for a more detailed study of diapause and the factors which influence it.

* As noted by Key (1960), the correct form of the name is *tessulatus*, not *tessulata*, which was used by Key (1957), the generic name having to be treated as masculine.

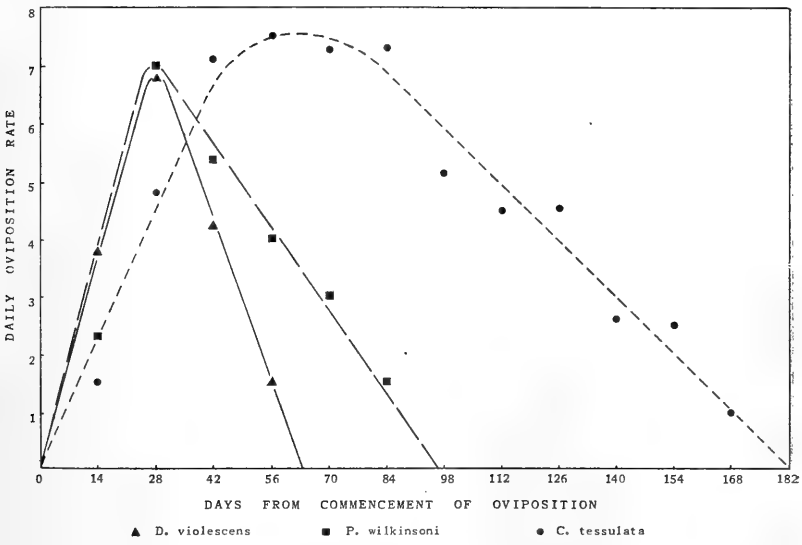
Parthenogenesis, which occurs frequently in the Phasmatodea, has been recorded for *C. tessulatus* and the investigation into diapause was extended to include the development of unfertilized eggs and to determine the extent to which parthenogenetic reproduction occurs in these three species.

Materials and Methods.

(*a*) *Procedure for Obtaining Eggs.*

Final instar nymphs of *P. wilkinsoni* and *D. violescens* were collected in the field from the Jenolan area in the Central Highlands during December, 1957, and kept in cages at Hurstville during oviposition. Final instar nymphs of *C. tessulatus*, the progeny of insects collected in 1956 from Tanban State Forest near Kempsey, were also kept at Hurstville. Throughout this period the insects were fed on *Eucalyptus andreana* Naud.

Fertilized eggs of each species were obtained from females which were kept in cages with males. These females have been described hereafter as mated females,



although it is possible, but very unlikely, that some had not mated. Eggs of each species were also obtained from females which had no contact with males and these eggs were used to study parthenogenesis. Such individuals have been referred to as unmated females. The total number of females used is shown in Table 6.

Mated females of the three species commenced to oviposit 12 days after the final moult and unmated females 15 days after. The average number of eggs produced by each female, both mated and unmated, was 257 for *P. wilkinsoni*, 206 for *D. violescens* and 691 for *C. tessulatus*. The daily oviposition rates when plotted against the average age of the respective females has been expressed in Text-figure 1.

(*b*) *Procedure for the Treatment of Eggs.*

Eggs were collected each week and separated into four groups, each group being eggs laid during a particular period of oviposition, as shown in Table 1.

These eggs were placed in moistened sterilized sand in round plastic containers. The depth of sand did not exceed one inch and moisture was added each month. These eggs were kept at Hurstville where they were exposed to environmental temperatures. Some eggs from mated females of each species were kept at Hurstville in plastic jars in the absence of sand to determine whether hatching or embryonic development was

affected by soil moisture. Maximum and minimum temperatures were recorded daily and these have been expressed in Table 2 as mean monthly maxima and minima for the holding period.

Eggs of the three species of the same parental origin as previously mentioned, but not divided into groups representing the various oviposition periods, were also similarly prepared and kept at a constant temperature of 76° F. Light was excluded from all eggs during the holding period.

Eggs of the three species, kept in the field in environments from which the parents were collected, were destroyed shortly after the initiation of the investigation and provided no worthwhile data.

(*c*) *Examination of the Embryos.*

Egg samples were taken each month from the containers, placed in fixative and later dissected. Some eggs were stained to distinguish early embryonic development. From such examinations it was possible to study the occurrence and duration of the diapauses and the progress of morphogenesis in the egg.

TABLE 1.

Emergence Periods in Relation to Oviposition—Mated Females—(Coastal Environment).

Species.	Period of Oviposition (1958).	First Hatching (1958–59).	Second Hatching (1959–60).
P. wilkinsoni ..	1 Jan.–15 Jan.	6 Sept. (1 emergence)	9 Aug.–25 Oct.
	15 Jan.– 7 Feb.	27 Sept. (1 emergence)	20 Aug.– 8 Oct.
	7 Feb.–28 Feb.	——	17 Aug.– 8 Oct.
	28 Feb.–28 Mar.	——	15 Aug.–29 Sept.
D. violescens ..	1 Jan.– 8 Jan.	1 Nov. (1 emergence)	9 Sept.–30 Dec.
	8 Jan.–22 Jan.	15 Sept.– 5 Jan.	30 Aug.–18 Jan.
	22 Jan.– 7 Feb.	19 Sept.– 7 Nov.	22 Aug.– 1 Feb.
	7 Feb.–28 Feb.	25 Sept.– 8 Dec.	24 Aug.– 4 Jan.
C. tessulatus ..	1 Jan.–22 Jan.	4 Aug.– 4 Nov.	28 Aug.–19 Sept.
	22 Jan.–21 Feb.	13 Aug.–18 Dec.	26 Aug.–29 Sept.
	21 Feb.–21 Mar.	24 Aug.–22 Nov.	6 June– 5 Oct.
	21 Mar.–18 April	27 Aug.–31 Dec.	9 Aug.–11 Oct.
	18 Apr.–16 May	22 Nov.–18 Jan.	11 Aug.– 3 Nov.
	16 May–13 June		2 May–16 Sept.

(*d*) *Hatching.*

First instar nymphs were removed from the containers, and emergences from those eggs kept at the coastal environment were counted and sexed. Hatching occurred mainly during the early mornings (1 a.m. to 6 a.m.) for all eggs kept at the coastal environment temperatures, while nymphs of *C. tessulatus*, which emerged from eggs at 76° F., appeared at all times and hatching was not restricted to any particular period of the day. The months during which hatching occurred are given in Tables 1 and 2.

In the absence of added moisture, emergences of *C. tessulatus* did not occur, while in *P. wilkinsoni* and *D. violescens* the percentage hatch was lower than that for eggs held in moist sand. A large number of nymphs of *P. wilkinsoni* and *D. violescens* were unable to detach their metathoracic legs from the chorion.

RESULTS.

Parthenogenesis and Sperm Storage.

In the Phasmatodea parthenogenesis occurs frequently and in some species whose reproduction is entirely parthenogenetic the male is unknown. It was anticipated that parthenogenesis would occur in the three species studied since parthenogenetic, as well as sexual reproduction, had been recorded for *C. tessulatus* by Hadlington and Hoschke (1959).

TABLE 2.
Emergences in Relation to Temperature.

Month and Year.	Hurstville Temperatures.		Emergences (% of Total Eggs).			Emergences (% of Total Eggs). *C. tessulatus* at 76° F. from 1/5/58 (1,110 Eggs).
	Mean Monthly Maximum.	Mean Monthly Minimum.	*P. wilkinsoni* (1,400 Eggs).	*D. violescens* (1,300 Eggs).	*C. tessulatus* (2,350 Eggs).	
February, 1958 ..	80	64	Nil	Nil	Nil	—
March	80	63	Nil	Nil	Nil	—
April	74	60	Nil	Nil	Nil	—
May	72	56	Nil	Nil	Nil	Nil
June	64	49	Nil	Nil	Nil	1·1
July	62	46	Nil	Nil	Nil	0·8
August	65	50	Nil	Nil	16·3	0·6
September	65	54	0·1	2·5	13·1	2·6
October	74	57	Nil	2·8	16·3	27·6
November	78	63	Nil	0·5	10·5	17·2
December	76	65	Nil	0·1	1·4	17·8
January, 1959 ..	79	67	Nil	0·1	Nil	2·2
February	80	68	Nil	Nil	Nil	0·3
March	78	64	Nil	Nil	Nil	1·3
April	74	61	Nil	Nil	0·1	1·3
May	68	52	Nil	Nil	Nil	0·2
June	64	48	Nil	Nil	Nil	0·5
July	64	46	Nil	Nil	0·1	0·1
August	66	48	10·1	0·2	6·2	0·3
September	69	55	33·2	13·0	12·8	—
October	72	56	0·7	6·2	0·6	—
November	75	64	Nil	4·5	0·1	—
December	78	64	Nil	2·5	Nil	—
January, 1960 ..	83	68	Nil	0·4	Nil	—
Total emergence ..	..	..	44·0%	32·8%	77·5%	72·6%

Eggs from unmated females of *P. wilkinsoni* and *D. violescens* yielded female individuals only, thus establishing thelytokous parthenogenesis for these species. In *C. tessulatus* deuterotokous parthenogenesis was recorded. Eggs from unmated females of *C. tessulatus* were collected at approximately monthly intervals over a period of six months and each group of eggs was held separately. There was a progressive increase in emergence numbers from eggs laid from the initial to the final oviposition period. Males emerged from eggs of the last oviposition period (Tables 3 and 4).

Field observations indicated that males and females were present in approximately equal numbers. The proportion of male and female progeny from mated females did not deviate significantly from the 50:50 sex ratio of males to females as shown in

TABLE 3.
Viability of Sperms—C. tessulatus.
Indicated by Proportion of Males in the Progeny from Eggs of Various Oviposition Periods. Expressed as percentage of total number of eggs.

Oviposition Period (1958).	Emergences—1958.		1958 Total.	Emergences—1959.		1959 Total.	Total 1958 and 1959.
	Males.	Females.		Males.	Females.		
1 Jan.–22 Jan. ..	44·5	39·0	83·5	2·0	1·5	3·5	87·0
22 Jan.–21 Feb. ..	43·0	39·0	82·0	2·2	3·2	5·4	87·4
21 Feb.–21 Mar. ..	41·4	37·6	79·0	4·6	4·6	9·2	88·2
21 Mar.–18 April ..	31·4	31·0	62·4	7·6	9·6	17·2	79·6
18 Apr.–16 May ..	9·0	6·6	15·6	29·2	24·0	53·2	68·8
16 May–13 June. ..	0·0	0·0	—	10·0	18·0	28·0	28·0

* No males survived after this date.

Table 5 and it appeared that the usual method of reproduction was sexual rather than parthenogenetic for these three species.

Females of *P. wilkinsoni* and *D. violescens*, which had been kept with males and then isolated for a period of one week, produced eggs at the end of this period of isolation, both male and female nymphs hatching from these eggs. When the same females were dissected after nineteen days' isolation, no viable sperms were found in

TABLE 4.
Parthenogenesis (C. tessulatus) *and the Incidence of Male Progeny in Relation to Oviposition.*
(Percentage of total eggs.)

Oviposition Period (1958).	First Emergence (1958).		Emergence (Males and Females).	Second Emergence (1959).		Emergence (Males and Females).	Total Emergence
	Males.	Females.		Males.	Females.		
1 Jan.–22 Jan. ..	0·0	1·0	1·0	0·0	0·5	0·5	1·5
22 Jan.–21 Feb. ..	0·0	2·0	2·0	0·0	1·4	1·4	3·4
21 Feb.–21 Mar. ..	0·0	0·8	0·8	0·0	4·2	4·2	5·0
21 Mar.–18 Apr. ..	0·0	0·4	0·4	0·0	8·0	8·0	8·4
18 Apr.–16 May ..	0·0	0·4	0·4	0·0	13·2	13·2	13·6
16 May–11 July ..	0·0	0·0	0·0	18·5	25·0	43·5	43·5

the spermathecae. Eggs laid by *C. tessulatus* females which had been in contact with males and then isolated for a period of ten weeks yielded male and female nymphs (Table 3).

The ability to store sperms thus occurred in the three phasmatid species, but was more pronounced in *C. tessulatus* than in the other two species. In high density populations the storage of sperms would not appear to be advantageous, but if the population was low and the chances of a female contacting a male less, then fertilization

TABLE 5.
Sex of Progeny from Mated and Unmated Females.
(Percentage of total emergences.)

Species.	Eggs from Mated Females.						Eggs from Unmated Females.					
	First Emergences.		Second Emergences.		Total.		First Emergences.		Second Emergences.		Total.	
	Males.	Females.	Males.	Females.	Males.	Females.	Males.	Females.	Males.	Females.	Males.	Females.
P. wilkinsoni ..	50	50	55·4	44·6	55·4	44·6	—	—	—	100	—	100
D. violescens ..	44·8	55·2	49·3	50·7	48·4	51·6	—	100	—	100	—	100
C. tessulatus ..	52·4	47·6	50·0	50·0	51·7	48·3	—	100	17·4	82·6	15·9	84·1

of eggs by stored sperms may be important. The storage of sperms would ensure that eggs, produced later in the life of the female, were fertilized, particularly since the female appears to live much longer than the male (Table 6).

Degeneration was greater in eggs from unmated females than in those from mated females (Table 7).

Embryogenesis.

The morphological development of embryos and the differentiation of the various structures have been described by Steele (1941) in her study of the embryonic behaviour of *Austroicetes cruciata* (Sauss.) and these aspects have not been considered in detail in this paper. Development and the movements of the embryos during embryogenesis appeared to be similar in all three species so that in describing the relevant aspects of embryogenesis the species are considered as one.

The embryo was first visible as a small plate-like structure in the region of the micropyle. The developing embryo, with its dorsal surface directed inwards towards the yolk, then moved posteriorly along the micropylar area towards the operculum during anatrepsis and in the opposite direction around the posterior pole during the early stages of catatrepsis. Throughout this development, the embryo was slightly folded. Towards the completion of catatrepsis it almost entirely occupied the chorion, the head being located at and facing the operculum, while the dorsal surface of the embryo lay along the micropylar area (Plate x, B). When in an advanced stage of

TABLE 6.
Adult Longevity—Coastal Environment.

Species.	No. of Insects.	Maximum (Days).	Average (Days).
P. wilkinsoni			
Female	27	130	80
Male	11	85	61
D. violescens			
Female	17	95	57
Male	11	61	42
C. tessulatus			
Female	15	210	147
Male	14	74	60

catatrepsis the embryo was pigmented, and the mandibles were strongly chitinized. Once embryogenesis was initiated, it was continuous for 12–14 weeks until late catatrepsis.

The stage prior to the formation of the platelet was not observed. Embedding and sectioning the eggs to study the nuclei were not successful and it was not determined at what point the diapause occurred prior to the appearance of the platelet.

The stage prior to the formation of the platelet is here referred to as "pre-embryonic" and is the stage at which the first diapause supervened in those eggs which had two diapauses. In this regard Lees (1955) recorded that no species was known in

TABLE 7.
Emergences and Embryonic Conditions of Eggs—Coastal Environment.
(Expressed as percentages of total eggs.)

Species.	From Mated Females.				From Unmated Females.			
	Emergences.	Dead Embryos.	Undeveloped Eggs.	Diseased.	Emergences.	Dead Embryos.	Undeveloped Eggs.	Diseased.
P. wilkinsoni	44·0	2·8	44·7	8·5	1·4	1·7	77·7	19·2
D. violescens	32·8	0·6	54·0	12·6	1·2	0·2	50·4	48·2
C. tessulatus	77·5	2·4	12·7	7·4	10·4	3·0	74·1	12·5

which an embryonic diapause supervened before the formation of the blastoderm, but Voy (1954), while studying the embryonic behaviour of *Clonopsis gallica* Charp. (Phasmatodea), recorded a non-developmental stage prior to visible embryogenesis and regarded this as preblastodermic. Apparently he could not be more precise about the occurrence of the diapause with respect to the nuclei.

In those eggs which hatched during the first year, the first diapause occurred when the embryo was fully formed so that this is here referred to as "post-embryonic". In eggs which had two diapauses, the second was a post-embryonic diapause.

These periods of suspended development coincide with the winter months when lower temperatures prevailed, while morphogenesis occurred during the summer and autumn months, usually during January-April when higher temperatures occurred.

The Occurrence and Duration of the Diapauses.

One or two diapauses, namely, pre-embryonic and post-embryonic, occurred in the eggs of all three species of phasmatids, but varied in their duration. The variability in the duration of the pre-embryonic diapause determined the length of life cycle.

The eggs of the three species hatched during the first, second and third years. However, only one-year and two-year life cycle eggs have been expressed quantitatively. Individuals having a three-year life cycle, while hatching, were not recorded and are included in the totals of undeveloped eggs in the respective tables.

TABLE 8.
Diapauses in Relation to One-, Two- and Three-Year Life Cycles.

Species.	One-year.	Two-year.	Three-year.
P. wilkinsoni			
First diapause	Post-embryonic.	Pre-embryonic.	Pre-embryonic.
Second diapause ..		Post-embryonic.	Post-embryonic.
D. violescens			
First diapause	Post-embryonic.	Pre-embryonic.	Pre-embryonic.
Second diapause ..		Post-embryonic.	Post-embryonic.
C. tessulatus			
First diapause	Pre-embryonic or Post-embryonic	Pre-embryonic	Pre-embryonic
Second diapause ..		Post-embryonic	Post-embryonic

The eggs of *P. wilkinsoni* having a one-year life cycle showed no indication of a pre-embryonic diapause, as the embryo commenced to develop soon after oviposition and progressed to a stage of advanced development when the post-embryonic diapause supervened. Hatching occurred from these eggs during the following spring. Two diapauses, namely, pre-embryonic and post-embryonic, occurred in eggs which produced two-year and three-year individuals.

The eggs of *D. violescens* appeared to behave similarly to those of *P. wilkinsoni*, although the proportion of one-year individuals was greater, as shown in Table 9.

TABLE 9.
Progeny from Mated and Unmated Females.

Species.	From Mated Females.					From Unmated Females.				
	First Emergence.		Second Emergence.		Total Emergence (%).	First Emergence.		Second Emergence.		Total Emergence (%).
	Males.	Females.	Males.	Females.		Males.	Females.	Males.	Females.	
P. wilkinsoni	1	1	340	274	44·0	—	—	—	18	1·4
D. violescens	34	42	173	178	32·8	—	2	—	6	0·6
C. tessulatus	713	649	237	237	77·5	—	20	37	185	10·5

The eggs of *C. tessulatus* produced one-year individuals of two types, namely, those which have no pre-embryonic diapause and over-winter in the post-embryonic diapause stage and hatch in spring and those which have a pre-embryonic diapause and hatch in the late spring or summer suggesting the avoidance of, or a shorter period for, the post-embryonic diapause. The eggs of *C. tessulatus* with two-year and three-year life cycles have either one pre-embryonic diapause or a pre-embryonic together with a post-embryonic diapause. When only one diapause occurred hatching took place during the late spring or summer suggesting the avoidance of the post-embryonic diapause. The

possible avoidance or reduced period of the post-embryonic diapause was indicated when embryogenesis occurred in the egg samples examined during the spring months.

The period of oviposition influenced, to some extent, the production of one-, two- and three-year individuals as shown in Table 4. Eggs laid during the earlier oviposition periods yielded a large proportion of one-year individuals, while two-year individuals predominated from the later periods.

Diapause in eggs from unmated females of each species was similar to those from mated females, yielding one-, two- and three-year individuals, although the percentages were much lower (Tables 9 and 10).

Effects of Temperatures on the Embryonic Behaviour.

(*a*) Field Environment Temperatures.

Richards (1952) and Campbell (1960) during their investigations recorded the predominance of the two-year life cycle for *P. wilkinsoni*. To determine the existence and proportion of the one-year life cycle in the climatic region naturally occupied by this species, eggs of *P. wilkinsoni* were collected from cage-held females which had been collected at Jenolan and these eggs were kept in moist sand in plastic containers buried one inch below ground level at 4,200 feet in the Jenolan area. Only two-year individuals (76%) were recorded from these eggs. The percentage of eggs which developed and subsequently hatched was greater than that (44%) recorded from eggs kept in a coastal environment.

TABLE 10.
One-year and Two-year Life Cycles of the Three Phasmatid Species.
(Percentage of total eggs.)

Species.	From Mated Females.			From Unmated Females.		
	One-year.	Two-year.	Undeveloped Eggs.	One-year.	Two-eyar.	Undeveloped Eggs.
P. wilkinsoni ..	0·1	43·8	44·8	0·0	1·2	77·7
D. violescens ..	5·8	27·0	54·0	0·1	0·5	50·4
C tessulatus ..	57·3	20·2	12·7	0·8	9·2	74·1

From dissection data for field-collected eggs from Nundle, Hanging Rock and Tuggolo State Forests in the Central Highlands, Campbell (1960) derived a figure of 20–30% embryonic development in eggs not parasitized. The low figure for embryonic development may be attributable to the large proportion of degenerated eggs which may have accumulated over several years, and thus represented more than one oviposition year.

Defoliation by *D. violescens* was recorded during alternate years from Bago State Forest in the Southern Highlands, thus suggesting predominance of the two-year life cycle. Campbell (1960), from his field data during his egg sampling work, was able to demonstrate that embryonic development had occurred in the December-February period and the eggs subsequently hatched during the following November and December, thus confirming the predominance of the two-year life cycle. Campbell recorded as much as 43% development in the eggs, but this figure may be greater as his material probably included degenerating eggs from previous oviposition years. As with *P. wilkinsoni* there was evidence which suggested that the development was higher for eggs in the field in a region naturally occupied by the species than when kept in a coastal environment.

A predominantly one-year life cycle was recorded for *C. tessulatus* (Hadlington and Hoschke, 1959), this being confirmed by laboratory results (Table 3). Individuals having a two-year life cycle appeared to occur in the field, but to only a minor degree. Both the natural environment of this species and the coastal environment at Hurstville are similar, and no marked deviation in the embryonic behaviour of this species was expected.

(*b*) *Coastal Environment Temperatures.*

The occurrence and relative proportions of the one-, two- and three-year life cycle individuals from eggs of the three phasmatid species kept at coastal environment temperatures has been given in Tables 9 and 10. A two-year life cycle predominated for *P. wilkinsoni* and *D. violescens* while a one-year life cycle predominated for *C. tessulatus.*

Embryogenesis, diapause and emergences of nymphs occurred at the coastal environment temperatures in all species, although the emergence of *P. wilkinsoni* and *D. violescens* nymphs was lower than that recorded from the field in the Central Highlands. Eggs of these two species do not appear to have received sufficient stimulus from the coastal environment; possibly the winter temperatures on the coast were not low enough and of sufficient duration during the first winter period to terminate the pre-embryonic diapause. However, many of these eggs remain viable until the following winter when the diapause may then be terminated, resulting in a three-year life cycle. Whether four-year individuals occur was not determined, but this possibility cannot be overlooked in any of the three species.

TABLE 11.

Monthly Average Daily Maximum and Minimum Temperatures for 30 Years.

(Weather Bureau data.)

Month.	Jenolan Caves.		Sydney.		West Kempsey.	
	Average Daily Max.	Min.	Average Daily Max.	Min.	Average Daily Max.	Min.
January	77·6	52·4	78·6	65·1	86·0	63·1
February	76·9	52·7	78·8	65·5	85·0	63·4
March	72·0	49·6	76·6	62·9	82·8	61·0
April	63·2	43·7	72·0	57·7	78·2	55·5
May	56·1	37·9	67·0	52·4	72·7	48·9
June	51·1	34·3	62·8	48·1	67·8	43·8
July	50·0	32·7	61·8	46·4	67·6	42·2
August	53·5	33·6	64·3	47·6	70·8	43·3
September	60·2	37·3	68·3	51·4	75·9	47·5
October	67·4	41·9	71·7	55·9	79·4	53·1
November	72·6	46·7	74·5	59·8	82·4	57·7
December	76·4	50·6	76·9	63·2	84·3	61·4

The emergence of *C. tessulatus* nymphs was greater than for the other two species, and this result would be consistent with the fact that the coastal environment temperatures at which these eggs were kept would more closely approach the temperatures of the climatic regions occupied by this species than the temperatures of the climatic regions occupied by *P. wilkinsoni* and *D. violescens* (Table 11).

(*c*) *Constant Temperature.*

P. wilkinsoni eggs kept at 76° F. did not hatch. Embryogenesis did not occur and the eggs deteriorated at this constant temperature. The temperature was not low enough to terminate the pre-embryonic diapause which would have permitted morphogenesis to be initiated.

D. violescens eggs kept at 76° F. also failed to hatch. However, in this species embryogenesis occurred and the embryo progressed to an advanced stage of catatrepsis and then degenerated. This temperature enabled the pre-embryonic diapause to be completed, allowing morphogenesis to occur, but it was not low enough to terminate the post-embryonic diapause and permit hatching.

C. tessulatus eggs kept at 76° F. hatched and emergences were not confined to any particular period of the day as with those eggs exposed to diurnal fluctuations. The eggs commenced to hatch one month after being exposed to 76° F., but the emergences were not related to the seasons. The total percentage emergence differed very little from that for eggs kept at coastal environment temperatures (Table 2). The constant

temperature of 76° F. enabled the pre-embryonic and post-embryonic diapauses to be completed, thus permitting morphogenesis and hatching to occur.

Discussion.

From the experimental data it appears that temperature, as a component of the environment, influences the diapause and embryonic behaviour of eggs of the three phasmatid species. Exposure to low temperatures for a sufficient period appears to ensure the completion of diapause, while the next phase of the development is dependent on higher temperatures for the completion of embryogenesis.

The occurrence of diapause in the eggs of the three species, in the various climatic zones occupied by each, ensures that the eggs may over-winter for one, two or more years and regulates the occurrence of morphogenesis and hatching to the most favourable periods. The optimum exposure to low temperatures was not determined, but there is evidence which suggests that there is variability within the eggs to the duration of these exposure periods which are necessary to terminate the diapause.

In the three species studied the two highland species, *P. wilkinsoni* and *D. violescens*, may be expected to have a lower optimum temperature for the termination of diapause than that for the coastal phasmatid, *C. tessulatus*. Lees (1955) has previously considered this in suggesting that the warmer the climate of the region occupied by a species the higher will be the optimum temperature required for the termination of diapause. The diapause and embryonic behaviour of these phasmatids appear to support his remarks.

The terms "diapause stage" and "diapause development" (Andrewartha, 1952) are used in the consideration of the diapauses in these phasmatids. The first and second periods during which morphogenesis appears to have ceased are referred to as the pre-embryonic and post-embryonic diapause stages respectively, while diapause development is used for the periods of physiological development in progress during the diapause stages and which must be completed as a prerequisite for the initiation or resumption of morphogenesis.

After oviposition, eggs producing two- or three-year individuals enter the diapause stage and some physiological development occurs at the low temperatures. Unless the temperature range for diapause development is sufficiently low and sustained, the egg will degenerate or fail to be stimulated by the higher temperatures which occur later and are necessary for morphogenesis.

Although the occurrence of four-year or longer life cycles was not investigated, these may occur in the three species in particular environments.

P. wilkinsoni.

For termination of the pre-embryonic diapause, eggs of *P. wilkinsoni* apparently require to be exposed to periods of sufficient cold, in terms of duration and intensity, to allow diapause development to proceed. This permits morphogenesis to occur as soon as the temperature of the environment enters the temperature range for morphogenesis, which is not reached until December in the Jenolan area when the average daily maximum is 76° F. Once initiated, this development proceeds until the embryo is in late catatrepsis, at which time it enters the post-embryonic diapause stage. When post-embryonic diapause development has been completed the young phasmatids emerge. The lower limit of the temperature range for emergence appears to be lower than that for morphogenesis and would be somewhere between the average daily maximum of 60–65° F. which occurs in September in the Jenolan area, and during August on the coast, as shown in Table 11. This is confirmed by the emergences in the field and from eggs kept on the coast (Table 1).

When kept at a constant temperature of 76° F. no development occurred in the eggs, although this temperature was within the temperature range for morphogenesis. In eggs of this species, from the Jenolan area, a sufficient exposure to a relatively low temperature range is an essential preliminary to the initiation of morphogenesis.

Eggs in the post-embryonic diapause stage, which have been kept at 76° F. after embryogenesis is complete, do not hatch, but after being exposed to periods of cold they

hatch when placed at 76° F. The intensity and duration of cold during the pre-embryonic diapause stage appear to determine whether morphogenesis will be initiated. Eggs vary in their threshold of exposure to chilling, but it was evident that percentage of eggs in which development occurs was greater for eggs kept in the highlands than on the coast, and this appears to operate through temperature as shown in Tables 2 and 11.

The occurrence of a three-year life cycle has not been determined in the field in the Central Highlands, but it has occurred from eggs kept on the coast. This would seem to be due to the higher minimum temperatures and shorter periods of exposure to such temperatures on the coast, so that diapause development is not completed in any one season. If three-year individuals occur in environments where plagues have occurred they would be in small numbers.

D. violescens.

In this species a number of eggs developed without the pre-embryonic diapause or this diapause was of a very short duration. These eggs over-wintered in the post-embryonic diapause stage and yielded one-year individuals. The eggs which produce two-year and three-year individuals have the pre-embryonic and post-embryonic diapauses and react to the evironment in a similar way to *P. wilkinsoni.*

When kept at 76° F. morphogenesis occurred without exposure to low temperatures, suggesting that this holding temperature was within the temperature range for pre-embryonic diapause development and also for morphogenesis. Emergences did not occur from these eggs, indicating that post-embryonic diapause was not terminated and the constant temperature of 76° F. was above the temperature range for post-embryonic diapause development.

While no results are available from field material of this species, the eggs may be expected to behave similarly to *P. wilkinsoni* in respect of the intensity and duration of cold when compared with eggs held in a coastal environment. Three-year individuals, if present in the field, would occur to a minor degree.

C. tessulatus.

In this species most eggs have only one diapause so that they over-winter in the post-embryonic diapause stage. In the eggs which produce two and three-year individuals, the pre-embryonic and post-embryonic diapauses occur during successive winters.

At 76° F. both pre-embryonic and post-embryonic diapause stages are completed, suggesting that this temperature was within the temperature range for pre-embryonic and post-embryonic diapause development and it was also within the temperature range for morphogenesis. All processes then operated at 76° F. so that emergences occurred at any time and were not confined to the periods after exposure to lower temperatures, although the seasonal production of individuals occurred from eggs kept at coastal environment temperatures. It may be noted from Table 11 that the average daily minimum temperature for Kempsey, where this species occurs in plagues, is lower than that for Sydney.

The most effective portion of the temperature range for the termination of diapause varies from one species to another (Hogan, 1960), and this appears to be related to the climatic zone occupied by each species. The warmer the climate of occurrence the higher are the optimum temperatures for the termination of diapause. The behaviour of *C. tessulatus* eggs, when compared with that of the other two species, appears to support this viewpoint, also expressed by other workers.

The period of oviposition appears to affect the production of one-year and two-year individuals in this species and this operates through the diapause stage. Eggs which were laid during the earlier oviposition period (January-March) were exposed to higher temperatures at which both pre-embryonic diapause development and morphogenesis would be completed, and such eggs over-wintered in the post-embryonic diapause stage. During the later oviposition periods (April-June) the temperature had fallen below that necessary for morphogenesis to be initiated, and these eggs over-wintered in the

pre-embryonic diapause stage. The effect of the oviposition period on the occurrence of the diapauses is masked by the incidence of parthenogenesis, but when the results in Tables 3 and 4 are compared it may be seen that the oviposition period is significantly related to the occurrence of the pre-embryonic diapause stage.

Acknowledgements.

The authors are indebted to Messrs. K. G. Campbell, K. M. Moore and L. H. Bryant of the Forestry Commission of New South Wales and to Mr. L. R. Clark, Division of Entomology, C.S.I.R.O., for their helpful criticism of the manuscript. The photograph is by Mr. R. Moulton, Forestry Commission of New South Wales.

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EXPLANATION OF PLATE X, B.

An embryo of *P. wilkinsoni* in a stage of late catatrepsis.

THE GENUS *PELARGONIUM* L'HER. EX AIT. IN AUSTRALIA.

By R. C. Carolin, University of Sydney.

(Four Text-figures.)

[Read 29th November, 1961.]

Synopsis.

Seven indigenous species of *Pelargonium* are distinguished and described, *P. helmsii* for the first time. *P. littorale* Hügel and *P. drummondii* Turcz. are reinstated. Introduced species are also considered. Some problems raised by the distributions of the various species are discussed.

Introduction.

The genus *Pelargonium* has attracted considerable attention due to the horticultural value of many of the species. It is not surprising, then, to find the most showy of the species occurring on the eastern seaboard of Australia being cultivated in Europe at quite an early date. *P. australe* was described by Willdenow in 1800 and it appears that it was widely cultivated even then. *P. inodorum* was described by the same worker a little later and, subsequently, the name was misapplied to a number of

Table 1.

Name.	Date.	Conspecific with.
P. AUSTRALE Willd.	1800	
var. *clandestinum* (L'Her. ex Hook f.) Hook. f.	1864	*P. inodorum* Willd.
var. *erodioides* (Hook.) Benth.	1863	*P. australe* Willd.
var. *major* Hook. f.	1855	*P. australe* Willd.
var. *glabrata* Hook. f.	1855	*P. australe* Willd.
P. clandestinum L'Her. ex DC.	1824	nom. nud.
P. clandestinum L'Her. ex Hook. f.	1853	*P. inodorum* Willd.
P. crinitum Nees in Lehm.	1844	*P. littorale* Hüg.
var. *congestum* Nees in Lehm.	1844	*P. littorale* Hüg.
P. DRUMMONDII Turcz.	1858	
P. drummondii sensu Hook. f., non Turcz.	1894	*P. capitatum* (L.) Ait.
P. erodioides Hook.	1834	*P. australe* Willd.
P. glomeratum (Andr.) Jacq.	1816	*P. australe* Willd.
P. HAVLASAE Domin.	1923	
P. HELMSII, sp. nov.		
P. INODORUM Willd.	1809	
P. inodorum sensu Sweet, non Willd.	1820–22	*P. australe* Willd.
P. LITTORALE Hüg.	1837	
P. RODNEYANUM Mitch. ex Lindl. in Mitch.	1839	
P. stenanthum Turcz.	1858	*P. littorale* Hüg.
Erodium peristeroides Turcz.	1863	*P. inodorum* Willd.
Geranium australe (Willd.) Poir.	1811	*P. australe* Willd.
Geranium glomeratum Andr.	1805	*P. australe* Willd.
Geraniospermum australe (Willd.) O. Ktze.	1891	*P. australe* Willd.
Geraniospermum rodneyanum (Lindl.) O. Ktze.	1891	*P. rodneyanum* Mitch. ex Lindl. in Mitch.

Australian species. Others have since been described, but Bentham (1863) admitted only two, reducing the others to synonymy of *P. australe* and one, *P. erodioides* Hook., to varietal rank. Knuth (1912) reinstated *P. inodorum*, equating it with *P. erodioides*. This action only served to increase the confusion surrounding the names, primarily caused by Sweet (1820–2) when he described inland forms of *P. australe* as *P. inodorum* (see below). Table 1 sets out the author's opinion with regard to the application of the various names that have been used for the indigenous taxa.

The characters used to distinguish between the sections of this genus are often connected with the habit of the plants. Collectors do not always obtain complete specimens in this respect and it must be urged that in future specimens should show the basal parts of the plant, even the roots, as these are often particularly important.

The habit conditions are summed in Figure 1 in which both indigenous and introduced species are represented. The species normally classified in sect. *Peristera* (Groups I and II below) form a very short, basal, more or less horizontal, perennial stem from which, each year, arise leafy, deciduous, flowering branches. These are apparently terminal and the growth of the basal, perennial stem is sympodial just as that of the deciduous branches. The perennial stems may be quite elongated when the plant is gradually becoming smothered in drifting sand and they are frequently branched. The root system of this group consists of a swollen, but not tuberous, taproot which may be branched. *P. rodneyanum* belonging to sect. *Polyactium* shows a

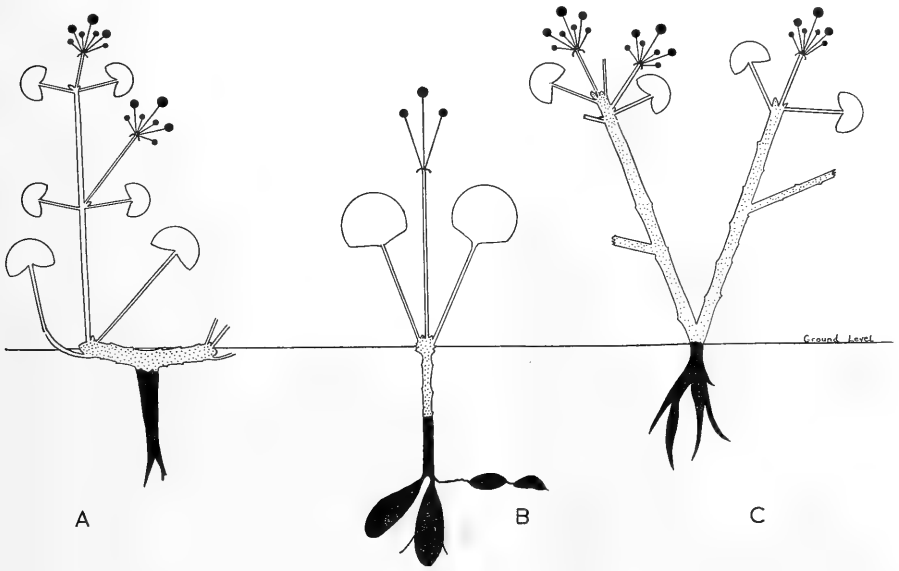

Fig. 1.—Habits of *Pelargonium* species. A. Groups I and II (in *P. drummondii* the perennial stems are more erect). B. Group IV. C. *P. capitatum*, *P.* × *asperum*, *P. domesticum*, etc. Roots and flowers, solid black; perennial stems, stippled; deciduous parts, white.

slightly different habit. The root system consists of a number of, or rarely one, root tubers attached to the main, slender root by very narrow roots. The basal perennial portion of the stem is sometimes elongated and narrow right at the base, but this seems to be a function of the habitat which is generally in rock crevices. The flowers in this group are borne on few-leaved deciduous stems. *P. havlasae* probably has much the same habit, although root tubers have not been observed on any of the specimens examined. The typical growth form of sect. *Pelargonium* is shown by the introduced species *P. capitatum* and *P.* × *asperum*, and others which are of less frequent occurrence. They do not show such an obvious differentiation of stem into perennial-basal and deciduous. The habit is definitely shrubby with the more or less leafless peduncles as the only consistently deciduous shoots. *P. drummondii* has a habit similar to that of the sect. *Peristera*, but the basal stems are larger and semi-succulent. Its sectional position is doubtful (see below).

Eichler (Blüthendiagramme) emphasizes the tendency towards cincinnal growth This is not only found in the vegetative development, but also in the inflorescence. This is a cymose umbel, commencing as a dichasium and eventually passing out into cincinni.

Odour is often a distinguishing character of *Pelargonium* species. Of the native species *P. inodorum* [*sic*] and *P. helmsii*, when making good growth, always have a characteristic odour. The single living collection of *P. littorale* which has been examined also had the same characteristic odour. The other indigenous species have an extremely weak odour which cannot be detected except when the plant is kept in an enclosed space for some time. The odour is not like that found in the other group.

Other characters that have provided the bases of this treatment are: (i) the number of fertile stamens, which for each species is variable within limits; (ii) the indumentum type; (iii) relative length of petals and sepals; (iv) colour of petals; (v) shape of sepals; (vi) length of calyx spur, which varies within quite wide limits in each species.

Taxonomy.

Pelargonium L'Her. ex Ait. (applying to species found in Australia only).

Annual or perennial herbs or low shrubs. *Leaves* simple or almost compound, dentate, lobed to deeply dissected, hairy with long simple hairs and short glandular ones or almost glabrous, often aromatic; margin sometimes undulate. *Flowers*

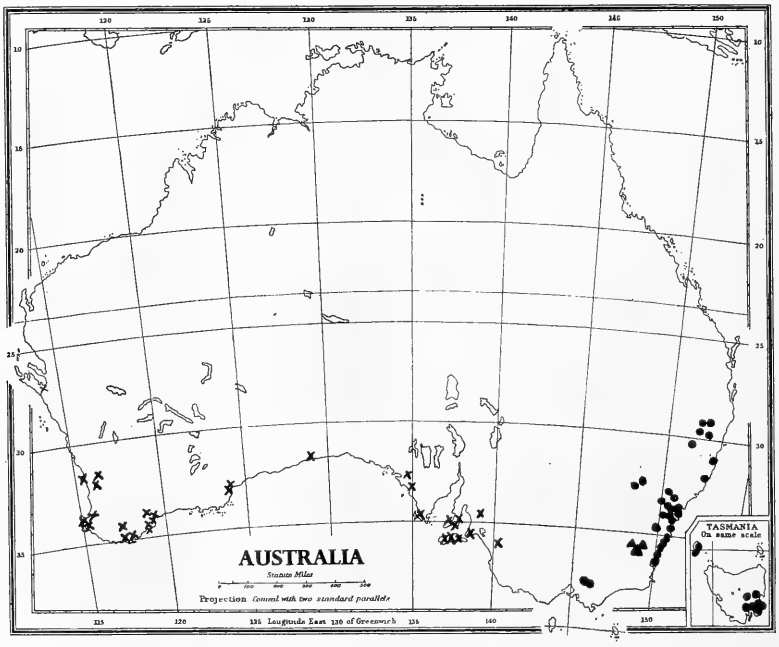

Fig. 2.—Map showing distribution of *Pelargonium* spp. *P. littorale*, ×; *P. helmsii*, ▲; *P. inodorum*, ●.

irregular, arranged in dichasia passing into monochasia in the ultimate branches and condensed into simple umbels; inflorescences terminal, themselves arranged in cincinni. *Sepals* 5, usually quincuncial, connate basally; posterior one with a spur or pocket adnate to the pedicel. *Petals* 5, usually convolute, free, often clawed, white to deep pink or purple; posterior ones usually larger and often marked with darker veins or spots. *Stamens* 10, 3–8 bearing anthers; filaments more or less lanceolate to elliptic, often irregularly united basally. *Ovary* 5-locular with two ascending ovules in each loculus inserted on the axis near the base, hirsute. *Fruit*, a schizocarp splitting into five mericarps each containing a single seed, open on the ventral suture and without a pronounced tuft of hairs on the "aril"; outer part of style persistent as a coiled awn terminal on the mericarp and with long hairs on the inner surface, glabrous

outside. *Rostrum* hirsute. *Seed* not distinctly reticulate, sometimes punctate and usually eventually released from the pericarp.

The groups indicated below are considered to have some taxonomic status, but until a complete revision of the genus is available that status must remain uncertain.

INDIGENOUS SPECIES.

GROUP I. Fertile stamens 3–5. Simple hairs patent, usually rigid. Nectary tube usually short. Petals usually scarcely longer than the calyx. Plants with characteristic odour. Sect. PERISTERA pro parte.

PELARGONIUM INODORUM Willd., *Enum. Plant. Hort. Reg. Bot. Berol.*, 702 (1809) et *Hort. Berol.*, t. 34 (1816).

Synonymy: *P. clandestinum* L'Her. ex DC., Prodr. 1: 660 (1824) nom. nud. *P. clandestinum* L'Her. ex Hook. f., *Flora N.Z.*, 41 (1853). *P. australe* Willd. var. *clandestinum* (L'Her. ex Hook. f.) Hook. f., *Handbook N.Z. Flora*, 37 (1864). *Erodium peristeroides* Turcz. in *Bull. Soc. Imp. Nat. Moscou*, 36: 592 (1863).

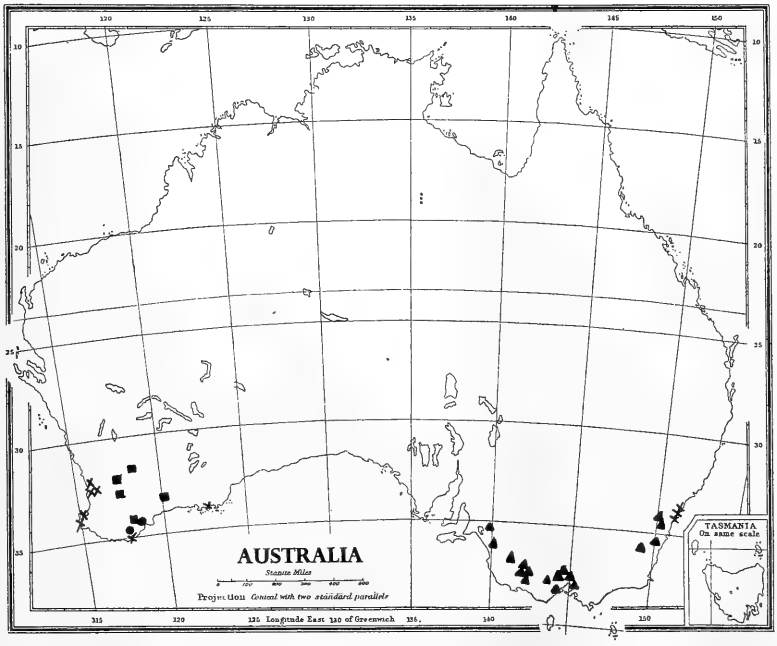

Fig. 3.—Map showing distribution of *Pelargonium* spp. *P. drummondii*, ●; *P. rodneyanum*, ▲; *P. havlasae*, ■; *P. capitatum* ×.

Weak, erect, annual or short-lived perennial, more or less odoriferous herbs with fleshy, tapering tap-roots. *Flowering* stems terete, 5–35 cm. tall, usually branched; simple hairs scattered over the surface, usually short but rarely long, patent and with shorter glandular hairs. *Leaves* opposite: laminae ovato-cordate, 0·8–4·0 cm. long, 0·8–5·0 cm. wide, often 5–7-lobed, crenate, scattered hairs present on both surfaces or upper surface quite glabrous; petioles slender, 1·0–4·0 (5·0) cm. long, slightly hairy; stipules brown, scarioso-membranous, deltoid, 2–4 mm. long, 1–3 mm. wide, sometimes drawn out into a short awn, ciliate; bracts brown, scarioso-membranous, narrow-lanceolate, *c.* 3 mm. long and 0·5–1 mm. wide, often shortly aristate, ciliate. *Peduncles* 3–8 cm. long. *Flowers* arranged in umbels of 3–14 flowers, sub-sessile or on slender pedicels up to 3 mm. long in flowering stage, lengthening to 2–10 mm. in fruiting stage. *Sepals* 5, united basally into a tube 1 mm. long or less; lobes broad-lanceolate or ovate, 2–4 mm. long (including a short mucro), 1·5–2·0 mm. wide, covered with usually short coarse

simple hairs with some very short glandular ones, membranous towards the margin; about as long as the mericarps and therefore not incurved around them in the fruiting stage; nectary tube 0·5–1 mm. long. *Petals* usually deep pink, ligulate; posterior ones 2–4 mm. long and 1 mm. wide, sometimes with darker veins; anterior ones smaller; all scarcely exceeding sepal lobes although sometimes half as long again. *Stamens* 10; filaments broadened below and irregularly united, 3–5 bearing anthers; others sterile, three of which are usually longer than the remaining ones. *Fruit*: mericarp pilose, obovoid, 2 mm. long, 1 mm. wide, terminated by a long awn; rostrum, 8–12 mm. long, upper glabrous region plus stigmatic lobes 1·0–1·5 mm. long. *Seeds* black or grey, striate, 1·5 mm. long, 1 mm. wide or less.

Range: Great Dividing Range and associated ranges extending onto the Western Slopes in Eastern Australia, Tasmania and New Zealand.

Habitat: Woodlands, mostly on acid rocks, but has been found on basaltic soils.

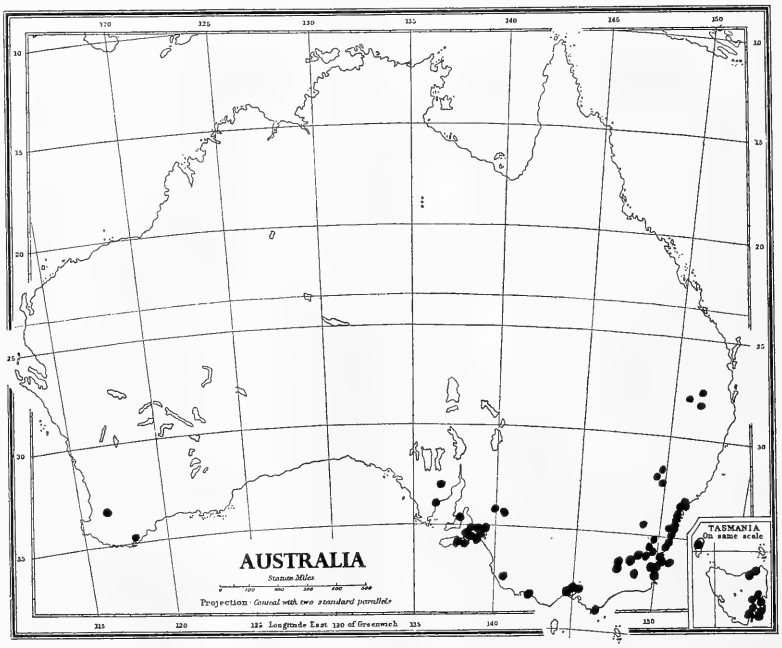

Fig. 4.—Map showing distribution of *Pelargonium* spp. *P. australe.*

Typification: Holotype: Willdenow no. 124, 35 (B). There is some confusion with regard to this name. Willdenow himself was partially responsible when he stated "Habitat ad Cap. b. Spei?" Sweet stated that this was an error, but his description and figure do not agree with Willdenow's, thus: Sweet: "Branches thickly clothed with soft villous hairs. . . . Leaves . . . thickly clothed on both sides with short villous hairs. . . ."; Willdenow: "Caules . . . glabriusculi. . . . Folia utrinque glabra."

Sweet's description and plate apply to an inland form of *P. australe.* He misapplied Willdenow's name. Many later authors perpetuated this mistake. Thus Bentham sank *P. inodorum* in *P. australe,* but the description that he gives for *P. australe* var. *erodioides* is more in keeping with Willdenow's diagnosis of *P. inodorum* than it is with the type of *P. erodioides* Hook. Knuth further confused the situation when he placed *P. erodioides* as a synonym of *P. inodorum.*

Photographs of the Holotype show that the Australian material included is almost certainly conspecific with it. Willdenow's diagnosis does not agree, strictly, in two respects: i.e., "corolla . . . calyce duplo majore" (it is uncommon to have such large

petals in this species) and "Filamenta decem, quorum duo brevissima sterilia septem vero apice filiformis antherifera" (none of the specimens known to this author have more than five fertile stamens, the usual condition is two very short and sterile, three or four long and sterile and four or five long and fertile: it is possible that Willdenow took some of the long sterile filaments to be fertile).

P. clandestinum Holotype: Banks, Nova Zealandia (L'Héritier n. 29) (GEN). This name was published by De Candolle, without description, as a synonym of *P. acugnaticum* Pet. Th. It was subsequently taken up by J. D. Hooker, citing "L'Héritier Geran. ined., A. Cunn. Prodr." (presumably a misprint for DC. Prodr.).

Erodium peristeroides Turcz. A series of *Syntypes*: Nova Zealandia Everard Home (KIEW photos SYD). Since writing the paper on *Erodium* (Carolin, 1958) material of these specimens has been forwarded from Kiew. There is little doubt that they belong to this species.

Discussion: Although *P. clandestinum* L'Her. ex DC was published as a synonym of *P. acugnaticum* Pet. Th., there appears to be no very close relationship between these two species. The indumentum and the calyx spur differ markedly (two specimens in N.S.W. and photographs of the type material in B.M. of *P. acugnaticum* were examined). Nor does there appear to be any substantial agreement between *P. inodorum* and *P. grossularioides* (L.) Ait., a South African species to which it has been compared several times. It would seem that no extra-Australian specimens should be referred to this species except those occurring in New Zealand. The specimens retained in the Dominion Museum, Wellington, N.Z., have all been examined and it seems that they are conspecific with the Australian material.

There is some variability within the species, particularly in Tasmania where forms with congested umbels occur. As intergrades with the typical form occur frequently it seems inadvisable to admit these variations to a definite category.

Selection of Specimens Examined: Queensland: Mt. Barney, Macpherson Range, E. Constable, 15.11.1952 (NSW24348); Mt. Ngun Ngun, Prof. R. Good, 6 Dec. 1956 (BRI 007603); Cunningham's Gap, F. M. Bailey (NSW42475). New South Wales: Morangarell, 30 m. from Temora, J. L. Boorman, 11.17 (NSW42504); Lookout Point. Gibraltar Range, E. F. Constable, 26 Apr. 1956 (NSW42508); Port Stephens, J. L. Boorman, 9.1911 (NSW42529); Narrabeen, H. Salassoo, no. 1025, 4.1.1953 (NSW2645); Jenolan Caves, W. F. Blakely, 11.99 (NSW42510); Concord, O. D. Evans, Nov. 1926 (SYD); Wentworthville, R. G. Tupper, 1933 (SYD); National Park, L. R. Fraser and J. W. Vickery, 11.1933 (SYD); Milton, R. H. Cambage, 22.12.11 (NSW42522); Big Badja, A. B. Costin, 1.1950 (NSW42507). Victoria: Dandenong Ranges, Dr. M., Jan. 1853 (MEL). Bass Strait: King's Island, Sm. Mcgowan (MEL); King's Island, W. S. Sayer, 11.87 (MEL). Tasmania: W. Archer, no locality (NSW42500 and 42699 pro parte); Circular Head, R. C. Gunn, nos. 1049 and 1842, 18.12.1837 (NSW42702).

Pelargonium helmsii, sp. nov.

Herbae perennes plerumque odoriferae. Caules floriferi teretes pilis brevissimis simplicibus glandulosisque vestiti. Lamina folii reniformis vel orbicularis 4·0–1·0 cm. longa, 4·5–1·0 cm. lata crenulata pilis brevissimis obtecta. Petiolus gracilis pilis brevissimis confertis vestita; stipulae deltoideo-lanceolatae; bractea ovato-lanceolatae. Flores 5–12 in umbella conferta dispositi. Sepala elliptico-oblonga 2–5 mm. longa 2–3 mm. lata fere obtusa pilis brevissimis dense vestita. Petala rosea ungulata. Stamina fecunda 4–5. Mericarpia pilosa 3 mm. longa 2 mm. lata, aristis 9–13 mm. longis. Semina nigra vel carnea.

Ascending odoriferous herbs up to 25 cm. tall with fleshy thickened tap-roots but not tuberous, and short perennial stems. *Flowering stems* terete, densely covered with very short simple and glandular hairs. *Leaves* opposite; lamina reniform-orbicular, 1·0–4·0 cm. long, 1·0–4·5 cm. wide, often shallowly lobed, crenate, covered with short scattered hairs; petioles slender, up to 13 cm. long, thickly covered with short hairs; stipules brown, deltoid or lanceolate, 4 mm. long, 3 mm. wide, scarioso-membranous; bracts ovate or broad-lanceolate, 2·5 mm. long, 1·5 mm. wide, scarioso-membranous,

acute, hairy, ciliate. *Peduncles* slender, 3–7 cm. long, pubescent. *Flowers* arranged in compact umbels of 5–12. *Pedicels* densely pubescent with very short, simple and glandular hairs, *c.* 2 mm. long. *Sepals* united basally into a short tube about 1 mm. long; lobes elliptico-oblong, 3–5 mm. long, 2–3 mm. wide, almost obtuse, thickly clothed with very short, simple and glandular hairs; spur less than 1 mm. long. *Petals* deep pink, more or less ungulate; posterior ones *c.* 8 mm. long and 3 mm. wide, sometimes with dark pink lines; anterior ones smaller. *Stamens* 10; filaments broadened and irregularly united basally, 4–5 fertile and bearing reniform anthers on short awns. *Fruit*: mericarp, hirsute, ovoid, *c.* 3 mm. long and 2 mm. wide, awn 9–13 mm. long, glabrous on outside but with long golden hairs on the inner surface; rostrum covered with simple hairs; glabrous upper region plus stigmatic lobes, *c.* 1 mm. long. Seeds smooth or minutely striate, 2·5 mm. long, 1 mm. wide, black or dark grey.

Range: High altitudes in N.S.W.

Habitat: Sub-alpine woodland (*Eucalyptus niphophila* woodland).

Typification: Holotype: Mt. Kosciusko, R. Helms, February, 1893 (NSW42523).

Named after the collector of the specimens which has been selected as the holotype.

Discussion: A species which is quite distinct from others, but which, apparently, has a very restricted distribution, being confined to the Kosciusko plateau. It is, moreover, not common in its native habitat.

Specimens Examined: New South Wales: Mt. Kosciusko, R. Helms, 1901 (NSW 425245); Mt. Kosciusko district, C. Skottsberg and A. B. Costin, 9.3.1947 (NSW42524); Snowy River below Charlotte's Pass, S. McKay, 21.1.1958 (SYD); White's River Hut near Guthega, R. Carolin, no. 794 (SYD).

Pelargonium littorale Hügel, *Bot. Arch.*, t. 5 (1837) et ex Endl. in *Enum. Plant. Hügel.*, 14 (1837).

Synonymy: *P. stenanthum* Turcz. in *Bull. Soc. Imp. Nat. Moscou*, 31: 419 (1858). *P. crinitum* Nees in Lehm., *Pl. Preiss.*, 1: 163 (1944) non Harv. et Sond. (1859–60). *P. crinitum* var. *congestum* Nees. in Lehm., *loc. cit.*

Erect or semi-prostrate, perennial, odoriferous herbs with fleshy tap-roots but not tuberous. *Flowering stems* angular or terete, up to 35 cm. tall, covered with scattered, long, spreading, villous hairs and short glandular ones. *Leaves* opposite; lamina ovato-cordate, slightly 5–7-lobed, crenate, (1·0) 2·0–4·0 cm. long, 1·0–3·0 (5·0) cm. wide, sparsely hairy particularly on the veins; petioles slender, 1·0–7·0 cm. long, sparsely villous-patent hairy; stipules brown, scarioso-membranous, ovate to broad-deltoid, up to 4 mm. long and 3 mm. wide, sparsely hairy, ciliate; bracts lanceolate to narrow-ovate, 4 mm. long and 1·5 mm. wide, ciliate. *Peduncles* 2–8 cm. long. *Flowers* arranged in umbels of 2–5 (7); pedicels slender, up to 2 cm. long in the flowering stage, often further elongating in the fruiting stage. *Sepals* united basally into a short tube *c.* 1 mm. long; lobes lanceolate or narrow-elliptic, 3–4 mm. long, 1·5–2·0 mm. wide, acute, sparsely covered with long, patent-villous hairs and minute glandular ones, membranous at margin, distinctly larger than the mericarps and incurved over them in the fruiting stage; nectary spur 1–3·5 mm. long. *Petals* usually deep pink; posterior ones broad-oblanceolate, scarcely ungulate, *c.* 6 mm. long and 2 mm. wide; anterior ones narrower. *Stamens* 10; filaments broadened and irregularly united below, 4–5 fertile, about 4 mm. long and bearing shortly oblong anthers. *Fruit*: mericarp hirsute, oblanceolate, 3 mm. long, 1 mm. wide, terminated by a long awn which is glabrous on the outer surface and bears long, white to golden hairs on the inner surface; rostrum 1·5–1·8 mm. long, hirsute; upper glabrous region plus stigmatic lobes *c.* 2 mm. long. *Seeds* brown to black, very minutely striate, *c.* 1·5 mm. long and 1 mm. wide or less.

Range: Western Australia and into South Australia.

Habitat: In fairly dry areas and often near the sea.

Typification: *Lectotype*: Swan River, Hügel (no. 44) (W photo SYD). The Director of the Botany Dept. of the Naturhistorische Museum Wien has kindly forwarded the pertinent material housed in his Institute. There are two sheets labelled "Swan River Hügel", neither of which, however, bears a number. The more complete

of these two is named "P. australe Willd. Endl. ipse" and the other is labelled "P. littorale Hügel". The former is fairly close to the type of *P. crinitum* Nees in Lehm., which is here reduced to synonym (see below). The latter corresponds more closely with Hügel's description and that supplemented by Endlicher, and to the illustration supplied in *Bot. Arch.*, particularly with respect to the length of the nectary spur. The specimen, however, is not exactly equivalent to this illustration and there is no evidence that it was the only element used in drawing up the diagnosis. It must, therefore, be selected as the lectotype. The shorter latin diagnosis accompanying the illustration in *Bot. Arch.* is followed by "Hügel msc." and can therefore be attributed to him. The longer latin diagnosis is attributed to "Endlicher msc.". Both are repeated in *Enum. Pl. Hügel* and the name is attributed there to Hügel. It would appear, then, that the original description is certainly Hügel's and that he should be recognized as the author of the name.

P. crinitum Nees in Lehm. *Syntypes*: In arenosis apertis prope oppidulum Freemantle, Decembri a. 1838, Preiss no. 1905: In solo sublimoso districtus Sussex, Decembri 1839, Preiss no. 1906. The material used by Nees in drawing up his original description has not been located, but specimens of these numbers have been forwarded from GEN (photos SYD) and a photograph of Preiss no. 1906 housed in S has been examined. This material falls within the limits of variation of *P. littorale* as defined above, although the nectary spur is rather longer than usual. Nees states: "A pelargonio littorali Endl. in Hüg. differt caulibus procumbentibus nec erectis, valde angulosis nec teretibus." There would appear to be all gradations between these contrasting characters and the best course seems to be to reduce *P. crinitum* to a synonym of *P. littorale*.

P. crinitum var. *congestum* Nees in Lehm. *Holotype*: Preiss no. 1903. Material of this number has been forwarded from LE, although the holotype itself has not been traced. Preiss no. 1901 is mounted on the same sheet. The specimens (6) included under no. 1903 show considerable variation and, in fact, represent the range of variability to be found in *P. littorale*. The two specimens on the extreme left-hand side (to the observer) correspond most closely to the type description (photo SYD). A photograph has also been forwarded from S and this sheet is rather more uniform, consisting of only two specimens. Once again there appear to be all gradations between the non-congested and the congested umbels; indeed to some extent these are represented on the Leningrad sheet. It does not seem advisable to admit this variety at present.

P. stenanthum Turcz. *Holotype*: Drummond Coll. V. no. 193 (KIEW photo SYD). *Isotypes*: K, GEN photos SYD. The specimen housed in Geneva was kindly forwarded for examination. It agrees quite closely with Preiss's specimens referred to *P. crinitum* by Nees as does the type description.

Selection of Specimens Examined: South Australia: Myponga, J. M. Black, 11.1906 (NSW42476); Kangaroo Island, J. Staer (NSW42479); Thistle Island, Spencer Gulf. J. H. Maiden, Jan. 1907 (NSW42477); Eyre Peninsula, Colton, near Venus Bay, Herb R. Tate, Oct. 1882 (AD95813034); Southern Yorke Peninsula, between Corny Point and Cape Spencer, Hj. Eichler, no. 13977, 26.9.1957 (AD95751017); Naracoorte, E. H. Ising, 25.10.1934 (AD95812074); Encounter Bay, J. B. Cleland, Jan. 1924 (AD95813045); Eucla, J. D. Batt, 1886 (MEL). Western Australia: Rottnest Island, G. M. Starr, nos. 17 and 53, 15.4.1956 (WA); Mt. Randall, Darling Range, C. A. Gardner, Aug. 1933 (WA); Chittering, R. D. Royce, no. 4717, Dec. 1952 (WA); Middleton Beach, King George's Sound, B. T. Goadby, no. 296, Dec. 1900 (NSW40494).

Group II. Fertile stamens 7–8, rarely 6. Simple hairs villous, pubescent or almost quite absent, not patent. Nectary spur usually quite distinct. Petals at least twice as long as sepals. Root non-tuberous. Sect. Peristera pro parte.

Pelargonium australe Willd., *Spec. Plant.*, 3: 675 (1800).

Synonymy: *P. glomeratum* (Andr.) Jacq., *Ec. Plant. Rar.*, 146 (1816). *P. erodioides* Hook. in *Journ. Bot.*, 1: 252 (1834). *Geranium glomeratum* Andr. *Geraniums*, vol. 2:

87 (1805). *Geraniospermum australe* (Willd.) O. Ktze., *Rev. Gen.*, 1: 94 (1891). *Unrecognized varieties*: *P. australe* var. *glabrata* Hook. f., *loc. cit.* *Misapplied names*: *P. inodorum* sec, Sweet, *Geraniaceae*, vol. 1 (1820–22).

Herbaceous scarcely odoriferous perennials with tough, more or less fleshy, but not tuberous, tap-root and short, often rhizomatous, perennial stems. *Flowering stems* terete, erect to semi-prostrate, up to 50 cm. long, branching, covered with long or short, soft villous hairs or pubescent or rarely almost glabrous, always with some minute glandular hairs. *Leaves* opposite; laminae almost orbicular to ovate, sometimes shallowly undulate, 5–7-lobed, sometimes obscurely so, crenate, pubescent or almost glabrous, 2·0–9·0 cm. long, 2·0–8·0 cm. wide or even larger; petioles up to 13 cm. long, villous to pubescent or glabrous; stipules deltoid, 3–4 mm. long and 3 mm. wide, acute, membranous, often hairy; bracts narrow-deltoid to lanceolate, *c.* 3 mm. long and 0·5 mm. wide, villous or pubescent especially on the thickened mid-rib or glabrous. *Peduncles* 3–10 cm. long, villous to pubescent and bearing an umbel of 4–12 flowers. *Pedicels* 0·2–1·5 cm. long (rarely longer) or flowers sub-sessile, often elongating during the fruiting stages, villous pubescent or almost glabrous. *Sepals* 5, united basally into a short tube; lobes lanceolate to narrow-oblong, 4–7 mm. long, 2–3·5 mm. wide, acute, villous pubescent or glabrous but almost always with numerous minute glandular hairs; nectary spur 1–8 mm. long. *Petals* 5, longer than the sepals, pink to white; posterior ones oblanceolate to obovate ungulate, *c.* 8 mm. long and 4–6 mm. wide, veins deep pink and often with deep pink spots; anterior ones narrow. *Stamens* 10; filaments broadened and irregularly united below, 7–8 fertile (rarely only 6) and bearing anthers; anthers oblong; pollen yellow to white. *Fruit*: mericarp villous to pubescent, ovoid, *c.* 2·5 mm. long and 1 mm. wide; awn 6–12 mm. long; rostrum covered with simple and glandular hairs, glabrous upper region plus stigmatic lobes 2–3 mm. long. *Seeds* oblong, black, or grey, very minutely pitted or smooth.

Range: Southern Australia, both inland and coastal, and into Tasmania.

Habitat: Coastal sand-dunes and acid, often granitic, rock outcrops inland.

Typification: *Holotype*: Willdenow no. 12478, sheet 1 (B photo SYD). The material on this sheet seems to be quite homogeneous.

Geranium glomeratum Andr. The type would appear to be the illustration accompanying the type description. The figure and Andrews' statement, ". . . known under the title of Botany Bay Geranium", indicates that the specimen originated from coastal sand-dunes. Sweet's figure of *P. australe* corresponds quite closely to the one under consideration.

P. australe var. *α major* Hook. f. "var. *α*" would seem to imply that Hooker regarded this as the type variety. He cites Gunn 61 and 787 (K photo SYD) which differ little from Willdenow's holotype.

P. australe var. *β glabrata* Hook. f. *Holotype*: Gunn. 658 (K). Until more is known about the inheritance of the "glabrous" condition it is advisable not to recognize this variety.

P. erodioides Hook. *Holotypes*: Mr. Lawrence, Van Dns Land 1833, no. 325 (K photo SYD). This specimen is mounted on the same sheet as some collections made by Gunn. It apparently represents inland forms of the species which this author is unwilling to accept as separate species at present (see discussion).

Discussion: This is an extremely variable species as constituted above, but it seems impossible, as yet, to recognize any constant, sub-specific taxa. The characters that are so variable are indumentum length, pedicel length, calyx spur length and habit. No constant correlation of differences has been noted. There seems little doubt that there are ecological races within this species as cultivation under garden conditions has shown no divergence from the parent field characters. Moreover, under such conditions, there has been quite distinct selective death of the coastal forms in normal garden conditions and the inland forms in very sandy soil. These experiments and breeding experiments are being continued. The forms from Eyre's Peninsula and associated islands and the Recherche archipelago may eventually prove to be distinctive enough to be admitted to a definite status.

Selected Specimens Examined: QUEENSLAND: Granite Hill, Darling Downs, S. L. Everist and L. J. Webb, no. 1366, 23.11.1946 (BRI007605); Stanthorpe, H. Wright, Dec. 1916 (BRI007614). NEW SOUTH WALES: Warrumbungle Ranges, G. W. Althofer, 23.3.1947 (NSW42533); Coree, Queanbeyan, R. H. Cambage, no. 3314, 9.12.11 (NSW26539); Upper Tumut River nr. Kiandra, Whitefield, 3.1924 (NSW42532); Boree, H. S. McKee, no. 534, 4.11.52 (SYD); Kosciusko, J. McLuckie and A. H. K. Petrie, 1.1925 (SYD); The Gib, Bowral, R. H. Cambage, no. 1468, 10.2.1906 (SYD); N. Coast. L. Leichardt, no, 168, 6.11.1842 (NSW42416); Curl Curl, T. G. B. Osborn, 5.1928 (SYD); Garie Beach, National Park, R. Carolin, no. 441, 18.3.1958 (SYD); Lake Conjola, G. L. Rodway, 26 Feb. 1933 (NSW42429); Brush Island, F. A. Rodway, 5 Sept. 37 (NSW42420). VICTORIA: Mt. Buffalo, H. C. E. Stewart, 6 Jan. 1950 (BRI007604); Enoch Point, J. George, 1882 (MEL); Wilson's Promontory, Musgrave (MEL). BASS STRAIT: King's Island, C. French, 11.87 (MEL); Rock Island, C. E. Lord (HO). TASMANIA: Lyell Highway, 64 miles from Hobart, R. Carolin, no. 1363, 16.1.1960 (SYD); Roaring Beach, N.E. of Nubeena, Tasman Peninsula, R. Carolin, no. 1805, 9.2.1960 (SYD). SOUTH AUSTRALIA: Waikerie, J. B. Cleland, 30.11.1913 (AD95830022); Murray Bridge, W. Ham, 26.3.1921 (AD95816006); Encounter Bay, J. B. Cleland, Jan. 1924 (AD95830019); Largs Bay, Herb. J. M. Black, 22.11.1916 (AD95813040); Ravine des Casoars, Kangaroo Island, J. B. Cleland, 2.2.1950 (AD95830006); Gawler Ranges, Dr. Sullivan (MEL). WESTERN AUSTRALIA: Gilakin Rock, C. V. Malcolm, 24.10.1959 (W.A.).

PELARGONIUM DRUMMONDII Turcz., in *Bull. Soc. Imp. Nat. Moscou*, 31: 421 (1858).

Ascending, very weakly odoriferous perennial with more or less erect semi-succulent sub-ligneous, pubescent perennial stems which are covered in the upper parts with persistent stipules and about 1 cm. wide. *Flowering* stems obscurely angled or terete, covered with a soft spreading pubescence often interspersed with longer villous hairs, *c.* 30 cm. tall and up to 4 mm. wide. Basal leaves apparently alternate; lamina cordate-reniform, obscurely 5-lobed, up to 4 cm. wide and 3 cm. long, crenate, pubescent on both surfaces: petioles pubescent, 10–15 cm. long, often more or less persistent. Leaves on the flowering stems similar but mostly opposite and with shorter petioles; stipules brown, scariose, deltoid-acuminate, 5–10 mm. long, 3–5 mm. wide, somewhat pubescent; bracts brown-yellow tinged with pink with a distinct mid-rib, lanceolate-deltoid, *c.* 5 mm. long and 1·5 mm. wide, pubescent, ciliate. *Peduncles* pubescent, up to 6 cm. long, bearing an umbel of 3–8 flowers each on a slender pedicel 8–12 mm. long. *Sepals* united basally into a tube *c.* 1·5 mm. long, covered with soft spreading villous hairs; lobes narrow-elliptic to elliptic, *c.* 5 mm. long and 2 mm. wide, acute, or with a very short mucro and membranous towards the margin; nectar spur 5 mm. long to almost obsolete. *Petals* pink; posterior ones obovate, ungulate, 14 mm. long, 12 mm. wide, with dark lines and spots marking them; anterior ones without darker lines and spots and usually narrower, 12 mm. long and 4 mm. wide. *Stamens* 10; filaments broadened and irregularly united below, 7 (4 long and 3 short) bearing anthers and somewhat longer than the others; pollen orange. *Fruit*: mericarp obovoid, villous; rostrum *c.* 14 mm. long, villous hairs ceasing very abruptly at the base of the upper glabrous region which, with the stigmatic lobes, is *c.* 4 mm. long. *Seeds* grey.

Range: *Western Australia*: Porongorup Ranges to Mt. Melville.

Habitat: Amongst granite boulders.

Typification: *Holotype*: Drummond coll. V 191 (KIEW photo SYD), isotypes K (photo SYD), MEL, NSW. Hooker misapplied this name, Hook. f., *Curt. Bot. Mag.*, ser. 3, 50: 7346 (1894), to *P. capitatum* (see below) and Knuth cites it as a synonym of both *P. australe* and *P. capitatum*. The specimen at Kew is the most complete; descriptions supplied by that institute show that the scraps housed in Sydney and Melbourne are conspecific with it. In general the petals of these specimens are pink and not "(in sicco) alba" as described by Turczaninow. The photographs supplied by Kiew leave little doubt that the collection was an homogeneous one.

Discussion: The species is clearly different from *P. capitatum*. The semi-succulent main stems, the softer pubescence, the pedicillate flowers, the shape of the bracts and

stipules all serve to separate them from each other. In addition it would seem that *P. drummondii* is not a species of the coastal sand-dunes like *P. capitatum*, but occurs further inland in rocky country. Turczaninow stated that it belongs to the "*Alchimiloideae*", a subsection of the section *Eumorpha* according to Knuth. Its affinities may indeed lie here or in sect. *Cortusina*, although its relationships with *P. australe* seem to be quite close. The author has been unable to relate these specimens to any extra-Australian species to date. It would seem, in fact, that the species is distinct. Well-located specimens are the result of only a few collections, from two ranges of hills, the specimens being well established away from habitation. In short it shows the distributional characteristics of a restricted species and not of an introduction which would usually be rather tenuously established near habitation or aggressively expansive. The final solution of the problem may well have to await a full-scale monograph on the genus.

Specimens Examined: Western Australia: Nancy's Peak, Porongorup Ranges, B. G. Briggs, 10.10.1960 (NSW52439 et SYD); Summit of Nancy Peak, Porongorup Ranges, R. D. Royce, no. 6118, 29 Oct. 1959 (WA); Mt. Melville, C. A. Gardner, Albany, Feb. 1939 (WA).

N.B. Mr. J. H. Willis of the State Herbarium of Victoria has kindly sent me some interesting notes on Drummond's various collections. From this it would appear to be highly probable that he collected from one of the areas mentioned in "Specimens Examined".

Group III. Roots tuberous. Fertile stamens 6–8. Simple hairs absent or if present then scarcely patent. Nectary-tube long. Petals much longer than sepals. Sect. Polyactium.

Pelargonium rodneyanum Mitch. ex Lindl. in Mitch., *Three exped.*, II: 44 (1839).

Synonymy: *Geraniospermum rodneyanum* (Mitch. ex Lindl.) O. Ktze., *Rev. Gen.*, 1: 94 (1891).

Erect perennials with basal perennial stems, the lower part of which may be a narrow vertical rhizome expanding above, and with a number of brown, red or whitish tuberous swellings on the roots sometimes arranged in chains. *Flowering stems* terete. 8–35 cm. tall, usually simple or once branched, covered with short glandular hairs, occasionally with some long simple hairs scattered over the surface. *Leaves* mostly on the basal stems, few on the flowering stems, opposite; laminae ovate-cordate or ovate, 2–4 cm. long, 1·5–4·0 (5·0) cm. wide, sometimes slightly 5–7-lobed, crenate, a few scattered hairs present on the veins; petioles slender, (1·5) 7·0 (10·0) cm. long; stipules yellow, scarioso-membranous, ovate to elliptic, 3–4 mm. long, 2–3 mm. wide, usually obtuse but sometimes acute, glandular-hairy, ciliate on the margin; bracts usually deltoid, occasionally lanceolate, 2–3 mm. long, 1–1·5 mm. wide, otherwise similar to the stipules. *Peduncles* often derived from the base of the plant. *Flowers*: 2–7 per umbel; pedicels slender, 1·3–2·2 cm. long, puberulent and rarely with a few spreading villous hairs. *Sepals* deep pink, united basally into a tube *c.* 1 mm. long; lobes lanceolate to narrow-elliptic, 3–5 mm. long, 1–3 mm. wide, acute, often with small mucro, puberulent with glandular hairs and a few short simple hairs which are sometimes quite absent; nectary spur (3)5–9 mm. long. *Petals* deep pink, very unequal; posterior ones obovate, 1·3–1·7 cm. long, 6–8 mm. wide, ungulate and with darker streaks and spots; anterior ones narrow sub-ligulate. *Stamens* 10; filaments broadened and irregularly united below, 7–8 fertile, longer than the others and bearing oblong anthers. *Fruit*: mericarp pilose, oblanceolate, 2 mm. long, 1 mm. wide, terminated by a long awn; rostrum 1·6–2·0 cm. long, hirsute, upper glabrous region plus stigmatic lobes *c.* 4 mm. long. *Seeds* dark grey, minutely striate, 1·5 mm. long, 1·0 mm. wide.

Range: South-eastern Australia and into South Australia.

Habitat: Usually amongst granitic outcrops and often growing from the clefts between the rocks.

Typification: *Holotype*: Major Mitchell's Expedition 1836, 21 June, no. 184 (CANTAB photo NSW).

Discussion: A fairly distinct species, although its relationships with the other groups are by no means clear as yet.

Selected Specimens Examined: New South Wales: Bungonia Lookout, nr. caves, E. F. Constable, 23 Jan. 1956 (NSW36703); Endrick River near Nerriga, F. A. Rodway, no. 995, 27 Nov. 1932 (NSW42455); Eucumbeen, W. H. Dillon, 1893 (MEL). Victoria: Grampian Mt., Victoria, E. H. Ising, no. 2321, 6 Jan. 1927 (AD95730012); Mt. Macedon, R. H. Cambage, 11.1.13 (NSW42463). South Australia: Lucindale, E. H. Ising, 13.12.1934 (AD95812075); Cave Range, west of Penda, Herb. Tate, 25.11.1882 (AD 95813028); 7 miles south of Coonalpyn, M. C. R. Sharrod, sine date (SYD).

Pelargonium havlasae Domin in *Vestn. Krel. Ces. Spolek*, Nauk 11: 49 (1923).

Erect herbs often with a thin erect rhizome terminated by the perennial basal stems. *Flowering stems* up to 15 cm. tall with a few short simple hairs and some minute glandular ones scattered over the surface, usually simple and terminated by a few-flowered umbel. *Leaves* mostly attached to the perennial stems; laminae ovato-cordate, 1·0–1·8 cm. long, 1·5–2·2 cm. wide, obscurely 5–7-lobed, crenate, sparsely hairy or sub-glabrous: petioles slender, 1·0–8·0 cm. long, sparsely hairy: stipules ovate, 3 mm. long, 2 mm. wide, acute, membranous, brown, scarcely hirsute or ciliate: bracts broad-lanceolate, *c.* 3 mm. long and 1·5 mm. wide, otherwise similar to the stipules. *Peduncles* mostly springing from the base of the plant and up to 15 cm. long. *Flowers*: 4 per umbel or very rarely solitary; pedicels slender, 15–30 mm. long in flowering stages, pubescent or puberulent with glandular hairs and some short simple ones. *Sepals* united basally into a tube *c.* 1 mm. long; lobes lanceolate or narrow-oblong, *c.* 4 mm. long and 2 mm. wide, acute, puberulent or rarely hirsute with short simple hairs and denser glandular hairs, membranous towards the margin; nectary spur 1–6 mm. long. *Petals* white or very pale pink with deeper veins; posterior ones obovate, 7–10 mm. long, 4–5 mm. wide, ungulate; anterior ones narrower and usually without the deeper veins. *Stamens* 10; filaments broadened and irregularly united below, 6–7 fertile, *c.* 6 mm. long, and somewhat longer than the rest; anthers oblong. *Fruit*: mericarp oblanceolate, *c.* 2·5 mm. long and 1 mm. wide, villous; rostrum covered with simple and glandular hairs; upper glabrous region plus stigmatic lobes 3–4 mm. long. *Seeds* not seen.

Range: Southern parts of Western Australia.

Habitat: Unrecorded, and so far not observed in the field by this author.

Typification: *Holotype*: A. A. Dorrien-Smith, W.A. (K).

Discussion: This species must be quite closely allied to *P. rodneyanum*, although no one has so far stated that it has tuberous roots. Field observations are badly needed on this species.

Selected Specimens Examined: Western Australia: Near Wagin, C. A. Gardner, no. 6474, 8 Oct. 1942 (WA); District Stirling, C. A. Gardner, no. 2087, 30 Sept. 1928 (WA); Beatley, R. Helms, Sept. 98 (NSW42470); Cowcowning, Max Koch, no. 1174, Sept. 1904 (AD95813014); Drummond, no. 30 (MEL) (collection uncertain).

Introduced Species. (The descriptions given below refer to Australian material only and are not intended to be complete but merely diagnostic.)

All these species, but for *P. fragrans*, are grouped in sect. *Pelargium* by Knuth. *P. fragrans* he places in sect. *Cortusina*.

Pelargonium capitatum (L.) Ait., *Hort. Kew*, 2: 425 (1789).

Synonymy: J. D. Hooker misapplied the name *P. drummondii* Turcz. to this species.

Straggling, odoriferous, shrubby, perennials up to 1 metre tall. Stems terete and covered with soft spreading villous hairs. *Leaves* alternate or opposite: laminae ovato-cordate in outline, 2–8 cm. long, 2–8 cm. wide, deeply 3–7-lobed, dentate, undulate, villous, petioles 2–6 cm. long, villous; stipules ovato-acuminate or acute, usually quite broad, *c.* 8 mm. long: bracts elliptic to oblong, *c.* 6 mm. long and 2·5 mm. wide, otherwise similar to the stipules. *Stamens* 10; filaments broadened and irregularly united below, pink above, about seven fertile and somewhat longer than the others; pollen

orange. *Fruit* villous; mericarp oblanceolate, 5 mm. long; awn *c.* 2 mm. long; upper glabrous part of villous rostrum plus stigmatic lobes *c.* 7 mm. long. *Seeds* brown reticulo-striate.

Range: A native of the Cape Peninsula, South Africa, introduced very early in the history of colonization, probably in shipping ballast, and now well established at various points around the coast.

Habitat: Sand-dunes.

J. D. Hooker's figure and description, *Curt. Bot. Mag.*, ser. 3, 50: 7346 (1894), of *P. drummondii* Turcz. leave little doubt that he was, in fact, dealing with *P. capitatum* in spite of his insistence on the similarities with *P. australe.* "Undershrubs 2 ft. . . . clothed with a soft more or less glandular fragrant pubescence, branches robust" is particularly significant. (Also see above under *P. drummondii.*)

Selection of Specimens Examined: Western Australia: Sea coast at Swanbourne, P. R. Gorrie, July 1938 (WA); Garden Island, March, 1941, B. T. Goadby (WA); Perth, R. Helms, 2.11.98 (NSW42440). New South Wales: Kurnell, R. Carolin, no. 530, 28.9.1958 (SYD); Cape Solander, L. A. S. Johnson, 20.10.1945 (NSW42435).

Pelargonium × asperum Ehr. ex Willd., *Sp. Plant.*, ed. 4, 3: 678 (1800).

Synonymy: (from Moore, 1955) *P. roseum* Willd. ex Spreng. non Ehr. nec (Andr.) Ait. *P. rosodorum* Hoffmansegg. *P. graveolens* L'Her. ex Ait. × *P. radens* H. E. Moore.

Shrubs up to 1 metre tall with a characteristic odour. *Stems* terete, erect, *c.* 6 mm. thick, covered with harsh hairs. *Leaves* alternate or opposite: laminae ovate in outline, margins recurved, up to 7 cm. long and 6 cm. wide, deeply more or less pinnately dissected into 5–7 lobes, dentate, hirsute with harsh hairs, aromatic, paler on the undersurface, petioles 4–10 cm. long, hirsute; stipules membranous-scariose ovate or deltoid, 7 mm. long, 4 mm. wide, ciliate; bracts lanceolate to narrow-ovate. *Peduncles* 3–6 cm. long bearing an umbel of 5–10 flowers. *Flowers* subsessile or with pedicels up to 6 mm. long. *Sepals* lanceolate to narrow-elliptic, 6–9 mm. long, 2–4 mm. wide, united basally into a very short tube, hirsute, membranous towards the margin and sometimes with a short mucro; nectary spur 2–4 mm. long. *Petals* pink, oblanceolate to obovate; posterior ones obovate, ungulate, 1–2 cm. long and about 5 mm. wide, marked with pink to purple lines and/or spots; anterior ones smaller and with smaller dark markings. *Stamens* 10; filaments broadened below, about six fertile bearing oblong anthers and somewhat longer than the others; pollen orange. *Fruit*: mericarp ovoid to oblanceolate with a terminal awn bearing harsh brown hairs on the inner surface; rostrum hirsute, upper glabrous part plus stigmatic lobes 5–7 mm. long. *Seeds* dark grey, ovoid, seed-set is usually poor when compared with the indigenous species.

Range: Introduced from the Mediterranean regions of Europe where it is cultivated for its volatile oils used in perfumes. Now well established around some cities and towns in southern Australia.

Habitat: Open places.

Selected Specimens Examined: New South Wales: Castle Crag, Sydney, H. S. McKee, July 1950 (SYD); Woy Woy, H. S. McKee, no. 6694, 25.12.1958 (SYD). South Australia: Mount Lofty Range, Victor Harbour and Happy Valley, J. M. Black (AD95813044); south of Ashville, 25 km. north of Meningie, M. C. Sharrad, no. 327, 3.11.1959 (SYD).

Discussion: The specimens previously referred to *P. graveolens* L'Her. ex Ait, are probably none of them strictly typical of that species. Moore (1955) provides a key to the cultivated species of *Pelargonium* and in it he distinguishes between *P. graveolens* and *P. radens* thus: "17. Margins of leaves rolled under, the lobes very deeply divided into narrow segments with short, stiff, rasp-like hairs on both surfaces . . . *P. radens.* 17* Margin of the leaves not rolled under, the lobes rather shallowly toothed with soft, slender hairs on both surfaces . . . *P. graveolens.*"

All the specimens examined which originated from naturalized localities in Australia fall between these two extremes. All possess more or less harsh hairs, all have leaf-margins rolled under to some degree and the dissection of the leaves is

extremely variable. Earlier in his treatment Moore discusses the position of *P.* × *asperum*. This, he states, is probably a hybrid between the two species under discussion. The plate which he reproduces from Roth. (1787) is not clear enough to distinguish the important points. He notes that the hybrid is very variable falling between the extremes of the two parents. It would appear that all the Australian material should be referred here.

PELARGONIUM DOMESTICUM L. H. Bailey. The very variable group of cultivated "show" Pelargonia covered by this name has become naturalized in a number of places. The nomenclature is extremely complex and it is proposed that this name be maintained for the time being.

Selected Specimens Examined: WESTERN AUSTRALIA: Yoongarallup, Bussleton district, R. D. Royce, no. 3899, 19 Oct. 1952 (WA). SOUTH AUSTRALIA: Near Finnis *ca.* 60 km. south of Adelaide, J. B. Cleland, 11.10.1949 (AD95829079). NEW SOUTH WALES: La Perouse, D. Kilgannon, 13.9.1949 (SYD). TASMANIA: Eaglehawk Neck, Tasman Peninsula, R. Carolin, no. 1817, 9.2.1960 (SYD).

PELARGONIUM FRAGRANS Willd. has been collected once from a naturalized (?) locality. It is a native of South Africa and is cultivated for its volatile oil.

Key to the Species.

1. Leaves deeply pinnately or palmately dissected; hairs harsh ..... *P.* × *asperum* Ehr. ex Willd.
1.* Leaves shallowly lobed or almost entire; hairs villous to pubescent or puberulent, soft.
2. Lobes of the leaf acute ..... *P.* × *domesticum* Bailey.
2.* Lobes of the leaf obtuse.
3. Fertile stamens 3-5 (rarely 6); perennial stems short and not succulent.
4. Hairs on the calyx short and coarse, petals seldom much exceeding sepals.
5. Hairs on the calyx dense; sepals obtuse ..... *P. helmsii* Carolin.
5.* Hairs on the calyx scattered; sepals acute ..... *P. inodorum* Willd.
4.* Hairs on the calyx long and patent, villous ..... *P. littorale* Hüg.
3.* Fertile stamens 6-8; very rarely 5 and then perennial stems semi-succulent.
6. Basal (perennial) stems short, thick, semi-succulent ..... *P. drummondii* Turcz.
6.* Basal stems not semi-succulent or plants shrubby.
7. Roots not tuberous; nectary spur seldom as long as calyx-lobes.
8. Bracts broad-ovate; habit shrubby (Fig. 1) ..... *P. capitatum* (L.) Ait.
8.* Bracts lanceolate; habit as in Fig. 1 ..... *P. australe* Willd.
7.* Roots tuberous; calyx spur as long as or longer than calyx lobes.
9. Corolla white to very pale pink ..... *P. havlasae* Domin.
9.* Corolla pink to pale purple ..... *P. rodneyanum* Mitch. ex Lindl. in Mitch.

GENERAL DISCUSSION.

This study has been made with reference to Australian species only. The sections of the genus into which other authors have placed these species are indicated, although it seems that a new critical analysis of these sections is required. The groups which have been indicated above are considered to be systematic units, the actual category should remain in abeyance until a complete monograph is attempted. Groups I and II show some affinities with *P. grossularioides* (L.) Ait., a complex South African species with apparently related taxa in Madagascar and western India. The genus is not recorded from South America, Oceania or Indonesia, although there is a species endemic to Tristan da Cunha. It seems, then, that it is most likely to be part of a small South African element in the Australian flora.

Some interesting points arise from a study of the distributions of the indigenous species. In Group I, which is a well defined unit, *P. helmsii* is the very high altitude representative found only on the highest parts of the continent; the other two species are geographically vicarious. The change, however, occurs not at the head of the Bight where most floristic changes in southern Australia occur, but somewhere in western Victoria. The determining factor in this case is probably something associated with the Eastern Highlands and their climate. With regard to *P. australe* it is interesting to note the paucity of material from Western Australia, where it is.

apparently, exclusively an inland species. The soft-leaved dune-form seems to have originated in the east and to have been confined there. The break occurs somewhere in South Australia or at the head of the Bight. *P. drummondii* is quite restricted. Group III shows a distribution resembling that of the two subspecies of *Erodium cygnorum* Nees in Lehm. (Carolin, 1958). *P. rodneyanum* occurs in the east and *P. havlasae* in the west. The arid, limestone country at the head of the Bight seems to have been a more effective barrier in this case than in that of the *Erodia*.

A survey of the chromosome numbers has not been completed, but it seems that there are differences in basic number between the indigenous species. The number Hare and Beuzenberg (1960) give for *P. inodorum* (n = 11) has been confirmed for the Australian material and *P. australe* has a number of 2n = 18. A subsequent paper will deal with this aspect when the survey is complete.

Acknowledgements.

Mr. P. F. Morris of the Victorian National Herbarium has kindly lent me some notes made by him during a visit to England. Dr. R. Melville and Dr. W. T. Stearn of the Royal Botanic Gardens, Kew, and British Museum, London, respectively, have helped considerably with the location of types and the description of those which could not be loaned. Dr. G. M. Schultze of Berlin-Dahlem has been particularly helpful with regard to Willdenow's types. The directors of the various State Herbaria in Australia have loaned material for some considerable time during the course of this work. Thanks are also due to the directors of those institutes enumerated in the text for lending valuable type material.

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THEODORE CLEVELAND ROUGHLEY, 1888–1961.

(*Memorial Series No. 19.*)

(With portrait, Plate xi.)

Theodore Cleveland Roughley, B.Sc., F.R.Z.S., who had been a member of the Linnean Society of New South Wales since 1925, its President in 1938–39, a Councillor from 1931 to 1956, and a Corresponding Member since 1957, died suddenly on 14th January, 1961, at The Entrance, Tuggerah, New South Wales.

Born at Dulwich Hill, Sydney, on 30th September, 1888, T. C. Roughley was educated at Sydney High School. He spent three years at the University of Sydney undertaking the medical course, but surgery and sickness were not to his taste, so he embarked on a career of scientific research and did not receive his degree of B.Sc. until years afterwards for his thesis on the oyster, published in 1933. On 21st August, 1911, he joined the staff of the Technological Museum, Ultimo, as Economic Zoologist, a post he held for 28 years. He delivered very many lectures and was a good after-dinner speaker, with a ready wit, and he contributed many articles on a variety of subjects to newspapers, magazines, scientific periodicals and to the *Australian Encyclopaedia.* He was an outstanding photographer and microscopist: he not only illustrated his own writings, but he photographed hundreds of illustrations for A. R. McCulloch's *Fishes of New South Wales.* His tall figure ensured success at athletics: he had played first grade cricket and baseball in early manhood and was proficient in tennis, golf and bowls. His hobby was the collection of books and works of art, himself being skilful at drawing, having studied under Julian Ashton.

The influence of Lawrence Hargrave (1850–1915) on man's pioneering efforts to fly was a lively topic for debate some years ago. Hargrave's models of flying machines had been presented to the Technological Museum, Sydney, and Roughley sought to establish Hargrave's rightful place as a pioneer of aviation. After most carefully appraising Hargrave's papers on aerodynamics and working with his actual models, Roughley concluded his appreciation of the other man's work as follows:

> "Although Hargrave's monoplanes were marvels of ingenuity and were propelled by internal combustion engines, the making of which showed his great resource, they played little part in the development of the modern aeroplane.
>
> "It is on his work on the box-kite that his fame must rest."

How Hargrave's models of box-kites went to Germany is related in the Technological Museum's Annual Report for 1919: 4. The present writer saw them in the Deutsches Museum, Munich, in 1936.

The Director (Mr. J. L. Willis) and the Keeper of Exhibits (Mr. H. L. Brown) of the Museum of Applied Arts and Sciences, Broadway, Sydney, to whom I am grateful for their help, inform me that in 1960 all Hargrave's still remaining models in the Deutsches Museum, Munich (except four engine models), were returned to their Institution, which was known as the Technological Museum in Roughley's days. Of the seventy-three models Hargrave sent to Germany, fifty-seven, including all the box-kites, were destroyed by Allied bombing during World War II.

In a review of Roughley's work, Ronald Monson pointed out in the *Daily Telegraph* newspaper, Sydney, 2nd July, 1949, p. 11:

"Using four large box-kites joined together, Hargrave, in 1894, launched himself into the air in a 21 miles-an-hour wind. He soared to 16 feet. In North Carolina in 1903 the Wright brothers made their first flights in the first power-driven aeroplane ever to fly, but the first aeroplane to fly in Europe—the one Santos-Dumont flew in France in 1906—was simply an arrangement of Hargrave box-kites. Voisin further

developed the box-kite plane and Farman produced his biplane by omitting the vertical sides of the series of box-kites which formed the wings of Voisin's plane. Thus Roughley demonstrated the direct evolution of the biplane from Hargrave's box-kites."

In 1928 Roughley conducted an interstate investigation of Australia's oyster resources and in 1929 we were shipmates aboard the Danish vessel "Dana" at the invitation of Professor Johannes Schmidt. An illustrated account of the voyage appeared in *The Australian Museum Magazine*. Roughley was also associated with the Great Barrier Reef Expedition to Low Isles.

Roughley was apparently first in the field in several fisheries matters. His photograph of a living flying fish, taken from the Danish research vessel "Dana" off the south Queensland coast in 1929 and reproduced in *The Australian Museum Magazine*, 3, 1929: 298, and in Danish and other publications was the first of its kind in the world. He encouraged F. A. Coombes in his experiments on softening and tanning shark-leather. He was responsible for the development of the fish-canning industry in Australia, encouraging local enterprise to tin prawns and mullet in the 1930s.* The migrations of the Australian marine "Salmon" (*Arripis trutta*) are still not completely understood, but Roughley considered that these fish could be sidetracked into pens at Narooma and in other coastal places so that their flavour could be improved and they would be available for canning on the spot. Unfortunately the fish did not appear at regular intervals at particular places so that several years without the appearance of shoals caused the idea to be shelved. However, canning developed rapidly in several States of the Commonwealth subsequently, using mullet, Perth herring, and tuna as well as the "Salmon" aforesaid.

Whilst our best prawning-grounds used to be considered to be inshore and in estuaries, Roughley, in the late 1930s, suggested that larger, more mature prawns would be found farther out to sea, as proved to be the case, with consequent expansion in the industry. The coloured plates in Roughley's books on fishes set a new standard of excellence in Australian ichthyology. Roughley was not a taxonomist, preferring to leave to specialists the identification of his specimens, but he named, in conjunction with Iredale, one new species of oyster and he was instrumental in donating many interesting specimens to the Australian Museum. In the field of economic zoology, however, his ability is amply demonstrated by the papers he produced.

The work which he made his own more than any other was the investigation of the biology of oysters. When he began, nothing was known of the life-history of Australia's commercial species, later to be known as *Saxostrea commercialis* Iredale & Roughley, and there were even prejudices against eating this delicious mollusc, at least the equal of any overseas. Roughley spent years studying the breeding and found that our oysters lay eggs into the water where they are fertilized, and that the very young are not retained in the gills as in the European species. In 1927 he announced his discovery of a sex change in the eastern Australian oyster which first functions as a male and later breeds as a female.

He had been a member of the Royal Zoological Society for many years, a Councillor from 1927 until recently, and was President from 1934 to 1936; the Society elected him a Fellow for his contributions to Australian zoology. Roughley was President of the Microscopical Society of New South Wales in 1926–27, Vice-President of the Aquarium Society, Sydney, and President of the Great Barrier Reef Game Fishing and Angling Club (1937), a member of the New South Wales Committee of the Council for Scientific and Industrial Research and of various aquarium, angling and sporting associations.

On 13th March, 1939, he transferred to the State Fisheries Branch of the Chief Secretary's Department, Sydney, where he was Research Officer, 1939, Deputy Controller of Fisheries in 1943–47, and ultimately became Superintendent of Fisheries. His administrative work was characterized by scrupulous fairness and integrity. In 1945 and 1946 he visited the United States of America to lecture about the Great Barrier Reef. After his retirement in September, 1952, he still took an active interest in

* *Technological Museum Annual Reports*, 1934, 1938, etc.

fisheries matters, and studied the oyster industries of the United States and the United Kingdom in 1956. He was well known in Australia for his Press comments, radio and television talks, and acted as adviser or referee in angling competitions. Indeed it was when staying at an hotel as inspector at a fishing contest that he was suddenly stricken. Mr. Roughley is survived by his widow, Mrs. Olive Roughley of Vaucluse (to whom I am grateful for assistance in the preparation of this memorial notice), and their son Mr. Clive Roughley and daughter, Norma (Mrs. W. Coombs), and two grandchildren.

Illustrated biographies of the late T. C. Roughley were published in the *Daily Telegraph* (Sydney) Magazine Section, 2nd July, 1944: 10–11, in *People*, 28th March, 1951: 28–31, and in the *Australian Monthly*, February, 1953: 63.

It is impossible to prepare a complete bibliography of Roughley's voluminous writings because hundreds of newspaper and magazine articles were contributed by him, some to ephemeral or obscure publications like certain angling journals and reports of organizations concerned with marketing fisheries products.

The appended bibliography is believed to cover the titles of all his major scientific papers and books, but some of these appeared in several editions, published in Great Britain and the United States as well as in Australia, so that collation of all editions has not been practicable, even in the fine libraries of the Australian Museum, Public Library, and Mitchell Library, Sydney, to which I am grateful for help.

G.P.W.

List of Publications by T. C. Roughley.

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1917. Edible Fishes. *The Australasian*, Oct. 27, 1917.
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1925. The Birth and Growth of an Oyster. *Austr. Mus. Mag.*, 2 (6): 187-194, figs 1-9.
1925. The Cultivation of the Oyster. *Austr. Mus. Mag.*, 2 (7): 235-242, 12 figs.
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* i.e., Riverstone.—G.P.W.

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* Though termed "second edition", I have not found any earlier edition of this paper which embodied two articles published in *Tech. Gazette N.S. Wales,* 13 (2), 1923 and 14 (1), 1924, which may thus have been regarded as the first edition.—G.P.W.

THE TAXONOMIC POSITION OF *ACTINOPTERIS INDICA* SRIVASTAVA.

By J. F. Rigby, B.H.P. Central Research Laboratories, Newcastle.

(Plate x, A; three Text-figures.)

[Read 25th October, 1961.]

Synopsis.

A number of specimens of *Actinopteris indica* Srivastava from the Permian of Queensland were examined. Sufficient information was available to include the species in the family Calamitaceae.

This was based on the absence of a resistant cuticle, the presence of a pith cast in the stem supporting the leaves and the nature of the leaves.

There are a number of undoubted specimens of *Actinopteris indica* Srivastava in an undescribed flora from Baralaba Colliery, Central Queensland. They form part of the collection made firstly by Miss B. Houston, now of the Queensland Geological Survey, and later supplemented by specimens collected by the manager of the colliery. The collection has now been incorporated into the museum of the Geology Department, University of Queensland.

The specimens were collected from the roof of the Dawson Seam in the Upper Bowen Series of Permian age.

Baralaba lies approximately 70 miles south-west of Rockhampton.

CALAMITACEAE.

Actinopteris indica Srivastava. (Plate x, A; Text-figs 1, 2, 3*a*, 3*b*).

Actinopteris indica Srivastava, *Palaeobotanist*, 3, 1954, p. 72, fig. 4, pp. 74-76, Pl. 3, fig. 26.

Approximately 30 specimens of this species were present, some of which formed almost complete whorls. A few whorls were connected by what appeared to be a thin stem, but was probably a pith cast. These specimens were attributed to Srivastava's species without hesitation. They differed from the type specimen in only one respect, in that they were smaller. Size is not generally a critical factor in distinguishing species.

Certain additional information obtained from the specimens was considered sufficient to place the genus in the family Calamitaceae.

Srivastava described it as *incertae sedis*. He referred to Feistmantel (1876, p. 76) who described the genus using *A. bengalensis* Feistmantel as the type species. Feistmantel considered it to be a fern. Zeiller (1902) reclassified it as possibly a new genus of the Equisetales; he considered each leaf whorl to have been formed into conical verticils similar to those of *Schizoneura wardi* Zeiller, as illustrated on his plate 6, figs 5-9.

Differences in the whorls of each species are that the leaves of *S. wardi* were joined only near their bases, whereas the leaves of *A. bengalensis* were joined for more than half their length. As a verticil of *A. indica* was similar to *A. bengalensis* in this and most other respects, we may compare *A. indica* directly with *S. wardi*. The verticil of *Actinopteris* must have been almost flat (see text-fig. 1), for if it were not, at least some of the leaves would have split along their junction or have torn apart during compression. It is suspected from the apparent epidermal cell structure as seen under low-power magnification that the individual leaves of a whorl were completely fused along their junction. The apical angle formed by a verticil of *S. wardi* lay between 90° and 120°, measured from Zeiller's illustration (*loc. cit.*).

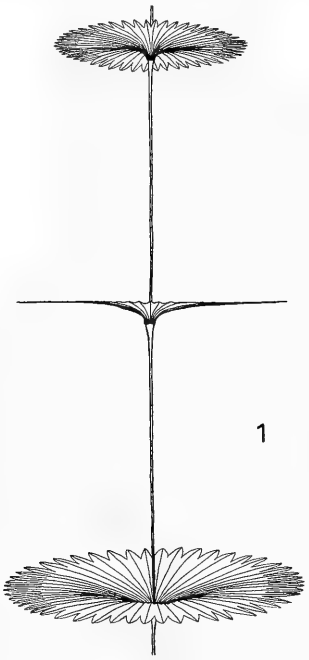
Arber (1905) and Dolianiti (1953) both shared Zeiller's opinion that *A. bengalensis* was probably not a fern, but a member of the Equisetales. Srivastava (1954) reviewed all evidence to date. After unsuccessfully endeavouring to prepare cuticles from a

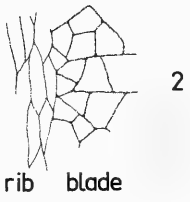
well-carbonized crust in a specimen of *A. bengalensis*, he concluded: "Is it possible that these plants do not possess a resistant cuticle? If this is so, then it is possible that Feistmantel was not altogether wrong in placing this plant in the ferns."

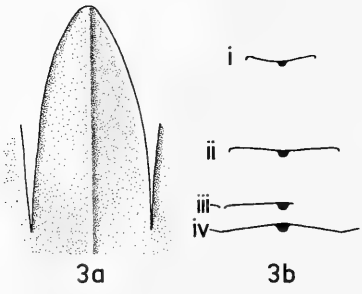
Schenk (1868), who described the genus *Actinopteris*, compared the nervation of the type species, *A. peltata*, with some recent ferns including *Trichomanes* species and *Lindsaya schomburgkii* Klotzsch. He excluded *A. peltata* from the genus *Cyclopteris*, where it had been placed previously, because of its orbicular nature.

The individual leaf whorls of *A. indica* contained from 46 to 52 leaves, each having a single, unbranched midrib, with secondary venation lacking.

The length of individual leaves measured from different whorls varied from 1·2 to 2·6 cm., but in most whorls the leaves were 1·7 cm. long (i.e., whorl 3·4 cm. in diameter). This is smaller than in the type specimen where they were 3 cm. long. The leaves were united for three-quarters of their length.







Text-fig. 1.—Reconstruction of part of a "branch" bearing verticils of *Actinopteris indica* Srivastava. The "branch" shown is the pith cast. The projection is natural size and in correct projection if the centre verticil were at eye level, and held six inches from the eye. The dimensions used are those of example 2, Specimen F31980 (see Plate x, A), as tabulated on Table 1.

Text-fig. 2.—Outlines of a few cells showing difference of structure in region of midrib, and of blade, in *Actinopteris indica* Srivastava. × 80 (approx.).

Text-fig. 3*a*.—The free portion of a single leaf of *Actinopteris indica* Srivastava viewed from below. × 7.

Text-fig. 3*b*.—Cross sections through the leaf of text-fig. 3*a* to show shape of leaf. × 7.

The most elliptical of the whorls is on specimen F31980 (this is the registered number of the specimen in the museum of the Geology Department, University of Queensland. All specimens described in this paper are housed in the museum of the Department). The individual leaflets vary in length between 1·7 cm. and 2·3 cm. Measured across the width of the leaf, at the point where the leaves become free, the leaf that was 1·7 cm. long was 3·0 mm. wide, and the leaf that was 2·3 cm. long was 2·1 mm. wide. Each leaf still had closely similar surface areas, so the ellipticity was probably caused during fossilization or subsequent folding of the beds.

Srivastava used, as one of his criteria to distinguish this species from *A. bengalensis* Feistmantel, a linear dimension (see his Table 1, p. 75, 1954). This criterion is not considered to be valid in distinguishing species, as size will depend on age of the plant and other factors, although if expressed as a ratio $\frac{\text{width of free segment}}{\text{length of leaf}}$ it may be valuable in undistorted specimens. His other criteria are sufficiently adequate to distinguish these species without any possible confusion.

The leaflets had slightly rounded acute apices (see text-fig. 3*a*), more acute than those illustrated by Srivastava. This appeared to be the only difference between the Indian and Australian specimens. The midrib appeared to reach the apex.

Each individual leaf was flexed slightly about the midrib downwards in the same direction as the side on which the midrib projected throughout the united part of the verticil. This is shown on text-fig. 3*b* (iv). The side with the midrib was assumed to be dorsal by analogy with published illustrations of other calamitalean foliage, i.e., the leaves were dorsiflexed. In the free part of the leaf, the edges were strongly enrolled, and the flexing of the leaf was away from the midrib. This is shown in the cross-sections of the leaf of text-figure 3*a*, varying from the united section of the leaf (text-fig. 3*b*; iv) towards the apex (text-fig. 3*b*; iii, ii and i). This made each whorl appear crenulate as well as being dentate. The crenulations may have been caused by slight distortion during compression, but as they were quite distinct on nine verticils, this would be unlikely. No leaf apices were found to have been folded during compression, so that the free portions of the leaves must have been sufficiently rigid to remain in the same plane as the united portion of the whorl, although the whole whorl was sufficiently thin not to tear when folded into the same plane as the supporting branch. The crenulations would add to this rigidity. No whorl was found where one-half of the verticil was folded back onto the other half. This, along with the slight distortion shown towards the centre of some verticils (e.g., the complete whorl in the lower centre of Plate x, A), supported the contention that they were slightly conical, as a cone would tear when folded.

The pith casts were ornamented with longitudinal striations; in specimen F31974 these appeared to be in paired groups. These represented vascular bundles. The internodes tapered gradually into the slightly swollen nodes. Two of the nodes appeared to have a series of small swellings around the leaf base. It was difficult to determine the relationship of these small swellings with the leaf parts, but they appeared to bear a relationship with the striations of the stem; they lay at either side of the paired vascular bundles. These were thought to represent swellings of the vascular bundles, where the bundles branched so as to give rise to the approximately 50 leaf midribs in each whorl. On specimen F31972 there was a suggestion of eight bunches of midribs in one verticil and seven in a second. If this were correct it would favour eight pairs of vascular bundles in the stem. Purely for mechanical reasons, the stem must have been considerably thicker than the pith cast. The thickening of the pith cast at the nodes appeared unusual.

No stems could be found, although their presence along the pith casts was evident. On Plate x, A, example 1 (the two incomplete verticils on the right hand side) shows a ridge in the upper, very incomplete verticil, which became a groove in the upper part of the lower verticil, then a ridge in the lower part of the same verticil. From the disposition of the midribs in each whorl it appeared that the tissue of the stem had vanished rapidly after deposition of the specimen, then the leaf had been pressed into the cavity formerly occupied by the tissue of the stem.

Another hypothesis that could be advanced to explain the identity of these specimens is that the pith casts represent a simple vascular cylinder or protostele covered by parenchymatous or other tissue and a cuticle that was not resistant to maceration. If this were so, then the vascular strands would not be visible. No tracheids were recovered, nor were any cell outlines visible in the pith casts.

The dimensions of a number of specimens are given in Table 1.

From this it appears that the plant bore slightly crenulate, flatly conical circular verticils of approximately 50 leaflets, united for three-quarters of their length, uninerved, with the nerve probably reaching the slightly rounded, acute apex. Stems having a very thin pith bore the verticils approximately at right angles separated by a distance of slightly less than one verticil diameter.

It would appear physiologically undesirable for such verticils to be borne any closer than this in a healthy plant because of shading. In other calamitalean genera the verticils appear to be borne at a distance approximately equal to one leaflet apart, *vide* numerous illustrations in Hirmer (1927). For the sake of stability, the stems were probably at least four times the thickness of the pith cast in the internode.

Only small fragments of calamitalean pith cast were found in the collection. They were too small for identification. Numerous other stems were found, but they were considered to be fern stems, probably belonging to *Sphenopteris* sp. *Sphenopteris* occurred frequently in the area.

TABLE 1.

Dimensions of several Specimens of Actinopteris indica *Srivastava.*

	1	2	3	4
Length of internode	33	upper 34 lower 35	28	unknown
Diameter at centre of internode	0·6	upper 0·4 lower 0·4	0·4	0·7
Mean diameter verticil				
Upper	40	26	32	30
Middle	—	36	—	—
Lower	unknown	40	37	—
Diameter of node				
Upper	1·0	unknown	0·9	0·9
Middle	—	0·8	—	—
Lower	unknown	1·0	unknown	—
Number of striations across width of internode	not visible	not visible	not visible	8 in paired bundles

Note: All measurements are in millimetres. 1 and 2 are on specimen F31980 (see Pl. x, A), 3 is on specimen F31972, 4 is on specimen F31974.

The specimens were preserved in a grey shale as compressions with some of the carbonaceous material still present. Specimens could be removed as Canada Balsam transfers following the technique of Walton (1928), but all attempts at oxidation maceration, viz. Schulze maceration, or in bleaching solution resulted in complete oxidation of the plant material. This, in itself, would suggest that the plant was not a spermatophyte.

Maceration was also attempted in either HCl or saturated $ZnCl_2$, the latter following the suggestion of Harris (1932, p. 4) that modern fern cuticles were preserved during maceration in a non-oxidizing, non-alkaline solution.

The surface of these specimens was examined in reflected light. Some cell outlines could be seen with difficulty (see Text-fig. 2 and Table 2). The cells adjacent to the veins were elongated along the length of the veins, whereas the cells of the lamina were cubic or polygonal. Neither balsam transfers nor cellulose acetate peels showed any additional detail.

Some specimens from Newcastle, N.S.W., discovered by Etheridge (1895) and described by Arber (1905) as *Phyllotheca etheridgei* bear a certain resemblance to these specimens.

P. etheridgei consisted of a series of whorled verticils borne on a thick, ribbed stem. A comparison of this species with *A. indica* is given below using Etheridge's fig. 1, Plate xvii (fig. 1 was reproduced by Arber as text-fig. 9 on page 27) and fig. 3 of Plate xviii with the specimen of *A. indica* illustrated as text-fig. 1 in this paper.

Actinopteris indica Srivastava.	*Phyllotheca etheridgei* Arber.
50 leaves per whorl.	20 or more leaves per whorl.
Leaf apex rounded.	Leaf apex pointed.
Sheath absent.	Leaf bases united to form a sheath.
Leaves fused for three-quarters of their length.	Leaves fused for seven-eighths of their length.
V notch where leaves become free.	U notch where leaves become free.
Diameter of node less than one-tenth of the length of a leaf.	Diameter of node approximately one-quarter of the length of a leaf.
Internode shows no more than eight vascular bundles in side view.	Internode shows at least eight vascular bundles in side view.

These two species have the following characters in common: Leaf whorls approximately the same size; leaf whorl flatly conical; whorls spaced approximately one verticil diameter apart along the stem; each leaflet bears a single median nerve.

A. indica may be compared with *Annularia* spp., e.g., *A. stellata*. This plant has been figured by numerous authors, including Seward (1898, p. 339). A comparison of *Actinopteris indica* with *Annularia stellata* is given below. It may be seen that

TABLE 2.

Dimensions of Cells on Leaf Surface of Actinopteris indica *Srivastava.*

	On Blade.	Along Vein.
Leaf 1	range $\begin{cases} 37 \times 25 \\ 18 \times 12 \end{cases}$	90 × 8
Leaf 2	40 × 32	80 × 10
Leaf 3 (largest in collection)	32 × 22	63 × 8
Leaf 4 (smallest in collection)	55 × 40	90 × 16

All dimensions are in μ.

A. indica possesses more features in common with *A. stellata* than with *Phyllotheca etheridgei.*

The following features are distinctive between these two species:

Actinopteris indica Srivastava.	*Annularia stellata* Schl.
50 leaves per whorl.	Fewer than 25 leaves per whorl.
Leaf apex rounded.	Leaf apex often mucronate.
Leaves fused for three-quarters of their length.	Leaves free, bases united.
Whorls spaced approximately one verticil diameter apart along the stem.	Whorls spaced approximately one-half verticil diameter apart along the stem.
Leaf whorls tend to be ovate-orbicular	Leaf whorls tend to be orbicular with the attachment eccentric.

These two species have the following characters in common: Diameter of the node less than one-tenth of the length of a leaf; leaf whorls borne on a slender stem; leaf whorls approximately the same size; each leaflet bears a single median nerve; margin of free portion of leaflets is enrolled; leaf whorls (?) slightly ensheathing. It is because of these common features that *A. indica* has been included in the family Calamitaceae. This raises the point that *A. indica* should no longer be included in the genus *Actinopteris*, but should be transferred to some other genus such as *Annularia*, or to a new genus. *Annularia ivini* Walkom has its leaves united for most of their length as does *Actinopteris indica*. Etheridge (1895), in his description of *Phyllotheca etheridgei* Arber, has mentioned that "The intercostal spaces are also crossed by the finest possible transverse striae, arranged in a festoon-like manner". This feature is

closely similar to the striae in *Annularia ivini* (Walkom, 1941, Pl. viii), but is absent in *A. stellata* and *Actinopteris indica.*

From this it appears that *Actinopteris indica* possesses many characters similar to members of the genus *Annularia,* but that it also possesses certain quite distinctive characters.

Acknowledgements.

The writer wishes to thank Professor Dorothy Hill, Research Professor of Geology in the University of Queensland, for allowing him the opportunity to examine the Baralaba Collection, for placing at his disposal all facilities required to make this examination while on a short visit to the University and for making valuable suggestions to improve the manuscript. Thanks are also due to Dr. H. K. Worner, Director of Research, B.H.P. Central Research Laboratories, Shortland, N.S.W., for arranging to have the manuscript prepared for publication and to Mr. S. Thompson, of the same organization, for his excellent photography. The writer's indebtedness to Dr. A. B. Walkom for suggesting that the writer might be allowed to examine this material and for assistance in the references is also acknowledged.

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EXPLANATION OF PLATE X, A.

Specimen F31980. *Actinopteris indica* Srivastava, showing verticils described in the text. The two verticils of example 1 (Table 1) are those running in a line at about 60° to the horizontal, along the right-hand side. The large verticil in the top right-hand corner was not measured. The three verticils of example 2 are bisected by the fracture in the rock, with the smallest verticil at the top of the plate. The specimen was illuminated from the bottom right-hand corner. Natural size.

THE CHROMOSOMES OF SOME AUSTRALIAN LIVERWORTS.

By Geoffrey K. Berrie, Department of Botany, University of Sydney.

(One Text-figure.)

[Read 29th November, 1961.]

Synopsis.

The chromosomes of four species of Australian liverworts are described as follows: *Riccardia maxima* Schiffn., n = 8, including a heteromorphic pair at meiosis; *Symphyogyna obovata* Tayl., n = 8, including a heteromorphic pair at meiosis; *Umbraculum flabellatum* Gottsche, n = 9, including a microchromosome; *Metzgeria furcata* (L.) Lindb., n = 9.

Some of the genera and species of Australian liverworts are widely distributed throughout the world, but many are relatively restricted in their distribution. There is only one chromosome record for Australian material, a count of n = 5 (plus a variable number of fragments) for *Phaeoceros laevis* (L.) Prosk. subsp. *carolinianus* Prosk. (Anthocerotales) from New South Wales (Proskauer, 1957).

The chromosome numbers characteristic of most liverwort genera are well known (Berrie, 1960), and since there is little variation within each genus it is generally only necessary to tabulate new records without detailed description. The four species of liverworts belonging to the Jungermaniales anacrogynae which are treated here all show features of special interest which make a slightly more detailed account desirable. The justification in each instance is either that the chromosome number is unusual for the genus (*Riccardia maxima*) or that these are the first full records published for a member of the genus concerned.

There are several points of special significance in the chromosome complement of a liverwort, to which reference will be made. These are: (i) the presence of sex chromosomes in some dioecious species, forming a heteromorphic pair at meiosis; (ii) the presence of a very small chromosome, the microchromosome, in the complement of some species; (iii) the presence of chromosomes which are largely heterochromatic (heteropycnotic), and stain differently from the other chromosomes at certain stages of mitosis and meiosis.

An aceto-orcein squash technique was used for all preparations.

Riccardia maxima Schffn. (Aneuraceae).

Riccardia maxima is dioecious, and is typical of the genus in all morphological features except its very large size. It is recorded from Java, Sumatra and Australia, and is quite common near waterfalls and at similar sites in the neighbourhood of Sydney. The population examined here was collected at Oxford Falls, near Sydney.

The gametic chromosome number is 8. Records for twelve other species of *Riccardia* are for n = 10, or a multiple of 10 (Berrie, 1960). Variation in basic chromosome number within a liverwort genus is unusual. At prophase of meiosis there is a distinct difference in size between the large heterochromatic parts of the constituents of one of the bivalents (Figure 1*a*). This bivalent presumably represents a pair of sex chromosomes. The difference in size is not great, and is difficult to detect at first metaphase and later stages of meiosis. *Riccardia pinguis* (L.) Gray and a number of other species have a similar sex chromosome pair (Berrie, 1960).

Symphyogyna obovata Tayl. (Dilaenaceae).

Symphyogyna obovata is dioecious, and is recorded from New Zealand and Australia. There is a record of the chromosomes for one species of this genus (*S. aspera*, n = 8, MacCormick, 1914; Berrie, 1960), but this early record requires confirmation. Material of *S. obovata* was collected beside a spring near Mount Wilson in the Blue Mountains, New South Wales.

At meiosis there are eight bivalents. The components of one bivalent are strongly heteromorphic, and heterochromatic (Figure 1*b*). The larger component is about twice the size of the smaller. This chromosome complement is very similar to that of species of *Pallavicinia*, a closely related genus.

UMBRACULUM FLABELLATUM Gottsche (Metzgeriaceae).

The distribution of *Umbraculum* (*Hymenophytum*) *flabellatum* is restricted to New Zealand and Australia. No chromosome records exist for *Umbraculum*, or for *Hymenophytum*. The material was collected from beside a spring near Mount Wilson in the Blue Mountains, New South Wales.

Observations were made on the apices of stolons of male plants. There are nine chromosomes, one of them a microchromosome (Figure 1*c*).

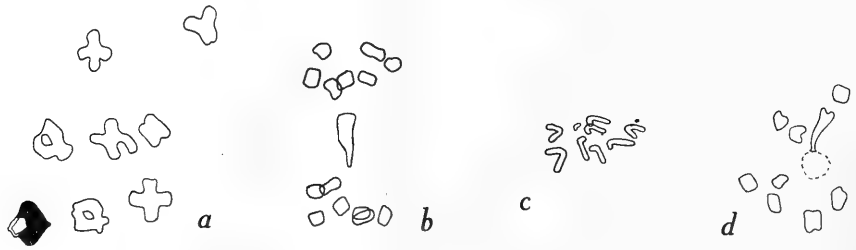

Figure 1.—The chromosomes of some Australian liverworts (×1,250). (*a*) *Riccardia maxima*, diakinesis (heterochromatin in black). (*b*) *Symphyogyna obovata*, first anaphase of meiosis, the components of the heteromorphic pair not yet separated. (*c*) *Umbraculum flabellatum*, one daughter nucleus at anaphase of mitosis. (*d*) *Metzgeria furcata*, prophase of meiosis.

METZGERIA FURCATA (L.) Dum. (Metzgeriaceae).

Metzgeria furcata is cosmopolitan. There are no well documented records of the chromosomes, and only an approximate chromosome number is available for this species (n = 8–10, Heitz, 1942).

The material came from an unidentified locality in New South Wales. The gametic chromosome number, counted at prophase of meiosis, is 9. There is no microchromosome. In all nuclei in the material examined the components of one large bivalent are in intimate terminal contact with the nucleolus (Figure 1*d*).

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ABSTRACT OF PROCEEDINGS

ORDINARY MONTHLY MEETING.

29th March, 1961.

Professor J. M. Vincent, President, in the chair.

The minutes of the last Monthly Meeting (30th November, 1960) were taken as read and signed.

The Chairman offered congratulations to Dr. R. N. Robertson on his election to Fellowship of the Royal Society.

The Chairman announced that library accessions amounting to 35 volumes, 512 parts or numbers, 24 bulletins, 15 reports and 36 pamphlets, total 622, had been received since last meeting.

The Chairman announced that, owing to the holding of the A.N.Z.A.A.S. meeting in Brisbane from 29th May to 2nd June, 1961, no Ordinary Monthly Meeting of the Society will be held in May.

The Chairman announced that by decision of Council surplus copies of the Macleay Memorial Volume and the Jubilee brochure would be available to members free on application.

PAPERS READ (by title only).

1. Seed Coat Anatomy and Taxonomy in *Eucalyptus*. III. By E. Gauba and L. D. Pryor.

2. Supplementary Note to a Revision of the Australian Rutelinae (Coleoptera: Scarabaeidae). By P. B. Carne.

3. New and Little-known Laelaptidae, Trombiculidae and Listrophoridae (Acarina) from Australasian Mammals. By R. Domrow.

ORDINARY MONTHLY MEETING.

26th April, 1961.

Professor J. M. Vincent, President, in the chair.

The following were elected Ordinary Members of the Society: Mr. J. A. Bishop, Lane Cove, N.S.W.; Miss Constance M. Jacobson, B.Sc., Bondi, N.S.W.; and Dr. Donald Walker, B.Sc., M.A., Ph.D., F.L.S., Canberra, A.C.T.

The Chairman announced that the Council had elected the following office-bearers for the 1961-62 session: Vice-Presidents: Dr. I. V. Newman, Dr. T. G. Vallance, Dr. S. Smith-White and Dr. Lilian Fraser; Honorary Treasurer: Dr. A. B. Walkom; Honorary Secretaries: Dr. A. B. Walkom and Dr. W. R. Browne.

The Chairman offered congratulations to Miss Barbara G. Briggs on obtaining the degree of Doctor of Philosophy in the University of Sydney for research in botany.

The Chairman drew the attention of members to the list of Rare Fauna issued by the Fauna Protection Panel. The list, which is exhibited on the Society's notice-board, includes 31 birds, 16 marsupials and 2 monotremes.

The Chairman announced that library accessions amounting to 11 volumes, 58 parts or numbers, 1 report and 2 pamphlets, total 72, had been received since the last meeting.

PAPERS READ.

1. The Effects of Forest Fires on three Species of Stick Insects (Phasmatidae Phasmatodea) occurring in Plagues in Forest Areas of South-Eastern Australia. By K. G. Campbell.

Discussion: Mr. Moore, who presented the paper for Mr. Campbell, answered many questions in the lively discussion which ensued. Of particular interest was his reference to spraying experiments in forest areas and the suggested possibility that other factors in the ecological situation could be upset thereby.

2. Observations on some Australian Forest Insects. 7. The Significance of the *Glycaspis* spp. (Hemiptera: Homoptera, Psyllidae) Associations with their *Eucalyptus* spp. Hosts; Erection of a New Subgenus and Descriptions of thirty-eight new Species of *Glycaspis*. By K. M. Moore.

Discussion: In the discussion questions were asked as to the reasons for the evident build-up of these insects. Mr. Moore suggested that the incidence of excessive rains over several successive years and perhaps also the influence of clay subsoils on moisture relationships could be important.

LECTURETTE.

An illustrated lecturette was delivered by Mr. D. K. McAlpine, of the Australian Museum. entitled "Collecting Insects in Tasmania".

ORDINARY MONTHLY MEETING.

28th JUNE, 1961.

Professor J. M. Vincent, President, in the chair.

Miss Lesley D. Clarke, Eastwood, N.S.W., was elected an Ordinary Member of the Society.

The Chairman offered congratulations to Dr. A. J. Nicholson on receiving the C.B.E. from Her Majesty the Queen; to Dr. I. M. Mackerras on the award of the Mueller Medal of the Australian and New Zealand Association for the Advancement of Science; and to Dr. T. C. Chambers on obtaining the degree of Doctor of Philosophy in the University of Sydney.

The Chairman announced that library accessions amounting to 33 volumes, 271 parts or numbers, 20 bulletins, 11 reports and 17 pamphlets, total 352, had been received since the last meeting.

The Chairman announced that the 2nd Annual Dinner of the Nature Conservation Societies will be held on Saturday, 14th October, 1961, at 6 p.m. Tickets 15s. each. Copies of the circular (with application form for tickets attached) are available at the Society's rooms.

PAPERS READ.

1. The Generic Position of the Australian Light-brown Apple Moth (Lepidoptera: Tortricidae). By I. F. B. Common.

2. Notes on the Morphology and Biology of *Caenoprosopon trichocerus* (Bigot) (Diptera, Tabanidae, Pangoniinae). By Kathleen M. I. English.

Discussion: In answer to a question Miss English said that there was no evidence that, in Australia, the blood-sucking tabanids had any public health significance.

3. A Study of Inheritance of Pathogenicity in *Puccinia graminis* var. *tritici*. By N. H. Luig and I. A. Watson.

Discussion: There was some discussion on the nature and significance of somatic hybridization as a means of causing breakdown of host resistance.

LECTURETTE.

An illustrated lecturette was delivered by Dr. A. R. H. Martin, Botany Department, University of Sydney, entitled "Pollen and its Chronological Significance".

ORDINARY MONTHLY MEETING.

26th JULY, 1961.

Professor J. M. Vincent, President, in the chair.

Dr. Aola M. Richards, M.Sc. (Hons.), Ph.D. (N.Z.), University of New South Wales, Sydney, was elected an Ordinary Member of the Society.

The Chairman announced that library accessions amounting to 23 volumes, 191 parts or numbers, 12 bulletins, 5 reports and 3 pamphlets, total 234, had been received since the last meeting.

PAPERS READ.

1. Larval Development of *Velacumantus australis*. By R. J. MacIntyre. (*Communicated by Dr. G. F. Humphrey.*)

2. Observations on some Australian Forest Insects. 8. The Biology and Occurrence of *Glycaspis baileyi* Moore in New South Wales. By K. M. Moore.

3. The Status of Nitrogen in the Hawkesbury Sandstone Soils and their Plant Communities in the Sydney District. III. The Sources of Loss of Nitrogen. By Nola J. Hannon.

4. The Reproduction and Early Life History of the Gastropod *Bembicium nanum* (Lamarck, 1822) (Fam. Littorinidae). By D. T. Anderson.

LECTURETTE.

An illustrated lecturette entitled "The New Zealand Glow-worm" was delivered by Dr. Aola Richards Lecturer in Zoology, School of Biological Sciences, University of New South Wales.

ORDINARY MONTHLY MEETING.

30th AUGUST, 1961.

Professor J. M. Vincent, President, in the chair.

Miss Lynette Bedford, B.Sc., King's Cross, Sydney, Miss Diane King, Croydon, N.S.W., Mr. G. C. Morrison, North Balgowlah, N.S.W., and Mr. P. D. Strong, Austinmer, N.S.W., were elected Ordinary Members of the Society.

The Chairman announced that library accessions amounting to 13 volumes, 108 parts or numbers, 6 bulletins, 4 reports and 3 pamphlets, total 134, had been received since the last meeting.

The Chairman drew the attention of members to the Jubilee Congress of Czechoslovak Botanists in Prague from 1st to 8th July, 1962.

PAPERS READ.

1. An Investigation of the possible Role of Biting Midges (Diptera, Ceratopogonidae) in the Transmission of Arthropod-borne Virus Diseases at Townsville. By Eric J. Reye and David J. Lee.

2. The Distribution and Inter-relationships of *Perga affinis* Kirby and *Perga dorsalis* Leach (Hymenoptera, Symphyta). By E. F. Riek.

3. Observations on some Australian Forest Insects. 9. A New Species of *Glycaspis* (*Glycaspis*) (Homoptera: Psyllidae). By K. M. Moore.

4. Leaf Rust on Wheat in Australia: A Systematic Scheme for the Classification of Strains. By I. A. Watson and N. H. Luig.

Discussion: In reply to a question as to whether the gene-for-gene theory operated between wheat and leaf rust, Professor Watson pointed out that, though the evidence for this was mostly with other host/fungus relationships, his own work was in line with this theory. Asked whether there were any wheats resistant to all known races

of the rust, Professor Watson said that no commercial variety was available with this property and that new varieties have been quickly attacked by new variants of rust. A broader genetic base confirming resistance is needed.

NOTES AND EXHIBITS.

Dr. I. V. Newman exhibited a longitudinal section of stem and taproot of *Macrozamia communis* showing the distribution of the main tissues, the form of the apical end of the stem and the relation of stem to taproot. The stem has primary tissues of far greater extent than is commonly produced by quick-growing plants, which is commonly attributed to a primary thickening meristem not in the immediately apical growing region. Because the rim of the apical end of the plant is higher than the apical centre, there must be a vertical component in this "thickening" meristem. A copy of an illustration of another cycad apex (*Microcycas calocoma* Foster, *Amer. J. Bot.*, 30, 1943, fig. 7) at a magnification of 250× showed a probable approximation to the cellular pattern in the immediately apical region, extending laterally only to the beginning of the primary "thickening" meristem region. There was reference to a similar situation in *Xanthorrhoea media* (Grass tree) in an exhibit shown to this Society by Mr. I. A. Staff at the November meeting last year. This type of meristematic organization is present in such wide-stemmed plants as these, the palms and the large cacti. These plants offer a very interesting field for a mathematical study of growth in the form of trigonometry of tissue development. The half-stem and taproot from which the section was cut were also exhibited.

Mr. W. J. Peacock exhibited slides showing subchromatids in *Vicia faba*. The photographs showed chromosomes of cells which have been irradiated with relatively low dosages of X-rays (36*r*). The two-side-arm bridge and Y-chromatid configurations are diagnostic for the existence of subchromatids, both being consequences of different patterns of subchromatid reunion and restitution. Demonstration of a bipartite structure of the chromatid is of particular significance in evaluation of recent studies of the mechanism of chromosome duplication.

Mr. K. E. W. Salter raised the question of whether the geographical distribution of Thynnidae which, so far as known, are confined to the Australian region, the Philippines and South America, could be explained on the hypothesis of a former land connexion between the countries concerned. The question gave rise to an impromptu discussion of the general hypothesis of Continental Drift.

ORDINARY MONTHLY MEETING.

27th September, 1961.

Professor J. M. Vincent, President, in the chair.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1962, 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 £1,600 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 1st November, 1961.

The Chairman announced that library accessions amounting to 15 volumes, 210 parts or numbers, 6 bulletins, 4 reports and 24 pamphlets, total 259, had been received since the last meeting.

PAPER READ.

1. Observations on the Life Cycle of *Stictodora lari* (Trematoda: Heterophyidae). By A. J. Bearup.

LECTURETTE.

An illustrated lecturette entitled "Geographical Patterns of Chromosome Change in the Australian Flora" was delivered by Dr. S. Smith-White, Department of Botany, University of Sydney.

The Chairman drew the attention of members to a meeting in Canberra on 21st October to discuss the formation of an Australian Freshwater Biological Association, particulars to be had from Dr. V. H. Jolly, Warragamba Dam, New South Wales.

ORDINARY MONTHLY MEETING.

25th October, 1961.

Professor J. M. Vincent, President, in the chair.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships, tenable for one year from 1st January, 1962, 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 £1,600 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 1st November, 1961.

The Chairman announced that library accessions amounting to 10 volumes, 120 parts or numbers, 5 bulletins, 2 reports and 12 pamphlets, total 149, have been received since the last meeting.

PAPERS READ.

1. The Taxonomic Position of *Actinopteris indica* Srivastava. By J. F. Rigby.
2. Re-discovery of a Little-known Victorian Frog. By Stephen J. Copland.

LECTURETTE.

A lecturette entitled "The Argentine Ant Eradication Campaign in Sydney", illustrated by colour film with commentary, was delivered by Mr. Gordon Pasfield, N.S.W. Department of Agriculture, Sydney.

ORDINARY MONTHLY MEETING.

29th November, 1961.

Professor J. M. Vincent, President, in the chair.

The Chairman announced that the Council had reappointed Mr. W. J. Peacock, B.Sc., to a Linnean Macleay Fellowship in Botany for one year from 1st January, 1962.

The Chairman announced that library accessions amounting to 26 volumes, 100 parts or numbers, 9 bulletins, 3 reports and 2 pamphlets, total 140, had been received since the last meeting.

The Chairman also announced to members of the Society that the Melbourne University Press will be publishing in January, 1962, a centenary volume on behalf of the Royal Society of Victoria. Members of the Society are offered a pre-publication price concession at £5/5/- per copy, post paid, the request for such concession to be made on a special order form, which should be applied for to the Melbourne University Press. The title of the volume is "The Evolution of Living Organisms", edited by G. W. Leeper (Australian retail price, £6/6/-, royal 8vo, full cloth, pp. xii, 460, 93 figures, 7 pages of half-tones, 31 tables, index). The address of the Melbourne University Press is Parkville, N.2, Victoria.

PAPERS READ.

1. Notes on Australian Mosquitoes (Diptera, Culicidae). I. The Life History of *Aedomyia venustipes* (Skuse). By G. W. Douglas.

2. Diapause and Parthenogenesis in the Eggs of Three Species of Phasmatodea. By P. Hadlington and E. Shipp.

3. The Genus *Pelargonium* l'Hér. ex Ait. in Australia. By R. C. Carolin.

4. The Chromosomes of some Australian Liverworts. By G. K. Berrie.

LECTURETTE.

Mr. R. C. Carolin, Department of Botany, University of Sydney, delivered a lecturette entitled "The Impact of New Techniques on Taxonomy".

LIST OF MEMBERS.

(15th December, 1961.)

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.
1927 *Albert, Michel Francois, "Boomerang", 42 Billyard Avenue, Elizabeth Bay, Sydney.
1940 *Allman, Stuart Leo, B.Sc.Agr., M.Sc., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W.
1959 Anderson, Donald Thomas, B.Sc., Ph.D., Department of Zoology, Sydney University.
1922 Anderson, Robert Henry, B.Sc.Agr., Royal Botanic Gardens, Sydney.
1927 *Armstrong, Jack Walter Trench, "Callubri", Nyngan, N.S.W.
1952 Ashton, David Hungerford, B.Sc., Ph.D., 92 Warrigal Road, Surrey Hills, E.10, Victoria.
1912 Aurousseau, Marcel, B.Sc., 229 Woodland Street, Balgowlah, N.S.W.

1952 Baehni, Professor Charles, Dr.sc., Conservatoire botanique, Université de Genève, 192, rue de Lausanne, Genève, Switzerland.
1961 Bain, Miss Joan Maud, M.Sc., 18 Onyx Road, Artarmon, N.S.W.
1949 Baker, Eldred Percy, B.Sc.Agr., Ph.D., Faculty of Agriculture, Sydney University.
1959 Bamber, Richard Kenneth, A.S.T.C. (Science), 113 Lucinda Avenue South, Wahroonga, N.S.W.
1950 *Barber, Professor Horace Newton, M.A., Ph.D., Department of Botany, University of Tasmania, Hobart, Tasmania.
1960 Barber, Ian Alexander, B.Sc.Agr., Department of Zoology, Sydney University.
1955 Barlow, Bryan Alwyn, B.Sc., Ph.D., Department of Botany, University of Queensland, George Street, Brisbane, Queensland.
1956 Barnard, Robert Alexander Stephen, 14 Grassmere Road, Lindfield, 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., c.o. Mr. L. H. Moore, H. W. Horning and Co. Pty. Ltd., 14 Martin Place, Sydney.
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), 28 Menangle Road, Camden, N.S.W.
1961 Bedford, Miss Lynette, B.Sc., 376 Victoria Street, King's Cross, N.S.W.
1952 Bennett, Miss Isobel Ida, Department of Zoology, Sydney University.
1960 Berrie, Geoffrey Kenneth, B.Sc., Ph.D., 202 Headland Road, Dee Why, N.S.W.
1948 Besly, Miss Mary Ann Catherine, B.A., Department of Zoology, Sydney University.
1961 Bishop, James Arthur, 46 Hallam Avenue, Lane Cove, N.S.W.
1958 Blake, Clifford Douglas, B.Sc.Agr., c.o. Department of Nematology, Rothamsted Experimental Station, Harpenden, Herts, England.
1941 Blake, Stanley Thatcher, D.Sc. (Q'ld.), Botanic Gardens, Brisbane, Queensland.
1929 Boardman, William, M.Sc., Zoology Department, University of Melbourne, Carlton, N.3, Victoria.
1960 Bourke, Terrence Victor, B.Sc.Agr., c.o. Post Office, Graman 5N, N.S.W.
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.
1949 Browne, Lindsay Blakeston Barton, Ph.D., C.S.I.R.O. Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1911 Browne, William Rowan, D.Sc., 363 Edgecliff Road, Edgecliff, N.S.W.
1952 Bunt, John Stuart, B.Sc.Agr., Ph.D., School of Agriculture, Sydney University.
1949 Burden, John Henry, 1 Havilah Street, Chatswood, N.S.W.
1931 *Burges, Professor Norman Alan, M.Sc., Ph.D., Professor of Botany, University of Liverpool, Liverpool, England.
1959 Burgess, The Rev. Colin E. B. H., 8 Deakin Avenue, Haberfield, N.S.W.

1960 Cady, Leo Isaac, "Milford", Saddleback Road, Kiama, N.S.W.
1959 Campbell, Keith George, D.F.C., B.Sc.For., Dip.For., 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., Department of Botany, Sydney University.**
1957 Casimir, Max, B.Sc.Agr., Flat 2, 36 Benelong Road, Cremorne, 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.
1959 Chippendale, George McCartney, B.Sc., Lindsay Avenue, Alice Springs, Northern Territory, Australia.
1947 Christian, Stanley Hinton, c.o. Malaria Control School, Department of Public Health, Minj, Western Highlands, New Guinea.
1932 *Churchward, John Gordon, B.Sc.Agr., Ph.D., 6 Kareela Road, Chatswood, N.S.W.
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 John Burton, M.D., Ch.M., C.B.E., 1 Dashwood Road, Beaumont, Adelaide, South Australia.
1957 Clinton, Kenneth John, School of Public Health and Tropical Medicine, Sydney University.
1956 Cogger, Harold George, B.Sc. (Gen.Sc.), 4 Blane Street, Granville, N.S.W.
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.
1956 Common, Ian Francis Bell, M.A., M.Sc.Agr., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1942 Copland, Stephen John, M.Sc., 15 Chilton Parade, Warrawee, N.S.W.
1947 Costin, Alex Baillie, B.Sc.Agr., C.S.I.R.O., Division of Plant Industry, P.O. Box 109, City, Canberra, A.C.T.
1908 Cotton, Professor Leo Arthur, M.A., D.Sc., 113 Queen's Parade East, Newport Beach, N.S.W.
1950 **Crawford, Lindsay Dinham, B.Sc., 4 Dalton Avenue, West Hobart, Tasmania.**
1955 Crocker, Professor Robert Langdon, D.Sc., Department of Botany, Sydney University.
1957 Crook, Keith Alan Waterhouse, M.Sc., Ph.D. (New England), Department of Geology, Australian National University, G.P.O. Box 197, Canberra, A.C.T.

1960 Dart, Peter John, B.Sc.Agr., Department of Botany, Sydney University.
1957 **Davies, Stephen John James Frank, B.A. (Cantab.), 61 Abbotsford Road, Homebush, N.S.W.**
1945 Davis, Professor Gwenda Louise, Ph.D., B.Sc., Faculty of Science, University of New England, Armidale, 5N, N.S.W.
1934 Day, William Eric, 23 Gelling Avenue, Strathfield, N.S.W.
1937 Deuquet, Camille, B.Com., 238 Rue Victor Rauter, Brussels 7, Belgium.
1953 Dobrotworsky, Nikolai V., M.Sc., Department of Zoology, University of Melbourne, Carlton, N.3, Victoria.
1954 Domrow, Robert, B.A., B.Sc., Queensland Institute of Medical Research, Herston Road, Herston, N.9, Brisbane, Queensland.
1960 Dorman, Herbert Clifford, J.P., A.S.T.C. (Dip.Chem.), Dip.Soc. Stud. (Sydney), Rodgers Street, Teralba 2N, N.S.W.
1954 Douglas, Geoffrey William, B.Agr.Sci., 226 Clarendon Street, East Melbourne, C.2, Victoria.
1946 **Durie, Peter Harold, M.Sc., C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly,** Brisbane, Queensland.
1952 Dyce, Alan Lindsay, B.Sc.Agr., C.S.I.R.O., Wildlife Survey Section, P.O. Box 109, City, Canberra, A.C.T.

1953 Edwards, Dare William, B.Sc.Agr., Forestry Commission of N.S.W., Division of Wood Technology, 96 Harrington Street, Sydney.
1947 Endean, Robert, M.Sc., Ph.D., Department of Zoology, University of Queensland, St. Lucia, Brisbane, Queensland.
1930 English, Miss Kathleen Mary Isabel, B.Sc., 2 Shirley Road, Roseville, N.S.W.
1957 Evans, Miss Gretchen Pamela, M.Sc., 27 Frederick Street, Taringa, Brisbane, Queensland.
1955 Evans, John William, M.A., D.Sc., Sc.D., 47 Bundarra Road, Bellevue Hill, N.S.W.

1955 ***Fairey, Kenneth David, Box 1176, G.P.O., Sydney.**
1957 Filewood, Lionel Winston Charles, 62 Dickson Avenue, West Ryde, N.S.W.
1953 Frame, William Robert, Goroka, New Guinea.
1930 Fraser, Miss Lilian Ross, D.Sc., "Hopetoun", 25 Bellamy Street, Pennant Hills, N.S.W.

1959 Gardner, Mervyn John, B.Sc.For., Dip.For., Forest Office, Baradine 6W, N.S.W.
1935 *Garretty, Michael Duhan, D.Sc., Box 763, Melbourne, Victoria.
1958 Green, John William, B.Sc. (Adel.), Department of Botany, University of New England, Armidale 5N, N.S.W.
1944 Greenwood, William Frederick Neville, 11 Wentworth Avenue, Waitara, N.S.W.
1946 *Griffiths, Mrs. Mabel, B.Sc. (*née* Crust), 89 Stock Road, Bicton, Western Australia.
1936 Griffiths, Mervyn Edward, D.Sc., Wildlife Survey Section, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
1939 *Gunther, Carl Ernest Mitchelmore, M.B., B.S., D.T.M., D.T.M. & H. (England), 29 Flaumont Avenue, Lane Cove, N.S.W.

1959 Hadlington, Phillip Walter, B.Sc.Agr., 15 Annie Street, Hurstville, N.S.W.
1952 Hannon, Miss Nola Jean, B.Sc., Ph.D., 22 Leeder Avenue, Penshurst, N.S.W.
1952 *Hansford, Clifford Gerald, M.A., Sc.D. (Cantab.), D.Sc. (Adel.), F.L.S., P.O. Box 66, Uvongo Beach, Natal, South Africa.
1917 Hardy, George Huddleston Hurlstone, "Karambi", Letitia Street, Katoomba, N.S.W.
1960 Hartigan, Desmond John, B.Sc.Agr., 75 Northwood Road, Northwood, Lane Cove, N.S.W.
1958 Hennelly, John Patten Forde, B.Sc., Highs Road, West Pennant Hills, N.S.W.
1951 Hewitt, Bernard Robert, B.A. (Qld.), B.Sc. (Syd.), M.Sc. (N.S.W. Univ. Tech.), Hunter Valley Research Foundation, P.O. Box 23, Tighe's Hill 2N, N.S.W.
1930 Heydon, George Aloysius Makinson, M.B., Ch.M., 9 Sirius Avenue, Mosman, N.S.W.
1938 Hill, Miss Dorothy, M.Sc., Ph.D., Department of Geology, University of Queensland, Brisbane, Queensland.
1943 *Hindmarsh, Miss Mary Maclean, B.Sc., Ph.D., 4 Recreation Avenue, Roseville, N.S.W.
1956 *Holder, Miss Lynette Anne, B.Sc., 48 Rutledge Street, Eastwood, N.S.W.
1932 Hossfeld, Paul Samuel, M.Sc., Ph.D., 132 Fisher Street, Fullarton, South Australia.
1953 *Hotchkiss, Arland Tillotson, M.S., Ph.D. (Cornell), Department of Biology, University of Louisville, Louisville 8, Kentucky, U.S.A.
1956 *Hotchkiss, Mrs. Doreen Elizabeth, Ph.D., B.A., M.A. (*née* Maxwell), 2440 Longest Avenue, Louisville, Kentucky, U.S.A.
1942 Humphrey, George Frederick, M.Sc., Ph.D., C.S.I.R.O. Marine Biological Laboratory, Box 21, Cronulla, N.S.W.

1960 Ingram, Cyril Keith, B.A., B.Ec., P.O. Box 12, Bathurst, N.S.W.
1938 Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., Australian Forestry School, Canberra, A.C.T.
1961 Jacobson, Miss Constance Mary, B.Sc., 9 Fletcher Street, Bondi, N.S.W.
1960 James, Sidney Herbert, M.Sc., 64 Reynolds Avenue, Bankstown, N.S.W.
1960 Jenkins, Thomas Benjamin Huw, Ph.D., Department of Geology and Geophysics, Sydney University.
1952 Jessup, Rupert William, M.Sc., 6 Penno Parade North, Belair, South Australia.
1956 Jobson, Arthur Edgar, 3 Wellington Road, East Lindfield, N.S.W.
1957 Johnson, Bruce, B.Sc.Agr., Ph.D., Waite Agricultural Research Institute, University of Adelaide, Private Mail Bag, Adelaide, South Australia.
1947 Johnson, Lawrence Alexander Sidney, B.Sc., c.o. National Herbarium, Royal Botanic Gardens, Sydney.
1945 Johnston, Arthur Nelson, B.Sc.Agr., 99 Newton Road, Strathfield, N.S.W.
1960 Jolly, Violet Hilary, M.Sc., Ph.D., 1 Twenty-Second Street, Warragamba Dam, N.S.W.
1958 Jones, Edwin Llewelyn, B.A., P.O. Box 196, Leeton 6S, N.S.W.
1930 Joplin, Miss Germaine Anne, B.A., Ph.D., D.Sc., Department of Geophysics, Australian National University, Canberra, A.C.T.
1960 Judd, Howard Kenniwell, Minnamurra Falls Forest Reserve, Box 14, P.O., Jamberoo, N.S.W.

1949 Keast, James Allen, M.Sc., M.A., Ph.D. (Harvard), Australian Museum, College Street, Sydney.
1951 Kerr, Harland Benson, B.Sc.Agr., Ph.D., 41 Badminton Road, Croydon, N.S.W.
1937 Kesteven, Geoffrey Leighton, D.Sc., c.o. Division of Fisheries and Oceanography, C.S.I.R.O., P.O. Box 21, Cronulla, N.S.W.
1957 Kindred, Miss Berenice May, B.Sc., 58 Caroline Street, Kingsgrove, N.S.W.
1961 King, Miss Dianne, 9 Royce Avenue, Croydon, N.S.W.

1956 Langdon, Raymond Forbes Newton, M.Agr.Sc., Ph.D., Department of Botany, University of Queensland, George Street, Brisbane, Queensland.
1932 Lawson, Albert Augustus, 9 Wilmot Street, Sydney.
1934 Lee, Mrs. Alma Theodora, M.Sc. (*née* Melvaine), Manor Road, Hornsby, N.S.W.
1936 Lee, David Joseph, B.Sc., School of Public Health and Tropical Medicine, Sydney University.
1943 Lothian, Thomas Robert Noel, Botanic Gardens, Adelaide, South Australia.
1957 Luig, Norbert Harold, c.o. Faculty of Agriculture, Sydney University.

1958 Lyne, Arthur Gordon, B.Sc., Ph.D., C.S.I.R.O., Sheep Biology Laboratory, P.O. Box 144, Parramatta, N.S.W.
1951 Macdonald, Colin Lewis, Grenfell Road, Cowra, N.S.W.
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LIST OF NEW NAME, NEW SUBGENUS AND NEW SPECIES.

VOL. 86.

New Name.

New Subgenus.

New Species.

INDEX.

1961.

CORRIGENDA, PROCEEDINGS, 1961.

P. 60, line 28—for *Isoodon macrourus*, read *Perameles nasuta*

P. 61, line 25—for *I. macrourus*, read *P. nasuta*

P. 71, line 36—*for* the same host, read *P. nasuta*

P. 76, line 9—*for* III & IV, *read* II & III

P. 82, lines 7, 8—*for* short-nosed bandicoot, *Isoodon macrourus* (Gould), *read* long-nosed bandicoot, *Perameles nasuta* Geoffroy

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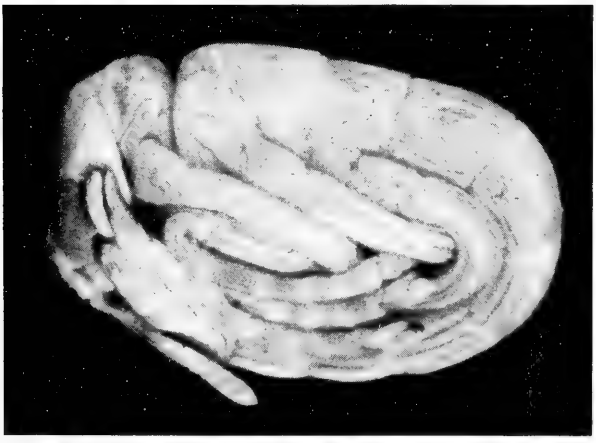
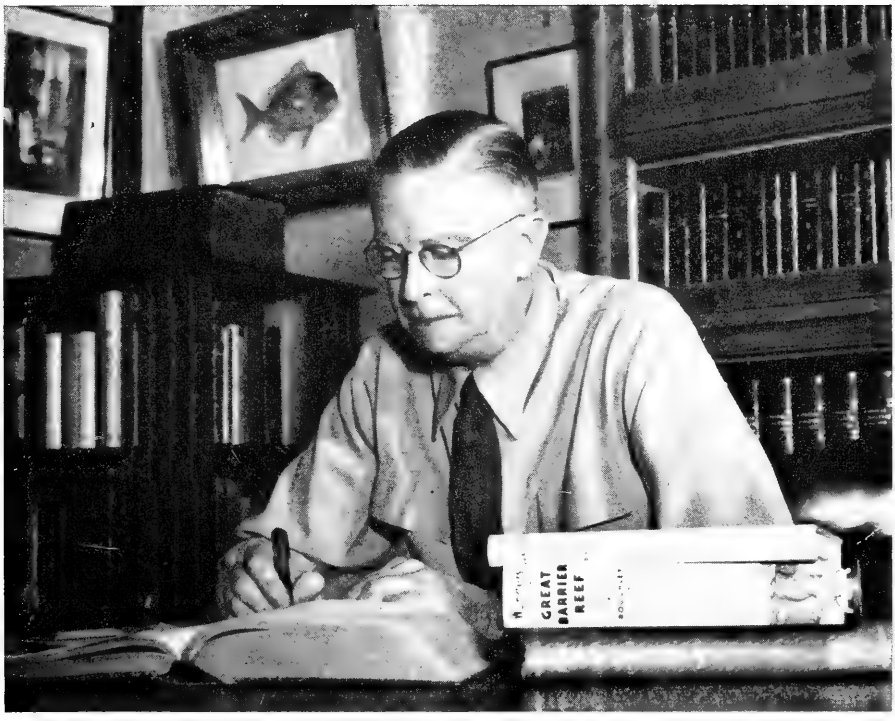
(Issued 20th February, 1962.)

Actinopteris indica Srivastava.

Plate x, B



Embryo of *Podacanthus wilkinsoni*.



T. C. Roughley.

NOTES ON AUSTRALIAN MOSQUITOES (DIPTERA, CULICIDAE). V.
Subgenus Pseudoskusea in Victoria.

By N. V. Dobrotworsky, Zoology Department, University of Melbourne.*

(Three Text-figures.)

[Read 28th September, 1960.]

Synopsis.

Adults of *Aëdes bancroftianus* Edwards and *Aëdes multiplex* (Theobald) are redescribed and the larvae of both species are described for the first time; the pupae of these species are figured. *Aëdes postspiraculosis*, n. sp., is described. An account is given of the biology and distribution of these species. *Aë. postspiraculosis* is closely related to *Aë. bancroftianus*, but can be distinguished not only by morphological traits, but also by its geographical distribution and biology. *Aë. bancroftianus* is stenogamous; *Aë. postspiraculosis* is eurygamous. The two species are sexually isolated and do not interbreed in nature where their distributions overlap. New records of the distribution of *Aëdes australis* (Erichson) are reported.

The subgenus *Pseudoskusea* of the genus *Aëdes* is represented in Victoria by four species. Three of these, *Aë. bancroftianus* Edwards, *Aë. postspiraculosis*, n. sp., and *Aë. multiplex* (Theobald), belong to group A—*Pseudoskusea*—which is characterized by Edwards (1932) as having: the vertex clothed with broad flat scales, no lower mesepimeral bristles, a very small eighth abdominal segment in the female, long cerci and no basal lobe on the coxite of the male terminalia. Group B—*Caenocephalus*—represented by *Aë. australis* (Erichson), is characterized by having: the vertex clothed with narrow scales only, lower mesepimeral bristles, a rather large eighth abdominal segment in the female, short cerci and a distinct basal lobe on the coxite of the male terminalia.

The species of Group A have very few traits in common with species from Group B. There is some similarity in the structure of the male terminalia, viz.: the absence of an apical lobe on the coxite and the absence of the harpago. These similarities, however, hardly justify the inclusion of the species of Group B in the subgenus *Pseudoskusea*; they should probably be placed in a separate subgenus, but this step should be deferred pending a revision of the subgenus *Pseudoskusea*.

Aëdes bancroftianus Edwards.

Aëdes bancroftianus Edwards, 1921, *Bull. ent. Res.*, 12: 74.

Distinctive Characters. Adult: Vertex clothed with broad, flat scales, dark brownish to creamy in colour. Male palps as long as proboscis or slightly longer. Post-spiracular area with only a median patch of scales. Fore and mid claws of female toothed, hind simple. Male terminalia: Coxites without apical and basal lobes, but with dense patch of hairs at base of coxites. Style with fine preapical setae. Harpago absent. Larva: Pigmented or white (in Queensland), antennae long, dark and curved. Head seta 5, single or 2-branched; 6, single. Seta 1 of VIIIth abdominal segment usually 2-branched, rarely 3-branched. Siphonal seta 1, long, 3-branched, arising at two-thirds of length from base. Distance between base of distal spine of pecten and base of seta 1 smaller than width of siphon at level of seta 1.

Description of Adult. Male. Head: Vertex clothed with broad, flat, pale or brownish scales; upright forked scales in front and towards neck, pale or dark. Proboscis and palps dark-scaled. Palps as long as proboscis with labella, or slightly

* This work was supported in part by a grant from the Trustees of the Science and Industry Endowment Fund of Commonwealth Scientific and Industrial Research Organization.

longer. Thorax: Integument dark brown. Scutum clothed with narrow scales either light brown or dark bronze in colour and becoming creamy around front margin and bare area; there may be two lines of dark scales extending from the scutellum for about half the length of the scutum. Scutellum with narrow pale-ochreous scales and 5–6 long bristles on each lobe. Anterior pronotum with elongate pale scales and bristles. Posterior pronotum with elongate dark brown scales. Post-spiracular area with only a median patch of scales and 9–12 bristles. Sternopleuron with large patch of broad scales extending from below pre-alar area along posterior edge; there are also several setae. Large patch of scales below upper mesepimeral bristles. Wing length: 3·1–4·0 mm. Knob of halters dark. Legs dark-scaled; front and mid femora pale below; hind femora pale except apical one-third or quarter and a dorsal line which are black. Fore tarsal claws unequal (Fig. 1, *b*, *c*, *d*); anterior claw with two teeth, posterior with one; mid claws unequal, both with one tooth; hind claws equal, simple. Abdomen: Tergites dark brown with basal creamy bands which may be very narrow. Sternites black-scaled, with basal lateral patches of pale scales which may join to form basal bands. Terminalia (Fig. 1, *a*): Coxite almost cylindrical, about four times as long as width at base; sternally and laterally with black scales and strong long bristles. Basal and apical lobes absent, but coxite has small dense patch of hairs at base. Style about three-fifths length of coxite, with distal third narrower and curved inwards; terminal spine long; 3–4 long, fine, preapical spines. Harpago absent. Lobes of IXth tergite small, with 5–6 setae.

Female. Females differ from males as follows: Palps about one-sixth length of proboscis. Wing length 2·7–4·1 mm. R_2 about twice its stem. Claws equal (Fig. 1, *e*, *f*, *g*); fore and mid claws toothed, hind claws simple. Tergites 2–4 with complete basal creamy bands, 5–6 with basal lateral creamy patches, sometimes forming basal bands. Sternites pale-scaled; apical black bands on sternites 4–6.

Variability. Adults from Queensland vary greatly in size and abdominal pattern. Typical females have the basal bands on the tergites well developed, but some specimens, particularly from Tarragindi, have unbanded tergites. The sternites also may be creamy scaled without apical black bands. In specimens with an unbanded abdomen the flat broad scales on the vertex are mainly dark, with only a few white scales mesially. Additional studies are required to decide the taxonomic status of the Tarragindi form.

New South Wales specimens are not as variable as those from Queensland. The posterior pronotum may have a patch of broad pale scales below; the venter is usually pale-scaled in females, but in males it may be black with lateral patches of white scales with or without basal creamy bands.

Victorian specimens are, in general, darker than those from New South Wales and Queensland, the upright scales on vertex, towards the neck, are almost black; the scutum has areas of dark almost black scales; the tergites are black-scaled with broad basal creamy bands; the venter in males may be almost black with lateral white patches, or may have scattered white scales particularly on sternite seven; in females the venter may be pale-scaled or may have an admixture of black scales; in some black scales may predominate.

The Western Australian specimens in general are similar to the Victorian specimens, but the flat wide scales on the lateral parts of the vertex are often dark, almost black, leaving only a small mesial area with pale scales. Among typical specimens there are small ones with the abdomen unbanded as in the Queensland form from Tarragindi.

Pupa. Details shown in Figure 1, *h*, *i*.

Larva (Fig. 1, *j*, *l*, *k*). Head and siphon pale (buff). Head as long as broad. Antennae dark, curved, spiculated, almost as long as head. Seta 1, 4–8-branched. Head seta 4, 1–3-branched; 5 and 6, single; 7, 3–5-branched; 8, single; 9, 3-branched. Mentum with central large tooth and 7–8 lateral teeth on each side. Prothoracic setae: 1, 2, 4, 5

and 6, single; 3, 2-branched; 7, 3-branched. VIIIth abdominal segment: seta 1, 2–3-branched; 2 and 4, single; 3, 4-branched; 5, 6-branched. Lateral comb patch of 70–80 fringed scales. Siphon tapering; index 4·0–4·5, mean 4·3. Pecten of 21–23 spines. Seta 1

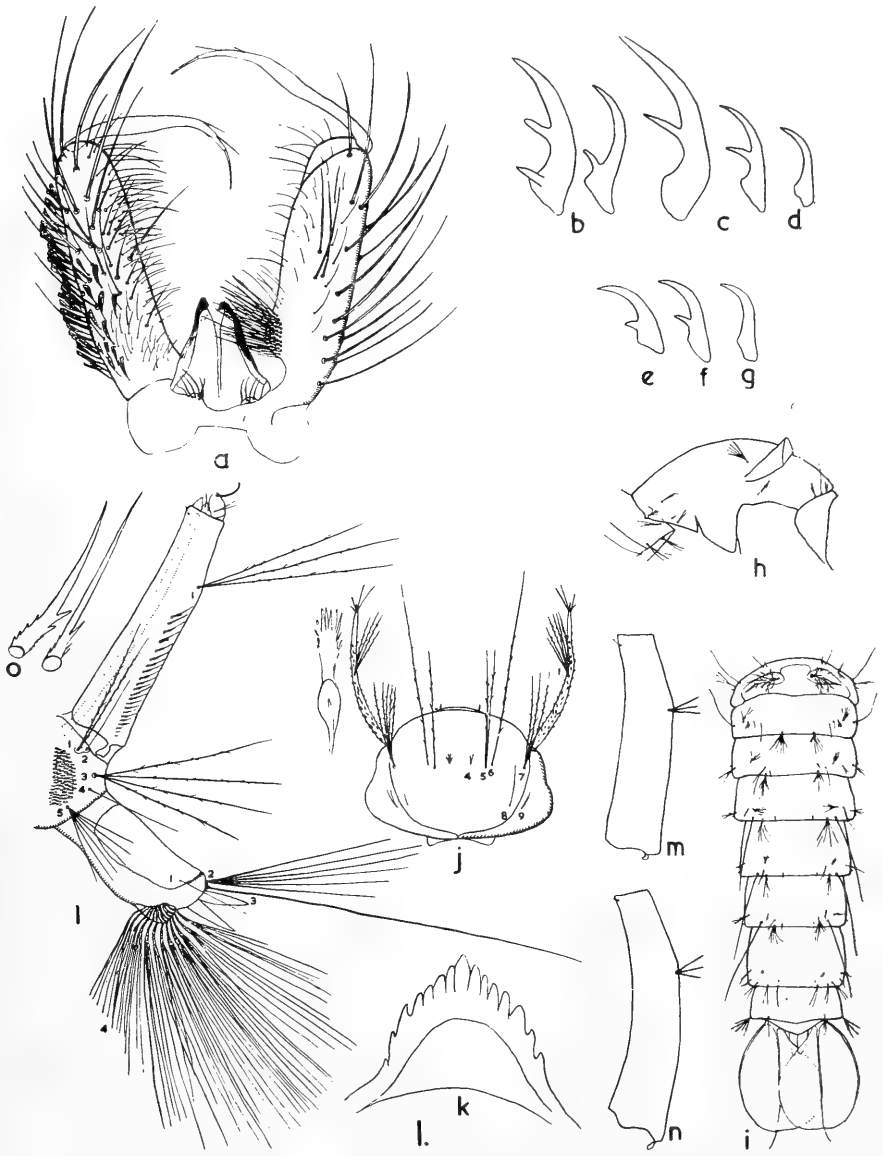


Fig. 1. *Aëdes bancroftianus* Edwards. *a*, ♂ terminalia, left coxite sternal aspect, right tergal aspect; *b-d*, ♂ tarsal claws: *b*, fore; *c*, mid; *d*, hind; *e-g*, ♀ tarsal claws: *e*, fore; *f*, mid; *g*, hind; *h-i*, pupa: *h*, cephalothorax and metanotum; *i*, abdomen; *j-n*, larva: *j*, head; *k*, mentum; *l*, terminal segments; *m*, *n*, siphons of larvae from Western Australia; *o*, pecten spine of larva from Euroa, Vic.

arising two-thirds length along siphon, long, usually 3-branched. Distance between base of distal spine of pecten and base of seta 1 smaller than width of siphon at level of seta 1. Siphonal tracheae very narrow. Anal segment: Seta 1 and 3, single; 2, 8–9-branched; 4 (ventral brush) of 11–12 tufts. Saddle covering about three-quarters of

dorsal part of segment. Anal papillae narrow, pointed, almost equal in length and about half length of saddle.

Variation of the Larvae. *Aë. bancroftianus* larvae collected at Mt. Gravatt, S. Qld., have "white body, light (buff) head and siphon, long black antennae" (E. N. Marks, personal communication). However, the larvae from Western Australia and Victoria have a pigmented body (the abdomen appears banded), and on this account are distinguishable, even to the naked eye, from the larvae of *Aë. postspiraculosis*, n. sp.

Larvae from different parts of Australia show a few significant variations. Thus larvae from Queensland (6 localities) have head seta 5 always single, seta 1 of VIIIth abdominal segment, 2-branched (1 specimen with 3 branches) and siphon index of 3·7–4·5, mean 4·0.

Larvae from Victoria (1 locality) have head seta 5 always 2-branched, seta 1 of VIIIth abdominal segment 2-branched and a siphon index of 4·0–5·0, mean 4·5.

Larvae from Western Australia (2 localities) have head seta 5 single or 2-branched, seta 1 of VIIIth abdominal segment 2–3-branched and a siphon index of 3·7–4·7, mean 3·7. The siphon is usually not straight, but is more or less backwards curved (Fig. 1, *m*, *n*).

Biology. *Aë. bancroftianus* is eurygamous. In Victoria it has been found breeding in freshwater pools during winter-spring months in the Euroa area. This is open plain country just north of the Dividing Range, with sparsely scattered eucalypts, mainly along creeks and roads. In 1958 it was breeding in a string of pools in a natural water course with almost vertical banks. No larvae were found in these sites in 1959, but they were present in a roadside ditch 2–2½ feet deep, with grassy edges and reeds in some places; the water was cloudy.

The larvae behave like those of *Aë. theobaldi* (Taylor): most of the time they lie on their backs on the bottom of the pool, or attach themselves to the sides, or to vegetation, by means of strong hook-like setae on the spiracular valves.

In Victoria the larvae of *bancroftianus* have been found alone or in association with *Aë. alboannulatus* (Macq.) and *C. p. australicus* Dobr. and Drumm. and occasionally with *Aë. rubrithorax* Macq. and *Aë. postspiraculosis*, n. sp.

In Queensland *bancroftianus* breeds in similar habitats: Tarragindi: "Series of isolated pools in natural water course; part sun; shallow to steep bare edge, 1 foot depth; no vegetation". Mt. Gravatt: "Isolated waterhole in stagnant creek; part sun, shade from trees; slightly muddy". Terry Hie Hie (Coll. A. L. Dyce): "Cleared hillside with very few green trees remaining; a string of waterholes in a small rain water creek; water muddy". Salisbury: "Waterhole is in partly dried water course; part shade; clay edge; depth 2 feet. Water discoloured". Camp Mt.: "Casual sunlit grassy pool". (E. N. Marks, personal communication.)

The larvae of *bancroftianus* in Queensland have been found in association with: *Aë. alboannulatus*, *Aë. vittiger* Skuse, *Aë. alternans* Westw., *Aë. rubrithorax* (i.e., *procax* Marks), *Aë. milsoni* (Taylor), *A. annulipes* Walk., *C. p. australicus*, *C. pseudomelaconia* Theo., *C. douglasi* Dobr.

Biting Habits. *Aë. bancroftianus* is a day biting mosquito which attacks man, dog, rabbit, cow and horse.

Distribution. It is widely distributed in Australia, but apparently is absent from the south-east part of Victoria south of the Dividing Range. Specimens have been examined from the following localities: QUEENSLAND: Julia Creek (M. Arden), Richmond (E. N. Marks), Longreach (E. J. Reye), Clermont (J. L. Wassell), Charleville (E. J. Reye), Roma (E. R. B. Marks)—all dry inland areas. Jimna (J. L. Wassell), Camp Mt. (E. N. Marks), Brisbane Suburbs: Tarragindi, Mt. Gravatt (P. J. Sparks), Salisbury (L. Angus)—all humid coastal, comparatively high rainfall areas. Lynd Range (J. L. Wassell), Wondae; Eidsvold (Type locality, T. L. Bancroft). NEW SOUTH WALES: Uralla, Ben Lomond, Chiswick, Exmouth, Bargibal, Bindarra (E. J. Waterhouse), Terry Hie Hie (A. L. Dyce), Merricumbene (A. L. D. and R. Lewis), Corowa (G. W.

Douglas). Northern Territory: Palm Valley about 70 m. w. Alice Springs (K. A. Walker). Western Australia: Moora, Onslow (E. J. Britten), Kojonup, Darkan, Piawaning (D. L. McIntosh), E. Dale Bridge (J. H. Calaby). Victoria: Bright (K. Myers), Mildura (N. Kent), Kilmore, Euroa, Seymour, Armstrong, Grampians, Steiglitz (N. V. Dobrotworsky), Castlemaine, Serpentine, Clunes (A. Neboiss), Maryvale (G. W. Douglas), Tubbut (E. Bass).

Aëdes postspiraculosis, n. sp.

Types. The type series were bred from larvae collected at Wattle Glen, Victoria (17.9.59). The holotype male, allotype female and ten paratypes have their associated larval and pupal skins. The holotype male, allotype female, six paratype males and six paratype females are in the collections of the National Museum, Melbourne. One paratype male and one paratype female are in each of the following collections: C.S.I.R.O., Division of Entomology, Canberra; School of Public Health and Tropical Medicine, Sydney, University of Queensland, Brisbane; British Museum (Natural History), London; U.S. National Museum, Washington.

Distinctive Characters. Vertex clothed with broad, flat scales pale mesially and dark laterally. Male palps shorter than proboscis with labella. Post-spiracular area with patch of scales medially and a second elongate patch on lower part between sub-spiracular area and sternopleuron. In female all claws simple. Male terminalia: Coxites without apical or basal lobe, but with dense long fine hairs at base of coxites. Style with thick preapical setae. Harpago absent. Larva: Milky-white. Head seta 5, single. Seta 1 of VIIIth abdominal segment 3-branched, rarely 4-branched. Siphonal seta 1, long, 3–5-branched, arising at two-thirds of length from base. Distance between base of distal pecten spine and seta 1 greater than width of siphon at level of seta 1.

Holotype Male. Head: Vertex clothed with broad, flat scales, pale mesially and darker laterally. Upright forked pale scales only towards neck. Proboscis and palps black-scaled. Palps slightly shorter than proboscis with labella. Thorax: Integument black. Scutum clothed with narrow brownish and yellowish-golden scales which become paler and broader around bare area. Scutellum with narrow pale scales and 10–11 long dark bristles on each lobe. Anterior pronotum with elongate pale scales and bristles. Posterior pronotum clothed with narrow and elongate brown scales, which become broader and paler below. Post-spiracular area with patch of scales and bristled medially and a second elongate patch on lower part between sub-spiracular area and sternopleuron. Sternopleuron with large patch of broad scales below pre-alar area and extending along posterior edge of sternopleuron; there are also several setae, two of them long and strong. Mesepimeron with large patch of scales below upper mesepimeral bristles; lower mesepimeral bristles absent. Wing length 4·0 mm. Wings dark-scaled with a few white scales at base of costa. Knob of halters pale-scaled. Legs: Dark-scaled; front and mid femora pale below; hind femora pale except tip and dark line dorsally. Fore tarsal claws unequal (Fig. 2, *b*, *c*, *d*); anterior claw with two teeth, posterior with one; mid claws unequal, both with one tooth; hind claws equal, simple. Abdomen: Tergites black-scaled, second with narrow creamy basal band, 3–6 with broad basal bands. Sternite 1 pale-scaled, 2–6 creamy basally, black apically and with some black scales medially on sternites 2–3. Terminalia (Fig. 2, *a*): Coxites almost cylindrical, with black scales and strong long black bristles sternally and laterally. Basal and apical lobes absent, but coxite has dense patch of fine long hairs at base. Style about three-fifths length of coxite, narrow, curved inwards on apical third, with 3–4 preapical spines at least two of which are almost as thick as appendage; appendage long, slender and almost straight. Paraproct with single tooth. Harpago absent. Lobes of IXth tergite small with 5–6 seta.

Paratype Males. The series of 10 paratype males does not show much variation. Palpi may be as long as proboscis without labella or slightly shorter. Scutal scales may be light brown except on fossa where they are dark brown. Wing length 3·7–4·0 mm. Black apical bands on sternites may extend mesially, forming a triangular black patch.

Allotype Female. This differs from the holotype as follows: Head: Upright forked scales are in front along eye margin and more numerous towards neck. Palps about one-sixth length of proboscis. Thorax: Scutal scales mostly dark brown, becoming pale around front margin and bare area; two small pale patches in front of bare area. Scutellum with 9–10 long bristles on each lobe. Wing length: 4·3 mm.; R_2 twice as long

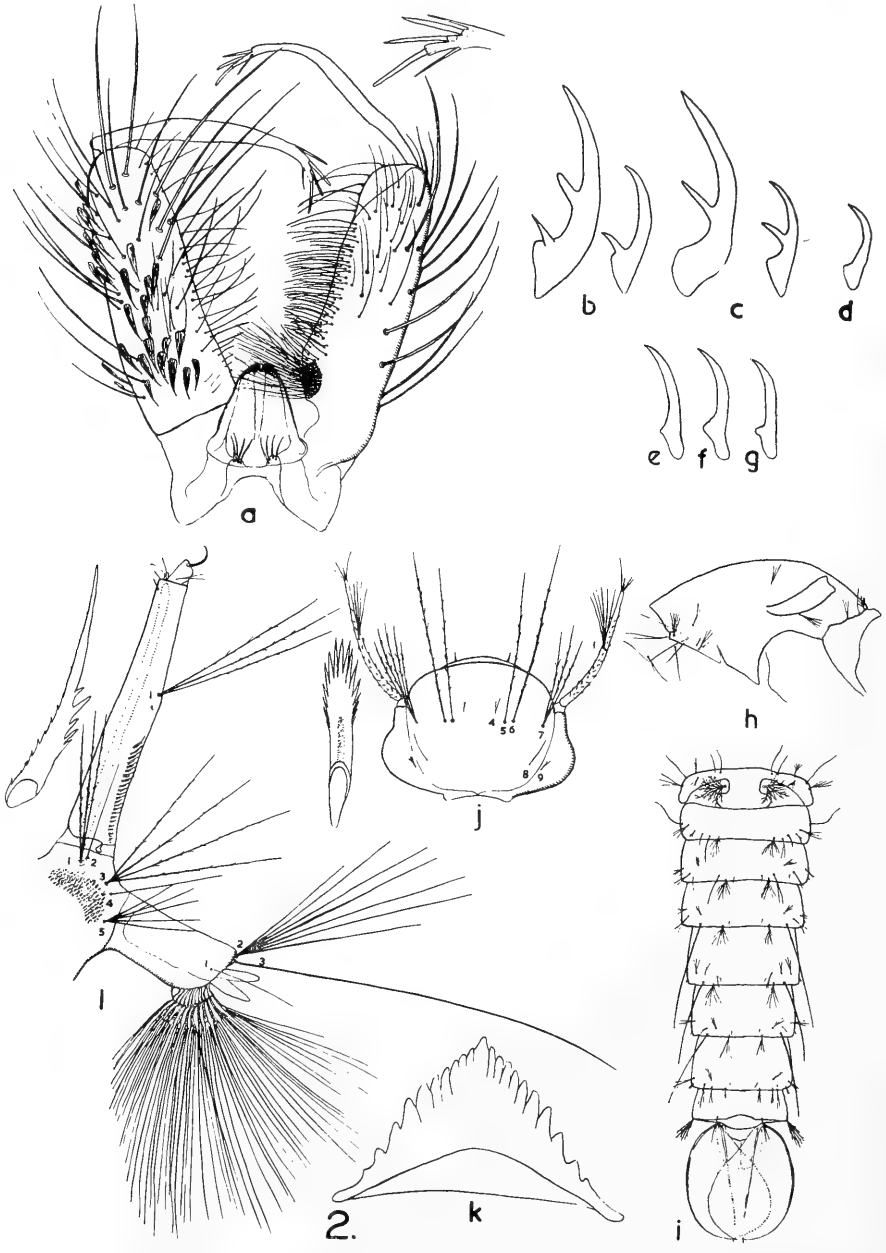


Fig. 2. *Aëdes postspiraculosis*, n. sp. *a*, ♂ terminalia, left coxite sternal aspect, right tergal aspect; *b-d*, ♂ tarsal claws: *b*, fore; *c*, mid; *d*, hind; *e-g*, ♀ tarsal claws: *e*, fore; *f*, mid; *g*, hind; *h-i*, pupa: *h*, cephalothorax and metanotum; *i*, abdomen; *j-l*, larva: *j*, head; *k*, mentum; *l*, terminal segments.

as its stem. All claws equal, simple (Fig. 2, *e*, *f*, *g*). Tergite 7, black. Sternites creamy-scaled with some admixture of black scales on segment 6; segment 7, black-scaled.

Paratype Females. The series of 10 paratype females does not show significant variations. Wing length: 4·0–4·3 mm.; R_2, 1·7–2·2 as long as its stem.

Pupa. Details shown in Figure 2, *h*, *i*.

Larva (Fig. 2, *j*, *l*, *k*). Milky white; head and siphon light brown, siphon becoming darker towards tip. Head: Antennae dark, thin, curved, spiculated, almost as long as head; seta 1, 4–7-branched. Head setae: 4, 2–4-branched; 5, 6 and 8, single; 5, single, rarely 2-branched on one side; 7, 4–5-branched (may be 3-branched on one side); 9, 2–5-branched. Mentum with long central tooth and 9–11 strong lateral ones on each side. Prothoracic setae: 1, 2, 3, 4, 5 and 6, single; 7, 3–4-branched. VIIIth abdominal segment: Seta 1, 3–4-branched; 2 and 4, single; 3, 4–5-branched; 5, 4–7-branched. Lateral comb patch of 60–70 fringed scales. Siphon tapering, with index 4·7–5·3, mean 5·0; pecten of 20–30 spines. Seta 1 arising two-thirds along siphon, long, usually 3-branched, may be 4–5-branched. Distance between base of distal pecten spine and seta 1 greater than width of siphon at level of seta 1. Siphonal tracheae very narrow. Anal segment: Seta 1 and 3, single; 2, 5–8-branched; 4 (ventral branch), of 11–12 tufts. Saddle covering three-quarters of dorsal part of segment. Anal papillae narrow, almost equal in length, about half length of saddle.

Biology. Aë. postspiraculosis is stenogamous. It is confined to wooded undulating country. Natural water courses which run only after heavy rains and retain water in holes for long periods provide the main breeding sites for this species. Water in such pools is usually cloudy. The pools may or may not have vegetation, but the banks are usually grassy; the depth varies from 1 to 2½ feet. The pools are usually shaded for part of the day and the water temperature remains below 20°C. even during the summer. The larvae behave like those of *Aë. bancroftianus* lying on their backs on the bottom for most of the time or attaching themselves to vegetation.

The number of generations depends on rainfall; in drier areas or during very dry summers there would be only spring and autumn generations, but in higher rainfall areas or during wet summers there may be two or more additional summer generations.

Mating occurs during the day. The males form small swarms of a dozen or two near the breeding sites; they move about close to the observer and near the ground, in "searching flights", and as females approach the observer, the males attack them. Coupling occurs in flight and is usually completed on the grass.

In the laboratory mating will take place in cages of 1 cubic foot capacity, if the mosquitoes have been induced to fly by shaking the cage or by just blowing into it. As soon as the females are in flight the males attack them and coupling can be observed.

The larvae have been found in association with *Aë. rubrithorax* (*queenslandis* (Strickl.)), *Aë. alboannulatus*, *Aë. waterhousei* Dobr., *Th. inconspicua* Lee, *C. p. australicus* and occasionally with *Aë. bancroftianus*.

Biting Habits. It is a day biting mosquito which attacks man; it usually prefers to settle on clothing rather than on bare skin.

Distribution. Aë. postspiraculosis is distributed widely on and south of the Dividing Range in Victoria and is also recorded from New South Wales and South Australia. Specimens have been examined from the following localities: NEW SOUTH WALES: Exmouth, Uralla (E. J. Waterhouse). VICTORIA: Lyonville, Ballan, Grampians, Kilmore, Steiglitz, Ringwood, Wattle Glen, Panton Hill, Hurstbridge, Eltham, Christmas Hills, Baxter (N. V. Dobrotworsky). SOUTH AUSTRALIA: Mt. Torrens (E. W. Lines).

Reproductive Isolation of Aë. bancroftianus *and* Aë. postspiraculosis.

Reproductive isolation of the two species was demonstrated by mating experiments.

Adults of *Aë. bancroftianus* were reared from larvae collected at Euroa, adults of *Aë. postspiraculosis* from larvae collected at Wattle Glen. In both groups the pupae

were segregated according to sex. All mating experiments were carried out at room temperature; the mosquitoes used were at least four days old. Successful mating was determined by examination of the spermathecae.

Aë. bancroftianus did not mate in cages of 6 cubic feet capacity even if there were 4–6 times as many males as females. In one experiment, for example, 11 females were caged with 45 males for 6 days; in another, 25 females were caged with 65 males for 14 days. Not a single female was fertilized in either experiment.

It was observed that the males remain inactive during the day and evening flying, only to feed on sugar solution. When disturbed they soon settled without making any attempts to copulate with females.

Aë. postspiraculosis, which mates readily in small cages, behaves quite differently. Males are very active; they often remain in flight for long periods and attack any flying females.

Preferential mating experiments (Table I) demonstrate that *postspiraculosis* males show complete preference for females of their own species and did not mate with *bancroftianus* females even when no choice was given.

TABLE 1.

Preferential Mating of the Males of Aë. postspiraculosis *with Females of* Aë. bancroftianus *and* Aë. postspiraculosis.

Number of			Fertilized.		Size of Cage.
Males.	Females.				
	bancroftianus.	*postspiraculosis.*	*bancroftianus.*	*postspiraculosis.*	
10	25	25	0	11	1 cub. foot
20	20	20	0	14	1 cub. foot
20	20	—	0	—	6 cub. feet

In one locality in Victoria (Steiglitz) both species have been breeding in large numbers in the same pool. Examination of the larvae and the adults from this locality revealed no intermediates; apparently the two species are reproductively isolated in nature and therefore *Aë. postspiraculosis* can be regarded as a good species.

Aë. postspiraculosis is the most recent species, which may be derived from *Aë. bancroftianus*. It apparently arose on the edge of the distribution of *Aë. bancroftianus* somewhere on the Dividing Range and then spread to the south-eastern cooler part of Australia.

AËDES MULTIPLEX (Theobald).

Skusea multiplex, Theobald, 1903, *Mon. Cul.*, III: 293–294. *Pseudoskusea multiplex*, Theobald, 1907, *Mon. Cul.*, IV: 192–193. *Aëdes multiplex*, Edwards, 1924, *Bull. ent. Res.*, 14: 386.

Distinctive Characters. Adult: Vertex clothed with broad, flat scales. Males: Palps as long as proboscis. Thorax clothed with narrow bronzy-black scales, with transverse band of ochreous scales across middle of scutum. Sub-spiracular and post-spiracular areas devoid of scales. Male terminalia: Coxites without apical and basal lobes, but with patch of hairs at base. Harpago absent. Larva: Head seta 5 and 6, 2-branched; seta 1 of VIIIth abdominal segment 6–7-branched. Seta 1 arising slightly beyond mid length of siphon, small, 2–3-branched.

Description of Adult. Male. Head: Narrow curved golden scales round eye margin. Vertex clothed with broad, flat, dark scales, sometimes pale. Proboscis and palps dark-scaled. Palps about as long as proboscis with labella. Thorax: Integument dark brown. Scutum clothed with narrow curved bronzy-black scales, with transverse band of ochreous scales across middle of scutum; this band may be broken into two lateral patches. Scutellum with narrow pale scales and 4–5 long bristles on each lobe. Anterior

pronotum with dark bristles only. Posterior pronotum with a few narrow bronze scales. Post-spiracular area with bristles only. Sternopleuron with large patch of broad white scales below prealar area and a second patch along posterior edge; the

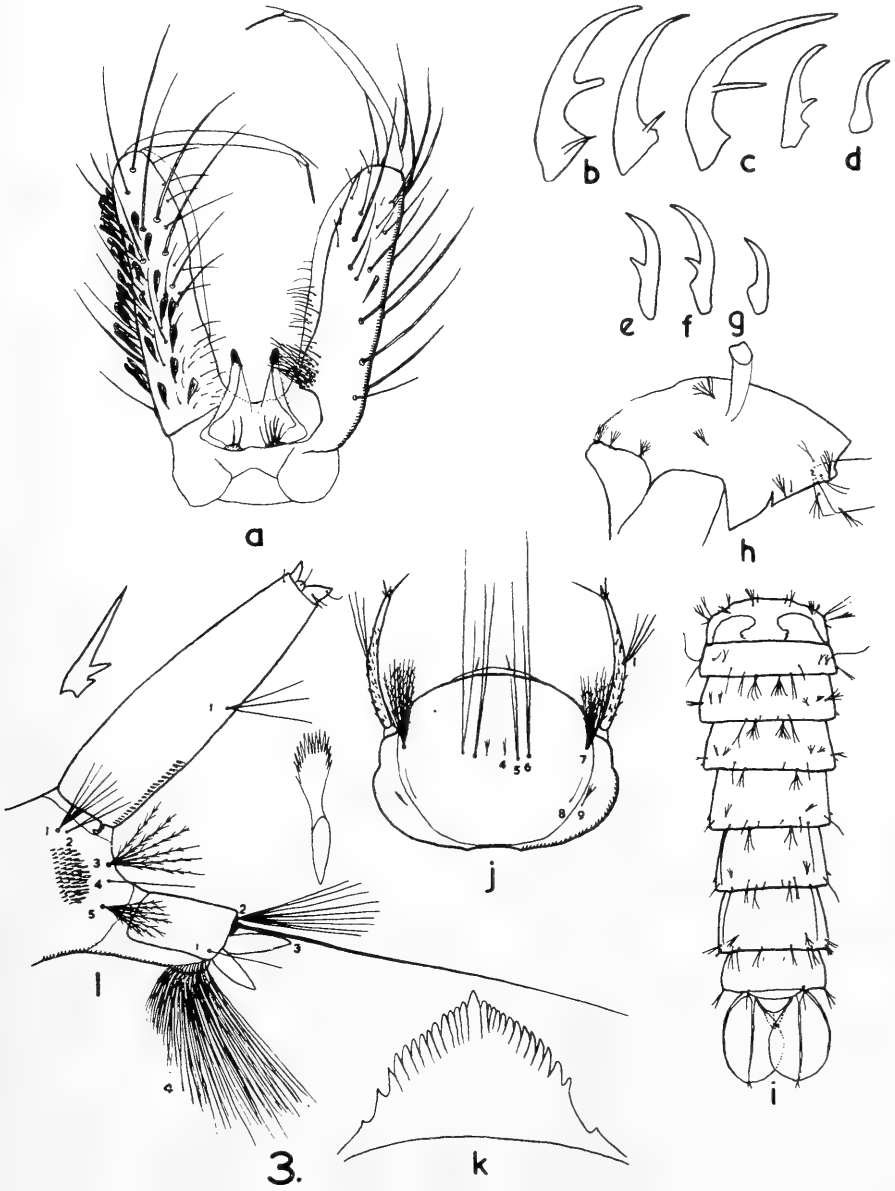


Fig. 3. *Aëdes multiplex* (Theobald). *a*, ♂ terminalia, left coxite sternal aspect, right tergal aspect; *b-d*, ♂ tarsal claws: *b*, fore; *c*, mid; *d*, hind; *e-g*, ♀ tarsal claws: *e*, fore; *f*, mid; *g*, hind; *h-i*, pupa: *h*, cephalothorax and metanotum; *i*, abdomen; *j-l*, larva: *j*, head; *k*, mentum; *l*, terminal segments.

two patches may join. Towards posterior edge of sternopleuron there are two strong bristles and several weaker ones. Large patch of scales below upper mesepimeral bristles; no lower bristles. Wing length about 3 mm. Knot of halters dark-scaled. Legs black, unbanded; fore and mid femora pale below, hind femora pale on basal half,

dark on apical half and with dark line dorsally. Fore tarsal claws unequal (Fig. 3, *b, c, d*); anterior claw with two teeth, posterior with one; mid claws unequal, both with one tooth; hind claws equal, simple.* Abdomen: Tergites black-scaled with narrow basal white bands on segments 2–7. Sternites white-scaled with apical black bands. Terminalia (Fig. 3, *a*): Coxite almost cylindrical, four times as long as their width at base, sternally and laterally with black scales and strong and weak bristles. Basal and apical lobe absent, but coxite with small patch of moderately long fine hairs at base. Style about three-fifths length of coxite, almost straight, narrowing apically with 3 fine spines; appendage long. Lobes of IXth tergite with 2–6 setae.

Female. Females differ from the males as follows: Flat, broad scales on vertex may be black except for some ochreous-white scales mesially. A few black forked upright scales in front of vertex and towards neck. Palps about one-sixth length of proboscis. Wing length: 2·9–3·6 mm., R_2 little less than twice its stem. Hind femora pale on basal two-thirds; apical third and dorsal line black. Claws equal (Fig. 3, *e, f, g*); fore and mid claws toothed, hind claws simple. Tergites with lateral basal patches of white scales; in addition there may be a median patch of white scales at base of segments 2 and 6, and narrow basal bands on segments 3–5. Sternites black-scaled with white basal bands.

Larva (Fig. 3, *j, l, k*). Head and siphon brownish, body whitish. Head about three-quarters as long as broad. Antennae about four-fifths length of head; seta 1, 3-branched. Head setae: 4, 3–6-branched; 5 and 6, 2-branched; 7, 8–12-branched; 8, single; 9, 4–5-branched. Seta 6 of 2 unequal branches, inner branch much thinner and about three-quarters length of outer one. Mentum with longer central tooth and 11–12 lateral teeth on each side. Prothoracic setae: 1, 2, 3, 5 and 6, single; 3, may be 2-branched; 4, 2-branched; 7, 3-branched. VIIIth abdominal segment: Seta 1, 6–7-branched; 2, 2-branched or single; 3, 6–7-branched; 4, single; 5, 6–7-branched. Lateral comb patch of about 60 fringed scales. Siphon almost cylindrical, slightly tapering apically; index 4·1–4·6, mean 4·4. Pecten of 18–24 spines; spines small with 1 or 2 teeth at base. Seta 1 arising slightly behind mid length of siphon, 2–3-branched, small. Anal segment: Seta 1 and 3 single; 2, 7–8-branched; 4 (ventral brush), of 11–12 tufts. Saddle covering about three-quarters dorsal part of segment. Anal papillae unequal, upper pair about half length of saddle.

Biology. Aë. multiplex is common only at Cabbage Tree Creek (East Gippsland) in Victoria. Larvae had not been collected in the field in Victoria. In Queensland they have been found in fairly shaded ground pools (e.g., at Tewantin) "in drying-out tea-tree swamps close to mangroves, water was fresh, discoloured, peaty soil, some dried grass or sedge". At Woombye larvae have been found alone in a shallow well with earth walls and covered with wooden clubs (E. N. Marks).

The larvae of *multiplex* have been found in association with *A. funereus* and *C. annulirostris.*

Biting Habits. Aë. multiplex is a day biting mosquito which attacks man.

Distribution. Aë. multiplex is a coastal species which is distributed from Queensland to East Gippsland, Victoria. Specimens have been examined from the following localities: Queensland: Tewantin (E. N. Marks), Maroochydore (Perkins and Wassell), Maoloolaha (E. N. Marks), Woombye, Endlo Creek, Forest Glen, Buderim (J. L. Wassell), Mountain Creek (Buderim), Myora, Dunwich (E. N. Marks): the last two localities are on Stradbroke I. New South Wales: Williamstown (K. J. Clinton). Victoria: Cabbage Tree Creek, Kalimna (N. V. Dobrotworsky).

Aëdes australis (Erichson).

Culex australis Erichson, 1842, *Arch. Naturgesch.*, 8: 270. *Culex crucians* Walker, 1856, *Ins. Saund. Dipt.*, 1: 432. *Culicada tasmaniensis* Strickland, 1911, *Entomologist*, 44: 181. *Caenocephalus concolor* Taylor, 1914, *Trans. ent. Soc. Lond.*, 46: 700. *Aëdes*

* In Theobald's (1907) description of the male it is stated that both fore claws have one tooth; apparently the small basal tooth was not noticed.

concolor, Edwards, 1924, *Bull. ent. Res.*, 14: 387. *Aëdes australis*, Mattingly and Marks, 1955, Proc. Linn. Soc. N.S.W., 80: 163–166.

Aëdes australis is a saltwater breeder and is one of the few mosquitoes which combine stenogamy with autogeny. Because of this it can be easily colonized in the laboratory and it has been closely studied by Woodhill (1936), Woodhill and Pasfield (1941) and more recently by O'Gower (1958). The taxonomic position of this species has only recently been clarified by Mattingly and Marks (1955).

To avoid unnecessary repetition of the description of this species only its distinctive characters and new records are given.

Distinctive Characters. Adult: Vertex with narrow curved golden scales. Palps shorter than proboscis without labella; last segment swollen. Post-spiracular area with large patch of broad black scales medially and a few pale scales below it. All female claws equal, toothed. Male terminalia: Apical lobe of coxite absent; basal lobe prominent with numerous setae. Harpago absent. Larva: Antennae and siphon short. Head seta 5, single; 6, 2-branched. Seta 1 of VIIIth segment 3–6-branched. Siphon index about 2; seta 1 moderately long, 7–8-branched, arising about mid-length of siphon. Anal papillae absent.

Distribution. Specimens have been examined from the following localities: Victoria: Wilson's Promontory, Phillip Island, Williamstown (N. V. Dobrotworsky). Tasmania: Randall's Bay, Bichem (J. G. Anderson).

Acknowledgements.

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THE PSORIC MITES PARASITIC ON BATS. XVI.*

A New Species of the Genus Teinocoptes Rodhain from the Fruit-Bat Pteropus conspicillatus in Queensland (Teinocoptidae, Sarcoptiformes).

By A. Fain, Prince Leopold Institute of Tropical Medicine, Antwerp.

(Communicated by Mr. R. Domrow.)

(Five Text-figures.)

[Read 28th September, 1960.]

Synopsis.

Teinocoptes domrowi, n. sp., is described from the spectacled fruit-bat, *Pteropus conspicillatus*, in north Queensland. The other eight members of the family Teinocoptidae are parasites of African pteropodids.

As far as is known, the mites of the family Teinocoptidae Fain are strictly confined to fruit-bats (Pteropodidae), and hitherto all the members of the family (eight species belonging to two genera, *Teinocoptes* Rodhain and *Chirobia* Fain) have been found in Africa. These mites are true parasites, and they live either partly or completely embedded in the skin of their hosts.

List of Species of the Family Teinocoptidae.

I. Genus *Teinocoptes* Rodhain, 1923.

Species.	Locality.	Host.	Sub-order and Family of the Host.
T. epomophori Rodhain, 1923 (genotype).	Belgian Congo.	*Epomophorus wahlbergi haldemanni* Hallow.	Megachiroptera ; Pteropodidae.
	Belgian Congo.	*Epomophorus labiatus minor* Dobson.	,,
	Ruanda-Urundi.	*Epomophorus anurus* Heuglin.	,,
	Belgian Congo.	*Epomops franqueti* Tomes.	,,
	Belgian Congo.	*Micropteropus pusillus* Peters.	,,
T. rousetti Fain, 1959.	Belgian Congo.	*Rousettus leachi* Smith.	,,
T. astridae Fain, 1959.	Ruanda-Urundi.	*Rousettus* sp.	,,
T. eidoloni Fain, 1959.	Ruanda-Urundi.	*Eidolon helvum* Kerr.	,,
T. auricularis Fain, 1959.	Zanzibar.	*Epomophorus w. wahlbergi* Sundevall.	,,
	Belgian Congo.	*Micropteropus pusillus* Peters.	,,
T. domrowi n.sp.	Australia.	*Pteropus conspicillatus* Gould.	,,

II. Genus *Chirobia* Fain, 1959.

Ch. congolensis Fain, 1959 (genotype).	Belgian Congo.	*Rousettus leachi* Smith.	Megachiroptera Pteropodidae.
Ch. squamata Fain, 1959.	Ruanda-Urundi.	*Rousettus* sp.	,,
	Belgian Congo.	*Rousettus a. angolensis* Bocage.	,,
Ch. otophaga Fain, 1959.	Zanzibar.	*Epomophorus w. wahlbergi* Sundevall.	,,

Recently, Dr. J. L. Harrison, of the Queensland Institute of Medical Research Field Station at Innisfail, collected on *Pteropus conspicillatus* a rather long series of a sarcoptiform mite, which his colleague, Mr. R. Domrow, kindly sent to me for study. These mites belong to the genus *Teinocoptes*, and represent a new species, which I have pleasure in naming in honour of Mr. Domrow.

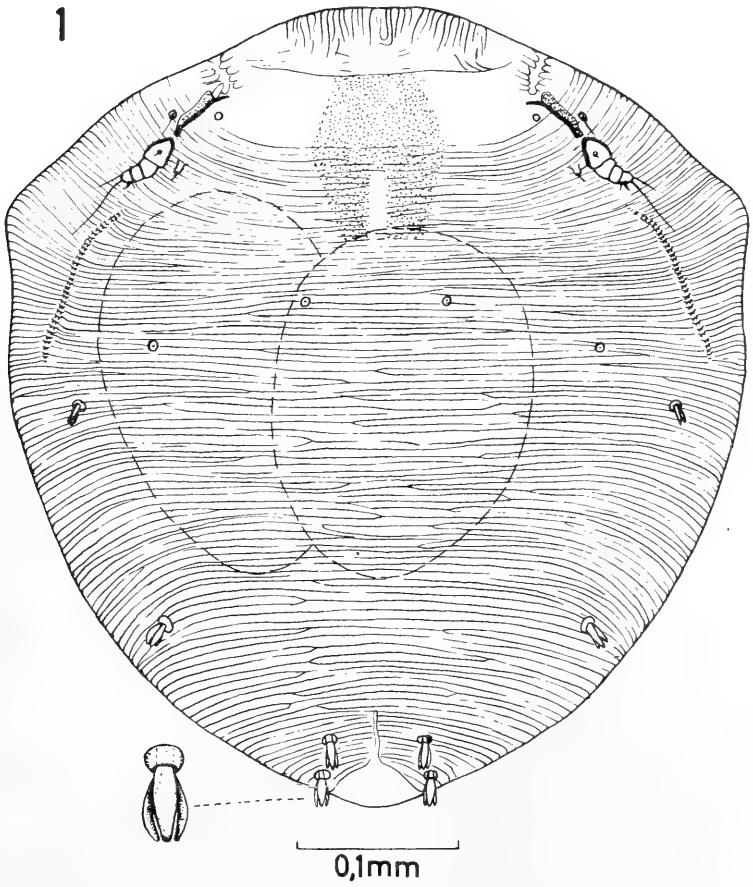
I wish to express my thanks to both these gentlemen for their kindness in having this interesting material sent to me.

* Other papers of this series have been published in various scientific journals.

TEINOCOPTES DOMROWI, n. sp.

Diagnosis. This new species is nearest to *T. auricularis* Fain in general appearance, but it differs from it in several features such as the characteristic structure of the chaetotaxy, the presence of a chitinous area behind the vulva, and the scaly structure of the larval cuticle.

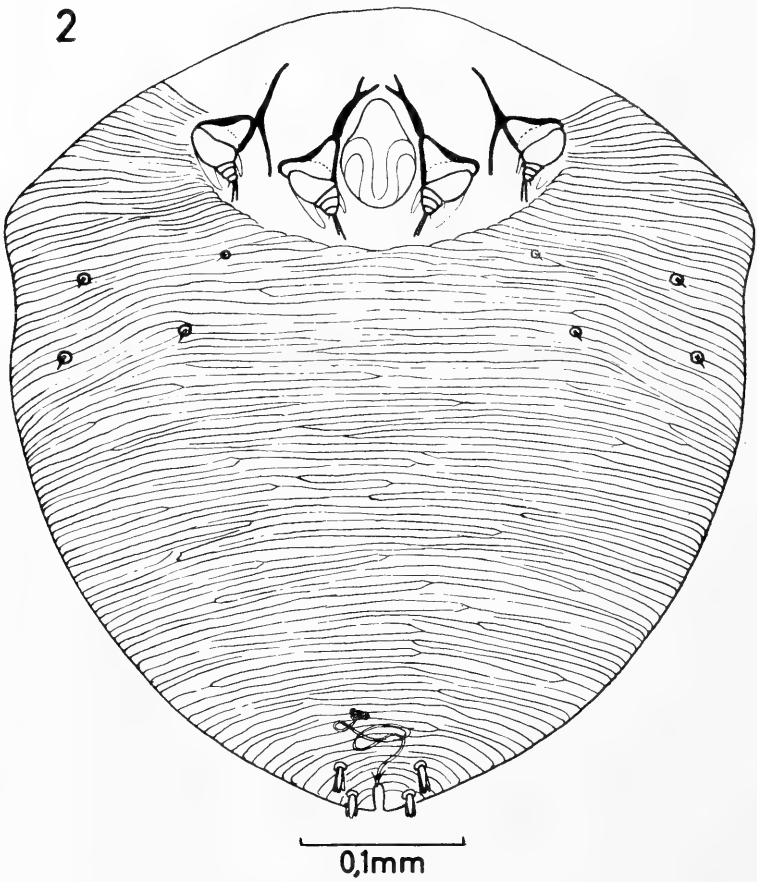
Female (holotype) (Text-figs 1–3). Body broadly conical or bell-shaped as in *Teinocoptes auricularis*, with an anterior flattened base bearing the legs, the mouth parts and the genital aperture, and a posterior rounded portion, on the summit of which



Text-fig. 1. *Teinocoptes domrowi*, n. sp., ♀, posteroventral view.

is located the anus. Length of idiosoma 510μ in the holotype, 450–540μ in five paratypes. Width at the level of the anterior border of the body 465μ in the holotype, 420–480μ in five paratypes. Cuticle completely striated, except in a small area behind the vulva, where it is finely verrucose. Dorsally the cuticle bears in the anterior third or fourth of the body four pairs of very small, short spines disposed in two transverse rows. Ventrally, at the same level as the dorsal spines, there are four small spines lying in a row, and laterally and slightly behind, two short but strong trifid hairs. The posterior third of the body bears laterally one pair of short, expanded trifid hairs. The anus is terminal, surrounded by eight expanded trifid hairs having the same shape as the posterolateral hairs, but slightly larger. The bursa copulatrix opens on a small papilla located on the dorsal side of the anus. It has a sinuous course, making six loops in

holotype (four to five in paratypes), and ends in a vesicular pouch located 30–60μ from the external papilla. Legs and mouth-parts as in *T. auricularis*; legs IV are vestigial, and represented only by a very short, slightly chitinized, and conical cuticular process bearing a short cylindrical, probably sensorial hair. The holotype contains two non-embryonated eggs measuring 240 × 162μ and 220 × 175μ. Some paratypes contain three eggs, of which one usually contains a fully developed larva. Size of the eggs in paratypes 220–270μ in length, and 150–180μ in width.

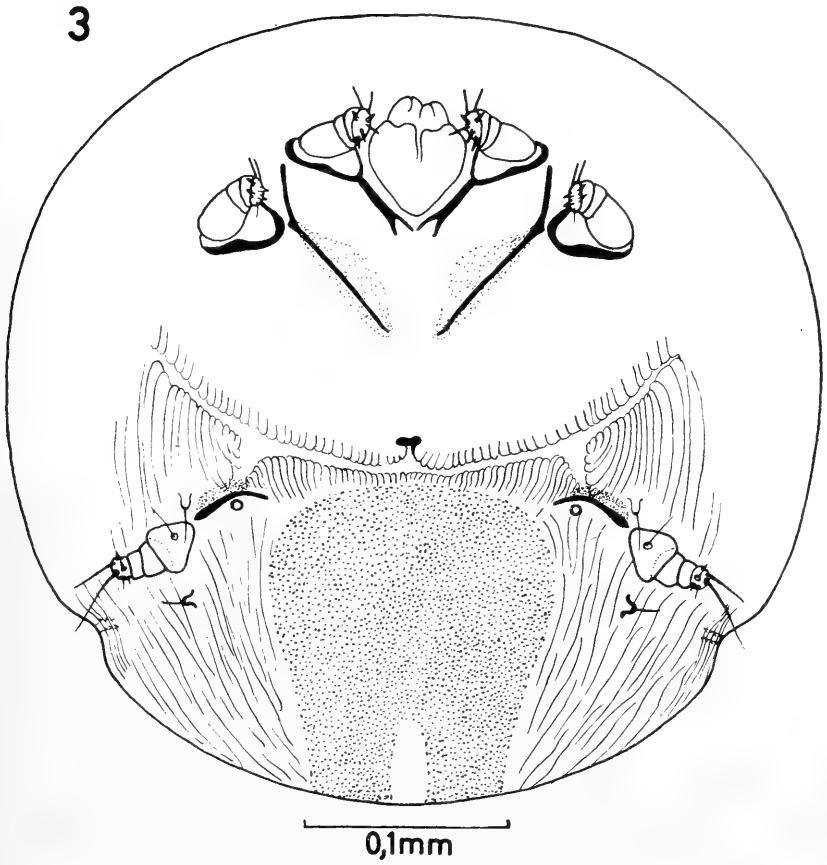


Text-fig. 2. *Teinocoptes domrowi*, n. sp., ♀, anterodorsal view.

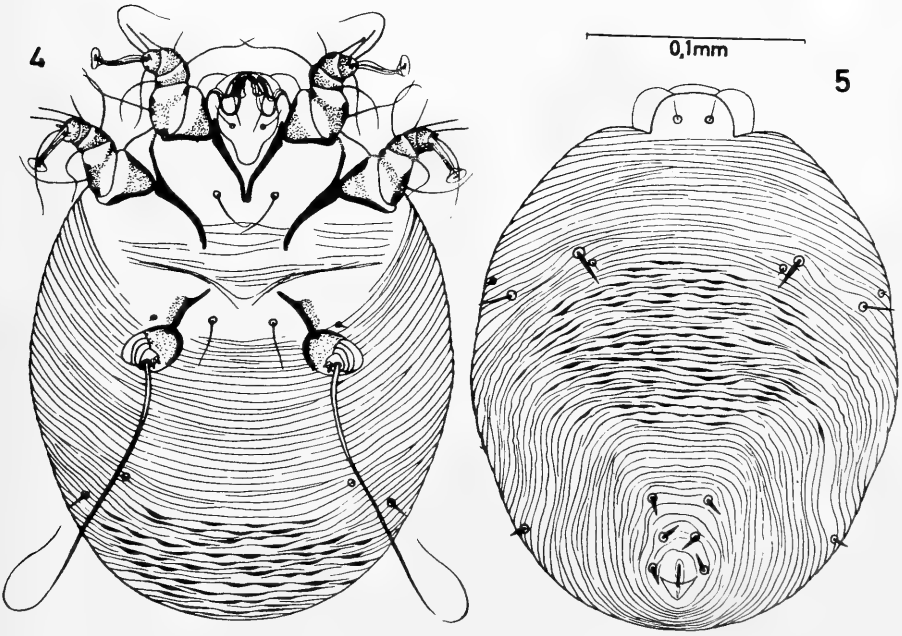
Nymph. The single nymph is 360μ long and 300μ wide. It is morphologically similar to the female, but there is no vulvar slit nor bursa copulatrix, and the lateral and perianal hairs are much smaller.

Larva (Text-figs 4–5). The length of three free larvae ranges from 225 to 230μ, the width from 180 to 200μ. General characteristics as in the other species of *Teinocoptes*. The larva of *T. domrowi* differs from all the other larvae of this genus by the scaly aspect of the cuticle of the opisthosoma. The anal area bears three pairs of lanceolate hairs much thinner than those of the adult female.

Localization of the Parasites. Dr. Harrison has noted that "all the mites were found attached to the extreme posterior margin of the interdigital flying membrane", and I have received from Mr. Domrow several pieces of the patagial skin, on which many specimens were still attached. All these mites were embedded, with the anterior third or fourth of the body in a cornified crateriform pouch formed by the host.



Text-fig. 3. *Teinocoptes domrowi*, n. sp., ♀, anteroventral view.



Text-figs 4-5. *Teinocoptes domrowi*, n. sp. Larva. 4, ventral view; 5, dorsal view.

Host. The spectacled fruit-bat, *Pteropus conspicillatus* Gould (Pteropodidae). Mundoo, near Innisfail, north Queensland, 29.vi.1959, J. L. Harrison coll.

Types. This mite is described from 24 specimens, comprising the type female and 23 paratypes (four larvae, one nymph, 18 females). The holotype female and paratype females, nymph and larvae, are in the Queensland Museum, Brisbane; paratypes are also in the South Australian Museum, Adelaide; United States National Museum, Washington; South African Institute for Medical Research, Johannesburg; Museum d'Histoire Naturelle, Paris; British Museum (Natural History), London; Musée de Tervuren; Institut Royal des Sciences Naturelles de Belgique, Brussels; and in the collection of the author.

Mr. Domrow has a further fifteen specimens from three bats of the same species, which I have not seen.

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————, 1959*a*.—Les acariens psoriques parasites des chauves-souris. XII. Deux nouvelles espèces des genres *Teinocoptes* et *Chirobia* chez des roussettes africaines (Sarcoptiformes-Teinocoptidae). *Bull. Ann. Soc. Roy. ent. Belg.*, 95 (11-12) : 336-341.

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THE INHERITANCE OF RESISTANCE OF *LINUM USITATISSIMUM* L. TO THE AUSTRALIAN *MELAMPSORA LINI* (PERS.) LÉV. RACE COMPLEX.

By H. B. Kerr.

[Read 26th October, 1960.]

Synopsis.

A physiologic race survey of the pathogen *Melampsora lini* (Pers.) Lév. was carried out at the Faculty of Agriculture, Sydney University, over the period 1948 to 1953. The races identified were used in studies of the mode of inheritance of resistance of the host varieties in the differential series. These studies confirmed the division of the Australian race complex into two major groups, Punjab-attacking and non-Punjab-attacking. The latter indicated the same pathogenic capacity as races previously identified by Flor from North and South American collections. With the exception of a resistance factor in Ottawa 770B, all the resistance factors operative against non-Punjab-attacking races had previously been identified by Flor in the respective differential varieties.

Several differential varieties carried one or more additional resistance factors which were effective against the Punjab-attacking collections but which had not previously been detected in these varieties by Flor. This emphasized the relative avirulence (restricted host-range virulence) of this division of the Australian *M. lini* complex, and stressed the uniqueness of this group already indicated by the race survey in terms of host-range and geographic distribution (Kerr, 1959), and by studies of uredospore germination as evidenced by the unusual high temperature tolerance (Kerr, 1958).

Three-way-cross material was used in most of these studies, and helped to establish the existence of only two allelic series in the linked *N* series previously identified by Flor in his differential varieties. There was no clear indication of the existence of allelic series of resistance factors other than those already located by Flor.

Introduction.

Henry (1930) was the first to examine the mode of inheritance of resistance of *Linum usitatissimum* L. to *M. lini*. He identified single genes in Ottawa 770B and Bombay and two factors in an Argentine selection. Myers (1937) carried the investigations further and determined the existence of two allelic series "L" and "M". At least three new loci were accounted for in Flor's subsequent investigations. These included two or more closely linked loci in the "*N*" series and loci independent of the "L", "M" and "*N*" series in the varieties Morye and Bolley Golden. By 1947, Flor had detected at least nineteen different factors conditioning the reaction of sixteen varieties of *L. usitatissimum* to his American races (Flor, 1947). This number has been added to since then.

The frequently noted inadequacy of a differential series evolved in one country to differentiate all the major races of the same pathogen in another country emphasizes the uniqueness of the rust flora of each country. Independent studies of host resistance should be undertaken in each country where the pathogen is an economic hazard, even when the differential series, on the basis of studies in the country of origin of the differential series, appears to carry only single factors for resistance in each variety. The studies dealt with in this paper were undertaken to determine whether the Australian races had the same pathogenic capacity as races previously identified by Flor.

The differential varieties analysed by Flor were used in these studies. It was intended to determine the number of resistance factors, hereafter called resgenes, effective in each variety against representative races of the non-Punjab-attacking group, and various collections of Punjab-attacking race 1, to determine the allelic identity of these resgenes, to discover whether other allelic series existed than those already listed

by Flor, to determine the number of loci involved in the linked "*N*" series, and to determine whether any of the differential varieties carried resgenes previously undetected by Flor.

It was also important to determine the range of resistance of the various resgenes to the Australian races as a basis for future breeding programmes aiming to incorporate rust resistance in commercial varieties of flax and linseed. For this reason Walsh and Koto were added to the series as potential sources of new resgenes.

Experimental Materials and Methods.

Genetical investigations were generally limited to the analysis of a single plant selection from each variety included in the differential series used in the physiologic race survey. Additional selections were occasionally included to check the homogeneity of some varieties.

Ottawa 770B, Newland, and Punjab, carrying the basic allels of the "L", "M" and "*N*" allelic series respectively, were used as the marker varieties for these loci in determining the allelic identity of the resgenes in the other varieties. They were generally satisfactory in the studies involving the Australian non-Punjab-attacking races. Koto was also found to be an excellent marker for the "*N*" series in studies with this race group. None of the above varieties was a satisfactory marker for the allelic series listed above in tests with Punjab-attacking race 1. Ottawa 770B and Newland were bifactorially resistant, Punjab was fully susceptible and another Koto factor than the "*N*" resgene conditioned resistance to this race. A new hybridization programme was therefore carried out after the first years of investigations using Abyssinian as the marker for the "*N*" series and Bison and Koto as the markers for the "L" allelic series. No satisfactory variety was available to mark the "M" locus. Investigations soon established the existence of two closely linked "*N*" loci. The Koto and Abyssinian "*N*" resgenes were allelic and were adopted as markers for one of the loci designated "1–N". The Punjab resgene occurred at the other locus designated "2–N" and was adopted as the marker for that locus.

F2 hybrids were studied during the earlier investigations, but 3-way-cross material was much more satisfactory in determining the allelic identity of different resgenes, particularly in those varieties carrying more than one resgene. 3-way hybrids were obtained by crossing F1 progeny with the all round susceptible variety F257. F257 was used as the pollen parent in order to avoid any risk of susceptible progeny appearing in non-segregating immune or resistant lines. This was most important, since self-fertilization, had F257 been the female parent, would have resulted in plants susceptible to every race and have led to the false assumption that the resgenes combined in the F1 hybrids were not allelic.

It was necessary to determine first the number of resgenes in a given differential variety, and the reaction of each resgene to various races of rust. The latter was particularly important in the case of varieties carrying more than one resgene. The reaction of such varieties to the various races of rust during the race survey might have stemmed from only one resgene, or a combination of resgenes. These results could best be obtained from material in which the variety under study, hereafter referred to as the "( )" variety, had been combined with the all round susceptible variety F257. F2 material proved more satisfactory than smaller amounts of 3-way-cross material. Where the difference between a single factor and a two factor resistance was indicated in F2 material by a difference between a 3 : 1 as against a 15 : 1 ratio, the difference was narrowed in 3-way-cross material to 1 : 1 versus 3 : 1.

The 3-way-cross material was of particular value in determining the allelic identity of the various resgenes in the "( )" varieties, particularly in those crosses involving a combination of resgenes at more than one locus. If a resgene in a "( )" variety were allelic with a resgene in a marker variety the two resgenes would be mutually exclusive in their distribution among the 3-way-cross seedlings combining the resgenes of these two varieties. One or the other resgene, but never both, would appear in the

same seedling. Should the resgene under study in a "( )" variety not be allelic with the resgene in the marker variety, the two resgenes would not be so mutually restricted in their distribution. The value of 3-way-cross material increased with the number of independent resgenes interacting, and was most strikingly useful in determining the allelic identity of the "*N*" resgene in Bolley Golden in a cross involving resgenes at four different loci.

Number of Resgenes Segregating Independently.	Number of F2 Plants Equivalent to One 3-way-cross Plant.
1	2
2	4
3	8
4	16
5	32

The following races were used on one or more occasions in testing the hybrids: Races 1, 2, 3, 4, 5, 6, 7, 8, 11, 13 and 17. Some, like races 1 and 2, with a restricted host range were used frequently. Others with a wider host range were used as uredospore material was available in the genetical analysis of the few varieties on which they were avirulent. Some races were identified too late in the genetical studies, and limitations of space and time prevented an adequate build up of others. For the method of uredospore storage and inoculation, see Kerr, 1959.

Accession 507 was adopted as the standard accession of Punjab-attacking race 1, the only Punjab-attacking race identified during the survey. Other accessions were included at intervals to determine whether the race was as pathogenically homogeneous as the physiological race survey indicated.

The plants studied by the excised shoot technique were grown out-of-doors out of range of infection. Special portable cold frames, glassed in all sides except the back, and holding about 120 4″ pots, were designed for the purpose. In order to reduce seedling losses the soil was steam sterilized for six hours at atmospheric pressure. 3-way-cross seed was always pre-germinated on blotting paper and transplanted into pots when the primary root was about ½″ in length. Eight to ten seedlings were sown in each 4″ pot and identified on emergence by loops of coloured, plastic-covered bellwire. Ten different combinations of colour and shape (five colours and two shapes per colour) were used to identify the sequences within each group of ten. Successive groups of ten were identified by the pot numbers. Bellwire was also an excellent means of labelling pot sown seedlings for rust reaction. The wire is cheap, extremely durable, and can be readily sterilized and cleaned for repeated use.

The seedlings were studied by the excised shoot technique instead of testing pot grown seedlings *in situ* (Kerr, 1951). Glasshouse space requirements were reduced to a minimum, the nutrient level was easily controlled, and the shoots grew with maximum vigour and minimum risk of loss once the early setbacks had been overcome.

Only three reaction levels (immune, resistant and susceptible) were differentiated in analysing the rust reaction of hybrids to the various races of rust (Kerr, 1959). It was often difficult to differentiate intermediate reactions high in the scale of susceptibility from susceptible reactions in the early stages of sporulation. These reactions were very common during studies of 3-way-cross Walsh hybrids. The difficulty was increased by the unusually heavy infection induced by the current inoculation technique. The difference became clear cut if the plants were left for sveral days or a week after sporulation. Reactions less than fully susceptible, however vigorous at the commencement of sporulation, deteriorated much more rapidly on standing than susceptible reactions, infection rarely spread to the stems, the leaves often became distorted and necrotic, and withered quickly.

During these studies Newland hybrids were notoriously susceptible to a root-rotting organism. This accounts for the common deficiency of Newland hybrids in these studies.

Experimental Results.

Notes on Tables Summarizing the Results.

The results have been summarized under the following headings.

Pedigree. The variety under investigation in each table is symbolized by brackets ( ). When a selection other than the survey selection has been involved in the cross the number of that selection is included in the brackets. (?) means selection used was not numbered.

e.g. Table 9. Punjab × (245) = Punjab × Ottawa 770B selection 245.

The pedigree lists the parents of the F1. Two types of progeny were derived from the F1, namely, F2 and 3-way-cross plants. The nature of the progeny is indicated in the same column as the pedigree by the symbols F2 or 3–W–C.

Parental Reaction. The reaction of the parent under investigation to each race is listed under the abbreviation of the parental name under Parental Reaction. The reaction of the marker variety in each hybrid is listed under the heading X.

Race. The Australian number of the race is given under this heading. When two races gave the same results they have been listed together. Unless otherwise stated the following accessions were used as representative of each race:

Race 1	Accession 507	Race 6	Accession 528
Race 2	Accession 492	Race 7	Accession 550
Race 3	Accession 511	Race 11	Accession 568
Race 4	Accession 578	Race 13	Accession 582
Race 5	Accession 519	Race 17	Accession 604

When accessions other than the above have been used this is indicated by the accession number included in brackets after the race number, e.g., race 2 (548).

Number of Resgenes Segregating. This refers to the number of resgenes (not resgene pairs) present in the F1 and effective against the race listed to the left of the table. Resgenes contributed by the two parents may be identical. The number of resgenes contributed by the parent under investigation is listed under the abbreviation of the parental name. The number of resgenes contributed by the other parent of the F1, referred to as the marker variety, is listed under the column X. When both parents carry resgenes conferring resistance to the same race the allelic identity of the resgene or resgenes of the marker parent is listed in brackets to the right of the number of resgenes. Lack of seedlings susceptible to that race indicates that resgenes in both parents occur at the same locus. The particular locus is marked by an asterisk (*).

P. The probability that the results obtained fitted the ratio expected was determined from χ^2 goodness of fit tests. A value of ·05 or higher was regarded as a satisfactory agreement. In a few cases P fell below ·05. This was sometimes due to poor infection resulting in a deficiency of susceptible seedlings. Even when this was not the case the results were accepted as a satisfactory fit if P exceeded ·01, provided no other more satisfactory hypothesis could be advanced to explain the results.

Number of Seedlings with Reactions Listed Below. Total: This refers to the number of plants tested with all the races. In many cases a greater number of plants were tested with individual races, but with successive excisions some parent plants sometimes succumbed to root rotting organisms.

Unless there was a clear cut difference between immune and resistant reactions seedlings giving either reaction were combined together for simplicity of analysis and classed as immune. Seedlings expected to give resistant reactions were often immune owing to slightly adverse incubation conditions.

Expected Ratio. This has been given when the resgenes of the two parent varieties in the F1 were segregating independently.

Symbolization of Resgenes. In recording the results the resgenes have been referred to by their allelic identity, e.g., "L", "M", "*N*" or "1–N" when the exact location of an "*N*" resgene is under examination. The identified resgenes are referred to in the discussion by their specific symbol without quotation marks.

Summary of Results obtained with each Variety. The varieties included in the studies of host resistance are shown in Table 1.

TABLE 1.

Variety.	Sydney University Accession Number.	C.I. Number.
Williston Golden	Fx 2	25–1
Akmolinsk	Fx 3	515–1
J.W.S.	Fx 4	708–1
Abyssinian	Fx 5	701
Kenya	Fx 6	709–1
Argentine	Fx 7	705–1
Very Pale Blue Crimped	Fx 9	647–1
Ottawa 770B	Fx 10	355
Argentine	Fx 11	462
Bison	Fx 13	389
Punjab	Fx 14	—
Walsh	Fx 86	—
F257	Fx 257	—
Morye	Fx 318	112
Newland	Fx 319	188
Bolley Golden	Fx 320	644
Italia Roma	Fx 321	1005–1
Leona	Fx 322	836
Tammes' Pale Blue	Fx 323	333–1
Koto	Fx 326	842

With one or more of the following races: 1, 2, 3, 4, 5, 6, 7, 8, 11, 13 and 17, used in tests of the above varieties.

Results obtained with Williston Golden Fx 2 C.I. 25–1. (Table 2.)

Williston Golden was fully susceptible to every race except Punjab-attacking race 1, and non-Punjab-attacking race 17, to both of which it was resistant. These two races seemed to give slightly different types of reaction.

The variety was monofactorially resistant to both races in the cross F257 × Williston Golden. Different resgenes appeared to condition the reaction to each race, but this was not confirmed, since the results given by the residue material tested to confirm this were obscured by high summer temperatures in the glasshouse.

The resegene conferring immunity to race 1 was inherited independently of the Abyssinian "*N*" resgene in the cross, Williston Golden × Abyssinian.

It was allelic with the Bison and Koto "L" resgenes in the crosses (Bison × Williston Golden) × F257 and Koto × Williston Golden.

Results from the cross (Bison × Williston Golden) × F257A tended to confirm the fact that different single resgenes conferred resistance to races 1 and 17. Williston Golden usually gave a completely immune reaction to race 1 in the test of its hybrids. The incubation conditions under which this lot of hybrids was tested were presumably more favourable to the pathogen. Some of the hybrids were resistant to race 1. Since the Bison "L" resgene always conditioned complete immunity, the resistant reaction must have been due to the Williston Golden "L" resgene. If the Williston Golden resgene also conferred resistance to race 17 all the hybrids resistant to race 1 should also have been resistant to race 17. Seven of the ten seedlings resistant to race 1 were susceptible to race 17.

Results obtained with Akmolinsk Fx 3 C.I. 515–1. (Table 3.)

Akmolinsk was susceptible to every race but races 2 and 4, to which it was resistant. This reaction varied from immunity to resistance.

TABLE 2.

Results obtained with Williston Golden.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		WG.	X.						I.	R.	S.		Total.	WG.	X.	
F257×( ) ..	1	R	S		I	S			77		23	3 : 1	1	1	0	0·8–0·9
F2	17	R	S		R	S			74		26	3 : 1	1	1	0	0·9–1·0
( )×Abyssinian ..	1	R	1		I	I	S		147		8	15 : 1	2	1	1 (N)	0·5–0·7
F2	2	S	I		I	S	S		122		33	3 : 1	1	0	1 (N)	0·2–0·3
				155	122	25	8					12 : 3 : 1				0·5–0·7
Bison×( ) ..	1 (507 621)	R	I		I	I	R	R	23	10		1 : 1	2	1	1 (L*)	0·05 approx.
A	17	R	S		R	S	R	S		17	16	1 : 1	1	1	0	0·8–0·9
3–W–C ..	2	S	S		S	S	S	S	All susceptible							
				33	14	9	3	7				1 : 1 : 1 : 1				0·05 approx.
Bison×( ) ..	1	R	I		I	I			16	All immune			2	1	1 (L*)	
3–W–C ..	17	R	S		I	S			7		9	1 : 1	1	1	0	0·8–0·9
	7	S	S		S	S			All susceptible							
( )×Bison ..	1	R	I		I	I	I		95	All immune			2	1	1 (L*)	
F2	17	R	S		I	R	S		74		21	3 : 1	1	1	0	0·5–0·7
				95	43	31	21					2 : 1 : 1				0·2–0·3
Koto×( ) ..	1	R	I		I	I			121	All immune			2	1	1 (L*)	
F2	2, 5	S	I		I	S			100		21	3 : 1	1	0	1	0·05–0·06
				121	100	21										

N.B.—Resistant reaction of Williston Golden to race 1 was commonly suppressed to immunity under the incubation conditions to which the hybrids were subjected.

TABLE 3.

Results obtained with Akmolinsk.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ak.	X.						I.	R.	S.		Total.	Ak.	X.	
F257×( ) ..	1	S	S		S	S			All susceptible							
F2	2	R	S		R	S			62		20	3 : 1	1	1	0	0·8–0·9
				82	62	20						3 : 1	1	1	0	
( )×Ottawa ..	1	S	I		I	I	S		13		4	3 : 1	2	0	2	0·8–0·9
770B.. ..	2	R	I		I	R	S		11	4	2	2 : 1 : 1	2	1	1 (L)	0·3–0·5
3–W–C ..	11	S	I		1	S	S		11		6	1 : 1	1	0	1	0·5–0·7
				17	11	4	2					2 : 1 : 1				0·3–0·5
( )×Newland .. F2	2	R	I	213	I	R	S		164	36	13	12 : 3 : 1	2	1	1 (M)	0·7–0·8
( )×Abyssinian .. F2	2	R	I	335	1	R			259	76		3 : 1	2	1	1 (1–N*)	0·3–0·5
( )×Koto ..	1	S	I		I	S	I	S	31		29	1 : 1	1	0	1	0·8–0·9
	2	R	I		I	I	R	R	31	28		1 : 1	2	1	1 (1–N*)	0·9–1·0
3–W–C ..	11	S	I		I	I	S	S	31		28	1 : 1	1	0	1	0·9–1·0
				59	17	14	14	14				1 : 1 : 1 : 1	3	1	2	0·9–1·0
( )×Bison ..	2	R	S		R	S			28		29	1 : 1	1	1	0	0·9–1·0
3–W–C ..	11	S	S		S	S			All susceptible							
				57	28	29						1 : 1				

It was monofactorially immune to race 2. The monofactorial resistance was confirmed in each of the crosses, which segregated for resistance to race 2.

The resgene conditioning resistance was inherited independently of the Ottawa 770B "L" resgene in the cross (Akmolinsk × Ottawa 770B) × F257. It was also inherited independently of the Newland "M" resgene in the cross Akmolinsk × Newland tested with race 2.

It was located in the same allelic series as the Abyssinian and Koto "*N*" resgenes at the "1–N" locus in the crosses Akmolinsk × Abyssinian and (Akmolinsk × Koto) × F257. Sufficient seedlings of the second cross were tested to prove that the Akmolinsk resgene was located at this locus, and not just closely linked with it.

Results obtained with J.W.S. Fx 4 C.I. 708–1. (Table 4.)

J.W.S. was immune to race 2, resistant to race 1, and susceptible to the other races. The reaction to race 1 varied from near immunity to near susceptibility. The reaction approximated so closely to susceptibility in hybrids that J.W.S. was regarded as the susceptible parent in hybrid lines tested with race 1.

Since all F2 hybrids of Ottawa × J.W.S. and reciprocal were immune to race 2, the J.W.S. factor was allelic with the Ottawa 770B "L" resgene conferring immunity to this race.

Results obtained with Abyssinian Fx 5 C.I. 701. (Table 5.)

Abyssinian was immune to races 1, 2 and 4 and susceptible to every other race.

A single Abyssinian resgene conditioned immunity to races 1 and 2 in the crosses Williston Golden × Abyssinian and Abyssinian × F257. This resgene was also effective against race 4 in the cross (Punjab × Abyssinian) × F257, which failed to segregate when tested with races 2 and 4, and conferred immunity to each of the three Punjab-attacking accessions, 507, 621 and 627.

The resgene segregated independently of the Ottawa 770B "L" factor in F2 hybrids of Abyssinian × Ottawa 770B and reciprocal tested with race 2. Lack of seedlings susceptible to race 1 suggested that the Abyssinian resgene was allelic or linked with the additional "*N*" factor in Ottawa 770B effective against race 1. This was confirmed in the tests of F2 and 3-way-cross hybrids of Abyssinian crossed with Punjab. The frequency of seedlings susceptible to race 2 was too low to assume independent segregation of the Abyssinian resgene and the Punjab "*N*" resgene. It could be accounted for by assuming close linkage between the two resgenes.

Results obtained with Kenya Fx 6 C.I. 709–1. (Table 6.)

Genetical investigations of this variety were limited to an analysis of resistance to race 1. The reaction of Kenya to the non-Punjab-attacking races (e.g., race 2) was too variable to permit satisfactory analysis.

Two independently inherited Kenya resgenes conferred immunity to race 1 in two independent lots of F2 hybrids F257 × Kenya.

Kenya was crossed with the varieties Koto and Abyssinian, both of which were monofactorially immune to race 1, and carried resgenes in the "L" and "*N*" allelic series respectively. Had both Kenya resgenes been independent of these two resgenes a trifactorial segregation was expected in the hybrids. 170/170 F2 hybrid of Koto × Kenya, 25/25 plants of (Koto × Kenya) × F257, 207/207 plants of Kenya × Abyssinian and 37/37 of (Abyssinian × Kenya) × F257 were immune to race 1. It was concluded that the two Kenya resgenes lay in the "L" and "N" allelic series respectively.

The immunity to race 1 of all 35 (Ottawa 770B × Kenya) × F257 plants and of all 234 Newland × Kenya (Selection 76) seedlings agreed with this conclusion, though, owing to fusarium wilt, there were insufficient seedlings to reach a definite conclusion. Both Ottawa 770B and Newland carried "*N*" resgenes effective against race 1.

Insufficient 3-way-cross plants were available to determine whether the Kenya "*N*" resgene was allelic with the Abyssinian resgene at the "1–N" locus, or whether it was closely linked with this locus.

TABLE 4.

Results obtained with J.W.S.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.			Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		JWS.	X.					I.	R.	S.		Total.	JWS.	X.	
F257×( )F2 ..	2	I	S		I	S		114		23	3 : 1	1	1	0	0·02–0·05
( )×Williston Golden F2	2	I	S		I	S		111		25	3 : 1	1	1	0	0·05–0·1
( )×Ottawa 770B	6	S	I		I, R	S		172		11	15 : 1	2	0	1	0·9–1·0
and F2	2	I	I		I	I		All immune				2	1	1 (L*)	
reciprocal				183	172	11	.								
( )×Newland and	6	S	I		I	S	S	108		35	3 : 1	1	0	1	0·9–1·0
reciprocal ..	2	I	I		I	I	S	86		6	15 : 1	2	1	1 (M)	0·9–1·0
F2				92	68	18	6				12 : 3 : 1				0·9–1·0
( )×Abyssinian ..	1	R	I		I	RS	RS	12	16		1 : 1	1	0	1	0·3–0·5
3–W–C ..	2	I	I		I	I	S	15		4	3 : 1	2	1	1 (1–N)	0·8–0·7
	6	S	S		S	S	S	All susceptible							
				19	9	7	3				2 : 1 : 1				0·3–0·5
( )×Punjab and	2	I	I		I	I	S	104		4	15 : 1	2	1	1 (2–N)	0·2–0·3
reciprocal	7	S	I		I	S	S	85		23	3 : 1	1	0	1	0·3–0·5
F2				108	85	19	4				12 : 3 : 1				0·5 approx.
( )×F527 F2 ..	2	I	S		I	S		124		38	3 : 1	1	1	0	0·5–0·7

TABLE 5.

Results obtained with Abyssinian.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ab.	X.						I.	R.	S.		Total.	Ab.	X.	
Williston F2 .. Golden×( )	2	I	S	131	I	S			99		32	3 : 1	1	1	0	0·9–1·0
( )×F257 F2 ..	1, 2	I	S	89	I	S			71		18	3 : 1	1	1	0	0·2–0·3
( )×Ottawa 770B	1	I	I		I	I	I		181	All immune			3	1	2 (1–N*)	
and reciprocal	2	I	I		I	I	S		173		9	15 : 1	2	1	1 (L)	0·3–0·5
F2	6	S	I		I	S	I		172		10	15 : 1	2	0	2	0·5–0·7
				182	163	10	9					14 : 1 : 1				0·5–0·7
( )×Punjab ..	1	I	S		I	S	I		52		12	3 : 1	1	1	0	0·2–0·3
F2	6	S	I		I	I	S		54		16	3 : 1	1	0	1	0·5–0·7
	2	I	I		I	I	I		All immune				2	1	1 (N*)	
				64	38	12	14					2 : 1 : 1				0·3–0·5
( )×Punjab ..	1	I	S		I	S	S	I	12		20	1 : 1	1	1	0	0·1–0·2
3–W–C ..	2	I	I		I	S	I	I	23		2		2	1	1 (2–N**)	
	6	S	I		I	S	I	S	14		11	1 : 1	1	0	1	0·5–0·7
				25	I	2	13	9				0 : 0 : 1 : 1				
Punjab×( ) ..	1 (621, 627, 507)	I	S		I	S	S	I	39		35	1 : 1	1	1	0	0·5–0·7
3–W–C ..	2, 4	I	I		I	S	I	I	69		3	1 : 0	2	1	1 (2–N**)	
	6, 7	S	I		I	S	I	S	37		28	1 : 1	1	0	1	0·2–0·3
				63	8	3	27	25				0 : 0 : 1 : 1				

N**=close linkage between "N" resgenes of the two parents.

TABLE 6.

Results obtained with Kenya.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions. Listed Below.			Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ke.	X.					I.	R.	S.		Total.	Ke.	X.	
F257×( ) F2 ..	1	I	S		I	S		133	7	2	15 : 1/63 : 1	$\frac{2}{3}$	$\frac{2}{3}$	0	
F257×( ) F2 ..	1	I	S		I	S		77		5	15 : 1	2	2	0	0·9–1·0
Ottawa 770B×( )	1	I	I		I	I	I	35	All immune			4	2	2 (L* 1–N*)	
3–W–C ..	2	R	I		I	RS	RS	12	16	(RS)	1 : 1	1	0	1	0·3–0·5
	6	R	I		I	R	S	12	9	7	2 : 1 : 1	2	0	2	0·5–0·7
				28	12	9	7				2 : 1 : 1				
Newland×(76) ..	1	I	I		I	I		234	All immune			4	2	2 (M, 1–N*)	
F2	2	R	I		I	RS		147	42	(RS)	3 : 1	1	0	1	0·3–0·5
				189	147	42									
Koto×( ) F2 ..	1	I	I		All immune			170	All immune			3	2	1 (L*)	
Koto×( )	1	I	I		I	I		25	All immune			3	2	1 (L*)	
3–W–C ..	2, 6	R	I		I	RS		10	8	(RS)	1 : 1	1	0	1	0·5–0·7
				18	10	8									
( )×Abyssinian ..	1	I	I		I	I		207	All immune			3	2	1 (1–N*)	
F2	2	R	I		I	RS		163	44	(RS)	3 : 1	1	0	1	0·2–0·3
				207	163	44									
Abyssinian×( ) ..	1	I	I		I	I		37	All immune			3	2	1 (1–N*)	
3–W–C ..	2	R	I		R	S		9	13	(RS)	1 : 1	1	0	1	0·2–0·3
	6	RS	S		RS	S									
				21	8	13					1 : 1				

RS = variable reaction ranging from resistance to susceptibility.

Results obtained with Argentine Fx 7 C.I. 705–1. (Table 7.)

The reaction of the Argentine 705–1 resgene to the non-Punjab-attacking races, particularly in hybrids, fluctuated too widely to permit satisfactory analysis under glasshouse conditions at Sydney. Investigations were limited to the analysis of resistance to race 1. Resistance to this race also fluctuated, sometimes too seriously to permit a satisfactory assessment of results.

A single Argentine resgene appeared to condition the reaction to race 1 in each of the crosses tested. This resgene was independent of the "L" and "*N*" loci marked by the two Ottawa resgenes.

The lack of race 1-susceptible seedlings in the cross Argentine × Newland suggested that the Argentine resgene was allelic with the Newland "M" resgene. The number of seedlings tested (150) was too small to be sure that Newland "M" and "*N*" resgenes were not segregating independently of the Argentine resgene. No other seedlings were available for further tests owing to heavy losses to *Fusarium*.

Results obtained with Very Pale Blue Crimped Fx 9 C.I. 647–1. (Table 8.)

Investigations of the variety were limited to the analysis of the resistance to race 1, the only race to which it was immune. A single V.P.B. Crimped resgene conditioned the immunity of F2 and 3–W–C seedlings to race 1 in each cross tested. The resgene segregated independently of the Abyssinian and Punjab "*N*" resgenes in the crosses V.P.B. Crimped × Abyssinian and V.P.B. Crimped × Punjab. It was allelic with "L" factors in the varieties Koto and Bison, since none of the seedlings of the following two crosses was susceptible to race 1, e.g., V.P.B. Crimped × Koto, V.P.B. Crimped × Bison.

Results obtained with Ottawa 770B Fx 10 C.I. 355. (Table 9.)

Ottawa 770B was immune to all races identified up to 1948. Since then it has been susceptible to several races discovered in Western Australia and one race in Victoria.

A single Ottawa 770B resgene, identified as Flor's L resgene, conditioned immunity to races 2 and 8 in the crosses F257 × Ottawa 770B and reciprocal. An additional Ottawa resgene conferred a variable resistant reaction to races 1 and 6 in the same crosses. This reaction ranged from near immunity with considerable necrosis and few pustules to a reaction with little necrosis and variable numbers of "3" pustules. It sometimes approximated to moderate susceptibility. There were never more than four or five pustules per leaf.

The Ottawa resgene, which conferred immunity to races 2 and 8, was also effective against race 13 in crosses (Punjab × Ottawa) × F257, (Ottawa 770B × Punjab) × F257. It was also effective against races 4 and 11 in the crosses (Ottawa 770B × Abyssinian) × F257 and (Abyssinian × Ottawa 770B) × F257.

The additional factor which conferred immunity to race 1 was also identified in Ottawa selections 244 and 245. It was effective against the three race 1 accessions 507, 610 and 613. It was allelic with the Abyssinian "*N*" resgene at the "1–N" locus. 182 3-way-cross seedlings of Abyssinian × Ottawa 770B pedigree were tested with race 1. All were immune. This number was ample to prove that the Abyssinian and Ottawa resgenes were allelic and not just closely linked. This was confirmed by results obtained with F2 and 3-way-cross hybrids of Ottawa × Punjab pedigree. The two seedlings susceptible to races 1 and 7 could only be accounted for by assuming close linkage between the Punjab "*N*" resgene at the "2–N" locus conferring immunity to race 7 and the Ottawa "*N*" resgene conferring immunity to race 1.

The Ottawa "*N*" resgene was also effective against the following additional non-Punjab-attacking races: Races 3, 5, 6 and 13. It was ineffective against races 2, 4, 8, 11 and 13 (Access 582).

Results obtained with Argentine Fx 11 C.I. 462. (Table 10.)

This variety was immune to every Australian race, but gave a moderately susceptible reaction to a New Zealand race. Its homozygosity was problematical in view of the occurrence of an occasional resistant or susceptible seedling during race survey tests.

TABLE 7.

Results obtained with Argentine 705–1.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ar.	X.						I.	R.	S.		Total.	Ar.	X.	
Punjab × ( ) F2	1	IR	S		IR	S			139		41	3 : 1	1	1	0	0·3–0·5
				180	139	41										
( ) × Bison ..	1	IR	I		I	S			21		13	3 : 1	2	1	1 (L)	0·5–0·1
3–W–C ..	2	RS	S	34	RS	RS			34	Mod. to fully susceptible			0			
J.W.S. × ( ) ..	1	IR	RS		R	R	S	S		11	15	1 : 1	1	1	0	0·3–0·5
3–W–C ..	2	RS	I		I	S	I	S	15		10	1 : 1	1	0	1	0·3–0·5
				22	5	5	9	3				1 : 1 : 1 : 1				0·3–0·5
( ) × Ottawa ..	1	IR	I		I	I	S		185		3	63 : 1	3	1	2 (L, 1–N)	0·9–1·0
770B ..	2	RS	I		I	S	S		150		38	3 : 1	1	0	1	0·1–0·2
F2				188	150	35	3					48 : 15 : 1				0·2–0·3
( ) × Newland F2	1	IR	I		I	S			150	All immune			3	1	2 (M, 1–N)	

IR = immune to resistant.
RS = resistant to susceptible.

TABLE 8.

Results obtained with Very Pale Blue Crimped.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		PBC.	X.						I.	R.	S.		Total.	PBC.	X.	
( )×F257 F2 ..	1	I	S		I	S										
				84	68	16						3 : 1	1	1	0	0·2–0·3
( )×Bison F2 ..	1	I	I		188	All immune							2	1	1 (L*)	
( )×Koto F2 ..	1	I	I		I	I			128	All immune			2	1	1 (L*)	
	5	S	I		I	S			94		34	3 : 1	1	0	1	0·5–0·7
				128	94	34										
( )×Abyssinian ..	1	I	I		I	S										
F2				140	138	2						15 : 1	2	1	1 (1–N)	0·05–0·1
( )×Punjab F2	1	I	S		I	I	S	S	130		37	3 : 1	1	1	0	0·3–0·5
	2	S	I		I	S	I	S	116		41	3 : 1	1	0	1	0·7–0·8
				157	97	34	19	7				9 : 3 : 1				0·1–0·2

TABLE 9.

Results obtained with Ottawa 770B.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ot.	X.							I.	R.	S.		Total.	Ot.	X.	
Punjab × (245) ..	1	I	S		I	I	S			183		14	15 : 1	2	2	0	0·5–0·7
F2	7	S	I		I	S	I			140		57	3 : 1	1	0	1	0·2–0·3
				197	126	57	14						11 : 4 : 1				0·3–0·5
Punjab × (245) ..	1	I	S		I	I	S	I	S	104		7	15 : 1	2	2	0	0·9–1·0
(244) × Punjab	2	I	I		I	I	I	S	S	103		8	15 : 1	2	1	1 (2–N)	0·5–0·7
F2	7	S	I		I	S	I	S	S	75		36	3 : 1	1	0	1	0·05–0·1
				111	69	28	6	7	1				11 : 3 : 1 : 1 : 0				0·3–0·5
( ) × Punjab ..	1 (507, 621, 627)	I	S		I	I	S	I		41		11	3 : 1	2	2	0	0·5–0·7
3–W–C ..	2, 13	I	I		I	I	I	S		42		9	3 : 1	2	1	1 (2–N)	0·2–0·3
	7	S	I		I	S	I	S		23		29	1 : 1	1	0	1	0·3–0·5
				52	12	20	11	9					1 : 1 : 1 : 1				0·1–0·2
Punjab × ( ) ..	1 (507, 610, 613)	I	S		I	I	S	I	S	21		9	3 : 1	2	2	0	0·5–0·7
3–W–C ..	2, 13	I	I		I	I	I	S	S	22		8	3 : 1	2	1	1 (2–N)	0·8–0·9
	7	S	I		I	S	I	S	S	13		17	1 : 1	1	0	1	0·3–0·5
				30	5	8	8	8	1				1 : 1 : 1 : 1 : 0				0·8–0·9
Bison × ( )	1	I	I		I	I	I			106	All immune			3	2	1 (L*)	
3–W–C ..	6	I	S		I	R	S			24	43	17	1 : 2 : 1	2	2	0	0·5–0·7
	2	I	S		I	S	S			47		45	1 : 1	1	1	0	0·9–1·0
				84	24	43	17						1 : 2 : 1				0·5–0·7
F257 × ( ) and	1, 6	I	S		I	I	S			90	30	8	12 : 3 : 1	2	2	0	0·5–0·7
reciprocal	2, 8	I	S		I	S	S			98		38	3 : 1	1	1	0	0·3–0·5
F2				136	98	30	8						12 : 3 : 1				0·5–0·7

TABLE 9.—*Continued.*

Results obtained with Ottawa 770B.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ot.	X.							I.	R.	S.		Total.	Ot.	X.	
( ) × Newland and reciprocal F2 ..	2	I	I	153	I 147	S 6							15 : 1	2	1	1 (M)	0·2–0·3
( ) × Abyssinian ..	1	I	I		I	I	I			34	All immune			3	2	1 (1–N*)	
3–W–C ..	2	I	I		I	I	S			22		5	3 : 1	2	1	1 (1–N)	0·3–0·5
	6	I	S		I	S	R			15	7	5	2 : 1 : 1	2	2	0	0·7–0·8
				27	15	7	5						2 : 1 : 1				0·7–0·7
Abyssinian × ( ) ..	1	I	I		I	I	I			38	All immune			3	2	1 (1–N*)	
3–W–C ..	2	I	I		I	I	S			26		11	3 : 1	2	1	1 (1–N)	0·5–0·7
	6	I	S		I	S	R			39		9	3 : 1	2	2	0	0·2–0·3
				37	17	9	11						2 : 1 : 1				0·7–0·8
( ) × Abyssinian ..	1	I	I		I	I	I			36	All immune			3	2	1 (1–N*)	
3–W–C ..	2	I	I		I	I	S			29		7	3 : 1	2	1	1 (1–N)	0·3–0·5
	11	I	S		I	S	S			19		17	1 : 1	1	1	0	0·7–0·8
	13 (602), 5	I	S		I	S	R			19	10	7	2 : 1 : 1	2	2	0	0·7–0·8
	7	S	S		S	S	S			36	All suscept.						
				36	19	10	7						2 : 1 : 1				0·7–0·8
Abyssinian × ( ) ..	1	I	I		I	I	I			74	All immune			3	2	1 (1–N*)	
3–W–C ..	2, 4	I	I		I	I	S			55		18	3 : 1	2	1	1 (1–N)	0·8–0·9
	11	I	S		I	S	S			38		35	1 : 1	1	1	0	0·7–0·8
	5	I	S		I	S	R			38	17	18	2 : 1 : 1	2	2	0	0·7–0·8
	7	S	S		S	S	S			73	All suscept.						
				73	38	17	18						2 : 1 : 1				

TABLE 10.

Results obtained with Argentine 462.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.			Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ar.	X.					I.	R.	S.		Total.	AR.	X.	
F257 × (263) ..	1	I	S		I	S	S	19		8	3 : 1	2	2	0	0·5–0·7
3–W–C ..	2, 7	I	S		I	I	S	23		4	7 : 1	3	3	0	0·2–0·3
				27	19	4	4				6 : 1 : 1				0·5–0·7
(?) × Williston	2	I	S		I	R	S								
Golden F2 ..				116	103	9	4	112		4	63 : 1/15 : 1	⅔	⅔	0	
F257 × (?)	1	I	S		I	I									
F2	6, 7	I	S		I	S									
	2	I	S		I	R									
				70	62	8					15 : 1	2	2	0	0·05–0·1
(260) × Ottawa ..	6	I	I		I	I	I	230	All immune or resist.					2 (1, 1–N)	
770B															
F2	2	I	I		I	I	S	294		11	15 : 1	2	1	1 (L)	0·05–0·1
	7	I	S		I	S	S	192		38	3 : 1	1	1	0	0·01–0·001
				230	192	28	10								
(252) × Ottawa	2	I	I		I	I	S	30		2	7 : 1	3	2	1	0·2–0·3
770B	6	I	I		I	I	I	32	All immune					2 (L, 1–N*)	
3–W–C ..	7	I	S		I	S	S	23		9	3 : 1	2	2	0	0·5–0·7
				32	23	7	2				6 : 1 : 1				0·1–0·2
(255) × Punjab ..	1	I	S		I	S									
F2				182	172	10					15 : 1	2	2	0	0·5–0·7
(254) × Punjab ..	1	I	S		I	S		20		2	3 : 1/7 : 1	⅔	⅔	0	
3–W–C ..	2	I	I		I	I		22	All immune					1 (2–N*)	
				22	20	2									

(?) = unnumbered selection.

TABLE 10.—*Continued.*

Results obtained with Argentine 462.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.			Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ar.	X.					I.	R.	S.		Total.	AR.	X.	
(254) × Punjab .. 3-W-C	2, 7	I	I					46	All immune					1 (2–N*)	
(255) × Punjab ..	1	I	S		I	S		57		8	7 : 1	3	3	0	0·9–1·0
3-W-C ..	2, 7	I	I		I	I		65	All immune					1 (2–N*)	
				65	57	8					7 : 1				0·9–1·0
(?) × Punjab and reciprocal F2	2	I	I					133	All immune					1 (2–N*)	
Concurrent × (?) ..	1	I	S		I	RS		21	22		1 : 1	1	1	0	0·8–0·9
3-W-C ..	2	S	S		S	S		43	All suscept.						
				43	21	22					1 : 1				0·8–0·9
Argentine Selection Used in Race Survey.															
F257 × ( ) ..	1	I	S		I	I	S	26		3	7 : 1	3	3	0	0·7–0·8
3-W-C ..	2, 7, 11	I	S		I	S	S	23		6	3 : 1	2	2	0	0·5–0·7
	13, 17			29	23	3	3				6 : 1 : 1				0·5–0·7
( ) × F257 ..	1, 2, 7, 11	I	S		I	S									
3-W-C ..	13, 17			33	27	6					3 : 1	2	2	0	0·3–0·5
F257 × ( ) B .. 3-W-C	2, 7	I	S		I	S		26		16	3 : 1	2	2	0	0·01–0·05
( ) × Concurrent	1, 2	I	S		I	S									
3-W-C ..				60	47	13					3 : 1	2	2	0	0·5–0·7

(?) = unnumbered selection.

TABLE 10.—*Continued.*

Results obtained with Argentine 462.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.			Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ar.	X.		I	S		I.	R.	S.		Total.	AR.	X.	
( )×Ottawa 770B	2	I	I		I	S									
3-W-C ..				40	32	8					7 : 1	3	2	1 (L)	0·1–0·2
)×Bison ..	1	I	I		I	I		110	All immune					1 (L*)	
3-W-C ..	2, 5, 7, 11, 13, 17	I	S		I	S		90		20					
				110	90	20					3 : 1	2	2	0	0·05–0·1
Newland×( ) ..	1	I	I		I	I	I	69	All immune					2 (M, 1-N*)	
3-W-C ..	2	I	I		I	I	S	69		10	7 : 1	3	2	1 (M)	0·9–1·0
	5	I	S		I	S	S	41		27	1 : 1	1	1	0	0·1–0·2
				68	41	17	10				4 : 3 : 1				0·1–0·2
( )×Newland ..	2	I	I		I	I	S	53		13	7 : 1	3	2	1 (M)	0·05–0·1
3-W-C ..	5	I	S		I	S	S	44		20	3 : 1	2	2	0	
Abyssinian×( ) ..	1, 2	I	I		I	I		26	All immune					1 (1–N*)	
3-W-C ..	8	I	S		I	S		19		7	3 : 1	2	2		0·8–0·9
				26	19	7									
Abyssinian×( ) .. 3-W-C	1, 2	I	I		I	I		81	All immune					1 (1–N*)	
( )×Koto	1	I	S		I	S		48		12	7 : 1	3	2	1 (L)	0·05–0·1
3-W-C ..	2	I	I		I	I		60	All immune					1 (1–N*)	
				60	48	12									

(?)=unnumbered selection.

Results obtained with Non-Survey and Survey Selections.

Several single plant selections were used in the early studies. The number of resgenes effective against race 2 varied. Three resgenes seemed to condition resistance in F257 × (263) 3–W–C, two or three (probably two) in (?) × Williston Golden; two in F257 × (?) and selections 252 and 255; one in selection 260 and none in an unnumbered selection Concurrent × (?). The number of resgenes effective against race 1 in the same selections varied from three to one. The variety was obviously heterozygous. This had been expected in view of the occurrence of occasional fully susceptible plants among seedlings used in the differential race survey, not only in Australia, but also in New Zealand. That there were so few susceptible seedlings in these survey tests could be attributed to the occurrence of at least two independently inherited resgenes which conditioned resistance to most, if not all, of the Australian races.

This heterogeneity stemmed either from the material originally introduced for study, or from contamination, by cross fertilization, with resgenes from other differential varieties during successive generations of seed propagation since their introduction. The results from the genetical studies tended to indicate the former situation.

A large number of different crosses, and different replicates within each cross, should have been available to clarify the genetic constitution of the survey selection of such a heterogeneous variety. Owing to limitations of time, and the fact that the variety had not had any differential function in separating races during the survey, studies of the variety were restricted to material available at the commencement of investigation.

On the evidence from Newland crosses the survey selection carried no resgenes at the "M" locus. Results obtained with Ottawa hybrids indicated an absence of resgenes at the "L" locus conditioning resistance to the NPA races. But the survey selection was heterozygous at this locus for a resgene conditioning immunity to PA race 1. This resgene was located in the 3-way-cross ( ) × Bison, but was absent in the 3-way-cross ( ) × Koto.

On this evidence the variety lacked resgenes conditioning immunity to the NPA races at the "L" and "M" loci. But the survey selection carried at least two independently inherited resgenes which conditioned immunity to a wide range of NPA races. One of these resgenes was probably located at an "*N*" locus. Hybrid material combining "1–N" resgenes from the marker varieties Ottawa 770B, Koto, and Abyssinian with resgenes from both the survey and non-survey Argentine 462 selections failed to segregate for susceptibility in tests with NPA races to which the marker "1–N" resgenes were immune. Tests of non-survey selections combined with Punjab suggested that Argentine 462 carried additionally a resgene at the "2–N" locus. The wide "*N*" resistance of Argentine survey selection might therefore have stemmed from the combined resistance of two less widely resistant resgenes.

While there was not final proof that the "*N*" resgene or resgenes of Argentine could be equated with one of the resgenes in the 3–W–C crosses F257 × ( ) and ( ) × F257 (conditioning immunity to races 2, 7, 11, 13 and 17), it was most reasonable to assume that this was the case. It was equally probable that the "*N*" resgene or resgenes conditioned immunity to race 5 (see ( ) × Bison 3–W–C). The other resgene with the same range of immunity must have been located at some other locus than the "L", "M" or "*N*" loci.

But for the results with Newland × ( ) 3–W–C, in which only one resgene appeared to condition immunity to race 5, it might have appeared that the survey selection was homozygous for the two sets of resgenes conditioning wide immunity to the NPA races. The results with this selection (assuming that the 41 : 27 segregation represents a one-factor ratio rather than a very aberrant two-factor ratio) suggested that the survey selection was heterozygous at at least one of the loci carrying the widely immune resgenes.

The existence, at an undesignated locus, of a resgene conferring resistance to a wide range of NPA races seemed to be fairly well established from these studies. This may

well have been the same factor as that determined in Morye. Argentine 462 was reported to carry much the same resgene complement as Morye except for the heterozygosity of one or two factor pairs in Argentine (Flor, 1947, pp. 242, 243). The probable occurrence of the same resgene at an undesignated locus in both varieties gave some measure of assurance that the Argentine 462 material used in the survey and genetical investigations was essentially true to type. But in view of the heterozygosity of the material (which seemed to be typical of this line as originally used by Flor, and later by other workers at Sydney University and in New Zealand) it was problematical whether the single plant selection used in the survey or any of the other selections carried the full range of Argentine 462 resgenes.

Results obtained with Bison Fx 13 C.I. 389. (Table 11.)

Bison was fully susceptible to every race but race 1. Its immunity to this race was conditioned by a single resgene. This resgene was allelic with the single Koto resgene conferring immunity to race 1, and with one of the two Ottawa 770B resgenes, which also conditioned immunity or resistance to this race. It segregated in a mutually exclusive distribution with the J.W.S. "L" resgene, which conditioned the race 2 immunity of 3-way-cross seedlings (Bison × J.W.S.) × F257. These results located it in the "L" allelic series.

Results obtained with Punjab Fx 14.

Punjab was immune to every Australian race identified during the current survey except race 1.

Without exception its immunity was derived from a single resgene. This resgene was very closely linked with the Abyssinian "N" resgene at the "1–N" locus, and the Newland and Ottawa 770B "N" resgenes conditioning the resistance of the following hybrids to race 1, e.g., (Newland × Punjab) × F257 and (Punjab × Ottawa 770B) × F257.

Results obtained with Walsh Fx 86. (Table 12.)

Walsh was the only linseed variety grown commercially in Australia. It was known to be rather heterogeneous. S. G. Burns identified at least six distinct lines in Queensland, and other workers frequently noted differences in flower colour within the variety. The heterogeneity was confirmed by the rust reaction of several single plant selections obtained from a commercial sample of seed. Fourteen of twenty-two lines were fully susceptible to race 11. Eight of these race 11-susceptible lines were also susceptible to race 12, five were immune, and the other segregated for resistance.

One of the single plant selections susceptible to race 11 was included in the differential series. With the addition of this selection, race 11, an important Walsh-attacking race, could be differentiated from race 10, a non-Walsh-attacking race with an otherwise identical reaction on the differential series.

Genetical Anlysis of Non-Survey Selections.

Three independently inherited resgenes conditioned immunity or resistance to race 1 in the crosses Walsh selection 160 × F257 F2 3–W–C, Walsh Selection 144 × J.W.S. Four Walsh resgenes may have conditioned the reaction of the hybrids in the first cross. Only one resgene seemed to be effective against the race in the 3–way–cross. Ottawa 770B × (149) 3–W–C.

Two or three, probably three, Walsh resgenes conditioned resistance to race 2 in the cross Walsh selection 160 × F257. Three resgenes were also effective against the race in the cross (Walsh selection 160 × F257) × F257. Only one Walsh resgene conferred resistance to the race in Concurrent × Walsh unnumbered selection, (Ottawa 770B × Walsh selection 149) × F257 and Ottawa 770B × Walsh selection 149 hybrids.

Sometimes one, at other times two or three Walsh resgenes conditioned resistance to races 6 and 7 in the above crosses.

Commercial Walsh was evidently very heterogeneous and a possible source of new resgenes.

TABLE 11.

Results obtained with Bison.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Bi.	X.						I.	R.	S.		Total.	Bi.	X.	
( ) × F257 ..	1	I	S		I	S										
F2	2	S	S		S	S										
				69	54	15						3 : 1	1	1	0	0·5–0·7
( ) × J.W.S. ..	1	I	RS		I	RS			19	20		1 : 1	1	1	0	0·8–0·9
3–W–C ..	2	S	I		S	I			25		22	1 : 1	1	0	1 (L*)	0·5–0·7
	6	S	S		S	S			32	All suscept.						
				32	15	17										
Koto × ( ) ..	1	I	I		I	I			17	All immune			2	1	1 (L*)	
3–W–C ..	2, 6	S	I		I	S										
				16	5	11						1 : 1	1	0	1	0·1–0·2
(293) × Ottawa ..	1	I	I		I	I	I		133	All immune			3	1	2 (L*, 1–N)	
770B and Ottawa	2 (492, 548)	S	I		I	S	S		103		30	3 : 1	1	0	1	0·5–0·7
770B × (284) ..	3, 6	S	I		I	R	S		103	21	9	12 : 3 : 1	2	0	2	0·5–0·7
F2				133	103	21	9					12 : 3 : 1				0·5–0·7
( ) × Ottawa and	1	I	I		I	I	I		133	All immune			3	1	2 (L*, 1–N)	
reciprocal.. ..	2	S	I		I	S	S		59		60	1 : 1	1	0	1	0·9–1·0
3–W–C ..	6	S	I		I	R	S		55	30	26	2 : 1 : 1	2	0	2	0·8–0·9
				111	55	30	26					2 : 1 : 1				0·8–0·9
(289) × Newland	1	I	I		I	I	S		99		2	63 : 1	3	1	2 (M. 1–N)	0·7–0·8
Newland × (292)	2	S	I		I	S	S		86		24	3 : 1	1	0	1	0·3–0·5
F2				86	62	22	2					48 : 15 : 1				0·7–0·8
Newland × ( ) ..	1	I	I		I	S										
3–W–C ..				32	29	3						7 : 1	3	1	2 (M 1–N)	0·5–0·7
(293) × Punjab and	1	I	S		I	S	I	S	133		22	3 : 1	1	1	0	Below 0·05
Punjab × (284) ..	2	S	I		I	I	S	S	118		37	3 : 1	1	0	1 (2–N)	0·7–0·8
F2				155	101	17	32	5				9 : 3 : 3 : 1				0·01 approx.

TABLE 12.

Results obtained with Walsh, Non-Survey Selections.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Wa.	X.							I.	R.	S.		Total.	Wa.	X.	
(160) × F257 ..	1	R	S		R	R	S				175	1	255 : 1	¾		0	
F2	2	R	S		R	S	S				172	4	63 : 1	¾		0	
				176	172	3	1						252 : 3 : 1				
(160) × F257 ..	2, 7	R	S		R	S											
				89	80	9							7 : 1	3	3	0	0·5 approx.
3–W–C ..	2	R	S		R	R	S				29	3	7 : 1	3	3	0	0·5–0·7
	6	R	S		R	S	S				26	6	3 : 1	2	2	0	0·2–0·3
				32	26	3	3						6 : 1 : 1				0·7–0·8
	1, 2	R	S		R	S											
				57	51	6							7 : 1	3	3	0	0·5–0·7
Concurrent × (?) ..	1	R	S		R	R	S				119	1	63 : 1	3	3	0	0·5–0·7
F2	2	R	S		R	S	S				98	22	3 : 1	1	1	0	0·05–0·1
				120	98	21	1						48 : 15 : 1				0·2–0·3
(?) × F257	1	R	S		R	S											
F2				188	184	4							63 : 1	3	3	0	0·5–0·7
(144) × J.W.S. ..	6	R	S		R	R	S				78	1	63 : 1	3	3	0	0·8–0·9
F2	7	R	S		R	RS	S				78	1	63 : 1	3	3	0	0·8–0·9
				79	73	5	1						60 : 3 : 1	3	3	0	0·7–0·8
J.W.S. × (142) ..	6	R	S		R	S											
F2				78	72	6							15 : 1	2	2	0	0·5–0·7
Ottawa 770 ×	1	R	I		I	I	I	S		68		8	7 : 1	3	1	2 (L, 1–N)	0·5–0·7
(149)	2	R	I		I	I	S	S		56		20	3 : 1	2	1	1 (L)	0·7–0·8
3–W–C ..	7	R	S		I	S	S	S		41		33	1 : 1	1	1	0	0·3–0·5
				73	41	13	11	8					4 : 2 : 1 : 1				0·3–0·5

(144) was resistant to race 11. 149 was susceptible to race 11.

The resistant reaction of Walsh was commonly depressed to immunity under the incubation conditions to which the hybrids were exposed.

(?) = unnumbered selection.

TABLE 12.—*Continued*

Results obtained with Walsh, Non-Survey Selections.—Continued

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Wa.	X.							I.	R.	S.		Total.	Wa.	X.	
Ottawa 770B ×	1, 6	R	I		I	I	I	I		206	All immune					2 (L, 1–N)	
(149)	2, 8 (555)	R	I		I	I	I	S		194		12	15 : 1	2	1	1 (L)	0·8 approx.
F2	11	S	I		I	I	S	S		155		51	3 : 1	1	0	1	0·9–1·0
	7	R	S		I	S	I	S		154		52	3 : 1	1	1	0	0·9–1·0
				206	115	40	39	12					9 : 3 : 3 : 1				0·7–0·8
Results obtained with Selection Used in Race Survey.																	
( ) × Bison	1	R	I		I	I	I	S		86		9	7 : 1	3	2	1 (L)	0·3–0·5
	2, 7	R	S		I	I	S	S		68		20	3 : 1	2	2	0	0·5–0·7
	6	R	S		I	S	S	S		47		41	1 : 1	1	1	0	0·5–0·7
3–W–C ..				93	48	23	13	9					4 : 2 : 1 : 1				0·8–0·9
	1	R	I		I	I	I	S		46		4	7 : 1	3	2	1 (L)	0·3–0·5
	2, 7	R	S		I	I	S	S		38		12	3 : 1	2	2	0	0·8–0·9
	5	R	S		I	S	S	S		25		25	1 : 1	1	1	0	1·0
				50	25	13	8	4					4 : 2 : 1 : 1				0·7–0·8
( ) × Concurrent ..	1, 2	R	S		R	S											
3–W–C ..	5, 7			48	23	25							1 : 1	1	1	0	0·7–0·8
Newland × ( ) ..	1, 2, 7	R	I		I	R	R			49	None suscept.					1 (M*)	
	13	R	S		I	R	S			36		13	3 : 1	2	2	0	0·8–0·9
3–W–C ..	5	R	S		R	S	S			29		20	1 : 1	1	1	0	0·1–0·2
				49	29	7	13						2 : 1 : 1				0·5–0·7
Punjab × ( ) ..	1	R	S		R	R	S	S			8	6					
3–W–C ..	2, 7, 13	R	I		R	I	R	I									
				14	6	2	1	5					1 : 0 : 0 : 1			2–(N**)	
( ) × Abyssinian A	1, 2	R	I		I	I	R	R		50	All immune					1 (1–N*)	
	5	R	S		R	S	R	S			23	27	1 : 1	1	1	0	0·5–0·7
3–W–C ..	7	R	S		S	S	R	R			27	23	1 : 1	1	1	0	0·5–0·7
	11	S	S		S	S	S	S		50	All suscept.						
				50	9	14	14	13					1 : 1 : 1 : 1				0·7–0·8

(2–N**) = close linkage.

TABLE 12.—*Continued.*

Results obtained with Walsh, Non-Survey Selections.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Wa.	X.							I.	R.	S.		Total.	Wa.	X.	
()×Abyssinian ..	1, 2	R	I		I	I	R	R		32	None suscept.					1 (1–N*)	
B	5	R	S		R	S	R	S			15	17	1 : 1	1	1	0	0·7–0·8
3–W–C ..	7	R	S		S	S	R	R			15	17	1 : 1	1	1	0	0·7–0·8
	11	S	S		S	S	S	S		32	All suscept.						
				32	8	9	7	8					1 : 1 : 1 : 1				0·9–1·0
()×Abyssinian ..	1, 2	R	I		I	I	R	R		32	None suscept.					1 (1–N*)	
C	5	R	S		R	S	R	S			48	34	1 : 1	1	1	0	0·1–0·2
3–W–C ..	7	R	S		R	S	R	R			60	22	3 : 1	2	2	0	0·7 approx.
				82	22	22	18	20					1 : 1 : 1 : 1				0·9–1·0
Koto×()	1	R	I		I	I	S			98		9	7 : 1	3	2	1 (L)	0·2 approx.
	2, 7	R	I		I	R	I			108	All immune/ res.					1 (1–N*)	
3–W–C ..	11	S	I		I	S	I			49		57	1 : 1	1	0	1	0·3–0·5
				106	40	57	9						3 : 4 : 1				0·3–0·5
Koto×()	1	R	I		I	I	I	S		65		20	3 : 1	2	1	1 (L)	0·7–0·8
	2, 7	R	I		I	I	I	I		85	All immune					1 (1–N*)	
3–W–C ..	5	R	I		I	I	S	I		68		17	3 : 1	2	1	1 (1–N)	0·2–0·3
	11	S	I		I	S	S	I		42		43	1 : 1	1	0	1	0·9–1·0
				85	22	26	17	20					1 : 1 : 1 : 1				0·5–0·7
()×Koto	1	R	I		I	I	I	S	S	89		33	3 : 1	2	1	1 (L)	0·5–0·7
3–W–C ..	2 5	R	I		I	I	S	I	S	95		27	3 : 1	2	1	1 (1–N)	0·3–0·5
	11	S	I		I	S	S	I	S	62		60	1 : 1	1	0	1	0·8–0·9
				122	45	33	11	17	16				3 : 2 : 1 : 1 : 1				0·8 approx.

The resistant reaction of Walsh was commonly depressed to immunity under the incubation conditions to which the hybrids were exposed.
(?)=unnumbered selection.

Genetical Analysis of Survey Selection.

The following results were obtained from two lots, A and B, of 3-way-cross plants of (Walsh × Abyssinian) × F257 pedigree derived from different F1 seeds in the same cross pollinated boll. All the seedlings were either immune or resistant to races 1 and 2, thus identifying a Walsh resgene allelic or closely linked with the Abyssinian "N" resgene. Different single Walsh resgenes conferred resistance to races 5 and 7. The resistant reaction to race 7 conditioned by one of these two Walsh resgenes was inherited in a mutually exclusive distribution with the immune reaction to races 1 and 2 conditioned by the Abyssinian resgene at the "1–N" locus. The Walsh resgene conferring resistance to race 7 was thus located at the "1–N" locus.

The same "1–N" Walsh resgene was identified in lot C of 3-way-cross plants of the same pedigree derived from an independent cross. But another resgene inherited independently of the "1–N" resgene conditioned resistance to both race 7 and race 5.

Three Walsh resgenes were thus differentiated and the survey selection was seen to be heterozygous. One resgene present in each of the three lots (A, B and C) was located at the "1–N" locus and conditioned resistance to races 1, 2 and 7 but not race 5. Another at some other locus conditioned resistance to race 5, but not to race 7. A third resgene also at another locus than the "1–N" conditioned resistance to races 5 and 7. The two different resgenes conditioning resistance to race 5 must have been allelic, since there was always one and never more than one Walsh resgene effective against race 5 in each of the eight Walsh 3-way crosses tested with this race. By the same token the two different resgenes conditioning resistance to race 7 were not allelic, but independently inherited. Some crosses gave bifactorial, and others gave monofactorial resistance to race 7.

Results obtained with the cross (Punjab × Walsh) × F257 tested with races 1, 2, 7 and 13 were not conclusive because of the few plants tested, but they confirmed the identification of a Walsh resgene at an "*N*" locus and could best be accounted for by assuming linkage between the Punjab "*N*" resgene conferring immunity to races 2, 7 and 13, and a Walsh resgene conferring resistance to these races.

The survey selection was not homozygous at the "1–N" locus for the resgene conditioning immunity or resistance to races 1, 2 and 7, since the single Walsh resgene effective against race 2 segregated independently of the Koto "1–N" resgene in the cross (Walsh × Koto) × F257. The Walsh "1–N" resgene was obviously missing from this cross. See also the 3-way cross Walsh × Concurrent where this same resgene is missing and only the resgene conferring resistance to race 5 and 7 is present.

A resgene conferring resistance to race 5 was located at the same locus as the Newland "M" resgene in the 3-way cross (Newland × Walsh) × F257. There were no susceptible seedlings and the immune reaction to races 1 and 2 conditioned by the Newland "M" resgene was inherited in a mutually exclusive distribution with the resistant reaction to race 5 conditioned by the Walsh resgene. This would locate the two previously mentioned allelic resgenes, which conferred resistance to race 5, in the "M" allelic series.

Resgenes were located at two loci in the survey selection. One of these loci, "1–N", was heterozygous for a resgene conditioning resistance to race 7, but not race 5. The other allel at this locus was ineffective against races 2, 5 and 7, and may have been ineffective against all the other races used. The "M" locus was heterozygous for two factors, one effective against races 1, 2, 5 and 7, the other effective against race 5 but not race 7.

Genetical Analysis of Morye Non-Survey Selections. Fx 318 C.I. 112. (Table 13.)

Results obtained from Morye crosses which segregated for susceptibility and immunity to race 2 could always be accounted for by assuming that three independently inherited resgenes were effective against race 2.

In the crosses involving Morye 303 the resgene conditioning resistance to race 2 was susceptible to race 7. Since race 6 gave the same results as race 7 in the crosses

TABLE 13.

Results obtained with Morye Non-Survey Selections.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Mo.	X.						I.	R.	S.		Total.	Mo.	X.	
(?) × Williston	2	I	S		I	R	S									
Golden F2 ..				121	110	9	2					60 : 3 : 1	3	3	0	0·2–0·3
F257 × (?)	2	I	S		I	R	S		47	7	8	6 : 1 : 1	3	3	0	0·9–1·0
3–W–C ..	6, 7	I	S		I	S	S		47		15	3 : 1	2	2	0	0·8–0·9
				62	47	7	8					6 : 1 : 1				0·9–1·0
F257 × (?)	1	I	S		I	I	S		17		1	7 : 1/15 : 1	¾	¾	0	0·3–0·5
3–W–C ..	2	I	S		I	R	S		16	1	1	6 : 1 : 1	3	3	0	0·3–0·5
	7	I	S		I	S	S		16		2	3 : 1	2	2	0	0·1–0·2
				18	16	1	1									
F257 × (189) ..	1	I	S		I	I	I	S	140	All immune		255 : 1	4	4	0	0·3–0·5
	2	I	S		I	I	S	S	137		3	63 : 1	3	3	0	0·5–0·7
F2	6, 7	I	S		I	S	S	S	130		10	15 : 1	2	2	0	0·5–0·7
				140	130	7	3	0				240 : 12 : 3 : 1				0·7–0·8
(198) × Newland	2	I	I		I	R	S		20		2	15 : 1	4	3	1 (M)	0·5–0·7
3–W–C ..	6	I	I		I	S	S		18		4	7 : 1	3	2	1 (M)	0·3–0·5
				22	18	2	2					14 : 1 : 1				0·7–0·8
Punjab × (193) ..	1	I	S		I	S										
F2				214	208	6						63 : 1	3	3	0	0·1–0·2
Punjab × (193) ..	1	I	S		I	S			62		6	7 : 1/15 : 1	¾	¾	0	
3–W–C ..	2, 7	I	I		I	I			68	All immune					1 (2–N*)	
				68	62	6						7 : 1/15 : 1				
(193) × Punjab	1	I	S		I	S			14		1	15 : 1/7 : 1	¾	¾	0	
3–W–C ..	2, 6	I	I		I	I			15	All immune					1 (2–N*)	
				15	14	1										
(303) × Ottawa	2	I	I		I	I	R		70	6	0	7 : 1	4	3	1 (L*)	0·2–0·3
770B	7	I	S		I	S	S		61		14	3 : 1	2	2	0	0·2 approx.
3–W–C ..				75	61	8	6					6 : 1 : 1				0·3–0·5
Ottawa 770B ×	2	I	I		I	I	R		90	13	0	7 : 1	4	3	1 (L*)	0·9–1·0
(303)	7	I	S		I	S	S		81		22	3 : 1	2	2	0	0·7–0·8
3–W–C ..				103	76	14	13					6 : 1 : 1				0·9 1·0

(?) = unnumbered selection.

(F257 × unnumbered Morye Selection) × F257, and (F257 × Morye Selection 189) × F257, it was assumed that the above resgene susceptible to race 7 was also susceptible to race 6. This resgene was located in the same allelic series as the Ottawa 770B "L" resgene. It was almost certainly the "L" factor located in Morye by Flor. The factor, now known as the Rio "L" factor in Flor's new monofactorially immune series, was immune to race 1, resistant to race 2 and susceptible to race 6 when tested later in the studies at Sydney.

All three Morye resgenes effective against race 2 in selection 198 were inherited independently of the Newland "M" resgene.

One of the two resgenes conferring immunity to races 2, 6 and 7 was located at an "*N*" locus, since none of eighty-three 3-way-cross seedlings (Punjab × Morye selections 193) × F257 and (Morye Selection 193 × Punjab) × F257 was susceptible to these races. Insufficient 3-way seedlings were available to determine whether the Morye resgene was allelic with the Punjab "N" resgene conferring immunity to the above races, or whether it was just closely linked with it.

A fourth Morye resgene appeared to condition immunity to race 1 in the cross F257 × Morye selection 189. This resgene was not present in all the selections. Only three Morye resgenes were effective against race 1 in the cross Punjab × Morye selection 193. Results from the other crosses, (F257 × unnumbered Morye selection) × F257, (Punjab × Morye selection 193) × F257 and (Morye selection 193 × Punjab) × F257, could be interpreted to indicate three or four Morye resgenes effective against race 1. The combined results from the last three crosses, i.e., 93 immune : 8 susceptible, fitted a four factor 15 : 1 ratio very satisfactorily. The fourth resgene must have occurred at the "M" locus or some other undesignated locus independent of the other unidentified locus. It was probably a new resgene.

Genetical Analysis of the Survey Selection.

Very little survey selection hybrid material was available for study. The two lines studied suggested that the survey selection was not true to type.

Results obtained with Newland Fx 319 C.I. 188. (Table 14.)

Newland was immune or resistant to twelve of the eighteen Australian races identified in the current race survey. Race 7 sometimes gave a resistant reaction, at others a completely immune reaction. No distinction was made between the two types of reaction, both of which were classified as immune.

Only one resgene operated against the five non-Punjab-attacking races with which Newland hybrids were tested, namely, races 2, 6, 7, 8 and 17. This resgene was allelic with the single resgene in Italia Roma operating against races 2, 7 and 17.

The survey selection and the two additional selections 306 and 314 carried an additional resgene only effective against race 1 accessions. It was effective against each of the race 1 accessions used, 507, 610 and 627. This resgene was inherited independently of the previously determined "M" resgene and the Bison and Koto "L" resgenes.

The additional resgene was closely linked with the Punjab "*N*" resgene. Had these two resgenes been allelic, none of the 3–W–C seedlings of Newland × Punjab pedigree would have been immune to both the PA and NPA race types. But four of one hundred and eleven such seedlings susceptible to the two race groups could only be accounted for by assuming that the extra Newland factor occurred at some other "*N*" locus than the "2–N" locus marked by the Punjab "*N*" resgene. It probably occurred at the "1–N" locus marked by the Abyssinian "*N*" resgene, but this could not be confirmed owing to lack of Newland × Abyssinian hybrids.

Results obtained with Bolley Golden Fx 320 C.I. 644. (Table 15.)

Analysis of Non-Survey Selections.

Two Bolley Golden resgenes were effective against races 2 and 7 in each of the non-survey selections 325, 326, 338, 339. One of these two conferred immunity to races 2 and 7. The other conditioned a resistant reaction, which ranged from immunity to

TABLE 14.

Results obtained with Newland.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ne.	X.							I.	R.	S.		Total.	Ne.	X.	
F257 × (314) and	1	I	S		I	R	S			95		3	15 : 1	2	2	0	0·2 approx.
(306) × F257 ..	2, 6	I	S		I	S	S			110		30	3 : 1	1	1	0	0·3–0·5
F2				98	70	25	3						12 : 3 : 1				0·1–0·2
( ) × Bison ..	1	I	I		I	S											
3–W–C ..				32	29	3							7 : 1	3	2	1 (L)	0·3–0·5
( ) × Bison and	1	I	I		I	I	S			99		2	63 : 1	3	2	1 (L)	0·7–0·8
reciprocal	2	I	S		I	S	S			86		24	3 : 1	1	1	0	0·3–0·5
F2				86	62	22	2						48 : 15 : 1				0·7–0·8
Punjab × ( ) ..	1 (507, 621)	I	S		I	I	I	S	S	42		13	3 : 1	2	2	0	0·8–0·9
3–W–C ..	2, 8 (564)	I	I		I	I	S	I	S	39		18	3 : 1	2	1	1 (2–N)	0·2–0·3
	5	S	I		I	S	S	I	S	27		30	1 : 1	1	0	1	0·5–0·7
				56	14	12	16	12		1			1 : 1 : 1 : 1 : 0				0·8–0·9
( ) × Punjab ..	1 (507, 610)	I	S		I	I	S	S		41		14	3 : 1	2	2	0	0·8–0·9
	2, 8 (564)	I	I		I	S	I	S		43		12	3 : 1	2	1	1 (2–N)	0·5–0·7
3–W–C ..				55	32	9	11	3					2 : 1 : 1 : 0				0·2–0·3
	1 (507, 610)	I	S		I	I	I	S	S	30		10	3 : 1	2	2	0	1·0
	2, 8 (564)	I	I		I	I	S	I	S	32		8	3 : 1	2	1	1 (2–N)	0·3–0·5
	5	S	I		I	S	S	I	S	26		14	1 : 1	1	0	1	0·05–0·1
				40	16	6	8	10	0				1 : 1 : 1 : 1 : 0				0·1–0·2

TABLE 14.—*Continued.*

Results obtained with Newland.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ne.	X.							I.	R.	S.		Total.	Ne.	X.	
( )×Punjab and	1	I	S		I	S	I			270		11	15 : 1	2	2	0	0·1–0·2
reciprocal	2	I	I		I	I	S			267		14	15 : 1	2	1	1 (2–N)	0·3–0·5
F2				281	256	11	14						14 : 1 : 1				0·1–0·2
(306)×Punjab and	1	I	S		I	I	S			262		22	15 : 1	2	2	0	0·3 approx.
reciprocal	2, 6	I	I		I	S	I			274		18	15 : 1	2	1	1 (2–N)	0·9–1·0
F2				276	242	14	20						14 : 1 : 1				0·5–0·7
Tammes' Pale Blue	1	I	I		I	I	I	S		58		1		3	1	2 (M, 1–N**)	
×( )	5	I	S		I	S	S	I		31		25	1 : 1	1	1	0	0·3–0·5
3–W–C ..	7	I	I		I	I	S	I		45		11	3 : 1	2	1	1 (M)	0·3–0·5
				56	30	14	11	1					2 : 1 : 1 : 0				0·5–0·7
Italia Roma×( ) ..	1, 2, 7	I	I							40	All immune			2	1	1 (M*)	
3–W–C																	
Italia Roma×( ) ..	1, 2, 7, 17	I	I		I	I				43	All immune			2	1	1 (M*)	
3–W–C ..	5	R	S		IR	S				23		20	1 : 1	1	1	0	0·5 0·7
				43	23	20											

TABLE 15.

Results obtained with Bolley Golden.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		BG.	X.							I.	R.	S.		Total.	BG.	X.	
J.W.S. ×	7	I	S		I	R	S										
(325) F2				242	189	31	22						12 : 3 : 1	2	2	0	0·02–0·05
(325) × J.W.S. ..	7	I	S		I	R	S										
F2				150	120	18	12						12 : 3 : 1	2	2	0	0·05–0·1
Concurrent × (338)	7	I	S		I	S											
F2				45	42	3							15 : 1	2	2	0	0·9 approx.
(339) × F257 ..	1	I	S		I	I	I	S		150	All immune		255 : 1	4	4	0	0·3–0·5
F2 .. .	2	I	S		I	I	S	S		130		6	15 : 1	2	2	0	0·3–0·5
	6	I	S		I	S	S	S		109		27	3 : 1	1	1	0	0·1–0·2
				136	109	21	6	0					192 : 48 : 15 : 1	4	4	0	0·5–0·7
F257 × (339) ..	1	I	S		I	I	I	S		139		1	255 : 1	4	4	0	0·5–0·7
F2	2	I	S		I	R	S	S		133		7	15 : 1	2	2	0	0·5–0·7
	6	I	S		I	S	S	S		112		28	3 : 1	1	1	0	0·1–0·2
				140	112	21	6	1					192 : 48 : 15 : 1				0·3–0·5
Total of last 2 lots				276	221	42	12	1					192 : 48 : 15 : 1				0·2–0·3
(338) × Punjab	1	I	S		I	I				100	All immune		255 : 1	4	4	0	0·5–0·7
F2	6	I	I		I	S				82		10	15 : 1	2	1	1 (2-N)	0·05–0·1
				92	82	10											
Concurrent × (338)	1	I	S		I	I	I	S		49		0	15 : 1	4	4	0	0·05–0·1
	2	I	S		I	R	S	S		40		9	3 : 1	2	2	0	0·2–0·3
3-W-C ..	6	I	S		I	S	S	S		27		22	1 : 1	1	1	0	0·3–0·5
				49	27	13	9	0					8 : 4 : 3 : 1				0·3–0·5
Punjab × (326) ..	1	I	S		I	I	I	S	S	54		4	15 : 1	4	4	0	0·8–0·9
	2, 7	I	I		I	I	S	I	S	53		5	7 : 1	3	2	1 (2 N)	0·1–0·2
3-W-C ..	6	I	I		I	S	S	I	S	46		12	3 : 1	2	1	1 (2-N)	0·3–0·5
				58	43	7	4	3	1				11 : 2 : 2 : 1 : 0				0·5–0·7

TABLE 15.—*Continued.*

Results obtained with Bolley Golden.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		BG.	X.							I.	R.	S.		Total.	BG.	X.	
Punjab × (321)	1	I	S		I	S											
3-W-C ..				29	28	1							15 : 1	4	4	0	0·5–0·7
F257 × (339) ..	1	I	S		I	I	I	S		19		2	15 : 1	4	4	0	0·5–0·7
	2	I	S		I	I	S	S		20		5	3 : 1	2	2	0	0·5–0·7
3-W-C ..	6	I	S		I	S	S	S		10		11	1 : 1	1	1	0	0·8–0·9
				21	11	5	3	2					8 : 4 : 3 : 1				0·8–0·9
Selection Used during the Physiologic Race Survey.																	
( ) × F257 ..	1 (507, 557)	I	S		I	I	S			35		2	15 : 1	4	4	0	0·8–0·9
3-W-C ..	5, 7, 11, 17	I	S		I	S	S			28		8	3 : 1	2	2	0	0·7 approx.
				36	28	6	2						12 : 3 : 1				0·9–1·0
( ) × Bison ..	1	I	I		I	I				85	All immune			5	4	1 (L*)	
3-W-C ..	3	I	S		R	S					43	42	1 : 1	1	1	0	0·9–1·0
				85	43	42											0·9–1·0
( ) × Koto ..	1	I	I		I	I	I	I		162	All immune			5	4	1 (L*)	
3-W-C ..	2, 7	I	I		I	I	I	S		123		15	7 : 1	3	2	1 (1–N)	0·5–0·7
	6	I	I		I	I	S	S		94		23	3 : 1	2	1	1 (1–N)	0·1–0·2
	13	S	I		I	S	S	S		63		55	1 : 1	1	0	1	0·3–0·5
				103	56	25	14	8					4 : 2 : 1 : 1				0·5 approx.
( ) × Ottawa 770B	6	I	I		I	I	I	S	S	34		3	7 : 1	3	1	2 (L, 1–N)	0·3–0·5
	2	I	I		I	I	S	I	S	31		7	7 : 1	3	2	1 (L)	0·2–0·3
3-W-C ..	7	I	S		I	S	S	I	S	24		13	3 : 1	2	2	0	0·1–0·2
				37	23	6	5	1	2				11 : 2 : 1 : 1 : 1				0·3–0·5
( ) × Newland ..	2, 6	I	I		I	I				16	All immune			3	2	1 (M*)	
3-W-C ..	5	I	S		I	S				13		3	3 : 1	2	2	0	0·5–0·7
				16	13	3							3 : 1				0·5–0·7

TABLE 15.—*Continued.*

Results obtained with Bolley Golden.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.					Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		BG.	X.							I.	R.	S.		Total.	BG.	X.	
( )×Punjab ..	1	I	S		I	I	I	I	S	29		1	15 : 1	4	4	0	0·5 approx.
	2	I	I		I	I	R	S	I	27		3	7 : 1	3	2	1 (2–N)	0·5–0·7
3–W–C ..	6	I	I		I	I	S	S	I	22		7	3 : 1	2	1	1 (2–N)	0·9–1·0
	13	S	I		I	S	S	S	I	17		13	1 : 1	1	0	1	0·3–0·5
				29	16	5	4	3	1				7 : 4 : 2 : 2 : 1				0·5–0·7
( )×Abyssinian ..	1	I	I		I	I	I			100	All immune			5	4	1 (1–N*)	
3–W–C Lot A	2	I	I		I	R	S			80		20	7 : 1	3	2	1 (1–N)	0·02–0·05
				100	67	13	20						6 : 1 : 1				0·05–0·1
Lot B	1	I	I		I	I	I	I	I	69	All immune			5	4	1 (1–N*)	
	2	I	I		I	I	I	R	S	66		3	7 : 1	3	2	1 (1–N)	0·02–0·05
	5	I	S		I	S	R	R	S	56		13	3 : 1	2	2	0	0·2–0·3
				69	37	10	7	12	3				4 : 1 : 1 : 1 : 1				0·2–0·3
Lot C ..	1	I	I		I	I	I	I		98	All immune			5	4	1 (1–N*)	
	2	I	I		I	I	R	S		84		16	7 : 1	3	2	1 (1–N),	0·2–0·3
	6	I	S		I	S	S	S		52		45	1 : 1	1	1	0	0·3–0·5
				97	52	13	16	16					4 : 2 : 1 : 1				0·05 approx.
Total ..	1				I	I	I			267	All immune			5	4	1 (1–N*)	
	2				I	R	S			230		39	7 : 1	3	2	1 (1–N)	0·3–0·5
				266	186	41	39						6 : 1 : 1				0·1–0·2

resistance according to the conditions of incubation. The first conditioned an immune reaction to race 6. The second was ineffective against this race in each of the three selections involved in the crosses tested with this race. Two additional resgenes were effective against race 1 in each of the four selections 321, 326, 388 and 339 involved in crosses tested with this race.

As far as the tests could determine the variety Bolley Golden was homozygous for four resgenes.

Analysis of Resistance of the Survey Selection to Non-Punjab-Attacking Races.

The survey selection agreed with above selections. Two resgenes conferred immunity or resistance to races 2 and 7. Both were also effective against races 5, 11 and 17. Only one of these resgenes was effective against race 6. Both resgenes and two additional independently inherited resgenes conferred immunity to race 1 in the cross (Bolley Golden × F257) × F257.

The two Bolley Golden resgenes effective against the non-Punjab-attacking races were inherited independently of the Punjab, Koto and Abyssinian "*N*" resgenes. Both were also inherited independently of the Ottawa 770B "L" resgene.

One was almost certainly allelic with the Newland "M" resgene. Only sixteen plants of (Bolley Golden × Newland) × F257 were tested with races 2 and 6. No further seed was available since this cross succumbed to *Fusarium* wilt, but since only two resgenes (one from each variety) were known to be effective against race 6 in this cross this number was probably sufficient.

Results obtained with Punjab-Attacking Race.

Two additional resgenes were effective against the two race 1 accessions (507 and 557) used in the study of the survey selection. One was located in the "L" allelic series. The other was probably located at the "1–N" locus. 267 3-way-cross plants of (Bolley Golden × Abyssinian) × F257 were immune to race 1. This conclusion was supported by results from the cross (Punjab × Bolley Golden selection 326) × F257. One of the fifty-eight plants tested in this cross was susceptible to both Punjab and non-Punjab-attacking race groups. This could only be accounted for by assuming that the Bolley Golden and the Punjab "*N*" resgenes were closely linked.

Results obtained with Italia Roma Fx 321 C.I. 1005–2. (Table 16.)

Italia Roma was immune to thirteen of the eighteen races determined in the race survey. Its reaction to other races varied about a norm of moderate susceptibility.

A single resgene conditioned immunity to NPA races in Italia Roma selections 345, 352, 353, 356, 362, an unnumbered selection and the selection used in the race survey.

The Italia Roma resgene and the "L" resgene of Ottawa 770B were inherited independently. The Italia resgene was also inherited independently of the Punjab resgene at the "2–N" locus. It was allelic with the Newland "M" resgene.

Two Italia resgenes, including the one already located, were effective against the three race 1 accessions, 507, 621 and 627, with which hybrids of the survey selection and selections 352, 353 and 356 were tested. The additional resgene was allelic with the J.W.S., Koto and Bison "L" resgenes. The immune reaction to race 2 and semi-resistant reaction to race 1 conditioned by the J.W.S. "L" resgene was inherited in a mutually exclusive distribution to the immune reaction to race 1 conditioned by one of the two Italia Roma resgenes in 3-way crosses of J.W.S. × Italia Roma pedigree.

Results obtained with Leona Fx 322 C.I. 836. (Table 17.)

Leona was susceptible to every race but races 1, 2, 4 and 17. Apart from reaction to race 1 it reacted very much like Abyssinian. It was not so intensively investigated as other varieties.

A single Leona resgene conferred immunity to race 2 in the cross (Leona × F257) × F257. This and another independently inherited resgene conferred immunity to race 1 in the same cross. Two Leona resgenes were also effective against race 1 in the crosses Leona × F257, (Leona × Bison) × F257 and Punjab × Leona.

TABLE 16.

Results obtained with Italia Roma.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		IR.	X.						I.	R.	S.		Total.	IR.	X.	
F257 × (356) ..	1	I	S		I	I	S		137		3	15 : 1	2	2	0	0·02–0·05
F2	2, 6	I	S		I	S	S		106		34	3 : 1	1	1	0	0·8–0·9
				140	106	31	3					12 : 2 : 1				0·05–0·1
(362) × Ottawa	2	I	I		I	I	S		95		4	15 : 1	2	1	1 (L)	0·3–0·5
770B F2	7	I	S		I	S	S		75		24	3 : 1	1	1	0	0·8–0·9
				99	75	20	4					12 : 3 : 1				0·5–0·7
Ottawa 770B ×	2	I	I		I	I	S		81		6	15 : 1	2	1	1 (L)	0·8 approx.
(345)	7	I	S		I	S	S		66		21	3 : 1	1	1	0	0·8–0·9
F2				87	66	15	6					12 : 3 : 1				0·2–0·3
(?) × Ottawa ..	6	I	I		I	I	R	S	205	10	4	3 : 1	3	1	2 (L, 1–N)	0·7–0·8
F2	2	I	I		I	I	S	S	205		14	15 : 1	2	1	1 (L)	0·9–1·0
	7	I	S		I	S	S	S	164		44	3 : 1	1	1	0	0·2 approx.
				208	164	30	10	4				48 : 12 : 2 : 1				0·3–0·5
( ) × Newland and reciprocal F2	2, 7	I	I						200	All immune			2	1	1 (M*)	
(352) × Punjab ..	1	I	S		I	I	S	S	90		5	15 : 1	2	2	0	0·5–0·7
F2	6	I	I		I	S	I	S	84		11	15 : 1	2	1	1 (2–N)	0·02–0·05
				94	79	10	4	1				57 : 3 : 3 : 1				0·05–0·1
Punjab × (353) ..	1	I	S		I	I	S		86		7	15 : 1	2	2	0	0·5–0·7
F2	13	S	I		I	S	S		75		18	3 : 1	1	1	0	0·2–0·3
				93	75	11	7					12 : 3 : 1				0·2–0·3

TABLE 16.—*Continued.*

Results obtained with Italia Roma.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		IR.	X.						I.	R.	S.		Total.	IR.	X.	
J.W.S.×( ) ..	1 (621, 627)	I	RS		I	RS			7		1	3 : 1	2	2	0	0·5–0·7
3-W-C ..	13	S	S		S	S										
				8	7	1										
( )×J.W.S. ..	1	I	RS		I	I	RS		40	12		3 : 1	2	2	0	0·7–0·8
3-W-C ..	2	I	I		I	S	I		39		12	3 : 1	2	1	1 (L)	0·8–0·9
	6, 7	I	S		I	S	S		27		25	1 : 1	1	1	0	0·7–0·8
				51	27	12	12					2 : 1 : 1				0·9–1·0
( )×Bison ..	1	I	I		I	I			30	All immune			3	2	1 (L*)	
3-W-C ..	2, 5, 7, 17	I	S		I	S			17		13	1 : 1	1	1	0	0·3–0·5
				30	17	13						1 : 1				0·3–0·5
( )×Koto ..	1	I	I		I	I			23	All immune			3	2	1 (L*)	
3-W-C ..	2, 5, 7, 17	I	I		I	S			19		4	3 : 1	2	1	1 (1–N)	0·3–0·5
				23	19	4										
Abyssinian×( ) ..	1 (621, 627)	I	I		I	S			13		2	7 : 1	3	2	1 (1–N)	0·9–1·0
3-W-C ..	13	S	S		S	S			15	All suscept.						
				15	13	2										
( )×Newland ..	1, 2, 7	I	I						40	All immune			2	1	1 (M*)	
3-W-C																
( )×Newland ..	1, 2, 7 17	I	I		I	I			43	All immune			2	1	1 (M*)	
3-W-C ..	5	R	S		IR	S			23		20	1 : 1	1	1	0	0·5–0·7
				43	23	20										

TABLE 17.

Results obtained with Leona.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Le.	X.						I.	R.	S.		Total.	Le.	X.	
( )×F257 ..	1	I	S		I	R	S									
F2				207	177	13	17		190		17	15 : 1	2	2	0	0·2–0·3
( )×Bison ..	1	I	I		I	S			40		4	7 : 1	3	2	1 (L)	0·3–0·5
3–W–C ..	7	S	S		S	S			39	All suscept.						
				39	35	4										
( )×F257 ..	1	I	S		I	I	S		68		2	15 : 1	2	2	0	0·2–0·3
F2 ..	2	I	S		I	S	S		55		15	3 : 1	1	1	0	0·3–0·5
				70	55	13	2					12 : 3 : 1				0·3–0·5
Punjab×( ) ..	1	I	S		I	I	S	S	164		13	15 : 1	2	2	0	0·5–0·7
F2	6	S	S		I	S	I	S	133		44	3 : 1	1	0	1	0·9–1·0
				177	120	44	12	1[1]				12 : 3 : 1 : 0				0·05–0·1
Abyssinian×( ) ..	1	I	I						35	All immune			3	2	1 (1–N*)	
3–W–C ..	7	S	S							All suscept.						

[1] Product of crossing over.

One of these two resgenes was allelic with Abyssinian resgene at the "1–N" locus. Neither Leona resgene was allelic with the Bison "L" resgene.

The results were inconclusive. But one resgene conditioning immunity to race 1 was located at the "1–N" locus. The other resgene did not occur in the "L" allelic series and may have been located at the "M" or some other locus.

Results obtained with Tammes' Pale Blue Fx 323 C.I. 333–1. (Table 18.)

Tammes' Pale Blue was moderately susceptible to race 17, but was classified as immune to the other seventeen races identified in the survey.

A single Tammes' Pale Blue resgene appeared to confer immunity to each of the non-Punjab-attacking races used in the tests of each of the following selections used in these studies, viz., selections 388, 390, 391, 395 and the survey selection.

The resgene effective against races 2 and 5 was allelic with the Abyssinian and Koto resgenes at the "1–N" locus. None of the seventy-nine 3-way-cross seedlings (Abyssinian × T.P.B. survey selection) × F257 was susceptible to race 2, and none of the fifty-one 3-way-cross seedlings (T.P.B. survey selection × Koto) × F257 was susceptible to race 5.

Another Tammes' Pale Blue resgene was effective against race 1. It occurred at another locus closely linked with the "1–N" locus. This was first indicated by the results obtained from F2 hybrids F257 × T.P.B. Selection 390. The plants susceptible to race 1 and immune to race 2, and others immune to race 1 but susceptible to race 2, could only be explained by assuming that resistance to these two races was derived from different single resgenes at closely linked loci.

This was confirmed by the crosses (T.P.B. survey selection × Ottawa 770B) × F257, and two lots of (Abyssinian × T.P.B. survey selection) × F257. Both the above varieties, with which Tammes' Pale Blue was crossed, carried a resgene effective against race 1 at the "1–N" locus. The occurrence of plants susceptible to race 1 in each of these crosses showed that the Tammes' Pale Blue resgene conferring immunity to race 1 was not located at the "1–N" locus. This was confirmed by results from T.P.B. × Newland 3–W–C. The second resgene probably occurred in the "2–N" allelic series. But Punjab × T.P.B. 3-way-cross material prepared to confirm this succumbed to *Fusarium* root rot.

Results obtained with Koto Fx 326 C.I. 842. (Table 19.)

Koto was immune to every race identified during the survey. A single resgene conferred immunity to each of the NPA races with which Koto hybrids were tested. These tests involved Koto Survey Selection and additional selections 397, 404 and 406. The results also established the homogeneity of the variety.

The Koto resgene segregated independently of the Ottawa 770B "L" resgene. This was confirmed by its independent segregation with the J.W.S. resgene in the cross (J.W.S. × Koto) × F257 tested with race 2. It was also inherited independently of the Newland and Italia Roma "M" resgenes.

It was located at the "1–N" locus marked by the Abyssinian "*N*" resgene. None of 75 plants (Koto × Abyssinian) × F257 was susceptible to race 2. The location was confirmed by results obtained from Koto × Punjab hybrids. F2 and 3-way-cross plants of this pedigree which were susceptible to race 2 could only be explained by assuming close linkage between the Punjab resgene at the "2–N" locus and the locus accommodating the Koto "*N*" resgene.

Another resgene conditioned immunity to race 1. This resgene was susceptible to NPA races, and segregated independently of the resgene effective against these races. It was allelic with the Bison, Bolley Golden, Italia Roma, Very Pale Blue Crimped and Kenya "L" resgenes.

Summary and Discussion.

Varieties used in physiologic race surveys must be maintained as pure lines. While *Linum usitatissimum* is a self-fertilizing species, the open nature of the flowers and constant activity of bees favours a small percentage of cross pollination at each

TABLE 18.

Results obtained with Tammes' Pale Blue.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.				Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		TPB.	X.						I.	R.	S.		Total.	TPB.	X.	
F257 × (390) ..	1	I	S		I	I	S	S	54		16	3 : 1	1	1	0	0·5–0·7
F2	2	I	S		I	S	I	S	52		18	3 : 1	1	1	0	0·8–0·9
				70	49	5	3	13				3 : 0 : 0 : 1				
(391) × Ottawa and	1	I	I		I	I	I		100	All immune			3	1	2 (L, 1–N*)	
Ottawa × (395) ..	2	I	I		I	I	S		97		3	15 : 1	2	1	1 (L)	0·1–0·2
F2	7	I	S		I	S	S		81		19	3 : 1	1	1	0	0·1–0·2
				100	81	16	3					12 : 3 : 1				0·2–0·3
(388) × Newland F2	2, 7	I	I		I	S			85		4	15 : 1	2	1	1 (M)	0·3–0·5
Selection used in Physiologic Race Survey.																
( ) × Ottawa 770B	1	I	I		I	I	S		42		1		3	1	2 (L, 1–N)	
3–W–C ..	7	I	S		I	S	I		22		21	1 : 1	1	1	0	0·8–0·9
				43	21	21	1					1 : 1 : 0				1·0
Abyssinian × ( ) ..	1	I	I		I	I	S		30		3		2	1	1 (1–N**)	
3–W–C ..	7	I	S		I	S	I		16		17	1 : 1	1	1	0	0·8–0·9
				33	13	17	3					1 : 1 : 0				
( ) × Newland ..	1	I	I		I	I	I	S	58		1		3	1	2 (M, 1–N**)	
3–W–C ..	5	I	S		I	S	S	I	31		25	1 : 1	1	1	0	0·3–0·5
	7	I	I		I	I	S	I	45		11	3 : 1	2	1	1 (M)	0·3–0·5
				56	30	14	11	1				2 : 1 : 1 : 0				
Abyssinian × ( ) ..	1	I	I		I	I	S		45		1		2	1	1 (1–N)	
3–W–C ..	2	I	I		I	I	I		46	All immune			2	1	1 (1–N*)	
	5, 8, 11	I	S		I	S	I		27		19	1 : 1	1	1	0	0·2–0·3
				46	26	19	1					1 : 1 : 0				
( ) × Koto ..	1	I	I		I	S			43		8	3 : 1	2	1	1 (L)	0·1–0·2
3–W–C ..	5	I	I		I	I			51	All immune			2	1	1 (1–N*)	
				51	43	8						3 : 1				0·1–0·2

(1–N**) = close linkage.

TABLE 19.

Results obtained with Koto.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.						Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ko.	X.								I.	R.	S.		Total.	Ko.	X.	
( ) × Abyssinian	1	I	I	13	I	S					9		4	3 : 1	2	2	1 (1–N)	0·3–0·5
3–W–C	2	I	I		I	I					25	All immune			2	1	1 (1–N*)	
( ) × Abyssinian	1	I	I		I	I	S				36		14	3 : 1	2	1	1 (1–N)	0·5–0·7
3–W–C	2	I	I		I	I	I				50	All immune			2	1	1 (1–N*)	
	5, 7, 11, 17	I	S		I	S	I				25		24	1 : 1	1	1	0	0·8–0·9
				49	11	24	14							1 : 2 : 1				0·8–0·9
( ) × Punjab	1	I	S		I	I	S				13		19	1 : 1	1	1	0	0·2–0·3
3–W–C	2, 6	I	I		I	S	I				22		1	1 : 0	2	1	1 (2–N)	
				18	5	1	12							1 : 0 : 1				0·05–0·1
(386) × Punjab	1	I	S		I	S	I				149		47	3 : 1	1	1	0	0·7–0·8
Punjab × (404)	7	I	I		I	I	S				195		1		2	1	1 (2–N)	
F2				196	148	47	1							3 : 1 : 0				0·7–0·8
( ) × Punjab	1	I	S		I	I	S	S	S	I	16		13	1 : 1	1	1	0	0·5–0·7
3–W–C	2	I	I		I	I	I	I	S	S	26		3		2	1	1 (2–N)	
	N.Z. TPB-attacking	S	I		S	I	I	S	S	S	13		16	1 : 1	1	0	1	0·5–0·7
	N.Z. 3	I	S		I	S	S	I	I	S	15		14	1 : 1	1	1	0	0·8–0·9
				29	8	8	5	5	2[1]	1[1]				1 : 1 : 1 : 1 : 0 : 0				0·7–0·8
Ottawa 770B × (404) and	1	I	I		I	I	I				186	All immune			3	1	2(L*, 1–N)	
(403) × Ottawa 770B	2	I	I		I	I	S				174		12	15 : 1	2	1	1 (L)	0·9–1·0
F2	7	I	S		I	S	S				143		43	3 : 1	1	1	0	0·5–0·7
				186	143	31	12							12 : 3 : 1				0·7–0·8

[1] Cross overs.

TABLE 19.—*Continued.*

Results obtained with Koto.—Continued.

Pedigree.	Race.	Parental Reaction.		Total.	Number of Seedlings with Reactions Listed Below.						Reaction to Each Race.			Expected Ratio.	Number of Resgenes Segregating.			P.
		Ko.	X.								I.	R.	S.		Total.	Ko.	X.	
(406) × Newland F2	2, 7	I	I		I	S					172		9	15 : 1	2	1	1 (M)	0·3–0·5
( ) × F257	1	I	S		I	I	S	S			9		7	1 : 1	1	1	0	0·5–0·7
3–W–C	2	I	S		I	S	I	S			15		15	1 : 1	1	1	0	1·0
				12	4	1	4	3						1 : 1 : 1 : 1				0·5–0·7
(397) × F257	1	I	S		I	S	I	S			126		39	3 : 1	1	1	0	0·5–0·7
F2	2	I	S		I	I	S	S			120		45	3 : 1	1	1	0	0•5 approx.
				165	94	26	32	13						9 : 3 : 3 : 1				0·5–0·7
(397) × F257	1	I	S		I	I	S	S			99		33	3 : 1	1	1	0	1·0
F2	2, 6	I	S		I	S	I	S			99		33	3 : 1	1	1	0	1·0
				132	73	26	26	5						9 : 3 : 3 : 1				0·9–1·0
J.W.S. × ( )	1	I	RS		I	I	RS	RS			6		12	1 : 1	1	1	0	0·1–0·2
3–W–C	2	I	I		I	S	I	I			22		3	3 : 1	2	1	1 (L)	0·1–0·2
				9	2	2	2	3						1 : 1 : 1 : 1				0·9–1·0
( ) × Williston Golden ..	2	I	S		I	S												
F2				139	101	38								3 : 1	1	1	0	0·5–0·7
( ) × Bison	1	I	I		I	I					17	All immune					1 (L*)	
3–W–C	2, 6	I	S		I	S					5		11	1 : 1	1	1	0	0·1–0·2
				16	5	11												
Newland × ( )	1	I	I		I	I	I	S			43		8	7 : 1	3	1	2 (M. 1–N)	0·3–0·5
3–W–C	2	I	I		I	I	S	I			24		12	3 : 1	2	1	1 (M)	0·2–0·3
	5	I	S		I	S	S	I			19		15	1 : 1	1	1	0	0·3–0·5
				34	14	4	11	5						3 : 2 : 2 : 1				0·3–0·5

generation of seed increase. Such varieties as Ottawa 770B, Very Pale Blue Crimped, Williston Golden and Tammes' Pale Blue had distinctive flower colour, and the first two had characteristic petal shape, controlled by recessive factors. Rogues resulting from cross pollination could be detected and removed without difficulty. Judging by the very small percentage of rogue plants in these varieties at the time they were taken over for these studies, cross pollination did not constitute a serious threat to the purity of these differential lines. Varieties with the common blue petal controlled by dominant petal colour and petal shape allels may have carried a small percentage of off type plants, despite careful selection for conformity to growing habit, etc. With varieties exhibiting characteristic differential reaction to races already identified the process of selection could be carried further. But Morye and Argentine 462 were immune to all races previously identified in Australia and all those identified during these studies. Several single plant selections of each variety were included in the preliminary genetical investigations. Whenever possible hybrid material was tested with races to confirm the genetic identity of the parents involved in the cross, additional to those minimally required to determine the allelic identity of the resgene under study in a given variety.

Only very occasionally had hybrid material to be rejected as not true to type. Apart from Argentine 462 the differential varieties included in the survey and genetical investigations were true to type. The Morye survey selection seemed to be an off type. This did not invalidate the listing of Morye as immune to all Australian races. Genetical studies with other selections and confirmatory tests of other single plant selections during the survey supplied independent evidence for the all round immunity of this variety.

The dichotomy of the Australian *Melampsora lini* race complex into non-Punjab-attacking (NPA) and Punjab-attacking (PA) groups was fully confirmed by these studies. This had been indicated during the race survey by the unique host and geographic range of the PA complex, and by the remarkable high temperature tolerance of this complex in the field. The last feature had been confirmed and emphasized by studies *in vitro* of uredospore germination.

Flor established a one-for-one correlation between pathogenic factors in *Melampsora lini* and resgenes in the host species for which they were specific. On this basis the results obtained during the genetical studies of host resistance in Sydney showed that the Australian NPA complex had substantially the same range of pathogenicity as the combined range of virulence of the North and South American races determined by Flor. Kenya, Argentine 705–1 and Very Pale Blue Crimped gave too variable a reaction to the NPA races, particularly in hybrid combinations, to permit adequate study of their respective resgenes with this group. Among the other varieties all the resgenes identified by Flor were found to function against one or more of these races. The discovery of a previously unidentified "*N*" resgene in Ottawa 770B was the only instance of a pathogenic factor in the NPA complex not present or detected among overseas races. This factor operated in races 3, 5, 6 and 13 (accession 602) found in Victoria, South Australia and Western Australia. It must have been introduced early in the history of the development of this race complex in Australia, although it might conceivably have been introduced into the NPA complex from the PA group. This seems unlikely (Kerr, 1959).

Ottawa 770B, J.W.S. and Morye carried "L" resgenes effective against NPA races. The Ottawa resgene conferred immunity to races 2, 4, 5, 6, 8, 11 and 13, and almost certainly those other non-Ottawa-attacking races to which it was not exposed in tests of Ottawa hybrids. It was identified as Flor's L factor. The J.W.S. resgene was equated with Flor's L2 factor. It conditioned immunity to race 2, but was ineffective against the other NPA races. The total range of effectiveness of the Morye "L" resgene was not determined. It conferred resistance to race 2, but was susceptible to the other two NPA races, 6 and 7, to which it was exposed. The Morye factor, now

known as Rio "L", was resistant to race 2 and susceptible to race 6 in later tests at Sydney. It was concluded that Morye used in these studies carried the L6 factor.

Newland, Bolley Golden, Italia Roma and Walsh carried resgenes at the "M" locus. The Newland resgene was identified with Flor's M factor. It conferred immunity to races 2, 6, 8 and 17. The same resgene was effective against race 7, which gave an unusual immune reaction, characterized by the development of occasional, small type "3" pustules. Inoculum built up from these pustules evoked the same reaction, so that it could not be attributed to contaminating spores. The M factor was almost certainly the factor conditioning immunity to all the other non-Newland-attacking races. It was ineffective against races 4, 5, 9, 13 and 14.

Bolley Golden and Italia Roma carried the same "M" resgene which was equated with Flor's M3 factor. This resgene conferred immunity to races 2, 5, 6, 7, 11 and 17. It was ineffective against races 3, 4, 12, 13 and 16. The reaction to race 5 differentiated the M and M3 factors. Walsh was heterozygous for two resgenes at the "M" locus. Both differed from the M and M3 resgenes in their susceptibility to race 11. The one, tentatively designated Mh, was susceptible to race 7. The other, designated Mw, was resistant to race 7. Both were effective against races 2 and 5. Both could be distinguished from the M1 factor of Williston Golden, the M2 factor of Buda (not included in the genetical studies, but included in the race survey), and the M5 factor of Argentine 705–1 by their resistance to race 5. Apart from the M4 factor which did not figure in these studies there were no other "M" factors with which these resgenes might be identified. One, and probably both Walsh resgenes, were distinct from previously identified "M" factors.

Flor had determined at least two factors at loci other than the "L", "M" or "N". The one factor, in Morye, and the other in Bolley Golden, may or may not have been allelic. The same two factors were identified in these studies. There was a similar factor in Argentine 462, which was presumed to be the same as that carried by Morye. The Morye factor conditioned immunity to races 2, 6 and 7, and probably most, if not all, of the other NPA races. The Bolley Golden factor conferred resistance to races 2, 5, 7, 11 and 17. It differed from the Morye factor in its ineffectiveness against race 6. This factor, rather than the M3 immunity factor, conditioned the resistant reaction of Bolley Golden to race 3.

Prior to these studies Flor had postulated a closely linked set of resgenes accommodating loci in the "*N*" series, but had not determined the number. During studies with the NPA races two loci were determined, although the possibility of a third, while very unlikely, had not been eliminated. The "*N*" resgene of Punjab was closely linked with the "*N*" resgenes of Abyssinian and Koto. The resgenes of the last two varieties were allelic. Abyssinian and Koto were used as marker varieties for one of the loci designated "1–N", and Punjab for the other locus designated tentatively (until cross checked with Flor) "2–N".

A large amount of 3–W–C material of Punjab × Koto and Punjab × Abyssinian pedigree was prepared to determine the frequency of cross-over between the "1–N" and "2–N" loci. Much of this succumbed to root rot. The results obtained with the residue were not considered adequate to determine this frequency with a high degree of accuracy. Results obtained with race 1 from other crosses were added to offset the deficiency. It had not been finally established that the Newland "*N*" resgene occurred at the "1–N" locus, or that the Tammes' Pale Blue resgene occurred at the "2–N" locus. But since there was no reason to suggest that either of these occurred at a third locus they were assigned to the "1–N" and "2–N" loci respectively. The results are summarized in Table 20. The agreement between results obtained with Newland and Tammes' Pale Blue respectively and the other hybrid lines justified the allocation of the factors carried by these varieties to the "1–N" locus.

Flor has since confirmed these results and designated the two linked loci "N" and "P". These agree with the "2–N" and "1–N" loci respectively. The degree of linkage is indicated by a crossing-over frequency of 9·6%.

Resgenes effective against the NPA group were located at the "P" locus in Akmolinsk, Abyssinian, Ottawa 770B, Tammes' Pale Blue, Koto, Walsh, Morye and Argentine 462.

The Akmolinsk factor was effective against only two of the NPA races, 2 and 4. It conditioned resistance to these two races and was equated with Flor's P1 resgene. The Abyssinian factor resembled this factor in its range of effectiveness. It conditioned immunity to races 2 and 4. It was equated with Flor's P2 factor. Studies with race 1 clearly differentiated the two resgenes. P1 was susceptible and P2 immune. The

TABLE 20.

Cross-over Frequency between "N" Loci.

Pedigree.	Race.	Resgenes Effective Against Race in Variety Listed.		Frequency of Susceptible C.O. Plants.	Frequency if only "N" Resgenes Segregating.
		First.	Second.		
Abyssinian × Punjab 3–W–C ..	2	P2	N	5/97	5/97
Koto × Punjab 3–W–C	2	P	N	4/52	4/52
Punjab × Ottawa, Ottawa × Punjab 3–W–C	1 and 2	N	P5, L	1/82	2/82
Combined results	—	—	—	—	11/231
Tammes' Pale Blue × Ottawa 770B 3–W–C	1	N2	P5, L	1/43	2/43
Abyssinian × Tammes' Pale Blue 3–W–C	1	P2	N2	4/79	4/79
Combined results	—	—	—	—	6/122
Punjab × Newland 3–W–C ..	1, 2, 5	N	P6, M	1/56	2/56
Newland × Punjab 3–W–C ..	1, 2, 5	P6, M	N	3/95	6/95
Tammes' Pale Blue × Newland 3–W–C	1	N2	P6, M	1/59	2/59
Combined results	—	—	—	—	10/210
Grand total	—	—	—	—	27/563

Ottawa 770B factor conditioned a resistant reaction to races 3, 5, 6 and 13 (accession 602). It was ineffective against races 2, 4, 8, 11 and 13 (accession 582). Following communication with Flor it was designated P5. The Tammes' Pale Blue factor differed from each of the above factors in its immunity to races 2 and 5, but susceptibility to race 1.

Flor determined the same resgenes in Tammes' Pale Blue and Koto at the "P" locus. The Koto "P" resgene identified in these studies conferred immunity to all the Australian NPA races, but the Tammes' Pale Blue "P" factor appeared to be ineffective against NPA race 17, though it may well have been effective against all the other NPA races. Apart from the reaction of Tammes' Pale Blue to race 17, the Koto and Tammes' Pale Blue "P" factors could have been equated. Both were susceptible to race 1 and to a New Zealand Tammes' Pale Blue-attacking race. Neither the "P" factor in Tammes' Pale Blue nor the "P" factor in Koto could have been contaminant resgenes introduced into these varieties by outcrossing. Either the Tammes' Pale Blue line or the Koto line differed at their source of origin from the lines used by Flor, or the reaction of Tammes' Pale Blue to race 17 was an aberrant reaction induced by minor modifying factors. The reaction to this race was always moderately susceptible, never type 4 fully susceptible. Moderate susceptibility usually equated with field resistance. It was possible, however, that race 17 represented the first appearance of a race capable of differentiating the supposedly identical Tammes' Pale Blue and Koto factors. Under the circumstances the potential identity of the factors was recognized

by equating both with Flor's P factor, though the possibility of differentiating them was recognized by adopting the subscripts P_t and P_k.

The Walsh "P" factor could be differentiated from other factors in the same allelic series by its resistance to race 7, but susceptibility to race 11. It was also effective against race 2 and race 13 (accession 582), but was ineffective against race 5. It seemed to be distinct from "P" factors identified by Flor, and has been tentatively designated Pw. Flor suggested the designation P7. Unfortunately, when these studies were concluded the factor had not been isolated. Walsh was rather heterozygous, and it is problematical whether the same resgene could be readily isolated from the variety again. It is obvious, however, that Walsh is a potential source of new resgenes.

According to Flor, both Morye and Argentine 462 carried the same factor in common with Koto and Tammes' Pale Blue. The results with Argentine 462 indicated a resgene at the "P" locus. But lack of race 1 susceptible seedlings in two lines of Abyssinian × Argentine three-way cross indicated that the Argentine "P" factor was immune to race 1. This would distinguish it from the "P" factors of Koto and Tammes' Pale Blue. The total range of effectiveness of this factor was masked by the probable occurrence of another resgene at the "N" locus. According to Flor's results the second Argentine factor should be the N2 resgene, identical with the factor in Tammes' Pale Blue. The N2 factor in Tammes' Pale Blue conditioned immunity to race 1, but it was susceptible to race 2. Results with Argentine 462 non-survey selections did not agree with this conclusion. There were no race 2-susceptible seedlings among three-way-cross hybrids of Argentine 462 × Punjab pedigree. It seemed possible, therefore, that the Argentine 462 material used at Sydney since the first race surveys differed from Flor's standard line in its "N" resgene constitution. This did not affect the results of previous physiologic race surveys, since this variety had given a consistently immune reaction and had not been used to differentiate races.

It was not possible to determine the differential reaction of the Morye "*N*" resgenes since two closely linked resgenes appeared to operate in this variety. Selection 193 (the only selection crossed with Punjab) carried a factor at the "N" locus effective against races 2 and 7. This could well have been Flor's N1 factor. The occurrence of the P factor at the other locus could not be established from the hybrid material available.

With the exception of the J.W.S. L2, Akmolinsk P1, Punjab N and Koto and Tammes' Pale Blue P factors, all the resgenes effective against any of the NPA races were also effective against PA race 1, and all those accessions of race 1 used in these studies. In addition, those resgenes in Very Pale Blue Crimped, Kenya and Argentine 705–1 which conditioned too variable a resistant reaction to permit their identification with NPA races were identified in studies with PA race 1 as the L3, L4 and M5 factors already postulated for them by Flor.

Several factors, previously unidentified in the differential series, were effective against PA race 1. These factors had been inoperative against overseas races and the Australian NPA complex. Bison carried an "L" factor, designated L9 following communication with Flor. "L" factors effective against race 1, but ineffective against all NPA races to which they were exposed, were also found in Bolley Golden, Italia Roma and Koto. While they may have been different factors, there was no evidence to indicate this. They were equated with the L9 resgene. These resgenes were evidently not rogue factors introduced into the above varieties by cross pollination. The survey selections were homozygous for the "L" factor, and all other selections studied carried an extra factor effective against race 1 but ineffective against the NPA group.

Previously undetected "*N*" resgenes were located in Newland, Kenya and Bolley Golden. The factors in Bolley Golden and Kenya were located in the "P" series. The Newland factor did not belong to the "N" series, but owing to lack of relevant hybrid lines could not be assigned definitely to the "P" series. Studies of crossing-over frequency, however, supplied strong evidence for the existence of only two closely linked loci. On the foregoing evidence the Newland factor was assigned to the "P"

series. The new factors were fully susceptible to all the NPA races, and immune to all the race 1 accessions to which they were exposed in hybrids. In the absence of evidence to the contrary they were identified as the same resgene. This resgene, following communication with Flor, was designated P6.

Another factor than the Pt factor already mentioned conditioned the immunity of Tammes' Pale Blue to race 1. It was ineffective against race 2. Its identification by Flor as the N2 factor indicated its effectiveness against some at least of the overseas races. It is highly probable that it confers immunity or resistance to some NPA races in Australia. Its differential reaction to races 1 and 2 clearly distinguished it from the Punjab N resgene.

A resgene located in Leona in tests with race 1 was equated with Flor's P3 factor. This factor was probably effective against NPA races 2, 4 and 17. A new resgene was determined in Leona additional to the P3 factor. It was independent of the P3 factor, and the "L" locus, and must have occurred at the "M" or an undesignated locus. It was tentatively designated X1. A new, but unallocated, factor also seemed to be effective against PA race 1 in Morye. Flor had postulated no more than three independent factor groupings (among them two closely linked factors, N1 and P). Results during studies of non-survey Morye selections with NPA races agreed with this. While the evidence was not conclusive, it seemed that the variety was heterozygous for a fourth independent factor effective against race 1. If this were so the new factor must have occurred at the "M" locus, or an undesignated locus independent of the previously determined, undesignated Morye locus. The final allocation of the Leona and Morye factors could not be determined owing to lack of time and hybrid material.

Genetical investigations of the resistance of a wide range of host varieties to the Punjab-attacking complex may well identify many more new resgenes. It will be important in determining the identity of these resgenes to obtain a variety or varieties deriving their resistance to race 1 from a single "M" resgene. The lack of such a marker variety was a considerable handicap in determining the identity of resgenes effective against race 1 during these studies.

Accession 507 was the standard race 1 accession used during these investigations. Other accessions, 557, 610, 613, 621 and 627, were occasionally introduced to cross check results with 507. They always gave the same results. This strongly confirmed the observation that the Punjab-attacking complex is a highly stable, uniform complex, exhibiting a minimum of pathogenic diversity. If it were not for the differentiation of PA races A, F and G by earlier workers (Waterhouse and Watson, 1941, 1943), it might be assumed that this group was represented by only one race, and that this race maintained itself vegetatively over its entire geographic distribution from year to year. Any diversity, however, at least in terms of reaction to the standard differentials drawn from the cultivated species, is relatively minor.

The distinctiveness of the PA group is emphasized by its extreme avirulence. This had already been indicated by the race survey. Race 2, the most avirulent of the NPA races, attacked four of the twenty differential varieties. Race 8, the next most avirulent NPA race, attacked seven of these varieties. Race 1 accessions evoked a fully susceptible reaction on only two of the varieties, Akmolinsk and Punjab. The former variety was susceptible to race 1 in the seedling stage only, and acquired a high degree of resistance later in development in the field.

The avirulence of the PA division was stressed by the genetical investigations. The new resgenes, P5 and P6, were ineffective against race 2, but conditioned immunity to race 1. New resgenes in Leona and Morye were likewise effective against race 1, but ineffective against race 2. Additionally race 1 commonly induced a reaction lower in the scale of immunity than NPA races. The Ottawa P5, Morye L6 and undesignated Bolley Golden factors conditioned a resistant reaction to those NPA races to which they were not fully susceptible. The same factors conditioned an immune reaction to race 1.

A given resgene interacting with NPA races gave either a compatible susceptible reaction or an incompatible reaction which varied according to the resgene. With some, the incompatible reaction was complete immunity, with others high resistance, and with others a variable resistant reaction, particularly variable in hybrid lines. The Ottawa 770B L, J.W.S. L2, Koto Pk, Abyssinian P2, Punjab N and Bolley Golden M3 factors gave immune reactions to all those races to which they were not susceptible. The Very Pale Blue Crimped L3, Kenya L4, Morye L6, Walsh Mw and Mh factors, Argentine 705–1 M5, Walsh Pw, Akmolinsk P1, Ottawa 770B P5 and Bolley Golden undesignated factor conditioned resistant reactions to the races to which they were not susceptible.

Although these studies, in the absence of controlled temperature and light facilities, could not be geared for such observations, it seemed that a resgene evidenced only two significant primary levels of reaction with the NPA races. It may yet be found that a resgene may manifest an intermediate, perhaps several intermediate levels of reaction, additional to the two extremes of incompatibility and compatibility. At present the evidence favours the two-level interaction interpretation of results. It is, therefore, all the more interesting that the Morye L6, Ottawa 770B P5 and undesignated Bolley Golden factors manifest two incompatible reactions, a resistant reaction to NPA races, and an immune reaction to race 1.

The very limited range of virulence of the PA division against a wide range of varieties of the cultivated species has already been used as evidence to suggest that the PA group is uniquely associated with the wild species *Linum marginale* in Australia (Kerr, 1959). If this is so it highlights the fact that the pathogenic capacity of the pathogen is very closely correlated with the resgene composition of the host. Careful studies of the wild species may reveal a range of resgenes approximating the diversity of these carried by the cultivated species. Such resgenes, if they exist, may well differentiate distinct races within the PA group. The PA group, however, in specializing on the wild species, has not accumulated those pathogenic factors which would increase its range of virulence among the cultivated varieties.

It may be significant that the L9 and P6 resgenes which are quite ineffective against the NPA races and North and South American races seem to be widely distributed among the differential varieties. The occurrence of the L9 factor in Bolley Golden and Koto probably represents a recent transfer of this factor from Bison. Bolley Golden was a selection of unknown origin made at North Dakota in 1924, where Bison was a prominent linseed parent. Koto was derived from the cross (Reserve × Morye) × Bison. There was less likelihood of any recent transfer of the L9 factor between Italia Roma and Bison. The former was first introduced into U.S.A. from Argentine in 1948. Bison was imported into U.S.A. from Ghent, Belgium, in 1911. There was no evidence to suggest that the occurrence of the P6 factor in Newland, Bolley Golden and Kenya stemmed from recent common parentage, or transfer of the factor from one of these varieties to the others.

It has been suggested that, by virtue of the mutability of most pathogens, the longer a resgene has been exposed to a pathogen, the less likely is that resgene to maintain its immunity to the pathogen. The more widely a given resgene has been distributed geographically, and through the species in different varieties, the less likely is that resgene to confer all-round immunity to a world-wide sampling of races. Conversely, the pathogen is most likely to carry virulent pathogenic factors and less likely to carry avirulent factors specific for those resgenes which are most widely distributed through the species. If the occurrence of such virulence factors in the pathogen confers positive survival value by extending the host range, avirulent factors allelic with them should be progressively eliminated from the pathogen. This might account for the absence from the NPA, and North and South American race complexes of avirulent pathogenic factors specific for the L9 and P6 factors. The avirulent factors specific for these resgenes, as well as virtually all the other resgenes carried

by the differential varieties, have not been eliminated from the Australian PA complex by virtue of its isolation from the cultivated species and specialization on a wild species lacking these resgenes.

The potential discovery of new resgenes when a differential series is introduced into a second geographically isolated country makes it important to integrate race surveys with genetical investigations of host resistance. It might be well in race surveys to use three-way-cross material derived from F1 hybrids of each differential variety crossed with such an all-round susceptible variety as F257 instead of the usual varietal material. (It is naturally assumed that such a variety as F257 may itself be found to carry hidden resgenes, and should be tested with each collection of rust received.) The excised shoot technique can be used to ensure the maximum production of progeny from a single F1 seed. It may be possible to develop this method so that a plant can be maintained indefinitely in vigorous vegetative growth, by frequent excision, and maintenance under conditions favouring such growth, and retarding the flowering cycle. It may even be possible to store excised shoots at low temperatures. New resgenes could be isolated from three-way-cross material with the minimum loss of time and effort.

The potential existence of new resgenes must necessarily make any equation of races identified at different localities, or at the same locality in different years, rather doubtful. Race 13 was isolated from accession 582 (the standard used in the genetical investigations) and accession 602. Both gave the same differential reaction during the race survey. The genetical investigations of host resistance showed that the line isolated from accession 602 was avirulent to the Ottawa 770B P5 factor. The P5 factor was, however, ineffective against the line isolated from accession 582. In such a situation race surveys must serve primarily to determine the range of virulence of the total race complex, the degree of recombination of old combinations, the rate of loss of already determined pathogenic factors, and the rate of appearance of new pathogenic factors. The discovery of specific races can be of only secondary importance. The situation would be different where the race complex is highly stable, as in the case of wheat stem rust in Australia.

The NPA complex, with its total range of pathogenicity approximating the combined potential of North and South America races, must stem from material introduced into Australia from overseas with the cultivated host. A great diversity of races may have been introduced before quarantine measures began to restrict the risk of further introductions. It may be that only a small number of races were introduced originally, and that the present diversity is the result of frequent mutation within the NPA complex since then. Whatever the explanation, the NPA complex now carries a range of virulence factors capable of attacking all but a very limited number of resgenes carried by the differential varieties. The Punjab N, Koto Pk, and probably also Morye N1 and undesignated factors conferred immunity to all the NPA races. The first two factors were, however, completely susceptible to race 1. The Morye factors may constitute the only source of immunity to all Australian races.

Despite the limited amount of useful all-round immune resgenes, the Koto immunity may constitute a useful source of all-round resistance. The Australian NPA and PA races had existed for at least thirteen years without any detectable hybridization *inter se*, with consequent pooling of their pathogenic potential. So long as this situation is maintained, any combination of the Punjab N factor or Koto Pk factor with a non-allelic factor conditioning resistance or immunity to race 1 will constitute resistance to all the races identified to date.

In summary these studies substantiate the resgene identification by Flor in U.S.A., while keying out a number of new resgenes effective against the PA complex, but ineffective against overseas races. At least two closely linked series of "*N*" allels were determined, and there was no evidence to suggest the existence of a third. Assuming only two linked loci the cross-over frequency was 9·7%.

The validity of the division of the Australian *Melampsora lini* race complex into the NPA and PA subgroups was further substantiated, lending weight to the thesis that the latter subgroup has possibly developed in isolation on the wild species *Linum marginale.*

The value of three-way-cross material was highlighted by its effectiveness in such a cross as Bolley Golden × Abyssinian tested with race 1, in which the presence of a Bolley Golden resgene at an "*N*" locus could be conclusively established from a study of 266 seedlings, and the existence of this resgene at the "P" locus fairly definitely established. Had these studies been continued it would have been comparatively easy to isolate new resgenes from the three-way-cross material.

The importance of carrying out genetical investigations of a differential series in a country before automatically equating their reaction to the race complex of a second country with the resgenes postulated for them by studies in the country of origin of the series is emphasized. This is true even if each member of the series is supposed to carry only one resgene. Koto, according to Flor, carried only a single resgene. The immunity of Koto to every Australian race of *M. lini* might have led to the mistaken assumption that this variety carried a useful resgene conferring all-round immunity, when in fact this stemmed from two independent resgenes, one effective against the PA complex and the other against the NPA complex.

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SECOND SIR WILLIAM MACLEAY MEMORIAL LECTURE. BRIDGING THE GAP BETWEEN RACE AND SPECIES.

By Theodosius Dobzhansky.*

[Delivered 29th June, 1960.]

I greatly appreciate the distinction of having been chosen to deliver the Second Sir William Macleay Memorial Lecture. It is a privilege to honour the memory of so remarkable a man. In our day, being a scientist is a profession and a source of maintenance. I do not for a moment imply that modern scientists are not dedicated to their work. Self-actualization through creative work is the greatest reward to any scientist worthy of his salt. We must, nevertheless, pay tribute to scientists of the bygone age, whose dedication to science was unmixed with compensations of material gain. Macleay is certainly one of the best representatives in your country of pioneer scientists of that age.

Linnaeus and Darwin were two great men, each a characteristic product of his time, whose names have become symbols of two biological philosophies, that of immutability and that of evolutionary origin of biological species. Two centuries after Linnaeus and one century after Darwin, we now feel certain that species are not immutable and that they arise by accumulation of changes, usually gradual ones. This process of origin of species leads, in at least a majority of sexually reproducing and cross-fertilizing organisms, from originally genetically similar local populations, through progressively more and more distinct geographic races, and finally to full-fledged species. The crux of the matter lies, then, in the demonstration that there is no gap between race and species, that the former is a stage in the development of the latter. A reading of Darwin's classic "On the Origin of Species" will show that Darwin in fact looked at the matter in this light—the core of his argument was that there is no basic difference between species and what he called varieties, which in most cases are what we prefer to call races or subspecies. Races are incipient species, although this certainly does not mean that every race will necessarily become a full-fledged distinct species in the future.

Having the advantage of hind-sight, we can see why it was that Linnaeus reached the wrong conclusion that species are separated by unbridgeable gaps. The animals and plants which he studied came predominantly from his native Sweden, some came from other countries of northwestern Europe, and only scattered specimens from the rest of the world. This is to say that Linnaeus was studying chiefly sympatric species, forms of life which live together in the same territory. Now, sympatric species actually are separated by genetic gaps and by corresponding morphological gaps. This is because sexually reproducing and cross-fertilizing populations, Mendelian populations in our present terminology, can live side by side without becoming fused into a single variable population only provided that the gene exchange between them is limited or excluded by reproductive isolating mechanisms. Species of sexually reproducing organisms are reproductively isolated Mendelian populations or, better, groups of Mendelian populations reproductively isolated from other such groups. The gaps between sympatric species are prima facie evidence that they are reproductively isolated.

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Genetic and morphological gaps may or may not exist between allopatric populations, i.e., populations living in different territories.* Dr. Wharton Mather, of the University of Queensland, and myself have been recently comparing representatives of the fly species *Drosophila serrata* Malloch from northern New South Wales, Queensland, New Guinea and New Britain. We find these populations slightly different in some visible traits, particularly those living in New South Wales and southern Queensland from those living farther north. But should we regard these populations as races of the species *Drosophila serrata*, or are we dealing here with more than one species? For the time being we do not know the answer. We shall have to study these populations in more detail, test them for their ability to interbreed, inquire whether these visibly different populations are ever found sympatrically, whether intermediate populations may be observed at some points, etc.

Now, our difficulty with *Drosophila serrata* is quite representative of the difficulties which systematists face when they study allopatric forms of life. It is often not easy to decide whether two or several populations which they observe are still races of the same species or already independent species. And this is the difficulty which systematists had to face increasingly more and more often when, as a result of the geographic exploration of the world in the late eighteenth and in the nineteenth centuries, zoological and botanical museums acquired materials from many different countries. The convenient gaps which separated sympatric species sometimes seemed to disappear. The predicament of the systematists proved to be a blessing to general biologists. For it suggested that species are not fundamentally distinct from races. First Lamarck and then Darwin and Wallace drew the necessary conclusion—species evolve from races. The centenary of Darwin and Wallace and the sesquicentenary of Lamarck were celebrated during the past two years. Their conclusions have been amply confirmed by subsequent work.

Nowadays it is no longer necessary to prove that the gap between race and species is sometimes bridged. This is an old story. But it is important to discover how it is bridged, especially since we have reasons to suspect that the means whereby speciation is accomplished, i.e., whereby reproducing isolating mechanisms are established between diverging populations, are not the same in all organisms. There exist different patterns of speciation. One of these patterns, perhaps one of the most interesting ones, in the sense of bridging the gap between race and species most plainly, is the formation of so-called rings or circles of races. Very briefly, a race "ring" is a series of races the adjacent members of which resemble each other closely, and are often connected by intermediates in the geographically intermediate zones. But the terminal members of the "ring" live together, sympatrically, differ usually more strongly than do neighbouring races elsewhere in the "ring", and yet do not interbreed and do not form intermediates. The result is an apparent paradox. If we observe the neighbouring allopatric populations we unhesitatingly place them in a single species; yet, the sympatric terminal forms behave exactly as full-fledged species do—they are reproductively isolated and do not form intermediates in the zone of their sympatric overlap.

"Rings" of races are on the whole not a frequent occurrence. Nevertheless, they have been described by various authors over the years in diverse organisms—butterflies and birds, beetles and salamanders, etc. The situation in the group of salamanders

* More precise definitions of sympatry and allopatry may be desirable. These terms may be defined in relation to the mean distance between points at which individuals of a given population are born and at which they give birth to their progeny. This distance is obviously a function of the migratory propensities of the form of life involved, or of the distributional versatility of its young, seeds, pollen, spores, etc. Sympatric individuals and populations are, then, those which live at points closer than this mean distance, and allopatric those at points greater than that distance. Allopatric populations of, say, snails may be found much nearer each other than those of, for example, birds, insects, or plants with wind-borne pollen.

belonging to the genus *Ensatina* is one of the most striking and best studied.[1] These animals occur in the mountains surrounding the great central valley of California, but not in the valley itself. Starting in the south, one finds increasingly distinct races of the salamander *Ensatina escholtzii* as one proceeds northwards along the Coast Ranges facing the Pacific Ocean, in the mountains of northern California south of the Oregon border, and again southward along the chain of the Sierra Nevada and Sierra Madre mountains. Nowhere a break seems to be found—neighbouring races merge into each other through series of transitional forms. But the ring is closed in the San Bernardino Mountains of Southern California, where two very differently-appearing salamanders occur together without intermediates.

The fly genus *Drosophila* contains probably between 600 and 700 described species (and doubtless many undescribed ones). Closely related species abound, but, owing to many forms of this genus being breedable in laboratory cultures, it is usually possible to establish unambiguously by experimental means whether a given pair of populations should be regarded as distinct species or as races of a single one. No instances of race rings were, however, known in *Drosophila* until found recently in the tropical American species *Drosophila paulistorum* Dobzhansky and Pavan.[2] It is because these flies are favourable for experimental work that this finding is particularly interesting. We are perhaps not over-optimistic to hope that the analysis can be pushed in *Drosophila* further and more easily than in previously known instances of the phenomenon of race rings.

The basic data concerning *D. paulistorum* can be summarized rather easily. We have in our laboratory in New York living strains of *D. paulistorum* from 25 different localities, ranging from Guatemala and the Island of Trinidad in the north to São Paulo in the south, and from the Pacific coast of Ecuador in the west to the Atlantic seaboard of Brazil in the east. With 25 strains, a total of 600 intercrosses could be made. About one-half of the possible intercrosses have actually been tried. The technique used was as follows. About a dozen virgin females of one strain are placed with a like number of males from another strain in a culture bottle, and left undisturbed for about a week at room temperature. If no larvae appear in the culture medium, the flies are transferred to a fresh bottle, and left there for another week. The non-appearance of larvae is taken to mean that the two strains do not cross. If hybrid larvae do appear, they are permitted to develop to adult flies, which are then tested for fertility in the same manner. Three types of results are observed in such experiments: (A) Fertile F_1 hybrids between the strains are obtained; (B) F_1 hybrids are obtained, which are fertile as females but completely sterile as males; (C) no hybrids are obtained.

On the basis of such tests we can distinguish six different races or incipient species, as follows:

(1) *Centro-American race.* Strains from Guatemala, Salvador, Honduras and Costa Rica.

(2) *Amazonian race.* Panama, Trinidad, upper Rio Negro (Içana), and Belem (state of Pará, Brazil).

(3) *Andean-South Brazilian race.* Llanos of Colombia, Ecuador, the eastern slope of the Peruvian Andes, Bolivia, southern Brazil (states of Minas Gerais, São Paulo, and the coast west of Rio de Janeiro).

(4) *Orinocan race.* Panama, Llanos of Colombia, Venezuela (Caripe), British Guiana (Georgetown).

(5) *Guianan race.* A single strain from Georgetown, British Guiana.

(6) *Transitional race.* Colombia (Santa Marta, Bucaramanga, Palmira, Buenaventura).

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[1] R. C. Stebbins, *Univ. California Publ. Zool.*, 48: 377-526 (1949), and *Evolution*, 11: 256-270 (1957).

[2] Th. Dobzhansky and B. Spassky, *Proc. Nat. Acad. Sci. U.S.A.*, 45: 419-428 (1959).

Intercrosses of strains of different geographic origin within a race easily produce numerous fertile hybrids. Intercrosses between races give a variety of results which can be summarized thus:

Centro-American × *Amazonian.*—Usually no progeny at all; in rare instances when hybrids are obtained the hybrid males are sterile.

Centro-American × *Andean-South Brazilian.*—Hybrids obtained quite easily in most crosses, but F_1 males are completely sterile. Fertile male hybrids have, however, been obtained in the crosses Guatemala ♀ × Santo Domingo (Equador) ♂ and Coroico (Bolivia) ♀ × Honduras ♂.

Centro-American × *Orinocan.*—Like the preceding; fertile male hybrids obtained only in crosses Panama ♀ × Salvador ♂ and Honduras ♀ × Llanos (Colombia) ♂.

Centro-American × *Guianan.*—Hybrids obtained, males sterile.

Amazonian × *Andean-South Brazilian.*—Mostly no progeny, but some crosses produce hybrids with sterile male sex.

Amazonian × *Orinocan.*—Mostly no progeny; some crosses yield hybrids the males of which are sterile.

Amazonian × *Guianan.*—No progeny.

Andean-South Brazilian × *Orinocan.*—Most crosses go easily and produce sterile male hybrids, but some crosses consistently fail, and one cross (Llanos, Colombia ♀ × Santo Domingo, Ecuador ♂) produces fertile hybrids of both sexes.

Andean-South Brazilian × *Guianan.*—F_1 hybrids with sterile males usually obtained; Dobzhansky and Spassky (*l.c.*) have recorded that the cross Guiana B ♀ × Santa Cruz, Bolivia ♂, gave fertile male hybrids, but subsequent tests showed this to be an error.

Orinocan × *Guianan.*—No progeny, except that Llanos (Colombia) ♀ × Guiana B ♂ gave a few hybrids, the males of which were sterile.

By far the most interesting are the crosses of the Transitional race strains to the strains of the other races. Only the Guianan race has failed to produce F_1 hybrids fertile in both sexes when crossed to any strain of the Transitional race. Otherwise at least one strain of the Transitional race yields fertile hybrids of both sexes with at least one strain of another race, and, vice versa, at least one strain of every race gives fertile hybrids with a strain of the Transitional race. However, thus far no Transitional strain has been found to be crossable to every other race.

To summarize, two salient facts emerge from the experiments described above. First, all the races of *Drosophila paulistorum* are genetically open systems, since they are potentially capable of exchanging genes with all other races, albeit sometimes only via a bridging strain of the Transitional race. Even the Guianan race, which appears to be the most distinctive one, produced some fertile interracial hybrids. Second, in at least three places, Panama, Llanos of Colombia, and Georgetown in British Guiana, there live two sympatric forms which fail to produce any hybrids at all.

We have, then, the apparently paradoxical situation observed also in other instances of "rings" of races. On the one hand, the species *D. paulistorum* preserves a single gene pool; a gene mutation or a favourable gene combination arising anywhere in the species is potentially able to penetrate into every population of the species. On the other hand, in at least three places named above, and doubtless in others which remain to be discovered, the process of speciation seems to have been completed. In these places we have sympatric populations debarred from gene exchange by reproductive isolating mechanisms. These sympatric populations behave like full-fledged species.

Two kinds of reproductive isolating mechanisms are operative between the races of *D. paulistorum.* The non-production of offspring in interracial crosses is due to sexual isolation. This is easily demonstrated by dissection of the females of one race which were exposed for a week or two to males of another race and failed to give a progeny. The sperm receptacles of such females are empty; the females are virgins. Sexual isolation is demonstrable also in many interracial crosses which do produce

offspring—usually only a single female, or only a minority of the females, are inseminated. The other isolating mechanism is, of course, the sterility of the hybrid males.

Thanks to the preliminary work of Malogolowkin and Ehrman,[3] the genetic mechanisms responsible for the hybrid sterility in *D. paulistorum* have been brilliantly analysed by Ehrman.[4] Ehrman studied the hybrids between the Centro-American race and the Amazonian and the Andean-South Brazilian races, using strains of each race in which the chromosomes were marked by mutant genes producing visible changes in the fly's external morphology. Such gene "markers" permit the distribution of certain chromosomes to be followed generation after generation in the interracial crosses. Ehrman found that a female carrying a mixture of the chromosomes of diverse racial origin produces sons all of whom are sterile. This is true even of females which have all the chromosomes but one of the same race. Now, in the progeny of such females, back-crossed to males of the race to which the majority of their chromosomes belong, half of their sons will be racially "pure", i.e., will have the chromosomes of one race only. Nevertheless, even such males are completely sterile. What happens is evidently that the presence of a foreign chromosome in the female so alters the structure of her eggs, presumably by some modification of the egg cytoplasm, that male individuals developing from these eggs are sterile, and this regardless of the chromosome complement which they come to possess after fertilization. Furthermore, any one foreign chromosome (the species has three pairs of chromosomes) suffices to induce this male sterility.

No previously analysed instance of hybrid sterility anywhere, either in the animal or in the plant kingdom, was due to a genetic mechanism of the above sort. The only analogy known is a mutant named "grandchildless" described in another species of *Drosophila*, *D. subobscura*, by Spurway.[5] But the grandchildless mutant is a genetic recessive which is not known to occur in nature. It is most interesting that the other isolating mechanism, the sexual isolation, operative in the interracial crosses of *D. paulistorum* has an entirely different genetic basis from the hybrid sterility. Dr. L. Ehrman kindly informs me that her preliminary experiments indicate that the sexual isolation is not cytoplasmic but apparently due to complexes of polygenes differing from race to race.

Dr. Ehrman infers, and I concur, that the hybrid sterility caused by the peculiar cytoplasmic effects was probably the primary, and the sexual isolation the secondary, reproductive isolating mechanism in *D. paulistorum*. As indicated above, the six races which we distinguish are mostly allopatric, occurring in different countries. They have become differentiated genetically, presumably in response to the different environments prevailing in their respective distribution regions, and their genetic differentiation happened to be of a kind which caused the peculiar male sterility in the interracial crosses. This obviously reduces the Darwinian fitness of the races where their geographic distributions touch or overlap. The development of sexual isolation removes this threat to fitness. When the races become sexually isolated, only intraracial and no interracial matings occur, and no sterile or otherwise inferior hybrids are produced. Sexually isolated races may now safely coexist in the same region, sympatrically, and this is, as we have seen, exactly what has been observed in at least three localities, in Panama, Venezuela, and in British Guiana. The sympatric non-interbreeding "races" behave, however, as if they belonged to distinct species. The gap between race and species has been bridged.

The question may arise, whether *Drosophila paulistorum* should still be treated as a single species, or should it be split into several species, so that no two races or subspecies would have to be recognized as sympatrically coexisting. I believe that the

[3] C. Malogolowkin and L. Ehrman, *Evolution*, 14: 266-270 (1960).
[4] L. Ehrman, *Evolution*, 14: 212-223 (1960).
[5] H. Spurway, *Jour. Genetics*, 49: 126-140 (1948).

name *D. paulistorum* should be applied to all its races or incipient species, including the sympatric ones. In any case, let us distinguish very clearly the nomenclatorial problem from the underlying biological problem. Nomenclature is a matter of convenience and expediency; it would be neither convenient nor expedient to split *D. paulistorum* into several species, because doing so would confront us with an insoluble problem of where to draw the lines between these species. *D. paulistorum* is a congeries of races, some of which have, in some parts of their geographic distribution areas, emerged as distinct species. Their biological status will appear to us different, depending upon whether we look at them in their totality or whether we consider them only in the regions of their sympatric overlaps with the other races or species.

In any case, we have a beautiful demonstration of Darwin's argument that ". . . species are only strongly marked and permanent varieties, and that each species first existed as a variety".

THERMOREGULATORY BEHAVIOUR IN A SPECIMEN OF *MORELIA SPILOTES VARIEGATA* GRAY (SERPENTES : BOÏDAE).

By Harold G. Cogger and Alex Holmes.

(Plate viii.)

[Read 26th October, 1960.]

Synopsis.

It is shown that a large carpet snake (*Morelia spilotes variegata* Gray), by absorbing solar heat during a fine day, is able to conserve much of this heat and maintain its body temperature well above that of its surroundings during the following cold night. This conservation is accomplished simply by tightly coiling its body, thus reducing the surface area available for heat exchange with the surrounding atmosphere. It is estimated that the surface area exposed to the surrounding atmosphere when the snake is coiled is only about 30-50% that of the surface area when the snake is uncoiled.

As heat uptake is dependent upon the availability of solar radiation, periods of unfavourable weather result in the equalizing of the snake's body temperature with that of its surroundings.

It is suggested that such a method of heat conservation may be important in the maintenance of normal digestive processes and in the incubation of the eggs.

Introduction.

The observations recorded below were made on a captive specimen of the carpet snake (*Morelia spilotes variegata* Gray) in the collection of one of the authors (A.H.).

The carpet snake is widely distributed throughout Australia, being absent only from the far south-eastern corner of the continent and from coastal New South Wales. The specimen under discussion is approximately eight feet in length. This species is largely nocturnal (both in captivity and under natural conditions), but it is frequently found basking or foraging during a fine day.

The specimen is kept in a small aviary, one end of which is enclosed, so that part of the aviary floor is exposed to direct sunlight from about 10 a.m. until 3.30 p.m. each day. As a result of his interest in certain lizard temperature recordings which were being carried out at the time, on the evening of August 24, 1959, A.H. made a rough determination of the temperature of this specimen by placing a thermometer among the coils of the snake. He was surprised to find that the temperature of the snake was some 20°F. above that of the surrounding air. The authors then decided to continue readings whenever the opportunity should present itself. In practice this resulted in several readings each morning and evening, except on week-ends when temperatures could be taken during the day.

These results are set out in Table 1.

Discussion.

Several qualifying comments should be made concerning the results obtained, for it was not the authors' intention to carry out an exact and quantitative experiment, but rather to show, in a qualitative way, the manner in which snakes of this family might maintain their temperatures well above that of their surroundings.

It was found that only by placing the recording thermometer in among the coils of the snake would the snake remain undisturbed. Although this may not appear to be a very accurate measure, on several occasions simultaneous recordings were made rectally, and on each occasion a reading was obtained within one or two F. degrees of the reading of the thermometer among the coils. It was, of course, essential not to disturb the snake, as once it had uncoiled considerable heat was lost before it resumed its former position. Although the use of a series of thermocouples to make continuous

or regular recordings of the pertinent temperatures (snake, air, substrate, etc.) would have added substantially to the significance of the results, it was considered that the low order of accuracy was offset by the magnitude of the temperature differentials obtained.

The specimen studied has been in captivity for some years, and it is assumed that its behaviour is, as much as possible, free from the disturbing influences which captivity initially supplies. Also, although it would be preferable to make a regular temperature record of the snake throughout the day, the week-end results have shown that such readings would not have materially affected the conclusions.

It will be noted that in fine weather the temperature of the snake at the end of the day varies between 9 and 20 F. degrees above the surrounding atmosphere, and that on the morning following each of these readings the temperature of the snake is still appreciably above that of its surroundings, even when the atmospheric temperature during the night has reached a much lower figure. Hence, although there is no way in which the snake can obtain heat during the cold night, it is evident that it must have an efficient mechanism for heat conservation. This is confirmed by the readings taken during a cloudy day and the following night and morning. In this case the body temperature of the snake falls to within one or two degrees of the surrounding air, and follows any fluctuation in the latter fairly closely. It is therefore evident that solar radiation is the principal source of the temperature differential between the snake and its surroundings.

An attempt was then made to account for both the heat intake during the day and the heat conservation during the night by studying the behaviour of the snake. This resulted in a ready explanation of the phenomena observed and the following pattern of behaviour was noted: On fine days the snake lies, outstretched or loosely coiled, in the sun, exposing a maximum surface area to the warming rays of the sun (Plate viii, *a*). However, as soon as the sun leaves the aviary, or when the temperature of the snake becomes excessive, the snake moves to a corner of the sheltered end of the cage and tightly coils its body so that part of the coils are against the cement sides of the enclosure (Plate viii, *b*). The cement walls were not found to become sufficiently warm to provide a source of heat during the night. As may be noted from the photograph there is a substantial layer of dry grass on the floor of the aviary, so that the snake is well insulated from the surrounding atmosphere except where its coils are actually exposed to the latter.

Direct exposure to the sun would enable the snake to absorb sufficient solar heat to raise its body temperature well above that of the surrounding shade temperature. The optimum temperature of the snake is not known, but it is probably in the vicinity of 90°F., for it was found that this was the maximum temperature attained by the snake during the warmest part of a sunny day (and when it could reduce its temperature simply by moving into a shaded part of its enclosure).

As it was apparent that heat loss and gain could only occur as a result of exposure of the surface of the body to the surrounding atmosphere or to solar radiation, an attempt was made to determine the surface area of the snake exposed to these sources under its various behaviour conditions. Although these figures were calculated very roughly, they are accurate enough to show the extreme significance of the differences in behaviour that have already been noted in the present paper.

Assuming the snake to have a mean diameter of 2–3 inches and, when coiled, the coil to be approximately 13 inches in diameter and 6 inches deep, it was estimated that the uncoiled surface area exposed to the surrounding atmosphere was approximately 500–700 square inches, whilst the coiled surface area was reduced to approximately 200–250 square inches. It is postulated that this proportional decrease in surface area available for heat exchange is largely responsible for the ability of the snake to maintain its body temperature well above that of its surroundings.

The significance of the surface-mass ratio of the body in thermoregulation and heat conservation has been discussed by many previous workers (including Cowles and

TABLE 1.

Day	Time a.m. p.m.	T_a °F	T_s °F	Daily Range + Weather
1	7.30	53	71	50-65
	8.45	53	71	
	9.45	50	69	
2	6.30	45	58	
	5.15	58	79	
	6.45	53	73	45-66
	7.30	51	71	
	10.00	51	68	
	11.00	51	67	
3	6.30	54	61	
	5.45	54	57	53-56
	6.45	54	55	
	11.15	53	54	
4	6.30	52	53	
	7.00	58	73	50-65
	8.45	57	71	
	9.45	56	66	
5	8.00	57	58	
	5.30	60	81	52-64
	8.00	57	76	
	9.00	56	72	
6	7.15	50	58	
	9.00	59	58	
	2.00	74	88	
	3.00	71	88	49-67
	6.25	69	78	
	7.15	61	77	
	8.30	60	74	
7	6.15	51	58	49-73
	7.15	64	79	
8	6.30	57	64	57-70
	6.00	66	82	
	10.30	62	73	
9	6.30	55	64	
	5.15	58	78	52-63
	6.30	58	74	
	7.30	57	72	
10	6.00	56	60	
	5.45	58	77	51-61
	7.45	57	73	
	9.30	57	70	
11	6.30	54	60	52-66
	10.45	57	70	
12	7.00	55	60	
	8.00	56	60	
	9.00	57	60	
	10.00	60	60	
	11.00	60	NR*	
	1.00	73	82	53-64
	2.00	71	80	
	3.00	66	79	
	4.30	63	77	
	5.30	62	74	
	6.30	59	68	
	7.30	59	71	
	8.30	58	70	
	9.30	57	68	
13	7.00	52	56	
	8.00	55	56	
	9.00	58	56	
	10.00	62	NR*	
	2.00	78	90	51-69
	3.00	78	87	
	4.00	71	86	
	5.00	68	82	
	6.30	64	78	
	7.30	62	76	
14	6.00	54	60	
	7.00	55	60	51-67
	5.30	65	74	
	8.30	62	69	
15	6.00	59	62	55-66
	10.45	61	68	
16	6.15	59	62	
	5.15	59	62	57-65
	6.15	59	61	
	9.45	57	60	
17	6.15	56	58	54-67
	10.30	61	70	
18	6.15	57	62	54-68
	5.45	66	79	
	6.45	65	77	
	7.45	64	76	
	9.00	63	73	
	10.15	62	71	
19	6.15	54	62	
	7.15	55	61	54-73
	5.45	68	82	
	7.15	63	73	
	8.30	64	75	
	9.15	63	74	
20	7.00	58	64	
	8.15	62	64	
	8.15	64	69	56-70
	10.15	67	NR*	
	5.00	69	82	
	6.00	66	79	
	7.00	65	77	
21	6.15	57	63	
	6.15	70	81	56-77
	7.30	68	78	
	9.00	66	76	
	10.00	66	74	
22	6.00	69	69	
	6.30	69	73	65-77
	7.30	66	72	
	8.30	66	71	
23	6.00	55	63	
	5.30	73	84	55-78
	6.30	72	82	
	10.15	66	77	
24	6.15	61	67	
	6.30	63	77	58-68
	7.15	61	75	
	Mid-ni.12.00	52	68	
25	6.00	48	62	48-71
	9.30	61	79	
26	8.00	60	66	56-72
	11.30	57	70	
27	7.30	55	63	
	2.15	63	79	
	4.00	61	70	50-62
	7.00	56	71	
	8.00	56	69	
28	6.00	52	61	51-65
	5.30	62	62	
29	6.00	54	60	
	5.15	63	79	52-65
	6.30	61	78	
	8.30	59	74	
30	6.00	55	67	
	4.15	68	78	53-63
	7.00	59	78	
	9.15	56	70	
31	6.15	51	62	48-70
32	6.15	56	63	53-63

Observations commenced on 25th August, 1959.

Daily range (A)indicates min. and max. temperatures in F°.

*NR indicates no reading.

CLEAR

INTERMITTENT CLOUD

CLOUDY

RAIN

Bogert, 1944; Gunn, 1942). However, it is also evident that absolute size alone is important in controlling the amount of heat exchange, even where the surface-mass ratio is constant.

Benedict (1932) found that it required approximately three hours for the body temperature of a large boa to fall to within 1°C. of the new environmental temperature when the snake was taken from 30·2°C. to 20·2°C. Such a result is apparently a product of the effects of large size and low surface-mass ratio.

Cowles and Bogert (1944) point out that relatively high temperatures are required for the maintenance of normal digestive processes. It is well known that pythons frequently take many days to digest a large meal. The advantages, under such circumstances, of maintaining a high body temperature, are obvious. In the temperate winter climate of Sydney, such a mechanism would possibly allow a large snake to feed during fine weather throughout the winter. However, the specimen discussed above abstained from feeding during the whole winter period.

The above authors also comment on the significance of the substrate as a source of heat for desert reptiles. The carpet snake is both arboreal and terrestrial and is found in a wide variety of habitat types. It is commonly found in the rain forests of the eastern and northern seaboards, in sclerophyll forests, in savannah grassland and in the arid central regions. Therefore, although it is evident that the substrate has not been an important source of heat in the present example (and this is probably also true where the species is found in forested regions), it may be of significance under arid terrestrial conditions.

Waite (1929) comments that python eggs ". . . are often protected by the mother snake, who coils her body around them. It has long been believed that the eggs are actually incubated, observations indicating that the temperature of the mother is raised during the 'sitting' period. If true, it is remarkable that the temperature of a cold-blooded reptile should be thus raised, but doubts have since been thrown on the somewhat imperfect observations, which need to be repeated before the statement can be fully accepted."

Similarly Loveridge (1945) writes that pythons ". . . not only lay eggs, but they guard and actually incubate them. For a cold-blooded reptile whose temperature supposedly depends on that of the surrounding atmosphere, this is indeed surprising. At various times, however, sundry investigators have slipped thermometers between the coils of brooding pythons and noted that the female was from one to twenty degrees warmer than her mate and from ten to thirty degrees warmer than the cage they occupied."

Benedict (1932) reviews the published data on incubation in pythons. Of particular interest are the results of Sclater (1862) who found that the temperature of a large incubating female python in the Gardens of the Zoological Society of London remained constantly above that of its surroundings. However, he also found that a male python in the same cage, although having a temperature always below that of the female, was still well above that of its surroundings. In discussing Sclater's results Benedict states that from ". . . the standpoint of our temperature studies, the results of Sclater are inexplicable because of the great difference between the temperature of the male python and the environment. If his measurements on the male python are true and there is this difference between the temperature of the environment and that of the male python, then it is a question of whether the male *as well as* [our italics] the female produces sensible heat. . . . Our direct calorimetric measurements rule out . . . the possibility of sensible heat being produced." Benedict offers the following suggestions to explain Sclater's results: (1) that Sclater may have been in error in determining the true environmental temperature; (2) that, contrary to Sclater's assumption, it was unlikely that the two snakes were subject to the same environmental conditions; (3) that heat may have been supplied to the female from the large mass of fermenting eggs.

It seems to the present authors that the first two factors are not of any great significance (as suggested by Benedict) and that variations in either would probably not account for the considerable temperature differential obtained by Sclater. It would seem that Benedict, though ruling out the possibility of the male producing sensible heat, is quite prepared to accept the latter in an incubating female.

However, the factors which have not been noted by Benedict, though supplied by Sclater, were, firstly, that the female python was 22 feet in length, whereas the male was only 14 feet. Secondly, the cage in which the pythons were kept was warmed with hot-water pipes. Hence, although a full description of the cage conditions was not given, one cannot rule out the possibility that the pythons obtained sufficient heat (possibly by conduction) to enable them to raise their temperatures well above their surroundings. It would also be reasonable to assume that in any form of heat conservation the larger female would be more efficient than her smaller mate.

The observations of Forbes (1881) provide confirmation (though with less extreme temperature differences) of Sclater's results. However, Benedict has applied the same criticisms to both results, so that our objections outlined above are equally valid when applied to Benedict's treatment of Forbes' results. Indeed Benedict concluded that Forbes' ". . . finding that the temperature of the male was many degrees above that of the air is, we believe, evidence of an error in establishing the true temperature of the environmental air."

Benedict apparently refused to accept the possibility of a temperature differential between a male python and its surroundings even though there was, at that time, considerable evidence in support of such a fact. However, although he could see no physiological mechanism to explain the internal generation of such heat, he does not appear to have explored the possibility of the snake conserving heat obtained from some external source. This is indeed surprising, for Forbes' results show that, although the air temperature was well below that of the snakes, the gravel in the cage (which was heated by hot-water pipes beneath the floor) was always at a temperature only slightly below that of the snake. It is not inconceivable that considerable heat would be absorbed by conduction where the snake was in contact with the gravel or the floor of the cage.

Benedict, in discussing his own work on an incubating python in the National Zoological Park in Washington, comments that the method of making a comparative study of the temperature of both male and female would have been of no value. This was because the conditions varied in different parts of the cage, and it would not have been possible to transport the male python to the same corner as the female without disturbing either or both of the snakes.

However, we cannot agree with Benedict on this point, for his aim was to determine temperature differences between the snakes and their surroundings, and these could have been readily established independently of the difference in environmental temperatures between the two snakes. The fact that the other two pythons in the cage remained coiled during most of the time that the temperatures were recorded would have greatly facilitated such a study. Surely if he felt that the results of previous experimenters were due to inaccuracies in their measurements of the environmental temperatures, the application of his refined experimental techniques to the other pythons in the cage would have done much to clarify these apparently anomalous earlier results.

The cage in which these pythons were kept was heated during the day by solar radiation, and according to Benedict this ". . . aided in developing a rather high temperature, although the sun at no time came in contact with the brooding python". It appears that one can assume that the temperature in the cage at some time reached a higher level than the maximum recorded by Benedict during his temperature measurements.

It seems to the authors that the fact that coiling is always associated with the higher temperature of these brooding pythons is of considerable significance, and it is

tentatively suggested that the mechanism described earlier may in part account for these past observations.

We mentioned our interest in the incubation of pythons to Mr. Eric Worrell, of the Australian Reptile Park, Gosford, and he kindly provided a summary of his observations, from which we have extracted the following:

"Frequently, diamond pythons (*Morelia spilotes spilotes*) brought to us produce eggs in captivity during January to March and for the first week or two the female coils tightly around the cluster but eventually deserts them. However, on three or four occasions the incubation period has been completed.

"The female crawls into a deep heap of leaf mould and produces her eggs in a cluster while entirely hidden. We frequently trod on the coiled snakes beneath the litter without them making their presence known. From twelve to thirty eggs about 50 mm. in length and about 27 mm. in diameter were produced and the incubation period appeared to be around 90 days, 93 days being the only occasion on which we were able to make a positive record.

"In the cases of the successful hatchings the females spent an hour or two every sunny morning absorbing every minute of sunlight that came in through the windows in the vivarium. A noticeable feature was that the snakes did not coil to sun-bask, but lay loosely outstretched.

"Another distinctive attitude was the method in which the female coiled around the eggs. This was always done very tightly so that not only was every egg completely hidden, but I feel positive that no air was able to escape between the coils.

"On one occasion at Ourimbah I was called to catch a python that had been crawling into a heap of dried bracken and leaf mould under lantana bushes. When I uncovered the snake it was coiled in the same characteristic pose that I have observed so often under captive conditions and I was able to presume, without first seeing them, that the snake's body enclosed a clutch of eggs."

It would appear from these observations, which we feel support our earlier contentions, that the efficiency of the heat-conserving mechanisms may be increased in incubating female pythons due to an exaggeration of their normal behaviour pattern.

Finally, it should be reiterated that many questions have been left unanswered. The rough nature of the observations, the lack of quantitative data, and the need to extend the observations over a wider range of winter and summer conditions are readily admitted by the authors to be notable shortcomings of the present paper. However, it is hoped that as we are unable, at present, to carry our observations beyond the stage discussed above such simple heat conserving behaviour may be of sufficient interest to other students to warrant its publication in such rudimental form.

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THE GENUS *CONOSTYLIS* R.Br.

II. Taxonomy.

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(Plates ix-x; ninety-six Text-figures.)

[Read 30th November, 1960.]

Synopsis.

The genus *Conostylis* has been examined critically, and twenty-three species are now recognized. All are described in detail, illustrated, and their distributions shown on outline maps.

Two new species and two new subspecies are described, and 18 new records of chromosome numbers (including six from genera other than *Conostylis*) given. A key to the species is included.

Problems concerning the family to which *Conostylis* and related genera should be assigned are mentioned, and intergeneric and interspecific relationships discussed.

Introduction.

The genus *Conostylis* R.Br. is endemic in the south-western portion of Western Australia; its range is practically that of the South-west Vegetation Province of Diels (1906) (Fig. 2). The plants are most common and prolific in heath and dry sclerophyll forest communities, but occur in all of the principal communities of the area, with the exception of the wet sclerophyll forest dominated by *Eucalyptus diversicolor*. One species, *C. candicans* Endl., occurs also on Rottnest Island and on Garden Island.

No monographic treatment of the genus has been published, the only comprehensive account of the genus being that of Bentham (1873). Of the total, at that time, of 46 validly described species, Bentham recognized 31. A further five species have since been described.

No species are known to be of any economic value. In view of the writer's difficulties in bringing the plants into cultivation it is not expected that they would become useful horticulturally.

In the early stages of the present work, it became evident that the existing taxonomic treatments of the genus were inadequate in dealing with certain critical groups of species. It was noted that these species were particularly prone to misidentifications in the herbarium specimens examined, and that many unnamed specimens were difficult to assign to a described species with any certainty. Therefore, an intensive investigation was conducted, in the field, the laboratory and the herbarium, in an attempt to resolve some of the difficulties.

More than 1,000 specimens have been examined, from the institutions listed below. The following abbreviations are those proposed by Lanjouw and Stafleu (1956), with the exception that the collection of the Department of Botany, University of Western Australia, is included with that of the State Herbarium of Western Australia under PERTH: The Queensland Herbarium, Brisbane (BRI), University of Cambridge, Botany School, Cambridge, Great Britain (CGE), Royal Botanic Gardens, Kew, Great Britain (K), Botanical Museum and Herbarium, Lund, Sweden (LD), National Herbarium of Victoria, Melbourne (MEL), Department of Botany, University of New England, New South Wales (NE), National Herbarium of New South Wales, Sydney (NSW), Fielding Herbarium, University of Oxford, Great Britain (OXF), State Herbarium of Western Australia (PERTH), Department of Botany, University of Western Australia (PERTH).

Photographs of type specimens were kindly made available by the Royal Botanic Gardens, Kew, and by the British Museum (Natural History), London, Great Britain.

Historical Survey.

The genus *Conostylis* was first described by Robert Brown in his *Prodromus* of 1810. He placed it in a new family, Haemodoraceae, together with *Haemodorum*, *Anigozanthos* and *Phlebocarya*, and described four species. One of these (*C. serrulata*) was first collected by Menzies in 1791 from King George's Sound and the remaining three by Brown himself at King George's Sound and Lucky Bay in 1801–2, while he was botanist with Flinders on the *Investigator*. The chronology of publication of these and all subsequent species is set out in Table 1.

The history of the taxonomic treatment of *Conostylis* is connected intimately with that of the monotypic genera *Blancoa* Lindl. and *Androstemma* Lindl. *Androstemma* was described by Lindley (1840)* with the single species *A. junceum*, but was united with *Conostylis* as *C. androstemma* by Mueller (1873); at the same time Mueller united *Blancoa* (1840) with *Conostylis* as *C. canescens*. The first synonymy was accepted by Bentham (1873)†, but he maintained *Blancoa* as a separate genus, stating that it was "much more nearly connected with *Anigozanthos*, but separated from both by characters which appear to be of full generic value, unless all the Australian Conostyleae be treated as sections of one comprehensive genus". This will be discussed later.

Assessment of Taxonomic Characters.

Habit. All species of *Conostylis* are perennial herbs, whose habit falls roughly into three classes: (1) caespitose, the rhizome being very short or absent (Fig. 1, *a-b*); (2) proliferous, in which the stem bears tufts of leaves at intervals at the nodes: branching of the stem may occur and scapes may arise from the upper nodes (Fig. 1, *c*); (3) stoloniferous, in which the plant is able to cover a considerable area by means of runners (Fig. 1, *d*). Combinations of these types of growth occur in many species. Habit is held to be of little taxonomic importance; a spreading, stoloniferous mode of growth is shared by such unrelated species as *C. stylidioides* F. Muell. and *C. seorsiflora* F. Muell, while no close taxonomic relationship exists between those groups of species whose growth is caespitose or proliferous. In defining two of the three series of his section *Euconostylis* Bentham used habit as an ancillary character: "Stems proliferous or stoloniferous" and "Stem short, rarely shortly proliferous", respectively.

Leaves. Great constancy occurs in the leaf characters of most species of *Conostylis*, particularly as regards the marginal spines and marginal veins. In a previous publication (Green, 1959) it was noted that anatomical characters of the leaves, especially the disposition of sclerenchyma, have some taxonomic value. In view of the difficulties experienced in using floral characters to define species limits in this genus, particular attention has been paid to the leaves. The external morphology of the leaves of many individual species of *Conostylis* is particularly uniform and distinct. Considerable variation occurs in the morphology of the leaves of *C. juncea* Endl. (as here emended), but this species is quite distinct on floral characters.

Scapes. The inflorescence, in most species, is borne on an erect scape which may be branched; the scape may be shorter (Fig. 1, *a*) or longer (Fig. 1, *b*) than the leaves, and usually bears several leaf-like bracts at intervals along its length. In the axil of an upper bract a small accessory scape and inflorescence may arise in a few species (e.g., *C. candicans* Endl.). Scapes are usually tomentose-woolly, but the tomentum is sometimes lost, probably by abrasion or weathering, in old scapes. Bentham placed some importance on the relative lengths of scapes and leaves, but this has been found a very variable character in some species (e.g., *C. aculeata* R.Br.) and one which has not proved of great use to the writer in classifying the genus.

Flowers. Three types of perianth are found: (1) tubular, in which the length of the perianth tube above the ovary greatly exceeds that adnate to the ovary (in *C. androstemma* (Lindl.) F. Muell. and *C. bealiana* F. Muell. only; Fig. 1, *e*); (2) campanulate, in which the free part of the tube is approximately equal in length to the

* Often quoted as 1839, but see *Flora Malesiana*, ser. I, vol. 4, CXCVII (1954).

† All subsequent undated references to Bentham refer to this work.

TABLE 1. (*Chronology of published species.*)

In this table the following information is given for each species: Date—Original Name—Type Locality—Type Collector and Date—Present Name.

1810—*C. aculeata* R.Br.—King George's Sound—Brown, 1801—*C. aculeata* R.Br. ssp. *aculeata.*
C. serrulata R.Br.—King George's Sound—Menzies, 1791—*C. serrulata* R.Br.
C. setigera R.Br.—King George's Sound—Brown, 1801—*C. setigera* R.Br.
C. breviscapa R.Br.—Lucky Bay—Brown, 1802—*C. breviscapa* R.Br.
1839—*C. juncea* Endl.—Cult. from seed—.....—*C. juncea* Endl.
C. candicans Endl.—Swan River*—Hügel—*C. candicans* Endl.
1840—*C. setosa* Lindl.—Swan River—Drummond, 1839, Mangles & Toward (3 syntypes)—*C. setosa* Lindl.
C. aurea Lindl.—Swan River—Drummond, 1839—*C. aurea* Lindl.
C. bracteata Lindl.—Swan River—Drummond, 1839, & Toward (2 syntypes)—*C. aculeata* R.Br. ssp. *bracteata.*
C. dealbata Lindl.—Swan River—Drummond, 1839—*C. candicans* Endl.
C. caricina Lindl.—Swan River—Drummond, 1839—*C. caricina* Lindl.
C. aemula Lindl.—Swan River—Mangles & Toward No. 76 (2 syntypes)—*C. setigera* R.Br.
Blancoa canescens Lindl.—Swan River—Drummond, 1839—*Blancoa canescens* Lindl.
Androstemma junceum Lindl.—Swan River—Drummond, 1839—*C. androstemma* (Lindl.) F. Muell.
1846—*C. propinqua* Endl.—Rottnest Island—Preiss 1400, 1839—*C. candicans* Endl.
C. sulphurea Endl.—Perth—Preiss 1382, 1839—*C. aurea* Lindl.
C. preissii Endl.—Darling Range—Preiss 1384, 1841—*C. aculeata* R.Br. ssp. *preissii* (Endl.), ssp. nov.
C. bromelioides Endl.—York—Preiss 1401, 1840—*C. aculeata* R.Br. ssp. *bromelioides* (Endl.), stat. nov.
C. melanopogon Endl.—Unknown—Preiss 1387, 1840—*C. setigera* R.Br.
C. festucacea Endl.—Southern River—Preiss 1386, 1841—*C. aculeata* R.Br. ssp. *preissii* (Endl.), ssp. nov.
C. graminea Endl.—Guildford—Preiss 1380, 1839—*C. caricina* Lindl.
C. discolor Endl.—Swan River—Preiss 1392, 1839—*C. setigera* R.Br.
C. assimilis Endl.—Kaudiap-Cape Riche—Preiss 1394, 1840—*C. setigera* R.Br.
C. pusilla Endl.—Unknown—Preiss 1388, 1840—*C. setigera* R.Br.
C. minima Endl.—Unknown—Preiss 1389, 1840—*C. setigera* R.Br.
C. psyllium Endl.—York—Preiss 1391, 1839—*C. setigera* R.Br.
C. ensifolia Endl.—Mt. Manypeaks-Cape Riche—Preiss 1402, 1840—*C. serrulata* R.Br.
C. occulta Endl.—Albany—Preiss 1404, 1840—*C. serrulata* R.Br.
C. misera Endl.—Mt. Barker—Preiss 1406, 1840—*C. misera* Endl.
C. spathacea Endl.—Darling Range—Preiss 1397, 1840—*C. serrulata* R.Br.
C. longifolia Endl.—Ballanggajalup-Cape Riche—Preiss 1396, 1840—*C. serrulata* R.Br.
C. involucrata Endl.—Perth—Preiss 1407, 1839—*C. juncea* Endl.
C. vaginata Endl.—Manypeak-Cape Riche—Preiss 1383, 1841—*C. vaginata* Endl.
1859—*C. seorsiflora* F. Muell.—Gardiner River—Maxwell, 1859?—*C. seorsiflora* F. Muell.
1872—*C. stylidioides* F. Muell.—Murchison River—Oldfield, *c.* 1859—*C. stylidioides* F. Muell
C. teretiuscula—Unknown—Oldfield, *c.* 1859—*C. teretiuscula* F. Muell.
C. filifolia F. Muell.—Unknown—Drummond—*C. filifolia* F. Muell.
1873—*C. petrophiloides* F. Muell. ex Benth.—Phillips River—F. Mueller—*C. petrophiloides* F. Muell. ex Benth.
C. villosa Benth.—Unknown—Drummond 311—*C. villosa* Benth.
C. drummondii Benth.—To the E. of King George's Sound (?)—Drummond—*C. villosa* Benth.
C. gladiata Benth.—To the E. of King George's Sound (?)—Drummond—*C. misera* Endl.
C. prolifera Benth.—Swan River, Murchison River—Drummond, Oldfield (two syntypes)—*C. stylidioides* F. Muell.
C. racemosa Benth.—White Peak, Champion Bay—Oldfield—*C. stylidioides* F. Muell.
C. spinuligera Benth.—Unknown—Drummond—species dubium.
C. laxiflora Benth.—Vasse River—Oldfield—*C. serrulata* R.Br.
C. cymosa Benth.—Blackwood River, Champion Bay, Greenough Flats, Busselton—Oldfield, Oldfield, C. Gray, Pries (four syntypes)—*C. aculeata* R.Br. ssp. *aculeata.*
1875—*C. bealiana* F. Muell.—Cape Arid—Maxwell, 1859—*C. bealiana* F. Muell.
1903—*C. dielsii* W. V. Fitzg.—Mingenew—Diels, 1901—*C. dielsii* W. V. Fitzg.
1904—*C. harperiana* W. V. Fitzg.—6-7 miles NE. of Bayswater—Fitzgerald, 1902—*C. aculeata* R.Br. ssp. *bracteata* (Lindl.), comb. et stat. nov.
C. robusta Diels—Chapman River—Diels 4152, 1901—*C. aculeata* R.Br. ssp. *robusta* (Diels), comb. et stat. nov.
C. phathyrantha Diels—Israelite Bay—Brooke—*C. phathyrantha* Diels.
C. psammophila Diels (nom. nud.)—.....—.....—*C. dielsii* W. V. Fitzg.

* The locality "Swan River" usually refers to the Perth district. It was, however, an early name for the whole colony of Western Australia and may sometimes be much less precise.

adnate part (most species; Fig. 1, *f*); (3) free, in which the perianth is completely divided above the ovary (in *C. breviscapa* R.Br. only; Fig. 1, *g*).

The indumentum of the outside of the perianth may consist of a woolly tomentum of branched trichomes (most species) or more or less simple hairs (e.g., *C. aurea* Lindl.; Fig. 62) or the perianth may be rough and more or less scarious, bearing an incomplete covering of long, slightly denticulate setae (in *C. juncea* Endl. only; Fig. 37). On the inside, the perianth is usually almost glabrous with a few scattered hairs.

The type of placentation of the ovules has been used as a diagnostic character. In many species the ovules are numerous and borne "all over in front" of the placenta (Bentham) (Fig. 1, *k*); in the remaining species the placenta is more or less recurved with the ovules ("few" or "several") borne on the under surface (Fig. 1, *l-m*).

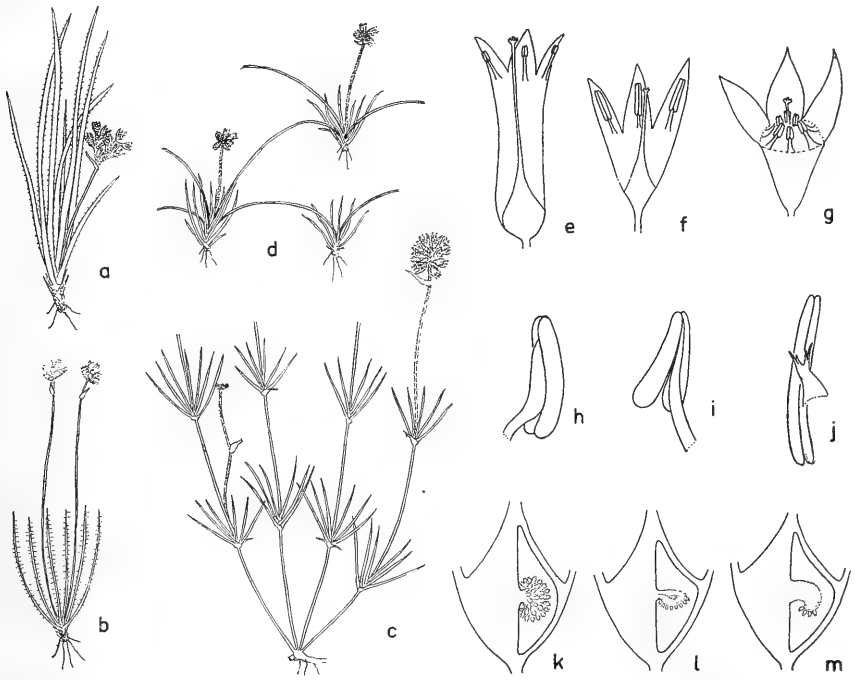


Fig. 1.—Morphological features of *Conostylis*. Habit: *a*, caespitose with scape shorter than the leaves; *b*, caespitose, scape longer than the leaves; *c*, proliferous; *d*, stoloniferous. Perianth: *e*, free part of the tube greatly exceeding that adnate to the ovary; *f*, free part slightly exceeding the adnate part; *g*, perianth divided to the adnate part. Anthers: *h*, joined in the lower third to a long, decurrent connective; *i*, connective short, apical; *j*, connective short, median, with erect appendages. Placentation: *k*, placenta covered all over with numerous ovules; *l*, peltate with the ovules recurved; *m*, recurved with few pendulous ovules.

In most species the anther connective is decurrent on the dorsal side of the anther, attached toward the base to the filament (Fig. 1, *h*). In *C. breviscapa* R.Br. the free thecae are pendulous from a small apical connective, although superficially this type may resemble the preceding (Fig. 5). In *C. aurea* Lindl. the filament differs from all other species in being short and strap-like, with the connective median and bearing two usually fringed erect appendages (Figs 1, *j*, and 64).

In several species, e.g., *C. setigera* R.Br., the stamens are in two series, those of the inner whorl being shorter (Fig. 44); those of most other species are uniseriate. The character of biseriate stamens is usually accompanied by some degree of biseriation of the perianth segments.

Fruit. The fruit is accompanied by accessory organs, viz., the persistent perianth and stamens, but is basically a loculicidal capsule. In many species development of

the fruit seems to be inhibited and the ovules of nearly all flowers abort. As a result, in these species the fruiting stage is observed infrequently in the field. Fruits appear to mature with fair regularity in *C. juncea* Endl. and *C. candicans* Endl., and it is interesting to note that the former was described from plants raised in Europe from seed.

Seeds. Seeds of only three species have been examined in any detail. These have been rugose, subelliptical in outline and about 1·5 mm. long (Fig. 96). Seeds of *C. candicans* and *C. aculeata* R.Br. ssp. *bracteata* (Lindl.), comb. et stat. nov., have been germinated and raised to 6-months-old seedlings (Fig. 96).

Chromosome Numbers.

The following chromosome numbers except for that of *Anigozanthos flavida*, are new records obtained from acetocarmine squashes of young anthers. Voucher specimens are filed in the Department of Botany, University of Western Australia. Chromosome numbers of some species of related genera are recorded because of their bearing on the intergeneric relationships of *Conostylis*.

n = 4. *C. breviscapa* R.Br.: Near Esperance.

n = 5. *C. androstemma* (Lindl.) F. Muell.: E. of Geraldton; Gooseberry Hill. *C. aurea* Lindl.: S. of Mingenew; Wattle Grove.

n = 7. *C. caricina* Lindl.: N. of Kalamunda. *C. setosa* Lindl.: Greenmount.

n = 8. *C. aculeata* R.Br. ssp. *aculeata*: Lesmurdie Hill. *C. aculeata* R.Br. ssp. *preissii*: Cape Naturaliste. *C. aculeata* R.Br. ssp. *robusta*: W. of Wicherina. *C. bealiana* F. Muell.: Near Esperance. *C. candicans* Endl.: Lharidon Bay; Near Esperance; Rottnest Island. *C. filifolia* F. Muell.: Cannington. *C. juncea* Endl.: Near Bassendean. *C. phathyrantha* Diels: E. of Esperance. *C. seorsiflora* F. Muell.: S. of Tambellup. *C. serrulata* R.Br.: Near Nannup. *C. stylidioides* F. Muell.: N. of Geraldton. *C. vaginata* Endl.: N. of Hopetoun.

n = 14. *C. setigera* R.Br.: Kings Park; SE. of Busselton.

n = 8. *Blancoa canescens* Lindl.: Bushmead.

n = 6. *Macropidia fuliginosa* (Hook.) Druce: Cultivated, Kings Park. *Anigozanthos bicolor* Endl.: Near Perth. *A. flavida* Redoute: Near Albany. *A. humilis* Lindl.: N. of Yerecoin; Cultivated, Kings Park. *A. manglesii* D. Don: Kings Park. *A. viridis* Endl.: Near Perth.

Pollen Morphology.

The pollen morphology of two species (*C. aculeata* R.Br. ssp. *bromelioides* (Endl.), stat. nov., and *C. dielsii* W. V. Fitzg.) has been described and illustrated by Erdtman (1952). Several features of these and other species are of palynological interest, although their taxonomic value cannot yet be ascertained fully. Many species contain, in their pollen, a certain proportion of multiporate grains. A mixture of 2- and 3-porate grains has been observed in *C. petrophiloides* F. Muell., *C. seorsiflora* F. Muell., *C. aculeata* R.Br. ssp. *bromelioides* (Endl.), stat. nov., *C. vaginata* Endl., *C. androstemma* (Lindl.) F. Muell., *C. caricina* Lindl. and *C. bealiana* F. Muell. Some 4-porate grains have been observed in *C. setosa* Lindl. and *C. setigera* R.Br., while multiporate grains (5- and up to 8-porate) have been observed in *C. phathyrantha* Diels.

In *Blancoa canescens* Lindl. the pollen is intermediate between, and scarcely distinguishable in morphology and average linear dimensions from, that of *C. vaginata* Endl. and *C. androstemma* (Lindl.) F. Muell. Pollen of *Anigozanthos*, *Tribonanthes* and *Phlebocarya* species was described by Erdtman (loc. cit.) and shown to be more or less closely related to that of *Conostylis*. The multiporate spherical grains of *Tribonanthes* afford a link between this genus and *Conostylis*, via *C. phathyrantha* Diels, whose pollen is, however, unique in the genus.

Erdtman (1954) has pointed out that, apart from the family Alismaceae and certain genera of the Amaryllidaceae, Araceae and Bromeliaceae, pollen grains with three or more rounded apertures are unknown outside of the dicotyledons.

Ecology.

Climate. The climate of the area has been dealt with by Diels (1906) and by Gardner (1944).

Geology and Soils. Detailed accounts of the geology are given by Jutson (1934) and by Clarke, Prider and Teichert (1944). The soils of the South-Western Agricultural region have been dealt with by Smith (1952). Generalized soil zones of the South-Western portion of the State are shown in Figure 3.

The Biotic Factor. Little is known of the effect of native animals on the growth of *Conostylis* plants. In some species, e.g., *C. aculeata* R.Br. and *C. candicans* Endl., the ovary is completely eaten out by insects. A young inflorescence is sometimes completely removed from the scape by insect damage. On Rottnest Island, Storr (1958) has observed slight grazing of *C. candicans* leaves by the native quokka (*Setonix brachyurus*), but it is probable that the plant is grazed by this animal only in cases of extreme shortage of other vegetation.

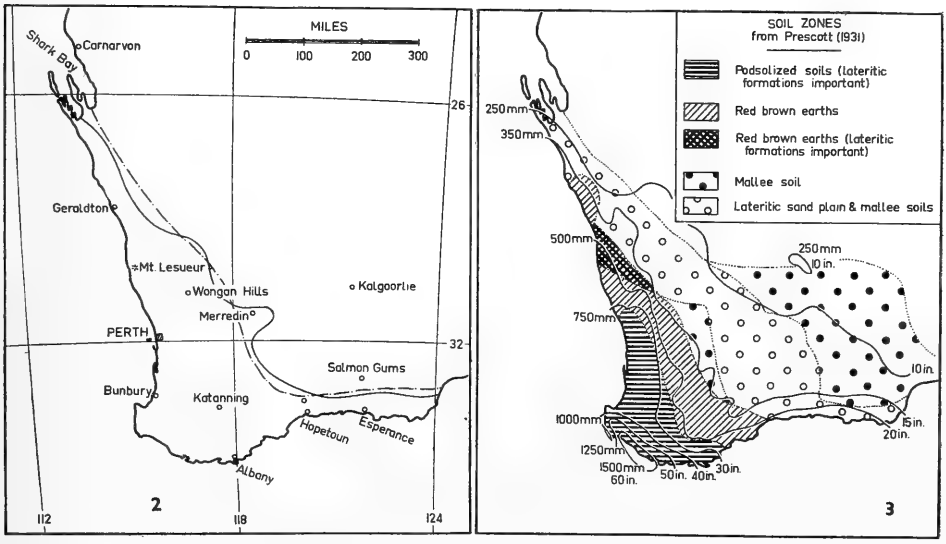


Fig. 2.—Distribution of *Conostylis*. The solid line shows the eastern limit of the genus, while the broken line shows that of the South-west Vegetation Province of Diels (1906).

Fig. 3.—Soils and annual average rainfall in the area of *Conostylis* distribution. Scale as in Fig. 2.

Fires. Several plants of *Conostylis* have been observed to recover rapidly from fire damage. Similarly, evidence of past fires has been found in the rhizomes of healthy plants. Both observations indicate that resistance to fires is a characteristic of members of the genus. Typically, young shoots develop from the unharmed rhizome soon after a fire, and flowering has been recorded within nine months in *C. vaginata* Endl., *C. aculeata* R.Br. and *C. androstemma* (Lindl.) F. Muell. Shoots of *C. candicans* make rapid vegetative progress during the first year following a fire.

Methods of Natural Propagation.

In many species of *Conostylis* a very low proportion of flowers produce mature seed under field conditions. Only in *C. juncea* Endl. are seeds found commonly in herbarium specimens, and this species was described from a plant raised from seed in Europe. In *C. aculeata* R.Br., *C. candicans* Endl., *C. caricina* Lindl. and *C. setosa* Lindl. seeds have been found in the field, but in most other species few or no ovules develop into seeds. Counts of seed-bearing fruits in the species referred to are shown in Table 2.

Seeds from *Conostylis* plants were collected at every opportunity in late 1956 and batches were tested for germination at intervals during the following year. Although a

variety of pre-treatments was used, no germination was obtained. In July, 1959, seeds of two species were incubated on moist filter paper at 18°C. in Armidale, New South Wales, and the following germinations were obtained: *C. candicans*, Rottnest Island: 39% (sample 216); *C. aculeata* ssp. *bracteata*, Kings Park: 23% (sample 151).

Since only one seedling of *Conostylis* has ever been observed in the field, these results show that the barrier to normal sexual reproduction in the genus may be at the establishment stage, rather than at germination.

In the absence of regular seed-setting, most species of the genus rely upon vegetative reproduction for their propagation. It has been noticed that those species in which some major taxonomic difficulties lie are those most strongly equipped for vegetative growth, e.g., members of the "*C. aculeata* complex" and the various forms included under *C. stylidioides* in the present treatment.

TABLE 2.

Ovule Development.

Species.	Locality.	Date, 1956.	Percentage of Flowers having				Number of Flowers in Sample.
			Seeds Shed.	Seeds Present.	Ovules Aborted.	Ovary Damaged.	
aculeata ssp. *aculeata*	Lesmurdie Hill.	9 Dec.	32	2	66	0	50
aculeata ssp. *bracteata*	Morley Park.	9 Dec.	38	2	24	36	50
candicans	Rottnest Island.	12 Nov.	0	30	50	20	50
candicans	Rottnest Island.	14 Nov.	9	32	28	31	148
candicans	Rottnest Island.	16 Nov.	0	17	21	62	468
caricina	Gooseberry Hill.	9 Dec.	66	0	34	0	50
setosa	Gooseberry Hill.	9 Dec.	10	14	8	68	50

INTERGENERIC RELATIONSHIPS.

Conostylis is closely related to four genera, all restricted to south-western Australia. The closest is undoubtedly *Blancoa*, the next closest probably are *Anigozanthos* and *Macropidia*, with *Tribonanthes* occupying a doubtful position.

In spite of Bentham's statement that *Blancoa* is closer to *Anigozanthos* than to *Conostylis*, there is some evidence that this is not the case. Morphologically, the flower of *Blancoa* fits better into the *Conostylis* range of characters with the discovery, since Bentham's publication, of *C. bealiana* F. Muell. The chromosome number of *Blancoa canescens* Lindl. is n = 8 (the predominant number of *Conostylis*), while all the species of *Anigozanthos* examined, as well as *Macropidia fuliginosa*, have n = 6. The pollen of *Blancoa* falls within the range of variation of size in *Conostylis* pollen; that of *Anigozanthos* resembles that of some species of *Conostylis*, but is morphologically distinct.

The present doubtful position of *Tribonanthes* is due partly to the fact that chromosome numbers could not be obtained, partly to its modified floral morphology compared with that of the other genera (although a possible connection has been observed between the anther appendages of *Tribonanthes* and those of *C. aurea*), and partly to its pollen morphology which agrees closely with one species only of *Conostylis* (*C. phathyrantha*).

THE FAMILY HAEMODORACEAE.

The family Haemodoraceae was first described by Robert Brown in 1810 to include the genera *Haemodorum*, *Conostylis*, *Anigozanthos* and *Phlebocarya*. In defining the genera, emphasis was placed on characters of the ovules (definite or indefinite) and the number of stamens (3 or 6). The delineation of the family by subsequent workers has

given rise to much confusion. Some authors have greatly increased its scope, while others have denied its existence as a distinct family, dividing its genera between the Liliaceae and Amaryllidaceae.

Lindley (1853) divides the family into two tribes with a third doubtful tribe, thus: Haemodoreae, Conostyleae and ? Vellozieae. He attempts to distinguish between the Amaryllids and the Haemodoraceae, but has to admit that although "there can be no doubt as to their real distinctness", the exact difference is difficult to express. He defines 13 genera and 50 species.

Bentham (1873) includes the two tribes Haemodoreae and Conostyleae in the Amaryllidaceae and expresses the opinion that a well-defined group of the same grade as the Iridaceae or Orchidaceae can only be formed by the union of Haemodoraceae, Hypoxidaceae and Amaryllidaceae. A decade later, Bentham and Hooker (1883) expand Lindley's conception of the family to include 26 genera and 120 species. They divide the family into four tribes, Euhaemodoreae, Conostyleae, Ophiogoneae and Conantherеae, but exclude the genera *Vellosia* and *Barbacenia* which they place in the Amaryllidaceae.

Rendle (1904) includes most of the genera in two tribes of the Liliaceae, the Ophiopogonoideae and the Aletroideae. He states that these tribes include "a few genera . . . which are often included in a distinct order (Haemodoraceae) owing to the more or less inferior ovary".

In the classification of Hutchinson (1934, 1959) the Haemodorales (as well as the Amaryllidales + Iridales) are shown as being derived phylogenetically from the Liliales. Hutchinson disagrees with Pax (1930) who had limited the family to Bentham and Hooker's first tribe, Euhaemodoreae, while transferring the second, Conostyleae, to the Amaryllidaceae. Hutchinson is firmly of the opinion that the two tribes should be united to form the Haemodoraceae which, with the genus *Aletris* removed to the Liliaceae, would then be natural and homogeneous, both in its facies and its general austral distribution. He distributes the remainder of Bentham and Hooker's tribes between the Liliaceae, Agavaceae and Tecophilaceae.

The critical treatment of Lemée (1939) admits that the problem is insoluble and resorts to the adoption of a combined family group Liliaceae-Haemodoraceae-Amaryllidaceae. In pointing out the difficulty encountered in characterizing the families he states: "Cela est impossible pour les 3 familles en question, les manières si différentes dont elles sont presentées et limitées dans les ouvrages les plus récents et les plus connus en témoignent suffisament."

Lawrence (1951) states that "there is a disagreement among phylogenists as to how much or how little this family embraces". His systematic treatment of the family places it between the Liliaceae and Amaryllidaceae, following Pax (1930).

There seems little relationship between the group of genera *Conostylis*, *Blancoa*, *Anigozanthos*, *Macropidia* and *Tribonanthes* on the one hand, and the Australian members of the Haemodoraceae (*Haemodorum* and *Phlebocarya*) on the other, although strong superficial resemblances occur between *Conostylis* and certain South African genera usually attributed to the Haemodoraceae, particularly *Dilatris* and *Lanaria*.

Erdtman (1952) recognizes a closely-knit group in the genera *Conostylis*, *Blancoa*, *Anigozanthos* and *Tribonanthes* on the basis of pollen morphology and hints that further investigation might suggest the desirability of raising the group to family status. The erection of such a family is not considered timely, in view of the difficulties in delineating the existing families of the Liliiflorae, and the writer is prepared, for the time being, to accept Bentham's (1873) tribe Conostyleae of the family Amaryllidaceae.

Taxonomic Treatment.

Bentham recognized only 31 of 46 described species, and it is with some hesitation that it is now proposed to reduce still further the number of species; yet close study of the plants, both in the field and in the laboratory, has convinced the writer that this genus has suffered, perhaps more than most, from the erection of large numbers of

poor species, principally by European botanists who had little acquaintance with plant populations in the field.

The drastic reduction in the number of species arises in two ways. Firstly, many of the populations previously regarded as species are closely related morphologically, yet more or less separated geographically, and most of these have been reduced to subspecific rank. Secondly, field work has revealed the absence of distinct discontinuities between some pairs of "species" and such species have been united on the grounds that their boundaries are arbitrary and quite impossible to define on observable characters. It is not claimed that the subjective interpretation of species has been eliminated, but when opportunities have arisen for placing species on a firmer foundation of fact than was previously possible, this has been attempted. Thus, the present revision, while presenting two new species and two new subspecies, recognizes a total of only 23 species. The total number previously described was 51.

Methods.

Data from the fields of gross morphology, cytology, anatomy and ecology have been brought together and an attempt has been made to place the species approximately in order of relative advancement. This must necessarily be highly speculative and largely subjective. The scheme is shown in diagrammatic form in Figure 95, and the order in which the species are described in the treatment below is a linear adaptation of this scheme.

The term *variety* has been abandoned in view of its increasing ambiguity, and the only infraspecific taxon used is the *subspecies*. This category is used for morphological variants which are geographically isolated from the type species. When it is considered that a previously described *variety* is of this kind, its status is altered to *subspecies*.

All specimens cited have been examined by the writer except where specifically indicated, but when large numbers of specimens have been recorded from identical localities, usually only one is cited. All critical or historically important specimens are included. Descriptions are based on the whole range of specimens seen.

Type specimens of new taxa will, wherever possible, be deposited in the State Herbarium of Western Australia and duplicates in the National Herbarium of Victoria.

Conostylis R.Br.

Conostylis R.Br., Prodr., 1: 300 (1810), ed. Nees, 1: 156 (1827); Bartl., Ord., 43 (1830); A. Rich, *Sert. Astrol.*, 80 (1834); Endl., *Gen.*, n. 1258, 172 (1837); Lindl., *App. Bot. Reg.*, 44, t.6 (1840); Dietr., *Syn.* II, n. 1046, 1614 (1840); Ench., 100 (1841); Brongn., *En. Genr.*, 23 (1843); Spach, *Veg. Phan.*, 13: 109 (1846); Benth., *Fl. Aust.*, 6: 428 (1873); Benth. & Hook., *Gen. Pl.*, 3: 676 (1883); Durand, *Gen. Phan.*, 411 (1888); Kuntze, *Gen. Pl.*, 1: 699 (1891); Dalla Torre & Harms, *Gen. Siphon.*, 1242, 78 (1900–07); Diels and Pritzel, *Fragm.*, 107 (1905); Ostenf., *Contrib.*, 3: 31 (1921); Pax & Hoffm. in Engl. & Prantl, 15a: 428 (1930); Lemée, *Dict. Descr.*, 2: 290 (1930). *Androstemma* Lindl., *App. Bot. Reg.*, 46 (1840).

Caespitose perennial herbs, low, or rising to some height by proliferous branching, the tufts compact, solitary or connected by stolons or rhizomes to nearby tufts and thereby covering often a considerable area. *Roots* fibrous arising close together from a short stem or at intervals along the rhizome densely pilose in the young root, often the hairs firmly enclosing particles of soil in a cylinder around the root, roots becoming glabrous and wiry with age. *Stem* short and undivided or long and sometimes branched, passing underground as a rhizome and bearing old leaf scales, or growing at or near ground level as a tough wiry glabrous stolon giving off roots and fascicles of leaves at the nodes, or arising above ground in a proliferous type of growth also with fascicles of leaves at the nodes. *Leaves* equitant and distichous at the base, soon becoming flat or terete above, linear, straight or falcate, narrowing to an acute but scarcely pungent tip, entirely green and glabrous or bearing on each margin simple or branched setae or cilia in one to several vertical series, or the whole leaf covered with a whitish more

or less woolly tomentum of usually branched hairs, sometimes the tomentum disappearing with age, usually the leaves longitudinally striate with the alternate nerves more pronounced and sometimes the marginal nerves fibrous and very prominent. *Scape* arising from the stem apex, surrounded by sheathing leaves, very short or as long as or longer than the leaves, usually covered with a whitish or yellow woolly tomentum of branched hairs, the scape simple or sometimes branched, bearing one to several bracts at intervals along its length, the bracts narrow-ovate, green and leaf-like or only the midline green and the margins broad, brown and membranous, the bracts glabrous or pubescent, sometimes as long as the leaves but usually much shorter. *Inflorescence* terminal, a simple or bifid dichasial cyme, extended or compressed sometimes to a several- to many-flowered head or sometimes reduced to a single flower, the inflorescence subtended by one or more scapose bracts which are narrow-ovate and leaf-like or sheathing and very broad and membranous. Sometimes also a small inflorescence occurs in the axil of the uppermost scapose bract. Flowers each subtended by a linear brownish bract much shorter than the flower. *Flowers* pedicellate, the perianth petaloid, narrow-turbinate or subcampanulate or long-tubular, invested outside with a close woolly yellow, reddish-yellow, brick-red, purplish-white or cream-coloured tomentum of mostly branched hairs which are sometimes longer near the base of the perianth, rarely the hairs simple to slightly denticulate. Perianth near the base adnate to the lower portion of the ovary, the tubular portion above short or sometimes very long or absent, at length divided into six linear-lanceolate or narrow-linear erect or spreading lobes, equal or the inner smaller, imbricate, the inner lobes often having broad margins on the dorsal side where the tomentum is shorter or absent, the lobes usually somewhat tomentose inside, the tube inside usually only slightly hairy, or glabrous. *Stamens* opposite the lobes, attached to the tube just below the level of the sinuses, erect or slightly incumbent, the filaments linear-filiform or sometimes dilated, the anthers oblong, erect, introrse, bilocular, dehiscing in longitudinal slits, the thecae confluent or rarely free almost to the apex, the connective usually attached near the base and decurrent, about two-thirds of the length of the anther, sometimes short and attached near the middle, rarely apical. *Ovary* semi-inferior, adnate to the perianth tube in the lower part, ovoid, trilocular, tricarpellary, syncarpous with a single style broadly conical at the base, equal in height to or slightly exceeding the anthers, trigonous, filiform above, the stigma minutely 3-lobed. Placentation axile, median, in either the free or adnate portion of the ovary, globose and bearing numerous orthotropous ovules all over its surface or peltate with the ovules relatively few and pendulous or reflexed. *Fruit* accessory, basically a capsule dehiscing loculicidally, the dissepiments rising to half the height of the fruiting chamber, the style splitting into three tardily, often remaining joined near the stigma for some time. Seeds usually fewer than the ovules, often very few or none as a result of abortion. Perianth and stamens persistent on the slightly swollen fruiting ovary.

Flowering period spring except one summer-flowering species (*C. breviscapa* R.Br.).

Chromosome numbers: n = 4, 5, 7, 8, 14.

Type species: *Conostylis aculeata* R.Br.

A key to the species follows the descriptions.

1. Conostylis breviscapa R.Br., *Prod. Fl. Nov. Holl.*, 1: 301 (1810).

Holotype.—(Photo only seen), Lucky Bay, South Coast, R. Brown 5627, 7.i.1802 (BM). Four separate pieces on holotype sheet (Plate ix, 3). *Isotype* in K (not seen). The type locality has been ascertained from Brown's unpublished field notes ("Bay I". see Burbidge, 1955).

Stems very short, somewhat branched; leaves flat, 10–30 cm. long and 1·5–2·5 mm. broad, glabrous except the woolly margins, the lamina prominently striate; inflorescence capitate, on a short scape 2–5 cm. long bearing at least one median leafy-bract exceeding the inflorescence; perianth pale creamy-yellow, 10–12 mm. long, shortly branched-tomentose outside, loosely hairy and often orange-coloured inside, divided completely to

the ovary into six nearly equal segments 5–6 mm. long; filaments slender, concealed by the pendulous anther thecae which are attached at the apex only to a short connective; style protruding slightly beyond the anthers; placentas bearing several reflexed ovules; fruiting perianth scarcely enlarging; seeds not seen. Chromosome number n = 4. (Plate ix, fig. 3; Figs 4–5, 72.)

Specimens examined. Old Telegraph Line, Hopetoun, Speck 8657, 10.1952; Gibson, near railway station, J. W. Green 1246, 3.1957; 8 miles N. of Esperance, Churchill 18, 8.1956; 7 miles N. of Esperance, J. W. Green 1245, 3.1957; Near Esperance, Butier, 12.1956; Shark Lake, near Esperance, Grewar, 12.1957 (PERTH); Near the Thomas River, Taylor, 1887 (MEL).

The very unusual stamens, together with the low chromosome number and the deeply dissected perianth, make this easily the most distinctive species in the genus. Bentham placed it in a Section of its own, with the remark: "The peculiar anthers and perianth of this plant might have afforded grounds for establishing it as a distinct genus . . ." It is also the only summer-flowering species of *Conostylis*.

A relationship between the haploid chromosome number of 4 and the predominating n = 8 in the genus is not at all definite but, in combination with the character of the perianth segments free to the ovary, may indicate that this species is related to the ancestor of some or all of the n = 8 species.

2. Conostylis bealiana F. Muell., *Fragm.*, 9: 50–1 (1875).

Holotype.—Prope promontorium Cape Arid, G. Maxwell, 1875 (MEL). Two pieces on holotype sheet.

Discrete tufts 10–15 cm. in diameter; stem shortly branched; leaves 10–15 cm. long and 1·5–2 mm. broad, longitudinally nerved, glabrous except the margins which bear fine appressed cilia; flowers solitary on pedicels about 5 mm. long; perianth orange to brick-red, 3–3·5 cm. long, velutinous with branched hairs outside, sparingly hairy inside, lobes 5–7 mm. long; bracts subtending the flowers 2–3, unequal, 4–12 mm. long, dilated at the base; filaments broad, anthers up to 2 mm. long, attached by a dorsal connective in the lower third; style slightly exserted beyond the perianth lobes; perianth enlarging slightly in fruit; seeds not seen. Chromosome number n = 8. (Plate x, fig. 6; Figs 6–9, 73.)

Specimens examined. 13 miles E. of Young River Station, J. W. Green 1240, 3.1957 (PERTH); 35 miles W. of Esperance, Willis, 9.1947 (MEL); 10 miles N. of Gibson's Soak, Brittan, 8.1951; 8 miles N. of Esperance, Churchill 17, 8.1956 (PERTH); Between Esperance Bay and Fraser's Range, Dempster (MEL); Near Carrabin, Salisbury, 8.1949 (PERTH).

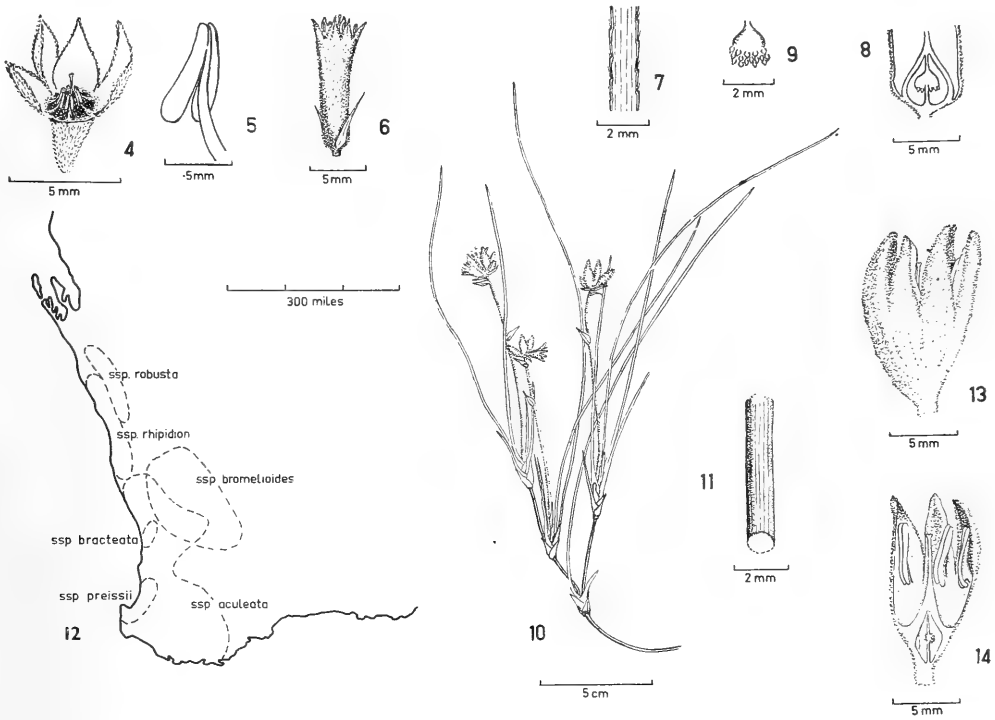
This species does not appear to be closely related to *C. androstemma*, as implied by Blackall (1954), because of the long tubular corolla. Rather, on the basis of chromosome number and morphology, pollen morphology, floral morphology and colour of the perianth, its affinities seem to lie with *Blancoa canescens* Lindl. *C. bealiana* therefore assumes importance in arguments on the inclusion of *Blancoa* in *Conostylis*, as proposed by Mueller (1840) (see also historical notes on *Conostylis*, above). The characters on which *Blancoa* is separated from *Conostylis* are that the ovules are in two rows in each loculus and the inflorescence is a unilateral raceme. The evidence is not conclusive, however, and current practice is followed, excluding *Blancoa* from the present treatment.

3. Conostylis serrulata R.Br., *Prod. Fl. Nov. Holl.*, 1: 300 (1810); *C. ensifolia* Endl. in Lehm., *Pl. Preiss.*, 2: 21 (1846); *C. occulta* Endl., *ibid.*, 22 (1846); *C. spathacea* Endl., *ibid.*, 22 (1846); *C. longifolia* Endl., *ibid.*, 22–3 (1846); *C. laxiflora* Benth., *Fl. Aust.*, 6: 439 (1873).

Holotype.—(Photo only seen), King George's Sound, A. Menzies (BM). Two separate pieces on holotype sheet.

Tufts discrete or sometimes the stem a shortly branched rhizome; leaves glabrous except the minutely denticulate-serrulate margins, 20–50 cm. long and 1·5–6 mm. broad, longitudinally striate, the nerves somewhat raised and prominently pale in colour, especially in dried specimens, but much less so towards the margin of the lamina which

is thin and not at all prominent; flowers in compact cymes on short pedicels about 5 mm. long or the inflorescence loose and occasionally rising to a height of about 10 cm. when the pedicels may be 1 cm. long; scape bearing usually 1–2 chaffy bracts up to 2 cm. long; perianth creamy or dull golden yellow with a smooth dense mat of branched hairs on the outside, sometimes with much longer hairs intermixed, glabrous inside, lobes equal, 7 mm. long, the perianth divided almost to the ovary; filaments short, anthers oblong and fairly short; style rather short; placentas covered by numerous ovules; ovary enlarging in fruit to a subglobular capsule 6–8 mm. in diameter. Seeds not seen. Chromosome number n = 8. (Plate ix, fig. 4; Fig. 74.)



Figs 4-11 and 13-14.—4, *C. breviscapa* R.Br., flower; 5, stamen (both from N. H. Speck 8657); 6, *C. bealiana* F. Muell., flower; 7, leaf surface (from J. W. Green 1340); 8, base of flower in longitudinal section; 9, placenta and ovules; 10, *C. filifolia* F. Muell., habit; 11, part of a leaf (both from J. W. Green 1716); 13, *C. aculeata* R.Br., ssp. *aculeata*, flower; 14, half flower (both from J. W. Green 1732).

Fig. 12.—*C. aculeata* R.Br. Distribution of subspecies.

Specimens examined. Near 26 mile peg, Albany Highway, J. W. Green 1725, 1739, 10.1957 (PERTH); Darling Range, L. Preiss 1397, 1.1840 (Type of *C. spathacea* Endl.) (LD, MEL); Jandakot, Blackall, 8.1939; S. of Wagin, Churchill, 1957; 8 miles E. of Collie, Butler, 9.1956; Yoongarillup, Busselton district, Royce 4538, 9.1953; Jindong, S. of Busselton, Royce 3403, 10.1950; Rosa Brook, E. of Margaret River, Royce 4627, 10.1953; Elgin, Royce 3113, 9.1949 (PERTH); Sources of the Blackwood River, Cronin, 1892 (MEL); Hoffman's Mill, Williams, 9.1932; Scott River, Brittan 52/9, 8.1952; Manjimup, Royce 2713, 9.1948; 3 miles NW. of Nannup, J. W. Green 1401, 7.1957 (PERTH); Vasse River, A. F. Oldfield (Type of *C. laxiflora* Benth.) (MEL); Red Gum Pass, Stirling Range, Morrison, 10.1902; Porongorups, Cashmore 69, 9.1939 (PERTH); Upper Kalgan River, Mueller, 1873 (K, MEL); Kalgan, Oldfield 590 (MEL); Lower Kalgan River, Royce 3728, 8.1951 (PERTH); King George's Sound, 10.1867; King George's Sound, Franklyn 82, 1884 (MEL); Near Albany, L. Preiss 1404, 10.1840 (Type of *C. occulta* Endl.); Between Balanggajalup and Cape Riche, L. Preiss 1396, 11.1840 (Type of *C. longifolia* Endl.); Between Mt. Manypeak and Cape Riche, L. Preiss 1402, 11.1840 (Type of *C. ensifolia* Endl.); Drummond 349 (LD, MEL); Drummond 758 (CGE, MEL); Drummond (MEL).

The somewhat variable nature of this species led to the erection by Endlicher in 1846 of several species which fail to stand in the light of subsequent investigation. Bentham's species *C. laxiflora* appears to be connected by a series of intermediates to typical *C. serrulata*.

Here is a species difficult to define on technical characters but which is unmistakeable once seen. Its distinctive appearance seems to depend chiefly on the slightly glaucous, striated, minutely serrulate leaves, and the perianth which is divided almost to the ovary.

4. Conostylis misera Endl. in Lehm., *Pl. Preiss.*, 2: 22 (1846); *C. gladiata* Benth., *Fl. Aust.*, 6: 434–5 (1873).

Haptotypes.—In solo arenoso inter frutices sylvae ad radices montis "Bokkenbop" v Barker, Plantagenet, L. Preiss 1406, 9.xi.1840 (LD, MEL).

Caespitose, with short stems; leaves glabrous, 5–10 cm. long, 2–5 mm. broad, often falcate, striate but not prominently so, the margins thin, quite entire or with a few very small distant setae, usually drying dark green or brown, not glaucous; flower usually solitary, on a short peduncle, the short scape bearing 2–3 acuminate brown bracts, the flower partly hidden in the sheathing leaf bases; perianth 1·5 cm. long, the indumentum smooth, of short branched hairs with longer hairs intermixed; lobes equal, about 8 mm. long, greatly exceeding the free part of the tube; filaments short, all equal, anthers long; placentas covered with numerous ovules. Chromosome number unknown. (Plate x, figs 4–5; Fig. 75.)

Specimens examined. Drummond (MEL); Drummond 761 (CGE).

Bentham (1873) referred the type of this species to *C. serrulata* R.Br. with the comment: "*C. misera* is a starved specimen with short leaves and only one or two flowers in the head, such as we have also from Drummond." Since haptotype specimens of *C. misera*, examined by the writer, agreed perfectly with Bentham's description of his own species *C. gladiata*, it seemed possible that the two were identical, but this was thought unlikely because *C. gladiata* was described in the same work as that in which Bentham had referred *C. misera* to *C. serrulata*. Although unable to examine the type of *C. gladiata* personally, the writer has examined a photograph of it and has forwarded photographs of Preiss 1406 and of the Drummond specimen cited above to Kew for comparison with the type. The results of these investigations have convinced the writer that *C. misera* and *C. gladiata* are conspecific, and the latter has therefore been reduced to synonymy.

5. Conostylis filifolia F. Muell., *Fragm.*, 8: 18 (1872); *C. festucacea* Endl. in Lehm., *Pl. Preiss.*, 2: 18 (1846).

Holotype.—J. Drummond (MEL). The holotype sheet comprises two separate pieces together with several flowers in a packet. *Type* also in K.

Straggling tufts up to 30 cm. diameter at the base, the stems loosely proliferous; leaves glabrous, filiform, often exceeding 35 cm. in length and 1–2 mm. in diameter; scapes much shorter than the leaves, bearing 1–2 ± median brown bracts; inflorescence loosely capitate; perianth yellow, about 12 mm. long, tomentose with branched hairs outside, glabrous inside, the lobes equal, about 5–6 mm. long; anthers linear, attached to the shorter filaments by a dorsal connective in the lower third, style ± equal to the stamens; placentas covered with numerous ovules; fruits and seeds not seen. Chromosome number n = 8. (Figs 10–11, 76.)

Specimens examined. About 5 miles W. of Dandaragan, Royce 5656, 10.1956; 5 miles W. of Moora, Brittan 52/26, 9.1952 (PERTH); Near Southern River, Preiss 1386, 9.1841 (LD, MEL); Cannington, Helms, 10.1898 (NSW 37828); Cannington, Helms, 11.1898 (NSW 37794); Canning Plains, ex herb. Fitzgerald, 10.1903 (NSW 37716); Cannington, Andrews, 9.1904 (NSW 37717, PERTH); Cannington, Morrison 20086, 10.1910 (NSW 37715); Cannington, Speck, 9.1948 & 10.1949 (PERTH); Kelmscott, Helms, 11.1898 (NSW 37734); South-west, Eames & Armstrong, 1937 (PERTH); Drummond (MEL); Hamilton (NSW 37811).

6. CONOSTYLIS ACULEATA R.Br., *Prod. Fl. Nov. Holl.*, 1: 300 (1810).

Holotype.—(Photo only seen), King George's Sound, R. Brown 5625, 1801 (BM). Four separate pieces on holotype sheet. (Plate ix, 1.) *Isotype* in K, MEL.

Stems short and tufted or rhizomatous or proliferously branched, with the leaves arising in distichous fascicles; leaves 10–45 cm. long and 1–6 mm. broad, the laminae glabrous and striate, the margins ± prominent with spines projecting at intervals along the whole leaf or sometimes near the apex only, rarely entire; inflorescence a loose or compact cyme or panicle or capitate, borne on a simple or branched scape shorter than or ± equal to the leaves; flowers usually 8–10 mm. long, the perianth yellow, branched-tomentose outside, glabrous or slightly hairy within, the lobes equal, 5–6 mm. long and usually exceeding the free part of the tube; filaments 1–1·5 mm. long, shorter than the anthers which may be 3–5 mm. long, attached in the lower third by a long adnate dorsal connective; style slender or slightly dilated near the base, equal to or slightly exceeded by the anthers; placenta covered all over with numerous ovules; perianth scarcely enlarging in fruit; seeds, where seen, oblong-ellipsoidal, about 1 mm. long and ± rugose. Chromosome number n = 8 in all subspecies examined. (Fig. 77.)

The complex of forms related to *C. aculeata* has proved a major stumbling block in the study of the taxonomy of the genus. The former species *C. bracteata* Lindl., *C. bromelioides* Endl., *C. preissii* Endl. and *C. robusta* Diels, although often recognizable morphologically, present many problems of identification when extreme forms are encountered. However, they occupy more or less isolated geographical ranges (Fig. 12) and it is proposed to reduce them to subspecific rank. Where the ranges meet or overlap, no cases have been recorded of two or more subspecies growing together, and it is probable that ecological isolation then operates. An undescribed form from the Geraldton area appears to have a similar status and is described below as a new subspecies of *C. aculeata*.

The inclusion of six subspecies under *C. aculeata* has meant enlarging slightly the specific limits of that species. *C. aculeata* now includes all forms whose floral structure agrees with *C. aculeata* R.Br. sens. strict. and whose leaves are flat and glabrous except for the usually stiff erect or divaricate spines or setae, borne on the rather prominent marginal nerve. In one subspecies the spines are restricted to the upper part of the leaves.

C. filifolia F. Muell., although closely related, seems distinct in having terete leaves, and no intermediates have been seen. The *C. aculeata* complex is closely related to *C. stylidioides* F. Muell. (through *C. aculeata* ssp. *rhipidion*, ssp. nov.) and to *C. candicans* Endl. (through *C. aculeata* ssp. *bracteata* (Lindl.), comb. et stat. nov.).

A key to the subspecies follows the subspecific descriptions.

6*a*. CONOSTYLIS ACULEATA R.Br. ssp. ACULEATA; *C. cymosa* F. Muell. ex Benth., *Fl. Aust.*, 6: 439 (1873).

Stems usually short, sometimes shortly proliferous; leaves 15–30 cm. long and 2–5 mm. broad, bearing rigid spines along the whole length of the margins, otherwise glabrous, striate on the laminae; spines of the leaf usually 2–3 mm. long, ± erect and making an angle of 10–35° with the margin which is usually slightly more prominent than the laminal striae; inflorescence a loose raceme, the scape branched, or a loose cyme, shorter than the leaves. Chromosome number n = 8. (Plate ix, fig. 1; Figs 13–15.)

Specimens examined. Middleton Beach, Andrews, 12.1902 (PERTH); Near Perth, Menzel, 10.1898 (NSW 37807); Swan River, 11.1877 (MEL); Wooroloo, Koch 1471 (BRI 003183); Between York and Perth, Mueller, 1877; Beverley, Tepper 29, 9.1892 (MEL); Jarrahdale, Andrews, 10.1905; Arthur River, Pearce, 9-10.1956; Harvey, Royce 3106, 9.1949; Mornington Bush Camp, Williams, 10.1932 (PERTH); Beenup, SW. Railway, Morrison, 11.1907 (NSW 37724); 2 miles S. of Tambellup, J. W. Green 1732, 10.1957 (PERTH); Collie, Hotchkiss & Eames, 9.1953 (NSW 37723); Yoongarillup, Busselton district, Royce 2416, 10.1947; 3159, 10.1949; 4539, 4540, 9.1953; Capel, Royce 2672, 9.1948; Elgin, Royce 3114, 9.1949; Noggerup, Quinlivan, early 10.1956 (PERTH); Banks of the Blackwood River, Oldfield 589c; Blackwood River, Wale...., 1868?; Blackwood River, Hester, 1871?; Sources of Blackwood River, Cronin, 1889 (MEL); Karridale, Lea, 10.1898; Karridale, Gardner, 11.1933; Darradup, W. of Nannup,

Royce 2992, 10.1948; Skippy Rock, Churchill, 12.1957 (PERTH); Balingup, Pulleine, 12.1917 (NSW 37825); Bridgetown, Quinlivan, 10.1956; Manjimup, Koch 2488, 11.1920; Manjimup, Royce 2721, 9.1948; Manjimup, Quinlivan, 10.1956 (PERTH); Pemberton, Koch 2377, 10.1919 (NSW 37735); Chowerup, Quinlivan, 9.1956; 10 miles W. of Mt. Barker, J. W. Green 1139, 3.1957 (PERTH); Mt. Barker, Fitzgerald, 11.1907 (NSW 37714); Deep River, Jackson, 12.1912 (NSW 37806); Boggy Lake, J. W. Green 873, 884, 922, 1023, 1083, 12.1956; Cranbrook, Quinlivan, 9.1956; 3 miles SW. of Tanterden, J. W. Green 1147, 3.1957 (PERTH); Base of Stirling Range, Mueller, 10.1867 (MEL); Porongorups, Burbidge (PERTH); Upper Kalgan River, Oldfield 589; Between Swan River and King George's Sound, Forrest, 1881; King George's Sound, Muir; King George's Sound, Webb, 12.1882 (MEL); King George's Sound, Vol....burgh, 1882 (BRI 003184); Albany, Helms, 11.1896 (PERTH); Albany, Menzel & Goadby 357, 10.1898 (NSW 37731); King George's Sound, Maiden, 9.1909 (NSW 37737); Lower Kalgan, Albany, Poole, 11.1943 (PERTH); Irwin's Inlet, Jackson, 11.1912 (NSW 37805); Lake Muir, Muir; Murchison River (?), Oldfield; Drummond (MEL); L. Preiss 1395 (LD, MEL).

6*b*. Conostylis aculeata R.Br. ssp. bromelioides, stat. nov.; *C. bromelioides* Endl. in Lehm., *Pl. Preiss.*, 2: 18 (1846); *C. aculeata* var. *bromelioides* (Endl.) A. J. Ewart in *Proc. Roy. Soc. Vict.*, 19: 37 (1906); *C. aculeata* var. *bromelioides* (Endl.) Domin in *J. Linn. Soc.*—Bot., 41: 256 (1912).

Haptotypes.—In solo sublimoso prope Avondale, York, L. Preiss 1401, 10.iv.1840 (LD, MEL).

Differs from ssp. *aculeata* chiefly in the leaves, whose very prominent fibrous margins possess rigid spines which are divaricate and sometimes even deflexed; leaves generally stouter and usually shorter; inflorescence loosely racemose or cymose, shorter than the leaves. Chromosome number n = 8. (Fig. 16.)

Specimens examined. Watheroo, Koch 1320, 10.1905 (NSW 37722); Moora, Maiden, 10.1909 (NSW 37730); Jibberding, Koch 1320, 10.1905 (MEL); Cowcowing, Koch 1253, 10.1904 (MEL, NSW37719, PERTH); Mogumber, ex herb. Fitzgerald, 10.1903 (NSW 37721); Mogumber, Helms, 10.1902 (PERTH); Avon district, Pritzel, 10.1901 (NSW 37720); York, Heal, 10.1889; E. Sources of Swan River, Eaton, 1889 (MEL); Tammin and Watheroo; Tammin, Pritzel 828, 10.1901; Near Narembeen, Blackall, 9.1929; Armadale, Helms, 8.1896 (PERTH); Near Mt. Churchman, Young (MEL).

6*c*. Conostylis aculeata ssp. robusta (Diels), comb. et stat. nov.; *C. robusta* Diels in Engl., *Bot. Jahrb.*, 35: 109–11 (1904).

Holotype.—(Not found), Champion Bay, in muddy slopes near the Chapman River, Diels 4152. Probably destroyed in 1943. *Neotype.*—Irwin River, West of Mingenew, C. A. Gardner 7725, 9.x.1945 (PERTH).

A large robust perennial, similar to ssp. *aculeata* in general appearance, but larger and coarser in most of its parts; leaves 25–40 cm. long and 6 mm. broad, often ± glaucous, the flowers borne in a large terminal head on a scape usually much longer than the leaves; branching may be shortly proliferous. Chromosome number n = 8.

Specimens examined. Murchison River, Oldfield (MEL); Murchison River, Speck, 9.1949; Junga Tank, Speck 966, 9.1953; Ogilvie, Gardner 8575, 9.1947; Eradu, Gardner 2642, 9.1931; 2 miles W. of Wicherina, J. W. Green E.160-1, 8.1956; Mullewa Plains, Gardner & Blackall, 9.1931; Irwin River W. of Mingenew, Gardner 7725, 10.1945 (PERTH); Hamilton 750, 1902 (NSW 37827).

6*d*. Conostylis aculeata ssp. rhipidion, ssp. nov.

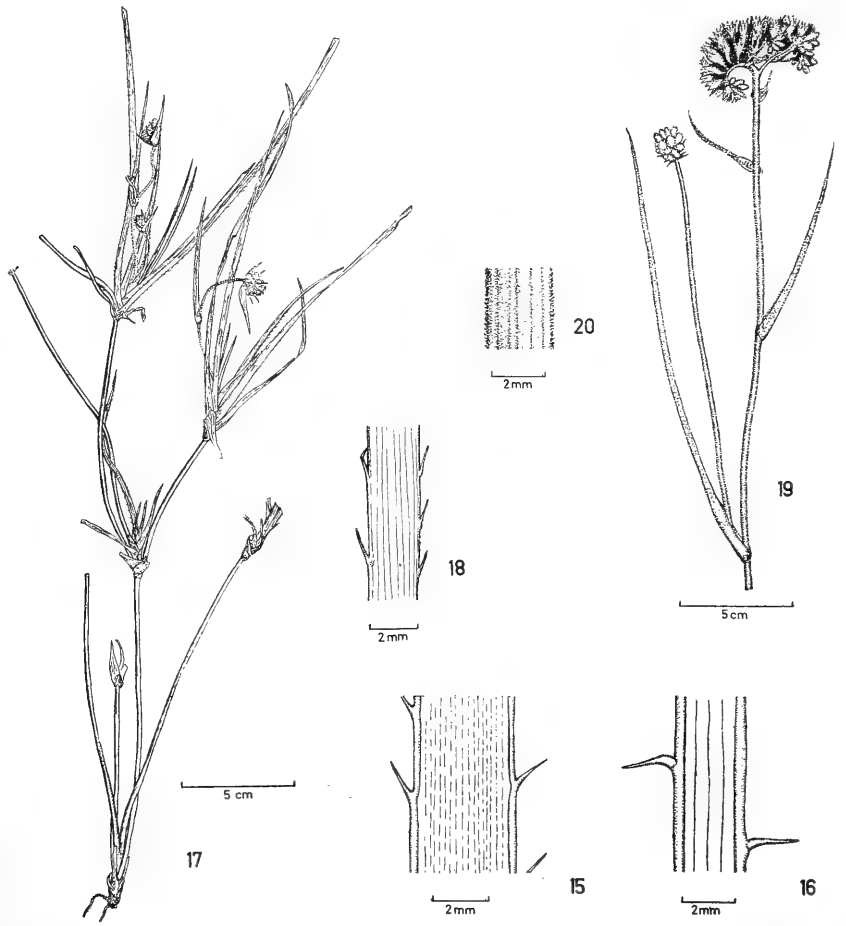
Holotype.—8 miles north of Geraldton, J. W. Green 427, 11.viii. 1956 (PERTH).

Sclerophyllosa, fruticosa, perennis, usque ad 60 cm. alta lataque; folia duriter spinosa et erecta, distichosa, in valde planata velut flabellos fasciculos in ramis proliferosis disposita plerumque 5–15 cm. longa et 2–3 mm. lata; inflorescentia capitata, bracteis 1–2 foliaceis aut fuscis ferme 2 cm. longis subtenta; scapo ferme longitudine foliis aequo aut longiore, plerumque 1–2 media foliacea bractea ferente; flores aliquantulo quam ssp. *aculeata* breviores.

Sclerophyllous shrubby perennial up to 60 cm. high and broad; leaves harshly spiny and erect, distichous, in markedly flattened fan-like fascicles on the proliferous branches, usually 5–15 cm. long and 2–3 mm. broad; inflorescence capitate, subtended by 1–2 leafy or brown bracts about 2 cm. long, the scape about the same length as the

leaves or longer, usually bearing 1–2 median leafy bracts; flowers somewhat smaller than in ssp. *aculeata*. Chromosome number n = 8. (Figs. 17, 18.)

Specimens examined. Cockleshell Gully within 2 miles of homestead, Blackall 3572, 8.1938, Cockleshell Gully-Mt. Lesueur, Plains near Cockleshell Gully, Blackall 3603, 8.1938; Hill River, Speck, 9.1952; Northampton District, Grieve, 8.1947 (PERTH); Between Geraldton and Northampton, Jessep, 9.1947 (MEL); 14 miles N. of Geraldton, Burbidge 2061, 9.1947; 12 miles N. of Geraldton, J. W. Green 434, 8.1956; 8 miles N. of Geraldton, Marchant 13, 8.1956; 8 miles N. of Geraldton, J. W. Green 427, 8.1956; White Peak, Gardner & Blackall 2053, 9.1926; Near White Peak, Gardner 2053, 9.1926; N. of Geraldton, Speck 406, 9.1953; 17 miles E. of Geraldton, J. W. Green 473, 8.1956 (PERTH).



Figs 15-20.—15, *C. aculeata* R.Br. ssp. *aculeata*, leaf surface (from J. H. Maiden, 1909); 16, ssp. *bromelioides*, leaf surface; 17, ssp. *rhipidion*, habit; 18, leaf surface (both from J. W. Green 427); 19, *C. candicans* Endl., scape and inflorescence; 20, leaf surface.

6*e*. CONOSTYLIS ACULEATA ssp. PREISSII (Endl.), comb. et stat. nov.; *C. preissii* Endl. in Lehm., *Pl. Preiss.*, 2: 18 (1846).

Haptotypes.—In asperis jugi Darling's-range districtus Perth, L. Preiss 1384, ix.1841 (LD, MEL).

Differs from ssp. *aculeata* chiefly in the more compact inflorescence and in the more marked proliferous branching; leaves 15–25 cm. in length, rarely exceeding 3 mm. in width, the marginal spines usually less rigid than in the other subspecies; scape usually slightly shorter than the leaves and bearing 1–2 bracts; inflorescence densely racemose appearing as a somewhat loose head. Chromosome number n = 8.

Specimens examined. Upper Swan River, Sewell, 1885 (MEL); Near Perth, Fitzgerald, 11.1902; Guildford, Andrews, 9.1902; Cannington, Speck, 9.1948; Lesmurdie, J. W. Green 1714, 9.1957 (PERTH); Kelmscott, Helms, 9.1898 (NSW 37734); Armadale, Stoward, 10.1911 (NSW 37728); Armadale, Gardner, 754A, 9.1920; Armadale, Storr, 9.1956; Mundijong, Andrews, 9.1903; Jarrahdale, Andrews, 10.1905; Harvey, Royce 3106, 9.1949 (PERTH); Bunbury, Oldfield (MEL); 6 miles S. of Bunbury, Burbidge, 9.1956; Busselton, Royce 3165, 10.1949 (PERTH); Cape Leschenault, Oldfield; Cape Naturaliste, Oldfield (MEL); Cape Naturaliste, Wilbur...., 1904 (NSW 37826); Yallingup, Maiden, 10.1909 (NSW 37729, 37774); Margaret River, Maiden, 10.1909 (NSW 37796); Blackwood River, McHard, 1874 (MEL); Karridale, Helms, 12.1898 (NSW 37782); Karridale, Gardner, 11.1933 (PERTH); Drummond, 1st coll. 753; Nornalup, Oldfield 588; King George's Sound, Mueller, 10.1867 (MEL).

6*f*. Conostylis aculeata ssp. bracteata (Lindl.), comb. et stat. nov.; *C. bracteata* Lindl., *App. Bot. Reg.*, 45 (1840); *C. harperiana* W. V. Fitzgerald in Proc. Linn. Soc. N.S.W., 28: 106 (1904).

Syntypes.—Swan River, J. Drummond, 1839; Swan River, Toward (CGE). Three pieces on syntype sheet.

Caespitose, the stems sometimes shortly proliferous; leaves usually 30–40 cm. long and 4–6 mm. broad, the laminae striate, with ± prominent fibrous margins, glabrous except for a few short rigid spines toward the apex, occasionally extending to the lower half or occasionally the leaves without spines; scape about the same length as the leaves, simple (or with a smaller scape and inflorescence arising from the upper scapose bract) bearing a dense globular head of numerous flowers. Chromosome number n = 8.

Specimens examined. Maylands, Andrews, 9.1903 (PERTH); Bayswater, Morrison, 9.1900 (NSW 37713); Bayswater, Andrews, 11.1902; Mt. Lawley, Gardner, 8.1936 (PERTH); Leederville, Helms, 8.1897 (NSW 37798, PERTH); Swan River, Drummond 751 (CGE, MEL); Lower Swan River, Helms, 1897 (PERTH); Perth, Deane, 11.1908 (NSW 37791); Observatory Grounds, Perth, J. W. Green 377, 10.1955 (PERTH); Claremont, ex herb. W. V. Fitzgerald, 8.1900 (NSW 37808); Near Claremont, Fitzgerald, 10.1901; Blackwall Reach, Andrews, 9.1904 (PERTH); Prope lacum "Kei-er-mu-lu" (Perth), Preiss 1405, 8.1839 (LD, MEL).

This subspecies forms a link between *C. aculeata* and *C. candicans*, on the basis of floral morphology, habit, and the presence of intermediate forms in the field. In some areas (e.g., in Kings Park, Perth) *C. aculeata* ssp. *bracteata* and *C. candicans* occur sympatrically. *Conostylis bracteata* Lindl. was re-described by Endlicher in 1846, who cited Lindley's earlier description (n. 204). Bentham (1873) saw that the types of *C. bracteata* Lindl. and *C. dealbata* Lindl. were very similar, and reduced the former to synonymy. At the same time he maintained "*C. bracteata* Endl." as a distinct species: this name is illegitimate since Endlicher cited Lindley's name. The writer is of the opinion that "*C. bracteata* Endl." represents the same population as *C. bracteata* Lindl., even though the types do not match exactly. Even if the population referred to by Bentham were considered taxonomically distinct, the later homonym would have to be discarded as invalid, and a new name chosen. While the close resemblance between *C. bracteata* Lindl. and *C. dealbata* is acknowledged, the latter is here reduced to synonymy with *C. candicans* on the basis of leaf indumentum. At one end of its range *C. bracteata* Lindl. is almost indistinguishable from *C. preissii* Endl., but the leaves of the latter tend to be narrower (less than 2 mm. broad). Both are retained here as subspecies of *C. aculeata.*

Conostylis harperiana W. V. Fitzg. is based on what appears to be an aberrant form of *C. aculeata* ssp. *bracteata*, having a hooked style, but otherwise indistinguishable from it. The rather precise locality (near the margin of a lagoon, 6–7 miles NE. of Bayswater) has been visited and searched thoroughly without revealing a trace of such a form, although *C. aculeata* ssp. *bracteata* is common in the area.

Key to the subspecies of C. aculeata *R.Br.*

1. Leaves bearing spines or setae along the whole length of the margins.
2. Marginal nerves strongly fibrous, much more prominent than those on the lamina; spines often deflexed ..... *b. bromelioides.*
2.* Margins of leaves not markedly prominent.
3. Leaves 6 mm. broad and 25-40 cm. long; flowers in large terminal heads on scapes usually exceeding the leaves ..... *c. robusta.*

3.* Leaves rarely exceeding 5 mm. broad and mostly 10-30 cm. long; scapes ± equal to the leaves or shorter.
4. Inflorescence very loose, much shorter than the leaves ..... *a. aculeata.*
4.* Inflorescence ± capitate.
5. Leaves in markedly flattened distichous fascicles on the proliferous branches; leaves and spines harshly pungent ..... *d. rhipidion.*
5.* Leaf fascicles not flattened, ± flaccid, spines not hard and pungent.
6. Leaves rarely exceeding 2 mm. in breadth ..... *e. preissii.*
6.* Leaves usually exceeding 2 mm. in breadth ..... *f. bracteata.*
1.* Marginal setae confined to the upper part of the mature leaf or the margin entirely glabrous ..... *f. bracteata.*

7. Conostylis candicans Endl., *Nov. Stirp.*, Dec. 3: 20 (1839); *C. dealbata* Lindl., *App. Bot. Reg.*, 45 (1840); *C. propinqua* Endl. in Lehm., *Pl. Preiss.*, 2: 17 (1846).

Holotype.—(Not found), South-western Australia, Huegel. Probably destroyed in 1943. *Neotype.*—Attadale, Perth, J. W. Green 519, 9.ix.1956 (PERTH).

Usually caespitose, the tufts up to 40–50 cm. diameter and 50 cm. high, sometimes the plants slender and rising by proliferous branching; leaves 15–40 cm. long and 3–6 mm. broad, entirely covered at maturity by a pale grey mealy tomentum or becoming ± glabrous in old age by abrasion; inflorescence often appearing a dense globular head, but the rhachis bifid and visibly so when the head is somewhat looser; bracts subtending the inflorescence often long and leaf-like, the scape bearing often two further leaf-like bracts, one ± median and the other above, the latter sometimes subtending a miniature scape and small inflorescence; perianth yellow, about 12 mm. long, tomentose outside and sparingly hairy inside, the lobes about 5 mm. long, filaments shorter than the linear anthers and attached by a dorsal connective in the lower third; style ± equal to the stamens; placentas covered with numerous ovules; perianth enlarging somewhat in the fruit; seeds about 1·5 mm. long, ellipsoidal and rugose. Chromosome number n = 8. (Figs 19–20, 78.)

Specimens examined. S. of Lharidon Bay, J. W. Green 1434, 7.1957; S. of Hamelin, Speck 887, 9.1953; Caves, Lake Logue, Speck, 9.1953 (PERTH); Champion's Bay, Guérin, 1871; Geraldton, Spalding, 1889; Upper Irwin, Guérin (MEL); Coorow, Helms, 10.1898 (NSW 37795 part); 4 miles N. of Bolgart, J. W. Green 544, 11.1936; Bolgart, Erickson, 9.1938; Watheroo, Quinlivan, 9.1956; Meenaar, J. W. Green 851, 11.1956; Greenmount, Kneip 27, 11.1940 (PERTH); Kalamunda, Stoward, 12.1911 (NSW 37766); Gooseberry Hill, J. W. Green 1719, 9.1957 (PERTH); Darling Range near Perth, Cleland, 190? (NSW 37763); Melville Park, Helms, 7.1897 (NSW 37801); Guildford, Andrews, 9.1902; Floreat Park, Storr, 8.1954; Cannington, Speck; Attadale, J. W. Green 519, 9.1956 (PERTH); The Chine, Helms, 9.1899 (NSW 37802 & 37829); Perth, Maiden, 9.1909 (NSW 37769); Perth, Maiden, 11.1909 (NSW 37823); Kings Park, Mauritzon, 8.1936 (LD); Kings Park, Vincent, 8.1934 (PERTH); Claremont, Morrison, 11.1908 (NSW 37761); Ad fl. Cygnorum, Preiss 1399, 12.1838 (LD, MEL); City Beach, 7½ miles W. of Perth, Willis, 9.1947 (MEL); Cottesloe, Helms, 9.1898 (NSW 37795 part); Cottesloe, Helms, 10.1899 (NSW 37768); Cottesloe, Lucas, 8.1928 (NSW 37762); Cottesloe, Solomon, 8.1932 (PERTH); N. Fremantle-Cottesloe Beach, Hiern, 9.1914; Near Fremantle, Preiss (CGE); Fremantle, Oldfield (MEL); District Swan, Pritzel, 8.1901 (NSW 37771); Near "Pointwater" (Perth), Preiss 1398, 7.1839 (LD, MEL); Swan River, J. Drummond, 1839 (Type of *C. dealbata* Lindl.) (CGE); Swan River, Drummond 752 (OXF); Swan River, Mylne (MEL); Karrakatta, Stoward, 7.1911 (NSW 37765); Nedlands, White 5181, 10.1927 (BRI 003180); Rottnest Island, L. Preiss 1400, 8.1839 (Type of *C. propinqua* Endl.) (LD, MEL); Rottnest Island, Walcott, 1881 (MEL); Rottnest Island, Fitzgerald, 11.1902 (NSW 37772); Rottnest Island, Baird, 8.1955; Rottnest Island, J. W. Green 497, 500, 501, 503, 8.1956 (PERTH); Rottnest Island, 1822 (CGE); Garden Island, Smith, 11.1948; Bibra Lake, 11.1917; Peron, McArthur, 9.1951 (PERTH); Armadale, Stoward, 10.1911 (NSW 37767); Princess Royal Harbour, Preiss 1403, 12.1840 (LD); 1 mile N. of Snake Spring near the Scott River, Churchill, 2.1957 (PERTH); Preiss 1399 (MEL); Coolgardie (?), Webster, 1900 (NSW 37764); Williamson, 8.1903; Drummond (MEL).

The greyish-white tomentum of the leaves of this species gives it an appearance quite unlike that of any other in the genus. Nevertheless, *C. candicans* shows strong affinities with *C. aculeata* (through *C. aculeata* ssp. *bracteata*) and with *C. stylidioides*. Floral structure is remarkably similar in this whole group of species, and intermediate forms have been found in the field. Bentham's *C. candicans* var. *leptophylla* is thought to represent a hybrid between *C. candicans* and *C. stylidioides* (e.g., where their ranges come together in the Greenough-Geraldton area), and *C. dealbata* may represent a

hybrid between *C. candicans* and *C. aculeata* ssp. *bracteata*. Bentham regarded *C. dealbata* as "very nearly allied to *C. candicans* and perhaps a variety connecting it with *C. Preissii* and *C. bracteata* Endl." (see discussion under *C. aculeata* ssp. *bracteata*). It is possible too that the little-collected *C. dealbata* may represent *C. candicans* in a senescent state in which most of the tomentum has been lost by abrasion or weathering: some of the leaves on the holotype of *C. dealbata* are indistinguishable from those of *C. candicans*.

Conostylis candicans is represented in the collection from Shark's Bay made by Dampier in 1699, one of the earliest records of an Australian plant in existence (Osborn and Gardner, 1939). This is also the most northerly record for the species; it has been recorded from Lharidon Bay (Shark's Bay area) by the writer and from south of Hamelin by N. H. Speck.

Seeds of this species have been germinated successfully by the writer and the seedlings are now about six months old. It is one of the few species in which viable seeds seem to be produced in any quantity.

8. Conostylis stylidioides F. Muell., *Fragm.*, 8: 17 (1872); *C. prolifera* Benth., *Fl. Aust.*, 6: 436 (1873); *C. racemosa* Benth., *ibid.* (1873).

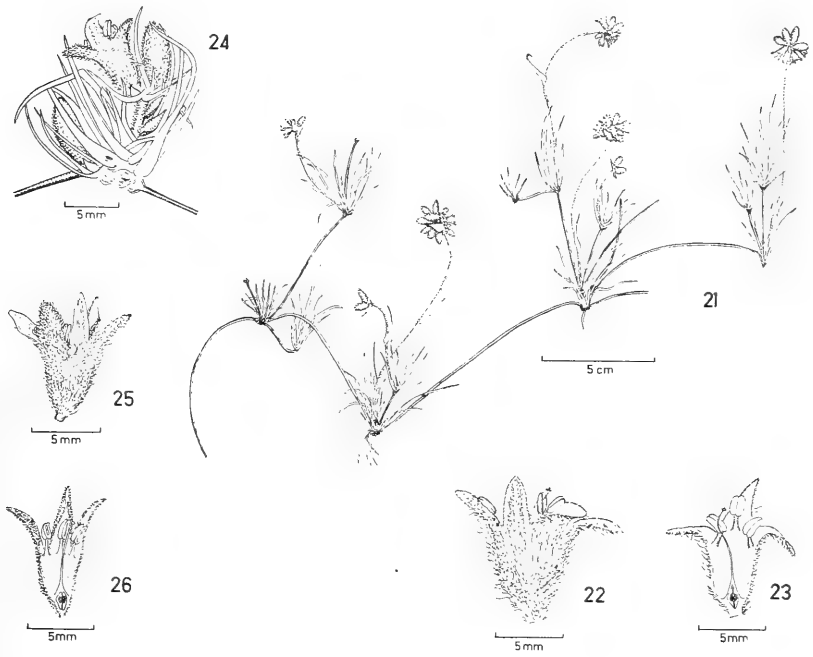
Lectotype.—In vicinia fluminis Murchisoni, August, A. F. Oldfield (MEL). Two separate pieces on the type sheet (top left and bottom right) are chosen as lectotype. *Isotype* in K (not seen) is inscribed: "Near Dolingara, Murchison River."

Small plants growing in discrete tufts 3–4 cm. high, or the tufts connected by a network of stolons, or rising to some height by proliferous branching; leaves flaccid, 1–10 cm. long and 1–2 mm. broad, green or ± hirsute, sometimes bearing minute erect setae on the margins; inflorescence loosely capitate on a simple scape as long as the leaves or much longer, the scape bearing usually a small ± leafy median bract in addition to the short inconspicuous bracts subtending the inflorescence; perianth campanulate, 10–12 mm. long with a tomentum of branched hairs outside, glabrous inside, the lobes about 5 mm. long; filaments very short bearing oblong anthers attached by a dorsal connective in the lower third; placentas covered with numerous ovules; fruits and seeds not seen. Chromosome number n = 8. (Figs 21–26, 79).

Specimens examined. Murchison River, A. F. Oldfield (Syntype of *C. prolifera* Benth.) (MEL); 30 miles N. of Ajana, Gardner & Blackall 590, 9.1931; 3 miles N. of Ogilvie, J. W. Green 453, 8.1956; 9 miles N. of Northampton, J.W. Green 447, 8.1956 (PERTH); Near Port Gregory, 10.1877 (MEL); 6 miles W. of Northampton, Gardner & Blackall, 9.1926; Northampton, Helms, 10.1898 (PERTH); Northampton, Spalding 1883 (MEL); 4 miles SE. of Northampton, J. W. Green 462, 8.1956; 3 miles SW. of Nanson, J. W. Green 469, 8.1956 (PERTH); Between Geraldton and Northampton, Blake 18096, 9.1947 (BRI 003178); Between Geraldton and Northampton, Jessep, 9.1947 (MEL); Base of Mt. Sewell near Oakabella, J. W. Green 444, 8.1956; Oakabella, C. Andrews, 9.1904 (NSW 37757, PERTH); 13 miles N. of Geraldton, J. W. Green 441, 8.1956; 12 miles N. of Geraldton, J. W. Green 431, 8.1956; 10 miles N. of Geraldton, J. W. Green 428, 8.1956; 10 miles NE. of Geraldton, J. W. Green 472, 8.1956 (PERTH); White Peak, Champion Bay, A. F. Oldfield (Type of *C. racemosa* Benth.); Champion Bay, Gray 71 (MEL); Chapman Plains, Morrison, 10.1903; Near Mt. Julia, 21 miles E. of Geraldton, J. W. Green 483, 485, 8.1956 (PERTH); Greenough's and Irwin's Rivers, 11.1877 (MEL); Inter flumina Moore et Murchison, Pritzel, 9.1901 (NSW 37755); Mullewa Plains, Gardner & Blackall 711, 9.1931 (PERTH); Mingenew, Fitzgerald, 9.1903 (NSW 37752); Yandanooka, Baird, 8.1929 (PERTH); Carnamah, Morrison, 11.1906 (NSW 37748); 6 miles E. of Ballidu, Royce 2110, 9.1947 (PERTH); Cowcowing, Koch 1240 (MEL, NSW, 37751, PERTH); Wongan Hills, Gardner, 9.1924 (PERTH); Tammin, Maiden, 9.1909 (NSW 37750); Near Mt. Caroline, Sewell, 1889 (MEL); 5-6 miles S. of New Norcia, Gardner 8678, 10.1947 (PERTH); Toodyay, Stoward, 8.1911 (NSW 37753); District Avon, Pritzel, 8.1901 (NSW 37754); Meenear, Gardner 7601, 9.1945; Northam, Gregory, 1901 (PERTH); Northam-Perth Highway 4-6 miles from Northam, Salasoo 108, 9.1949 (NSW 37749); Beverley, 9.1918 (PERTH); Swan River, J. Drummond 76 (?760) (OXF); J. Drummond 760 (Syntype of *C. prolifera* Benth.) (MEL).

Field studies, especially in the Geraldton area, have shown that Bentham's distinctions between *C. stylidioides*, *C. prolifera* and *C. racemosa* are quite unworkable; in one case, different parts of a single specimen fell into each of the three species. Apart from this extreme case, the distinctions break down as a result of a large

number of specimens which do not fit well any of the species. There seems no alternative but to reduce Bentham's two species to synonymy with *C. stylidioides* and to enlarge slightly the circumscription of that species. Bentham's *C. candicans* var. *leptophylla* is undoubtedly closely related to *C. stylidioides* (see discussion under *C. candicans*). In addition a single- or very few-flowered form (represented by only two collections, East of York, A. Eaton, 1889 (MEL) and Cunderlin, ex herb. W. V. Fitzgerald, viii.1903 (NSW 37775, PERTH)) has come to light and seems to be an extreme form of *C. stylidioides* (see Figs 24–26).



Figs 21-26.—21, *C. stylidioides* F. Muell., habit; 22, flower; 23, half flower (all from J. W. Green 431); 24, habit; 25, flower; 26, half flower (all from East of York, A. Eaton).

9. Conostylis seorsiflora F. Muell., *Fragm.*, 1: 158 (1859).

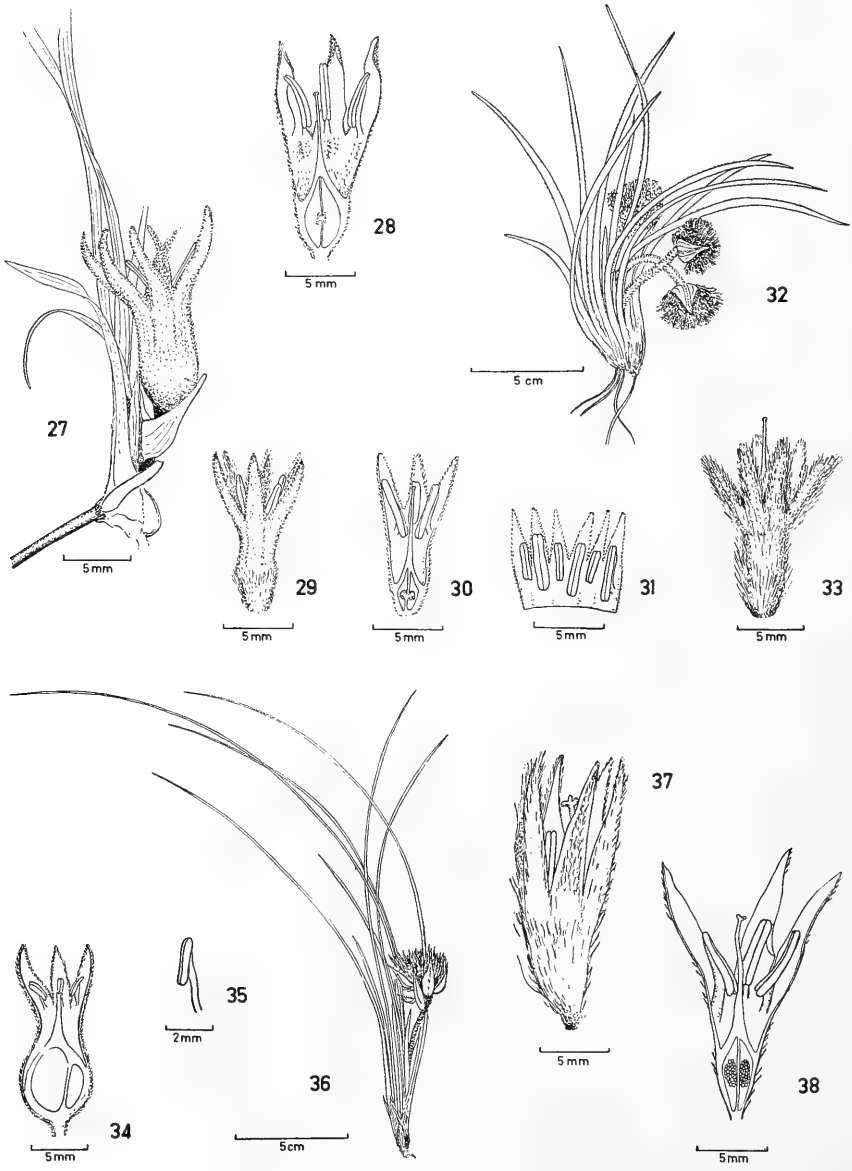
Holotype.—Ad ripas fluvii Gardner River, G. Maxwell 69 (MEL). Holotype sheet comprises one piece together with several flowers in a packet.

Prostrate mats 3–4 cm. in diameter, connected together by stoloniferous branches to form a network up to 40 cm. across; leaves 3–8 cm. long and up to 1 mm. diameter, ± tomentose but often the mature leaves glabrous; inflorescence mostly single-flowered on short scapes which bear usually a median leafy bract about 15 mm. long with two linear bracts subtending the flower; perianth bright yellow (becoming greenish in the fruit), about 13 mm. long, shortly tomentose outside with branched hairs, loosely hairy inside, the lobes about 7 mm. long; filaments short, bearing linear anthers on a dorsal connective in the lower third; style ± equal to the stamens; placentas covered with numerous ovules; perianth enlarging in the fruit; seeds not seen. Chromosome number n = 8. (Plate x, fig. 7; Figs 27–28, 80.)

Specimens examined. 2 miles S. of Tambellup, J. W. Green 1731, 10.1957 (PERTH); W. end of Stirling Range, Mueller; N. of Stirling Range, Mueller, 10.1867; Banks of the Gairdner River, Maxwell 69 (MEL); Near Jacup, Andrews, 10.1903 (PERTH); Near Oldfield River, Mueller (MEL); 18 miles W. of Young River Station, J. W. Green 1234, 3.1957; 12 miles N. of Esperance, Blackall 1062, 10.1931 (PERTH); Near Cape Arid, Maxwell, 1875 (MEL).

A species of interest because of its single- or very few-flowered inflorescence. It may be related to *C. misera* Endl., but the writer is of the opinion that the few-flowered

condition in these species has been brought about by convergence, and that *C. seorsiflora* is probably more closely related to *C. stylidioides* F. Muell. which it resembles in flower structure and habit. The chromosome number of the two latter species is n = 8; that of *C. misera* is unknown, but that of its closest relative, *C. serrulata* R.Br., is n = 8. Hybridization experiments may eventually help to elucidate relationships here.



Figs 27-33.—27, *C. seorsiflora* F. Muell., inflorescence (from J. W. Green 1234); 28, half flower (from J. W. Green 1731); 29, *C. vaginata* Lindl., flower; 30, half flower; 31, perianth spread to show stamens (all from Hopetoun, G. Grewar); 32, *C. petrophiloides* F. Muell. ex Benth., habit; 33, fruit (both from J. W. Green 1194).

Figs 34-38.—34, *C. phathyrantha* Diels, fruit, showing zygomorphic development of the ovary; 35, stamen (both from C. A. Gardner 2890A); 36, *C. juncea* Endl., habit; 37, flower; 38, half flower (all from J. W. Green 507).

10. Conostylis vaginata Endl. in Lehm., *Pl. Preiss.*, 2: 23 (1846).

Haptotypes.—In arenoso-calcareo inter Manypeak et Cape Riche districtus Plantagenet, L. Preiss 1383, xi.1841 (LD, MEL).

Stems much branched, forming a straggling plant rarely more than 10 cm. high, the rhizome rooting at intervals and spreading to cover an area 30–40 cm. in width; leaves arising in tufts from the sheathing old leaf bases, 3–10 cm. long and 1 mm. broad, terete, sulcate and entirely glabrous; inflorescence capitate with rarely more than five flowers in the head, subtended by imbricate scarious sometimes brownish bracts, about half the length of the flowers; scapes short; perianth 10–13 mm. long, bright yellow, tomentose outside and glabrous or slightly hairy within, the lobes equal, 5–6 mm. long; filaments shorter than the anthers, flattened and ± dilated at the base, 1 mm. long, anthers about 3 mm. long, connective dorsal, attached in the lower third; style filiform; placentas bearing several pendulous ovules; fruiting perianth scarcely enlarging and quickly deciduous; seeds not seen. Chromosome number n = 8. (Plate x, fig. 1; Figs 29–31, 81.)

Specimens examined. Nornalup, Upper Kalgan River, Oldfield 587: Upper Kalgan, Mueller, 10.1867 (MEL); Kalgan River, Andrews, 10.1903; S. Stirling Plain, Baird, 10.1951 (PERTH); Between Mt. Manypeaks & Cape Riche, Preiss 1383, 11.1840 (LD); Middle Mt. Barren, Gardner 9157, 9.1948 (PERTH); West Mt. Barren, Maxwell (MEL); West Mt. Barren, Gardner 2239, 10.1928; 3 miles N. of Hopetoun, Brittan, 8.1951; 2 miles N. of Hopetoun, J. W. Green 1222, 3.1957, 1 mile N. of Hopetoun, Royce 3668, 8.1951; 1 mile N. of Hopetoun, J. W. Green 1471, 8.1957 (PERTH); Hopetoun, Maiden, 11.1909 (NSW 37670); Hopetoun, Grewar, 10.1957; Bremer Bay, Wellstead, 1900 (PERTH); Near the Thomas River, Taylor, 1887; Swan River to Cape Riche, Drummond 444 (CGE, MEL).

This is a very distinctive species, by virtue of the terete leaves, very straggling habit and the conspicuous bracts subtending the few-flowered inflorescence. The last character is shared with *C. petrophiloides* F. Muell., but it is not thought that the two species are closely related. The placentation is of the less common pendulous type, and the species is restricted geographically and ecologically to the sand heaths along the extreme south coast from Nornalup to the Thomas River.

11. Conostylis petrophiloides F. Muell. ex Benth., *Fl. Aust.*, 6: 431 (1873).

Holotype.—Flats on the Phillips River, F. Mueller (MEL).

Small discrete tufts up to 5 or 10 cm. wide; stems short, unbranched; leaves flat, glabrous except for small marginal hairs, prominently nerved, 15–25 cm. long and 1–4 mm. broad; scape 5–17 cm. long, usually with one median chaffy bract 2–3 cm. long and 6 mm. broad; inflorescence capitate with numerous pale yellowish-white flowers in a head 2–3 cm. in diameter which is subtended by two large broad concave hyaline or coloured bracts about half as long as the flowers; perianth about 15 mm. long, bearing on the outside a loose woolly-villous indumentum, the inside sparingly hairy, lobes equal, about 7 mm. long; anthers linear, 5–6 mm. long on short slender filaments 1·5–3 mm. long, ± dilated at the base; connective attached in the lower third; style slender, scarcely protruding beyond the stamens; placentas dilated with several reflexed ovules; fruiting perianth scarcely enlarging; seeds not seen. Chromosome number unknown. (Figs 32–33, 82.)

Specimens examined. York, Heal, 10.1889 (MEL); District Avon, in apertis arenosis, Pritzel, 10.1901 (NSW 37698); Near Mt. Caroline, Sewell, 1889 (MEL); Tammin, Gardner 327A, 9.1933; Corrigin-Quairading, Blackall 3272, 10.1933; Near Bruce Rock, Blackall, 9.1929; Newdegate, Blackall 1289, 11.1931 (PERTH); Between Swan River and King George's Sound, Forrest, 1881 (MEL); 17 miles W. of Ravensthorpe, J. W. Green 1194, 3.1957; Hopetoun, Andrews, 10.1903 (PERTH).

The few locality records suggest an unusual distribution pattern: almost in a straight line from York to Hopetoun, but without records in the dry Corrigin-Lake Grace section (Fig. 82). It appears that the species had once a more extensive range, skirting this unfavourable area on the south-western side. This is the only disjunct distribution pattern in the genus and is therefore of value in suggesting that this and perhaps other species are contracting in area.

Morphologically, the species does not have any close relatives, although the bracts subtending the inflorescence resemble those of *C. vaginata*. The chromosome number is unknown, but the species seems allied more to the *C. aculeata* group than to any other group or species in the genus.

12. Conostylis phathyrantha Diels in Engl., *Bot. Jahrb.*, 35: 111 (1904).

Holotype.—(Not found), Israelite Bay, Brooke. Probably destroyed in 1943. *Neotype.*—Inland from Israelite Bay, N. H. Brittan 53/95, 1.xi.1954 (PERTH).

Stems short, leaves markedly distichous, ± falcate, black and shining at the base, glabrous except the faintly papillose margins, obscurely nerved, 20–22 cm. long and 3–5 mm. broad; flowers on pedicels about 5 mm. long, each flower subtended by a small bract, the inflorescence loosely cymose, subtended by a linear-lanceolate bract about 1 cm. long; scape short, the whole inflorescence about 6 cm. high, perianth yellow, 12–15 mm. long, the lobes equal and about 5 mm. long, branched-tomentose outside; filaments very dilated at the base, attenuate towards the apex and bearing an anther about 2 mm. long, the connective dorsal, in the lower third; style ± equal in height to the stamens; placentas covered all over with numerous ovules; ovary enlarging in fruit, the loculi (in all fruiting specimens examined) zygomorphic. Seeds not seen. Chromosome number n = 8. (Plate x, fig. 2; Figs 34–35, 83.)

Specimens examined. 35 miles W. of Esperance, Willis, 9.1947 (MEL); 5 miles N. of Gibson's Soak, Brittan, 8.1951; 3 miles N. of Gibson's Soak, Royce 3563, 10.1951; Gibson's Soak, Gardner, 9.1934; Point Malcolm, Gardner 2890A, 10.1931 (PERTH).

A little-known species because of the remoteness of its area of distribution. The significance of the zygomorphic fruit (Fig. 34) could not be ascertained from the few specimens examined; it may prove to be the result of insect damage. The multiporate pollen is unique in the genus and may provide a link between *Conostylis* and *Tribonanthes*.

13. Conostylis juncea Endl., *Nov. Stirp.*, Dec. 3: 19 (1839); *C. involucrata* Endl. in Lehm., *Pl. Preiss.*, 2: 23 (1846).

Holotype.—(Not found), Cultivated in Huegel's garden from seed from South-western Australia. Probably destroyed in 1943. *Neotype.*—Beechboro, Perth, J. W. Green 512, 2.ix.1956 (PERTH).

Discrete tufts up to 10 cm. diameter at the base, the stems unbranched; leaves terete or flat, 10–50 cm. long and 1–4 mm. broad, glabrous or sparingly hirsute, especially at the base, usually fairly prominently nerved; inflorescence in the bud concealed in the surface layers of the soil, the flowers emerging to just above ground level or borne on a loosely woolly scape commonly about 5 cm. long or sometimes up to 15 cm., the inflorescence subtended and often ± enclosed by 2 or 3 broad ovate-lanceolate membranous bracts with green midribs, capitate and few-flowered; perianth bright yellow or greenish-yellow, 15–20 mm. long, bearing long, rigid, simple or minutely denticulate hairs outside, without the woolly tomentum of branched hairs found in all the other species, glabrous inside, lobes equal, about 10 mm. long; filaments much shorter than the anthers which are about 5 mm. long and attached near the base by a slender connective extending along the dorsal side of the loculi; style exceeding the anthers; placentas densely covered with numerous ovules; fruiting perianth enlarging slightly and becoming dry and membranous when the hairs are seen to arise from small tubercles; seeds commonly found, 1·5 mm. long and ellipsoidal, the surface uniformly rugose. Chromosome number n = 8. (Figs 36–38, 84.)

Specimens examined. Bindaminna Road, Moore River, Speck, 9.1952; Gingin, Blackall 2958, 10.1932; 5 miles W. of Gingin, Royce 4724, 12.1953; Caversham, Marchant 23, 9.1956; Gnangarra, Gardner, 7678, 9.1945 (PERTH); Forrestfield, Souster 530, 10.1946 (NSW 37758); Kalamunda, Gardner, 9.1928 (PERTH); Welshpool to Kalamunda, Maiden, 9.1909 (NSW 37760); Maida Vale Road, near Poison Gully, J. W. Green 1711, 9.1957; Wattle Grove, J. W. Green 490, 8.1956; Wattle Grove, Baird, 9.1956; Beechboro, J. W. Green 511, 512, 513, 9.1956 (PERTH); Hampden, Clarke (MEL); Midland Junction, Andrews, 8.1902; Guildford, Andrews, 8-9.1902; Helena Valley Road, Bushmead, J. W. Green 487, 8.1956; Bassendean, J. W. Green 507, 9.1956 (PERTH); Bayswater, Helms, 8.1899 (NSW 37832); Maylands, Andrews, 9.1903

(PERTH); Leederville (or Perth?), Helms, 7-8.1897 (NSW 37800); Perth, Maiden, 9.1909 (NSW 37776); Near Perth, ex herb. Fitzgerald, 7.1901 (NSW 37777); do. x.1902 (NSW 37779); Attadale Estate, McAleer, 1950; Attadale, J. W. Green 518, 9.1956; South Perth, Carne, 8.1923; Como, Vincent, 7.1934; Canning Bridge, Royce, 9.1950 (PERTH); Swan River, Drummond 755, 756 (CGE, MEL); Fremantle, Oldfield (MEL); Cannington, Kissane 63, 9.1948; Cannington, Speck, 8.1948 & 10.1949; Cannington, Gardner, 9.1920 (PERTH); Kelmscott, Helms, 9.1898 (NSW 37830); Armadale, Gardner 753, 9.1920 (PERTH); Serpentine, ex herb. Fitzgerald, 9.1901 (NSW 37759); Near Pinjarrah-Mandurah Road, near Serpentine River, Wilson 826, 8.1957; Pinjarrah, Blackall, 9.1937 (PERTH); Waroona, Berthoud, 7.1907 (NSW 37790); Yarloop, Willis, 9.1947 (MEL); Coolup, Royce 3757, 9.1951 (PERTH); Cleland (NSW 37778); L. Preiss 1407 (Type of *C. involucrata* Endl.) (LD, MEL).

Although the holotype could not be examined, the species is sufficiently distinct to allow of the identification of the specimens cited above, by comparison with the original and subsequent published descriptions (Endlicher in Lehmann, 1844–48; Bentham, 1873).

The only distinction drawn between Endlicher's two species *C. juncea* and *C. involucrata* is that the leaves of the former are almost or quite terete, while those of the latter are flat but often narrow. The writer has no hesitation in uniting the two under the earlier name *C. juncea*, since terete and flat leaves can be found on a single plant.

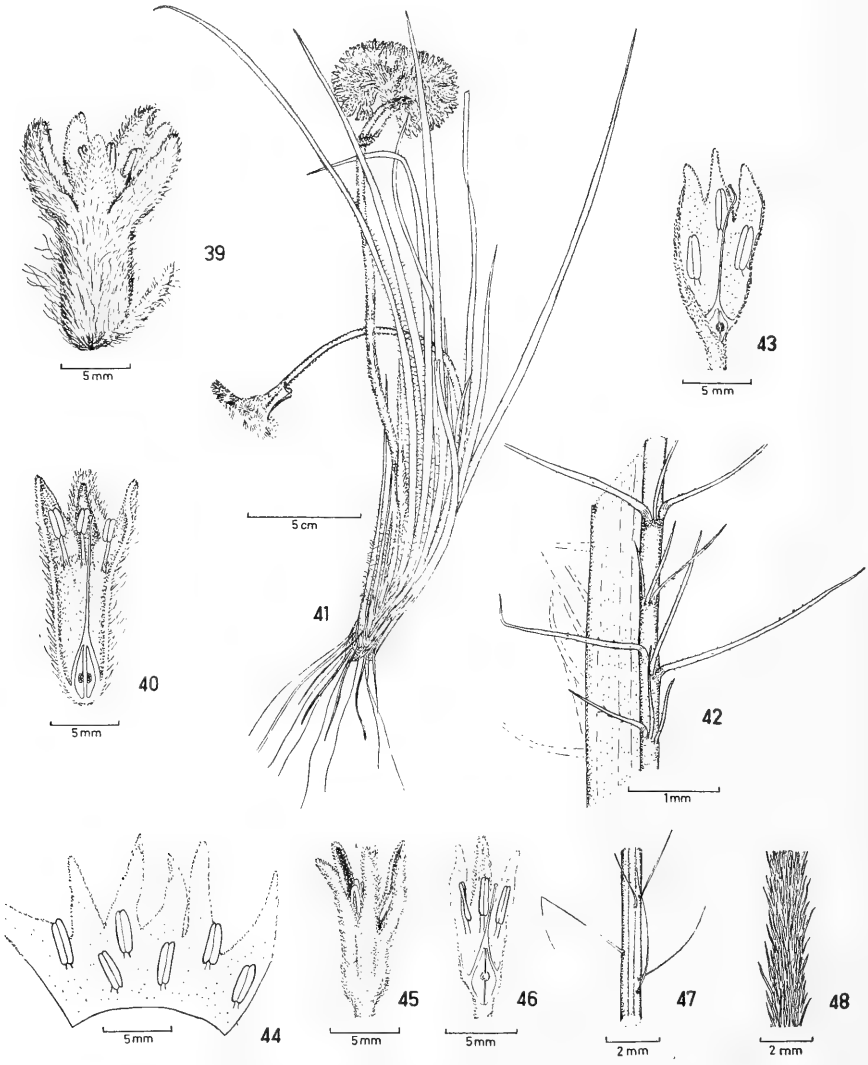
14. Conostylis setosa Lindl., *App. Bot. Reg.*, 44 (1840).

Syntypes.—Swan River, Drummond, 1839; Swan River, mountains rare, Toward; Swan River, J. Mangles (CGE).

Discrete tufts, often consisting of a few leaves and a single scape, the number of scapes rarely more than 3 or 4; stem short, leaves 20–30 cm. long and 3–4 mm. broad, longitudinally striate, the leaves glabrous except for two or more ranks of long spreading white setae on each margin; inflorescence usually very large, up to 5–6 cm. in diameter, densely cymose or capitate, the scape 20–25 cm. long; scapose bract median, leaf-like and 3–4 cm. long, those subtending the inflorescence shorter than the flowers; perianth purplish-cream or creamy-white, about 2 cm. long, covered outside with a loose silky tomentum of hairs which are branched at least at the base, ± woolly inside; lobes narrow, up to 1 cm. long, spreading in the flower and about as long as the cylindrical tube; filaments slender, bearing narrow anthers attached by a dorsal connective in the lower third; stamens and perianth lobes ± uniseriate; style ± equal to the stamens; placentas dilated with several reflexed ovules; perianth scarcely enlarging in the fruit; seeds not exceeding 2 mm. in length, ovoid-oblong and minutely rugose. Chromosome number n = 7. (Figs 39–41, 85.)

Specimens examined. 5 miles NE. of Bullsbrook, J. W. Green 1726, 10.1957; Near Red Hill, J. W. Green 1723, 10.1957 (PERTH); Upper Swan River, 11.1877; Between York and Perth, Mueller, 11.1877 (MEL); National Park, on Great Eastern Highway, J. W. Green 855, 11.1956 (PERTH); Swan View, Goadby (BRI 003179); Swan River, Mueller, 11.1877 (MEL); Swan River, Drummond 749 (CGE, MEL); Swan River, Mylne; Swan River, Preiss (CGE); Lower Swan River, Gribble (MEL); Parkerville, Scott, 1936 (NSW 37706); Wooroloo, Koch 1473, 9.1906 or 10.1907 (MEL, NSW 37705); Darlington, Morrison, 10.1910; Darlington, Williams, 9.1931; Darlington, Roark, 9.1949 (PERTH); Gooseberry Hill, Morrison, 10.1897 (NSW 37702); Gooseberry Hill, Helms, 10.1897 (PERTH); Gooseberry Hill, Helms, 10.1899 (NSW 37780); Gooseberry Hill, Gardner, 10.1933 (PERTH); Kalamunda, Stoward, 10.1911 (NSW 37710, PERTH); Kalamunda, Jutson 70, 10.1915 (NSW 37707); Kalamunda, 10.1928 (PERTH); 3 miles S. of Kalamunda, J. W. Green 368, 10.1955 (PERTH); Smith's Mill, Darling Range, Morrison, 11.1899 (NSW 37701); Montium Darling Range, Preiss 1406, 9.1841 (LD, MEL); Darling Range, Forrest, 1880 (MEL); Montium Darling Range, Pritzel, 11.1900 (NSW 37711); Darling Range, Koch 1473, 10.1906 (NSW 37708); Lesmurdie, Souster 550, 10.1946 (NSW 37704); Sawyer Valley, Mundaring, Willis, 9.1947 (MEL); Canning Dam, Kissane 14, 11.1948 (PERTH); Fremantle, Lukin, 1874 (MEL); Peel Estate, G. D. Vincent, 9.1934; Jandakot, Blackall, 8.1939; Armadale, Andrews, 10.1902; Armadale, Fitzgerald, 10.1903; 5 miles NE. of Bullsbrook, J. W. Green 1726, 10.1957 (PERTH); Jarrahdale, ex herb. Andrews, 10.1905 (NSW 37709); Dwellingup, Hotchkiss & Eames, 9.1953 (NSW 37699); Ex Gunn's Tasmanian Herb. (NSW 37820); Cleland (N.S.W. 37712); Morrison, Between 1897-1911 (NSW 37700); Near Wundowie, Salasoo 500, 11.1949 (NSW 37703); Zamia, 9.1926 (PERTH); King George's Sound (?), Webb, 1880; Preiss 1398; Preiss 1498 (MEL); Hamilton 422, 1902 (NSW 37813); Hamilton, 1902 (NSW 37818).

Although restricted in its area of distribution, this species is an attractive one and therefore well collected. It has been referred to as *C. discolor* Endl. (Gardner, 1959, and earlier editions), but the two are not easily confused; *C. discolor* is a form of *C. setigera* R.Br. with brick-red flowers (see also discussion under *C. setigera*), while the perianth of *C. setosa* is morphologically distinct and the colour purplish-cream or



Figs 39-48.—39, *C. setosa* Lindl., flower; 40, half flower; 41, habit (all from J. W. Green 1723); 42, *C. setigera* R.Br., part of leaf (from J. W. Green 517); 43, half flower; 44, perianth spread to show stamens (both from J. W. Green 515); 45, *C. teretifolia*, sp. nov., flower: 46, half flower (both from W. E. Blackall 3562); 47, part of leaf (from Mt. Lesueur, N. H. Speck); 48, *C. villosa* Benth., part of leaf (from Drummond 311).

creamy-white. In addition, the typical biseriation of the stamens in *C. setigera* does not occur in *C. setosa* and the two species have different chromosome numbers. The leaves of some forms of *C. setigera* closely resemble those of *C. setosa*, and it is thought that the former, a polymorphic and widely distributed species, may have arisen by tetraploidy from the latter which is highly restricted geographically and ecologically.

15. Conostylis setigera R.Br., *Prod. Fl. Nov. Holl.*, 1: 300–1 (1810); *C. aemula* Lindl., *App. Bot. Reg.*, 45 (1840); *C. melanopogon* Endl. in Lehm., *Pl. Preiss.*, 2: 18 (1846); *C. discolor* Endl., *ibid.*, 20 (1846); *C. assimilis* Endl., *ibid.*, 20 (1846); *C. pusilla* Endl., *ibid.*, 20 (1846); *C. minima* Endl., *ibid.*, 21 (1846); *C. psyllium* Endl., *ibid.*, 21 (1846).

Holotype.—(Photo only seen), King George's Sound, R. Brown 5626, xii.1801 (BM) (Plate ix, 2). Six separate pieces on holotype sheet.

Discrete tufts to 5–6 cm. in diameter; stems short; leaves variable in size, usually 6–30 cm. long and 2–3 mm. broad, flaccid or ± erect, longitudinally striate, glabrous except for the marginal setae which are minutely branched, soft, spreading or appressed, usually prominently white, but sometimes blackened, often arranged in several clearly visible vertical ranks on each margin; inflorescence capitate bearing about 5–10 flowers on a scape which is usually shorter than the leaves; scapose bracts 1 or 2, often one long and leaf-like; bracts subtending the inflorescence short; perianth narrow-campanulate, 10–12 mm. long, yellow or yellow suffused to a greater or less degree brick red (drying purplish), woolly-tomentose with branched hairs outside, shortly woolly inside, the lobes 4–5 mm. long and biseriate, the inner whorl smaller than the outer; filaments shorter than the oblong anthers, the stamens biseriate, the inner borne lower than the outer; style ± equal to the stamens; placentas dilated with several reflexed ovules; perianth scarcely enlarging in the fruit, the fruits and seeds frequently not developed; seeds ellipsoidal, rugose, about 1 mm. long. Chromosome number n = 14. (Plate ix, fig. 2; Figs 42–44, 86.)

Specimens examined. Piawaning, J. W. Green 759, 11.1956 (PERTH); Moora, Cleland 50, 10.1908 (NSW 37678); Quairading, Waters 106, 9.1957; Toodyay Road, near Red Hill, Baird, 9.1956; 17 miles W. of Northam, J. W. Green 541, 10.1956; Near Junction of Northem & York Roads, J. W. Green 524, 525, 526, 10.1956 (PERTH); On the Northam-Perth Highway, 3-4 miles from Northam, Salasoo 12, 9.1949 (NSW 37672); In arenosis sylvae districtus York, L. Preiss 1391, 9.1839 (Type of *C. psyllium* Endl.) (MEL); "Currie" (York), Preiss 1393, 4.1840 (LD); York, Wells (MEL); Top of Mt. Bakewell, Sargent 550, 9.1907 (NSW 37812); Boxvale, 50 miles E. of York, Wells (MEL); Meenaar turnoff, Great Eastern Highway, J. W. Green 853, 11.1956 (PERTH); Wooroloo, Koch 1468, 9.1906 or 1907 (MEL, NSW 37685); Darlington, Helms, 9.1898 (NSW 37673); Darlington, Williams, 9.1931 (PERTH); Mahogany Creek, Fitzgerald, 12.1907 (NSW 37674); Smith's Mill, Stoward 13, 10.1911 (NSW 37680); Montium Darling Range, Pritzel, 10.1901 (NSW 37683); Mundararing, Helms, 7.1897 (NSW 37799 p.p.); Mundaring Weir, Bick, 8.1926 (BRI 003182); Government Road, Bassendean, J. W. Green 508, 9.1956; Maylands, Andrews, 8.1903; Bushmead, J. W. Green 1718A, 9.1957; Maida Vale Road, J. W. Green 1712, 9.1957 (PERTH); Welshpool to Kalamunda, Maiden, 9.1909 (NSW 37675); Cannington, Hotchkiss & Eames, 9.1953 (NSW 37671); Lower Swan River, Gribble, 1887 (MEL); Ad fl. cygnorum, L. Preiss 1392, 10.1839 (Type of *C. discolor* Endl.) (LD, MEL); Swan River, Drummond (OXF); Swan River, Mangles; Swan River, Toward 76 (Syntypes of *C. aemula* Lindl.) (CGE); Swan River, Helmich; Swan River, Mylne (MEL); Floreat Park, Storr, 8.1954; Floreat Park, Marchant 22, 9.1956 (PERTH); Leederville, R. Helms, 9.1899 (NSW 37679); Circa urbiculam Perth, Preiss 1390, 7.1839 (LD, MEL); Perth, Maiden, 10-11.1909 (NSW 37784-8); Perth, Sheath, 12.1910 (NSW 37676, 37833); Kings Park (PERTH); Como, Vincent, 7.1934; Attadale, J. W. Green 517, 9.1956; Mt. Pleasant, J. W. Green 514, 515, 516, 9.1956 (PERTH); Near Perth, ex herb. Fitzgerald, 10.1902 (NSW 37684); Fremantle, Oldfield (MEL); Kelmscott, Andrews, 9.1902 (PERTH); North Dandalup, Willis, 9.1947 (MEL); Dwellingup, Blackall, 9.1937; Mornington Mills, Williams 114, 1932; 3 miles S. of Donnybrook, Royce 2319, 10.1947 (PERTH); Busselton, Pries, 1870 (MEL); Yoongarillup, Busselton distr., Royce 3160, 10.1949 & 4537, 4541, 4548, 9.1953 (PERTH); Vasse's River, Pries (MEL); Cape Naturaliste, Wilburd, 9.1904 (NSW 37810); Blackwood River, Mueller, 12.1877 (MEL); Mt. Johnson, Churchill, 3.1957 (PERTH); Upper Hay River, Warburton, 1870 (MEL); Noggerup, Quinlivan, early 10.1956; Darradup, W. of Nannup, Royce 3005, 10.1948 (PERTH); Greenbushes, Ostenfeld 52, 9.1914 (NSW 37669); Manjimup, Quinlivan, 10.1956 (PERTH); 8-10 miles from Nornalup, Pulleine, 12.1917 (NSW 37667); 10 miles NW. of Tambellup, Pearce, 10.1956; Tenterden, Quinlivan, 9.1956; 3 miles SW. of Tenterden, J. W. Green 1148, 3.1957; about 6 miles SW. of Tenterden, J. W. Green 1140, 3.1957; Kendenup, Quinlivan, 9.1956 (PERTH); N. of the Stirling Range (MEL); NW. Plantagenet, Pritzel, 9.1901 (NSW 37668); Porongerup, Knight, 1870; Foothills of Porongerups, 20 miles N. of Albany, Willis, 9.1947; S. of the Stirling Range, Mueller, 10.1867 (MEL); Lowden (Preston), Koch 2002, 10.1913 (NSW 37677); Upper Hay River, Warburton, 1873 (MEL); Narrikup, Quinlivan, 9.1956; 5 miles W. of Albany, J. W. Green 870, 12.1956 (PERTH); Mt. Lindsay, Webb 67, 1881? (MEL); Albany, Menzel, 9.1898 (NSW 37686);

Mt. Clarence, Albany, White 5307, 11.1927 (BRI 003181); Albany, Preiss 1379, 11.1840 (MEL); King River, Albany, Brittan, 8.1951 (PERTH); Kalgan, Oldfield 586c (MEL); 14 miles E. of Albany, J. W. Green 857A, 12.1956; Albany-Manypeaks, N. H. Brittan, 10.1951 (PERTH); Bow River, Jackson, 11.1912 (NSW 37804); In arenosis inter Kaudiap et Cape Riche, L. Preiss 1394, 11.1840 (Type of *C. assimilis* (Endl.) (LD); Bremer River, Webb, 1884; Interior of Cape Arid, towards the Great Bight; L. Preiss 1388 (Type of *C. pusilla* Endl.); L. Preiss 1389 (Type of *C. minima* Endl.); Drummond 754, 757; L. Preiss 1387 (Type of *C. melanopogon* Endl.) (MEL).

The delineation of *C. setigera* (probably the most common and widespread species in the genus) has proved difficult. Field studies resulted in a progressive broadening of the writer's concept of the species until all of the species cited above in the synonymy were included, with the exception of *C. psyllium* Endl. This species was at first kept separate because of its occurrence in one area (near Tenterden) with *C. setigera* (sens. strict.): it was assumed that infraspecific taxa of a single species could not occur sympatrically while remaining morphologically distinct (and the two populations did appear distinct). Yet in the herbarium it was impossible to separate the two "species" when specimens from a number of localities were brought together. It seemed desirable, therefore, to reduce *C. psyllium* to synonymy, making *C. setigera* a very broad species, but one whose limits can at least be defined. Some of the forms previously regarded as species may eventually prove to be good subspecies, but at present there is little evidence to support the erection of formal infraspecific taxa.

The chromosome complement of *C. setigera* has not been examined in good preparations and the number quoted must be regarded as somewhat doubtful. Should the haploid number of 14 be confirmed by later work, it seems likely that *C. setigera* may prove to be a tetraploid derivative of the related and highly restricted species *C. setosa* Lindl. (whose number of n = 7 is, incidentally, more certain).

In the closely related species, *C. villosa* Benth. and *C. crassinerva*, sp. nov., the structure of the flowers (including the characteristic biseriate stamens) is almost identical with that of *C. setigera*, although these species appear to be distinct in their leaves.

16. Conostylis teretifolia, sp. nov.

Holotype.—Cockleshell Gully, within 2 miles of the homestead, W. E. Blackall 3562, 25.viii.1938 (PERTH).

Caespitosa, caulide brevi aut breviter rhizomatoso; folia teretia, sulcata, 5–10 cm. longa, et ferme 1 mm. lata, setas usque ad 4 mm. longas extendentes canas ferentia; scapo foliis longitudine aequo aut multo longiore, nonnumquam bracteam brevem mediam foliaceam, sed semper bracteam parvam ovato-acuminatam scariosam sub inflorescentia capitata ferente; perianthus 10–11 mm. longus, indumentum luteum aut subrubrum e setis ramosis compositum extra, et laneo-tomentosum intra ferens, lobis 4–5 mm. longis; antherae lobaeque perianthi uniseriatae; filamenta 2 mm. longa, antheris longitudine aequa, dorsi conexu sub medio fixa; stylus tenuis, aliquanto antheras superans; placentae quaeque non multa infra reflexa ovula ferentes; perianthus fructuosus non multum aucta; semina inobservata.

Caespitose, stems short or shortly rhizomatous; leaves terete, sulcate, 5–10 cm. long and about 1 mm. broad, bearing spreading white setae up to 4 mm. long; scapes as long as or much longer than the leaves, sometimes bearing a short median leafy bract in addition to a small ovate-acuminate scarious bract below the capitate inflorescence: perianth 10–11 mm. long with a yellow or reddish indumentum of branched hairs outside, woolly-tomentose inside, the lobes 4–5 mm. long; anthers and perianth lobes uniseriate; filaments 2 mm. long, as long as the anthers, attached by a dorsal connective below the middle; style slender, slightly exceeding the anthers; placentas bearing several reflexed ovules from the under-side; fruiting perianth scarcely enlarging; seeds not seen. Chromosome number unknown. (Figs 45–47, 87.)

Specimens examined. Three Springs, Blackall 4890, 9.1940; Mount Lesueur, Speck; 10 miles W. of Moora, Brittan 52/31, 9.1952 (PERTH); Between York and Hampton Plain, Sayer & Carlson, 8.1888; E. Sources of the Swan River, Heal, 1889; Sources of Swan River, Eaton, 1889; Adams, 1890 (MEL).

Although appearing closely related to *C. setigera* R.Br., this species differs from it in two important respects: the stamens are uniseriate and the leaves terete. It is thus less closely related than are *C. villosa* Benth. and *C. crassinerva*, sp. nov., whose flowers are almost identical with those of *C. setigera*. The present species also differs from most forms of *C. setigera* in the length of the foliar setae.

17. Conostylis villosa Benth., *Fl. Aust.*, 6: 433 (1873); *C. drummondii* Benth., *ibid.*, 433–4 (1873).

Holotype.—(Not seen), Swan River, Drummond 311, 1845 (K). *Isotypes* in CGE, MEL.

Caespitose; leaves flat, 12–20 cm. long and 1–2 mm. broad, loosely villous with soft hairs, often silvery-white and sometimes ± spreading; inflorescence capitate, many-flowered, the scape markedly white-tomentose when young and 6–12 cm. long with 1–2 leaf-like bracts; perianth yellow, sometimes tinged or almost wholly purplish-red, 12–15 mm. long, the lobes 5–7 mm. long, tomentose outside and inside; stamens biseriate, filaments 1·5 mm. long and anthers 2 mm. long; style ± equal to the outer stamens; placenta bearing several ovules reflexed from the under surface; ovary scarcely enlarging in fruit, seeds linear-oblong, 1·5 mm. long. Chromosome number unknown. (Figs 48, 88.)

Specimens examined. 5 miles S. of Calingiri, J. W. Green 563, 11.1956 (NE 005567, PERTH); 5 miles N. of Bolgart, J. W. Green 559, 11.1956 (NE 005566, PERTH).

This extremely little-known species differs from *C. setigera* R.Br. only in the leaves which are covered all over with a loose tomentum at maturity, and some botanists may prefer to regard it as a subspecies of *C. setigera*. However, uncertainty surrounds the definition and occurrence of the species, and such a step is considered unwise in the absence of more complete field data. The specimens cited above appear closest to this species, but they do not agree perfectly with the type.

The writer is unable to separate *C. drummondii* Benth. from this species; the leaves of *C. drummondii* are described as being "covered with a close whitish tomentum and a few longer appressed hairs intermixed", while those of *C. villosa* are "hairy all over" (Bentham). However, the type of the former has not yet been examined, and it may prove to be distinct. (See also remarks under *C. dielsii* W. V. Fitzg.)

18. Conostylis crassinerva, sp. nov.

Holotype.—Top of Mount Lesueur, N. H. Speck (PERTH).

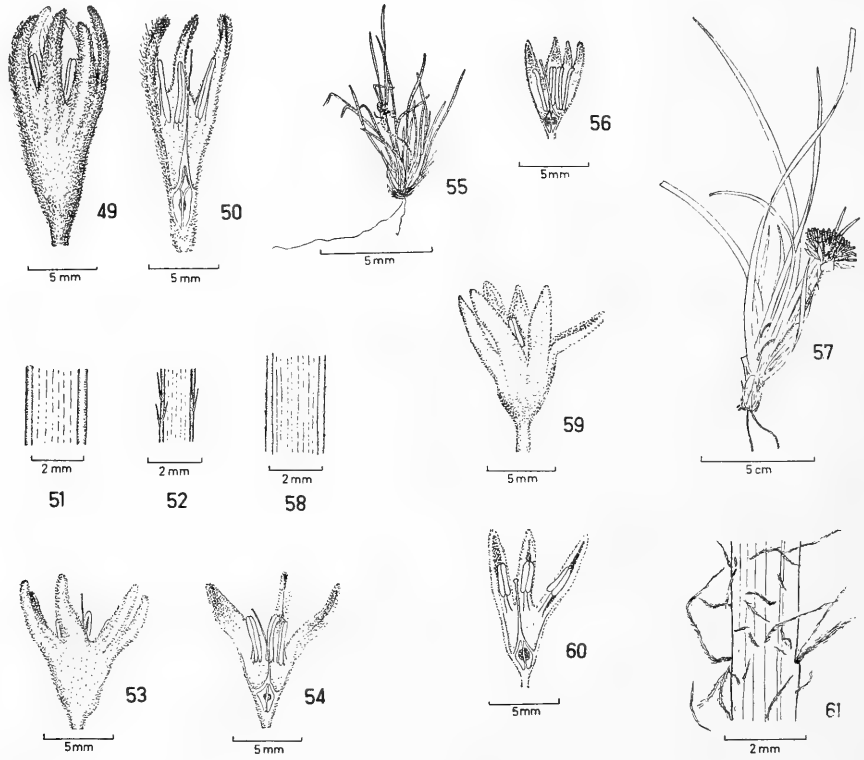
Caespitosa, caulide brevi; folia usque ad 15 cm. longa, ferme 3 mm. lata, marginibus conspicuis fibratisque glabris, aut setas moliter appressas ferentibus; scapi longitudine foliis aeque aut breviores, inflorescentia capitata, bracteum longum foliaceum prope basim et dua breviora plus minusve foliacea inflorescentiam subtendentia ferentes; perianthus luteus aut subruber 10–12 mm. longus, tomentum laxum capillarum ramosarum et prope basim capillarum complurium longiorum minute denticulatarum extra ferens et intra breviter laneus, lobis 5–6 mm. longis; stamina lobaeque perianthi uniseriatae aut minime biseriatae; filamenta brevissima ferme 1 mm. longa, antheras lineares 5 mm. longas dorsi convexu sub medio ferentia; stylus tenuis et plus minusve longitudine staminibus aequus; placentae in parte ovarii adnata dispositae, quaeque non multa infra reflexa ovula ferentes; fructus et semina inobservata.

Caespitose, stem short; leaves up to 15 cm. long and about 3 mm. broad, the margins prominent and fibrous, glabrous or with softly appressed hairs; scapes as long as or shorter than the leaves, the inflorescence capitate; scape bearing a long leaf-like bract near the base with two shorter, ± leaf-like bracts subtending the inflorescence; perianth yellow or reddish, 10–12 mm. long, covered outside with a loose tomentum of branched hairs with a few longer, minutely denticulate hairs near the base, shortly woolly inside, the lobes 5–6 mm. long; stamens and perianth lobes uniseriate or very slightly biseriate, filaments very short, about 1 mm. long, bearing long linear anthers 5 mm. long on a dorsal connective just below the middle; style slender and ± equal to

the stamens; placentas in the adnate portion of the ovary bearing several reflexed ovules from the under-side. Fruits and seeds not seen. Chromosome number unknown. (Plate x, fig. 11; Figs 49–52, 89.)

Specimens examined. Solley's Farm, about 5 miles N. of Hill River, Churchill 69.0, 9.1957; Approximately 7 miles SE. of Mount Lesueur, Churchill 95.2, 9.1957; Hill River, Speck, 9.1951 & 9.1953 (PERTH).

Although known from only a few localities, in the Hill River district, this species appears distinct from its nearest relative, *C. setigera* R.Br. It differs from that species in the prominent leaf margins which do not bear long marginal setae, and in the stamens and perianth lobes, which are ± uniseriate.



Figs 49-61.—49, *C. crassinerva,* sp. nov., flower; 50, half flower; 51-52, leaf surfaces (all from Hill River, N. H. Speck); 53, *C. dielsii* W. V. Fitzg., flower; 54, half flower (both from E. Pritzel 528); 55, *C. teretiuscula* F. Muell., habit; 56, flower (both from J. W. Green E214); 57, *C. caricina* Lindl., habit; 58, leaf surface; 59, flower; 60, half flower (all from J. W. Green 1713); 61, leaf surface (from J. W. Green 584).

19. Conostylis dielsii W. V. Fitzgerald in *J. Proc. Muell. Bot. Soc. W. Aust.*, 1: 82 (1903); *C. psammophila* Diels in Engl., *Bot. Jahrb.*, 35: 109 (1904) (nomen nudum).

Holotype.—In fruticetis arenosis inter flumina Moore et Murchison, E. Pritzel 528, viii.1901 (NSW 37736).

Discrete tufts, stem shortly rhizomatous; leaves up to 10 cm. long and 1 mm. broad, flat, invested all over with a soft white woolly tomentum of simple hairs; scapes equal to or slightly exceeding the leaves and bearing a dense cyme or the inflorescence capitate; scape bearing usually one ± median bract, leaf-like, with a smaller bract subtending the inflorescence; perianth pale creamy-yellow, about 1 cm. long, the indumentum closely tomentose of branched hairs outside, glabrous or slightly hairy inside, the lobes ± equal, about 5 mm. long; filaments slender, short, bearing linear anthers by a dorsal connective in the lower third; styles slender, shorter than or ± equal to the

stamens; placentas dilated with several reflexed ovules; fruits and seeds not seen. Chromosome number unknown. (Plate x, fig. 8; Figs 53–54, 90.)

Specimens examined. Mingenew, ex herb. Fitzgerald, 9.1903 (NSW 37735).

With the original description. Fitzgerald states that this species is allied to *C. drummondii* Benth., differing chiefly in foliage and inflorescence. Since there is no evidence that Fitzgerald saw the type of *C. drummondii* (now in Kew), it is thought that the above remark is the result of his comparison with Bentham's original description of *C. drummondii.* The latter is a somewhat doubtful species, but is probably identical with *C. villosa* Benth. (see remarks under that species); in any case there is no doubt that *C. villosa* is more closely related to *C. setigera* R.Br. than is *C. dielsii.* The elucidation of these relationships must await examination of the type of *C. drummondii,* as well as further field data on all of these little-known species.

20. Conostylis teretiuscula F. Muell., *Fragm.*, 8: 18 (1872).

Holotype.—A. F. Oldfield (MEL).

Caespitose; leaves ± terete, 5–12 cm. long and 1 mm. broad, silvery-villous; inflorescence few-(5–8)flowered, compact, on a thin woolly-tomentose scape 3–4 cm. long, bearing a narrow median bract 6 mm. long; perianth pale creamy-yellow, 6–8 mm. long, the lobes 4–5 mm. long, tomentose outside and inside; filaments 1 mm. long, anthers 4 mm. long; style slightly exceeding the stamens; placenta covered all over with numerous ovules; fruits not seen. Chromosome number unknown. (Figs 55–56. 91.)

Specimens examined. About 7 miles N. of Marchagee, J. W. Green E.214, 6.1957 (NE 005564, PERTH); 12 miles N. of Watheroo, J. W. Green E.203, 6.1957 (NE 005565).

The relationships of this species are most obscure. From the three specimens examined it appears distinct and bears a superficial resemblance, in flowers and leaves, to *C. dielsii* W. V. Fitzg. However, the placentation suggests affinities with the *C. aculeata* group. Bentham remarks that it "requires further investigation". The writer's specimens, cited above, appear to be the only collections known beside the type and one is in very young bud only.

21. Conostylis caricina Lindl., *App. Bot. Reg.*, 45 (1840); *C. graminea* Endl. in Lehm., *Pl. Preiss.*, 2: 19 (1846).

Holotype.—Swan River, J. Drummond, 1839 (CGE). Two separate pieces on holotype sheet. *Isotype* in K (not seen).

Discrete tufts up to 30 cm. diameter; stems very short; leaves 10–25 cm. long and 2–3 mm. broad, longitudinally striate with prominent fibrous margins, glabrous except for minute marginal setae, rarely loosely villous on the leaf surface; inflorescence a dense or ± loose few-flowered head with about 6–8 flowers in 2–3 fairly regular rows, the pedicels up to 1 cm. long; scape 4–8 cm. long, usually with a single brown membranous median bract; perianth creamy-yellow with a close velvety tomentum of branched hairs outside, perianth 15 mm. long, the lobes narrow-linear, about 6 mm. long and greatly exceeding the short tube above the ovary and producing a characteristic claw-like appearance, especially in the fruit; filaments short and thick, bearing linear anthers, attached by a dorsal connective in the lower third; style ± equal to the stamens; ovules numerous, ± reflexed from the stipitate placentas; perianth enlarging slightly in fruit; seeds rugulose, 2 mm. long, oblong-ellipsoidal. Chromosome number n = 7. (Figs 57–61; 92.)

Specimens examined. Murchison River, Oldfield (MEL); 2 miles N. of Yerecoin, J. W. Green 587, 11.1956 (PERTH); Upper Swan River, Sewell, 1883? (MEL); Toodyay, Royce 4316, 9.1953; Toodyay Road, near Red Hill, Baird, 9.1956; 5 miles N. of Pearce Air Station, Royce 3834, 8.1952; Near Perth, Helms?; Guildford, Andrews, 9.1902 (PERTH); Supra urbiculam "Guildford", L. Preiss 1380, 8.1839 (Type of *C. graminea* Endl.) (LD, MEL); National Park, 9.1953; Darlington, Williams, 9.1931 (PERTH); Darlington, Morrison, 10.1907 (NSW 37737); Darling Range, Koch 1698, 9.1907 (MEL, NSW 37739); Montium Darling Range, Pritzel, 9.1901 (NSW 37741); Mahogany Forest, York Road, Jones, 1881 (MEL); Top of Gooseberry Hill Road, J. W. Green 1713, 9.1957; Kalamunda, Vincent, 9.1934; Bellevue,

Blackall, 8.1939; Wattle Grove, Storr, 8.1954 (PERTH); Kelmscott, Helms, 9.1898 (NSW 37742, 37831); Armadale, Morrison, 8.1902 (NSW 37738); Preiss 1385 (LD, MEL); Gardner 7025 (9025?) (PERTH).

The claw-like appearance of the fruiting perianth gives this species a characteristic appearance; the species has a certain "look" which is difficult to define, but other contributory features are the even, felted, creamy-yellow indumentum of the perianth and the few-flowered inflorescence which is shorter than the leaves.

The Yerecoin specimens cited above have loosely hairy leaf surfaces in the mature plant, and may be a subspecies of *C. caricina*, or even a distinct species. This form is known only from one collection, in late flowering. The record from the Murchison River is thought to be erroneous. Apart from the Yerecoin collection, *C. caricina* is known only from a small area in the Darling Range, where it occurs mainly on lateritic sandy soils.

The fact that the chromosome number is the same as that of *C. setosa* Lindl. does not seem to be significant; the two species are not closely related morphologically.

22. Conostylis aurea Lindl., *App. Bot. Reg.*, 44 (1840); *C. sulphurea* Endl. in Lehm., *Pl. Preiss.*, 2: 17 (1846).

Holotype.—Swan River, J. Drummond, 1839 (CGE). Two separate pieces on holotype sheet. *Isotype* in K (not seen).

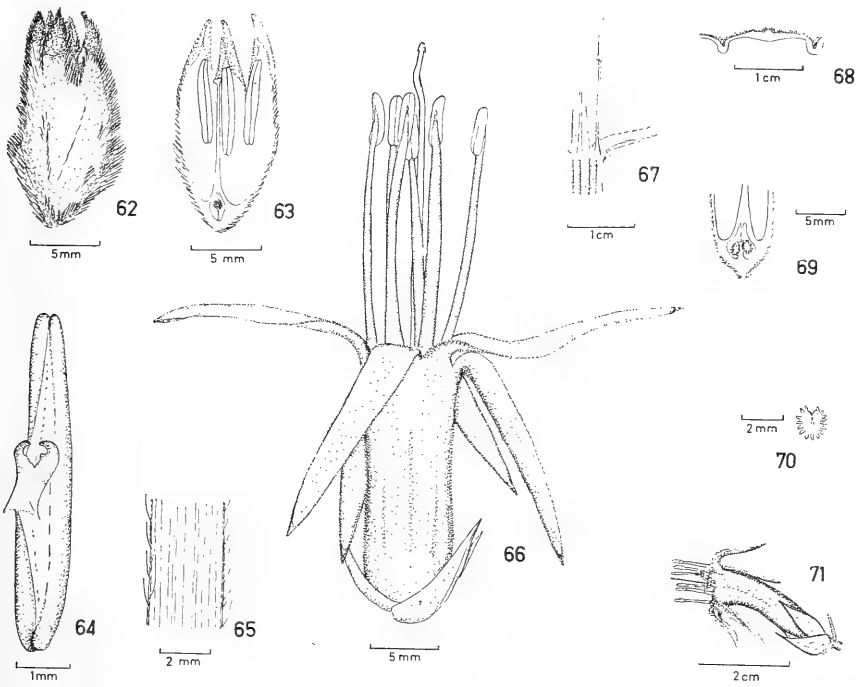
Discrete tufts up to 30 cm. in diameter; stem short, unbranched; leaves usually 15–30 cm. long and 1·5–4 mm. broad, usually glabrous on the lamina, striate, with a row of small appressed cilia on the margins, sometimes the lamina sparingly hairy and frequently covered with a mucilaginous excretion causing the leaves to stick to drying papers; inflorescence ± capitate on a very short scape or the scape as long as or exceeding the leaves; bracts on the scape 1–2, the median usually silky-woolly, those subtending the inflorescence small and ± concealed; perianth 15–20 mm. long, golden or pale yellow, sometimes tinged with purplish red, densely woolly-tomentose outside with simple and branched hairs, glabrous inside, the lobes 6–7 mm. long; filaments short and flat, attached to the long linear anthers by a median, dorsal connective bearing a pair of simple or denticulate dorsal appendages, at least in the young flowers; style ± equal to the stamens; placentae borne in the free portion of the ovary, stipitate and dilated with many reflexed ovules; ovary enlarging slightly in fruit; seeds not seen. Chromosome number n = 5. (Plate x, fig. 3; Figs 1, *j*, 62–65, 93.)

Specimens examined. Murchison River, 10.1877 (MEL); Murchison River, Speck, 9.1949 (PERTH); Greenough's and Irwin's Rivers, 11.1877; Geraldine, Oldfield (MEL); 1 mile W. of Wicherina, J. W. Green 479, 8.1956; W. of Coorow, Blackall 3972, 9.1938; Three Springs, Blackall 4407, 8.1940; Cockleshell Gully, within 2 miles of Homestead, Blackall 3555, 8.1938; N. of Diamond of the Desert Spring, Gardner 8480, 10.1946; Top of Mt. Lesueur, Speck, 1952; Hill River, Gardner 9056, 8.1948; Hill River, Speck, 9.1951; Minegarra-Mt. Misery, Speck, 9.1951; Piawaning, J. W. Green 760, 11.1956; 2 miles N. of Yerecoin, J. W. Green 1485, 8.1957 (PERTH); Toodyay, Oldfield (MEL); Julimar Track, between Toodyay & Bindoon, Gardner 8719, 10.1947; Near Red Hill, J. W. Green 1724, 10.1957; 5 miles N. of Pearce Air Station, Royce 3836, 8.1952; Gnangarra, Gardner 7679, 9.1945 (PERTH); Watheroo (or Jibberding?), M. Koch 1322, 10.1905 (Type of *C. aurea* var. *longiscapa* A. J. Ewart) (MEL, NSW 37696); Kalamunda, Stoward, 10.1911 (NSW 37691); Welshpool to Kalamunda, Maiden, 9.1909 (NSW 37690); Bassendean, J. W. Green 509, 9.1956; Guildford, Fitzgerald, 10.1902?; Bushmead, J. W. Green 1718, 9.1957 (PERTH); Bayswater, Morrison, 7.1897 (NSW 37682); Bayswater, Main, 10.1941; Maylands, Andrews, 9.1903 (PERTH); Perth, Maiden, 10.1909 (NSW 37692); Bull's Creek, Preiss 1381, 11.1841 (LD, MEL); Preston Creek, Perth, L. Preiss 1382, 7.1839 (Type of *C. sulphurea* Endl.) (LD, MEL); Perth, Morrison, 9.1898 (PERTH); Near Perth, Fitzgerald, 10.1902 (NSW 37694); Swan River, Drummond (CGE, OXF); Swan River, Helmich; Lower Swan River, Gribble (MEL); District Swan, Pritzel, 11.1900 (NSW 37695); South Perth, McAleer, 1950 (PERTH); Melville Park, Helms, 7.1897 (NSW 37689); Fremantle, Oldfield (MEL); Cannington, Speck, 1948; Armadale, Gardner 754, 9.1920 (PERTH); Cape Naturaliste, Oldfield (doubtful locality), Drummond 750, 759 (MEL); Hamilton, 1902 (NSW 37688); Cleland (NSW 37693); Ashby 133, 9.1946; Gardner 9344; Gardner 10229 (PERTH).

This is a polymorphic species, but one in which the writer has been unable to define subspecies. Ewart (1906) described one rather extreme form as a variety (*longiscapa*), but this seems to be connected to var. *aurea* (sens. Ewart) by intermediate forms.

Considerable differences occur in forms growing on laterite and on sand, the scapes of the former being far shorter than the leaves and of the latter equal or longer, but again intermediates are found in intermediate situations. The various forms are united by the possession of peculiar erect anther appendages (Figs. 1, *j*, 64); this is a unique feature of this species and has not been previously described.

This species appears to have no close relatives in the genus, but the chromosome number of n = 5 may be a reduction from a species having n = 7, or the prevailing n = 8.



Figs 62-71.—62, *C. aurea* Lindl., flower; 63, half flower; 64, stamen (all from J. W. Green 509); 65, leaf surface (from J. W. Green 1718); 66, *C. androstemma* ssp. *androstemma*, flower (from J. W. Green 1386); 67, stamen and portion of perianth; 68, portion of perianth tube in cross section; 69, ovary and base of flower in longitudinal section; 70, peltate placenta from above; 71, ssp. *argentea*, ssp. nov., flower (traced from a colour photograph, J. W. Green 1467).

23. Conostylis androstemma (Lindl.) F. Muell., *Fragm.*, 8: 19 (1873); *Androstemma junceum* Lindl., *App. Bot. Reg.*, 46 (1840).

Holotype.—Swan River, J. Drummond, 1839 (CGE).

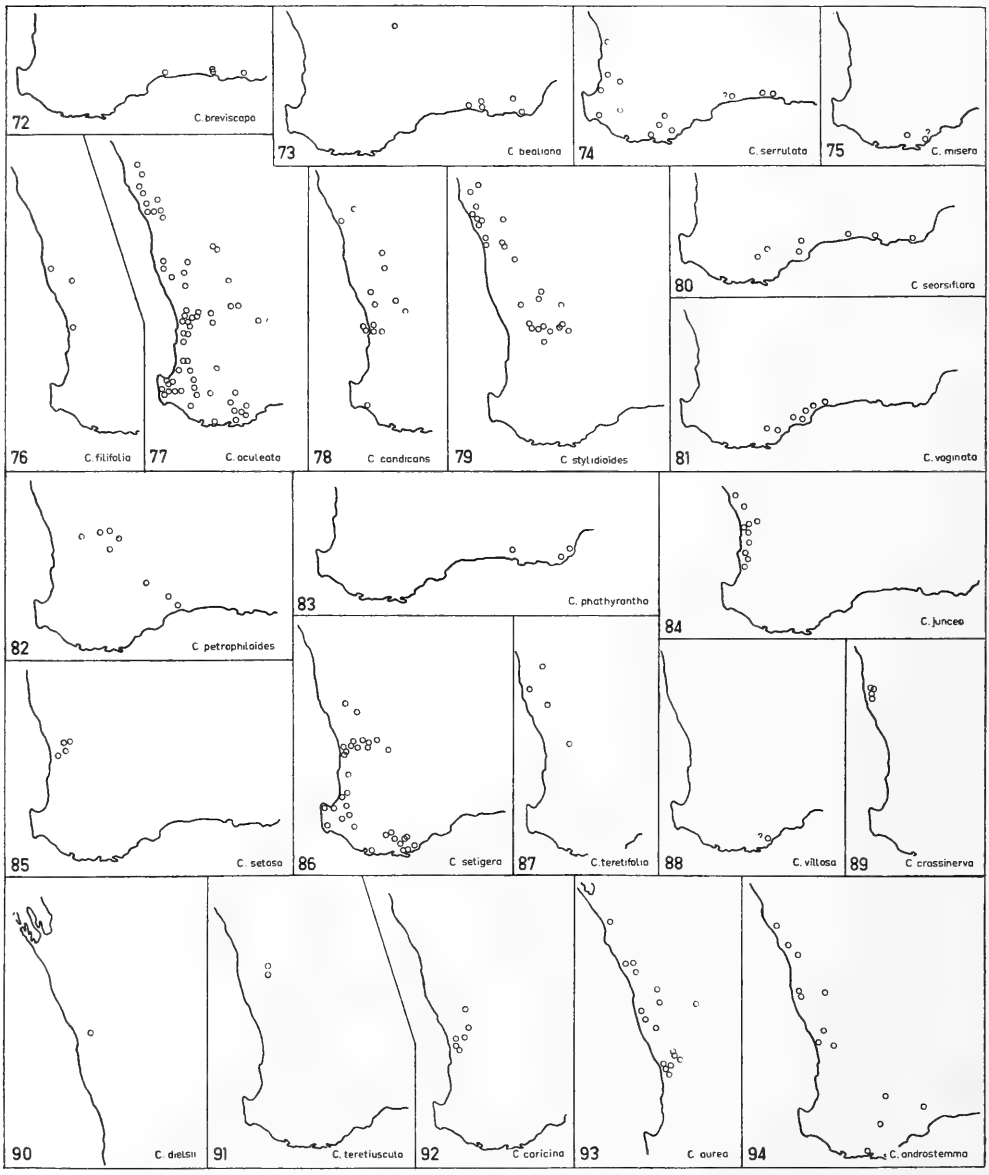
Discrete tufts up to 30 cm. in diameter, but usually smaller; stem short, unbranched, the leaves arising close to the base; leaves terete or flat and narrow, glabrous or silvery-tomentose, longitudinally striate, 10–30 cm. long, about 1 mm. broad; flowers solitary, on very short pedicels and subtended by 3–4 scarious or reddish bracts 5–10 mm. long; perianth tube pale yellow, about 3·5–4 cm. long; tomentose with branched hairs outside, glabrous inside, the lobes narrow, 1·5–2 cm. long, equal, spreading at the time of flowering; filaments filiform, erect, equal, about 1–2 cm. long, the anthers with a dorsal connective in the lower third; style equal to or slightly exceeding the stamens; placentas peltate, bordered by about 15 ovules, in the adnate part of the ovary; perianth scarcely enlarging in the fruit; seeds not seen. Chromosome number n = 5 in ssp. *androstemma*.

A variant of this species has been collected from several different localities which are geographically removed from the main area of occurrence of the typical form, and the variant is therefore described below as a new subspecies.

23*a*. Conostylis androstemma (Lindl.) F. Muell. ssp. androstemma.

Leaves terete, glabrous; flowers subtended by scarious bracts about 5 mm. long. Chromosome number n = 5. (Plate x, figs 9–10; Figs 66–70, 94.)

Specimens examined. 10-20 miles N. of Northampton, Blake 18108, 9.1947 (BRI 002846); South Hutt, Oldfield; Between the rivers Murchison & Irwin, Sewell (MEL); 32 miles E. of Geraldton, J. W. Green 1373, 7.1957; 35 miles E. of Geraldton, J. W. Green 1374, 7.1957



Figs 72-94.—Distribution of species of *Conostylis*. Scale as in Fig. 2.

(PERTH); Greenough Flats, Jones, 1878 (MEL); 3 miles W. of Strawberry, J. W. Green 1367, 6.1957 (PERTH); Upper Irwin, Gwerin (MEL); Mingenew, J. W. Green 1386, 7.1956; 6 miles S. of Mingenew, J. W. Green 1389, 7.1957; 2 miles N. of Arrino, J. W. Green 1365, 6.1957 (PERTH); Between Moore and Murchison Rivers, Pritzel 379, 6.1901 (NSW 37745); 3 miles N. of Maya, J. W. Green 1510, 8.1957; Cockleshell Gully-Mt. Lesueur, Blackall 3608, 8.1938; Lateritic Hills, Hill River, Gardner, 6.1943; Hill River, Speck, 9.1951; 4 miles E. of

Watheroo, Main, 7.1955; W. of Bindoon, Royce 3826, 7.1952; Gnangarra, Perry, 6.1946; Darlington, Morrison, 7.1902 (NSW 37744); Darlington, Andrews, 7.1902 (PERTH); Darlington, Morrison, 10.1907 (NSW 37743); Darlington, Williams 42, 6.1931; Gooseberry Hill, 6.1914 (PERTH); Darling Range, Koch 1735, 10.1907 (NSW 37746); Smith's Mill, Helms, 8.1898 (NSW 37747); Nicholson Road, Cannington, McMillan, 1956 (PERTH); Swan River, Drummond 762 (MEL, OXF); Swan River, Mylne (MEL); Albany, Green, 1911 (NSW 37834); Swan River, Preiss 1409 (LD, MEL, NSW 37835); Brittan 19.753, 7.1951 (PERTH).

23*b*. Conostylis androstemma (Lindl.) F. Muell. ssp. argentea, ssp. nov.

Holotype.—Whitish clayey sand, associated with *Eucalyptus incrassata*, 24 miles E. of Ongerup, J. W. Green 1467, 3.viii.1957 (PERTH).

Haec differt a ssp. *androstemma* bracteis subrubris ferme 10 mm. longis, flores subtendentibus et foliis quae sunt plana, angusta, argenteovillosa et perianthi tuba quae plerumque est plus minusve curvata.

Differs from ssp. *androstemma* in the reddish bracts, about 10 mm. long, subtending the flowers, in the leaves which are flat, narrow, and silvery-villous, and in the perianth tube which is generally slightly curved. (Figs 71, 94.)

Specimens examined. Near Kukerin, Gardner 1741, 9.1925; E. of Wishbone, Gardner & Blackall, 9.1925 (PERTH); 100 miles N. of Stirling Range, Muir, 1879; Far inland from King George's Sound, Hassell, 1882 (MEL); 39 miles E. of Ongerup, J. W. Green 1469, 8.1957; 33 miles W. of Ravensthorpe, J. W. Green 1189, 4.1957 (PERTH).

Reference has been made, in the historical survey of the genus, to the original description of this species in the genus *Androstemma* Lindl., and to its subsequent union with *Conostylis* by Mueller. Mueller (1873) gave no reasons for the new combination, merely pointing out the character of the long filaments as a point of difference from *Anigozanthos*.

The evidence in favour of inclusion of *Androstemma* in *Conostylis* is: Similarity of leaf anatomy and morphology and structure of the gynoecium and fruit; similarity of flower colour and indumentum. The evidence in favour of its separation from *Conostylis* is: Distinctive perianth structure (ribs and long spreading lobes); anthers borne on long, erect filaments; peltate placentation with bordering ovules. It seems impossible to make a decision in the absence of experimental evidence. Current practice, as laid down by Bentham, is therefore followed in the present paper.

It has been mentioned, under *C. bealiana* F. Muell., that the inclusion of these two species in the same section (Blackall, 1954) seems an artificial arrangement. *C. bealiana* was unknown to Bentham (being described in 1875), and Blackall placed it beside *C. androstemma* in his key, on the basis of the long tubular corolla. Evidence from the fields of cytology, palynology and floral morphology suggests that this similarity is a case of parallel evolution and is of no phylogenetic significance.

Artificial Key to the Species.

1. Anther connective apical or median; stamens uniseriate.
2. Anther connective apical, without appendages; filament slender; perianth divided to the ovary. Esperance district ..... 1. *C. breviscapa* R.Br.
2.* Anther connective median, bearing erect dorsal appendages; filament broad and strap-like; perianth tube present above the ovary. Murchison River to Darling Range ..... 22. *C. aurea* Lindl.

1.* Anther connective decurrent, attached to the filament near the base of the anther; stamens uniseriate or biseriate.
3. Leaves terete.
4. Perianth tube above the ovary exceeding 1 cm.; filaments much longer than the anthers. Widely distributed ..... 23. *C. androstemma* (Lindl.) F. Muell.
4.* Perianth tube above the ovary less than 1 cm.; filaments not appreciably longer than the anthers.
5. Mature leaves covered all over with a loose or dense indumentum.
6. Stamens uniseriate or nearly so.
7. Leaves sparsely covered with prominent long, usually white setae; inflorescence capitate; placenta recurved with few ovules; perianth often purplish. Inland, N. of Perth ..... 16. *C. teretifolia*, sp. nov.
7.* Leaves densely covered with a silvery white tomentum; inflorescence loose; placenta covered all over with numerous ovules; perianth yellow. Extremely rare ..... 20. *C. teretiuscula* F. Muell.

6.* Stamens biseriate. Extremely rare. ..... 17. *C. villosa* Benth.
5.* Mature leaves mostly glabrous.
8. Anthers alternatively long and short; Hopetoun district ..... 10. *C. vaginata* Endl.
8.* Anthers all equal. Mostly Swan River district and to the north.
9. Perianth densely tomentose, with branched hairs; habit loosely spreading; buds developing above ground. Cannington, Hill River district .... 5. *C. filifolia* F. Muell.
9.* Perianth with sparse, simple or minutely denticulate hairs; habit caespitose; buds developing in the surface layers of the soil. Often some flat leaves present. Perth to Geraldton, mostly within 30 miles of the coast ..... 13. *C. juncea* Endl.
3.* Leaves flat.
10. Leaves densely grey-tomentose.
11. Inflorescence usually bifid (often appearing capitate externally); habit caespitose or proliferously branched; leaves more than 2 mm. broad. Often on limestone soil, from Shark Bay to Flinders Bay ..... 7. *C. candicans* Endl
11.* Inflorescence ± capitate but the rachis not bifid; habit caespitose; leaves less than 2 mm. broad. Mingenew district ..... 19. *C. dielsii* W. V. Fitzg.
10.* Mature leaf blades (except the margin) usually glabrous, or bearing a loose indumentum, not densely felted.
12. Leaf margins bearing rigid spines or quite glabrous for part or all of their length. Widely distributed ..... 6. *C. aculeata* R.Br.
12.* Leaf margins minutely serrulate or papillate, or bearing setae which are not rigid.
13. Perianth tube greatly exceeding the lobes; perianth often completely brick red or reddish yellow. South coast, from near Young River to E. of Esperance .... 2. *C. bealiana* F. Muell.
13.* Perianth tube above the ovary ± equal to or shorter than the lobes; perianth yellow or sometimes tinged with purplish red.
14.* Inflorescence several- to many-flowered.
15. Leaves 4-5 mm. broad; flowers almost hidden within the leaf bases. Extremely rare ..... 4. *C. misera* Endl.
15.* Leaves 1-2 mm. broad; flowers not hidden.
16. Perianth more than 15 mm. long; leaves more than 3 cm. long. Stirling Range to E. of Esperance ..... 9. *C. seorsiflora* F. Muell.
16.* Perianth less than 12 mm. long; leaves less than 3 cm. long. Near York .... 8. *C. stylidioides* F. Muell.
14.* Inflorescence several- to many-flowered.
17. Mature leaf blades (besides the margins) invested regularly with sparse simple or minutely denticulate hairs.
18. Perianth tube very short; perianth claw-like in fruit; perianth indumentum short and dense; leaf margins prominent. Yerecoin district .... 21. *C. caricina* Lindl.
18.* Perianth tube above the ovary ± equal to the lobes; perianth with at least some long hairs; leaf margins not prominent.
19. Stamens biseriate; leaves almost terete; placenta recurved with few ovules. Bolgart district ..... 17. *C. villosa* Benth.
19.* Stamens uniseriate; leaves narrow but flat; placenta covered with numerous ovules. Murchison River to Beverley. ..... 8. *C. stylidioides* F. Muell.
17.* Mature leaf blades glabrous.
20. Leaf margins with minute hairs or papillae.
21. Perianth with long, silky hairs; inflorescence capitate, subtended by broad, conspicuous, scarious bracts. York to Hopetoun .... 11. *C. petrophiloides* F. Muell
21.* Perianth indumentum short and dense; inflorescence capitate or loose; bracts subtending the inflorescence narrow and ± leaf-like.
22. Scape much longer than the leaves. Murchison River to Beverley .... 8. *C. stylidioides* F. Muell.
22.* Scape equal to or shorter than the leaves.
23. Leaves falcate, shining, black at the base; ovary often zygomorphic, inflorescence very loose. Esperance to Israelite Bay .... 12. *C. phathyrantha* Diels.
23.* Leaves ± straight, dull green; ovary actinomorphic.
24. Placenta recurved; perianth claw-like in fruit. Darling Range. .... 21. *C. caricina* Lindl.
24.* Placenta covered with numerous ovules.
25. Perianth tube very short. Darling Range to E. of Albany .... 3. *C. serrulata* R.Br.
25.* Perianth tube above the ovary ± equal to the adnate part. Mainly Murchison River and Champion Bay districts ..... 8. *C. stylidioides* F. Muell.
20.* Leaf margins glabrous, or with soft, usually branched, setae.
26. Leaf margins quite glabrous; perianth with sparse simple or minutely denticulate hairs; scape very short; buds developing in surface layers of the soil. Perth to Geraldton, mostly within 30 miles of the coast ..... 13. *C. juncea* Endl.

26.* Leaf margins setose; perianth indumentum dense; scape ± equal to the leaves or longer; buds developing above ground.
27. Marginal setae yellowish, in a single row on each margin; placenta covered with numerous ovules. Busselton district ..... 6. *C. aculeata* R.Br.
27.* Marginal setae white (rarely black), usually prominent and in two or more distinct vertical rows on each margin; placenta recurved with few ovules.
28. Stamens biseriate; perianth yellow or purplish-yellow or quite purplish-red. Widely distributed ..... 15. *C. setigera* R.Br.
28.* Stamens ± uniseriate; perianth purplish-creamy white or quite creamy-white. Darling Range ..... 14. *C. setosa* Lindl.

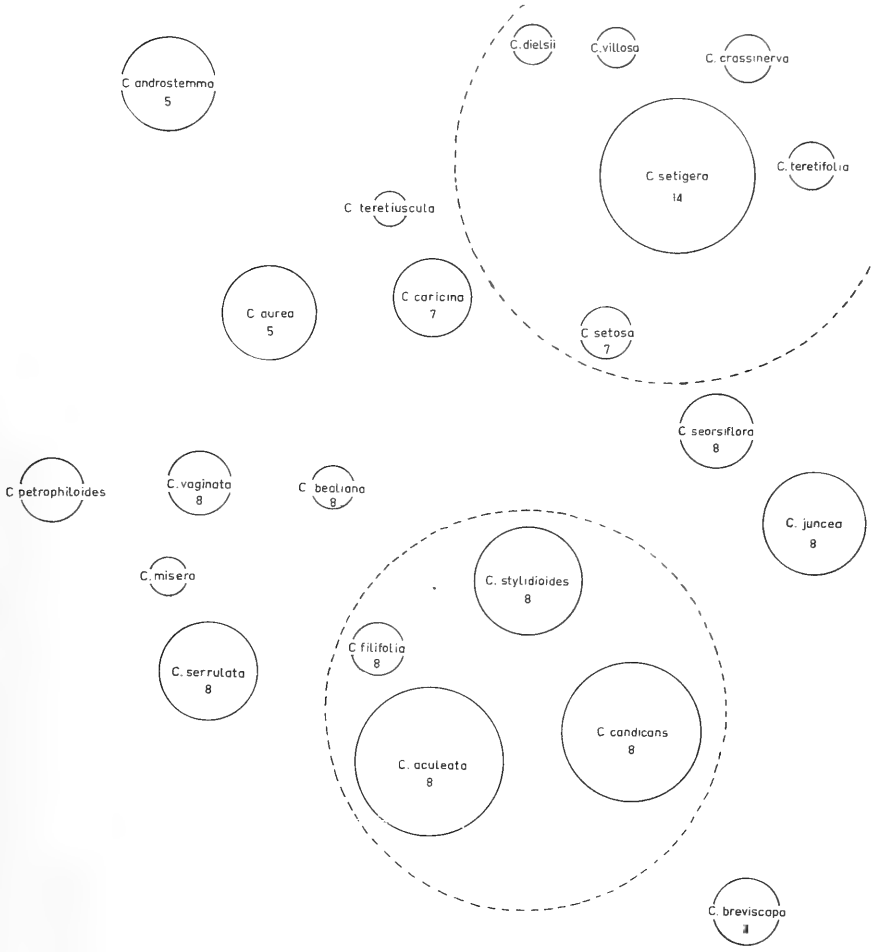


Fig. 95.—Diagrammatic representation of possible interspecific relationships.

Species Dubium.

Conostylis spinuligera F. Muell. ex Benth., *Fl. Aust.*, 6: 438 (1873).

Haptotype: J. Drummond (MEL).

Specimens from the single known collection of this species have been examined by the writer. It appears to belong to the *C. aculeata* group, but does not agree well with any of the well-known taxa in that group.

Interspecific Relationships.

The immediate relationships of the various species of *Conostylis* were mentioned with the descriptions above. The writer's impression is that the genus as a whole

shows, firstly, two well-defined species groups, and, secondly, a number of "loose ends"—species whose affinities are obscure or uncertain.

The probable phylogenetic relationships of the genus, in so far as it has been possible to speculate from existing data, have been set out in diagrammatic form in Figure 95: while it is not suggested that any existing species have evolved from any other existing species, some present-day species appear less specialized than others and may therefore be said to be more "primitive". Such species are placed near the bottom of the chart, while those which are morphologically more highly specialized are placed near the top: the lateral disposition of the species is governed purely by convenience in drawing the diagram. The size of the species circles is very roughly

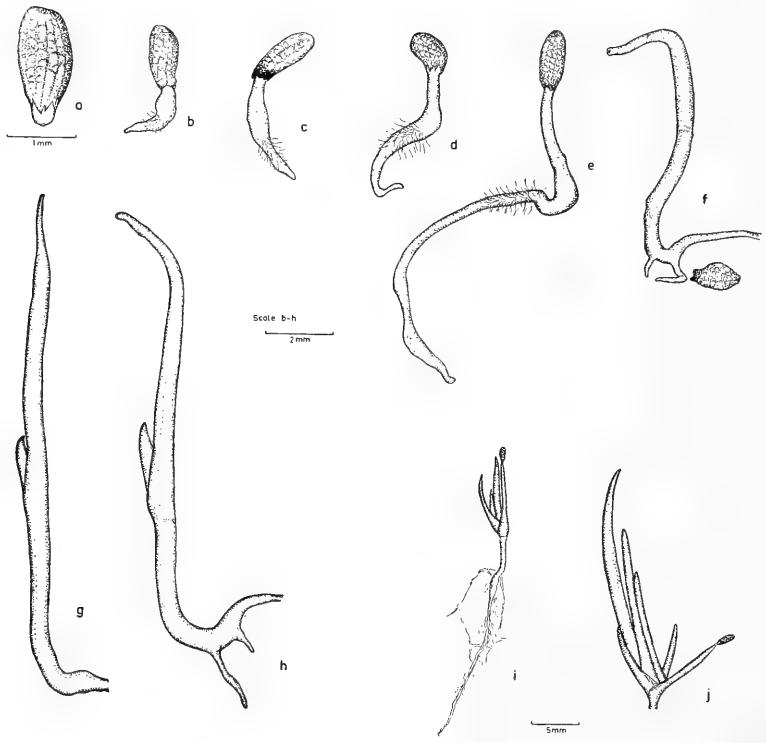


Fig. 96.—Germination and early seedling development in *C. candicans* Endl. *a*, germinating seed, approx. 20 days after incubation; *b-h*, seedlings at various stages of development, *a-f*, approx. 20, and *g-h*, 55 days after incubation; *i-j*, leaf development, shown in two seedlings drawn 110 days after incubation.

proportional to the estimated numbers of individuals within the total area of distribution of the species. Haploid chromosome numbers are shown where known. The dotted circles enclose the two major groups of species, within each of which the species are undoubtedly closely related.

The single species *C. breviscapa* shows several morphological characteristics which may be regarded as primitive, e.g., free perianth segments above the ovary, and free anther thecae; its chromosome number is half that of many other species in the genus, suggesting that it is most closely related to an ancestral form having the basic chromosome number.

On the other hand, *C. androstemma* is considered to have the most highly specialized floral structure, and it is postulated that its chromosome number is derived from the predominating n = 8 by reduction, perhaps in two stages. Two species exhibit a long tubular corolla (*C. androstemma* and *C. bealiana*), but in view of the following facts,

this is considered to be due to convergence, *C. bealiana* being much less highly advanced: (1) *C. androstemma* shows further floral modifications, e.g., long filaments and a peculiar peltate placentation (presumably the most advanced type, see Fig. 1, *k*, *l*, *m*); (2) the chromosome number of *C. bealiana* is the same as that of the *C. aculeata* group, and its placentation is of the same type.

The species *C. setigera* and its relatives are considered to be relatively highly advanced because of floral modifications (the usually biseriate stamens and recurved placentation) and because the chromosome numbers are different from those of *C. breviscapa* and *C. aculeata*. The haploid number of *C. setigera* itself appears to be 14, possibly a simple polyploid derivative of the n = 7 of *C. setosa*. The latter species may have evolved from the n = 8 series by reduction. The two species *C. setosa* (n = 7) and *C. setigera* (*n* = 14) are closely related on leaf morphology, and it is interesting to note that the former is highly restricted in its distribution while *C. setigera* is one of the most common and widespread species in the genus.

Among the remaining species, few clues to phylogenetic relationship are evident. The writer has been unable to recognize clear-cut groups of species such as those associated with *C. aculeata* and *C. setigera*.

Four species, *C. serrulata*, *C. bealiana*, *C. seorsiflora* and *C. juncea*, are placed near the *C. aculeata* group on the basis of chromosome number and/or placentation. *Conostylis petrophiloides* is placed near *C. vaginata* because of somewhat similar involucral bracts, and *C. misera* seems related to *C. serrulata* on leaf morphology. Some rearrangement must be expected when these species are more fully studied.

Several species, whose chromosomes are as yet unknown, seem very closely related to *C. setigera* (*C. teretifolia*, *C. crassinerva* and *C. dielsii*). Their floral morphology is almost identical.

The position of *C. teretiuscula* is perhaps the most problematical of all. The species is poorly known, but a slight resemblance between its floral structure and that of *C. caricina* has resulted in its being placed near that species. It may also be related to the *C. setigera* group, many of whose members it resembles in habit and habitat. It is placed above *C. caricina* in the diagram chiefly to show its probable lack of affinity with the *C. aculeata* group.

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EXPLANATION OF PLATES IX-X.

Plate ix.—Type specimens of four species of *Conostylis* described by Robert Brown in 1810. 1. *C. aculeata*, type species of the genus. 2. *C. setigera*. 3. *C. breviscapa*. 4. *C. serrulata*. (By courtesy of the British Museum.) The scale is the same for all the photographs

Plate x.—*Conostylis* specimens. 1. *C. vaginata* Lindl., Oldfield 587. 2. *C. phathyrantha* Diels, C. A. Gardner 2890A. 3. *C. aurea* Lindl., Drummond, 1839 (holotype). 4-5. *C. misera* Endl., Preiss 1406. 6. *C. bealiana* F. Muell., R. D. Royce 3526. 7. *C. seorsiflora* F. Muell., Stirling Range, F. Mueller. 8. *C. dielsii* W. V. Fitzg., Mingenew, W. V. Fitzgerald. 9. *C. androstemma* (Lindl.) F. Muell. ssp. *androstemma*, South Hutt River, Oldfield. 10. Ditto, Preiss 1409. 11. *C. crassinerva* sp. nov., Mt. Lesueur, N. H. Speck (holotype). (Fig. 3 by courtesy University of Cambridge.)

THE FAMILY SPELEOGNATHIDAE IN AUSTRALIA (ACARINA).

By Robert Domrow, Queensland Institute of Medical Research, Brisbane.

(Thirty-one Text-figures.)

[Read 26th October, 1960.]

Synopsis.

The three known Australian species of speleognathid mites (intranasal parasites of vertebrates) are redescribed. They are *Speleognathus australis* Wom., whose normal host appears to be cattle, *Speleognathopsis derricki* (Wom.), n. comb., from *Rattus assimilis*. *R. conatus* and *R. rattus* in Queensland, and *Lawrencarus angelae* (Wom.), n. comb., from native frogs in South Australia and north Queensland.

The mites of this apparently old family are intranasal parasites of a wide variety of mammals and birds, although one small genus is restricted to frogs and toads. Males do not seem to be common and, from what little is known, the entire life history is spent in the nasal passages of the host. All species are characterized by extremely simple gnathosomes, and by very strong paired claws, which may be completely retracted into a deep dorsodistal pit on the tarsi. The most striking diagnostic character is, however, a sclerotized subcuticular, mesh-like armour on the legs. As a result of their obligatory internal parasitism, most species are otherwise extremely delicate. This delicacy is paralleled by a marked trend toward reduction in many characters, and minor individual variants are common. It is important to recognize these variations, and it seems unlikely that the six genera and ten subgenera proposed for this group are all valid. A conservative system is followed here.

Of the approximately 40 known species, three are Australian. *Speleognathus australis*, upon which Womersley (1936) based the family, was found free-living on the surface of cattle and horse troughs in South Australia. Fain (1956*a*, 1956*b*) has since taken this species in the nasal cavities of cattle in Africa. Numerous specimens are now available.

The other two Australian species, however, are based on single specimens. They are *Speleognathopsis derricki* from *Rattus assimilis* (Queensland), and *Lawrencarus angelae* from a native frog (South Australia). Both these species have recently been rediscovered in north Queensland in the type or related hosts.

The original descriptions of all three species now seem somewhat generalized, and Mr. Womersley has suggested to me that I provide fresh ones.

Genus Speleognathus Womersley.

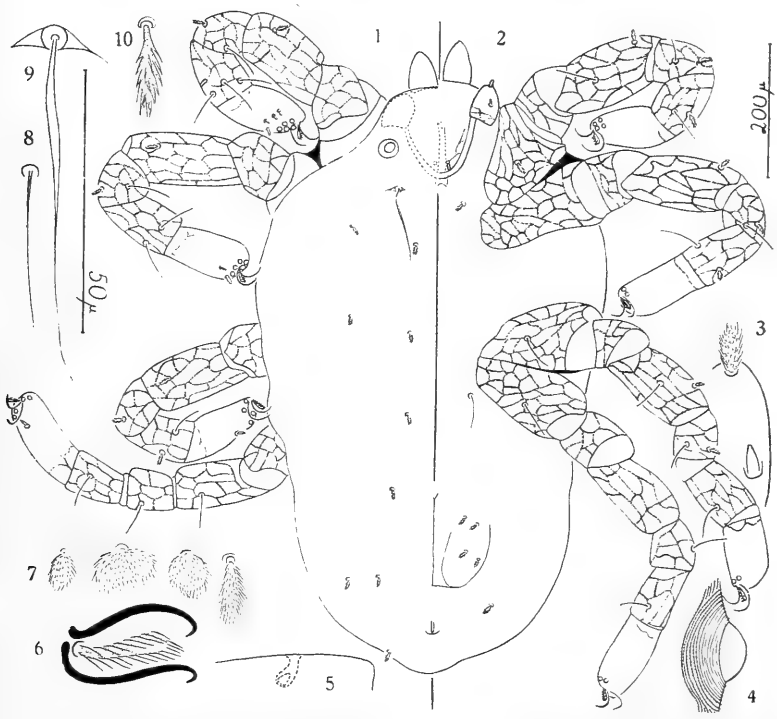
Speleognathus Womersley, 1936, p. 313. Type species *Speleognathus australis* Womersley, 1936.

Speleognathus australis Womersley, 1936.

Speleognathus australis Womersley, 1936, p. 313. *Speleognathus bovis* Fain, 1956*a*, p. 156.

Female.—*Dorsum*: Dorsal shield entirely absent. Sensillae somewhat swollen basally, but finer apically, 67–74μ long. Eyes large and with distinct corneae; in distended specimens they are set dorsally, but in unfed specimens they are anterolateral. Corneae clear, convex, and surrounded by concentric cuticular striae. Dorsal setal pattern 4.4.2.2.4.(2), all the setae being ramified (R). Cuticle striate-punctate. Peritremes have not been detected. *Venter*: With 2R setae between coxae I & II, and two slender nude setae (S) just behind coxae IV. Genitalia elongate, flanked by three or four pairs of ramified setae. Genital discs absent. Anus small, flanked by single

pair of ramified setae. (It is difficult to decide whether the last pair of dorsal setae should be classed as dorsals or as anals.) *Gnathosoma* somewhat longer than broad, deeply set beneath anterior part of body; with pair of ramified setae basoventrally, and containing an elongate, sclerotized structure. Chelicerae very weakly attached, and frequently much displaced in mounted specimens. Palpi with single free segment, which bears swollen barbed seta apically, and nude sensory rod laterally. *Legs* six-segmented, with strongly sclerotized subcuticular reticulation both dorsally and ventrally on all segments except tarsi. Setal pattern as follows: coxae R.O.S.S., femora 2R.S/2R/2R.S/S, genua 2R.2S/2R.2S/2R.S/2S, tibiae R.4S/R.3S/R.2S/2S, tarsi 12.8.7.7. Tarsi I have three dorsal, five distal, and four ventral setae; tarsi II one dorsal, five distal, and two ventral setae; and tarsi III & IV one dorsal, four distal, and two ventral



Text-figs 1-10.—*Speleognathus australis* Womersley. Female, slightly compressed. 1, dorsum; 2, venter; 3, palp in ventral view; 4, eye; 5, cone-like sensory seta in pit in tibia I; 6, claws and pulvillus; 7, from left to right, ventral, distal (two), and dorsal setae on tarsus II; 8, simple seta on femur IV; 9, sensilla; 10, ramified seta at end of body.

setae. The more proximal tarsal setae are swollen and barbed, the more distal ones globular and barbed. Tarsi I & II with minute nude sensory rod dorsally. Tibia I with minute cone-like sensory seta set in pit on dorsal surface. Each tarsus deeply excavate dorso-distally, forming deep pit, into which two claws can be completely retracted. Pulvilli simple, held up between claws, but with hairlets directed ventrally. *Length* of body excluding gnathosoma 792–848μ; some smaller, shrivelled specimens measure 550–715μ. All specimens appear to be females. They are pale yellowish-brown, with somewhat darker legs.

Variation: Most characters have been checked about fifteen times each. The following minor variations were noted: coxal formula R.O.S.O. in 1 of 15; coxal formula O.O.S.S. in 1 of 15; one ramified seta behind coxae IV in 1 of 13; tibia I R.3S in 1 of 15; tibia IV 3S in 2 of 16.

Material examined: The holotype (ACC726) of this species (as well as those of the two species described below) has been examined through the courtesy of Messrs. H. M. Hale and H. Womersley, Adelaide, who have also sent me one of Dr. Fain's specimens. I am further indebted to Dr. R. V. Southcott, Adelaide, for the loan of nine topotypic specimens, collected on the surface of water in cattle and horse troughs, Glen Osmond, South Australia, 2.vi.1935, 27.vii.1935, 11.iii.1936, 11.iv1936, 17.vi.1936, 13.i.1937, and 6.iii.1937, R.V.S. (ACC 735, 737, 739, 741, 742, 744, 748). Dr. Southcott mentions (*in litt.*, 31.iii.1960) that he has seen no live specimens since 1941.

Note: It is of interest that Fain's 21 African specimens of *S. bovis* (= *S. australis*) were collected in the frontal and maxillary sinuses of two of three "*bovidés*" examined.

Genus Speleognathopsis Cooreman.

Speleognathopsis Cooreman, 1954, p. 428. Type species *Speleognathopsis galli* Cooreman, 1954, p. 429.

Speleognathopsis derricki (Womersley, 1954), n. comb.

Boydaia derricki Womersley, 1954, p. 65. *Astrida derricki*, Fain, 1956c, p. 36.

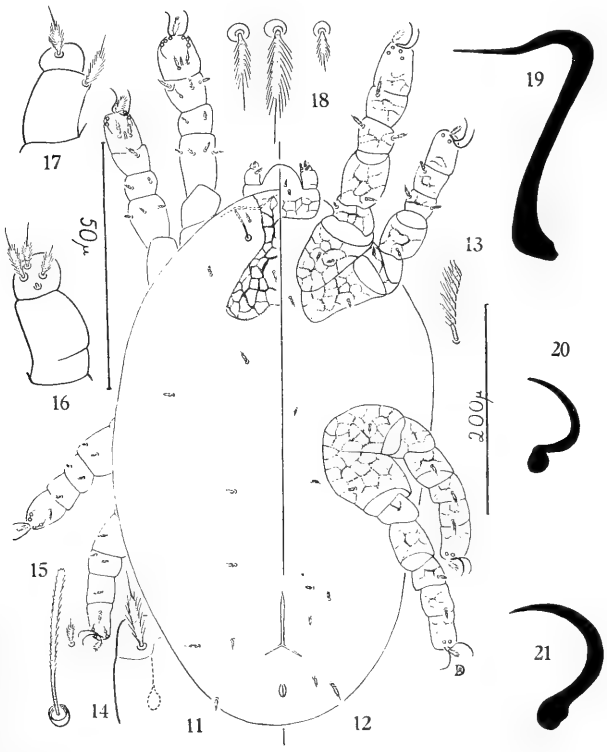
Female.—*Dorsum*: Dorsal shield subcuticular, in form of stout inverted Y, with irregular, reticulate sclerotized pattern, except for clear subcircular central zone bearing two setae. Sensillae set near junction of arms of shield, very weakly clavate, finely barbed, and 29–32μ long. Eyes absent. Dorsal setal pattern (including presensillary setae) 2.4.4.2.2.4.2. All setae stout or even clavate, with barbs along shaft, and longer terminal filament. Cuticle very minutely striate-punctate. The pattern of striae is as shown in the original description. On the legs the striae are in general longitudinal. Weakly defined peritremes are present above gnathosoma. *Venter*: With one pair of setae between coxae I & II, and two pairs between coxae III & IV. Genitalia in form of slender inverted Y, flanked by three pairs of setae; genital discs absent. Anus flanked by two pairs of setae, of which outer pair are largest setae on mite. *Gnathosoma* slightly broader than long, with reticulate pattern basoventrally. Two pairs of minute setae are also present on ventral face. Palpi with two free segments, although a third incipient segment may perhaps be traced ventrally. Basal segment with one dorsodistal seta; apical segment with one dorsal and three ventral setae, in addition to extremely minute basoventral sensory rod. *Legs* six-segmented, with reticulate pattern ventrally. Setal pattern as follows: coxae 2.1.1.1, trochanters 1.1.0.0, femora 5.4.3.1, genua 4.4.3.3, tibiae 4.2.2.2, tarsi 12.8.7.7. Tarsi I have two dorsal, six apical, and four ventral setae; tarsi II have two dorsal, four apical, and two ventral setae; tarsi III & IV one dorsal, four apical, and two ventral setae. On tarsi I & II, between the two dorsal setae, is a short nude sensory rod. Tibiae I dorsodistally with an internal "flagelliform" structure similar to that described by Boyd (1948) for *Boydaia sturni*. Each tarsus deeply excavate dorsodistally to accept retracted claws. Pulvillus as in *Speleognathus australis*. *Length* of body excluding gnathosoma 396–462μ; some smaller, shrivelled specimens measure about 363μ. All specimens examined are of the same facies, and are apparently females. One contains a six-legged embryo.

Variation: All the characters described above have been checked in about 15 specimens, while bilateral characters have been checked up to 30 times. Most characters are quite constant, but the following minor variations have been noted: only one seta in 4th dorsal row in 1 of 17; an additional seta in 5th dorsal row in 1 of 17; genital setae 3.2 in 1 of 17; genital setae 3.4 in 1 of 17; intercoxal setae 2.2.1 in 1 of 14; coxal setae 2.1.1.2 in 2 of 29; genual setae 3.4.3.– in 1 of 19; genual setae 4.4.3.2 in 1 of 19; seta on basal palpal segment apparently absent in 1 of 15.

Larva.—*Dorsum*: Dorsal shield absent, as are the reticulations on gnathobase and legs. Sensillae as in adult, but shorter, 17μ long. Eyes absent. Dorsal setal pattern 4.4.2.2.4.2; presensillary setae probably absent. *Venter*: With one pair of setae between coxae I & II, and another pair between coxae III. No trace of genitalia. Anus flanked by two pairs of setae, of which the posterior pair is stronger. *Gnathosoma*: As in

female. *Legs* six-segmented. Setal pattern as follows: coxae 2.1.1, femora 5.4.3, genua 4.4.3, tibiae 4.2.2, tarsi probably 10.6.5. At least tarsus I with nude sensory rod dorsally. Flagelliform structure in tibia I doubtful. Legs I and II shaped as in adult, but tibiae and tarsi III much expanded, the tarsus possessing a single, much enlarged claw as figured, and apparently lacking a pulvillus. *Length* of body excluding gnathosoma 288μ.

Material examined: The holotype female, the only specimen previously known, collected free-living on *Rattus assimilis*, Mt. Glorious, S.E. Queensland, 6.viii.1951, E. H. Derrick; also 55 females and one larva collected recently in the noses of rats as follows:



Text-figs 11-21.—*Speleognathopsis derricki* (Womersley). Female, slightly compressed. 11, dorsum; 12, venter; 13, pulvillus; 14, "flagelliform" structure inside tibia I; 15, sensilla and presensillary seta; 16 and 17, palp in ventral and dorsal views, respectively; 18, from left to right, middorsal, dorsal (tarsus I), and coxal setae; 19, tarsal claws III of larva; 20 and 21, tarsal claws I of larva and adult, respectively.

From 16 *R. assimilis*, 23 mites: I. Secondary rain-forest, Dinner Creek, near Innisfail, north Queensland, J. L. Harrison. Two mites 28.x.1958; 1 mite 12.xi.1958; 2 mites 19.xi.1958; 1 mite 2.xii.1958; 1 mite 10.xii.1958; 2 mites 10.xi.1959. II. Rain-forest, Etty Bay Hills, and Flying Fish Point, near Innisfail, J.L.H. and R.D. One mite 3.iv.1959; one mite 7.v.1960. III. Rain-forest, Crawford's Lookout, Palmerston National Park at 1,200 feet, near Innisfail, J.L.H. and R.D. Two mites 5.iii.1959; 1 mite 20.iii.1959; 1 mite 7.vi.1960. IV. Rain-forest, Palmerston National Park at 2,200 feet, R.D. Two mites 7.iv.1959; 2 mites 8.iv.1959; 2 mites 9.iv.1959; 1 mite 16.iv.1959. V. Mangrove swamp, Flying Fish Point, J.L.H. One mite 4.v.1960.

A further 44 *R. assimilis* were examined from the above localities (and also Dunkinju Ck.) throughout the year, but no speleognathids were found. Five of the infested rats also had intranasal *Walchia* larvae, one also had intranasal *Laurentella* larvae, and two had both *Walchia* and *Laurentella* larvae (Trombiculidae).

From 10 *R. conatus*, 16 mites and one larva: I. Sugar cane, near Innisfail, J.L.H. Three mites and one larva 10.ii.1960; one mite 15.vi.1960; 3 mites 17.vi.1960; one mite 21.vi.1960; one mite 21.vi.1960; two mites 21.vi.1960; one mite 22.vi.1960; one mite 22.vi.1960; one mite 23.iii.1960. II. Grass and brush on river bank beside sugar cane, J.L.H. Two mites 15.vi.1960.

A further eight *R. conatus* from similar localities were also examined, but no speleognathids were found.

From 12 *R. rattus*, 16 mites: I. House, Water Street, West Innisfail, J.L.H. Three mites 2.ix.1958; 2 mites 4.ix.1958. II. House, Innisfail, J.L.H. and R.D. One mite 23.ii.1959; one mite 23.ii.1959; one mite 13.v.1960; one mite 13.v.1960; one mite 8.vi.1960. III. Grass or sugar-cane on bank of Johnstone River, near Innisfail District Hospital, J.L.H. One mite 11.ix.1958; 2 mites 14.i.1959; 1 mite 7.v.1959. IV. Sugar-cane, Daradgee, near Innisfail, R.D. One mite 26.ii.1959. V. Grass and pumpkins, Goondi, near Innisfail, J.L.H. One mite 25.v.1960.

A further 37 *R. rattus* were also examined from similar localities throughout the year, but no nasal mites of any kind were found.

The incidence of these mites is therefore low. In the following figures, the numbers represent *R. assimilis*, *R. conatus* and *R. rattus* from left to right. Four mites were found in 0/1/0 rats, three mites were found in 0/1/1 rats, two mites in 7/2/2 rats, one mite in 9/6/9 rats, and no mites in 44/8/37 rats. The three host rats have characteristic ecological requirements (Harrison, 1960), but seem to be equally infested. No difference can be seen between the mites from the three hosts.

The mites are found deep in the nasal passages of the rats, usually 15–20 mm. behind the nostrils. They are velvety white, and run quickly over the mucus and blood in the opened nasal cavity. The trombiculid mites they are sometimes associated with are very sluggish, and occur more anteriorly, among the turbinal laminae (see Audy and Nadchatram, 1957).

The following 108 mammals have also been examined for nasal mites, but no speleognathids were found:

Marsupials.		
Dasyuridae:	*Antechinus flavipes godmani*	1
Peramelidae:	*Perameles nasuta*	16
	Isoodon macrourus	17
Rodents.		
Muridae:	*Hydromys chrysogaster*	1
	Melomys cervinipes / *M. lutillus*	35
	Uromys caudimaculatus	27
	Mus musculus	8
Bats.		
Rhinolophidae:	*Rhinolophus megaphyllus*	1
Pteropodidae:	*Pteropus conspicillatus*	2

Notes: Womersley (1954) originally assigned this species to *Boydaia* Womersley, 1953 (genotype *Speleognathus sturni* Boyd, 1948). In *B. sturni*, a bird parasite, a dorsal shield is never present. Later, Fain (1956c) removed *derricki* to *Astrida* Fain, 1955, accepting Womersley's statement that eyes are present. I have been unable to see eyes in the present series, but the dorsal shield is distinct. I would therefore prefer to remove *derricki* to *Speleognathopsis* Cooreman, 1954, disregarding, with Clark (1960), the three subgenera proposed by Fain (1958).

Genus Lawrencarus Fain.

Lawrencarus Fain, 1957, p. 250. Type species *Riccardoella ewert* Lawrence, 1952, p. 747.

LAWRENCARUS ANGELAE (Womersley, 1953), n. comb.

Boydaia angelae Womersley, 1953, p. 83. Not *Boydaia angelae*, Fain, 1956*b*, p. 647 (= *Lawrencarus eweri*).

Female.—*Dorsum*: Dorsal shield entirely absent. Anterior sensillae slightly thickened in basal half, but extremely attenuate in distal half, 69–72μ long; one or two minute barbs appear to be present where attenuation commences. In the holotype, the posterior sensillae are present, while in the specimen illustrated only one posterior sensilla is present, the other being replaced by an ordinary, basally barbed body seta. In the third specimen, at least one posterior sensilla is present. Eyes absent. Dorsal setal pattern 2.2.2.3 in specimen illustrated. Presensillary setae present in holotype only. All setae slightly thicker and shortly barbed basally, but with extremely fine filament distally (this filament is extremely hard to see if obscured by the cuticular pattern, but is present on all setae in both species of the genus). Cuticle very minutely striate-punctate. Weakly defined peritremes present behind gnathosoma. *Venter*: With one pair of setae between coxae I & II, and two pairs between coxae III & IV. Genitalia in form of inverted Y, flanked by three or four setae on each side; genital discs absent. Anus small, flanked by two pairs of setae, the exterior pair being the stronger. *Gnathosoma* slightly longer than wide, with weak reticulations ventrally in holotype only; with two setae on ventral face. Palpi with one short rounded free segment, bearing dorsodistal and distal seta, and inner nude sensory rod. *Legs* six-segmented, with weak reticulate pattern ventrally in specimen figured; the holotype, however, has strong reticulations dorsally and ventrally.* Setal pattern as follows: coxae 0.0.1.0, femora 2.2.2.0, genua 4.4.2.1, tibiae 4.3.2.2, tarsi 12.8.8.8. Tarsi I have two dorsodistal, six distal, and four ventral setae; tarsi II-IV two dorsodistal, four distal, and two ventral setae. On tarsi I & II, either between or outside dorsodistal setae, a short nude sensory rod. Tibiae I dorsodistally with minute cone-like sensory seta set in small pit. Each tarsus deeply excavate dorsodistally to accept retracted claws. Pulvillus simple, with five or six fine, curved filaments. *Length* of body excluding gnathosoma 527μ. All three specimens appear to be females.

Variation: Apart from the variation in the dorsal setal pattern and posterior sensillae, the only other variant I have seen is a seta on coxae IV on one side of one specimen.

Material examined: Of *L. angelae*, the holotype female (previously the only known specimen), from the mucus under the tongue of a frog, *Limnodynastes tasmaniensis*, Adelaide, 23.x.1952, M. L. Angel. Also two white females (one damaged), from the mouth of a native frog, secondary rain-forest, Dinner Ck., N.Q., 19.i.1960, J. L. Harrison. The nasal cavities of four toads (*Bufo marinus*) were also examined, but no mites were found (February-March, 1959, R.D.).

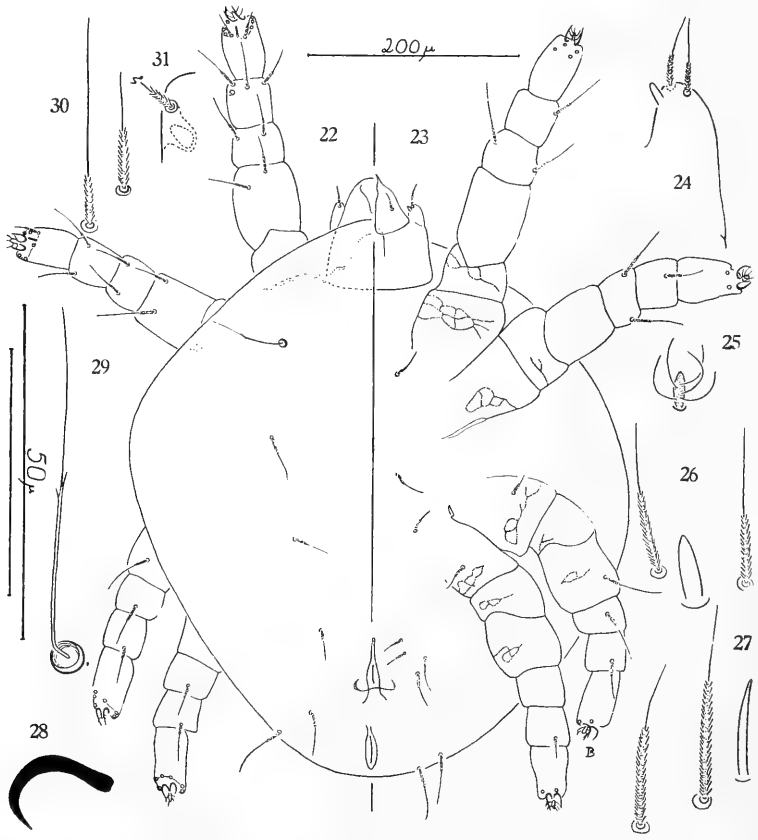
Of *L. eweri*, three females from the nasal cavities of *Bufo regularis*, Pietermaritzburg, R. F. Lawrence, and Astrida, January, 1956, A. Fain. This African species has also been recorded from *B. superciliosus* and perhaps from *B. carens* (Fain, 1958; Lawrence, 1952). I am most grateful to Dr. A. Fain, Antwerp, for the gift of two of these specimens.

Notes: The genus *Bufo* does not occur naturally in Australia, although one introduced species is present. This is the cane toad, *B. marinus*, introduced from Central America by way of Hawaii and Fiji. In north Queensland, it is common in all habitats from suburban gardens to rain-forest, but its range does not yet approach Adelaide. The two stocks which yielded *Bufo* and *Limnodynastes* have been long separated geologically, since the late Mesozoic, so the recognition of both described species seems justified. They may be separated by the anogenital setae, the number of which is correlated with geographical distribution. An excellent description of *L. eweri* has been given by Lutfy (1960).

* The degree of sclerotization depends both on the age of the specimen on mounting, and the strength of the clearing agent used.

Fourteen to seventeen pairs of anogenital setae present; sensory rod on tarsus I slender, set outside the two dorsodistal setae. African. ..... *L. eweri.*
Five or six pairs of anogenital setae present; sensory rod on tarsus I stout, sometimes set between the two dorsodistal setae. Australian. ..... *L. angelae.*

There are also minor differences in the leg setation. In *L. angelae*, genua and femora III have two setae each, and tarsi III & IV eight. In the three specimens of *L. eweri* I have seen, genua III have three or four setae, femora III one or two, and tarsi III & IV seven. The difference in the setae on tarsi II and IV (dorsodistals paired in *angelae*, but single in *eweri*) is perhaps significant, but the variation in the other segments parallels that discussed above for *Speleognathus australis* and *Speleognathopsis derricki.*



Text-figs 22-31.—*Lawrencarus angelae* (Womersley). Female, rather compressed. 22, dorsum; 23, venter; 24, palp in dorsal view; 25, pulvillus; 26 and 27, dorsodistal and sensory setae on tarsus I of *L. angelae* and *L. eweri,* respectively; 28, tarsal claw I; 29, sensilla; 30, from left to right, setae on genu I and tarsus II; 31, cone-like sensory seta in pit in tibia I.

One final comment is necessary. Fain (1956*b*, 1957) quotes Womersley (*in litt.*) as follows: in *L. angelae*, "there are a few barbed setae on the ventral surface other than the genital and ventral in my unique specimen, but unfortunately this area is in a bad condition to ascertain the number and arrangement". Actually, in the holotype, the dorsal cuticle has been ruptured anteriorly, and folded back beyond the end of the body. The setae in question, then, are not additional genitoanals, but simply the displaced dorsal series. At least thirteen are visible (excluding the presensillary and genital setae), so the dorsal setal pattern probably normally approaches that figured by Womersley.

Acknowledgements.

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————, 1954.—Another new species of *Boydaia* (Speleognathidae ; Acarina) from Australia. *Trans. Roy. Soc. S. Aust.*, 77 : 65-66.

STUDIES ON AUSTRALIAN THYNNIDAE. IV.

Results of Study in the British Museum.

By K. E. W. Salter.

[Read 30th November, 1960.]

In the Thynnidae there is much confusion and it is uncertain whether some species are to be accepted as valid or as synonyms. From the check lists (Salter, 1953, and Given, 1954) it is estimated that, of the total of 501 species then described, only about 490 can be regarded as authentic. This group was last revised in 1907–1910 by Rowland E. Turner, and in subsequent years a large number of species were added by that author. Today, there are so many more new species to be described that the original keys and descriptions are no longer adequate and a major revision of Thynnidae is in progress.

Obviously such a monograph could never be attempted without a fairly complete collection of correctly identified Thynnidae from the whole of Australasia and the adjacent islands, and, in order that such a collection might be assembled, about 5,400 thynnids were borrowed from the Macleay Museum, the N.S.W. Department of Agriculture, the South Australian Museum, the West Australian Museum and the National Museum of Victoria. From this large collection, representatives of many species were selected for subsequent identification in the British Museum, and to this end I sailed for England on 10th June, 1958, returning to Sydney on 24th September, 1959. Although time did not permit the completion of this project in its entirety, the following results were obtained:

Total number of species of Australasian Thynnidae: Identified and brought back to Sydney (males), 383; included in type material located in Australia, 16; with co-types available to me in U.S.A., 4; illustrated either by photographs or drawings, 44; not photographed or drawn as extension of time had expired, 2; with types which are either lost or unavailable at present, 15; known from the female sex only, 26.

Considered in all probability to be valid (as at 1953), 490.

As there are so many species of thynnid, and as the sexes are so dissimilar, it seems advisable to concentrate principally on the males for the present. Consequently, as there are twenty-six species which are known only from the female sex, the total number of species to be considered for the time being can be reduced to 464. Further, as an additional sixteen species are included in the types available in Australia, we now have 399 identified species here, and thus the total number outstanding amounts to sixty-five. Of the sixty-five species, there are four co-types which can be borrowed from the U.S.A. when they are required, and forty-six types in the British Museum, duplicates of which could not be found. There are twelve types which have not as yet been examined and three others which are presumed to be lost. As a step towards the ultimate recognition of the forty-six unduplicated types in the British Museum, 467 photomicrographs and eighty-seven drawings were made. The 467 photomicrographs illustrate forty-four of these unique B.M. types and, of these, 280 were in colour and 187 in monochrome. Unfortunately, two types had to be omitted because my extension of time had expired.

Since my return to Sydney, my first and most pressing task has been to find duplicates of as many species as possible, so that the specimens on loan to me might be returned with all possible speed. This section of the work is still in progress and

will involve an examination of all the collections of Thynnidae in Australia. By means of this set of identified thynnids, more than 3,100 specimens have been determined, and, thanks to additional loan material, the total number of thynnids for examination in this investigation now exceeds 7,000 specimens. It is safe to say that this collection is the largest assemblage of Thynnidae in existence.

In conclusion, I would like to express my very sincere appreciation of the wonderful assistance which has been given to me by the Directors of more than a dozen museums and institutions both in Australia and overseas, who have kindly lent me material or have permitted me to study the thynnids housed in their departments. Space is too limited here, but the help that has been thus extended to me by so many has been truly magnificent, for without this full co-operation it would have been quite impossible for the revision of the Thynnidae ever to be attempted. In particular, I wish to thank Dr. I. H. H. Yarrow of the British Museum, Professor G. C. Varley of Oxford and Dr. J. van der Vecht of Leiden.

ABSTRACT OF PROCEEDINGS

ORDINARY MONTHLY MEETING.

30th March, 1960.

Dr. I. V. Newman, President, in the chair.

The Chairman announced that library accessions amounting to 45 volumes, 383 parts or numbers, 32 bulletins, 12 reports and 33 pamphlets, total 505, had been received since last meeting.

PAPERS READ (by title only).

1. The Subgenus *Ochlerotatus* in the Australian Region (Diptera, Culicidae). III. Review of the Victorian Species of Perkinsi and Cunabulanus Sections with Descriptions of Two New Species. By N. V. Dobrotworsky.

2. Revision of the Genus *Acrotriche* R.Br. (Epacridaceae). By Betsy R. Paterson.

3. Notes on Metamorphic and Plutonic Rocks and their Biotites from the Wantabadgery-Adelong-Tumbarumba District, N.S.W. By T. G. Vallance.

4. Ariciid Polychaetes in Australia. By D. T. Anderson.

ORDINARY MONTHLY MEETING.

27th April, 1960.

Dr. I. V. Newman, President, in the chair.

The following were elected Ordinary Members of the Society: Dr. G. K. Berrie, Wingala, N.S.W.; Messrs. T. V. Bourke, Graman, N.S.W.; H. C. Dorman, Speers Point, N.S.W.; D. J. Hartigan, Northwood, N.S.W.; K. J. Horne, Sydney; Dr. T. B. H. Jenkins, Sydney University; Dr. Violet H. Jolly, Warragamba Dam, N.S.W.; Messrs. R. M. Moore, Canberra, A.C.T.; P. E. Reavell, King's Cross, Sydney; B. W. Salkilld, Abbotsford, N.S.W.; and A. G. Thorne, Neutral Bay, N.S.W.

The Chairman announced that the Council had elected the following office-bearers for the 1960-61 session: Vice-Presidents, Dr. T. G. Vallance, Dr. S. Smith-White, Dr. Lilian Fraser and Mr. S. J. Copland; Honorary Treasurer: Dr. A. B. Walkom; Honorary Secretaries, Dr. A. B. Walkom and Dr. W. R. Browne.

The Chairman announced that library accessions amounting to 10 volumes, 147 parts or numbers, 3 bulletins, 2 reports and 4 pamphlets, total 166, had been received since the last meeting.

The Chairman offered congratulations to Dr. Ida A. Browne on the award of the Society's Medal of the Royal Society of New South Wales for 1959.

The Chairman announced that the Tenth Pacific Science Congress of the Pacific Science Association will be held at Honolulu from 21st August to 6th September, 1961.

PAPERS READ

1. Spontaneous Chromosome Breakage in *Astroloma pinifolium*. By S. Smith-White and Alison McCusker.

Discussion: In answer to questions, Dr. Smith-White explained the difference between break of the whole chromosome, the chromatid and a sub-chromatid unit, and that it was only the chromatid break that could fit the pattern of pollen sterility, if such breaks were the cause of sterility.

2. Preliminary Studies in Population Estimation of Two Species of Stick Insects (Phasmatidae Phasmatodea) occurring in Plague Numbers in Highland Forest Areas of South-Eastern Australia. By K. G. Campbell.

Discussion: The discussion by the author and several members centred round the efficacy and economics of control measures, such as spraying, releasing sterility-bearing mutants and releasing parasites, particularly in view of the crop concerned being long term over many years and not merely an annual crop. The problem is one not only of a crop, but of land-cover in relation to conservation. Control may have to be viewed as a long-term ecological project.

3. Australian Mosquitoes described by Macquart. I. Species in the Paris Museum, *Aëdes* (*Finlaya*) *alboannulatus* (Macquart), *Aëdes* (*Finlaya*) *rubrithorax* (Macquart), *Aëdes* (*Ochlerotatus*) *albirostris* (Macquart). New Synonymy and a New Species from New Zealand. By J.-M. Klein and Elizabeth N. Marks.

4. Australian Mosquitoes described by Macquart. II. Species in Bigot's Collection, *Aëdes* (*Ochlerotatus*) *nigrithorax* (Macquart). New Synonymy. By Elizabeth N. Marks.

5. A New Tree-Frog (Genus *Hyla*) from Queensland. By Stephen J. Copland.

LECTURETTE.

An illustrated lecturette was delivered by Mr. H. G. Cogger, entitled "Environmental Adaptations in Australian Reptiles".

Discussion: The very diverse evolutionary development described, from the point of view of adaptation, of lizards in Central Australia led to a vigorous discussion. It was emphasized that the surface/volume ratio was shown as significant (as it is in relation to plants). The chief discussion was on the conflict between ideas of time required for such evolution among the lizards, as among the chenopodiaceous plants of the interior, and of time commonly ascribed by geologists for the existence of this desert interior.

ORDINARY MONTHLY MEETING.

25th May, 1960.

Dr. I. V. Newman, President, in the chair.

Mr. N. J. Williams, B.Sc., Miranda, N.S.W., was elected an Ordinary Member of the Society.

The Chairman offered congratulations to the following members on the award of the Ph.D. degree: Drs. B. A. Barlow, B.Sc., J. J. Lawrence, M.Sc., and G. E. Sullivan, M.Sc. (N.Z.).

The Chairman announced that Library Accessions amounting to 13 volumes, 134 parts or numbers, 4 bulletins, 3 reports and 5 pamphlets, total 159, had been received since last meeting.

The Chairman drew the attention of members to the fact that there will be no Ordinary Monthly Meeting in June. On Wednesday, 29th June, 1960, at 8 p.m., the second Sir William Macleay Memorial Lecture will be delivered by Professor Th. Dobzhansky in the Main Hall of Science House, 157 Gloucester Street, Sydney, the subject being "Bridging the Gap between Race and Species". All interested are invited.

PAPER READ.

1. 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. By Y. M. Upadhyaya and E. P. Baker.

Discussion: There was a short discussion centring round the nature of the physiological features which conferred resistance to the parasite and the mechanism of a general resistance to a range of strains of parasite.

NOTES AND EXHIBITS.

On behalf of Dr. A. R. Woodhill, the President exhibited a photograph of a Nemestrinid fly hovering in mid air, taken by Dr. A. J. Nicholson in the late 1920s and coloured by hand by Miss Burns. This is one of many photographs of living insects taken by Dr. Nicholson prior to 1930.

The President, Dr. I. V. Newman, exhibited two three-year-old seedlings of *Pinus radiata*, dried for more than two years. One had then been given the normal treatment for reconditioning collapsed wood, followed by one day in 70% alcohol plus 10% of glycerine to maintain a moist condition on drying again. This reconditioned seedling originally showed the needles more firmly attached than those of the untreated seedling, but it is now damaged by animals during storage. However, the needles, after five years, still endure a narrow U-bend without breaking, in contrast to the untreated needles. Possibly such reconditioning may be of use for examination of old material in herbaria.

Dr. E. P. Baker exhibited a series of morphological variants in cultivated barley concerning for the most part inflorescence characteristics. Most of these are single gene differences from the normal phenotype in each case. Certain chlorophyll mutants were also exhibited again genetically simple in inheritance. A taxonomic classification of cultivated barleys was shown and discussed, particularly in relation to certain of the inflorescence mutants.

Dr. A. R. H. Martin and Mr. Bruce Thom exhibited aerial photographs and maps of the Bulahdelah–Myall Lakes region, demonstrating a wide variety of coastal land forms associated with a marine transgression and its recession stages.

Dr. G. K. Berrie exhibited a small collection of liverworts collected in Australia. The study of liverworts in Australia is almost an open field. Although many of the plants are very similar to those in other continents, there are certainly some interesting plants to be found. Dr. Berrie at Sydney University welcomes specimens of liverworts for identification. Collection of liverworts (and mosses) is particularly easy, as they may simply be wrapped up in newspaper and dried, and will return to their original appearance on moistening.

Dr. T. G. Vallance exhibited specimens of chlorite schist containing porphyroblasts of garnet (almandine-spessartine) about ¼" in diameter. This unusual rock occurs near the Bathurst Granite at the abandoned Mount Apsley Mine, Cow Flat district. The material was probably formed by metasomatic alteration of normal pelitic sediment.

Dr. F. V. Mercer exhibited photographs to show the degree of differentiation of cells of the higher plants, maize, and in the cell of a primitive plant, a member of the blue-green algae. Electron micrographs of a portion of a leaf cell of maize showed the differentiation of the protoplast into chloroplasts, mitochondria, endoplasmic reticulum and membranes, whereas the protoplast of the blue-green cell is apparently not differentiated into cytoplasm and organelles.

Mr. R. K. Bamber exhibited coloured slides illustrating the staining reaction of pit membranes. He had examined the reaction of pit membranes of a number of woody dicotyledons and conifers to lignin and cellulose stains. In most cases the pit membranes of ray and axial parenchyma and fibres are not stained by lignin-sensitive stains (safranin and Fuelgen's), but are brightly stained by cellulose-sensitive stains (fast green). Tyloses, which develop from the pit membrane of ray parenchyma, also react in the same manner as the pit membrane. This reaction could not always be obtained with the pit membrane of the bordered pits of vessels, fibre tracheids and tracheids.

SIR WILLIAM MACLEAY MEMORIAL LECTURE.

29th June, 1960.

The second Sir William Macleay Memorial Lecture was delivered in the Main Hall, Science House, 157 Gloucester Street, Sydney, on Wednesday, 29th June, 1960, at 8 p.m., by Professor Th. Dobzhansky, Department of Zoology, Columbia University, New York City, U.S.A. The title of the lecture was "Bridging the Gap between Race and Species". (For full text of lecture, see pages 322-327.)

ORDINARY MONTHLY MEETING.

27th JULY, 1960.

Dr. I. V. Newman, President, in the chair.

The Chairman informed the meeting that the second Sir William Macleay Memorial Lecture had been duly given on 29th June by Professor Th. Dobzhansky before an audience of about 170 people.

The following were elected Ordinary Members of the Society: Messrs. A. F. Batley, A.C.A., Wahroonga, N.S.W.; P. J. Dart, B.Sc.Agr., Sydney University; Dr. A. A. Racek, Sydney University; and Mr. D. C. Wildon, B.Sc.Agr., Sydney University.

The Chairman referred to the death, on 26th May, 1960, of Dr. J. J. Lawrence, of the School of Public Health and Tropical Medicine, University of Sydney. He had been a member of the Society since 1946.

The Chairman offered congratulations to Dr. R. N. Robertson on his appointment to the Chair of Botany in the University of Adelaide.

The Chairman announced that library accessions amounting to 37 volumes, 362 parts or numbers, 72 bulletins, 9 reports and 30 pamphlets, total 510, had been received since the last meeting.

PAPERS READ.

1. *Tegea atropicta* Stäl (Hemiptera, Reduviidae), an Unusual Predator of Termites. By M. Casimir.

Discussion: The possibility of use of the predator for control of termites seems remote. Reference was made to the paucity of close relatives of *Tegea atropicta*, in view of the long evolutionary time presumed to be necessary for the development of such a precise predatory procedure. Possible additional experimental procedures were mentioned.

2. The Subgenus *Ochlerotatus* in the Australian Region (Diptera, Culicidae). IV. Review of Species of the *flavifrons* Section. By N. V. Dobrotworsky.

3. On Two Species of *Epilachna* (Coleoptera: Coccinellidae) from Australia. By George O. Stride and Esme P. Warwick. (*Communicated by Dr. D. F. Waterhouse.*)

4. The Structures Involved in the Presentation of Pollen to Visiting Insects in the Order Campanales. By R. C. Carolin.

5. Floral Structure and Anatomy in the Family Stylidiaceae Swartz. By R. C. Carolin.

Discussion of two papers by R. C. Carolin: Reference was made to organogeny in relation to interpreting the position of the stigmatic surface in *Leschenaultia* and to the possible relationship of this to the conditions present in *Lobelia*.

NOTES AND EXHIBITS.

Mr. Gilbert P. Whitley exhibited an original letter from Charles Darwin to John Murray, of Maryborough, Queensland, the text of which was as follows:

Down,
Beckenham, Kent.

Railway Station
Orpington. S.E.R.

Jan. 6.80
Dear Sir,

I am much obliged to you for your kindness in having taken the trouble to send me the specimens of Drosera, with which I am well acquainted. It is *D. binota* vel *dichotoma.*

Dear Sir
Yours faithfully
CHARLES DARWIN.

The President offered congratulations to Dr. Marie E. Phillips on her appointment as Botanist, Parks and Gardens Section of the Department of the Interior, and invited her to speak about the development of a botanical garden on the slopes of Black Mountain at Canberra, A.C.T. Dr. Phillips explained that on the mountain slopes where the scientific aspect of the garden would be located a collection of Australian plants in Family groups had been growing in size for several years and is now being vigorously extended. The forwarding of seeds of suitable native species would be welcomed by Dr. Phillips.

LECTURETTE.

A lecurette, illustrated by colour slides, entitled "Notes on the Vegetation of Nigeria", was delivered by Dr. G. K. Berrie.

ORDINARY MONTHLY MEETING.

31st AUGUST, 1960.

Dr. I. V. Newman, President, in the chair.

The following were elected Ordinary Members of the Society: Messrs. L. I. Cady, Kiama, N.S.W.; H. K. Judd, Jamberoo, N.S.W.; and E. K. Noffz, North Sydney.

The Chairman offered the congratulations of members to Dr. Lilian Fraser on her appointment as Chief Biologist of the N.S.W. Department of Agriculture.

The Chairman drew the attention of members to Subscribers' Day at the Muogamarra Sanctuary on 3rd September, 1960.

The Chairman mentioned the preliminary notice of a conference of European Malacologists in London in 1962.

The Chairman announced that library accessions amounting to 7 volumes, 96 parts or numbers, 3 bulletins, 5 reports and 4 pamphlets, total 115, had been received since last meeting.

PAPERS READ.

1. Antarctic Phytoplankton Studies. By E. J. Ferguson Wood.

Discussion: The author, describing the background to this purely taxonomic paper, mentioned the appearance of occasional Antarctic diatoms off the N.S.W. coast, thus tracing the source of upwellings. The discussion ranged over the corresponding possibilities of pollen for tracing the origin of air masses, and the possible use of radioactive tracers added to Arctic waters for finding the time taken for the water concerned to travel from the Antarctic. The author also mentioned occurrence of dimorphic frustules — epithecal valve of one species, hypothecal valve of another species. The discussion concerned the genetic and taxonomic aspect of this unusual feature.

2. The Genus *Theobaldia* (Diptera, Culicidae) in Victoria. II. By N. V. Dobrotworsky.

3. The Larval Ecology of *Aëdes australis* (Erichson) (Diptera, Culicidae) in the Sydney Area. By A. K. O'Gower.

4. Contributions to the Flora of New South Wales: New Species and Combinations in *Acacia* and *Blechnum*. By Mary D. Tindale.

Discussion: The discussion related to *Acacia* and centred round some criteria used in taxonomic determination in the genus, namely, the range of number of pairs of pinnae and the testing of different flowering times by growing together in one locality species with different times for flowering.

NOTES AND EXHIBITS.

The President, Dr. I. V. Newman, gave a brief report on the Conservation Conference held on Saturday, 13th August, 1960, at which he represented the Society.

Delegates are sent to the Conference by societies and organizations interested in all aspects of nature conservation. The matters before the Conference are of three main kinds: (*a*) General policy and planning for conservation, (*b*) wide matters of protest or advocacy, e.g. kangaroo meat and stock route preservation, and (*c*) local protests, e.g. about filching reserved land for commercial development. The Conference decided to become a council — a continuing body — with a committee to operate between the annual meetings on some matters as directed by the council. It was felt that the new status as a council with committee would enable the annual meeting to deal more adequately with policy and advance work, the many local problems being largely handled by the committee.

Among other resolutions were: A recommendation that all aspects of the protection of fauna and flora and reservations for those purposes be brought under the administration of one government department under the one ministerial control; a resolution supporting further research by the C.S.I.R.O., and the Fauna Protection Panel on the kangaroo meat problem. On a motion deploring poplars in Martin Place, a committee was set up to seek a compromise, if desirable, by substituting Australian trees.

Mr. J. F. Rigby exhibited a specimen of an isolated *Glossopteris* fructification, *Hirscutum* cf. *dutoitides* Plumstead, from Permian Illawarra Coal Measures at Kembla Heights, near Wollongong. The specimen was compared with the South African species, *H. dutoitides*, as it was not attached to a *Glossopteris* leaf and was smaller in size than the South African specimens, although identical in all other respects with those described as the fertile half of the cupule.

Mr. P. Dart exhibited some peas treated with gibberellic acid. This remarkable plant growth-promoting substance was first discovered by a Japanese plant pathologist, Kurosawa, in 1926. Information on gibberellins and their effects on plant growth has been accumulating at an ever-increasing tempo since then. One of the early discoveries was that gibberellin application allows some mutant dwarf plants to grow into the normal tall forms. A dwarf variety of garden pea, "Greenfeast", treated at the three-leaf stage with small amounts of gibberellic acid (0·5μg/plant) demonstrated this marked growth stimulation. This contrasted with the almost complete lack of response with a similarly treated tall variety, "Telephone".

Dr. T. G. Vallance noted that a statement in his Presidential Address (Proc. Linn. Soc. N.S.W., 85, 1960, p. 10) referring to the first use of the rock-name *spilite* in the Australian geological literature should be modified. The name appears as early as 1873 in Gerard Krefft's "Catalogue of the Minerals and Rocks in the Collection of the Australian Museum" (Govt. Printer, Sydney, 1873) and was applied to "a laminated rock, interspersed with small particles of Calc Spar". All six of Krefft's samples were from France or Germany.

Dr. Vallance also contributed some remarks on the corduroy granulite found at Cooma, N.S.W. The "corduroy" ribbing in this rock has been interpreted as a bedding feature (G. A. Joplin, Proc. Linn. Soc. N.S.W., 67, 1942, p. 178). In outcrops recently exposed after flooding in Spring Creek, about ½ mile N.E. of "Kia Ora", Cooma, it can be seen that the rocks have been folded into a series of small anticlines and synclines the axes of which plunge gently to the north. Corduroy ribbing is parallel to bedding on the flanks of the folds but cuts directly across bedding in the crests and troughs. The ribbing is evidently an axial-plane schistosity structure and is developed only in the sandy beds.

Dr. D. F. McMichael showed colour transparencies of some recently discovered marine gastropods of the family Volutidae. These shells have been found in recent years by a number of research vessels carrying out trawling and dredging operations around the Australian coast. Several of these species are new and others represent "lost" species, the range and habitat of which had previously been unknown.

Dr. W. R. Browne exhibited some colour slides illustrating the geology and physiography of the Nandewar Mountains.

ORDINARY MONTHLY MEETING

28th September, 1960.

Dr. I. V. Newman, President, in the chair.

Dr. Ilma M. Brewer, Darling Point, Sydney, was elected an Ordinary Member 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, 1961, from qualified candidates. Each applicant must be a member of the 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 £1,600 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 2nd November, 1960.

The Chairman announced that library accessions amounting to 14 volumes, 129 parts or numbers, 9 bulletins, 8 reports and 5 pamphlets, total 165, had been received since last meeting.

PAPERS READ.

1. Notes on Australian Mosquitoes (Diptera, Culicidae). V. Subgenus *Pseudoskusea* in Victoria. By N. V. Dobrotworsky.

2. The Psoric Mites parasitic on Bats. XVI. A New Species of the Genus *Teinocoptes* Rodhain from the Fruit-bat, *Pteropus conspicillatus*, in Queensland. By A. Fain. (*Communicated by Mr. R. Domrow.*)

Discussion: The question was raised as to whether there is any evolutionary-geographical significance in the newness of the parasite species on the only Australian representative of an essentially African family of animals.

Lecturette:

A lecturette entitled "The Natural History of New Caledonia", illustrated by colour transparencies, was given by Miss Elizabeth C. Pope.

ORDINARY MONTHLY MEETING.

26th October, 1960.

Dr. I. V. Newman, President, in the chair.

Miss Joan M. Bain, M.Sc., Artarmon, N.S.W., and Mr. Ian A. Barber, B.Sc.Agr., Sydney University, 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, 1961, from qualified candidates. Each applicant must be a member of the 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 £1,600 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 2nd November, 1960.

The Chairman announced that library accessions amounting to 7 volumes, 192 parts or numbers, 4 bulletins, 3 reports and 21 pamphlets, total 137, had been received since last meeting.

PAPERS READ.

1. The Inheritance of Resistance of *Linum usitatissimum* L. to the Australian *Melampsora lini* (Pers.) Lév. Race Complex. By H. B. Kerr.

2. The Family Speleognathidae in Australia (Acarina). By Robert Domrow.

Discussion: In answer to the question as to why it is necessary for re-description, an answer was given that there are very many cases of the older descriptions of organisms which in the light of today are quite unsatisfactory and need to be re-done.

3. Thermoregulatory Behaviour in a Specimen of *Morelia spilotes variegata* Gray (Serpentes: Boïdae). By Harold G. Cogger and Alex Holmes.

Discussion: The discussion centred round problems of measurement and the effect of different forms of coiling. Analogy was made with circinate vernation of the fern as a possible means of minimizing some adverse environmental factors.

LECTURETTE.

A lecturette entitled "Genetical and Biological Studies in the Western Australian Country-side", illustrated by colour slides, was given by Messrs. S. H. James and W. J. Peacock.

ORDINARY MONTHLY MEETING.

30th NOVEMBER, 1960.

Dr. I. V. Newman, President, in the chair.

Mr. C. K. Ingram, B.A., B.Sc., Bathurst, N.S.W., Miss Margaret M. Mackay, B.Sc.Hons. (St. Andrews), M.Sc. (Sydney), M.I.Biol., Longueville, N.S.W., and Miss Doreen T. O'Malley, Paddington, N.S.W., were elected Ordinary Members of the Society.

The Chairman announced that the Council had appointed Mr. William James Peacock, B.Sc., to a Linnean Macleay Fellowship in Botany for one year from 1st January, 1961.

The Chairman read a resolution sponsored by the National Parks Association of N.S.W. and subscribed to by the Society.

The Chairman drew the attention of members to the launching recently of the Ecological Society of Australia and to its objects, forthcoming meetings and the subscription to the Society.

The Chairman announced that library accessions amounting to 16 volumes, 118 parts or numbers, 19 bulletins and 2 reports, total 155, had been received since last meeting.

PAPER READ.

The Genus *Conostylis* R.Br. II. Taxonomy. By J. W. Green.

NOTES AND EXHIBITS.

Mr. Ian A. Staff displayed some specimens of the genus *Xanthorrhoea*, which showed evidence of secondary thickening of the caudex (stem). The caudex is composed of four obvious zones. A central cylinder of relatively constant diameter is presumed to have been derived from the combined actions of the apical and primary thickening meristems, the latter being similar to the primary thickening meristems of many other woody Monocotyledons, e.g., palms, *Dracaena*, *Aloe*. Surrounding this central cylinder is a zone of woody material formed by the action of a secondary thickening meristem (cambium), which is continuous with the primary thickening meristem, and extends, roughly in the shape of a cylinder, to the base of the caudex. This region is delineated by the frequency and arrangement of vascular bundles in the regions mentioned. The next zone is the region of secondary thickening meristem, which has already been mentioned. Lastly, there is a region of secondary parenchyma underlying and partly engulfing the persistent resiniferous leaf bases. The base of the caudex shows a marked widening, which is probably related to excessive lateral growth of the plant in the seedling stage. Three specimens of *Xanthorrhoea arborea* (transverse and longitudinal slabs) were prepared for exhibition by the Division of Wood Technology, Forestry Commission of N.S.W. A fourth specimen was of a partly decayed caudex of *Xanthorrhoea media*, which was almost devoid of leaf bases.

Dr. W. R. Browne exhibited (1) colour-photographs of part of New England Park from Point Lookout, indicating the great amount of denudation that has occurred since

the first uplift of the area in late Miocene (?) time, and (2) colour-photograph of Trap-featuring in Tertiary basalt between Point Lookout and Dorrigo.

Mr. K. E. W. Salter contributed a Note on the Results of Thirteen Months' Study in the British Museum (see pages 382-3).

LIST OF MEMBERS.

(15th December, 1960.)

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.**
1927 ***Albert, Michel Francois, "Boomerang", 42 Billyard Avenue, Elizabeth Bay, Sydney.**
1940 ***Allman, Stuart Leo, B.Sc.Agr., M.Sc., Entomological Branch, Department of Agriculture, Farrer Place, Sydney.**
1959 **Anderson, Donald Thomas, B.Sc., Ph.D., Department of Zoology, Sydney University.**
1922 **Anderson, Robert Henry, B.Sc.Agr., Royal Botanic Gardens, Sydney.**
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