



THE
PROCEEDINGS
OF THE
LINNEAN SOCIETY
OF
NEW SOUTH WALES

FOR THE YEAR
1959
VOL. LXXXIV.

WITH TWENTY-THREE PLATES.
287 Text-figures.

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ANNUAL GENERAL MEETING.
25th MARCH, 1959.

The Eighty-Fourth Annual General Meeting was held in the Society's Rooms, Science House, 157 Gloucester Street, Sydney, on Wednesday, 25th March, 1959.

Dr. S. Smith-White, President, occupied the chair.

The minutes of the Eighty-Third Annual General Meeting, 26th March, 1958, were read and confirmed.

PRESIDENTIAL ADDRESS.

Presidency of the Linnean Society of New South Wales confers both an honour and an obligation. I should like to express my thanks to the Society for the former. I feel that there is an obligation on the President, in presenting the address, to maintain the standards of past years. I hope I will not fail the Society in this respect.

I should like to thank Dr. W. R. Browne and Dr. A. B. Walkom for their continued services as Honorary Secretary and Honorary Treasurer-Editor. They have served us for so long and have served us so well that we must be careful not to take their services for granted. I should also like to express appreciation to Miss G. L. Allpress, our Assistant Secretary, for her continued loyalty; the efficient management of the daily affairs of our Society and the maintenance of our Library reflect our indebtedness to her.

The Society's PROCEEDINGS for 1958, Volume 83, Parts 1 and 2, were published in 1958, and Part 3 in March, 1959. Volume 83 consists of 387 pages, 6 plates and 392 text-figures. A grant of £125 was made by the Commonwealth Publications Fund Committee towards the cost of publication of "Catalogue of Australian Mammals and their Recorded Internal Parasites", by Dr. M. Josephine Mackerras, and payment for a two-colour plate to illustrate a paper by E. Gauba and L. D. Pryor, entitled "Seed Coat Anatomy and Taxonomy in *Eucalyptus*. I", was made by the Department of the Interior, Canberra, A.C.T. Printing of illustrations by collotype was considered by Council and it was resolved that appropriate action be taken to let prospective authors know of the availability of collotype illustrations for their papers, under certain conditions, including one that the author bear half the cost above that of a corresponding half-tone block. A minimum number of eight plates was another proviso, as for any number less than eight the cost would be prohibitive.

During the year twelve new members were added to the list, two members died, nine members and one associate member resigned, and two were removed from the list under Rule vii. The numerical strength of the Society at 28th February, 1959, was: Ordinary Members, 223; Life Members, 32; Corresponding Members, 2; total, 259.

The resignation from Council of Mr. A. J. Bearup was regretfully accepted by Council at its February, 1959, meeting and Dr. I. V. Newman was elected in his place. Mr. Bearup resigned on account of ill health. We greatly appreciate his services to and interest in the Society and offer him our best wishes for his speedy recovery.

New holland blinds for our suite of offices and meeting room, a steel filing cabinet and twenty-five new, comfortable, modern seats have been purchased during the year.

On 19th June, 1958, the first Sir William Macleay Memorial Lecture was delivered by Professor A. A. Abbie, of Adelaide, to a large audience in the hall in Science House. The title of the lecture was "Timing in Human Evolution" and the preliminary part was devoted to interesting facts in the lives of the Macleays, and Sir William Macleay in particular (see PROCEEDINGS, 83, 1958: 197-213).

Lectures were given at the following meetings: April, National Parks in New South Wales, by Mr. Allen A. Strom; September, The Natural History of Australian Echinoderms, by Miss Elizabeth C. Pope; and October, Whales and Whaling, by Mr. W. H. Dawbin. No ordinary monthly meetings were held in June or August, 1958. A symposium was held in July, 1958, on "Origin and Distribution of Australian Fauna and Flora", in which a leading part was taken by Professor R. L. Crocker, Dr. J. W. Evans and Mr. Gordon Packham. We express our thanks and appreciation to all lecturers for their contributions to the programmes of the meetings. Members also showed keen interest in bringing notes and exhibits and entering into the interesting discussions which often took place.

The relatively small attendances at ordinary monthly meetings have been causing the Council some concern, and in an endeavour to meet the convenience of members the time of meeting was altered to 6 p.m., without, however, any marked improvement resulting. The matter of increasing attendances is still under consideration and suggestions by members would be welcomed.

Library accessions from scientific institutions and societies on the exchange list amounted to 1,727 compared with 1,858 in the previous year. Requests for library loans from members and institutions were as numerous as in the past years. The following donations to the library were made: (1) Sir Gavin de Beer, two books, "The Origin of Species", by Charles Darwin (a reprint of the sixth edition with a preface by Sir Gavin de Beer) (1958), and "Evolution by Natural Selection", by Charles Darwin and Alfred Russell Wallace (with a foreword by Sir Gavin de Beer) (1958); and (2) Captain R. Lloyd Jones, three books by Alvin Boyd Kuhn, Ph.D., "The Lost Light" (1940), "Who is this King of Glory?" (1944) and "Shadow of the Third Century" (1949). Council decided to purchase "Scientific Serials in Australian Libraries" and amendment sheets as published from year to year. Exchange relations were entered into with a number of institutions. The PROCEEDINGS were offered to Museo Civico di Storia Naturale di Venezia, Venice, Italy; Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales de Buenos Aires, Argentina, and North Queensland Naturalists' Club, Cairns, North Queensland (in addition to Abstract of Proceedings already sent). Reprints were offered in exchange to: Service de Parasitologie Végétale, Institut Pasteur, Paris, France (Zoological and Entomological); Institute of Entomology, Academia Sinica, Peking, China (Entomological); Facultas Rerum Naturalium Universitatis Comenianae, Bratislava, Czechoslovakia (Botanical); National Geological Library, Peking, China (Geological); Université de Dakar, Faculté des Sciences, Dakar, French West Africa (Marine Zoology); Museo de Historia Natural "Javia Prado", Universidad Nacional Mayor de San Marcos, Lima, Peru (Geological); and Mammals Research Institute, Polish Academy of Sciences, Bialowieza, Poland (Zoological and Entomological). A resumption of the exchange of publications with Naturwissenschaftlicher Verein, Hamburg, Germany, took place during the year.

The total net return from the Society's one-third ownership of Science House for the year was £1,303 10s. 9d. A second Neon sign advertisement has been erected on Science House.

The Society contributed the sum of £5 5s. stg. towards the commemoration of the Bicentenary of the foundation of the Royal Botanic Gardens, Kew, England.

Linnean Macleay Fellowships.

In November, 1957, the Council reappointed Miss Nola J. Hannon and Mrs. Mary B. Williams to Fellowships in Botany for 1958.

Miss Hannon resigned her Fellowship on 11th April, 1958, to take up an appointment as a lecturer in the N.S.W. University of Technology (now University of New South Wales). She has since obtained her Doctorate of Philosophy.

During 1958 Mrs. Williams continued a study of the freshwater algal family Characeae. This work was drastically interrupted when the Department of Botany of the University of New England was destroyed by fire in February, 1958. The whole

of her personal collection of herbarium material and slides was lost. Part of the collection of Characeae of the N.S.W. National Herbarium was recovered in severely damaged condition and that of the Melbourne National Herbarium in moderately damaged condition. Fortunately, a large proportion of the data already accumulated from this material was saved. The loss of the material itself, however, has been a severe handicap to making a complete study of the group. During the remainder of the year an attempt was made to sort through the data on hand, but many gaps were found and the work has not been completed. Meanwhile, in collaboration with Mr. T. C. Chambers, certain races of *Nitella cristata* Al.Br. were grown in various environments differing in factors of light, temperature, and photoperiod. The results of this experiment will be incorporated in a joint paper to be presented later. Mrs. Williams did not seek reappointment to a Fellowship for 1959.

In November, 1958, Miss Alison McCusker, M.Sc., was appointed to a Fellowship in Botany for 1959. Miss McCusker proposes to undertake cytological investigations in the family Epacridaceae, including (1) the sexual system of *Leucopogon melaleucoides* (A. Cunn. ex DC.), (2) a comparison of pollen developments and breeding systems in populations of *Astroloma pinifolium* (Benth.) in eastern New South Wales and western Victoria, and (3) the production of two types of pollen in *Acrotriche divaricata* (R.Br.). We extend to Miss McCusker our best wishes for a successful year's research work.

Linnean Macleay Lectureship in Microbiology.

Dr. Y. T. Tchan, Linnean Macleay Lecturer in Microbiology, University of Sydney, has furnished a report of his activities for the year ending 31st December, 1958, as follows: Teaching and administrative duties occupied a large proportion of the year but time was found for the following research: (1) Soil fertility test. This work has been continued. Experiments showed that the algal assay technique can be used for the estimation of nitrogen, phosphorus, sulphur and magnesium. In addition the possibility of estimating certain trace elements has been under investigation. Many difficulties still have to be overcome but it is likely that the method may prove suitable for iron, manganese and molybdenum. A paper has been accepted for publication (*Plant and Soil*, 1959). (2) The study of nitrogen fixation by free living micro-organisms has made some progress. A paper has been published on the subject of cytochromes of *Azotobacter* (Moss and Tchan, *PROC. LINN. SOC. N.S.W.*, lxxxiii, 1958, Part 2, p. 161). (3) With the N-fixing-algae, work is in progress to obtain a general technique for isolation of bacteria-free algal cultures using antibiotics.

Obituaries.

It is recorded with regret that the following members died during the year:

SIR DOUGLAS MAWSON, D.Sc., B.E., F.R.S., an Honorary Life Member of the Society, who had been a member since 1905, died in Adelaide, South Australia, on 14th October, 1958. He was born in 1882 at Frizinghall, near Bradford, England, came to Australia as a boy, and was educated at Fort Street School, Sydney. He graduated B.E. (1902) and B.Sc. (1905) at the University of Sydney and D.Sc. (1909) at the University of Adelaide. He contributed only two papers to the Society's PROCEEDINGS (in 1905 and 1906) but always retained a keen interest in the Society in spite of his residence in South Australia and his many sojourns in Antarctica. For fuller biographical accounts of Sir Douglas Mawson see *Aust. J. Sci.*, v. 21, No. 5, p. 134 (December, 1958) and *Nature*, v. 182, No. 4645, p. 1273 (8th November, 1958).

MR. DONALD FORD ROSS died in Sydney on 4th July, 1958. He had been a member of the Society since 1945.

DR. WALTER GEORGE WOOLNOUGH, who died on 28th September, 1958, at the age of 82, was a notable figure in the geological life of Australia. He had filled with distinction important academic positions in Adelaide, Sydney and Perth, and was the first Geological Adviser to the Commonwealth Government. He joined this Society in

1899 and contributed five papers to the PROCEEDINGS. Though he resigned in 1933, he still maintained an interest in the Society and on numerous occasions rendered valued help by translating communications in foreign languages.

PRESIDENTIAL ADDRESS.

Pollen Development Patterns in the Epacridaceae.

A Problem in Cytoplasm-Nucleus Interaction.

Tetrad pollen is generally characteristic of the Order Ericales. In the tribe Styphelioideae of the Epacridaceae this tetrad form has been altered by the regular failure of three pollen grains in each tetrad, to produce apparently single monad grains. In its most extreme form, monad development involves cytoplasmic polarity and nuclear migration in the mother cell following meiosis. This extreme monad form probably originated roughly contemporaneously with the origin of the tribe. In some genera and species it has suffered further modification, to give variable or segregating pollen tetrads and reversion to regular pollen tetrads. These patterns of pollen development are described and illustrated. An attempt is made to offer a general hypothesis to explain the mechanism of monad development and to follow up the evolutionary consequences of this hypothesis.

(For full text see pp. 8-35.)

The Honorary Treasurer, Dr. A. B. Walkom, presented the balance sheets for the year ended 28th February, 1959, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A. (Aust.), and his motion that they be received and adopted was carried unanimously.

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

President: T. G. Vallance, B.Sc., Ph.D.

Members of Council: R. H. Anderson, B.Sc.Agr.; A. N. Colefax, B.Sc.; J. W. Evans, M.A., D.Sc., Sc.D.; Dorothy A. Thorp, B.Sc.; T. G. Vallance, B.Sc., Ph.D.; and J. M. Vincent, D.Sc.Agr., Dip.Bact.

Auditor: S. J. Rayment, F.C.A. (Aust.).

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

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				14,367	11	4
				34,367	11	4
Current Liabilities—						
Bookbinding Account	1,138	6	1			
Income Account	660	4	4			
Suspense	51	3	10	1,849	14	3
				£36,217	5	7

ASSETS.

	£	s.	d.	£	s.	d.
Fixed Assets—						
Commonwealth Loans, at cost ..	15,048	10	0			
Debentures:—						
Metropolitan Water, Sewerage and Drainage Board, at cost	4,844	7	6			
Science House (one-third share), at cost	14,835	4	4	34,728	1	10
Current Assets—						
Cash in Hand	10	0	0			
Commercial Banking Co. of Sydney, Ltd.	1,479	3	9	1,489	3	9
				£36,217	5	7

INCOME ACCOUNT. Year Ended 28th February, 1959.

	£	s.	d.	£	s.	d.
To Salary				742	0	0
" Printing Proceedings	1,095	10	6			
" Printing Reprints	496	11	0			
" Blocks	249	6	4	1,841	7	10
" Insurance	67	7	7	13	7	11
" Postage	35	6	8			
" Petty Cash				102	14	3
" Audit	16	16	0			
" Printing and Stationery	159	17	6			
" Expenses	106	17	8			
" Cleaning	40	2	6			
" Bank Expenses	3	11	0			
" Library	130	8	9			
" Furniture and Painting	194	6	6			
" Sir Wm. Macleay Memorial Lecture	76	0	0	727	19	11
" Transfer to Contingencies Reserve Account				1,500	0	0
" Balance to 1959-60				660	4	4
				£5,587	14	3

	£	s.	d.	£	s.	d.
By Balance from 1957-58				1,252	12	8
" Subscriptions:—						
1958-59	390	12	0			
Arrears	27	6	0			
In Advance	4	4	0			
Associate	10	0	0			
" Entrance Fees	422	12	0			
" Interest	12	12	0			
" Science House	729	9	0			
" Rent	1,303	10	9			
" Sales	11	0	0			
" N.S.W. Government Grant	408	12	1			
" Fellowships Account (surplus income at 28th February, 1959, transferred)	200	0	0			
" Bank Expenses	499	10	8			
" Sale of Reprints	4	2	11			
" Postcard Sales	561	0	8			
" Printing Grants	2	14	6			
" Sundry Sales	144	9	0			
	35	8	0			
				£5,587	14	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, 1959, 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, 1959, as shown by the books. Certificates of the investments have been inspected.

Sydney, 11th March, 1959.

S. J. RAYMENT, Chartered Accountant (Aust.), Auditor.

4th March, 1959.

A. B. WALKOM, Hon. Treasurer.

LINNEAN SOCIETY OF NEW SOUTH WALES.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

Balance Sheet at 28th February, 1959.

	£	s.	d.		£	s.	d.
LIABILITIES.				ASSETS.			
Accumulated Funds—				Fixed Assets—			
Amount bequeathed by Sir William Macleay ..	35,000	0	0	Commonwealth Loans, at cost ..	30,449	0	0
Surplus Income Capitalized	20,843	14	1	Metropolitan Water, Sewerage, and Drainage Board, at cost ..	16,956	14	9
				Rural Bank of N.S.W., at cost ..	2,172	15	0
				Loan on Mortgage	6,035	0	0
				Current Assets—	55,613	9	9
				Commercial Banking Company of Sydney Ltd.	230	4	4
	£55,843	14	1		£55,843	14	1

INCOME ACCOUNT. Year Ended 28th February, 1959.

	£	s.	d.		£	s.	d.
To Salaries of Linnean Macleay Fellows	843	8	9	By Interest	2,099	10	8
" Research Expenses	45	0	0				
" Balance, being Surplus Income transferred to General Account	499	10	8				
" Capital Account	711	11	3				
	£2,099	10	8		£2,099	10	8

AUDITOR'S REPORT TO MEMBERS.

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Sydney, 11th March, 1959.

S. J. RAYMENT, Chartered Accountant (Aust.),
Auditor.

A. B. WALKOM,

Hon. Treasurer.

4th March, 1959.

LINNEAN SOCIETY OF NEW SOUTH WALES.

BACTERIOLOGY ACCOUNT.

Balance Sheet at 28th February, 1959.

LIABILITIES.		ASSETS.	
£	s. d.	£	s. d.
Accumulated Funds—		Fixed Assets—	
Amount bequeathed by Sir William Macleay	12,000 0 0	Commonwealth Loans, at cost ..	15,320 0 0
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—			18,320 0 0
Income Account at 28th February, 1959	86 19 7	Current Assets—	
	£18,406 19 7	Commercial Banking Company of Sydney, Ltd.	86 19 7
			£18,406 19 7

INCOME ACCOUNT. Year Ended 28th February, 1959.

	£	s. d.	£	s. d.
To University of Sydney (towards salary of Lecturer)	700	0 0	By Balance from 1957-58	127 3 0
" Insurance	13	5	" Interest	660 10 0
" Balance to 1959-60	86	19 7		
	£787	13 0		£787 13 0

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Sydney, 11th March, 1959.

S. J. RAYMENT, Chartered Accountant (Aust.), Auditor.

4th March, 1959.

A. B. WALKOM,
Hon. Treasurer.

PRESIDENTIAL ADDRESS.

POLLEN DEVELOPMENT PATTERNS IN THE EPACRIDACEAE.

A PROBLEM IN CYTOPLASM-NUCLEUS INTERACTION.

By S. SMITH-WHITE.

(Plates i-ii; twelve text-figures.)

[Delivered 25th March, 1959.]

Synopsis.

Tetrad pollen is generally characteristic of the Order Ericales. In the tribe Styphelieae of the Epacridaceae this tetrad form has been altered by the regular failure of three pollen grains in each tetrad to produce apparently single monad grains. In its most extreme form, monad development involves cytoplasmic polarity and nuclear migration in the mother cell following meiosis.

This extreme monad form probably originated roughly contemporaneously with the origin of the tribe. In some genera and species it has suffered further modification, to give variable or segregating pollen tetrads, and reversion to regular pollen tetrads.

These patterns of pollen development are described and illustrated. An attempt is made to offer a general hypothesis to explain the mechanism of monad development and to follow up the evolutionary consequences of this hypothesis.

The interests of this Society are very diverse, and over the years presidential addresses have covered an equally diverse field. Many have presented reviews of the fields of knowledge and research in which the president of the year has had standing. It is not my intention to follow this custom. Instead, I propose to present and discuss a problem peculiar to a group of Australian plants which has interested me for many years but on which there is practically no published information.

My story concerns the characteristics of mature pollen and the patterns of pollen development found in the tribe Styphelieae of the Epacridaceae, and it involves differentiation at the intracellular level. Problems of differentiation provide one of the central themes of present-day biology, and I believe you will find my story unusual and interesting. I cannot provide the answers, but I am prepared to do some guessing. It has been said that the tortoise can make no progress until he sticks out his neck! I will become involved not only in cell polarity and cytoplasmic gradients, and the immediate reactions of nuclei to these cytoplasmic conditions, but also, in the long term, in the consequences of cytoplasmic polarity on nuclear genotype.

THE POLLEN OF THE STYPHELIEAE.

In the Order Ericales, and particularly in the major family of the Order, the Ericaceae, the pollen is characteristically matured in tetrads. Only in the monogeneric family Clethraceae do the individual pollen grains separate during maturation. In the Epacridaceae tetrad pollen is also produced, and this form is, to my knowledge, uniformly characteristic of the tribe Epacrideae. In the Styphelieae, however, there is an unusual diversity of pollen types.

The Monad Pollen Type.

As early as 1810 Robert Brown observed that in this tribe the pollen may be either tetrad or single. Brough (1924) described the pollen of *Styphelia longifolia* as being single. In my experience, truly single pollen grains do not occur within the

tribe. Each apparently single pollen grain is a tetrad containing one good pollen grain and three aborted and empty cells, all enclosed in a common thick exine. The terms "pseudomonad" and "monodynamosporous tetrad" have been used for the somewhat similar pollen type found in the Cyperaceae (Selling, 1947; Erdtman, 1952), but they seem unwieldy and unnecessary. The term *monad* is sufficient to distinguish this type from single pollen grains and will be used in this address.

The main features of the development of monad pollen in *Styphelia* and in *Leucopogon* have been described in the PROCEEDINGS of this Society and elsewhere (Smith-White, 1948*a*, 1955*a*, 1955*b*). In the pollen mother cell (PMC) immediately following meiosis, the four microspore¹ nuclei are uniformly spaced, either in tetrahedral or quadrant arrangement (Text-fig. 1, *a*). Before partition of the mother cell cytoplasm occurs, migration of the nuclei takes place; three cluster at one end of the cell and the fourth moves to, or remains in, an isolated position at the opposite end (Text-fig. 1, *b*). Cell walls are then laid down and the microspores are constituted. These microspores are *initially* very unequal in size (Text-fig. 1, *c*) and unlike in potential. The differentiation of the one functional and the three non-functional microspores occurs at a very early stage, either immediately following or perhaps during meiosis. All four microspores undergo some development, and there is some thickening of the cell walls surrounding the small ones. Very soon, however, the three minor microspores die (Text-fig. 1, *d*, *e*). As Barber has shown in *Uvularia* (1941) the opportunity for intercellular compensation is then lost and the small microspores can derive no advantage from their association with the large one to compensate them for their own deficiencies.

Subsequent growth of the tetrad and its increase in size with maturation is entirely due to the large microspore. The aborted cells become compressed and obscured (Text-fig. 1, *g*, *h*). In the functional microspore the pollen grain mitosis occurs at a rather late stage of development, and after very considerable increase in size. This PG mitosis shows an inversion of the usual polarity characteristic of the PG mitosis in many flowering plants (Sax and Husted, 1936; Brumfield, 1941; La Cour, 1949; de Almeida and Sampaya, 1950), in that the short pole of the mitotic spindle is directed radially outwards from the centre of the tetrad, and the generative nucleus, and later the generative cell, is derived from this outer pole (Text-fig. 1, *f*, *g*). Finally, the generative cell migrates into the centre of the pollen grain and its boundary becomes indistinct (Text-fig. 1, *h*).

This pattern of pollen development is the most frequent one in the tribe. It has been termed the *Styphelia* type, or S-type, since it was first found and is most fully developed in that genus. It is not usually associated with visible meiotic abnormalities.

Normal tetrad pollen (T-type), similar to that of the Ericaceae and the Epacrideae is also found in the Styphelieae, but is much less frequent. It is known to me in 11 species in the genera *Acrotriche*, *Cyathodes*, *Pentachondra*, *Trochocarpa*, *Leucopogon*, *Brachyloma* and *Lissanthe* (Table 8). Three other pollen types are also found in the tribe and involve patterns of development intermediate between the S-type and the T-type, in a sense linking them together. These will be described and considered after the implications of the S-type monad pattern of development have been discussed.

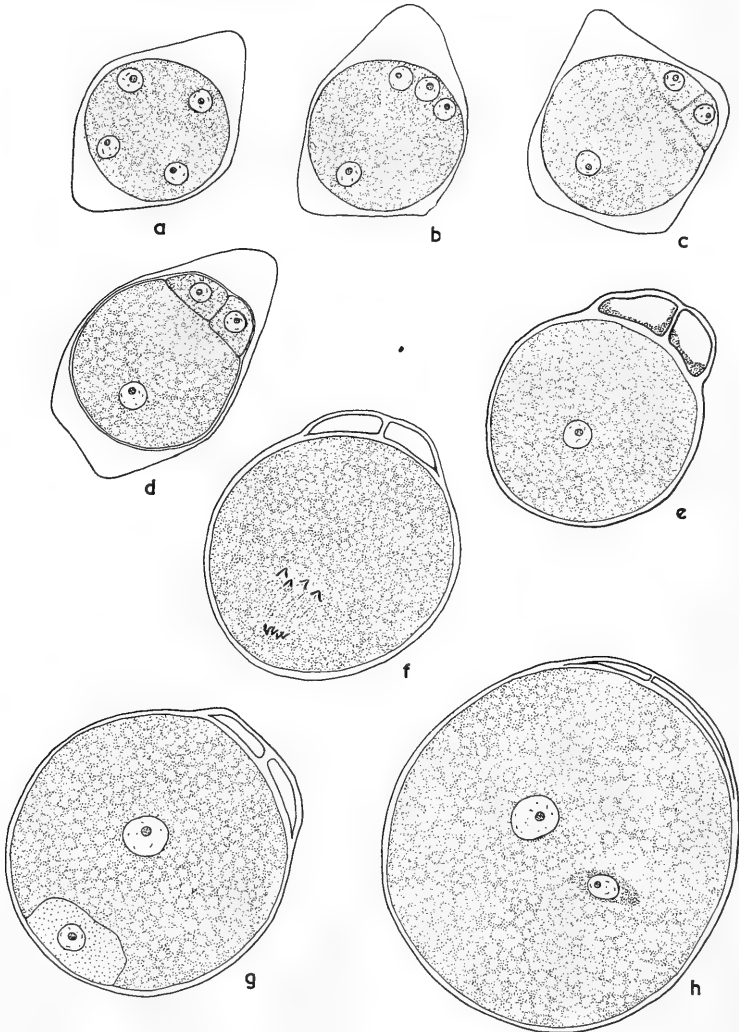
The Implications of the Styphelia Pattern of Development.

The unlike fates of the microspore nuclei in the *Styphelia* mother cell demonstrate the existence of differentiation within the cell. This differentiation may be in the cytoplasm or in the nuclei, or more probably in both.

Intracellular polarity, i.e., the development of substantive gradients between different parts of the cell cytoplasm, is not infrequent and is perhaps a necessary concomitant of all primary cellular differentiation (Mather, 1948). Such gradients

¹I propose to use the term *microspore* for the four daughter cells of a PMC until they reach the stage of the first gametophytic mitosis, the pollen grain mitosis. After this mitosis they become binucleate *pollen grains*.

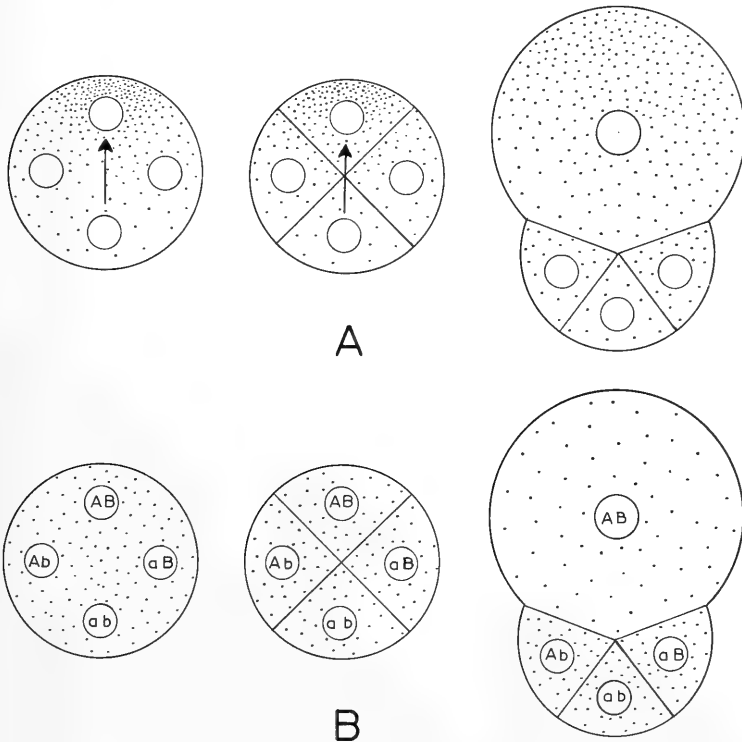
are evident in animal eggs, in blood precursor cells (La Cour, 1944), and in pollen grains (Geitler, 1935; Ostergren, 1947; La Cour, 1949). Similar gradients occur in embryo sacs (Darlington and La Cour, 1941; Darlington and Mather, 1949; Brock, 1954) and probably control the various patterns of embryo sac development which have been described and illustrated by Maheshwari (1950).



Text-fig. 1.—Pollen development in *Styphelia longifolia*. \times ca. 1150.

Very often intracellular differentiation can be related to the existence of physiological or tissue gradients in the surrounding tissues or, more generally, to a polarity of the surrounding environment: intracellular polarity is imposed from outside. Such is not always the case. La Cour (1949) and de Almeida and Sampaya (1950) have shown that the orientation of the pollen grain mitosis and the differentiation of the generative and vegetative nuclei are determined in relation to the centre of the original pollen mother cell. Each mother cell must be a centre of development of polarity. In the monad pattern of development each mother cell also seems to be a centre of origin of differentiation. There is a random orientation of the monads to the anther axis, and no general tissue gradient can be inferred. The monads are not

arranged in opposite pairs, as would happen if differentiation originated at the premeiotic mitoses. The control of monad development must be intracellular and local; in fact the usual and normal pollen grain polarity in many angiosperms and the exceptional polarity in the pollen mother cells of the *Styphelieae* responsible for monad development, are so similar in action that the former might well be the source of the latter. A slight precocity in the development of the PG polarity, bringing it forward only one cell generation, may be the fundamental change involved in the origin of *Styphelia* type pollen. Two examples of a greater precocity, causing the intrusion of polarity into the premeiotic mitosis, have been reported by La Cour (1949) and by Holden and Mota (1956).



Text-fig. 2.—Two hypotheses of monad development. A. Cytoplasmic determination. B. Nuclear (chromosomal) determination.

There seems no alternative to the view that cytoplasmic polarity is involved in the control of the monad pattern of pollen development, but it may not be sufficient. In dealing with a possible case of polarized segregation in *Bombardia*, Catchside (1944) has reasoned that it must involve both (i) a polarity in the cytoplasm or in the spindle, and (ii) some difference between the genes, which show a differential response to this polarity. His reasoning is equally valid where the units are whole chromosomes or whole nuclei. In monad development this nuclear differential could consist merely in the spatial arrangement of the four microspore nuclei or of the meiotic spindles in relation to the cytoplasmic axis. With the usual tetrahedral or quadrant arrangements one nucleus would often lie closer to the "effective" cytoplasmic pole than the other three, so that it might outgrow and suppress its sisters. This hypothesis is illustrated in Text-figure 2A.

The hypothesis needs a further brief consideration. Two features suggest that it is incomplete. It might be expected that occasionally two of the four nuclei would be approximately equally favoured in position so that dyads would be produced.

However, dyads have not been seen in any species of *Styphelia*, and in *Leucopogon juniperinus* only one dyad has been seen among over 300,000 monads. The system of control is extraordinarily efficient. La Cour (1949) has shown that in *Scilla* misorientation of the pollen grain mitotic spindle in relation to the cytoplasmic polarity may be brought about by experimental shock treatment, and that this misorientation leads to a failure of nuclear differentiation. The second feature which calls for an addition to the hypothesis is the occurrence of nuclear migration. Can a qualitative difference in nuclear response arise as a result of a quantitative difference in the concentration of some cytoplasmic activator? This problem also exists in the normal pollen grain differentiation and it emphasizes the similarity of the two systems.

Both of these features can be satisfied by a simple addition to the hypothesis. A spatial orientation of the division spindles in the cytoplasmic gradient could lead to an unequal distribution of non-chromosomal or non-genic nuclear materials and thus to a constitutional difference between the four nuclei. This constitutional difference could then condition the qualitative difference in response and the system would become self-reinforcing and reliable.

A second hypothesis is presented in Text-figure 2B merely to be eliminated. It involves chromosomal segregation and requires very precise and unlikely conditions. It requires the segregation of two loci of lethals A/a and B/b, which must be placed on the same chromosome pair at such a distance that one chiasma, and one only, is always formed between them. It thus requires chiasma localization. It also requires the maintenance of permanent hybridity by a system of complementary survival of AB pollen grains and ab embryo sacs. These conditions are unlikely. Again, it would be expected that such a system would break down in polyploids, but monad pollen is characteristic of both diploid and polyploid species, and even of the permanent triploid *Leucopogon*. The monad system breaks down only in secondary polyploids. The most serious objection to this second, segregational hypothesis, however, is that it is independent of cytoplasmic conditions and renders the assumption of cytoplasmic polarity superfluous. Thus it cannot explain nuclear migration and it isolates the pattern of monad development from the very similar patterns of differentiation in pollen grains and embryo sacs, where segregation is not possible.

At the present stage the first hypothesis must be favoured. Monad development is related to pollen grain differentiation and is determined and controlled by a cytoplasmic polarity and a consequent non-chromosomal nuclear differential, dependent upon the spatial relationship of the four microspore nuclei to the cytoplasmic polarity. However, with the intrusion of cytoplasmic polarity into the mother cell during meiosis, cytoplasmic control of segregation becomes a logical possibility, provided heterozygosity is present and provided that permanent heterozygosity can be maintained. In this connection the case of *Leucopogon juniperinus* is particularly instructive.

The Special Case of Leucopogon juniperinus.

This species is a permanent triploid numerical hybrid belonging to a section of the genus in which the haploid number is four. The pollen is similar to that of *Styphelia* and is of the extreme S-type, with marked nuclear migration occurring in the pollen mother cells. The somatic chromosome number in the species is 12, and at meiosis four bivalents are regularly formed, leaving four chromosomes as univalents. In the pollen mother cells the univalents show polarized segregation, all passing to the same pole with a frequency greatly in excess of binomial expectation (Smith-White, 1948). This polarized univalent behaviour is apparently present also in the embryo sac mother cell meiosis (Smith-White, 1955b). Permanent hybridity is maintained by complementary gametic survival, whereby the univalents are regularly excluded from the functional pollen and equally regularly are included in the functional embryo sacs. This system is illustrated diagrammatically in Text-figure 3.

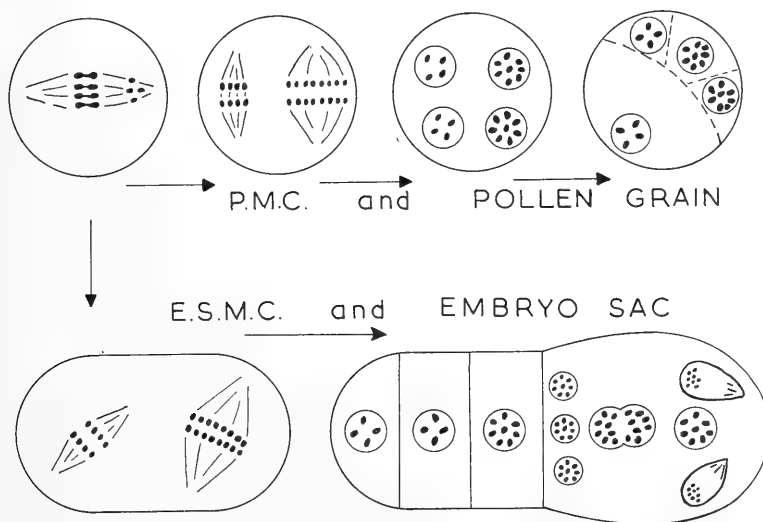
A similar controlled and polarized segregation of univalents occurs in the first meiotic divisions in embryo sac mother cells in *Rosa canina* (Tackholm, 1922; Hurst, 1931; Gustafson, 1944). In this species complex there are seven bivalents which show

normal segregation, and 21 or 28 univalents all of which pass to the micropylar pole of the embryo sac mother cell at Anaphase 1 and are thus included in the embryo sacs. The system of *Rosa canina*, which has been called semi-apomictic by Darlington (1939), differs from that of *Leucopogon juniperinus* in that in *Rosa canina* there is no control of univalent segregation in the pollen mother cells.

There can be no question or doubt that the S-type of monad pollen is antecedent to the condition of triploidy in *Leucopogon juniperinus*. The species yields evidence of fundamental importance for the analysis of the problem of monad development.

(1) It shows that the monad pattern need not be upset by triploidy. Therefore, chromosomal segregation is unlikely to be a primary cause of the differentiation.

(2) It emphasizes the presence in the pollen mother cell of a cytoplasmic gradient and it defines the time of action of this gradient, which must be developed during or before the metaphase of the first meiotic division. Polarity operates at a time when it could influence the segregation of unbalanced chromosomes.



Text-fig. 3.—The complementary gametic system in *Leucopogon juniperinus*. The four univalents are regularly included in the embryo sacs, and excluded from the pollen.

(3) It demonstrates that unbalanced chromosome univalents can and do react to the cell polarity, whereas paired chromosome bivalents, which are subject to the much stronger forces of centromere repulsion, are not free to do so.

Swanson (1958) has discussed the literature dealing with preferential chromosome segregation and a repetition is not necessary here. A short account of cases which may be relevant to our problem will suffice.

There is some evidence that preferential segregation is often a function of the centromere or of heterochromatin in the centromere region. This is true of trisomic segregation in triplo-IV *Drosophila melanogaster* (Sturtevant, 1936) and of X chromosomes in the same species (Novitski, 1951, 1954; Sandler and Braver, 1954) in *Sciara* (Metz, 1938; Crouse, 1943) and in B-chromosomes in Maize (Roman, 1947a, 1947b). In Maize heterozygous for a terminal knob on chromosome 10 (Rhoades, 1942, 1952) preferential segregation, leading to the inclusion of the knobbed chromosome 10 in the functional (chalazal) megaspore, is associated with neocentric activity of the abnormal heterochromatic knob. It is therefore significant that clonally-inherited chromosomes or chromosome segments, such as the univalents of *Rosa canina* and *Leucopogon juniperinus*, B-chromosomes, and the differential segments of sex chromosomes, are very often heterochromatic.

The controlled segregation of XY_1Y_2 or of X_1X_2Y sex chromosomes, which is known in *Humulus japonicus* (Kihara and Hirayoshi, 1932), in *Rumex acetosa* (Kihara and Ono, 1925, 1928) and in several groups of insects, including some Orthoptera, Dermaptera and Heteroptera (lists and references given by Darlington, 1937, and White, 1954), is determined by the properties of associated centromeres (Darlington, 1937, p. 362) and is not relevant to our problem. The segregation of sex chromosomes in sex mechanisms of the X_1X_2O type found in spiders (White, 1954) and the $X_1X_2X_3X_4O$ type in *Euceraphis*, where all the X chromosomes pass to the same pole, and the co-orientation of X chromosomes at M2 in *Cimex* (Darlington, 1940) cannot be explained in the same way. Swanson (1958) does not suggest an explanation for such behaviour, but a mechanism described by Catcheside (1950) in *Parthenium argetatum* could be operative. In this species, heterochromatic B-chromosomes show secondary association during meiotic prophase. Thus they tend to approach the metaphase I plate from the same direction, lie all on the same side of the A-chromosome bivalents, and pass together to the same anaphase pole.

Catcheside's mechanism implies preferential but not polarized segregation. It is not sufficient to explain univalent behaviour in *Rosa canina* embryo sac mother cells or in *Leucopogon juniperinus* pollen mother cells. It could, however, suffice to explain univalent segregation in embryo sac mother cells of the latter species, since the four univalents move together to either the micropylar or chalazal poles, apparently with equal frequency. In the embryo sac mother cells of *Rosa canina* and the pollen mother cells of *Leucopogon juniperinus* an additional mechanism is necessary to direct the univalents to a particular pole. Since in both there is other evidence of an intracellular cytoplasmic gradient, it is not unreasonable to suggest that this cytoplasmic gradient is the determining cause. The *Parthenium* behaviour then becomes superfluous, and in fact secondary association of the univalents of *Leucopogon juniperinus* during prophase has not been observed.

(4) Finally, *Leucopogon juniperinus* demonstrates that the same system of intracellular differentiation operates in both the pollen mother cells and the embryo sac mother cells in respect to univalent segregation, but that the consequences, the elimination or retention of the univalents in the pollen grains and in the embryo sacs, are different (Smith-White, 1955b). This difference must be dependent upon the different tissue environments of the anther and ovule. A surrounding tissue polarity is present in the ovule and is evidenced by the development of the micropylar megaspore rather than the chalazal one. A tissue gradient is not present in the anther.

The morphological uniformity and widespread but discontinuous distribution of this triploid species suggest that it is of very considerable age. In the course of time the univalents, subject to purely maternal inheritance, may have become vital in embryo sacs and lethal in pollen, but they cannot provide the primary cause of the monad pattern of development. The opposite contention, that the system which determines the S-pattern also influences univalent segregation, would, however, seem to be valid. The conditions which determine complementary gametic survival and which stabilize hybridity in the triploid are also present in diploid species; there is in fact pre-adaptation to permanent hybridity. Conditions which provide an opportunity for the reinforcement of a cytoplasmic control of the monad pattern of development by a chromosomal or segregational mechanism are demonstrable in the triploid and can be inferred in the diploids.

Modification of the Monad Pattern of Development.

Some species of *Leucopogon* (e.g. *L. revolutus*, Smith-White, 1955a) produce monad pollen which, when mature, is scarcely distinguishable from the S-type already described. In development, however, there is an absence of nuclear migration following meiosis, so that the four microspores are initially of equal size. Despite this apparent equality, three microspores in each tetrad regularly die at a very early stage of development. The term *modified monad* and the abbreviation S'-type will be used to designate this modification and the abbreviation M-type will be used to include both S-type and S'-type.

The S'-type of monad development is associated, so far as is known, with regular meiosis. It is still necessary to infer the existence of an intracellular cytoplasmic differentiation to account for the different fates of the four microspores and for the stability of the system, even though there is no direct evidence of cell polarity affecting nuclear movement. The distinction between the S- and S'-types is in fact quantitative rather than qualitative. In *L. ericoides* there is evidence of nuclear migration, but it is of lesser degree than that usual in *Styphelia*, and the initial size-inequality of the four microspores is also of lesser degree, although still quite distinct. In *Melichrus urceolatus* there is variation within anthers, some mother cells showing marked nuclear migration and others showing little or none.

This quantitative intergradation between the S-type and S'-type of development suggests that the control mechanism involved in monad development is itself quantitative, and it makes any classification of species into two classes, with S-type pollen and S'-type pollen respectively, such as was attempted earlier (Smith-White, 1955*a*), difficult and arbitrary.

Breakdown of the Monad Pattern.

It might be anticipated that the S'-type of pollen development would involve a lesser degree of cytoplasmic differentiation than the extreme S-type and that it might therefore be more easily subject to breakdown. This is the case. Comment has already been made upon the remarkable stability of the S-type system in *Styphelia* and in *Leucopogon juniperinus*. By comparison, *Leucopogon virgatus* ($n = 10$), which has S'-type pollen, shows a relative instability, with occasional or even frequent breakdown of the monad system leading to the formation of dyads and very exceptionally of triads. In a population of this species at Rylstone, N.S.W., 50 plants have been examined. Of these, many show no breakdown or a negligible degree of breakdown with less than 0.1% of dyads. Others produced dyads with a frequency of 1-2% in every anther and two have a breakdown frequency exceeding 10%. Data from eleven selected plants of this population, presented in Table 1, illustrate the range of behaviours.

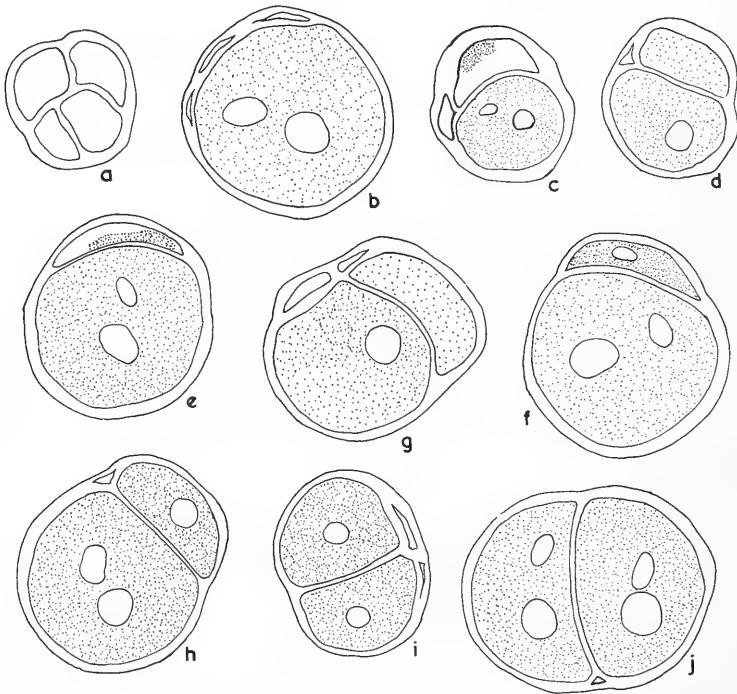
TABLE 1.
Breakdown of Monad Type Pollen in L. virgatus R.Br. at Rylstone, N.S.W.
Tetrad-type Proportions.

Plant.	Percentage Frequency of Tetrad Types.					N.	Ratio Dyads/ Monads.
	0s.	1s.	2s.	3s.	4s.		
57/4	37.85	62.15	0.00	0.00	0.00	1638	—
57/11	0.75	99.25	0.00	0.00	0.00	1196	—
57/7	2.55	97.41	0.04	0.00	0.00	2240	0.00045
57/3	3.08	96.73	0.19	0.00	0.00	3244	0.0019
58/56	2.66	97.05	0.29	0.00	0.00	13634	0.0022
57/2	6.24	93.34	0.42	0.00	0.00	2371	0.0045
57/1	4.68	94.34	0.98	0.00	0.00	4810	0.0103
58/94	0.61	96.04	3.35	0.00	0.00	9586	0.0349
58/73	39.17	57.53	3.30	0.00	0.00	3360	0.058
57/10	3.01	87.28	9.67	0.04	0.00	2625	0.111
58/8	1.37	88.46	10.06	0.11	0.00	4740	0.114

Several features in this breakdown of the monad type need to be emphasized. In some plants there is produced an appreciable frequency of nullads (i.e. completely aborted tetrads, in which the usual single pollen grain has failed to develop), but high nullad frequency does not appear to be associated with either high or low dyad frequency. Secondly, breakdown leading to dyad formation is not an all-or-nothing process. When a dyad is formed instead of the more usual monad, the two developed grains in the dyad may be equal in size and both either apparently viable or partially degenerate, or they may be slightly or grossly unequal (Text-fig. 4, *a-j*; Plate i, figs. 1-12). All degrees of breakdown, from the perfect monad to the full dyad, occur

in the same anther. The classification into monads and dyads given in Tables 1 and 2 thus involves an arbitrary decision of the degree of development which should be scored. In the data, grains showing development of a second cell equal to or greater than that illustrated in Text-figure 4, *f*, have been scored as dyads.

It will be observed that there are two different quantitative aspects of breakdown. These are (1) variation in frequency and (2) variation in degree. Breakdown does not involve a switch from one developmental pathway to another, and the control system of monad development must be itself quantitative. The behaviour supports the inference which was made earlier, i.e. the hypothesis that monad development is dependent upon intracellular cytoplasmic differentiation and polarity.



Text-fig. 4.—Monad breakdown in *Leucopogon virgatus*. \times ca. 1150. *a*. Nullad. *b*. Normal monad. *c*, *d*. Degenerate dyads. *e-h*. Degrees of monad "breakdown". *i-j*. Dyads.

In Tables 2A and 2B data are given for individual flowers and anthers, to show the extent of variation in the frequency of breakdown within plants. It is clear that significant differences occur between flowers and even between anthers of the same flower, and such differences must be environmentally determined. A comparison of Tables 1 and 2 shows that intraplant differences are of a substantially lower order than are interplant differences. It may be inferred that there are genotypic differences between plants in the population affecting the stability of the monad developmental system and that where the system is weak, buffering against environmental breakdown is marginal.

The precise nature and mode of action of environmental factors on monad breakdown remain to be determined, but they will probably be susceptible to experimental study. It is probably significant that there can be a substantial lapse of time, perhaps as much as a week, between the occurrences of meiosis in the five anthers of one flower, and that meiosis may commence at almost any time of the day or night. Thus it is possible that temperature at the time of meiosis or at some other critical stage of development could be an important factor in breakdown.

TABLE 2A.

Variation in Monad Breakdown within Plants. *L. virgatus R.Br., Rylstone, N.S.W.*
 Variations between flowers within plants. 58/56, 58/73, 58/94 and 58/8 (triads omitted).

Flower.	Plant 58/56. Percentage Frequency of Tetrad Types.			N.	Flower.	Plant 58/94. Percentage Frequency of Tetrad Types.			N.
	Os.	1s.	2s.			Os.	1s.	2s.	
1	2.57	97.32	0.11	4508	1	0.58	96.75	2.67	2955
2	2.43	97.05	0.52	4783	2	0.56	95.87	3.57	3195
3	3.02	96.78	0.21	4343	3	0.70	95.58	3.73	3436
Total ..	2.66	97.05	0.29	13634	Total ..	0.61	96.04	3.35	9586
Contingency $\chi^2=18.40$. P<0.001.					Contingency $\chi^2=6.78$. P=0.15.				
Flower.	Plant 58/73. Percentage Frequency of Tetrad Types.			N.	Flower.	Plant 58/8. Percentage Frequency of Tetrad Types.			N.
	Os.	1s.	2s.			Os.	1s.	2s.	
1	42.20	54.49	3.31	1147	1	0.85	86.84	12.31	1649
2	42.66	54.27	3.08	1137	2	1.82	93.16	5.02	1374
3	32.25	64.22	3.53	1076	3	1.52	86.50	11.97	1712
Total ..	39.17	57.53	3.30	3360	Total ..	1.37	88.55	10.07	4735
Contingency $\chi^2=32.03$. P<0.001.					Contingency $\chi^2=59.37$. P<0.001.				

TABLE 2B.

Variation in Monad Breakdown within Plants. *L. virgatus R.Br., Rylstone, N.S.W.*
 Variations between anthers and flowers in 58/8.

Flower.	Anther.	Percentage Frequencies of Tetrad Types.					Total.
		Os.	1s.	2s.	3s.	4s.	
1	1	0	93.30	6.42	0.28	—	358
	2	1.90	88.08	9.76	0.27	—	369
	3	0.77	82.26	16.97	0	—	389
	4	0.62	90.0	9.38	0	—	160
	5	0.80	81.96	16.71	0.53	—	377
	Totals ..	0.85	86.63	12.28	0.24	—	1653
2	1	2.83	88.68	8.49	0	—	318
	2	2.01	94.63	3.02	0.34	—	298
	3	0.60	94.89	4.50	0	—	333
	4	0.65	96.13	3.23	0	—	155
	5	2.58	92.62	4.80	0	—	271
	Totals ..	1.82	93.09	5.02	0.07	—	1375
3	1	1.28	83.89	14.83	0	—	391
	2	0.50	87.69	11.80	0	—	398
	3	0.81	84.84	14.34	0	—	244
	4	2.24	85.62	12.14	0	—	313
	5	2.73	89.89	7.38	0	—	366
	Totals ..	1.51	86.50	11.97	0	—	1712
Grand totals	1.37	88.46	10.06	0.11	—	4740

Neglecting triads, contingency, total $\chi_{23} = 137.6$. P<0.001.
 " " " between flower totals $\chi_4 = 59.37$. P<0.001.

Variable Pollen Tetrads.

Breakdown of the monad system connects the S- and S'-types with still another, that of segregating or variable pollen tetrads. This type was first reported in *Astroloma pinifolium* (Smith-White, 1948a) and has been designated as the *Astroloma* type or A-type. Similar segregating tetrads were later reported in *Astroloma conostephioides*, *Brachyloma preissii*, and *Acrotriche fasciculiflora* (Smith-White, 1955a). Since then the type has been found in eight additional species in *Acrotriche*, *Brachyloma*, *Leucopogon* and *Lissanthe* (cf. Table 3, in which information is also given on chromosome numbers and on the pollen types of other species of the same genera).

In A-type pollen development meiosis is followed by the partition of the pollen mother cell into four apparently equal microspores. All, any or none of these may

TABLE 3.
Species of the *Styphelieae* showing Tetrad Segregation.
A-type Pollen.

Genera and Species.	Number of Plants Examined.	Number of Plants with A-type.	Chromosome Number n.	Associated Meiotic Irregularities.	Characteristics of Congeners.		
					n.	Number of Spp.	Pollen Type.
<i>Astroloma</i>					4	14	S
<i>pinifolium</i> Benth. . .	>100	All	7	Fragmentation Inversion hybridity			
<i>conostephioides</i> F. Muell. . .	>100	All	7				
<i>Acrotriche</i>						9	3
<i>cordata</i> R.Br.	3	3	Not known	Hetero- chromatin			
<i>fasciculiflora</i> Benth. . .	20	All	9				
<i>divaricata</i> R.Br.	5	1	9				
<i>depressa</i> R.Br.	2	2	Not known				
<i>Brachyloma</i>					9	1	S, T
<i>ericoides</i> Sond.	3	3	Not known	Possible fragmentation			
<i>preissii</i> Sond.	6	6	7				
<i>scortechinii</i> F. Muell. . .	1	1	Not known				
<i>Lissanthe</i>					7	1	T
<i>montana</i> R.Br.	10	2	14	Gynodioecism			
<i>strigosa</i> R.Br.	50	1	7				
<i>Leucopogon</i>					4, 6 7, 10		S, S' T
<i>metaleucoides</i> A. Cunn. . .	15	15	Not known	Gynodioecism			

then abort, yielding five categories of tetrad in the mature anther — nullads, monads, dyads, triads and full tetrads (Text-fig. 5; Plate ii, figs. 1-6).

Within genera, A-type pollen is associated either with the S- and S'-types or with the full tetrad T-type. Unfortunately, chromosome numbers are not known for all species, but so far as is known the A-type is not associated with the haploid numbers of 4 or 6. In four cases it is associated with abnormal meiotic conditions.

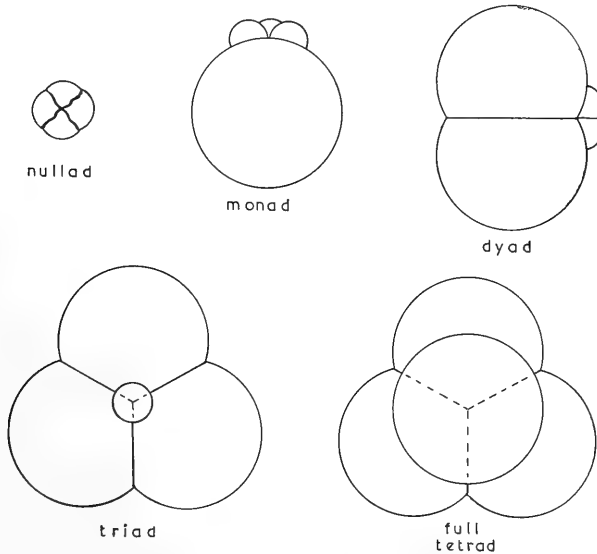
The details of pollen development subsequent to meiosis in the twelve species listed differ only in minor respects. The following description, however, applies particularly to *Astroloma pinifolium*.

Following meiosis the microspore nuclei assume a tetrahedral or a quadrant arrangement within the mother cell. There is no nuclear migration and the four microspores are initially equal in size. Inequality becomes apparent only after the cell walls separating the microspores have become appreciably thickened, but before there is any considerable increase in size, and is evident in the degeneration of the cytoplasm in some cells (Text-fig. 6, a-h). As in the development of monad pollen, aborting

microspores fail after the opportunity for intercellular compensation has been lost. It is not clear whether the deficiencies which lead to death are nuclear and chromosomal, as in *Uvularia* (Barber, *l.c.*), or whether they are cytoplasmic and related to the gradients involved in S-type monad development.

The pollen grain mitosis occurs in surviving microspores after these have undergone considerable growth and is similar to the pollen grain mitosis in *Styphelia* in respect to the reversal of generative-vegetative pole polarity as compared with *Scilla* and *Luzula* (Text-fig. 6, *g, h*).

In mature pollen, aborted cells are very small and completely devoid of cytoplasm. In some plants, however, a second kind of degeneration occurs; microspores or pollen grains die at a late stage of development, and as a consequence of this late death are little smaller than surviving pollen grains, and contain collapsed and deep-staining



Text-fig. 5.—A-type pollen. The five categories of tetrads.

cytoplasm. This type of death is sporadic in its occurrence and is apparently unrelated to the basic pollen development system of the tribe. Consequently, in scoring tetrad type frequencies late death has generally been ignored.

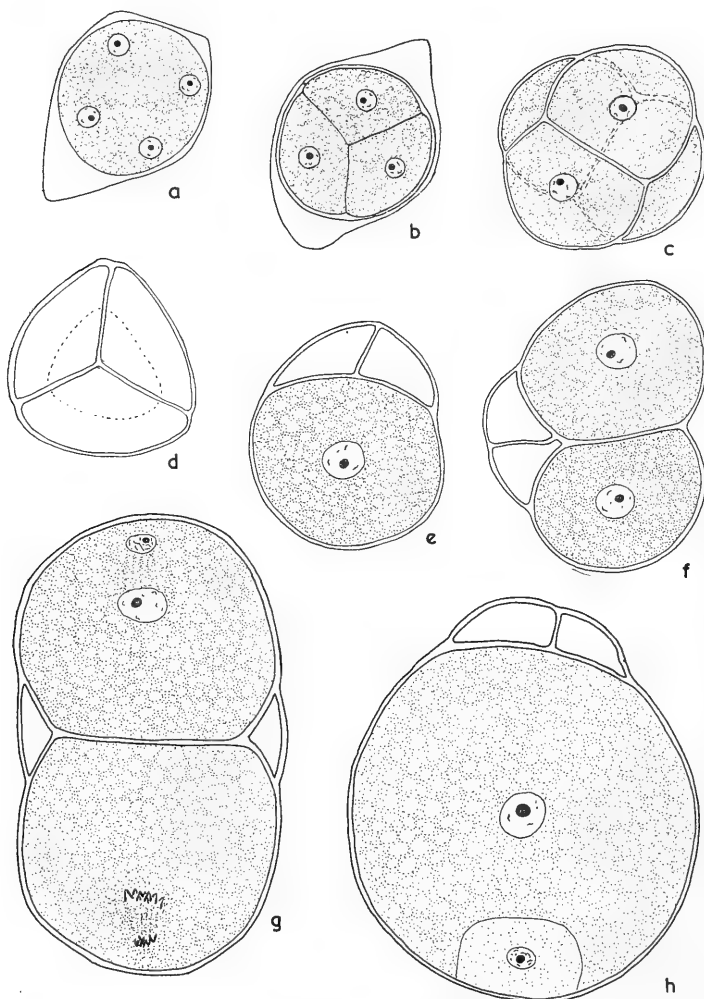
It could well be that full development of pollen grains at the time of anther dehiscence, as judged by their size and the condition and stainability of their cytoplasm, is not a consistent indication of their functional viability. Only one of the two or three grains in dyads and triads might in fact be functional. Observations on pollen germination in nectar (Table 4) deny this possibility. The two grains in any dyad each have a germination potential equal to that of single pollen grains in monads and are independent of each other in this respect ($\chi^2 = 1.01$, $P = 0.4$). It seems likely that the same independence would apply to the several pollen grains in triads and in full tetrads.

Tetrad Segregations in A-Type Pollen.

In A-type pollen the tetrahedral arrangement of the young microspores and the distortion caused by the growth of the good grains prevent any possibility of the recognition of the planes of the first and second divisions. Analysis of the segregations is thereby severely limited and can be made only on the basis of unordered tetrads. The shapes of the frequency distributions of the five categories of tetrad in the various species, and even in different plants within species, are often very different,

as will be seen from an inspection of the data in Tables 5, 6 and 7 and from the photographs in Plate ii. In respect to segregation characteristics, each species requires individual study and analysis. Such analysis will not be attempted here.

In Tables 5 and 6 a selection has been made to illustrate the diversity of segregation behaviour in different plants of the two species of *Astroloma*, and Table 7 presents data for most of the other species which were listed in Table 3. The



Text-fig. 6.—Pollen development in *Astroloma pinifolium*. \times ca. 1150.

selection of data in each table has been made to emphasize the fact that there is an almost complete range, from distributions with a modal class of monads (e.g. *A. pinifolium* 58/1005, Table 5) to others with a modal class of full tetrads (e.g. *Leucopogon melaleucoides* and *Brachyloma scortechinii*, Table 7). A-type pollen segregations thus connect the type of behaviour previously described in *Leucopogon virgatus* with the regular full tetrad T-type pollen. There is in fact a continuous series of pollen types within the Styphelieae, from the extreme S-type with nuclear migration characteristic of *Styphelia* itself, through the S'-type to S''-type with breakdown, leading to A-type variable tetrads and finally to regular full tetrads.

Diocism and Gynodioecism in the Styphelieae.

Before I undertake a general discussion of the problem of pollen development which I have outlined, I want to describe another feature of the Styphelieae which may appear to be quite unrelated. This is the occurrence of dioecism and of gynodioecism in several species.

TABLE 4.
Pollen germination in Astroloma pinifolium Benth.
A. In Monads.

Germinated.	Not Germinated.	Total.	Percentage Germinated.
181	150	331	54.8

B. In Dyads.

Both P.G.'s Germinated.	One P.G. only Germinated.	Neither P.G.'s Germinated.	Total Dyads.	Percentage P.G. Germination.
41	59	34	134	52.6
Expected on basis of independence. $(p+q)^2$.				
37.08	66.81	33.11		
$\chi^2=1.91$. $P=0.4$				

TABLE 5.
Pollen Tetrad Segregation Data. Astroloma pinifolium Benth.
A. East Coast Districts.

Plant.	Tetrad Type Frequencies Percentage.					N.	Percentage Pollen Fertility.
	0s.	1s.	2s.	3s.	4s.		
A. East Coast Districts.							
E51/1 ..	4.0	30.8	48.7	15.3	1.2	2336	44.7
W54/9 ..	16.2	39.7	32.8	10.5	0.8	3464	35.0
A53/1 ..	20.8	35.1	34.9	8.6	0.6	11322	33.2
O55/1 ..	20.0	39.8	30.3	9.1	0.8	1721	32.7
W54/5 ..	26.5	43.3	25.0	4.7	0.3	3603	27.2
M53/3 ..	40.0	37.3	18.7	3.7	0.3	8022	21.5
W54/6 ..	60.1	31.5	7.5	0.85	0.05	5878	12.3
B. Grampians District, Victoria.							
58/1008 ..	6.60	16.57	75.79	0.33	0.71	2408	43.0
58/1001 ..	4.31	20.82	74.16	0.05	0.66	1974	43.0
58/1005 ..	12.29	71.49	16.14	0.04	0.04	2571	26.0
58/1007 ..	30.28	59.46	10.26	0.00	0.00	2758	20.0
58/1016 ..	16.61	71.10	12.25	0.04	0.00	2776	23.9

Localities: A., Audley. E., Evans Head. O., Oatley. W., Warrah. M., Malabar.

The majority of flowering plants are hermaphrodite. Dioecism is comparatively rare, but perhaps 75% of the families, and nearly all the larger families, include some dioecic species (Yampolsky, 1922; Lewis, 1942). Whether the primitive angiosperm was unisexual or bisexual may never be known with any certainty, but in many families there can be little doubt that dioecism is a secondary and derivative condition.

Dioecism makes outcrossing obligatory. It ensures a high rate of genetic recombination and allows the maintenance of genetic heterogeneity and adaptability.

TABLE 6.
Tetrad Segregation Data. *Astroloma conostephioides* F. Muell.

Plant.	Tetrad Type Frequencies Percentage.					N.	Percentage Pollen Fertility.
	0s.	1s.	2s.	3s.	4s.		
A. Adelaide District.							
55/107 ..	3.8	30.0	64.2	0.9	1.1	1872	41.4
55/115 ..	19.8	20.9	47.9	5.2	6.2	3185	39.3
55/116 ..	20.5	55.1	22.3	1.7	0.4	2405	26.6
55/104 ..	46.5	51.6	1.9	0.0	0.0	3200	13.9
55/101 ..	61.0	37.2	1.8	0.0	0.0	2479	10.2
B. Grampians District.							
58/214 ..	8.5	13.2	77.1	0.1	1.1	1621	43.0
58/201 ..	0.5	46.8	35.6	11.9	0.6	1281	39.0
58/401 ..	8.8	30.8	59.0	0.7	0.7	2843	38.4
58/210 ..	15.4	58.6	25.5	0.0	0.5	2182	27.9
58/212 ..	14.0	72.0	13.9	0.0	0.1	1637	25.1
58/101 ..	18.1	66.8	15.0	0.0	0.1	2102	24.2

TABLE 7.
Examples of Tetrad Segregation in Other Species.

Species and Plant.	Tetrad-type Proportions Percentage.					N.	Percentage Pollen Fertility.
	0s.	1s.	2s.	3s.	4s.		
<i>Acrotriche</i>							
<i>cordata</i> R.Br.							
58/1	0.94	10.20	31.89	33.76	23.21	853	67.0
<i>depressa</i> R.Br.							
58/1	23.35	54.39	21.22	1.04	0.00	3554	25.0
<i>fasciculiflora</i> Benth.							
54/6	4.08	32.32	52.74	10.67	0.18	1640	42.6
54/5	7.84	40.67	45.79	6.06	0.00	2326	37.6
54/8	18.24	43.68	32.31	5.61	0.16	1891	31.4
54/12	90.12	7.39	2.44	0.05	0.00	4008	3.1
<i>Brachyloma</i>							
<i>ericoides</i> Sond.							
58/0	3.96	7.74	82.64	1.23	4.43	1060	48.6
58/1	1.62	6.94	90.71	0.06	0.67	1786	47.8
58/2	22.18	57.54	20.04	0.12	0.12	1677	24.6
<i>preissii</i> Sond.							
50/49	3.07	31.68	45.00	20.15	0.09	1171	45.6
52/16	2.29	23.46	53.66	20.52	0.07	1530	48.2
52/35	19.90	48.06	27.75	4.29	0.00	955	29.1
<i>scortechinii</i> F.M.							
51/1	0.43	1.44	5.33	21.61	71.18	694	90.4
<i>Leucopogon</i>							
<i>melaleucoides</i> A. Cunn.							
T58/12	4.82	21.72	34.80	29.59	9.07	3342	54.1
/20	3.20	14.84	32.24	35.03	14.69	3942	55.7
/15	3.95	18.73	27.57	30.83	18.92	2024	60.9

It is the predominant feature of the sexual systems in animals, but in plants the same end is achieved more often by other means, and particularly by self-incompatibility, which are perhaps more suited to the circumstances of non-mobility and the mechanisms of pollen transference (Mather, 1940; Westergaard, 1958).

Gynodioecism is a system where a population or a species contains individuals which are hermaphrodite and others which are male sterile, i.e. functionally female.

Sporadic male sterility is known in many normally hermaphrodite plants (Lewis, 1942). Established gynodioecism as a feature of the breeding system of a species has been studied in about a dozen species of flowering plants and is known to be particularly frequent in the Labiateae. Frankel (1940) suggested that such systems may be more frequent in other families than is indicated by actual records.

Normal dioecism is maintained in natural populations by the segregation of a pair of allelic sex genes, linked blocks of genes, or sex chromosomes. Lewis (1941) has shown that gynodioecic systems cannot be easily maintained on the same basis—stability can only be achieved where the male-sterile plants are more than twice as seed-fertile as the hermaphrodite ones, and the frequency of male-sterile individuals must be less than 50% of the population. Chromosomal (or genic) gynodioecism is frequent in experimental stocks of cultivated plants, but is rare in natural populations (cf., however, Lewis and Crowe, 1956). On the other hand, cytoplasmic systems of gynodioecism are more frequent in wild species. In such systems, maternally inherited cytoplasm determines whether an individual will be hermaphrodite or male-sterile. The method permits a delicate control of outcrossing without being dependent upon an extreme advantage in seed set of male-sterile plants.

In the Ericales the normal condition is monoecism with perfect bisexual flowers. Dioecism is rare and must be derived. However, Bentham (1869) observed that some species of the Stypheleae show "partial dioecism". Apart from the normal condition of hermaphroditism, three rather different modifications of the sexual system occur within the tribe. These are: (i) complete dioecism, (ii) gynodioecism comprising hermaphrodite and male sterile plants, and (iii) androgynodioecism, where hermaphrodites, male-sterile (female) plants, female-sterile (male) plants and male-sterile/female-sterile (neuter) plants occur in the population.

In *Monotoca elliptica* R.Br. at Woy Woy, N.S.W. (Smith-White, 1955c) male-fertile plants are completely seed-sterile and dioecism is complete in the functional sense although poorly developed pistils are present in the flowers of male plants and antherless staminodes are present in the females. Bentham (*l.c.*) has stated that in coastal populations of this species dioecism is incomplete, but in the Woy Woy population male-fertile plants are completely seed-sterile. The frequencies of male and female plants in the population are equal—one count gave 138 male and 146 female plants—and a simple sex gene or sex chromosome segregation is indicated.

A similar functionally dioecious system occurs in *Monotoca scoparia* R.Br. at La Perouse, and possibly also in *Leucopogon hookeri* Sond. at Kosciusko. Godley (1957) has reported dioecism in *Cyathodes* spp. and in *Leucopogon fasciculatus* in New Zealand. *Cyathodes divaricata* Hook. and *C. parviflora* R.Br. in Tasmania also include male sterile plants (Smith-White, 1955c) but it is not known whether dioecism is complete in these two species. A system of gynodioecism including female and hermaphrodite plants probably occurs in *Leucopogon melaleucooides* A. Cunn. at Torrington, N.S.W. (McCusker, unpublished data). In *Leucopogon hookeri* Sond. at Barrington, however, male, female and hermaphrodite plants exist.

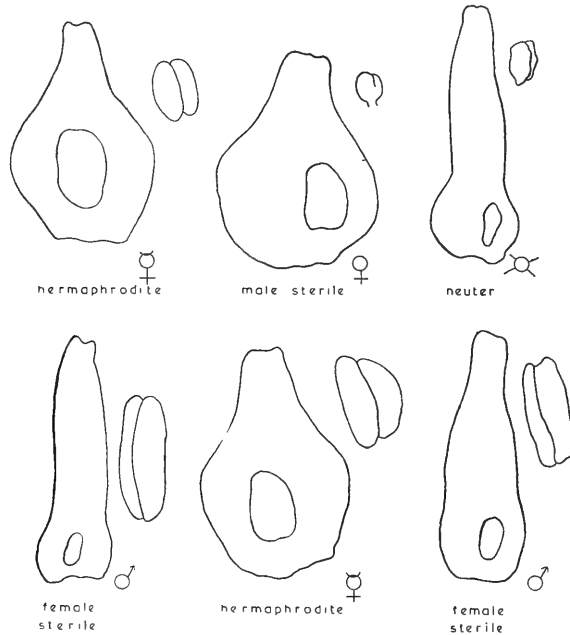
The sexual system in *Lissanthe montana* R.Br. at Kosciusko is still more complex, the population including hermaphrodites, males, females and neuters (Text-fig. 7). There is, however, a complete intergradation of sex types, since male plants show variation from "strong" to "weak" in respect to the size and pollen content of anthers, and female plants vary in pistil development and fertility. Hermaphrodite plants usually have less well-developed pistils than females and smaller anthers than males.

In field counts of the frequencies of male-fertile and male-sterile plants the following results were obtained.

	Male-fertile. ♂ + ♂	Male-sterile. ♀ + ⊗
At Kosciusko Summit	37	63
Roadside, 4½ miles below summit	58	42
Roadside, 6 miles below summit	48	32
Charlotte's Pass	56	44
Spencer's Creek	58	42

With the exception of the Summit counts, the frequencies are consistent and indicate a preponderance of male and hermaphrodite plants.

Sexual differentiation in *Monotoca scoparia* connects the complete dioecism of *M. elliptica* with the sex-strength system of *Lissanthe montana*, since male plants in some populations of *M. scoparia* show a limited seed set. There can be little doubt that the systems of sexual polymorphism found in the several species of the Styphelieae are related.



Text-fig. 7.—Representative pistils, ovules, and anthers from male, female, hermaphrodite and neuter plants of *Lissanthe montana*. $\times 20$. The two female-sterile plants represented differ slightly but consistently in the size of their aborted ovules.

The occurrence of complete dioecism in some species or in some populations, and of male and neuter plants in others, precludes the operation of a cytoplasmic system of sex determination. A cytoplasmic system of gynodioecism does not and cannot lead to complete dioecism since with the latter the cytoplasm of the whole species must be of the maternal, female type. A complex genetic segregational system of determination must be present in *Lissanthe montana*. Such a system may have become progressively simplified and stabilized to give complete dioecism in *Monotoca*.

Crane and Lawrence (1931) have described an experimentally produced sexual system in *Rubus idaeus* which depends on segregation at two independent gene loci. Males are ffMm or ffMM, and females are Ffmm or FFmm. Crosses between females Ffmm and males ffMm yield both hermaphrodite FfMm and neuter ffmm individuals. A similar system is known to occur in *Vitis* species (Negrul, 1936; Oberle, 1938). Another two-factor model is suggested for the Labiate *Origanum vulgare* by Lewis and Crowe (1956). These cases provide models for the interpretation of dioecism and gynodioecism in the Styphelieae, with the proviso that the actual system must be a good deal more complicated in *Lissanthe*.

GENERAL DISCUSSION.

1. *The Evolutionary Relationships of the Pollen Types.*

The maturation of pollen in tetrads is not uncommon in the Angiosperms. Sometimes it may be characteristic only of individual species or genera, as in *Leschenaultia* (Goodeniaceae, Martin and Peacock, 1959, in MSS.) and in *Acacia* (Mimosaceae,

Newman, 1934), or it may be characteristic of whole families such as the Winteraceae, the Droseraceae, and the Juncaceae. A survey of its occurrence (Wodehouse, 1936; Erdtman, 1952) establishes the fact that it must have had many independent origins. Indeed the establishment of the tetrad form from the more usual single condition requires only the persistent cohesion of the post-meiotic microspores, and in genera which normally produce single pollen grains unusual conditions may lead to this cohesion. Thus La Cour (1949) has shown that heat shock may have such an effect in *Scilla*. Levan (1942) has described a gene in *Petunia* which conditions the maturation of tetrad pollen.

Since tetrad pollen is generally characteristic of the Order Ericales, excepting only the monogeneric Clethraceae, it is a possible but by no means necessary assumption that it had a monophyletic origin approximately contemporaneous with the origin of the Order. Had there been separate origins of the character within the several families or tribes it might be expected that several taxa within the Order would have retained the true single pollen condition, and this does not appear to be the case.

Any assumption of multiple or polyphyletic origins of monad type pollen in the Styphelieae is not permissible. The type is not found elsewhere among the Angiosperms. Only in the Cyperaceae is there any parallel behaviour (Juel, 1900; Stout, 1912; Piech, 1928; Tanaka, 1940, 1941), and the details of pollen development in the two families are quite different. Within the Styphelieae—and also within the Cyperaceae—the monad form must have had a single origin from a prior tetrad form, and this origin must have been contemporary with the origin of the tribe itself. The descriptions which have been presented earlier show that the monad pattern of development must be determined by a quantitative cytoplasmic system which must itself be under ultimate nuclear control. The whole system must be complex, and it would seem more likely that it could break down on several occasions than that it should have had several independent origins.

Since both full tetrad and monad pollen types occur within the tribe, and since the latter must be derived from an earlier tetrad condition, it could be supposed that the tetrad type, where it occurs within the tribe, is actually primitive. Alternatively, the hypothesis may be suggested that the tetrad type within the tribe results from the loss of the conditions necessary for monad development. The first view cannot be maintained. Table 8 summarizes the three-way relationship between genera, basic chromosome number and pollen types. The genera were established by Robert Brown, and although later botanists have not always recognized them as having generic status (Mueller, 1868; Drude, 1898; Maiden, 1916) they have never denied their reality as natural groups and have merely reduced them to sectional rank within a single genus *Styphelia*.

It has been inferred (Smith-White, 1955a) that the basic numbers in the Styphelieae are $x = 4$ and $x = 6$, and that the numbers 7, 9 and 10 are derived by polyploidy and secondary change. This view is necessary in *Astroloma* particularly, where the basic haploid number is 4 in fourteen species all with monad pollen, and where two species have $n = 7$ and segregating tetrad pollen.

A consideration of the information in Table 8 shows that if the full tetrad T-type pollen is truly primitive within the tribe it is necessary to assume that the S-type has originated on several occasions or that the recognized genera have no phyletic meaning. It would also mean that the haploid numbers 7, 9 and 10 must be more primitive and that the numbers 4 and 6 must have originated several times, and always in association with an origin of the monad pollen type. Such a view is untenable.

Accepting the view that the origin of the monad type was contemporaneous with the origin of the tribe, and that the primitive basic number was $x = 6$, the S-type pattern was not upset by the origin of the 4-chromosome genom. The full tetrad T-type pollen in species of *Acrotriche*, *Lissanthe* and *Leucopogon* must then represent separate and independent breakdowns of the monad pattern, and it is significant that

such breakdowns are always associated with the origin of secondary basic numbers. Also, the S'-type of development, the partial breakdown in *L. virgatus*, and the segregating tetrads in twelve species belonging to four genera must represent stages in a transition back from monad to full tetrad pollen. This reversion does not do violence to the general concept of the irreversibility of evolution.

It is known that tetrad segregation in *Astroloma pinifolium* and in *Astroloma conostephioides* is associated with abnormal chromosomal conditions and behaviour during meiosis, and these abnormalities are in part responsible for the observed

TABLE 8.
Genera, Pollen Types and Chromosome Numbers in the Styphelieae.

CHROMOSOME NO. (n)	4	8	16	6	12	24	10	11	7	14	9	Un-known
Styphelia	M ₇ ^S											
Astroloma	M ₁₄ ^S	M ₁ ^S	M ₁ ^S						V ₂			
Conostephium		M ₂ ^S										
Melichrus		M ₂ ^S										
Leucopogon ♂ Pleuranthus	M ₇ ^S	M ₁ ^S		M ₅			M ₁ ^I					
Leucopogon ♂ Perojoa				M ₄	M ₂	M ₁	MT ₁	M ₉				
Monotoca					M ₂ ^D							
Cyathodes				M ₂			* ₂ ^D				T ₁	
Leucopogon ♂ Heteranthesis										T ₁ ^D	V ₁ ^D	
Lissanthe									T ₂	T ₁ ^D		V ₁
Pentachondra										T ₁		
Brachyloma									V ₁		MT ₂ ₁	V ₂
Acrotliche											T ₃ ₁	V ₃
Trochocarpa							T ₁					
TOTALS NUMBERS OF SPP.	M ₂₈ ^S	M ₆ ^S	M ₁ ^S	M ₉	M ₆	M ₁	MT ₂ ₁	M ₉	T ₂ ₃	T ₃ ₁	MT ₂ ₅ _{V₁}	V ₇

LEGEND

M MONAD TYPE

V VARIABLE POLLEN TETRADS

M^S MONAD TYPE Microspores initially unequal

T REGULAR FULL TETRADS

M^I MONAD TYPE Microspores initially equal

D SPECIES WITH DIOECISM or PARTIAL DIOECISM.

SUBSCRIPTS—Nos. of Species.

* POLLEN TYPE UNKNOWN

segregations. In *Lissanthe strigosa* only a single plant amongst more than fifty is known to show segregation and in this species it is necessary to assume that the segregation is derived directly from the full tetrad condition. If, however, the monad type is the primitive one within the tribe, unusual cytoplasmic conditions must be associated with segregation, and in some of the species, particularly in *Astroloma* and *Brachyloma*, segregation must be derived directly from the monad type. It is probable that the behaviour, even when not directly derived from the monad type, is dependent upon a preadapting evolutionary history involving monad pollen, cytoplasmic differentiation or polarity, and possibly the cytoplasmic control of chromosome segregation. This view is further supported by the high frequency of the occurrence of tetrad segregation within the tribe compared with its low frequency in other families with

tetrad pollen, and by the quantitative intergradation which connects the extreme monad and the full tetrad types.

2. *A Deductive Hypothesis.*

The treatment of the problem of pollen development in the *Styphelieae* so far has been descriptive and inductive. The main conclusions which have been reached may be enumerated.

Firstly, all the patterns of pollen development in the tribe are related in causation. They constitute parts of one large problem. One general hypothesis must be capable of explaining and relating all the modifications of this causal system, and an attempt to formulate such an hypothesis is worth while.

Secondly, the monad pattern of pollen development has had a single origin, roughly contemporaneous with the origin of the tribe itself, and may be regarded as the primitive condition within the tribe. Although the monad type must have originated from an earlier tetrad condition, full tetrad pollen, where it occurs within the tribe, is derived by the breakdown of the monad type. Tetrad segregation must also be related to the monad type.

Thirdly, from a consideration of the implications of the *Styphelia* type of monad development, it is inferred that the control of the monad system is primarily cytoplasmic and there must be a cytoplasmic polarity within the mother cell. Cytoplasmic polarity must mean that certain vital constituents attain a gradient distribution within the general "body" cytoplasm of the cell. Chromosomal homozygosity may be assumed as an initial condition, and differential nuclear migration is determined by position.

Fourthly, the permanent triploid *L. juniperinus* demonstrates that unbalanced univalent chromosomes are sensitive to this gradient and control of their segregation follows as an immediate consequence. Any control of the segregation of homozygous paired chromosomes is impossible and meaningless, but such control may extend to structurally heterozygous bivalents provided this heterozygosity involves sensitive chromosome segments. Support for this suggestion comes from evidence discussed earlier (page 13), that preferential segregation is often a function of heterochromatin.

Fifthly, the triploid species also shows that a similar control operates in the embryo sac mother cells, but under the influence of a different tissue environment. The conditions necessary for complementary gametic selection are present and confer preadaptation to permanent hybridity.

Finally, cytoplasmic differentiation must be under genotypic control. It is quantitative and complex. Change in genetic balance consequent upon change in the basic genom predisposes to the loss of polarity in the mother cell.

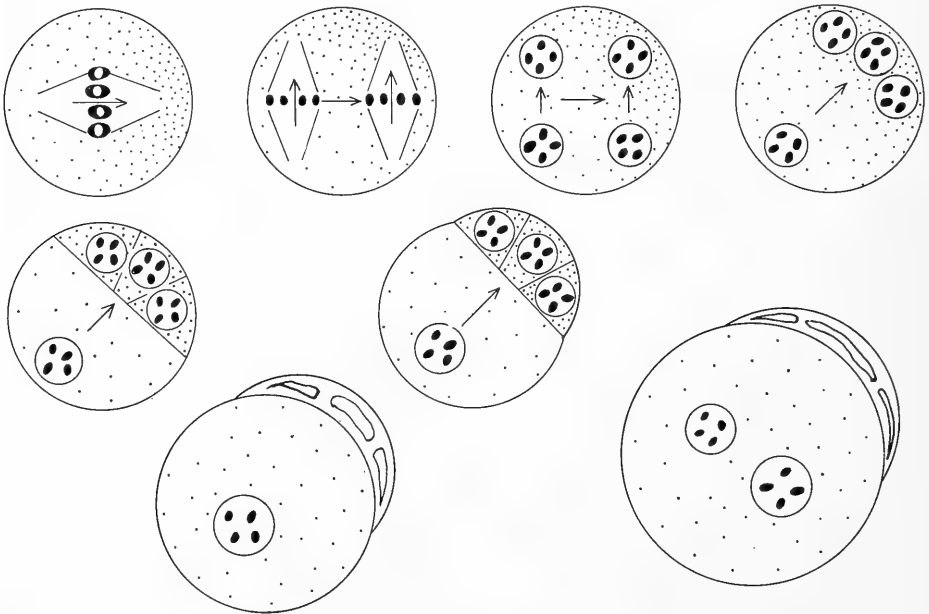
The Initial Operation of the System.

These conclusions may be taken to constitute a fundamental system and an attempt will be made to deduce its evolutionary consequences. Text-figure 8 illustrates the immediate operation of the system in pollen development in a homozygous diploid with four pairs of chromosomes. Polarity causes a gradient distribution of certain cytoplasmic constituents (stippling) and also of non-chromosomal nuclear materials. Nuclear migration is one result. Microspore survival is determined by the positions of the nuclei in the mother cell; that microspore survives which receives an adequate supply of both the polarized materials and of the "body" cytoplasm, and this would obviously be the isolated nucleus at the "negative" end of the polarity, since, getting the major share of the body cytoplasm, it would also get sufficient of the polarized constituents.

The operation of the same system in the ovule is illustrated in Text-figure 9. Intracellular conditions in the P.M.C. and in the E.S.M.C. are the same, but the

closely enveloping ovule tissue maintains a linear arrangement of the second division spindles and of the megaspores, and precludes nuclear migration. An ovule tissue gradient, not present in the anther, permits the development only of the micropylar megaspore.

Conditions of megaspore competition are thus different from those of microspore competition. The intracellular E.S.M.C. polarity may favour either the micropylar or the chalazal ends. In the former case (Text-fig. 9, left) the micropylar megaspore receives a major share of the polarized cytoplasmic components and an equal quarter-share of the body cytoplasm. A functional embryo sac is produced. Where, however, the intracellular polarity favours the chalazal end and operates against the tissue gradient, the micropylar megaspore gets insufficient polarized constituents and aborts; the micropylar megaspore commences to develop, but fails at an early age, and no functional embryo sac is produced (Text-fig. 9, right). The direction of the intracellular



Text-fig. 8.—The control of pollen developing in a diploid species. A cytoplasmic polarity (stippling) determines nuclear migration and survival. Cf. text.

mother cell gradient is apparently independent of the ovule tissue gradient, since species with monad pollen show a maximum of 50% seed fertility.

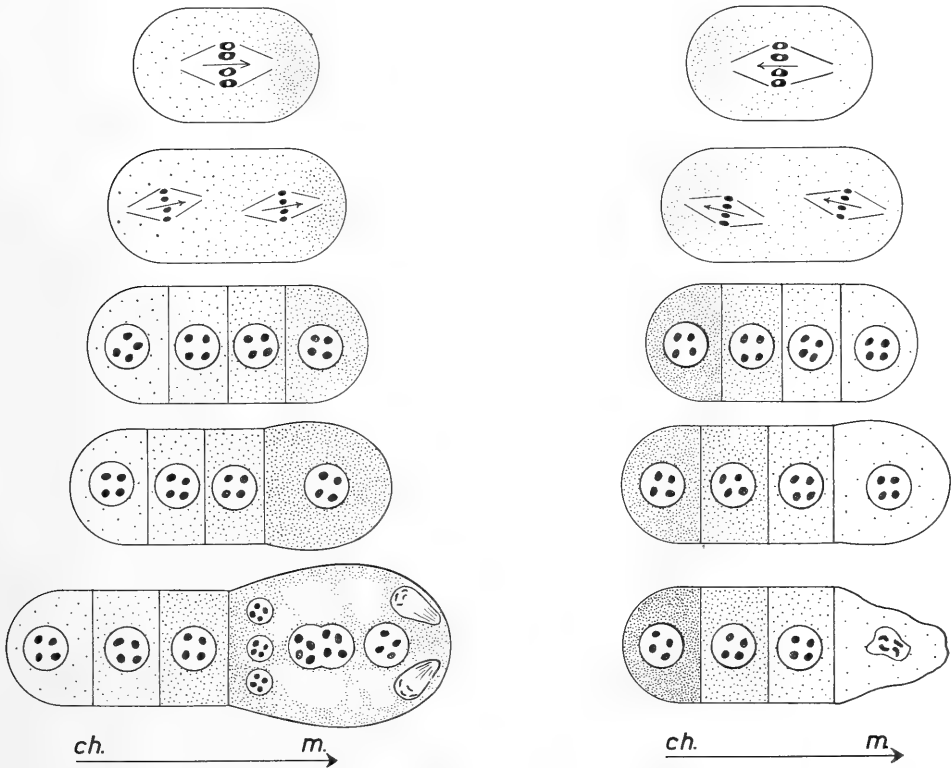
The hypothesis set up is admittedly superficial, since the nature of the gradient cannot be suggested. It is, basically, an hypothesis of the interaction of two different kinds of competition, balanced against each other differently in the pollen and embryo sac developmental sequences. Functional pollen grains are developed only from the "negative" end of the cytoplasmic axis, and functional embryo sacs come only from the "positive" end of the same axis. If unbalanced chromosomes are sensitive to cell polarity there is preadaptation to the maintenance of permanent hybridity.

The Operation of the System in the Triploid.

The operation of this system in the triploid *Leucopogon* is illustrated in Text-figures 10 and 11, and these figures need very little further explanation. When the triploid was first formed, presumably following hybridization, the exclusion of univalents from the effective pollen, and their inclusion in the effective embryo sacs would be an immediate consequence of the prior conditions of pollen and embryo sac development.

This initial control probably is not the final one. The univalents would be subject to a predominantly maternal inheritance and, since lethal mutations are relatively frequent, they could in the course of time accumulate pollen lethals preventing the survival of the exceptional grains which might contain them. Selection would also favour the accumulation in them of genes favourable to embryo sac development, and there would then be no retreat from permanent hybridity.

It is possible that a similar system is responsible for the maintenance of univalents in the *Rosa canina* complex. In these roses there is no polarity in pollen development, and univalents are eliminated in the pollen line only by the intolerance of genetic unbalance. In the embryo sacs, however, conditions must be very similar to those in



Text-fig. 9.—The control of embryo sac development in a diploid species. There is interaction between an ovule tissue gradient favouring the micropylar megaspore (bottom arrows) and a cytoplasmic polarity (stippling). The latter may favour either end of the megaspore-tetrad. Cf. text.

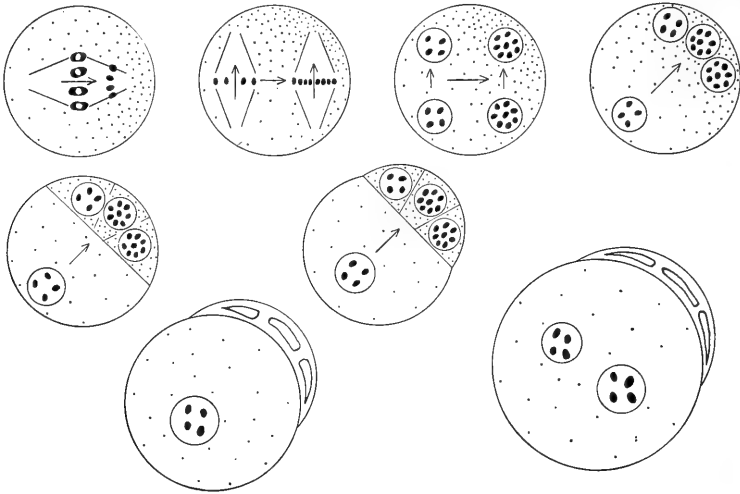
L. juniperinus and an initial tendency for the univalents to be inherited in the maternal line would then be strengthened by selection both of genes necessary for embryo sac development and of more reliability in polarized segregation, as suggested by Darlington (1939).

The Origin of Permanent Hybridity in Diploid Species.

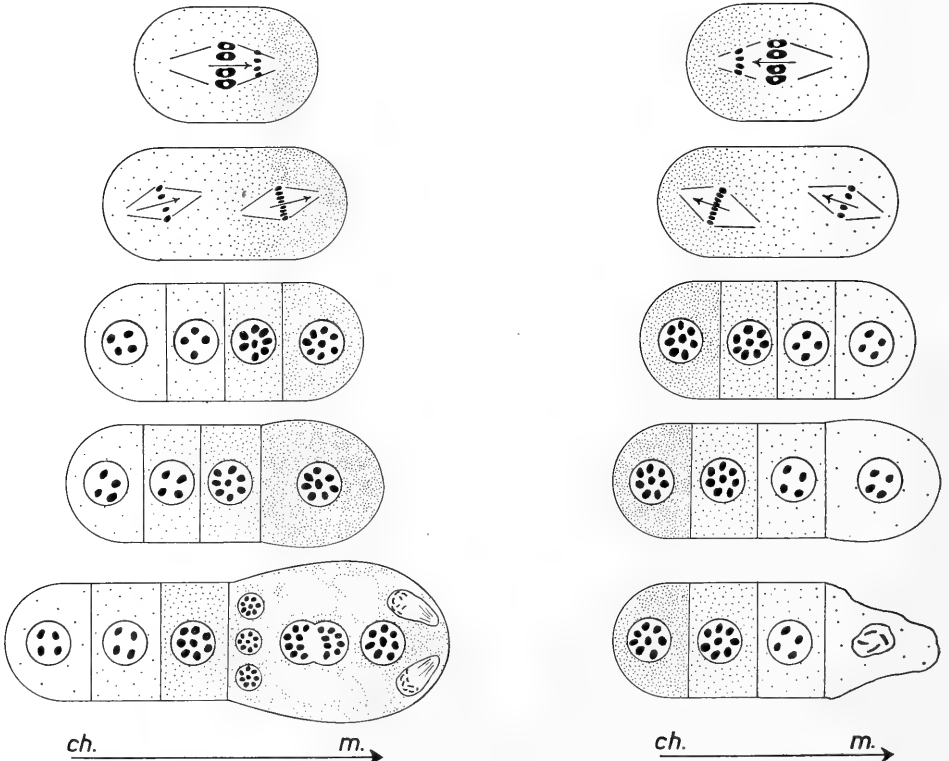
If, as has been inferred, cytoplasmic control of segregation can extend to structurally heterozygous bivalents, it would be possible for permanent structural hybridity to be established in diploid species possessing monad pollen. It will be

assumed that structural hybridity may arise adventitiously in any species, but that in sexual species with a normal genetic system it will usually be eliminated.

One necessary condition, for permanence, is some degree of chiasma localization, but this is not a serious restriction, since chiasmata are rarely or never strictly

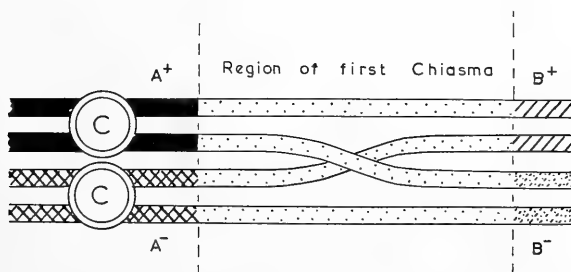


Text-fig. 10.—The control of pollen development in the triploid *Leucopogon juniperinus*. Univalents are "gradient-positive" and are excluded from the functional pollen. Cf. text.



Text-fig. 11.—The control of embryo-sac development in the triploid *Leucopogon juniperinus*. The univalents, being "gradient-positive", are included in the functional embryo sacs. The univalents of the triploid are strictly maternal in inheritance. Cf. text.

terminal or strictly adjacent to the centromeres. Text-figure 12 illustrates a bivalent in which there is one chiasma, with the proximal and distal regions excluded from the chiasma region. The bivalent can be extended to a second chiasma region without affecting the subsequent argument provided the first and second chiasma regions do not overlap, i.e. provided there is a degree of chiasma localization. An adventitious structural change, adjacent to the centromere, would cause an orientation of the bivalent at first metaphase, with the more sensitive segment directed towards the positive end of the cell polarity. As with the univalents in the triploid, this controlled segregation would favour the exclusion of the positive reacting chromatin from the pollen and its inclusion in the embryo sacs, and the negative responding chromatin would be favoured in the pollen. Similarly, an adventitious structural hybridity distal to the chiasma region, and perhaps with neocentric activity or acting indirectly through the centromere (Darlington, 1956), could cause a non-random orientation of the chromatids at the second division. It is not necessary that this control should be near-perfect in the beginning, but only that it should be substantial, since selection would then favour its greater stabilization. Adventitious structural hybridity would be maintained by the complementary gametic selection imposed by the cytoplasmic system.



Text-fig. 12.—Diagram of a bivalent with a single chiasma and some localization. The proximal and distal segments lie outside the chiasma region. Cf. text.

With this cytoplasmic system operative, a reinforcement with a genetic mechanism would be almost inevitable. Bennett (1956) has demonstrated that even in species with more normal genetic systems there is an appreciable prospect of the establishment of balanced lethal mechanisms within non-crossover segments. In the system suggested here there would be no selection against pollen-lethal mutations in the maternally inherited gradient-positive segments nor against embryo sac lethals in the paternal gradient-negative segments. This would lead to the reinforcement of the cytoplasmic control of the monad pattern of development by a more rigid system involving chromosomal segregation and permanent balanced gametic lethals. Referring again to Text-figure 12, if A and a represent "positive" and "negative" proximal segments, and if B and b represent similar segments distal to the chiasma region, we have precisely the segregational scheme mentioned and rejected earlier (Text-figure 2b).

There is an important complication, however. In *Styphelia* there are four pairs of chromosomes, and each is equally liable to the consequences of cytoplasmic polarity. In each bivalent there is a single proximal position (i.e. on both sides of the centromeres) and two distal positions (one on each chromosome arm) which are protected from crossing over and which are therefore potential sites for structural hybridity. With maximum complexity the constitution of a diploid *Styphelia* or *Astroloma* could be:

S A T	U B V	W C X	Y D Z
— — —	— — —	— — —	— — —
s a t	u b v	w c x	y d z

where the dots represent centromeres and the symbols represent "positive" (capitals) and "negative" (lower case) segments. This segregational system could reinforce,

but not replace, cytoplasmic control, since it would break down if subjected to random segregation. Further, it could not operate on the bivalents in the *caninae* roses, since there is no polarity and therefore no possible control of bivalent segregation, in the pollen mother cells of *Rosa*.

The Breakdown of the System.

It has been found that loss of the monad pattern is associated with secondary polyploidy and change of genetic balance. Secondary polyploidy does two things. It brings a reduplication of a large part of the genom and it causes a loss of polarity in the pollen mother cells. In *Astroloma*, with $x = 4$, the two species with A-type pollen both have $n = 7$. Assuming the full structural hybridity illustrated above, their constitutions would become

S A T	U B V	W C X	Y D Z	U' B' V'	W' C' X'	Y' D' Z'
s a t	u b v	w c x	y d z	u' b' v'	w' c' x'	y' d' z'

It is not necessary to assume that genetic differentiation should occur in all seven proximal positions and all 14 distal positions. The loss of cell polarity would open the system to segregation. Assuming segmental heterozygosity in all positions except those in the unrepeated chromosome, and either duplicate or alternate interactions between the repeated parts of the genom (i.e. either auto- or allopolyploidy), pollen tetrad segregation would result, with frequencies of the five possible tetrad types:

Percentage frequencies.

Interaction	nullads	monads	dyads	triads	full tetrads
Duplicate	75.73	24.64	2.50	0.127	0.003
Alternate	97.10	2.83	0.022	0.0002	0.000007

Thus, following loss of polarity, the initial pollen fertility would be extremely low provided full complexity had been attained. However, selection should tend gradually to undo the system previously built up under the protection of polarity, and simpler patterns of segregations such as those actually observed would result. Ultimately, the whole segregating system might be eliminated, giving reversion to the full tetrad type. It would be expected that the interaction relationships of the reduplicated genomes would be different in the several independent origins of secondary ploidy within the tribe. Also, the selective reduction of the segregating system would vary in each case; it would be rapid in the absence of the accumulation of pollen and embryo sac lethals on the "negative" and "positive" segments respectively, but slow and perhaps almost impossible in the event of such accumulation. The different species would show differences in the ease and rate of reversion to the full tetrad condition.

The Origin of Dioecism and Mixed Sexuality.

The chromosomal system wherein certain segments are inherited solely through the embryo sacs and where alternative segments are solely paternal, has some similarity with ordinary sex mechanisms. A very simple system of mixed sexuality can be deduced on such a basis.

In the simplest case, structural hybridity A/a may be assumed in a single segment, where A is positive to cell polarity and a is negative. Segment A has accumulated deficiencies which act as gametic lethals in the pollen, and similarly a has accumulated embryo sac deficiency lethals. With secondary ploidy there is a reduplication of these segments, giving either the constitutions A/a A/a (autopolyploidy) or A/a A'/a' (allopolyploidy). This is the simplest form of the system already deduced. There is also a loss of polarity. The only new assumption necessary is that in individuals homozygous for A/A or A'/A' there is anther abortion, and that in individuals a/a or a'/a' there is pistil abortion. Three genotypes of embryo sacs, AA', Aa', and aa', and three of

pollen grains, Aa' , aA' , and aa' , are possible, and in the sporophyte there are seven genotypes and four phenotypes:

$\frac{AA}{Aa'}$	$\frac{AA}{aA'}$	$\frac{AA'}{aa'}$	$\frac{Aa'}{aa'}$	$\frac{aA'}{aa'}$	$\frac{Aa'}{Aa'}$	$\frac{aA'}{aA'}$
Female		Her-	Male		Neuter	
		maphrodite				

There is an interesting feature of this system. Starting with any frequencies of the seven possible genotypes, and in the absence of selection, the system will rapidly approach a stable equilibrium in which the proportions p and q of A and a , and p' and q' of A' and a' , are equal, and in which the four phenotypes have the proportions 0.24 females, 0.35 hermaphrodites, 0.24 males and 0.17 neuters, which may be further summed to 0.59 male-fertile and 0.41 male-sterile. These are close to the actual proportions observed in *Lissanthe montana* at Kosciusko. The occurrence of such a stable equilibrium, which of course might be modified by other factors of selection, would mean that the system could be readily established once the necessary prior conditions were provided. In this respect it resembles the relatively simple case where selection favours a heterozygote A/a over either homozygote A/A or a/a .

The system also resembles fairly closely the two-factor mechanisms which have been described in *Rubus idaeus* and in *Vitis*, referred to earlier in this address. However, it is capable of much greater complexity, where heterozygosity might be established in similar non-crossover segments in other chromosomes, and it is capable of giving a complex sex-strength system which seems to be necessary in *Lissanthe montana*. It is also capable of being modified in the direction of complete dioecism.

SUMMARY.

The most frequent, and perhaps the most characteristic pollen type in the Stypheleae is the monad. Monad pollen is derived from the tetrad form by the regular failure of three microspores in the young tetrad. In its most extreme form, monad development involves nuclear migration in the mother cell following the conclusion of meiosis.

Other pollen types found in the tribe include modified monads where nuclear migration is absent, variable pollen tetrads, and regular pollen tetrads.

An attempt has been made to show that all pollen types in the tribe must be related at the level of causation, and that the extreme monad type is the basic one within the tribe. Its establishment must have been roughly contemporaneous with the origin of the tribe. The other pollen types represent breakdown or loss of the monad pattern of development.

The monad pattern of development necessarily implies the development of cytoplasmic differentiation or polarity within the pollen mother cell. This polarity may possibly be related to that which is normal in angiosperm pollen grains.

Conditions in a permanent triploid *Leucopogon* demonstrate that this polarity is present in the mother cell during the first meiotic division, and also that unbalanced chromosomes (univalents) may be sensitive to it. The permanent triploid also demonstrates the existence of a mechanism of complementary gametic selection. This mechanism must be antecedent to the origin of triploidy and its presence can be inferred in diploids.

Using these inductive conclusions, an evolutionary hypothesis has been presented to explain and relate the different pollen types. According to this hypothesis, structural hybridity could be maintained in diploid species by a mechanism similar to that demonstrated in the triploid. Loss of polarity, accompanying secondary ploidy and change of genetic balance would then give rise to the variable tetrad pollen type.

The hypothesis permits the deduction of a system of mixed sexuality and unstable dioecy which is adequate to explain actual conditions in a number of species of the tribe.

The hypothesis is admittedly a speculative one. Its only merit may be that it permits a unification of several problems within the group. It is, however, capable of experimental testing, and I hope to be able to contribute in this way, in the future, either to its establishment or its downfall.

Acknowledgements.

I am indebted to Miss A. McCusker for observations and data on pollen tetrad segregation in *Leucopogon melaleucoides*, *Lissanthe strigosa* and *Acrotriche divaricata*, and to Mr. L. D. Williams, of Meningie, S.A., for bringing to my notice the occurrence of tetrad segregation in *Acrotriche cordata*, *A. depressa*. and *Brachyloma ericoides*, and for supplying material of these species.

I am grateful to Miss Margaret Woodward for the preparation of many of the diagrams.

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EXPLANATION OF PLATES I-II.

Plate i.

Breakdown of monad development in *Leucopogon virgatus*, Plant R57/10.

Plate ii.

Variable Tetrad Pollen.

1. *Astroloma pinifolium* × 150. 2, 3. *Astroloma conostephioides* × 150. 4. *Acrotliche fasciculiflora* × 300. 5. *Leucopogon melaleucoides* × 300. 6. *Brachyloma ericoides* × 300.

PHYSIOLOGICAL SPECIALIZATION OF *MELAMPSORA LINI* (PERS.) LÉV.
IN AUSTRALIA.

By H. B. KERR.

(Plates iii-iv; three Text-figures.)

[Read 25th March, 1959.]

Synopsis.

A physiologic race survey of the pathogen *Melampsora lini* (Pers.) LéV. was carried out at Sydney University over the period 1948 to 1953. Several important new races were recorded indicating a marked change in the pathogenicity of the pathogen in Australia since the first surveys undertaken by Waterhouse and Watson. Particular attention is drawn to the difference in host range and geographic distribution of the Punjab-attacking and non-Punjab-attacking race groups.

INTRODUCTION.

Physiologic specialization in *M. lini* was first demonstrated by Flor in 1935, although others were aware of physiologic differences within the species as early as 1865. By 1935 Flor had identified fourteen races on nine differential varieties. Since then Flor has modified and increased his differential series on which he had differentiated 127 races by 1945 (Flor, 1945). Other races were detected by workers in Canada, Europe, Australia, South America and India (Straib, 1939; Waterhouse and Watson, 1943; Vallega, 1944; Prasada, 1948). The differential varieties currently used by Flor are monofactorially resistant or immune to the races identified by him, and could effectively differentiate over a million races which might be realized by random recombination of genes already detected in the pathogen.

According to McAlpine (1906), *M. lini* was first identified in Australia in 1889 on cultivated flax *Linum usitatissimum*. It was also common on native flax *L. marginale*. He assumed that it had been introduced from overseas.

Flax and linseed, especially flax, have been grown on a small scale since the earliest colonial days. Acreages remained very small until the 1939-1945 war. Prior to 1939 the yearly sowings of flax averaged less than 2,000 acres. This increased to a peak of 61,000 acres in 1944, followed by a progressive decline to acreages of less than 5,000 acres between 1950 and 1952. Commercial crops of flax were limited to Victoria, South Australia, Western Australia and Tasmania.

Blue Riga, the main flax variety in Victoria prior to 1937, and Concurrent and Liral Crown, the dominant varieties in the southern States during and after the war years, were highly susceptible to the majority of the Australian races identified since 1943. Rust-resistant varieties began to replace them (Thomas and Millington, 1946), but the pathogen continued to be a serious hazard to flax crops (Cass Smith and Harvey, 1946).

Linseed acreages also increased during the war years and remained at a moderately high level for some time afterwards. Moderate acreages were grown in New South Wales and Queensland as well as the southern States as late as 1953, when these studies were closed. The first commercial crops of Punjab suffered severely from rust, but the linseed growing industry was reestablished with Walsh, which has been generally resistant to *M. lini* in all States since its introduction.

Following serious outbreaks of rust in the early war years Waterhouse and Watson (1941 and 1943) commenced a survey of the pathogen. Flor's series of eleven differential varieties and Argentine 705-1 constituted the first set of differential varieties. The first survey keyed out a unique race which differed significantly from

all overseas races in its avirulence on Bison, a variety susceptible to all these races. It was designated race A, and was highly virulent on Punjab. Later studies determined five additional races, B to F. Most of the collections of rust were from commercial crops, but several were from *L. marginale*. The latter, with one exception, were identified as races A or F, both Punjab-attacking and avirulent on Bison. Watson continued the survey beyond 1943 but failed to detect any significant change in the rust population up to 1945. A further survey was carried out by Charles in 1947 on an extended host series of eighteen varieties including the original twelve. This was continued by Kerr in 1948 prior to the project dealt with in this paper. These studies determined seven additional races G to O. In addition, Charles reclassified the original six races A to F, adding to their description reactions given by them on six additional varieties (Millikan, 1951).

EXPERIMENTAL METHODS AND MATERIAL.

The differential series previously used by Charles (1947) was adopted during the current studies. To these were added Koto, a variety showing promise as a useful immune parent, and a selection of Walsh, the only commercial variety of linseed grown in Australia. Owing to impurity Williston Brown was later dropped from the series. The differential varieties are listed below.

Variety.	Sydney University Accession Number.	C.I. Number.
Buda	Fx 1	—
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	—
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

Collections of rust were received from Queensland, New South Wales, Victoria, South Australia and Western Australia. The collections were received during spring and early to mid-summer. They were cultured on the unnamed variety F257, which was found to be more susceptible to the Australian collections than the previously used variety, Concurrent. The uredospore inoculum was collected and stored in small, glass, cork-stoppered phials in a refrigerator at 0° to 2°C.

The studies were carried out in the glasshouses at Sydney University during the cooler months of the year from April to late October. Temperature and light intensity and duration fluctuated according to conditions out of doors. This was offset by the occasional use of radiators and incandescent lights during winter, when the equipment was available.

The reaction of the differential varieties was read after about 10 to 14 days, depending on conditions during incubation. Flor's system of reaction classification was adopted as far as possible, but the wide range of reaction induced by fluctuations

in the environment prevented very fine distinctions. Only three types of reaction were finally distinguished: immune (including consistently immune or highly resistant), resistant (including the wide range of rather variable intermediate reactions from resistant to moderately susceptible), susceptible (including highly susceptible reactions sometimes depressed to moderate susceptibility by adverse environmental conditions). (See Plate iii.)

Each collection was tested at least twice, and particular attention was paid to the varieties giving reactions rather sensitive to the environment. The varietal screening method was used to confirm the occurrence of new races, along with the use of single spore cultures.

Adequate precautions were taken to prevent contamination of the races in the glasshouse. Races were cultured where possible on varieties immune to the other races



Text-fig. 1.—Maps of linseed and flax growing States indicating main flax and linseed growing districts, and districts from which *Melampsora lini* specimens were received.

cultured in the same house. They were subcultured no more than twice a year and sometimes only once a year.

The spore dusting inoculation technique used by Flor (1935) and Waterhouse and Watson (1941) did not always give satisfactory results during these studies. A more laborious method was adopted, but this resulted in consistently heavy infection. A drop of water was placed on the crown of young unfolded leaves of each seedling. Uredospores were spread on the surface of water in a petri dish and transferred by spatula to the seedling tip. At first poor germination of uredospores stored for more than two months sometimes necessitated reinoculation. It had been the practice to check the percentage germination of the residual spores left in the petri dish. While germination was generally good on the seedling tips, it was not uncommon to discover that the spores had generally failed to germinate on the water in the petri dish. This was attributed to diffusion of substances from the host tissue into the terminal drop of water. Boiled aqueous host extract was found to induce consistently maximum germination in stored spores sown on the surface of the extract. Experiment showed that it was generally sufficient to spread stored spores on the surface of concentrated

host extract before transfer to the terminal drop of water on the seedling to ensure good germination. When spores had been stored for long periods it was sometimes sufficient to leave the spores on concentrated host extract for several minutes before transfer to the seedling. To ensure good germination host extract was used to moisten the seedling tips.

The excised shoot technique was used during most of these studies to conserve bench space and ensure a ready supply of seedling tips for inoculation (Kerr, 1951).

During these studies a technique was developed to preserve rust reactions for comparison with results obtained later. Leaves were preserved under Scotch tape on semi-absorbent paper and stored in the dark in a refrigerator at 0° to 2°C. After two years there was no appreciable deterioration, the leaves and reaction closely resembling freshly collected material.

EXPERIMENTAL RESULTS.

The Effect of the Condition of the Shoot on the Rust Reaction.

The condition of the host during the incubation period played an important role in determining the reaction of most varieties. The most susceptible varieties usually developed a measure of resistance as the shoots became more fibery with age.

Bison was fully susceptible to every Australian race, except race 1, and F257 was fully susceptible to every race in the early seedling stage. Race 6 was cultured on both varieties under identical conditions, on young succulent excised shoots of F257 which remained succulent during the incubation period, and on older excised shoots of Bison which were quite succulent when inoculated, but became rather fibery later. Both varieties gave a susceptible reaction after 10 days. After three weeks the infected Bison leaves had withered and yielded very little inoculum. F257 continued to yield very heavy loads of uredospores. A quantitative assessment of the degree of active infection at this time was given by the number of excised stems of each variety with prominent uredosori. Only fourteen of thirty-two excised shoots of Bison had uredosori on the stem. Thirty-nine of the forty-one shoots of F257 showed prominent uredosori on the stems. Bison had obviously acquired some measure of resistance to race 6.

The degree of succulence of the inoculated shoot was more important than the age of the parent plant in determining reaction. Since succulence was largely determined by environmental factors, rather than any inherent characteristic of the host, during the first month or so after excision of the shoot, the value of standardizing growing conditions at the optimal was apparent.

The Effect of the Environment on Host Reaction.

Recognition of the significantly different reactions of each variety in the differential series to different races of rust is fundamental to the success of any physiologic race survey. Since no two varieties behave alike, each must be studied individually to determine the number of significantly different reactions and the extent to which each reaction is subject to environmentally induced fluctuations.

The lack of temperature and light control facilities at Sydney accentuated the importance of this aspect of the work. Variations in the environment often induced changes in reaction as great as that considered adequate for the differentiation of races. The reaction of several varieties to both races 2 and 13 was suppressed in the direction of greater resistance under the very warm incubation conditions in the glasshouse during late October and early November. The variety Very Pale Blue Crimped was immune to race 2 under these conditions, although it gave a fully susceptible reaction to race 2 under the optimal conditions (15° to 20°C.) prevalent earlier in the year.

Races 1 and 2 were tested in the field at Sydney to determine their capacity to survive in the uredospore stage during spring and summer. The former was highly virulent on Punjab and moderately virulent on F257 in the glasshouse under optimal conditions, and the latter was avirulent on Punjab but highly virulent on F257. Both were well established on their susceptible hosts in September. Periodic sowings of

both varieties were made to ensure a constant supply of young infectable plants. As the temperature increased during November and December, Punjab continued to be heavily infected by race 1. The poor infection of F257 reflected the lack of tolerance of race 2 to high summer temperatures and the relative immunity of the variety to race 1 under these conditions.

Reaction Levels.

After careful consideration of all the results obtained with each accession it was decided to recognize no more than three distinctly different reactions in each variety. In most cases only two significantly different types of reaction were differentiated. Some varieties may have had more significantly different reactions than the number finally attributed to them. But in view of the wide variations in light intensity and temperature during tests and between different tests of each accession, it was considered unwise to postulate a greater number than that finally decided upon.

It is proposed to designate significantly different reactions within a variety "reaction levels". There seems to be no conclusive evidence to show whether the reaction of a variety to all possible races of a given pathogen ranges by almost imperceptible stages from complete immunity to complete susceptibility, or whether there is only a limited number of different reactions. If the former is the case the term reaction level has little meaning, the number of levels determinable being limited only by the degree of environmental control and accuracy of observation. The results obtained during this and most other rust surveys, and Flor's genetic investigations of virulence and avirulence in *M. lini* seem, however, to support the thesis that there is only a limited number of reaction levels. This assumption underlies the use of the term reaction levels.

In the final analysis races should be differentiated from each other and described in terms of these reaction levels. A double descriptive system would seem to be necessary. The rust reaction of a variety to any race is the product of the interaction of a gene or genes in the pathogen and corresponding genes in the host, modified by the environment, and possibly also by modifying genes in the race and host. No two varieties are likely to have the same range of reactions. The resistant reaction of Walsh was characteristic of that variety and differed noticeably from the resistant reaction of Akmolinsk to the Australian races. The initial descriptive terminology should be sufficiently comprehensive to define these differences.

However, fine differences in the resistant reaction of varieties are irrelevant in the final race classification. These differences are no more relevant than those induced by the environment. Final decisions on race status must necessarily be intravarietal. Two races can be differentiated only if the reaction of one differs significantly from the reaction of the other on the same variety under the same conditions. The finer differences of reaction usually given in a final race analysis have therefore been ignored in this survey, and the terms immune, resistant, and susceptible adopted. Immunity and susceptibility are probably synonymous with complete incompatibility and complete compatibility respectively between host and pathogen. Resistance includes the intermediate range of reaction probably synonymous with intermediate incompatibility. The use of the term seems quite valid, since such reactions less than completely susceptible generally agree with field resistance.

Reaction Levels of the Differential Varieties.

The following is a brief summary of the number of reaction levels determined for each of the differential varieties.

BUDA: 2: susceptible and a highly variable resistant reaction.

WILLISTON GOLDEN: 2: susceptible and resistant. The resistant reaction tended towards immunity and was characterized by necrosis and a variable number of pustules rarely exceeding Flor's type "3-". A slight difference in reaction between races 1 and 17 was too fine to justify differentiation of two intermediate reactions.

AKMOLINSK: 2: susceptible and resistant. The latter approximated fairly closely to Flor's type "1" reaction. The susceptible reaction to race 1 may have been slightly lower in the scale of susceptibility than that evoked by other races. The variety appeared to have a measure of resistance to Punjab-attacking race 1 later in development, but in the seedling stage under optimal growing conditions it was fully susceptible.

J.W.S.: 3: susceptible, resistant, immune. The resistant reaction to race 1 ranged from almost complete susceptibility to near immunity according to the conditions of incubation and the inoculation technique used.

ABYSSINIAN: 2: susceptible and immune. The susceptible reaction was sometimes depressed slightly to moderate susceptibility.

KENYA: 3: susceptible, resistant, and immune. The resistant reaction was characterized by necrosis, type "2" and occasional type "3-" pustules. The susceptible reaction was sometimes reduced to moderate susceptibility.

ARGENTINE 705-1: 2: a highly variable resistant reaction varying from near immunity to near susceptibility, and a rather variable susceptible reaction commonly depressed to moderate susceptibility.

VERY PALE BLUE CRIMPED: 3: susceptible, resistant, and immune. The resistant reaction ranged from near immunity to type "2" reaction. The susceptible reaction was most commonly reduced to moderate susceptibility. It was very subject to variations in incubation conditions.

OTTAWA 770B: 2: susceptible and immune. Two very stable reactions.

ARGENTINE 462: 1: immune.

BISON: 2: full susceptibility, immune. Both reactions were extremely stable.

PUNJAB: 2: susceptible and immune. The susceptible reaction to the only race to which it succumbed was one of the most virulent noted during these studies.

WALSH: 2: susceptible and resistant. The reaction to race 1 approximated more closely to immunity than that given by other non-Walsh-attacking races. The resistant reaction to these latter races was characterized by severe necrosis, with occasional type "2" pustules. The susceptible reaction was rather low in the scale of susceptibility.

MORYE: 1: immune.

NEWLAND: 2: susceptible and immune. Several races gave a delayed resistant reaction some time after completion of the usual incubation period. It was characterized by isolated and never abundant type "3" pustules. There was no necrosis. Uredospores taken from these pustules and built up on fully susceptible F257 failed to induce a more susceptible reaction. The pustules did not represent contaminant races. The races evoking this reaction more commonly gave complete immune reactions. The sparsity of type "3" pustules and the inconsistent development of the reaction did not justify differentiation of a resistant reaction level.

BOLLEY GOLDEN: 3: susceptible, resistant, and immune. The resistant reaction agreed with Flor's type "1", but was often depressed to immunity. Small isolated non-necrotic pustules like those recorded for Newland were sometimes associated with this reaction.

ITALIA ROMA: 2: susceptible and immune. There seemed to be a resistant reaction, but it was not sufficiently consistent to differentiate it from the slightly variable immune reaction. The susceptible reaction was quite commonly depressed to moderate susceptibility and occasionally to a resistant reaction.

LEONA: 2: susceptible, sometimes depressed to moderate susceptibility and a slightly variable immune reaction.

TAMMES' PALE BLUE: 2: susceptible and immune. Some immune reactions developed occasional type "3" pustules rather like those reported for Newland and Bolley Golden. The susceptible reaction varied about a norm of moderate susceptibility.

KOTO: 1: immune.

TABLE 1.
Details of the Virulence of Races Identified During the Survey on the Differential Varieties Designated by University Ex. Accession Number.

Race.	1 Bl.	2 WG.	3 Ak.	4 JWS.	5 Ab.	6 Ke.	7 Arg.	9 PBC.	10 Ot.	11 Arg.	13 Bl.	14 Pu.	86 Wa.	318 Mo.	319 Ne.	320 BG.	321 IR.	322 Le.	323 TPB.	326 Ko.
1	R	R	S	R	I	I	R	I	I	I	I	S	R	I	I	I	I	I	I	I
2	S	S	R	I	I	R	R	S	I	I	S	I	R	I	I	I	I	I	I	I
3	S	S	S	S	S	S	R	S	I	I	S	I	R	I	I	R	S	S	I	I
4	S	S	R	S	I	S	R	S	I	I	S	I	R	I	I	S	I	S	I	I
5	S	S	S	S	S	S	S	S	I	I	S	I	R	I	S	I	S	S	I	I
6	S	S	S	S	S	R	S	S	I	I	S	I	R	I	I	I	S	S	I	I
7	S	S	S	S	S	S	S	S	I	I	S	I	R	I	I	I	S	S	I	I
8	S	S	S	S	S	R	R	S	I	I	S	I	R	I	I	I	S	S	I	I
9	S	S	S	S	S	R	S	S	I	I	S	I	R	I	S	I	S	S	I	I
10	S	S	S	S	S	S	S	S	I	I	S	I	R	I	I	I	S	S	I	I
11	S	S	S	S	S	S	S	S	I	I	S	I	R	I	I	I	S	S	I	I
12	S	S	S	S	S	S	S	R	I	I	S	I	R	I	I	S	S	S	I	I
13	S	S	S	S	S	S	S	S	I	I	S	I	R	I	S	S	S	S	I	I
14	S	S	S	S	S	S	S	S	I	I	S	I	R	I	S	I	S	S	I	I
15	S	S	S	S	S	R	S	S	I	I	S	I	R	I	I	I	S	S	I	I
16	S	S	S	S	S	S	S	S	I	I	S	I	R	I	J	R	S	S	I	I
17	S	R	S	S	S	S	S	S	I	I	S	I	R	I	I	I	S	S	I	I
18	S	S	S	S	S	R	S	R	I	I	S	I	R	I	I	I	I	S	S	I

I = Immune. R = Resistant. S = Susceptible.

Races Identified During the Physiologic Race Survey.

On the basis of the reaction levels determined for each variety eighteen races were detected among sixty-two accessions collected in the field. These races were numerically designated, instead of following the alphabetical system previously adopted by Waterhouse and Watson (1943). This was considered advisable for three reasons. The frequency of occurrence of new races would soon have exhausted the reservoir of English alphabet symbols. The differential series adopted in the current survey included two varieties not used in any prior survey. The reaction given by Buda (used in previous surveys) to Punjab-attacking accessions was not considered sufficiently reliable to justify separation of races on this variety. The last two points complicated comparison of races differentiated in this and earlier surveys. A new system was therefore adopted to avoid confusion with results obtained in earlier surveys.

The reaction of each race on the differential series is listed in Table 1. A key for the identification of each race was also devised (Table 2).

TABLE 2.

Key for the Identification of Australian Races of Melampsora lini Determined in the Current Survey.

	Race
Punjab: Susceptible	1
Punjab: Immune.	
Ottawa 770B: Immune.	
Walsh: Susceptible	11
Walsh: Resistant.	
Newland: Immune.	
Very Pale Blue Crimped: Resistant.	
Argentine 705-1: Resistant	8
Argentine 705-1: Susceptible.	
Kenya: Resistant	18
Kenya: Susceptible	12
Very Pale Blue Crimped: Susceptible.	
Abyssinian: Immune	2
Abyssinian: Susceptible.	
Bolley Golden: Immune	6
Bolley Golden: Resistant.	
Argentine 705-1: Resistant	3
Argentine 705-1: Susceptible	10
Newland: Susceptible.	
Abyssinian: Immune	4
Abyssinian: Susceptible.	
Bolley Golden: Immune.	
Kenya: Resistant	9
Kenya: Susceptible	5
Bolley Golden: Susceptible	13
Ottawa 770B: Susceptible.	
Newland: Immune.	
Williston Golden: Resistant	17
Williston Golden: Susceptible.	
Kenya: Resistant	15
Kenya: Susceptible.	
Italia Roma: Immune	7
Italia Roma: Susceptible	16
Newland: Susceptible	14

Comparison of Races Identified During the Current Survey with Races Identified Earlier.

Comparison of races identified in the present survey with those identified by previous workers was complicated by slight differences in the varieties used and by differences in the system of reaction classification. Four different reactions were assigned to Kenya, Argentine 705-1, and Very Pale Blue Crimped by other workers. This was considered an unjustifiably fine distinction of reactions during this survey, and only three reactions were assigned to Kenya, and two to each of the last two varieties. Despite this, there was sufficient common ground for comparison.

Comparison with results obtained in the first survey by Waterhouse and Watson in 1941 and 1943 suggested a marked change in the rust population in Victoria and Western Australia. A more intensive survey would probably have revealed the same situation in South Australia.

Eight of the twelve races identified from Western Australia since 1948 were distinctly different from races detected between 1940 and 1942. Among them five new races could be designated even on the restricted differential series used by Waterhouse and Watson. Races 2 and 4 were more avirulent on the original differential series used in Survey I than earlier non-Punjab-attacking races, and races 7, 14, 15, 16 and 17 were highly virulent on Ottawa 770B, immune to all Australian races identified during the earlier survey.

Six of the thirteen races identified in Victoria since 1948 were distinctly different from races identified in Survey I. Each of the six could be differentiated from each other on the original Survey I differential series. Races 2 and 4 were less virulent than non-Punjab-attacking races identified in Survey I. Races 8, 12 and 18 differed from Survey I races in their resistant reaction on Very Pale Blue Crimped, and race 14 was the first Ottawa 770B-attacking race recorded in the State.

Fewer collections were received from South Australia, and correspondingly fewer races were identified. But one of the five identified since 1948, race 2, differed from the four races recorded in 1943.

The race position remained unchanged in New South Wales, where both collections received were Punjab-attacking.

No collections were received from Queensland prior to 1948. The seven received and identified since then were identified as race 1, a Punjab-attacking race.

A marked shift in the race population was noted when races identified by Watson, Charles, and Kerr between 1943 and 1948 were compared with races identified in the current survey. Prior to the current survey, only three Newland-attacking races had been identified. There were no Bolley Golden or Ottawa 770B-attacking races, and Walsh was relatively free from infection in the field until 1948. This survey identified six Newland-attacking races, 4, 5, 9, 12, 13 and 14, each of them apparently different from already determined Newland-attacking races. Five Ottawa 770B-attacking races, 7, 14, 15, 16 and 17, and three Bolley Golden-attacking races, 4, 12 and 13, were detected. An important Walsh-attacking race, race 11, was discovered in Victoria.

Only four of the races identified in this survey bore any close resemblance to races identified by previous surveys. Races 6 and 10 agreed fairly closely with Charles' races C and E respectively. Race 2 was identical with race K. The latter race was identified by Kerr in 1948. It was later found to give slightly different reactions on J.W.S., Akmolinsk, Kenya, and Argentine 705-1 than those listed by Millikan (1951). Race 1 was probably a composite of races A and F, since the reaction of Buda was not used to separate races in this survey as it had been to differentiate races A and F in earlier surveys.

Races A and F were differentiated by their reaction on Buda, and since this variety was rejected during the current survey, differentiation between races A and F was impossible. Race 1 cannot be equated with either of the former races and must be equated with both. Its reaction differs somewhat from that indicated for races A and F on two of the differential hosts. This could be attributed to the inoculation technique adopted in this survey. This induced a more virulent reaction than the spore dusting method of earlier surveys. When race 1 was inoculated onto J.W.S. and Akmolinsk by the latter method it gave virtually the same reactions, immune and resistant respectively, as those noted by Waterhouse and Watson for races A and F for these two varieties.

It was concluded that fourteen of the eighteen races identified in this survey had not been recorded before in Australia, namely races 3, 4, 5, 7, 8, 9, 11, 12, 13, 14, 15, 16, 17, and 18. Some of these races may have been present in the field when earlier

surveys were carried out, but may have been overlooked because insufficient districts were sampled, or because they constituted only a very small part of the total rust population at that time. But the very high percentage of new races among those identified in the current survey suggests a marked change in the race complex since the first surveys were carried out.

TABLE 3.
Distribution of Australian Races in Time and State.

State.	Year.	Race.																		Total.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Western Australia.	1948	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	1	4
	1949	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2
	1950	1	—	—	—	—	—	—	—	1	—	—	—	1	2	—	—	—	—	5
	1951	—	—	—	—	3	—	—	—	—	—	—	—	2	—	1	1	1	—	8
South Australia.	1948	—	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3
	1950	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2
	1951	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
	1952	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Victoria.	1948	—	1	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	4
	1949	1	2	1	1	1	1	—	2	1	—	1	—	—	—	—	—	—	—	11
	1950	—	—	—	1	—	—	—	—	—	1	—	1	—	—	—	—	—	—	3
	1951	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	2
	1952	—	—	2	—	—	—	—	—	—	2	—	—	—	1	—	—	—	—	5
Queens- land.	1948	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
	1952	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6
New South Wales.	1949	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
	1952	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Total of each race	..	15	6	4	3	9	2	1	2	2	5	1	1	3	3	1	1	1	2	62

Races Detected in Each State During the Survey.

- Queensland Race 1.
- New South Wales Race 1.
- Victoria Races 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 14, 18.
- South Australia Races 1, 2, 3, 5, 10.
- Western Australia Races 1, 2, 4, 5, 7, 9, 13, 14, 15, 16, 17, 18.

Geographic Distribution of Each Race and the Major Race Groups.

The distribution of the eighteen races according to the year of collection and State is given in Table 3. The districts in each State in which each race was found and a summary of the race complex of each State are listed in Table 4.

There was a remarkable diversity of non-Punjab-attacking races in the flax-growing southern States, and a complete absence of any of these races in the eastern linseed-growing States, New South Wales and Queensland.

There was no one dominant race among the seventeen non-Punjab-attacking races found in the south, although races 2, 5 and 10 occurred with a slightly greater frequency than the others. This follows the pattern of Flor's findings in the United States. Only two non-Punjab-attacking races, 2 and 5, occurred in all three southern States. Nine races were restricted to a single State.

Newland-attacking races were widely distributed in the southern belt during this survey, but were already established before the survey. Ottawa 770B-attacking races

by contrast were recorded in Australia for the first time since this survey began. There was no trace of such a race among the four hundred or more collections analysed previously. In 1948 Western Australian departmental officers reported sparse infection of Ottawa 770B seedlings in a small experimental plot at Kojunup. They attributed it to varietal impurity. The first Ottawa-attacking race, race 7, was identified in 1949 in a collection from Boyup Brook. Another Ottawa-attacking race, race 14, was identified from the same district in 1950. Three other Ottawa-attacking races, races 15, 16 and 17, were discovered in 1951 in the same area at North Boyup Brook, Newbicum, and Kulikup respectively. No further collections were received from the State, but a member of the local Department of Agriculture wrote that "The

TABLE 4.

Details of the State and District of Occurrence of the Races Determined during this Survey.

Race 1.	Queensland : Gatton 1948, Hermitage and Toowoomba 1952, Biloela 1950.* N.S.W. : Castle Hill 1949, Tibooburra 1952, Curlewis 1950.* Victoria : Lake Bolac 1949, Werribee 1953.* South Australia : Waite Institute 1950, 1952, Corry Point 1951. Western Australia : Boyup Brook 1950.
Race 2.	Victoria : Lake Bolac 1948, Winchelsea, Colac 1949. South Australia : Laura 1948, Waite Institute 1951. Western Australia : Boyup Brook 1949.
Race 3.	Victoria : Winchelsea 1949, Thorpdale 1952. South Australia : Maclaren Vale 1948.
Race 4.	Victoria : Werribee 1949, 1950. Western Australia : Mayanup 1948.
Race 5.	Victoria : Myrtleford 1948, Lake Bolac 1948, 1949. South Australia : Undalaya, 1948. Western Australia : Kojunup 1948, North Boyup Brook, Benjinup 1951.
Race 6.	Victoria : Colac 1948, Winchelsea 1949.
Race 7.	Western Australia : Boyup Brook 1949.
Race 8.	Victoria : Lismore, Casterton 1949.
Race 9.	Victoria : Winchelsea 1949. Western Australia : Boyup Brook 1950.
Race 10.	Victoria : Colac 1950, Drouin 1951, Thorpdale 1952. South Australia : Laura 1950.
Race 11.	Victoria : Casterton 1949.
Race 12.	Victoria : Birregurra 1950.
Race 13.	Western Australia : Boyup Brook 1950, Mayanup 1951.
Race 14.	Victoria : Thorpdale 1952. Western Australia : Boyup Brook 1950.
Race 15.	Western Australia : North Boyup Brook 1951.
Race 16.	Western Australia : Newbicum 1951.
Race 17.	Western Australia : Kulikup 1951.
Race 18.	Western Australia : Kojunup 1948. Victoria : Lismore 1951.

* Not positively identified as race 1 at Sydney University, since no viable inoculum was received, but definitely Punjab-attacking races, and therefore closely related to race 1, if not actually race 1.

Ottawa-attacking race (group) was very active (in 1952), and will, I think, considerably lower the fibre value of commercial crops of Wada". It seemed to have supplanted the old races. Until then the race group had been confined to Western Australia, but in early December, 1952, race 14 was identified on a specimen of Rust Resistant Norfolk Earl growing in Government experimental plots at Thorpdale, Victoria.

Field infection of Walsh, the only commercially grown linseed variety in Australia, was relatively insignificant until 1948. Although Walsh had not yet been included in the differential series, it is fairly certain from the above observation that no major Walsh-attacking race was then present. Race 11 was discovered in a collection from Casterton, Victoria, in 1949. It was highly virulent on the rather mixed commercial variety, attacking 70% of the seedlings in glasshouse tests at Sydney. The single plant selection, previously resistant to already identified Australian races, was fully susceptible. Despite its virulence and an abundance of susceptible host material in the field, it did not appear to have spread. But since the conclusion of this survey

there has been a report of a new Walsh-attacking race at Thorpdale and Casterton (Debrett, 1954).

Bolley Golden-attacking races were found in Victoria and Western Australia. Race 17, already mentioned as an Ottawa-attacking race, was the first occurrence of a Tammes' Pale Blue-attacking race in Australia. It was located at Kulikup in Western Australia.

Race 1 was the only Punjab-attacking race identified during the survey. It was the most common of the eighteen races and was detected in fifteen of the sixty-two collections. It occurred in all five States from which the collections were received. It was most common in Queensland. It was less common in New South Wales, Victoria, South Australia and Western Australia. But there was ample evidence from information supplied by officers of the State departments of agriculture and in the literature to indicate a more widespread occurrence.

Two Punjab-attacking accessions from New South Wales were identified as race 1. One was obtained from Tibooburra on wild flax, *L. marginale*. The other was obtained from linseed experimental plots at Castle Hill, near Sydney. Both districts were hundreds of miles from any known source of infection from commercial varieties of flax or linseed. Race 1 or a closely related race was also present in experimental plots at Curlewis in the north-western wheat belt. Several flax and linseed varieties were sown at the University Experiment Station, Curlewis, in May, 1950. The seed was disease-free, and there was no known source of rust inoculum in any of the commercial crops grown within 500 miles of the district. Punjab and Imperial, which in tests at Sydney University were immune to every race identified in this survey except race 1, were heavily infected by the end of September. The spores received on specimens sent from the district were inviable on receipt, but the race was almost certainly race 1 or a closely related race. The other varieties, including Concurrent, were uninfected. Since this variety was fully susceptible to all the non-Punjab-attacking races identified during this and previous surveys the immunity of this variety at Curlewis was strong proof of the absence of non-Punjab-attacking races from the district.

Rust was also noted on *L. marginale* at Pucuwan, 11 miles from Temora in the south-western wheat belt, during a field trip in November, 1948. Mr. Evans, of the Sydney University Botany Department, also reported that rust was quite common on the species near Sydney. Since twelve of thirteen collections received from the species since 1941 were Punjab-attacking races it is reasonable to infer that Punjab-attacking races were present near Pucuwan in 1948 and are common near Sydney in most years.

Only one collection of race 1 was received from Victoria during this survey, but seed of the differential varieties and F257 was sent to Mr. P. Debrett, of the Victorian Department of Agriculture, in 1952. Owing to excessive rain he was unable to make sowings in the Werribee district until late in the year. Punjab became heavily infected during February. The other varieties were immune. Since no inoculum was forwarded, the exact nature of the race is unknown. But since it was a Punjab-attacking race, it was probably race 1 or a closely related race. Since Bison and F257 were not infected, none of the common non-Punjab-attacking races could have been present in the field at that time of the year.

Four collections of race 1 were received from South Australia, one from *L. marginale* growing at Corry Point in 1951, and three from Punjab-type Indian linseed varieties growing at Waite Agricultural Institute. The race was present each year from 1950 to 1952 and constituted four of the ten collections received from the State.

One collection of race 1 was received from Western Australia. It was found as a mixture with race 14 on supposedly Concurrent plants growing at Boyup Brook in 1950. It must have been more common, since fifteen of twenty-eight rust collections sent in from the State in 1942 were identified as race A by Waterhouse and Watson.

The first Punjab-attacking collection from Queensland was collected from linseed growing at Gatton in 1948. No further collections were received from the State until

1952, but during that year special efforts were made to determine whether race 1 was the only race present in Queensland.

Records were kindly forwarded by the Plant Introduction Officer of the Commonwealth Scientific and Industrial Research Organization at the Cooper Laboratory, Lawes, Queensland, giving the mean intensity of rust infection in this district of the differential varieties used by Waterhouse and Watson and of Liral Crown and Concurrent. Results obtained in 1948 and 1949 showed that only Punjab-attacking races were present. Tests were discontinued in later years, but up to the end of this survey there was no record of infection of varieties such as Bison and Concurrent, known to be susceptible to all of the non-Punjab-attacking races of the southern States.

Seed of the varieties Punjab (susceptible only to race 1) and F257 (susceptible to all the races, including race 1) was distributed to experimental stations at Warwick, Hermitage, Toowoomba, and Kingaroy in 1952. They were grown under conditions most likely to induce infection, but remained uninfected at Kingaroy and Warwick. Infection of both varieties was reported at Hermitage in mid-November. The race

TABLE 5.

Distribution of Major Race Groups in Australia.

<i>Punjab-attacking Race Group: Race 1.</i>
Queensland: Gatton, Hermitage, Toowoomba, Biloela.
N.S.W.: Castle Hill, Tiboorurra, Curlewis.
Victoria: Lake Bolac, Werribee.
South Australia: Waite Institute (Adelaide), Corry Point.
Western Australia: Boyup Brook.
<i>Ottawa 770B-attacking Races: 7, 14, 15, 16 and 17.</i>
Victoria: Thorpdale.
Western Australia: Boyup Brook, North Boyup Brook, Kulikup, Newbieup.
<i>Newland-attacking Races: 4, 5, 9, 12, 13 and 14.</i>
Victoria: Winchelsea, Lake Bolac, Birregurra, Werribee, Myrtleford, Thorpdale.
South Australia: Undalaya.
Western Australia: Mayanup, Kojunup, North Boyup Brook, Benjinup, Boyup Brook.
<i>Bolley Golden-attacking Races: 4, 12 and 13.</i>
Victoria: Birregurra, Werribee.
Western Australia: Mayanup, Boyup Brook.
<i>Walsh-attacking Race: 11.</i>
Victoria: Casterton.

was not identified, but three collections received from the same district between September and October were identified as race 1.

The varieties were sown at three localities in the Toowoomba district. Sowings were made at regular intervals and a close check kept on each plot. No rust was recorded at one of the locations. Both varieties were infected in early December at the other locations. F257 was moderately infected. Punjab was heavily infected. The rust was identified as race 1. Sowings were made on 6th January, 1953, and at fortnightly intervals for some time afterwards. Every attempt was made to induce healthy succulent growth to encourage infection, but no rust was recorded on either variety after December.

Rust has appeared at Biloela Experiment Station, 560 miles north of Brisbane. This was almost certainly race 1 or a related race, since rust specimens sent to Sydney from the area in October, 1950, were from Punjab and Imperial.

Notes on the Cultivated and Wild Hosts in Australia.

Concurrent was highly susceptible in the seedling stage to all the races identified during the survey. It was somewhat less susceptible to race 1 than the other races in the seedling stage, and infection was usually restricted to the leaves, rarely spreading to the stems. Later in maturity it seemed to acquire complete immunity to the Punjab-attacking races. The same mature plant resistance seemed to be effective against the new highly virulent Ottawa-attacking races of Western Australia. This was not apparent until 1951. The first Ottawa-attacking race, race 7, was

collected at Boyup Brook from the variety Boyup in 1949. The following year race 14 was identified from two collections of Concurrent. Eight collections were received from neighbouring areas in 1951. The three collections from Concurrent yielded non-Ottawa-attacking races. Three different Ottawa-attacking races were isolated from the Wada specimens. This suggested that Concurrent was resistant to the most recent Ottawa-attacking races. The Western Australian Department of Agriculture late in 1952 reported that Concurrent was then free of rust although Wada was seriously affected.

Excised shoots of Concurrent were inoculated and incubated with an Ottawa-attacking race, race 17, and a non-Ottawa-attacking race, race 6. The two sets of shoots were kept under identical conditions in the same part of the glasshouse until sporulation and for several weeks afterwards. Both sets of shoots became heavily infected within two weeks. Shortly afterwards the race 6 infection spread to the stems, and subsequent shoot growth was stunted. Race 17 infection was restricted to the leaves, and the shoots recovered and continued vigorous growth (Plate iv, 2).

TABLE 6.
Races Isolated from the Varieties and Species Listed Below.

Host.	Races.
<i>Linum usitatissimum</i> :	
Concurrent	1, 4, 5, 13, 14.
Liral Crown	2, 3, 5, 8, 10.
Walsh	3, 6, 8, 11, 12, 18.
Wada	9, 10, 13, 15, 16, 17.
Boyup (A3)	3, 5, 7, 13.
Punjab, Imperial	1.
Unidentified flax varieties, probably Concurrent or Liral	
Crown	2, 4, 5, 10, 18.
<i>Linum marginale</i>	1.

Wada and Boyup were developed as rust-resistant varieties to replace Concurrent and Liral Crown. Tests at Sydney University showed that both varieties carried an appreciable percentage of off-type plants susceptible to most of the non-Punjab-attacking races with which they were tested. Both were fully susceptible in the seedling stage to the Ottawa-attacking races. But Boyup, like Concurrent, from which it is reported to have derived by natural crossing with Wada, seemed to have mature plant resistance to these races in the field. The two collections received from Boyup, Western Australia, in 1951 yielded non-Ottawa-attacking races, and a letter from the Department of Agriculture in November of 1952 stated that it was not as badly infected as Wada in the field.

The commercial variety Walsh contained up to 20% seedlings susceptible to many of the non-Punjab-attacking races. The occurrence of these susceptible plants probably gave rise to the many reports of important new Walsh-attacking races from the southern flax-growing districts. Race 11 was the only race to which most Walsh seedlings were fully susceptible, but eight of twenty-four single plant selections from the commercial variety were immune to this race. The occurrence of race 11 at Casterton in 1949 posed a considerable threat to the linseed-growing industry, but up to 1952 no further specimens of this race were received from Victoria. A report from Victoria in 1954 would seem to indicate the appearance of a new Walsh-attacking race in the Casterton and Thorpdale districts.

Linum marginale is probably an important host of *M. lini* in Australia. It is native to Australia and has been a host to *M. lini* since the first recorded observations of rust in the country. (The species is common in New Zealand, where it is regarded as an important carry-over host, particularly during winter. New Zealand crops are spring sown. Unlike Australia, there is an abundance of cultivated host material during summer, but a dearth of the host during winter.) It was reported from

Western Australia: "The evidence is clear in this State that *L. marginate* is an important hold over host for the rust fungus." The species is quite common in Victoria and South Australia. It has been found at such widely separated places in New South Wales as Sydney, Bourke, Curlewis, Tibooburra and Armidale.

It appeared to be much more restricted in its occurrence in Queensland. One report indicated that it had never been seen in the Lawes district or on the Darling Downs. The Government Botanist reported that the species was not common and the four localities from which specimens had been received were in the southern portions of the State towards the New South Wales border.

The species is not homogeneous in its reaction to *M. lini*. During the course of these studies, seed of the species was received from several States. The different lines were sown and tested for reaction to race 1 and several of the non-Punjab-attacking races. The lines tested were immune to several accessions of race 1 and also races 2, 6 and 7. Other lines, however, have been susceptible to race 1.

Factors Affecting the Incidence of the Rust in the Field.

The yearly and seasonal incidence of rust was directly correlated with the availability of susceptible material. Flax acreages have diminished steadily since the last war from 61,000 acres in 1944 to approximately 12,000 acres in 1948, and approximately 4,800 in 1950. This was paralleled by a reduction in the number of collections of rust received from the field.

Most of the crops were harvested by the end of December, leaving a sparse supply of volunteer plants to carry the rust over the hot summer months of January and February in the uredospore stage. This partly accounts for the fact that few samples of rust were received from the field later than December. Details of the earliest and latest collections of rust received from the field are given in Table 7. The dates given

TABLE 7.
Details of the Earliest and Latest Collections of Rust Received from Each State.
1948-1952.

State.	Earliest Collection.	Latest Collection.
Queensland	8th September.	13th December.
New South Wales	26th September.	22nd November.
Victoria	3rd August.	23rd December.
South Australia	9th October.	15th January.
Western Australia	10th September.	4th December.

in this table do not indicate the earliest or latest appearances of *M. lini* in the field in* the uredospore stage, but do help to indicate roughly the periods of maximum development of the rust in the uredospore stage.

The rust is evidently most abundant in the field in the uredospore stage from early September to December. Lack of rust before this period can be attributed to low field temperatures.

Observations in the field and in the glasshouse at Sydney and reports from workers in other States indicate that Punjab-attacking race 1 is better able to survive higher summer temperatures than the non-Punjab-attacking races in the uredospore stage. Non-Punjab-attacking race 2 was unable to survive summer temperatures in the field at Sydney. But Punjab-attacking race 1 survived without difficulty and caused severe infection.

The high temperature tolerance of Punjab-attacking races was also apparent from Mr. P. Debrett's report on the infection of varieties forwarded to him at Werribee in 1952. Punjab was severely infected during February, 1953. Non-Punjab-attacking races were much more common than Punjab-attacking races in his district up to December

in earlier years. But they were unable to maintain themselves in the uredospore stage during late summer, since Bison and F257, highly susceptible to these races, were uninfected during February.



Text-fig. 2.—Climatic map of Australia indicating mid-summer isotherms of flax and linseed growing States.

Approximately 1,000 miles further north, at Toowoomba, even Punjab-attacking races were less able to survive summer in the uredospore stage. Race 1 was present in the field until late December but failed to cause infection of susceptible material during January and February.

TABLE 8.
Summer and Winter Temperatures of Potential Flax Growing Districts in Australia.

State.	District.	Mean Temperature during Mid Winter. °F.	Mean Temperature during Summer. °F.
Tasmania.	Lannceston	47	64
Western Australia	Bunbury	55	73 Dec.-Jan.
	Katanning	50	70 Dec.-Jan.
	York	50	76 Dec.-Jan.
South Australia.	Waite Institute ..	50	70 Dec.-Feb.
	Millicent, Kapunda ..	Much the same as Waite Institute.	
	Mt. Barker, Clare ..		
Victoria.	Colac	43	64 Dec.-Feb.
	Leongatha	44	64 Dec.-Feb.
	Wangaratta	44	72 Dec.-Feb.
	Myrtleford	38	70 Dec.-Jan.
New South Wales	Albury	44	73 Dec.-Feb.
	Cootamundra	38	72 Dec.-Feb.
	Glen Innes	38	68 Dec.-Jan.
	Inverell	44	73 Dec.-Jan.
	Bathurst	38	68 Dec.-Jan.

Although non-Punjab-attacking races lacked tolerance to high temperature they were able to survive in the field in the uredospore stage in some districts in the southern States when the host was available. Rusted Walsh plants were received

from Mount Gambier in South Australia in mid-January, 1953. The rust was inviable on receipt. But since Walsh is completely immune to race 1, the only Punjab-attacking race identified during this survey, it is safe to attribute the infection in this instance to a non-Punjab-attacking race.

Since summer temperatures played an important role in regulating the seasonal incidence of rust, efforts were made to determine summer temperatures of the flax- and linseed-growing areas of Australia.

TABLE 9.
Summer Temperatures in Western Australia Flax Growing Districts.

Month.	Average of 40 years. °F.				
	Bridgetown.			Katanning. Mean.	York. Mean.
	Mean.	Maximum.	Hottest Day.		
November	61.9	76.4	103	63.7	67.8
December	66.4	82.3	105	68.5	73.7
January	69.1	85.5	109	71.1	76.4
February	68.6	85.3	115	70.6	76.1
March	65.3	80.4	105	66.8	71.7

Climatic graphs prepared by Dr. Forster (1941) to determine suitable areas for flax production in Australia yielded the information found in Table 8. Additional information was furnished by the Western Australian Department of Agriculture for Western Australian flax areas (Table 9). Temperatures at representative areas on the Darling Downs and other districts in Queensland were obtained from S. G. Gray's report on variety trials, 1950 (Table 10).

These figures agreed with the climate maps indicating the major temperature zones in Australia during the summer. It will be noticed that none of the Queensland districts had a mean temperature during January of less than 71°F. Some at least of the flax-growing districts of the southern States had a mean temperature during January of 70°F. or less. This fact is highlighted by the January (mid-summer) isotherms. Most of the southern flax-growing areas of Victoria, South Australia and Western Australia lie in a moderately temperate zone by comparison with the linseed-growing areas of north-west New South Wales and Queensland.

TABLE 10.
Mid Summer and Mid Winter Temperatures in Queensland Linseed Growing Districts. °F.

Month.	Mean Monthly Temperature.				
	Lawes.	Toowoomba.	Pittsworth.	Killarney.	Nanango.
January	77.2	71.2	74.1	71.9	74.1
July	56.1	50.7	51.4	59.0	51.2

Additional Comments on the Virulence of Punjab-Attacking and Non-Punjab-Attacking Races.

The results already summarized indicate an important division within the *M. lini* complex between the Punjab-attacking and the non-Punjab-attacking races. Observations not directly relevant to the survey were made during the course of these studies, which confirmed the difference between the pathogenicity of the two race groups.

It was possible within the reaction level of susceptibility to distinguish varying levels of virulence. Such distinctions could be readily defined by noting the following.

1. The extent of infection. In cases of milder susceptibility the uredosori were entirely or almost entirely restricted to the leaves, seldom spreading to the stems. In cases of extreme susceptibility the uredosori developed as vigorously on the stems as on the leaves.

2. The extent of plant recovery. In cases of mild susceptibility the inoculated plants commonly recovered and resumed normal growth unless deliberate attempts were made to induce further infection. In cases of extreme susceptibility plant growth was severely retarded or completely checked. Natural secondary infection of new growth was common.

3. Varieties showing the most severe susceptible reactions commonly developed heavy infection by the spore dusting technique. Varieties giving a milder reaction developed a very sparse infection by the spore dusting method.

Without exception non-Punjab-attacking races evoked a maximally virulent susceptible reaction on the variety F257. This variety was also susceptible to race 1, but invariably gave a less virulent susceptible reaction. A quantitative assessment of the difference in virulence of the non-Punjab-attacking and the Punjab-attacking races on F257 is summarized in Table 11. With the majority of the seedlings inoculated

TABLE 11.

Stem Infection of Pot Grown Seedlings Inoculated 7th May, 1953. Read 29th May, 1953.

Race.	Variety.	Number of Stems with Uredosori.		
		Heavy Infection.	Very Mild Infection.	No Infection.
1	F257	2	18	—
1	Punjab	19	—	4
6	F257	12	—	5
2	F257	10	—	5

with NPA races infection spread to the stem, producing prominent uredosori from which considerable quantities of inoculum could be drawn. Only two of the twenty seedlings inoculated with race 1 developed many stem uredosori. Eight stems were scarcely infected, and ten stems developed only a few scattered pustules. Race 1, however, gave a reaction of maximum virulence on Punjab seedlings, nineteen of twenty-three seedlings developing a heavy crop of uredosori on the stem.

In another test with excised shoots the milder virulence of race 1 on F257 was reflected in the almost complete lack of natural secondary infection after sporulation of the primary infection. Only one shoot showed any appreciable secondary infection. Only six secondary pustules developed on the other twenty-five shoots. The extreme virulence of the same race on Punjab resulted in heavy secondary infection of twenty-one of the thirty-four shoots.

Spore dusting bulk inoculation resulted in heavy infection of Punjab plants dusted with uredospores of race 1, placed in a moisture chamber and sprayed at intervals. F257 plants treated simultaneously in the same chamber developed only a light infection (Plate iv, 1 and 3).

The susceptibility of Punjab to race 1 was one of the most virulent reactions noted during the course of these studies. Punjab-attacking races from New Zealand induced a much milder reaction. Australian race 1 and New Zealand Punjab-attacking races 3 and 13 were cultured on Punjab excised shoots. The Australian race 1 accessions 507, 610, 613 and 624 from different sources in Queensland, and accession 621 from South Australia induced a maximum susceptible reaction with typical type 4 pustules. Infection spread to the stems; the plants became stunted and did not resume normal growth. Shoots inoculated with the New Zealand races developed type 3 pustules.

After three to four weeks the infected leaves died and normal growth resumed. Infection did not spread to the stems (Table 12).

TABLE 12.
Comparison of Virulence of Australian and New Zealand Punjab-attacking Races.

	Race 1 Accessions.					New Zealand Races.	
	507	610	613	621	624	3	13
Stems with uredosori ..	51/53	9/9	8/8	11/11	7/9	0/18	0/19

A NOTE ON UREDOspore MORPHOLOGY.

Measurements were made of uredospores of races 1, 2, 6 and 7 over a period of two weeks. The spores were collected from susceptible plants cultured under identical conditions and stored at 0° to 2°C. in the refrigerator for no more than four weeks. The spores were prepared for measurement by dusting onto a drop of specially prepared lacto-phenol on a thoroughly clean microscope slide. They were covered lightly with coverslips and checked after at least half an hour under the oil immersion objective. Provided all excess lacto-phenol was blotted up and the immersion oil was very fluid the coverslip remained firmly fixed to the slide as the slide was moved under the objective. The tube of the microscope was extended until each division on the scale in the eyepiece corresponded to 1 μ . At this level of magnification the image of the spores was clearly resolved. The spore concentration was adjusted beforehand so that the spores were fairly widely separated from each other. The movement of the slide was manipulated by a mechanical stage. To avoid biased selection of spores all the spores were measured which appeared completely within the field in the movement of the slide from left to right. Several samples of uredospores of each race were studied and one hundred spores were measured per sample.

Differences between the spores of different races were never significantly greater than differences between samples of the same race. Results obtained with one sample of spores are given in Table 13.

TABLE 13.
Uredospore Morphology (in μ) of Three Races Cultured under Identical Conditions and Collected 23rd May, 1953.
(Measured 23rd May, 1953.)

Race.	Average Length.	Range.	Average Breadth.	Range.
1	21.4	(18-25)	18.5	(15-21)
2	20.7	(16-24)	18.0	(15-20)
7	20.6	(16-25)	17.8	(15-20)

DISCUSSION.

The most striking feature of the race survey was the dichotomy of the Australian *Melampsora lini* race complex into the Punjab-attacking (PA) and non-Punjab-attacking (NPA) groups. This division paralleled differences in temperature tolerance in the field, and *in vitro* in the uredospore stage (Kerr, 1958), differences in host range in the field and in glasshouse tests, differences in the continuity of individual race members within each group in time and space.

None of the NPA races had so restricted a host range as PA race 1. Race 2, the least virulent of the NPA races, was highly virulent on four of the twenty differential

varieties. All the other NPA races were highly virulent on at least seven of the differential varieties. PA race 1 attacked only two of these varieties. J.W.S. gave an immune or fully susceptible reaction to the NPA races. Race 1 gave a variable resistant reaction even more marked in hybrids involving this variety. Bison was completely susceptible to all NPA races, as well as all races in America and New Zealand. It was immune to race 1.

The division between the PA and NPA groups was not an arbitrary classificatory division such as existed between the Ottawa-attacking and non-Ottawa-attacking races of Western Australia, determined by a single pathogenic factor. It seemed to be an important natural division. This might suggest that the difference was physiologic and that incompatibility prevented intergroup hybridization. This was ruled out by Charles's report (personal communication) of hybridization between races of the two groups in the glasshouse at Sydney University in 1947. There was no appreciable difference in uredospore morphology to indicate subspecific difference.

Hybridization between the two groups with progressive breakdown of the present differences might therefore have been expected. But there was no evidence that this had occurred since the first survey in 1940. Hybridization should eventually have produced among a wide range of races, races virulent on both Bison and Punjab, and others avirulent on both varieties. Since single factors condition virulence on these two varieties, the chances against the appearance of such races following hybridization were by no means great. Other widely virulent races, avirulent on Bison, and Punjab-attacking races lacking the high temperature tolerance of PA race 1 should also have appeared. The absence of such races from the field between 1940 and 1952 confirms the view that the PA and NPA race groups exist as two non-interpenetrating closed systems.

The existence of the two-group system poses several questions. How did the two systems originate? How is the dichotomy maintained and how long is it likely to continue? The answer to the second query is likely to suggest a solution to the first. If the difference did not stem from physiologic incompatibility it must have been maintained by factors external to the pathogen. Host and non-host environmental factors must have maintained the balance between the two groups.

The two groups did not occur together in the field on the same host varieties. The NPA group parasitized the commercial flax crops and were isolated on a number of occasions from the commercial linseed variety Walsh. The PA group, with one exception, was isolated from *Linum marginale*, a wild host, or such linseed varieties as Punjab and Imperial, which were not grown commercially and which were immune to all the NPA races. One collection of PA race 1 was received from Concurrent, a common host to the NPA group, but the plant yielding the race may well have been a rogue. This variety, fully susceptible to most NPA races from the seedling to the mature plant stage, was susceptible to PA race 1 in the seedling stage only. The difference in host range may have militated against hybridization of the two race groups.

The geographic distribution of the NPA group would seem to have been regulated primarily by temperature and to a lesser extent by host. There was an abundance of susceptible host in the southern flax-growing States. In the north the only commercial host was the linseed variety Walsh. Since this variety was generally resistant to the NPA races this might have militated against the epidemic development of the common NPA races in New South Wales and Queensland. But since the variety carried an appreciable percentage of off-type susceptible plants this could not account for the total absence of the NPA group from these States. Mid-summer temperatures in the linseed growing districts of these States exceeded the optimal, and possibly the maximum for development of the pathogen in the uredosoral state in the field. The combination of general host resistance and adverse summer temperatures probably accounted in large measure for the absence of the NPA groups. Summer temperatures in much of Victoria, South Australia, and Western Australia exceeded the optimal and possibly the maximum limits within which the NPA group could maintain itself

vegetatively in the uredosoral stage. But the more southern sections where flax was most commonly grown had a sufficiently mild summer to permit the group to aestivate successfully if not prolifically in this stage.

The occurrence of the PA group in all the flax- and linseed-growing parts of Australia, emphasized particularly by earlier race surveys, and also in districts where the commercial host was not grown or was restricted to very small experimental sowings presented one of the most interesting problems raised by the survey. Race 1, the only representative of this group identified during the current survey, was by far the most common race. It was the only Australian race found in all five States included in the survey. But it had the most restricted host range of all races identified during the survey. All commercial flax and linseed varieties were immune to it in the field. Such race 1-susceptible varieties as Punjab and Imperial were grown on far too small a scale and in too few localities for them to be considered the natural host of the PA group in the field. This suggested that the PA group did not maintain itself on the cultivated species, but rather on a widely distributed wild species. Such a host could be *Linum marginale*, native Australian flax. With the possible exception of parts of Queensland at a distance from the New South Wales border, this species was found in all flax- and linseed-growing districts of Australia, in many cooler highland districts bordering these districts, and at Tibooburra in inland New South Wales.

It would be interesting to know to what extent the distribution of the PA group was limited by higher summer temperatures. The common occurrence of the group in New South Wales and Queensland, at such places as Tibooburra in the former State and Biloela in the latter State, showed clearly that race 1 was much more tolerant to high summer temperatures in the field than NPA races. It was able to aestivate vegetatively in the uredosoral stage at Sydney, although an NPA race was completely eliminated from the field during the summer. Similar observations were made at Werribee in Victoria. In the linseed-growing zones of north-west New South Wales and Queensland, where summer temperatures are considerably higher, the pathogen may retreat to the cooler highland districts, just as the pathogen retreats from the hot plains of India (Prasada). While the only positive evidence from Queensland showed that race 1 did not survive in the uredosoral stage at Toowoomba beyond mid-summer, the race may well survive in cooler microlocal zones within such upland districts. The possibility of its survival on the inland plains was by no means ruled out, in view of the presence of the race at Tibooburra.

The mode of survival of the two race groups from year to year seemed to differ considerably. Within the NPA group there was little evidence that a given race maintained itself for long periods or spread to any great extent from its centre of origin. In view of the multiplicity of races during the current survey, and the marked change since earlier surveys, the sexual cycle must constitute a major phase in the history of this group. It seems unwise to assume that two collections of rust from different States or from the same State in different years were genetically identical and vegetatively related, even though they gave the same reaction on a given set of differential varieties.

Exhaustive race surveys were carried out by Cruickshank (1952, 1956) in New Zealand over what, by comparison with Australian conditions, was a relatively restricted area. There was a considerable carry-over of races in successive years. Since genetical investigations of host resistance and studies of uredospore longevity were being carried on simultaneously with the race survey, and since the writer was dependent on the kindness of field workers from other States for the supply of infected material, the same detailed survey of flax- and linseed-growing districts could not be carried out to assess the degree of carry-over of races within the NPA complex from one year to another. But a comparison of results obtained in the survey under discussion with results obtained in previous surveys, particularly in Western Australia, showed clearly that there had been a considerable shift in the NPA complex within a period of ten to thirteen years.

Ottawa-attacking races were restricted to a small section of Western Australia between 1949 and 1951. The first race, race 7, was identified in 1949. Another race, race 14, was found in 1950, and three new races, 15, 16 and 17, were isolated in 1951. One would judge from this evidence alone that the NPA complex was in a state of constant pathogenic flux. Race 14 was the first such race to be identified in another State, when it appeared in Victoria in 1952. It is impossible to determine whether the two occurrences of this race so separated in time and space stemmed from a common source or whether the race in Victoria developed *in situ*. But unless infected material was transferred between the two States it seems wisest to postulate independent origin.

Although a given race within the NPA complex may have failed to survive from one year to the next, new virulence factors, especially those with a high positive survival value, were not eliminated. The new factor conditioning virulence on Ottawa 770B soon became well established in the NPA complex of Western Australia even though the original race which carried it did not seem to have survived or spread. A factor or factors conditioning wide virulence on the heterogeneous variety Walsh appeared in race 11 in Victoria in 1949. The race did not seem to survive. Had it done so, specimens of such a potentially serious race would certainly have been forwarded from the district for analysis. But the new virulence factors evidently survived, though masked in less virulent races, eventually recombining in an important Walsh-attacking race reported from the same district in 1954.

The evident importance of the sexual cycle in the propagation of the NPA complex indicates the need for a careful study of this phase in the field. While there would not appear to be a Statewide suppression of the uredosoral stage in Victoria during summer, there did appear to be complete recession of this stage in some districts. This should increase the importance of the teleutospore stage as a carry-over phase. All stages in the life cycle of *M. lini* have been recorded on the cultivated host in New Zealand, as well as on the indigenous wild species *L. monogynum*. An intensive survey of southern flax-growing districts in Australia should indicate a like situation. This situation is most likely to obtain in the vicinity of flax mills, where harvested flax is stacked prior to processing. These stacks, by bringing together infected host and possibly different races from several districts, by buffering the teleutospore material against excesses of high summer temperature and ensuring a constant supply of volunteer plants, must provide those conditions by which the pathogenic potential of the pathogen is brought together, recombined and carried over from season to season. A visit to several flax mills near Melbourne in 1947 indicated an abundant supply of heavily infected volunteer plants.

It would be interesting to know to what extent the NPA race complex was affected by the growth cycle of the cultivated host. Mild temperatures and abundant supply of immature susceptible host ensured a maximum proliferation of this group during spring and early summer in Australia. High summer temperatures and lack of host following harvest resulted in an annual recession of the uredosoral stage, complete in some districts, partial in others according to local temperatures and supply of susceptible volunteer plants. Even if the recession were only partial and the volunteer plant population were entirely non-selective in its carry-over, it is highly improbable that the old balance of races would survive to the following year. The more severe the recession of the uredosoral stage in any year, the more prominent should be the role of the teleutospore as the carry-over phase, the more marked should be the change in the NPA complex in the following year. The diversity of races in the NPA complex and the marked change since the first survey could not, however, be attributed primarily to the Australian crop cycle. In New Zealand, with its much milder summer temperatures and spring sowings, *M. lini* maintained itself throughout the year in the vegetative uredosoral stage. The same multiplicity of races was found, though there was a considerable carry-over of old races in successive years.

The history of the PA group differed strikingly from the NPA group. Only one PA race, race 1, was detected during the four years of this survey. Specimens of this race were received from Western Australia, South Australia, Victoria, New South

Wales and Queensland. In the last two States it was located at such remote districts as Tibooburra and Biloela. Three Punjab-attacking races were identified in earlier surveys. They were differentiated by reactions on varieties not considered reliable for race differentiation in the current survey. Such differences as then existed were extremely fine and none of the three PA races had a range of virulence exceeding the least virulent of the NPA races. Such differences within the PA group as existed between 1940 and 1942 presumably still existed between 1948 and 1952, but could no longer be detected with the then used differential series and the currently recognized reaction levels of these varieties. Allowing for possible minor fluctuations of the nature indicated above there was no change in the pathogenicity of the PA complex from the first survey in 1940 to the completion of this survey in 1952. This contrasted with the NPA group within which fourteen of the eighteen races identified during this survey were recognizably different from races identified in earlier surveys. This suggested that the PA race group maintained itself entirely vegetatively in all parts of Australia or that the group, if it completed the sexual cycle, was pathogenically homozygous and homogeneous for those factors conditioning its avirulence on the eighteen immune members of the differential series. Both factors probably contributed to the uniformity of the PA group in time and space. Owing to the pressure of the several lines of investigation, race 1 teleutospores were not studied to determine the degree of homozygosity of this race. This could be a very useful study, which might throw much light on the unusual geographic and time patterning of this group.

Paralleling the remarkable pathogenic uniformity of the PA group was an equally notable uniformity in high temperature tolerance. This feature was lacking from the NPA group (Kerr, 1958) and must have contributed substantially to the PA group's capacity to penetrate and maintain itself in New South Wales and Queensland in a northerly sweep into higher temperature zones far beyond the line of the NPA group. If this tolerance were conditioned by a number of factors operating in complement, and some or all heterozygous, it might have contributed to the stability of the PA group by militating against the survival of off types lacking this tolerance. This seems unlikely since such races could have survived in the more temperate zones of the southern States. The mode of inheritance of high temperature tolerance could perhaps be determined relatively simply by studying the germination of uredospores of different segregates on host extract at temperatures in the vicinity of 20°C. (Kerr, 1958). It seems possible, assuming that the PA group completes the sexual cycle, that it is homozygous for those factors determining high-temperature tolerance, as well as those factors conditioning avirulence on the eighteen immune differential varieties. It would follow that mutations which might have resulted in the appearance of recessive factors conditioning virulence on some at least of these immune varieties have occurred very infrequently, if at all. With so many pathogenic factors involved it is surprising that no change in the pathogenicity of the PA group was registered over a period of twelve years.

Whether or not the sexual cycle played a major part in the survival of the PA group, it was evident that race 1 survived summer quite readily in the field in the uredosporal stage in areas where the NPA complex was suppressed. Given a year-round supply of susceptible host, the PA group could maintain itself vegetatively without difficulty in the southern States and in New South Wales, at least as far north as Sydney. This should certainly have tended to stabilize the pathogenicity of the group and might account in large measure for the uniformity of the group in time and space.

The manner of origin of new races is posed again by these studies, but no conclusive evidence can be brought forward to support either of the two major theories. In brief, these theories may be summarized as follows: (1) Mutations at loci conditioning virulence are relatively frequent. Potential new races, many with widened host range, are constantly being generated. (2) Mutations occur very infrequently. Any appreciable variation in virulence is the product of centuries of accumulation of mutant genes. Genes previously masked by dominant avirulent alleles or present in too low a frequency to ensure detection, even in the most thorough survey, may

suddenly manifest themselves long after their origin when a change in the host complex suddenly confers a high positive survival value on races homozygous for such virulence factors.

Although no conclusive evidence for either theory can be drawn from the data presented in this paper, a line of investigations may be suggested which could lead to some definite decisions. The potential of such studies would depend to some extent on the validity of conclusions concerning the origin of the PA group. But even if such conclusions, to be dealt with shortly, are not valid, the study could yield useful information so long as the NPA and PA groups continue to coexist as non-interpenetrating systems.

Delaying consideration of this for the present it should be noted that while the evidence from the PA group tends to suggest that mutations are very infrequent, the evidence from the NPA group could be interpreted in favour of the theory that new races are constantly being generated by mutation of old races. Any evidence for this must assume that the change cannot be accounted for by introduction of new factors from outside sources. This assumes rigid policing of quarantine laws. The need for rigid quarantine measures has been fully recognized by those in a position to import seed. Such quarantine measures have become increasingly strict during the period 1940 to 1952, as flax and linseed assumed increasing economic importance. Prior to the war, when acreages were extremely low, lesser precautions seem to have been taken, and one outbreak at least of the pathogen in this period was attributed to contaminated imported seed.

While no natural quarantine barrier exists between the eastern States or these States and South Australia, there is an extensive desert barrier between Western Australia and the more easterly States. For this reason it seems reasonable to assume that the occurrence of an Ottawa-attacking race for the first time in Victoria several years after the first appearance of such a race in Western Australia represents an independent development of this race group. The development of this race group followed the release of new, supposedly resistant varieties, carrying Ottawa resistance. These varieties were developed within Australia. Had the appearance of the Ottawa-attacking group coincided with large-scale importation of seed this might have indicated that the race group traced its origin to the country of origin of this seed. That this was not so lends weight to the assumption that the group developed *in situ* in Western Australia. That Ottawa-attacking races probably developed independently in two States separated by a major quarantine barrier suggests that the Ottawa virulence factor either took its source in both States from recent mutations or was already present in the race complex in sufficient frequency to ensure its manifestation within a very short time of a change in the host from an unfavourable to a favourable population.

Since 1947 races avirulent on Abyssinian (races 2 and 4), avirulent on Williston Golden (race 17), and avirulent on Very Pale Blue Crimped (races 12 and 18) appeared in the Australian NPA complex for the first time. Previous evidence rules out the possibility that factors conditioning avirulence on these varieties were derived from the PA group. Genetic studies suggested that the Williston Golden factor conditioning resistance to PA race 1 differed from the factor conditioning resistance to NPA race 17. The new avirulence factors may have been introduced from overseas, though the introduction of three such factors in so short a time seems unlikely. They may have been present in the original race complex at a very low frequency and escaped detection. But since three factors were involved, since they could not have been masked by dominant alleles, and since several hundred collections were analysed during earlier surveys this is by no means certain. The possibility of their origin by recent mutation cannot be ruled out.

It remains to determine the manner of origin of the two race groups. Many of the races now present in Australia stemmed from introduced races. McAlpine, reporting the first record of rust in this country, concluded that *M. lini* had been introduced from overseas. A rust epidemic in Victoria was attributed to the same cause in 1936.

Flor, in a personal communication, noted that the NPA races resembled those obtained by him by hybridization of North American and South American races. He suggested that races had been introduced from North America and Europe and had hybridized in Australia with more widely virulent races from South America.

The PA group almost certainly derived from some other source. Up to 1952 no such race as race 1, avirulent on Bison, had been recorded in North or South America. The avirulence of the North and South American races on Bolley Golden and Newland was conditioned by two factors and one factor respectively. The avirulence of PA race 1 on these varieties was conditioned by four and two factors respectively. Punjab-attacking races were identified in New Zealand, but none was avirulent on Bison (Cruickshank, personal communication). New Zealand Punjab-attacking races 3 and 13 (reclassified 10 and 8 respectively) (Cruickshank, 1956) were compared at Sydney with several Australian accessions of race 1. The New Zealand races were much less virulent on Punjab than the Australian accessions. *Linum marginale* was not included as a source of rust during the New Zealand race surveys (Cruickshank, personal communication), although it is an important hold-over host for the pathogen in that country. There is no information about the race complex present on this species, but the absence of Australian Punjab-attacking race types from commercial crops growing in the same districts as the wild species is in line with the assumption that the Australian PA group does not occur in New Zealand.

Indian races closely resembled the Australian PA group in their virulence on Bombay (carrying the same gene for resistance as Punjab) and avirulence on Bison and most of the differential varieties. If the Indian races possess the high temperature tolerance of the Australian PA group, and carry four factors and two factors respectively conditioning avirulence on Bolley Golden and Newland, the case for the derivation of the Australian PA group from India is strong.

This, however, cannot rule out the possibility that the PA group is endemic to Australia. Had the PA group been introduced in the same manner as the NPA group it is surprising that the two groups did not merge their pathogenic potential. Probably accounting for this and supplying the most critical evidence was the almost exclusive association of the native Australian flax *Linum marginale* with the PA group. Twelve of thirteen races collected from the wild species between 1940 and 1952 were Punjab-attacking races.

Wild flax species are common hosts to *M. lini* in all countries in which the pathogen has been studied, *L. monogynum* in New Zealand, *L. rigidum*, *L. lewisii*, *L. angustifolium* and *L. sulcatum* in America, as well as several species in Europe. It would be surprising if the native Australian species had only been host to *M. lini* since the settlement of the country. According to McAlpine, the pathogen was first identified on the cultivated host in 1889. Waterhouse obtained records of the pathogen on *L. marginale* at Como near Sydney in 1887. It seems reasonable to assume that the association of *M. lini* with the wild species predated the introduction of races from overseas. If this were so it is strange that the original race complex should be so repressed by introduced races that twelve of thirteen races isolated from the wild host between 1940 and 1952 were a race or races of Indian origin. The races isolated from the wild host may well have represented the original Australian *M. lini* complex. This was supported by the occurrence of race 1 on *L. marginale* at Tibooburra in the extreme north-west of New South Wales, a location so far removed from districts where the cultivated host was grown that derivation of the pathogen from the cultivated host seemed most unlikely in this instance. Identification of the pathogen at Pucuwun near Temora and at Curlewis added confirmation. Although Curlewis fell within areas where linseed was being grown commercially there was no known source of *M. lini* in the commercial crops. An exhaustive personal survey in the north-west of New South Wales, from Tamworth to Moree, failed to detect the slightest trace of rust in any of the commercial crops. Close checks by officers of the Department of Agriculture were equally fruitless. No commercial crops of flax or linseed were grown within 150 miles of Sydney, but a competent observer reported

that the wild species was commonly infected with rust in the Sydney area. The presence of the pathogen in New South Wales was almost certainly independent of the cultivated host.

The only evidence against these conclusions was the similarity of the Australian PA group and Indian races. This cannot be ignored, but it is by no means conclusive. It is not unreasonable to suppose that Australian and Indian races should be pathogenically similar. They might well trace back to a common source.

The association of the NPA complex with the cultivated host, *L. usitatissimum*, was reflected in the accumulation of a wide range of virulence factors specific for resistance factors carried by the various varieties within the species. The almost total lack of these factors in the PA group (stressed even more by the genetic investigations of host resistance to race 1) could be postulated as further evidence that the PA group was adapted to the wild species rather than the cultivated species. The PA group, despite its apparent pathogenic homogeneity, may well have accumulated a range of as yet undetected virulence factors for resistance factors in *L. marginale*. Since some lines of *marginale* were resistant to race 1 there must be diversity within the species. Should a thorough study of the wild species and the races present on it confirm the above, the case for an original Punjab-attacking *Melampsora lini* complex would be strong. No detailed study of the wild species has yet been made in Australia. Various lines were received from different States during these studies. Attempts were made to hybridize several of these lines with different varieties of *L. usitatissimum* using both species as female parents. The two species were completely incompatible.

If the wild species is the natural host of the PA group, this group should be able to maintain its distinctive identity as effectively in the future as it did between 1940 and 1952. A thorough study of this race complex might then indicate the extent to which the pathogen may generate new mutant virulence factors. This is impossible with the NPA complex where the possibility of introduction of new races from overseas can rarely be ruled out with complete certainty, and where the frequency of the individual virulence factors is controlled by not infrequent changes in the host complex. The presence of pathogenic factors in the PA complex specific for factors in the cultivated host could be used to determine the rate at which such factors are generated. Such factors, unless also fortuitously specific for or associated with some factor specific for resistance factors in the wild species, should be present at a frequency determined by the balance between the natural rates of generation and loss.

These studies confirm the well-established fact that a change in the host complex is generally followed by a change in the pathogen race complex. New varieties were released to counter the susceptibility of the common flax varieties Concurrent and Liral Crown. Shortly after the release of Wada and Boyup, Ottawa-attacking races appeared for the first time in Australia and soon dominated the Western Australia NPA complex. This stresses the need for combined resistance already emphasized by Watson and Singh (1952).

The range of combined resistance in *Linum usitatissimum* is greatly reduced by the limited number of loci in the host determining resistance to *Melampsora lini*. But this may be offset to some extent by the constant pathogenic flux of the NPA group. Flor (1946) established a one-to-one correlation between resistance factors in the host and specific virulence factors in the pathogen. Avirulence was always dominant to virulence. The greater the number of resistance factors in a host variety, the less likely is the pathogen to accumulate the requisite virulence factors homozygously in the one race. If the pathogen survives via the teleutospore stage rather than vegetatively from one season to another, the survival of a given complex of virulence factors becomes increasingly uncertain in a mixed race situation the greater the number of virulence factors involved.

During these studies, Wada, with its resistance derived from a single Ottawa factor, succumbed to an Ottawa-attacking race soon after its release for commercial production. While the original race did not survive, the Ottawa-attacking virulence

factor carried over in the race complex from one year to the next in Western Australia. Walsh, by contrast, the only commercially grown linseed variety, grown for a considerable period over a wide geographic range, remained effectively immune or resistant to the Australian PA and NPA race groups. One Walsh-attacking race appeared in one district in Victoria, but did not spread or survive to the next year. Genetic studies have shown that Walsh, though heterozygous, owes its resistance to at least three factors.

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EXPLANATION OF PLATES III-IV.

Plate iii.

- 1.—Fully susceptible type 4 reaction. Compound pustules with no chlorosis. Leaves rarely distorted. Note small newly developing non-compound pustules on same leaf. $\times 3\frac{1}{2}$.
- 2.—Typical fully susceptible reaction without compound pustules. No chlorosis and infection general over whole leaf surface. $\times 3\frac{1}{2}$.

3.—Fleck type immune reaction. Small chlorotic flecks over most of leaf surface. $\times 3\frac{1}{2}$.

4, 5, 6.—Various intermediate resistant reactions with pustules of varying size and varying degrees of chlorosis and necrosis. Infection often localized to part of the leaf, and leaf commonly misshapen. $\times 3\frac{1}{2}$.

Plate iv.

1.—Bulk inoculation of F257 with race 1. Fairly heavy production of uredosori on leaves, but very few developing on stems. Plants recovered and still growing vigorously. $\times \frac{1}{2}$.

2.—Two sets of excised shoots of Concurrent inoculated and incubated at the same time under identical conditions with an Ottawa-attacking race, race 17 (LHS), and a non-Ottawa-attacking race, race 6 (RHS). Note complete recovery of shoots inoculated with race 17 and the clean uninfected stems. Shoots inoculated with race 6 developed heavy stem infection and failed to resume normal growth. $\times \frac{1}{2}$.

3.—Bulk inoculation of Punjab with race 1. Very heavy development of uredosori on leaves and stem. Growth of shoots severely retarded. $\times \frac{1}{2}$.

THE FAMILIES OF CYCADS AND THE ZAMIACEAE OF AUSTRALIA.

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(Four Text-figures.)

[Read 25th March, 1959.]

Synopsis.

The general classification of the Cycadales is reviewed and grounds are put forward for the recognition of three families: Cycadaceae (*Cycas*), Stangeriaceae, fam. nov. (*Stangeria*) and Zamiaceae (remaining genera). A taxonomic revision of the Australian members of the Zamiaceae is provided. Three genera, all endemic, are recognized: *Lepidozamia* Regel (2 spp.), *Macrozamia* Miq. (14 spp.: 6 in sect. *Macrozamia*, 8 in sect. *Parazamia*), and *Bowenia* Hook. ex Hook. f. (2 spp.). New taxa are described and new combinations made as follows: *Lepidozamia hopeites* (Cookson) L. Johnson (fossil species), *Macrozamia communis*, *M. diplomera* (F. Muell.) L. Johnson, *M. lucida*, *M. stenomera*, *M. pauli-guilielmi* W. Hill and F. Muell. ssp. *plurinervia* and *flexuosa* (C. Moore) L. Johnson. The name *M. spiralis* (Salisb.) Miq. is shown to be correctly applied to the species known as *M. corallipes* Hook. f. The species known as *M. spiralis* in Queensland and New South Wales are the n. spp. *M. lucida* and *M. communis* respectively. Keys and discussions are provided for all taxa and the very confused synonymy is reviewed and clarified.

INTRODUCTORY.

This study has arisen out of the necessary revision of the New South Wales species of *Macrozamia* for the forthcoming *Flora of New South Wales*, part 1 (in press). It was clear from the outset that the specific limits needed clarification and that the nomenclature was in a state of chaos. Moreover, it soon became evident that generic as well as specific concepts were at issue and this in turn led to a consideration of the general taxonomy of the cycads.

PART I. THE FAMILIES OF CYCADS.

General.

It has been customary to refer all the true living cycads (universally accepted as the order Cycadales) to a single family, Cycadaceae, variously divided by different authors into subfamilies, tribes and subtribes. Schuster (1932, p. 63) gives a synopsis of these arrangements. Amongst these categories, however, all authors have recognized a suprageneric taxon including *Cycas* alone. In recent times only Wettstein (1923) has placed *Cycas* in a family (Cycadaceae *sensu stricto*) by itself, grouping the remaining genera as Zamiaceae. The latter family had, however, been established much earlier by Reichenbach (1837), though several cycad genera were then unknown.

Taxonomists have a tendency to recognize very inclusive families in the more unfamiliar groups of plants. The cycads are rather few, they are all very different from other living plants and they are clearly related to each other; consequently most botanists, impressed by this apartness, are content to lump them together and to minimize the differences within the group. Now all taxonomic classification, at least above the specific level, is to a considerable degree subjective as regards the status of admittedly related taxa. To take familiar examples from the flowering plants, the dismembering of the Leguminosae *s. lat.* into the three families Mimosaceae, Caesalpiniaceae and Papilionaceae must be more subjectively based than the exclusion of Paeoniaceae from Ranunculaceae. In the former case few will deny that the segregate groups have a closer phylogenetic relationship among themselves than any one of them has to other living families; the claim for family status rests on the

rather indefinable (though not unreal) degree of difference between, and coherence within, the groups. In the latter case morphological, anatomical and cytological grounds exist (Eames, 1953; Cronquist, 1957) for believing that *Paeonia* is in fact closely allied to certain families (the Dilleniales line) quite different from Ranunculaceae, and that it has been placed in the latter family on the basis of superficial resemblance; this is an objectively based segregation, provided that the general system of families in the dicotyledons is accepted as a frame of reference.

The small, self-contained group of the cycads lacks any such established frame of reference and the case for segregate families is thus scarcely a *provable* one. It is nevertheless a reasonable one. We can show that certain genera have many characters in common and could easily be derived from a common ancestral population which (at this stage) would still be quite different from the conceivable ancestors of other living genera. There are, furthermore, no links or breakdowns between these groups. Thus the groups are natural and their distinctions indicate evolutionary divergence at an early stage in the history of the Order. To justify family status we can apply to no fixed criterion, but can say that the differences are of such a nature that common ancestry for the whole assemblage must be very remote and that each of the family groups must be the result of considerable evolution since the divergence, the present members doubtless being relict forms with many lost relatives. Unfortunately, the fossil record of the true cycads is scanty (see, for instance, Cookson, 1953) in contrast to those of their distant relatives the Mesozoic Bennettitales and the broad, more or less ancestral, chiefly late Palaeozoic group of the Pteridosperms, and it is not at present likely to throw much light on evolution within the Cycadales.

On the principles outlined above, the Cycadales may be classified in three families: Cycadaceae *s. str.*, Stangeriaceae and Zamiaceae, the last of which may be subdivided (with less assurance) into tribes. The genera as commonly recognized are entirely natural with the exception of *Macrozamia*, from which *Lepidozamia* must be excluded (see below, p. 83).

There is little point in detailing the history of the many previous classifications, but of the more recent systems three may be mentioned. Hutchinson (1924) recognized two tribes, Cycadeae (*Cycas*) and Encephalarteae, the latter comprising the following subtribes: Encephalartinae* (*Dioon*, *Macrozamia*, *Encephalartos*), Stangeriinae* (*Stangeria*), Zamiinae* (*Bowenia*, *Ceratozamia*, *Microcycas*, *Zamia*); this is a reasonable arrangement and comes close to that adopted here apart from differences in status and Hutchinson's curious placing of the distinctive Stangeriinae between his other two more similar subtribes. I have used Hutchinson's key to some extent in devising the one hereunder. Pilger (1926) recognized five subfamilies, of which the first four were monotypic, containing *Cycas*, *Stangeria*, *Bowenia* and *Dioon* respectively; the fifth subfamily (Zamioideae) included the remaining genera without subdivision. The only merit of this is the recognition of *Stangeria* as rather distinctive. The subfamilial segregation of *Bowenia* and *Dioon*, while retaining such genera as *Zamia* and *Macrozamia* in a single equivalent taxon, is a characteristically unrealistic consequence of the analytical "key-character" used as a basis of classification. Schuster (1932), the latest monographer of the Cycadales, has two subfamilies, Cycadoideae (*Cycas*) and Zamioideae, the latter comprising eight tribes, each containing but a single genus! He does not say what purpose this is meant to serve.

The present system, unlike those of Pilger and Schuster, is derived not by the use of key-characters, but synthetically by marshalling like genera together using the whole complex of their characters, and analytically by the recognition of fundamental and irreconcilable differences. Parallelism and convergence are pitfalls, as usual, and grouping within the Zamiaceae is difficult. As to characters, the three very different systems of leaflet venation are surely of greater evolutionary significance and more difficult to derive from each other than are some of the different conditions in

* Given here in the correct forms under the present International Code of Botanical Nomenclature (Lanjouw, 1956); Hutchinson wrote "Encephalartinae", "Stangeriinae" and "Zamiinae".

reproductive characters traditionally considered of more importance. When critically examined, these latter, with the exception of those distinguishing *Cycas*, are seen to be nothing more than modifications of the shape and regularity of arrangement of the essentially similar sporophylls.

The chromosome numbers (from Darlington and Wylie, 1955) are not particularly enlightening in the cycads. They support the distinction of *Cycas* ($x = 11, 12?$), but in the Zamiaceae, while $x = 9$ is found in five genera and $x = 8$ in two (*Zamia* has both numbers), one genus (*Microcycas*) has $x = 13$. *Microcycas* agrees morphologically with the other Zamiaceae, but its chromosome number at least suggests a long history as an independent genus. The female gametophyte of *Microcycas* is remarkable for the very large number of archegonia and the male for the large number of spermatozoids produced (Chamberlain, 1919). The genus has no resemblance to *Cycas*, and certainly does not seem to be generally primitive in the Zamiaceae. Its chromosome number presents an intriguing problem, assuming, of course, that the count is correct. Finally, *Stangeria* has $x = 8$ but is very different from the two Zamiaceae (*Zamia* and *Ceratozamia*) with this number. The course of caryotype evolution is obscure.

The characters of the Cycadales as a whole may be found in any of the standard works (e.g. Schuster, 1932); *The Living Cycads* (Chamberlain, 1919), though semi-popular in style, still provides an excellent extended account and comparative discussion.

*Key to the Families and Genera.**

CYCADALES.

1. Pinnae with a single thick midrib and no lateral veins, circinate involute in bud. Female sporophylls not forming a determinate cone but spirally arranged in a terminal mass, and falling separately at maturity, the central axis eventually continuing vegetative growth (male sporophylls in definite cones). Female sporophylls with a pinnatifid, pectinate or toothed "lamina", ovules 2-several, marginally inserted proximal to the lamina, obliquely directed outwards ("ascending"). Trunk clothed with old frond-bases. $x = 11, 12?$ Old World tropics I. CYCADACEAE.
1. *Cycas*.
- 1.* Pinnae (or pinnules) with many lateral or longitudinal nerves, usually straight in bud (frond circinate as a whole in *Ceratozamia*). Sporophylls of both sexes in determinate cones, the female sporophylls scale-like, more or less peltate with a thickened and laterally expanded end on the axis-facing margins of which the 2 (sometimes 3 in *Lepidozamia* and rarely 3 or more in other genera) inward-facing ("inverted") ovules are inserted. Caudex various.
2. Pinnae pennineined, with a definite midrib and numerous transverse parallel dichotomously-branched lateral veins, convolute in bud. Sporophylls imbricate but in almost vertical rows. Caudex subterranean, naked (frond-bases deciduous). Superficially fern-like plants. $x = 8$. E. and S.E. Africa II. STANGERIACEAE.
2. *Stangeria*.
- 2.* Pinnae (or pinnules) lacking a midrib, with numerous more or less parallel longitudinal nerves (dichotomously-branched near the base), imbricate but not convolute in bud. Sporophylls and caudex various. $x = 8, 9, 13$ III. ZAMIACEAE.
3. Sporophylls imbricate, not in vertical rows. Caudex clothed with persistent frond- and cataphyll-bases. Pinnae not obviously articulate, though somewhat deciduous when old in a few species.
4. Cones axillary (sometimes erect and appearing falsely terminal, but not terminating main axis). Ovules sessile on the sporophyll. Female sporophylls greatly thickened towards the ends and tightly imbricate, glabrous or tomentose but scarcely woolly. $x = 9$. Australia and Africa a. Tribe *Encephalarteae*.
5. Sporophyll-ends acutely or bluntly pointed or with a terminal spine (sometimes reduced to a narrow transverse wing, but never a facet). Cones sessile or stalked. Australia.
6. Cones sessile or subsessile; sporophyll-ends tomentose, produced into a spreading obtuse to acute but not spinescent wing, curved upward or downward. Successive crowns of fronds markedly separated by broad series of cataphylls. Pinnae inserted on the adaxial midline of the rhachis. Frond-bases shortly tomentose. E. Australia 3. *Lepidozamia*.

* The terminology is the same as that used in Part II (see p. 77). Hutchinson's (1924) key and the excellent vegetative key of Regel (1876) have been used freely in constructing this one which, however, is based as far as possible on actual material. The key does not, of course, give all the distinguishing characteristics of the taxa. Each genus has a characteristic facies due to the form and arrangement of the fronds and their segments.

- 6.* Cones stalked ("pedunculate"); sporophyll-ends glabrate, often glaucous, at least the females subterminally compressed to form a more or less vertical surface, on which (in both sexes) the margins form a transverse ridge terminating in a rigid more or less erect spine. Successive crowns of fronds little separated by a few cataphylls. Pinnae inserted near the edges of the rhachis. Frond-bases silky or woolly with long hairs. $x = 9$. Australia 4. *Macrozamia*.
- 5.* Sporophyll-ends truncate, more or less prismoidal, with a 4- or 6-sided terminal facet, somewhat decurved. Cones sessile. $x = 9$. Africa 5. *Encephalartos*.
- 4.* Cones (sessile or shortly stalked) terminating growth of the main stem, which continues vegetative growth sympodially from the base of the cone (the subterminal "cone-dome" ultimately engulfed by the new growth so that the trunk appears continuous). Ovules usually borne on a short stalk-like outgrowth (false funicle) of the sporophyll. Female sporophylls somewhat thickened but loosely imbricate at least at the ends (which are reduced in *D. spinulosum*), the woolly ends flattened and erect. $x = 9$. Central America b. Tribe *Dioëae*.
6. *Dioon*.
- 3.* Sporophylls apparently valvate, arranged in vertical rows, their ends (at least in the females) hexagonal or rhomboid. Caudex various, often naked. Cones terminal (always?) in origin, on the main stem or short branches, though often pushed aside by new stem growth. Pinnae definitely articulate at the base or, if not, then fronds decompound c. Tribe *Zamiëae*.
7. Sporophylls either shortly woolly or 2-horned at the end. Trunk robust, clothed with leaf-bases and cataphylls or at length naked. Fronds simply pinnate, pinnae articulate.
8. Sporophyll-ends obtuse or truncate, not horned, tomentose with short, crisped hairs. Frond-bases and cataphylls said to be at length deciduous. $x = 13$. Cuba 7. *Microcycas*.
- 8.* Sporophyll-ends 2-horned, not tomentose. Frond-bases and cataphylls persistent. $x = 8$. Mexico 8. *Ceratozamia*.
- 7.* Sporophylls truncate, not woolly or horned. Caudex naked, usually slender or short, sometimes subterranean. Fronds either decompound or, if simply pinnate, then the pinnae articulate.
9. Fronds simply pinnate, pinnae articulate at the base. $x = 8, 9$. Tropical N. and S. America 9. *Zamia*.
- 9.* Fronds decompound, pinnae and pinnules not articulate at the base. $x = 9$. N.E. Australia 10. *Bowenia*.

Enumeration and Discussion.

In this paper I can neither list the detailed synonymy nor deal at length with the extra-Australian taxa, other than those newly established herein. Those interested may consult the monograph of Schuster (1932) for generic descriptions and bibliography, but will be wise not to rely on it, especially at the specific level. Probably all the larger genera need thorough revision, on modern lines, by workers familiar with most of their species in the field.

I. Family CYCADACEAE L. C. Rich.* in Pers., *Enchir.*, 2 (1807), 630.

As here restricted this includes only the genus *Cycas*. This is the most distinct of all the genera of cycads and in many respects preserves the most primitive characters, especially in the frond-like megasporophylls and their loose undifferentiated arrangement. However, *Cycas* cannot be considered to represent a form ancestral to the other living genera, since its single-veined pinnae could hardly have given rise to either the Stangeriaceous or the Zamiaëous condition.

The circinate vernation of the pinnae (not the whole frond) is an apparently primitive feature. The much greater specialization of the male as compared with the female structures is the most remarkable feature of the family. This indicates that determinate male and female cycad "cones" may not be homologous as complete structures, but only in so far as they are aggregations (attained at different stages) of sporangium-bearing reduced determinate branch-systems (sporophylls) more or less

* As "Cycadeae" but in family rank.

equivalent to the fronds which (phylogenetically speaking) are somewhat less reduced, similar but sterile branch-systems.

1. *CYCAS* L. Type species: *C. circinalis* L.

Perhaps 20 species, extending to Madagascar and East Africa but chiefly in South-East Asia, tropical Australia and the western Pacific. Chromosome numbers: $x = 11, 12?$ ($2n = 22$, but 24 in one count).

Schuster (1932) recognizes only eight species but his treatment would appear to be no sounder than that of *Macrozamia* (see below, p. 72). *Cycas* is much in need of satisfactory revision but this would certainly require a wide knowledge of the species in the field and extensive living and herbarium collections from the whole of its wide range. Much herbarium material is practically useless. For these reasons I have not attempted to deal with the Australian species. The synonymy also is most complex and confused, as in *Macrozamia*. A difficult and protracted task awaits any responsible monographer of the genus.

II. Family STANGERIACEAE L. Johnson, fam. nov.

I can trace no previous publication of this taxon in family rank.

Familia inter Cycadilibus frondium pinnis unicostatis arcte penninerviis (venis dichotomis rectiusculis) vernatione rectis sed convolutis* distincta. Sporophylla utriusque sexus conos determinatos formantia, squamiformia peltataque, mascula sporangiis multis infra instructa, feminea ovulas duas versus axem coni directas in marginibus gerentia. Chromosomata ut $x = 8$ numerata.

Genus typicum (unicum): *Stangeria* T. Moore.

Stangeria has not usually been considered as distinct as *Cycas* from the other cycad genera, and indeed there is no apparent character in the reproductive structures inconsistent with its inclusion in the Zamiaceae. However, the view that "good" taxa above the rank of species (or even species in some opinions) must always differ in reproductive characters is surely an example of archaic formalism lacking any firm evolutionary basis. "Good taxonomic characters" have no absolute significance and can be evaluated only in relation to the whole complex of circumstances in particular cases. A "conservative" character in one series of organisms may be quite radically modified in a closely related series or even in individual species within the same series. Evolutionary processes are no respecters of "characters", and useful as generalizations about characters may be when discussing trends, to apply them dogmatically in classification is to reduce taxonomy to a formal game rather than a branch of biology. This is in contrast to the view of Davis (1952, p. 149).

It is clear that the strongly-developed midrib and the many crowded, spreading, lateral veins of *Stangeria* pinnae must develop by organogenetic growth processes considerably different from those which produce the longitudinally-nerved midribless frond segments of the *Zamiaceae*. Neither condition is easily derivable from the other.† This implies an early separate development along two lines from some ancestral group with a more generalized vascularization of the fronds.

Anyone familiar with living plants of all or most of the cycad genera must be struck by the divergent appearance of *Stangeria*. Its fern-like, rather Marattiaceous, aspect is quite unlike that of any of the Zamiaceae or of *Cycas*. The resemblance to a *Marattia* or an *Angiopteris* is, of course, due to convergent, or perhaps more properly to parallel, evolution of a similar frond pattern from the more primitive forms of megaphyllous leaf (major determinate branch system) found in the very early

* The vernation of the pinnae is usually described (e.g. by Schuster, 1932) as plicate; in the living material which I have examined the young pinnae are strongly convolute and certainly not plicate, except perhaps at the tips.

† It is conceivable that the simply pinnate frond of *Stangeria* is equivalent to a bipinnate type of Zamiaceous frond (cf. *Bowenia*) in which individual pinnules have undergone "phylogenetic fusion". However, this seems very doubtful and *Stangeria* could still not be derived from anything like the known Zamiaceous genera—certainly not from *Bowenia*.

Pteropsida. There is no particular relationship between the groups, which differ profoundly in reproductive structures and internal anatomy. On the other hand, the difference between *Stangeria* and the Zamiaceae is certainly not superficial, and suggests that some of their reproductive resemblances may be due to parallel development from early proto-cycadalean ancestors. With little doubt the naked tuberous stem and the geophytic habit are secondary and do not imply any relationship between *Stangeria* on the one hand and *Bowenia* or *Zamia* on the other.

Such internal schisms notwithstanding, the unity of the Cycadales as a whole seems clear. The correspondence of all three families in structure and organization is too close to be the result of convergence from unlike ancestors, though parallel development of different lines from a common ancestral group seems probable. For a comparative discussion of homology, parallelism and convergence, and their significance in classification, see Simpson (1945, pp. 8-12). In the present paper I have attempted to apply principles of evolution-reflecting classification developed from considerations similar to those so admirably expressed by Simpson in this remarkable *tour de force*.

2. STANGERIA T. Moore. Type species: *S. eriopus* (Kunze) Nash (*S. paradoxa* T. Moore).

A single variable species (as usually treated) in south-east Africa. Chromosome number: $x = 8$ ($2n = 16$).

III. Family ZAMIACEAE Reichenb., *Handb.* (1837), 139.

Eight genera and perhaps 80 species in the tropical to warm-temperate regions of Africa, Australia and North and South America.

The Zamiaceae appear to be a natural group. All the genera certainly agree in many fundamentals of structure despite considerable diversity of detail and size. The characteristic longitudinal dichotomous venation has already been stressed when discussing the other two families. The basic chromosome number $x = 9$ predominates, with $x = 8$ (a reduction? Not found in the apparently more primitive genera) in two genera and the anomalous-seeming $x = 13$ in *Microcycas*. Chamberlain (1919) indicates various reduction and specialization series from genus to genus, but these are by no means always concurrent in different organs and it is obvious that, although some of them have a greater number of advanced features than others, the living genera do not represent an evolutionary series but rather the present end-points of a number of different lines, doubtless cognate with others now extinct. To judge from the phylogenetic series which many authors put forward even today for Recent organisms of all kinds, it is still necessary to state this evolutionary platitude.

With some diffidence I have attempted to arrange the genera into three tribes. These are perhaps not entirely natural (especially Zamieae, which includes the rather non-conforming *Microcycas*), but they do bring together similar genera, some of which are undoubtedly not too distantly related.

Phytogeographers should beware of basing any far-reaching arguments upon the distributions of these rather tentatively defined tribes.

a. Tribe ENCEPHALARTEAE (Miq.) L. Johnson, comb. nov.*

Three genera, in Australia and Africa.

These genera have relatively few advanced features, though certain specializations are found. Although each genus is very distinct, a true relationship seems likely. F. Mueller at various times united them under *Encephalartos* and indeed suggested sinking this under *Zamia*; he did not believe in evolution (see below, p.—), but in the individual creation of species and the consequent artificiality of genera. Affinity, apart from mystical connotations, meant merely resemblance in certain chosen characters.

* Cycadaceae ("Cycadeae") tribe Encephalarteae Miq., *Prodr. Syst. Cycad.* (1861), 5. Schuster (1932, p. 64) attributes this to himself, in spite of his citation on p. 63 of its use by Miquel and other authors.

3. LEPIDUZAMIA Regel. Type species: *L. peroffskyana* Regel.

Two species in tropical and subtropical eastern Australia. Chromosome number unknown.

Discussed in detail in Part II (p. 83).

4. MACROZAMIA Miq. Type species: *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn. (see p. 87).

Fourteen species in subtropical and warm-temperate Australia. Chromosome number: $x = 9$ ($2n = 18$).

Discussed in detail in Part II (p. 87).

5. ENCEPHALARTOS Lehm. Type species to be selected by a monographer.

Fifteen–twenty species in Central and South Africa. Chromosome number: $x = 9$ ($2n = 18$).

The genus still needs some revision, but the tropical species have been fully treated by Melville (1957).

b. Tribe DIŌEAE (Schuster) L. Johnson, comb. nov.*

A single genus in Central America.

This tribe was rather meaningless as set up by Schuster, since all his tribes were unigeneric. However, *Dioon* does stand somewhat apart from the Encephalarteae, their common characters being chiefly merely the generally primitive ones of the family. It may be convenient to allot it a tribe to itself. The cones are terminal (according to Chamberlain's studies), as in the Zamieae, but *Dioon* differs considerably from that tribe in other characters.

6. DIOON Lindl. Type species: *D. edule* Lindl.

Three (or more?) species in Central America (chiefly Mexico). Chromosome number: $x = 9$ ($2n = 18$).

Dioon and *Lepidozamia* have the least modified megasporophylls in the Zamieae. They are otherwise not particularly alike.

c. Tribe ZAMIEAE.†

Four genera, in America and Australia.

As stated above, this tribe possibly includes the products of convergence rather than close affinity. The genera are grouped mainly on the regular arrangement of the sporophylls in the cone, in which definitely vertical orthostichies are apparent. The sporophylls are, of course, at the same time arranged in parastichies (spirals) as in the other tribes. Phyllotactic modification to the regular vertical arrangement could easily have taken place more than once. *Bowenia* is geographically isolated from the other genera and its resemblance to *Zamia* in sporophylls, cones and habit could be secondary, at least in part. *Microcycas* has 13 gametic chromosomes and some gametophytic peculiarities, and thus stands rather apart from the other genera. *Ceratozamia* shares the number $x = 8$ with some species of *Zamia*, but this probably does not indicate any special relationship. In habit, at least, *Ceratozamia* seems more primitive than *Zamia* and its sporophylls are distinctive. These American genera and *Bowenia* need

* Cycadaceae tribe Diŏeae ("Diooneae") Schuster, Pflanzenr., IV, i (1932), 64. Schuster's spelling is to be corrected, as above. Since *Dioon* is from the Greek $\delta\iota\omicron$ and $\omega\nu$, and the stem of the latter, transliterated, is "ō-" (cf. "oospore", "Oidium"), then the stem of the compound is surely "Dio-". Under the I.C.B.N. the tribal ending "-eae" must be added to the stem. Classical Latin authors, supposing them to have used such a word at all, would doubtless have latinized it to the less outlandish-looking "Dioveae". One may perhaps enter a protest against the too common pronunciation of *Dioon* to rhyme with "soon"; it rhymes with "so on". Lindley's original publication as "*Dion*" was a mere slip, later corrected.

† As the tribe containing the type, this requires no author citation. It was first established as Cycadaceae ("Cycadeae") tribe Zamieae Reichenb., *Consp. Regn. Veg.* (1828), 40. (Not seen; the reference is from Schuster (1932, p. 63). On p. 64 he cites his own name as author, though Zamieae had been used by many earlier workers.)

a comparative study, with taxonomic rather than purely morphological principles in mind. Whether the cones are in fact always terminal in origin, as stated by Chamberlain (1919), needs to be confirmed. The cones of *Ceratozamia*, at least, appear lateral to the external view.

7. *MICROCYCAS* (Miq.) A.DC. Type species: *M. calocoma* (Miq.) A.DC.

A single species in Cuba. Chromosome number $x = 13$ ($2n = 26$).

I have seen no living plants of this genus and little herbarium material. Regel (1876) states that the frond-bases and cataphylls ("perulae") are at length deciduous, leaving a naked stem. By contrast, Hutchinson (1924) keys out the genus on its "trunk . . . covered with persistent leaf-bases and prophylls". This is a character of some importance in other genera. As stated above, the position of *Microcycas* is in some doubt. It does, however, show a number of resemblances to *Zamia*.

8. *CERATUZAMIA* Brongn. Type species: *C. mexicana* Brongn.

About four species in Mexico. Chromosome number: $x = 8$ ($2n = 16$).

A distinctive genus. Its relationship is not certain, but appears to be rather distantly with *Zamia*. The fronds are more or less circinate in veneration.

9. *ZAMIA* L. Type species: *Z. floridana* L. (lectotype, Hutchinson, 1924).

About 30-40 species in the tropics of the New World. Chromosome number: $x = 8$, 9 ($2n = 16, 18$).

Like *Cycas*, *Zamia* needs a modern monographic treatment, in this case by an American worker. Regel's genus *Aulacophyllum* (Regel, 1876) is worthy of reconsideration. Regel was a discerning worker and his treatment of cycad genera was sound. *Aulacophyllum* may be as good a genus as the equally neglected *Lepidozamia*.

10. *BOWENIA* Hook. ex Hook. f. Type species: *B. spectabilis* Hook. ex Hook. f.

Two species in north-eastern Australia. Chromosome number: $x = 9$ ($2n = 18$).

This is the only living cycad with truly decompound fronds, though *Stangeria* and *Macrozamia* may have forked pinnae. Discussed in detail in Part II (p. 109).

PART II. THE ZAMIACEAE OF AUSTRALIA.

Historical.

Early authors.

Since Salisbury described *Zamia spiralis* (now *Macrozamia spiralis* (Salisb.) Miq.) in 1796, many authors have contributed to the systematics of the Australian Zamiaceae. No useful purpose would be served by a detailed account of their treatments and the progress, and at times regression, in the classification over the last century and a half. All the relevant references and an index of names may be found hereunder, in the formal systematic treatment. The more important landmarks and workers, however, may be briefly mentioned.

Miquel established the genus *Macrozamia* in 1842, the three known species (under a single name) having previously been referred at first to *Zamia* and later to *Encephalartos*. This Dutch botanist studied the cycads in general for some thirty years and published numerous short and long papers on the group. Although many confusions are inevitably found in this early work, his studies are marked by a steady progress in understanding at both generic and specific levels, and his general discussions and contributions to cycad morphology are as praiseworthy as his taxonomic contributions. Unquestionably Miquel remains pre-eminent among taxonomic cycadologists and (the period taken into account) is overshadowed only by Chamberlain in the morphological field. Several of these studies (Miquel, 1861, 1863, 1868, 1869) are of particular importance. The first is a concise general review of the cycads of the world, while the second is a revision of the Australian members in which he reduced *Macrozamia* and the recently described *Lepidozamia* Regel to sections of *Encephalartos* and set up also the section *Parazamia*. The 1868 and 1869 papers are French and Dutch versions respectively of part of a series of morphological and taxonomic papers, of which the most important to us deals with the "Cycadëen van extratropisch Nieuw-

Holland", namely *Macrozamia* (restored here to generic rank, and embracing *Lepidozamia* as a section) and *Bowenia*.

F. Mueller (latterly F. von Mueller) published numerous notes and brief commentaries between 1858 and 1889 (see references in formal section). On the credit side he made known a number of newly-discovered species, stimulated collection and increased the knowledge of distribution; unfortunately this was counterbalanced by serious confusion of quite dissimilar species (most notably *M. miquelii* with *M. fawcettii*) and thirty years of vacillation between recognition of *Macrozamia* and its inclusion in *Encephalartos*. Each change of opinion was accompanied by a new combination or two. Mueller had little field knowledge of these plants, despite his residence in Australia.

A notable cycadologist whose work is largely overlooked was Regel, who gathered a large collection of living plants at the then St. Petersburg Botanic Garden and paid particular attention to the most useful and significant vegetative characters of the genera. Among his many papers, two (Regel, 1857, 1876) are of special importance, dealing respectively with the new genus *Lepidozamia* (the distinctive characters of which subsequent authors have not properly appreciated) and with a general revision of all the Cycads. This little-known work is essentially more sound than later reviews of greater pretensions.

J. D. Hooker (1863, 1872) described the distinctive genus *Bowenia*. A. De Candolle (1868) produced a useful monograph largely following Miquel. In the *Flora Australiensis*, Bentham (1873), working in England from inadequate herbarium material, provided a better treatment than did Mueller on the spot, but, as he was himself aware, it is not very satisfactory. Successful cycad studies require years of familiarity with the plants.

In a modest paper, Charles Moore (1884) gave the most realistic account yet published of the eastern species of *Macrozamia* (including *Lepidozamia*). Unlike other authors, Moore had the advantage of an extensive and critical field knowledge of most of the species. He also studied them side by side in the garden and laid the foundations of the present cycad collection in the Sydney Botanic Gardens. Apart from understandable partial confusion of the species now defined as *Macrozamia diplomera*, *M. heteromera* and *M. stenomera* (see p. 105) and neglecting minor matters of nomenclature with which he did not concern himself, the only flaws in his account arose from following Mueller with undue respect. Virtually the same arrangement was used in condensed form by Moore and Betche (1893).

At various times, but especially in the *Queensland Flora*, F. M. Bailey (1902) reviewed the Queensland species. As with Moore, some field experience put Bailey in touch with reality, though not all of his species can now be maintained.

From this encouraging position Maiden and Betche (1916) reverted to confusion by reducing all but one of the true *Macrozamia* species of New South Wales to their inflated concept of *M. spiralis*, claiming that they were all connected by intergradation. This is not so.

Schuster's monograph.

As a greater anticlimax, Schuster (1932) produced his monograph in *Das Pflanzenreich*. In his treatment of *Macrozamia*, despite its comprehensive scope and superficial aspect of detailed finality, Schuster so profusely introduces new and profound confusions in taxonomic concepts of every rank and in nomenclature, so blatantly contravenes the rules of priority, and so unreliably cites both synonymy and specimens that the work is quite egregious even for a compendium of such unequal quality as *Das Pflanzenreich*. Despite several years of unfortunately necessary detailed study of this work, I can form no idea of the principles, if any, which Schuster followed in arriving at his conclusions. Virtually identical plants, even the same specimens, are referred to entirely different species. Most diverse species are treated as subspecies, varieties or forms under a single (misapplied!) name, often appearing more than once in quite

different branches of this elaborate false hierarchy, while species closely allied to some of these are given full specific rank. For instance, Schuster places materials of *M. heteromera* as (i) (the typical variety of) an independent species, but there confused with two other species; (ii) a form of a variety (the type form of which is a different species) of this same species; (iii) a form of a variety of a subspecies of "*M. tridentata*", this form being a mixed concept of two species, the variety a mixed concept of four other species, and so on through the higher categories. With one or two partial exceptions, his arrangement and circumscription of all taxa from sections down to forms bear almost no relation to the real affinities and the distinctions between the species in nature. The result is a jumble which almost defies disentanglement. It is hard to see why Schuster did not follow the earlier treatments which, though imperfect, should have been a useful guide.

In most branches of science worthless work may be forgotten and need not hinder progress; taxonomy is bedevilled by the requirement that no validly published name may be ignored. Thus taxonomists spend much of their time in unprofitable antiquarianism rather than scientific study. So that future students of Australian Zamiaceae need not repeat much of this labour, and perhaps to help those in charge of overseas cycad collections who have naturally had recourse to Schuster's monograph in naming their plants, I have provided a table (Table 1) interpreting his usage.

Further details may be found in the synonymy of the various species in the formal section, below. In using this tabulation one should bear in mind that in any subdivided taxon Schuster's method was to describe and list first all material which he treated as typical and to follow this by his first named subsidiary category; (supposedly) typical subdivisions were not named in the lower rank. For example, his "*Macrozamia tridentata*" has two named and numbered subspecies, but these are preceded by a description and citations applying only to what one must consider as the "typical" subspecies (though the term has little meaning here; how Schuster regarded it one can only guess). Similarly his first subspecies includes three named varieties exclusive of the "typical" variety and so on. In Table 1 the total ambit of his inclusions ("concept" is hardly the word) under any one taxon must be obtained from the sum of the interpretations of its subdivisions.

In order to achieve finality in this tedious matter the identity of these "synonyms" and specimens has been checked with great care, and the reductions, as amplified in the formal section, may be accepted as authoritative according to the concepts of the present treatment. All cases of residual doubt or ambiguity are clearly indicated. Column 2 of the table gives the present correct position of the type(s) of the basionyms (and absolute nomenclatural synonyms) of Schuster's names, not the actual basionym itself. The latter may be determined from the synonymy in the formal section. Similarly, column 4 lists the correct positions of the types of the various alleged synonyms cited by Schuster, excluding the absolute synonyms.

Schuster's descriptions are frequently largely copied or translated from those of other authors and do not necessarily apply to the specimens or synonyms cited with them.

Present Study.

Scope.

This paper aims to present a fully-documented and definitive taxonomic revision of, and commentary on, all species of the three Australian genera of Zamiaceae. Amongst these the New South Wales species have received most attention, and indeed have most needed it.

No new cytological or anatomical investigations have been made, but the results of such studies are taken into account in forming taxonomic judgments. General ecological observations have been made and their taxonomic significance assessed. Economic and horticultural aspects lie outside the scope of this paper, but have been borne in mind in the course of the work. Evolutionary and theoretical questions are discussed when relevant.

TABLE 1.

Name Used by Schuster (1932) (spellings corrected).	Correct Name in the Present Revision. [<i>Macrozamia</i> spp. belonging to sect. <i>Parazamia</i> marked (P), others belong to sect. <i>Macrozamia</i> .]		
	Basionym (present correct position).	Specimens Cited.	"Synonyms" Cited (excl. Invalid Names and Absolute Synonyms) (present correct position).
<i>M. tridentata</i> (Used in contravention of priority, since Schuster's circumscription included the types of several earlier names, viz. <i>Z. spiralis</i> Salisb., <i>Z. pallida</i> Salisb., <i>Z. pungens</i> Ait.)	<i>Macrozamia</i> or <i>En- cephalartos</i> sp., un- identifiable (juv.) (= <i>Z. tridentata</i> Willd.)	<i>M. miquelii</i> . <i>M. communis</i> . (and perhaps <i>M.</i> <i>lucida</i> (P) by in- ference).	<i>M. miquelii</i> . <i>M. communis</i> . <i>M. spiralis</i> (P). <i>Zamia</i> , <i>Encephalartos</i> or <i>Macrozamia</i> sp.? (<i>Z. pallida</i> Salisb.).
ssp. <i>mountperriensis</i> ("mountperryensis")	<i>M. miquelii</i> .	<i>M. miquelii</i> .	
var. <i>miquelii</i> (nom. illegit.) . .	<i>M. miquelii</i> (lectotype) and <i>M. fawcettii</i> (P).	<i>M. miquelii</i> .	<i>M. miquelii</i> . <i>M. fawcettii</i> (P).
f. <i>milkaui</i> (nom. illegit.)		<i>M. miquelii</i> (juv.). <i>M.</i> or <i>Enceph.</i> sp. (juv.) (= <i>Z. tridentata</i> Willd.)	<i>M.</i> or <i>Enceph.</i> sp. (= <i>Z. tridentata</i> Willd.).
f. <i>oblongifolia</i>	<i>M. miquelii</i> .	<i>M. communis</i> (juv.).	
var. <i>mackenzii</i>	<i>M. miquelii</i> .	<i>M. miquelii</i> .	
var. <i>douglasii</i>	<i>M. miquelii</i> .	<i>M. miquelii</i> .	
ssp. <i>cylindrica</i>	<i>M. miquelii</i> .	<i>M. miquelii</i> . <i>M. communis</i> . <i>M. moorei</i> .	
var. <i>secunda</i>	<i>M. secunda</i> (P).	<i>M. secunda</i> (P). <i>M. pauli-guilielmi</i> ssp. <i>plurinervia</i> (P).	
var. <i>corallipes</i>	<i>M. spiralis</i> (P).	<i>M. spiralis</i> (P).	<i>M. spiralis</i> (P).
f. <i>wallsendensis</i>		<i>M. communis</i> (semi- juv.).	
f. <i>dielsii</i>		<i>M. spiralis</i> (P).	
f. <i>vavilovii</i>		<i>M. communis</i> ? or <i>M. miquelii</i> ?	
var. <i>pungens</i>	<i>Encephalartos</i> sp. ? (obscure, not Aus- tralian).	<i>M. communis</i> . <i>M. miquelii</i> . <i>M. moorei</i> <i>M. lucida</i> (P).	<i>Zamia</i> . <i>Enceph.</i> or <i>Macroz.</i> sp. ? (<i>Z. pallida</i> Salisb.).
f. <i>hillii</i>		<i>M. miquelii</i> or <i>M. communis</i> ? (or even <i>M. riedlei</i> ?).	<i>M. miquelii</i> or <i>M. communis</i> ? (or even <i>M. riedlei</i> ?)
f. <i>diplomera</i>	<i>M. diplomera</i> (lecto- type) and <i>M. heteromera</i> (P).	<i>M. diplomera</i> . <i>M. heteromera</i> (P).	

TABLE 1.—Continued.

Name Used by Schuster (1932) (spellings corrected).	Correct Name in the Present Revision. [<i>Macrozamia</i> spp. belonging to sect. <i>Parazamia</i> marked (P), others belong to sect. <i>Macrozamia</i> .]		
	Basionym (present correct position).	Specimens Cited.	"Synonyms" Cited (excl. Invalid Names and Absolute Synonyms) (present correct position).
<i>M. moorei</i>	<i>M. moorei</i> .	<i>M. moorei</i> .	
<i>M. flexuosa</i>	<i>M. pauli-guilielmi</i> ssp. <i>flexuosa</i> (P).	<i>M. pauli-guilielmi</i> ssp. <i>flexuosa</i> (P). <i>M. p.-g.</i> ssp. <i>pluri-</i> <i>nervia</i> (P).	
<i>M. heteromera</i>	<i>M. heteromera</i> (P) (lectotype) and <i>M. diplomera</i> .	<i>M. heteromera</i> (P). <i>M. stenomera</i> (P). <i>M. diplomera</i> .	
var. <i>dicranophylloides</i>		<i>M. stenomera</i> (P).	
var. <i>tenuifolia</i> (nom. illegit., later homonym).		<i>M. stenomera</i> (P).	
f. <i>harmsii</i>		<i>M. heteromera</i> (P).	
<i>M. pauli-guilielmi</i> ("pauli-guilelmi") ..	<i>M. pauli-guilielmi</i> ssp. <i>pauli-guilielmi</i> (P).	<i>M. pauli-guilielmi</i> ssp. <i>pauli-guilielmi</i> (P). <i>M. p.-g.</i> ssp. <i>flexuosa</i> (P.) <i>M. p.-g.</i> ssp. <i>pluri-</i> <i>nervia</i> (P).	<i>M. pauli-guilielmi</i> ssp. <i>pauli-guilielmi</i> (P).
<i>M. fawcettii</i>	<i>M. fawcettii</i> (P).	<i>M. fawcettii</i> (P). <i>M. pauli-guilielmi</i> ssp. <i>flexuosa</i> (P). <i>M. p.-g.</i> ssp. <i>pluri-</i> <i>nervia</i> (P).	
<i>M. platyrachis</i> ("platyrhachis")	<i>M. platyrachis</i> (P).	<i>M. platyrachis</i> (P).	
<i>M. denisonii</i> (Used in contravention of priority.)	<i>Lepidozamia</i> <i>peroffskyana</i> .	<i>L. peroffskyana</i> . <i>L. hopei</i> .	<i>L. peroffskyana</i> .
var. <i>hopei</i>	<i>L. hopei</i> .	<i>L. hopei</i> .	
<i>M. preissii</i> (Used in contravention of priority.)	<i>M. riedlei</i> .	<i>M. riedlei</i> . <i>M. macdonnellii</i> .	<i>M. riedlei</i> . <i>M. macdonnellii</i> .
ssp. <i>dyeri</i>	<i>M. riedlei</i> .	<i>M. riedlei</i> .	
<i>M. Sect. Polyorientales</i> (nom. illegit.) ..	As to type sp. <i>M. §Macrozamia</i> .	<i>M. §Macrozamia</i> (part). <i>M. §Parazamia</i> (part).	
Subsect. <i>Attenuatae</i> (nom. illegit.) ..	<i>M. §Macrozamia</i> .	<i>M. §Macrozamia</i> (part). <i>M. §Parazamia</i> (part).	
Subsect. <i>Acutae</i>	<i>M. §Parazamia</i> .	<i>M. §Parazamia</i> (part).	
Subsect. <i>Curvatae</i>	<i>M. §Parazamia</i> .	<i>M. §Parazamia</i> (part).	
<i>M. Sect. Monoorientales</i> (nom. illegit.) ..	<i>Lepidozamia</i> (Genus).	<i>Lepidozamia</i> (Genus).	
<i>M. Sect. Monooccidentales</i> (nom. illegit.)	<i>M. §Macrozamia</i> .	<i>M. §Macrozamia</i> (part).	

TABLE 1.—Continued.

Name Used by Schuster (1932) (spellings corrected).	Correct Name in the Present Revision. [<i>Macrozamia</i> spp. belonging to sect. <i>Parozamia</i> marked (P), others belong to sect. <i>Macrozamia</i> .]		
	Basionym (present correct position).	Specimens Cited.	"Synonyms" Cited (excl. Invalid Names and Absolute Synonyms) (present correct position).
<i>Bowenia spectabilis</i>	<i>B. spectabilis</i> .	<i>B. spectabilis</i> .	
var. <i>serrulata</i>	<i>B. serrulata</i> .	<i>B. serrulata</i> . <i>B. spectabilis</i> (?).	<i>B. serrulata</i> .

Basis.

The materials used are: (1) The herbarium and museum collections of the New South Wales National Herbarium (NSW), together with certain material from the Botanic Museum and Herbarium, Brisbane (BRI), the National Herbarium, Melbourne (MEL), the Museum of Applied Arts and Sciences, Sydney (TECH), and the Botany Department, University of Sydney (SYD). Since the outstanding problems were centred in New South Wales, only selected specimens from the other State herbaria were examined. Their full collections will, of course, fill in details of distribution, but are not likely to affect the conclusions, at least without concurrent field study. (2) The living cycad collections in the Royal Botanic Gardens, Sydney. (3) Natural populations of the following species: *Lepidozamia peroffskyana*, *Macrozamia moorei*, *M. macdonnellii*, *M. communis*, *M. diplomera* (limited observation), *M. lucida*, *M. spiralis*, *M. secunda*, *M. heteromera*, *M. stenomera* and *M. pauli-guilielmi* (especially ssp. *plurinervia*). The only species not examined either in the field or the garden are *L. hopei*, *M. platyrachis* and *M. riedlei*. The last certainly needs some field study. (4) Published and unpublished illustrations and descriptions. Information solely derived from such descriptions, except when they are very clearly fully reliable, is specified as such in the text.

Outlook.

Since systematists are notoriously individualistic, it is always helpful to appreciate a particular worker's standpoint and philosophical approach to the subject. Underlying the present treatment is the conviction that taxonomic classification, in one way or another, should reflect, if not express, the results of evolution. When little palaeontological evidence is available one can do this only by inference, using the accumulated knowledge of what is known to have happened in other and especially related groups of organisms, and evidence of every possible kind must be evaluated and taken into account. Bearing in mind genetic, evolutionary and ontogenetic principles, one must try to determine the most probable relative phylogenetic relationships and divergences of the various individuals, populations and groups of populations, and decide their taxonomic status accordingly. The success of this method depends greatly on the student's knowledge and insight, but on a balance of probabilities it leads to more satisfactory conclusions than those obtained by the static or formalistic approach, which rejects evolutionary speculation and depends solely on morphological differences and resemblances in their own right. It is well known that similar conclusions may often be reached from these really quite fundamentally different starting points. That they quite often lead to different conclusions is frequently forgotten.

I have, of course, used the customary, chiefly macroscopic and external, morphological characters in the keys and descriptions. However, characters as such were not regarded as the basis of taxonomic decisions, but rather as indices of the natural populations or groups of populations between which, on grounds of evolutionary

probability, if not direct evidence, we can infer relationship. It is often held that the best taxonomic characters are those which are selectively neutral. The existence of truly selectively neutral characters is dubious; practically every characteristic of a line of organisms is in some sense adaptive, within the range of genetic possibilities open to the particular group. Though selection may operate chiefly on some genetically and developmentally correlated characters rather than those we observe as taxonomic differences, any deleterious effects will tend to be minimized by adaptive compensation (Stebbins, 1950, pp. 121-123). There are, of course, many genetic and physiological balances and counterbalances, multiple genetic effects, and time-lags, and some characters do appear fixed because they are adapted not to the external environment, but rather to the complex of balanced organization within the organism itself in such a way that any uncoordinated change is disadvantageous.

Such characteristics are indeed of great taxonomic value and phylogenetic significance, but they are not confined to any particular set of organs, and one cannot uphold the often expressed view that, in the vascular plants, leaf and stem characters have less taxonomic value than reproductive characters. Variations in over-all shape and size, whether due to genic or direct environmental differences, cause little upset in the complex processes of the plant; such variations are indeed most common in vegetative organs, but may be found in the reproductive system as well. For instance, cone and sporophyll size varies considerably, both according to conditions and (apparently) genetically, within single species of *Macrozamia*.

In short, my attitude to taxonomic theory in relation to evolution is in general similar to that of Simpson (1945, 1953), with the difference that my emphasis is on the *classification* of the present-day plants in the light, where possible, of the *evolution* of their ancestors. To fit arrays of organisms widely separated in geologic time into a single classificatory system is often impossible. Organisms are related both to their contemporaries and to their forebears, but the relationships are not comparable.

Concepts.

The *genera* of cycads are too clearly distinct and too coherent in themselves to cause much argument as to status. This applies as well to *Lepidozamia* as to the currently-accepted genera. Botanists (except Regel) have simply neglected to look at it or think critically about it. The characters by which genera differ may be anything at all, according to the particular case.

A *species*, in this normal sexual group, is taken to be a population or group of similar populations effectively isolated in nature *by any means* which prevents a degree of interbreeding sufficient to cause large-scale merging in characters with related but genotypically and phenotypically consistently different populations. This is a crude but practical definition. The category cannot be precisely defined, and populations may occur which could reasonably be called either species or subspecies.

A *subspecies* I take to be a geographically or ecogeographically characterized population (or group of populations) consistently and recognizably different in several respects from, but intergrading to a considerable degree with neighbouring populations. A subspecies must be coherent as a population, that is, there must be much more breeding within the subspecies than between them. A variation of the definition is that if subspecies A and B merge, but a third very similar group C is isolated, C may be regarded as another subspecies rather than a distinct species.

The category of *variety* is not used for reasons given below (p. 108).

Morphological terminology.

Much confusion and false argument could be saved by a precise rationalized terminology for comparative morphology, to be clearly distinguished where necessary from non-committal, purely descriptive terms. In the present case one must bear in mind that most structures of cycads are not homologous with those bearing similar names in the Cordaite-*Ginkgo-Ephedra* (Eames, 1952)-Taxad-Conifer (Florin, 1948, 1954)

group* with which they are commonly grouped as "Gymnosperms". (It is high time that this term and "Pteridophyta" were relegated to the history of botany. Their continued use misleads not only students but learned botanists into the belief that they apply to natural groups.) The cycads, of course, belong to the Pteropsida, in company with the true fern groups both ancient and modern, Pteridosperms, the *Glossopteris* (*Scutum*) group (Plumstead, 1956), Bennettitales, Caytoniales, *Welwitschia*, *Gnetum* (Eames, 1952, p. 96) and, with little doubt, the Angiosperms. It does not follow that every organ called by the same name in these groups is homologous, though many are so, at least in a broad sense.

In general I have used terms which either (a) are well known to be descriptive and without comparative morphological significance, or (b) have a definite morphological sense which applies correctly to the cycads. However, a few terms fall between these categories and need comment.

Frond is used rather than "leaf", to indicate that these organs are generally comparable to the fronds of a fern, that is to say, they clearly show their derivation from the branch-systems of early Pteropsida, but have become two-dimensional and of quite determinate and predominantly intercalary growth. The leaves of Angiosperms may be homologous, but are certainly rather dissimilar structures. The "leaves" of non-pteropsids are either not at all or only in a very broad sense homologous.

Petiole is used as a descriptive term, without morphological significance, for the frond-stalk proximal to the first pinnae. *Stipe(s)*, used for the equivalent of the petiole in ferns, is traditionally used for the stalk of the megasporophyll in the cycads.

Rhachis is used for the frond-axis from the lowest pinnae onwards.

Pinna is used for the primary frond-segments. *Pinnule* is used only for the ultimate segments of *Bowenia*, whether these are borne on a secondary rhachis or on the end of the primary rhachis. The term is not applied to the segments of the bifurcating pinnae of some species of *Macrozamia*. "Leaflet", like "leaf", is not used.

Cataphyll, rather than "scale-leaf", which is scarcely apt here, is used for "reduced" leaves.

Cone (in Latin descriptions *conus* rather than *strobilus*) is used in a non-committal descriptive sense. The cycad cone is not at all equivalent to the female cone of conifers (a compound strobilus), nor is it really equivalent to the male cone of the same group, since the sporophylls are not homologous. Both terms "cone" and "strobilus" are used for a number of non-homologous structures; for comparative purposes they need replacement by special terms of obvious significance. I suggest *stroboid* for the cycad "cone", *strobe* for the male (or single unit of a female) conifer cone, *synstrobe* for the female conifer cone, *anthoid* for the Bennettitalean bisexual structure, but I shall pursue this matter elsewhere. Further simple, euphonious terms of obvious meaning are necessary for "cones" of Lycopods, Lepidodendrids, and the Sphenopsida. Such a terminology would add to precision, while retaining a degree of simplicity of language.

Cone-stalk† (*axis coniger*) is preferable to the usual "peduncle" (which it is not, since it bears the approximate equivalent of a single flower) or "pedicel" which suggests a more slender structure.

Sporophyll is used in preference to "cone-scale". The structure is quite different from the complex female cone-scale of the conifers. Admittedly it is not really homologous with the sporophyll of the male conifer strobilus and certainly not with the "sporophyll" of the Lycopods. Again the term is used in the non-committal sense of a simple (or

* For this great branch of the vascular plants the terms *Pityopsida* or *Pityophyta* (according to rank) are suggested as etymologically preferable to *Coniferopsida* and *Coniferophyta* (cf. Arnold, 1948), which are Latin-Greek mongrel terms. *Pitys* is Greek for a pine and is also the name of a genus of Palaeozoic near-conifers. Since the I.C.B.N. fortunately does not enjoin respect of priority in naming higher groups, we may surely choose to use euphonious, well-formed and meaningful names.

† Peduncle is used in my forthcoming account in the *Flora of New South Wales*, due to its use in the earlier ms. of that work.

apparently so) sporangium-bearing organ more or less equivalent to a "leaf" of the same plant.

Melville (1957) has introduced an elaborate special terminology to describe the various angles and faces of the sporophylls of *Encephalartos*. These terms certainly facilitate description of the very geometrical sporophyll-ends in that genus, where, moreover, these details are of taxonomic importance. In the Australian genera, however, they are not necessary and frequently not applicable. I have simply referred to the *sporophyll-end*, its *wing* and its *spine*. The last two (in *Macrozamia*) are actually continuations of the margins and the end of the lamina of the sporophyll. The sporophyll-end is the swollen portion distal to the stipe, and the descriptions apply especially to its outer surface on the cone, which really includes both adaxial and abaxial faces.

Male and *female* (rather than "microsporangiate", etc.) are applied freely to the cones and sporophylls (and plants). The sexual differentiation, which is finally expressed in the gametes, is carried back into the sporophyte, and I see no more objection to the use of sexual terms for a plant sporophyte than for an animal diplont, such as a man. *Megasporophyll* is, however, used at times (not in the descriptions).

Ovule is used for the megasporangium with its integument. The term is a descriptive one not implying complete homology in different groups. The same applies to *seed*.

All such terms as "flower", "stamen", "staminate", and "anther", though they have been widely used, especially on the continent of Europe, in cycad and conifer descriptions, are better confined to the angiosperms.

Taxonomic criteria.

Certain characters have proved useful for the recognition and formal definition of the taxa, though these are not necessarily more essential than others less useful. The keys and descriptions herein merely differentiate, circumscribe and partially describe the natural populations in terms of the readily observed external morphology. No character, as such, is essential to any one taxon. The correct identification of an individual is the determination of the natural population of which it is part, not the key-characters which it possesses. The latter are merely a generalization, as accurate as possible. For example, plants of *Macrozamia communis* may rarely be found with spirally twisted fronds, contrary to the key and descriptions. These aberrant plants are still constituents of the population defined as *M. communis* and the key (as a 99+ per cent. generalization) is not wrong. The dimensions given, in particular, are not to be considered absolute; cycads are especially variable in this respect. Nevertheless, the dimensions used in the keys apply to all the specimens actually examined, and there should not be many departures from them.

The characters which have been found useful will be evident from the keys and the discussions under the genera and sections. They need not be detailed here. In all the Australian Zamiaceae, many vegetative characters are quite as consistent as those of the cones, and these are given prominence in the keys. They will be especially useful in *Macrozamia* section *Parazamia*, in which cones are irregularly produced and frequently only vegetative individuals may be found; the cones are much the same throughout this group.

Juvenile and semi-juvenile plants are usually indeterminable unless their geographic origin is known. Only adult plants (old enough to bear cones) are described herein (see below, p. 89). The shapes of rhachis and petiole change somewhat on drying, as the parenchymatous tissue shrinks and the sclerenchyma is externally revealed as ridges. As far as possible both living and dried material is described.

Morphological and anatomical studies.

The detailed morphology, anatomy and life-history of the cycads have attracted a great deal of attention, especially from Chamberlain and his students. This work, of great importance in the comparative morphology of the vascular plants generally,

cannot be discussed here, and it is assumed that any serious student of cycads is familiar with its chief conclusions. The most notable Australian study is that of Brough and Taylor (1940) on *Macrozamia communis* ("*M. spiralis*" in their usage). The bibliography of their paper will provide an entry to the morphological literature.

Chromosome numbers.

All the Australian species cytologically examined have the chromosome number $2n = 18$, except for an early count ($n = 12$) on *M. riedlei* (q.v.), which needs confirmation. The numbers are cited after the descriptions of the genera and species. No chromosome count has yet been made in *Lepidozamia*.

Distribution.

The detailed distribution is indicated under each species and the present distribution patterns, which show much vicariism, are discussed under the genera.* Not a great deal can be said about past distribution (but see the discussion under *Lepidozamia hopei*, p. 86). *Macrozamia* section *Macrozamia* must have extended across the southern half of the continent during the Tertiary, though not necessarily continuously at any one time. Section *Parazamia* and the other two genera are confined to eastern Australia. The nearest relationships of *Lepidozamia* and *Macrozamia* appear to be with the African *Encephalartos*, but since the cycads in general are a relict group with scattered surviving genera, not too much weight can be placed on this. *Bowenia* is very different from the other Australian Zamiaceae, and is probably closer to some of the American genera. Again, the phylogeographic significance of this is hard to evaluate in an ancient and fragmented group.

Table 2 gives the distribution by States. No Zamiaceae occur in Victoria, Tasmania or South Australia. It must be kept in mind that this table excludes *Cycas* (Cycadaceae s. str.) which has species in the tropical parts of Western Australia, the Northern Territory and Queensland. Distribution maps are given under the respective genera and sections, below.

Speciation.

While little can be said about details of the evolution of the genera and sections, the distribution patterns suggest that the more recent speciation in the Australian Zamiaceae has been dependent on geographic isolation of segments of formerly continuous populations, associated with differentiation in response to environmental changes. This classical ecogeographic speciation is perhaps not quite complete in some cases especially in *Macrozamia* section *Parazamia* (see p. 100).

There is no evidence of recent polyploidy in any of the living cycads. The universal dioecism would make successful polyploidy unlikely, though not impossible. Outbreeding is, of course, complete. Some local ecotypic differentiation is found in the more widespread species (see discussions under the individual sections and species of *Macrozamia*).

Hybridism.

As would be expected in anemophilous, dioecious plants, all (so far as known) with the same number of chromosomes, some natural hybridism is found in *Macrozamia* where the species come into contact. Some introgressive hybridization is possible in the case of *M. diplomera* (q.v.), but in general the hybrids do not appear to be of much importance. A few spontaneous hybrids have arisen in the *Macrozamia* collections in the Sydney Botanic Gardens.

Particular cases are discussed under the respective parental species (below, or in Johnson, in press), but the following apparent hybrids have been found in the field or in herbarium collections: *M. diplomera* × *M. heteromera*, *M. lucida* × *M. moorei*, *M. heteromera* × *M. secunda*, *M. heteromera* × *M. stenomera*, *M. pauli-guilielmi* ssp.

* The subdivisions of New South Wales are defined as in the *Flora of New South Wales* (Anderson, in press).

plurinervia × *M. stenomera* (or perhaps *M. heteromera*). Others may be expected. All of these have been recognized by obviously intermediate frond characters and their occurrence as single or infrequent individuals in mixed communities of the apparent parents. Cones have not been available and no progenies could therefore be raised.

Ecology.

The particular ecology is discussed under each taxon. Most species grow in *Eucalyptus* (sclerophyll) forest, but *Lepidozamia hopei* (and to some extent *L. peroffskeyana*) and *Bowenia spectabilis* may be found in certain sites within or near

TABLE 2.

	Qld.	N.S.W.	N.T.	W.A.
Number of genera	3	2	1	1
Number of species	9 (2 : 5 : 2)	12 (1 : 11 : 0)	1	1
<i>Lepidozamia</i>				
<i>hopei</i>	+			
<i>peroffskeyana</i>	+	+		
<i>Macrozamia</i>				
(Sect. <i>Macrozamia</i>)				
<i>moorei</i>	+	+		
<i>riedlei</i>				+
<i>macdonnellii</i>			+	
<i>miquelii</i>	+	+		
<i>communis</i>		+		
<i>diplomera</i>		+		

(Sect. <i>Parazamia</i>)				
<i>platyrachis</i>	+			
<i>lucida</i>	+	+		
<i>spiralis</i>		+		
<i>secunda</i>		+		
<i>heteromera</i>		+		
<i>stenomera</i>		+		
<i>pauli-guilielmi</i>	+	+		
ssp. <i>p.-g.</i>	(+)	(+)*		
ssp. <i>plurinervia</i>	(+)*	(+)		
ssp. <i>flexuosa</i>		(+)		
<i>fawcettii</i>		+		
<i>Bowenia</i>				
<i>spectabilis</i>	+			
<i>serrulata</i>	+			

* Intergrades only.

rainforest. Only one species, *M. macdonnellii*, occurs under really arid conditions, and even this is confined to the refugium of the Central Australian range system where conditions are somewhat better than elsewhere in the interior. The species of *Macrozamia*, in contrast to the other two genera, are usually associated with other sclerophyllous species of the "Australian" floristic element. The plants are rather slow-growing, but by no means as excessively so as sometimes stated (see *Lepidozamia peroffskeyana*, p. 86). Apogeotropic roots regularly form coralloid end-systems containing Cyanophyta (Nostocaceae: *Anabaena* and perhaps *Nostoc*) (Fritsch, 1945, pp. 872-4). These blue-green algae may be in a symbiotic relationship with the cycad plant. Nitrogen-fixing bacteria (e.g. *Azotobacter*) also occur in these nodules in a number of cycads (refs. in Thieret, 1958).

Economics.

Like other cycads, the Australian Zamiaceae contain toxic substances (Hurst, 1942; Webb, 1948; Gardner and Bennets, 1956) which are at times responsible for poisoning

of stock, especially cattle. For this reason they have been killed out in certain areas. In view of their great botanical interest and the low pastoral quality of much of the land on which they occur, their destruction is particularly unfortunate. Nevertheless, in the past some botanists, especially in Queensland and Western Australia, have joined the agriculturists in issuing publications recommending methods of poisoning the plants.

The starchy endosperm of the seeds, and sometimes the pith of the caudex, served the aborigines as food, as *Cycas* still does in Arnhem Land (Specht, 1958), after washing and roasting to remove the poison. Various cycads are used similarly in other continents. Thieret (1958) gives a comprehensive review of the literature on the economics of cycads, but much of the cited information is out of date.

In horticulture, various species are to be seen in home and occasionally public gardens in Australia, but many species have been cultivated under glass in European collections, especially during the nineteenth century. The description of such plants (usually from vegetative and often semi-juvenile material) has been responsible for much of the extraordinary confusion of the nomenclature.

Taxonomic Revision.

Note.

This paper will be followed very shortly by the publication of the first parts of the *Flora of New South Wales* (ed. Anderson, in press). My treatment of the Zamiaceae forms Part 1 of this work. For reasons of space, descriptions (except Latin descriptions of new taxa), detailed synonymy and lists of specimens of the New South Wales species are not given in the present paper, but will be found in the *Flora*. Reference to the latter is made where necessary in the text hereunder. A complete index of synonyms, however, is given below (p. 113).

For most purposes the keys herein will be sufficient for identification, especially if the geographical origin of the material is known, but for critical investigation this revision and the *Flora* must be used in conjunction. I regret this necessity.

Family ZAMIACEAE Reichenb.

Sporophylls of both sexes in definite simple cones, of determinate growth. Cones dioecious, rather large, axillary or terminal, with numerous scale-like sporophylls arranged spirally or apparently in vertical rows; male sporophylls (microsporophylls) with many small, globose sporangia more or less clustered in groups (sori) in two collateral sometimes confluent areas on the undersurface, sporangia dehiscent by slits; female sporophylls (megasporophylls, macrosporophylls) simple, consisting of a barren stipes and an expanded and thickened end, the latter bearing two (rarely three in *Lepidozamia*) sessile ovules on its axis-facing margins ("inner surface"). Pollen wind-borne; fertilization by naked multiflagellate spermatozooids. Seeds large, from sub-globular to subcylindrical or variously angled, with a broad chalazal area and more or less apiculate micropylar end, seed-coat with a fleshy outer layer and a woody inner layer; (haploid) endosperm present, cotyledons two, germination hypogeal.

Somewhat palm-like plants; stem subterranean to tall, not or little branched, with a crown of spirally arranged pinnate or bipinnate leaves (fronds) and interspersed rudimentary leaves (cataphylls), leaf-bases persistent and clothing the stem, or deciduous. Fronds usually straight and folded in bud (circinate in *Ceratozamia* of Mexico); leaf-segments without a midrib, with few to many longitudinal nerves, straight, not circinate, in bud.

A family of eight genera and about 80 species, with a scattered distribution in tropical to warm-temperate parts of N. and S. America, Australia and Africa.

For a key to the tribes and genera see Part I, p. 66.

Australian members: Tribe Encephalarteae: I. *Lepidozamia*; II. *Macrozamia*. Tribe Zamieae: III. *Bowenia*.

I. LEPIDOZAMIA Regel.

Regel in *Bull. Soc. Imp. Nat. Mosc.* (1857), n. 1, 182, and in *Gartenfl.* 6 (1857*), 11, *ibid.* (1870), 227, (1875), 42 and (1876), 4, also in *Acta Hort. Petrop.*, 4 (1876), 294; Miq., *Prodr. Syst. Cycad.* (1861), 10; A.D.C., *Prodr.*, 16, pt. 2 (1868), 547 (as "Genus dubium").

Typification: *L. peroffskeyana* Regel. TYPE SPECIES (the sole original species).

Synonymy:

Catakidozamia W. Hill in *Gard. Chron.* (Nov., 1865), 1107 (type sp.: *C. hopei* W. Hill). [This is to be regarded as a combined "generico-specific" description, since only one valid species was included, though "*C. macleayi*" was mentioned as a *nomen nudum*. Schuster (1932, p. 86), who seems to have cited many publications without seeing them, has followed *Index Kewensis* in giving the author as T. Hill. The generic name evidently circulated amongst European gardeners (e.g. Haage and Schmidt) as "*Katakidozamia*", and is thus cited, in synonymy, by Regel (1876, both papers), but without reference to Hill. Schuster mis-cites it as "*Katikidozamia*".]

Encephalartos Lehm. sect. *Lepidozamia* (Regel) Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 371.

Macrozamia Miq. sect. *Lepidozamia* (Regel) Miq., in *Arch. Néerl.*, 3 (1868), 253, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 56.

Macrozamia sect. *Monoorientales* Schuster, *Pflanzenr.*, IV, i (1932), 88, nom. illegit. (exactly equivalent to the above).

Palm-like plants with a usually unbranched trunk clothed by the persistent leaf-bases, often tall, all parts shortly pubescent to tomentose when young, but some glabrescent with age. Fronds numerous, large, simply pinnate, not twisted. Cataphylls abundant, fleshy, linear-subulate, shortly tomentose, mostly in series alternating with the successive crowns of fronds. Base of petiole swollen, shortly tomentose. Pinnae numerous, spreading, inserted more or less alternately along the adaxial midline of the rachis, falcate, slightly narrowed but not callous at the base, stomata confined to lower surface. Cones of both sexes almost or quite sessile, large, axillary among the cataphylls of the crown, the spirally-arranged sporophylls tomentose at the ends, not spiniferous. Male sporophylls with a linear-spathulate fertile region and a more or less triangular-rhomboid, laterally expanded end, deflexed in spiral series at sporangial dehiscence. Female sporophylls with an elongated, terete to subangular stipes and a dorsiventrally biconvex, laterally expanded, somewhat deflexed, shortly tomentose end bearing two or sometimes three ovules on the inward-facing margins (inner surface), tapered into the flattened, more or less acute, at first deflexed, but on drying more or less upturned, ultimate tips. Outer seed-coat fleshy, red or yellowish, inner coat hard.

Endemic in the eastern coast region of Australia, with two species, one in tropical Queensland, the other in subtropical Queensland and the north coast of New South Wales, in wet sclerophyll forest and around rainforest (Text-figure 1).

Except by Regel himself, *Lepidozamia* has been generally placed under *Macrozamia* ever since its Australian origin was known (the type species was described from a garden plant in the then St. Petersburg, of unknown origin, and was at one time thought to be from Mexico). However, it is quite as distinct as any other genus of *Zamiaceae*, and I can see no especially close affinity with *Macrozamia*.

Encephalartos, *Macrozamia* and *Lepidozamia* would all appear about equally similar—and dissimilar—and if they appear to stand together apart from other *Zamiaceae*, this is perhaps due to the absence of certain advanced or specialized characteristics, rather than to any very positive features in common. They can, of course, be made to stand together in a key, but keys are an unsafe guide to relationships.

Lepidozamia is readily distinguished from *Macrozamia* by the almost or quite sessile cones, the quite differently-shaped sporophyll-ends which lack the characteristic

* Later than the first-cited reference. I have not seen the four *Gartenflora* references, which are quoted from Regel's second 1876 paper.

spinescent modification of *Macrozamia* and moreover are closely tomentose-pubescent with short hairs, the short swollen rather than laterally expanded and shortly rather than silky-woolly tomentose petiole-bases, the fleshy subulate shortly-tomentose cataphylls, the structurally more involute rhachis with median insertion of the falcate pinnae which lack callous bases, the straight torque-free veneration of the fronds and the more open crown with frond-series markedly interrupted by wide cataphyll-series. Furthermore, as Thomas and Bancroft (1913) and, in a more exhaustive study, Cookson (1953) have found, the epidermal anatomy of the species referred to *Lepidozamia* differs strikingly from that of *Macrozamia* proper. In *Lepidozamia* the long axes of the epidermal cells are oblique or transverse to the long axis of the pinna, in contrast to the longitudinal orientation in *Macrozamia*.



Text-fig. 1.—Distribution of *Lepidozamia*: 1: *L. hopei*; 1a: site of *L. hopeites* fossils; 2: *L. peroffskyana*.

A remarkable feature is the presence in some cones of a number of megasporophylls with three ovules. I have not been able to obtain sufficient fresh material of such sporophylls to determine the original position of the third ovule. It appears to be inserted above and between the other two, though rather to one side, but is probably lateral in ontogeny as in the Cycadales generally. The pluriovulate condition would appear to be a primitive feature, and indeed the unspecialized sporophylls suggest that *Lepidozamia* is relatively primitive in the Zamiaceae. Chamberlain (1909, p. 410) has recorded up to five or six abortive ovules in a cone of *Dioon spinulosum* and, as a rarity, as many as four ovules in *Zamia* and *Ceratozamia*. In *Lepidozamia*, however, the condition is more common and all three ovules may develop into seeds.

In very young seedlings the pinnae arise from the margins of the upper surface of the rhachis, as in *Macrozamia*. In successive fronds these margins are found to be closer together (relative to the increasing diameter of the rhachis) until the apparently median insertion of the adult stage is attained. This, of course, appears to be a specialization. The fronds superficially somewhat resemble those of *Ceratozamia*, but the sporophylls are very different.

Regel established his genus on vegetative material alone, and maintained it later (1876) when he had knowledge of the cones. In this he showed greater discernment than other cycadologists, though Miquel was aware that it was a rather distinctive

group and, of course, Hill recognized it as *Catakidozamia*. The name *Lepidozamia* refers to the scale-like frond-bases clothing the stem.

Schuster (1932) inexplicably (unless his arrangement was based, as the meanings of his Greek-Latin hybrid names suggest, not on morphology but on geography) placed his section *Monoorientales* (= *Lepidozamia*) between his other two sections of *Macrozamia*, although the latter contain extremely closely allied species.

Key to the Species.

1. Broadest pinnae 17-30 mm. broad, 20-40 cm. long, 17-30-nerved. N. Queensland 1. *L. hopei*.
 1.* Broadest pinnae 7-14 mm. broad, 10-32 cm. long, 7-14-nerved. S. Queensland and N.S.W. 2. *L. peroffskeyana*.

1. *L. HOPEI* Regel* in *Gartenfl.* (1876), 6, and in *Acta Hort. Petrop.*, 4 (1876), 296.

Typification: Based on a living plant cultivated by Haage and Schmidt, doubtless originally from Hill. The brief description unmistakably refers to this species.

Synonymy:

Catakidozamia hopei W. Hill in *Gard. Chron.* (Nov., 1865), 1107 ("from tropical Eastern Australia").

Macrozamia hopei W. Hill ex F. M. Bail., *Syn. Queensl. Fl.*, Suppt. 1 (1886), 52 (from "Daintree and Johnstone Rivers". To be considered as a new publication; Bailey did not cite Hill's earlier binomial or description, though he attributed his new binomial to Hill), and *Queensl. Fl.*, 5 (1902), 1506; also W. Hill ex C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 116, nomen nudum.

M. denisonii C. Moore & F. Muell. var. *hopei* (W. Hill) Schuster, *Pflanzenr.*, IV, i (1932), 101 [this may be taken as truly based on Hill's name of 1865, which is the earliest cited].

Trunk 2-20 m. tall. Fronds numerous, at first suberect, later spreading, 2-3 m. long on adult plants, more or less puberulous, especially the rhachis, but glabrescent with age; petiole 30-60 cm. long (the short, much swollen, shortly tomentose base ca. 3-4 cm. long), rounded to angular beneath, angled or (when dry) keeled and broadly two-furrowed above, or sometimes very slender and laterally compressed (when dry); rhachis more or less rounded when living but when dry angular beneath, more or less laterally compressed, angled to the median pinna-bearing keel above. Pinnae 160-200 or more, spreading but recurved-drooping towards the ends, entire, shining above, recurved-falcate, broadly strap-shaped, 20-40 cm. long (lower somewhat shorter than the median ones, but never very short and spinescent), 15-30 mm. broad, with 15-30 scarcely raised nerves beneath, tapered to the acute apex, slightly contracted at the base, with stomata on the undersurface only. Cones sessile, usually solitary, axillary but often appearing quasi-terminal, surrounded at the base by several rows of fleshy, velvety-tomentose, subulate-tipped cataphylls. Male cones not seen, doubtless similar to those of *L. peroffskeyana*. Female cones ovoid, sometimes somewhat contracted at the base, 40-60 (or more?) cm. long, 20-25 (-30?) cm. diam.; sporophylls ca. 5-8 cm. long, 3.5-6.5 cm. broad, the shortly tomentose end deflexed, but the extreme tip often again upturned. Seeds 4-5.5 (-6?) cm. long, 2.5-3.5 cm. thick, outer coat fleshy, bright red when ripe.

Distribution: North-east Queensland from the Daintree River (or further north?) to the Rockingham Bay region in hilly country near or within rainforest.

Specimens examined: Babinda Creek, P. R. Messmer, 12.viii.1954 (NSW.30536); Bellenden Ker, C. T. White 1295, iii.1922 (NSW.40971); Cardwell, H. L. White, vii.1911 (NSW, cone material only).

* This is not nomenclaturally based on *Catakidozamia hopei* W. Hill, the publication of which appears to have been unknown to Regel. Regel cited "*Katakidozamia Hopei* h. Haage et Schm.", a garden name of no validity, though, of course, derived ultimately through horticultural channels from Hill. Regel's *Gartenflora* reference is the earlier of the two; it was cited in the other 1876 paper.

L. hopei, one of the tallest of all cycads, is reputed to reach a height of up to 20 m. It is very similar to *L. peroffskeyana* in most respects, but is readily distinguished by its broad pinnae. Cookson (1953) describes clear differences in details of epidermal anatomy between the two species. I have not seen sufficient cone material to determine whether there are significant differences in these organs. If so, they are certainly not very great, and Bailey's (1902) key is not reliable. In Bentham's treatment (1873, pp. 253-4) the species is not distinguished from "*M. perowskianä*", but since Bailey's time it has been generally recognized as specifically distinct, except by Schuster.

Although *L. hopei* is at present confined to the wet tropics and is replaced further south by *L. peroffskeyana*, a plant very similar to the former grew in Victoria during the early Tertiary. This is the following:

LEPIDOZAMIA HOPEITES (Cookson) L. Johnson, comb. nov. (sp. foss.).

Basionym: *Macrozamia hopeites* Cookson in *Phytomorphology*, 3 (1953), 307, f. 1-5.

Typification: "collected from a sandy bed exposed during 1947 and 1948 on top of the early Tertiary brown coal at the Lucifer Mine, Bacchus Marsh, Victoria". Fragments of pinnae. Nat. Mus. Vic. P15781 is the HOLOTYPE.

Cookson's description and beautifully clear photographs of the epidermal anatomy of these pieces show the unmistakable resemblance to *L. hopei*. The epidermis of *L. peroffskeyana* differs from these in detail, and that of *Macrozamia* is very different in orientation and shape of the cells. Dr. Cookson described the species as a *Macrozamia* pending completion of the present revision (Cookson, *l.c.*, p. 311), but was aware at the time of the considerable differences between *Lepidozamia* and *Macrozamia*, which her studies have indeed established more firmly.

The former occurrence of this plant, rather than one resembling *L. peroffskeyana*, in Victoria illustrates the risk involved in deducing past history from present distribution. It may be, of course, that whereas little change has taken place in the tropical segment of a former single population, the more southern segment has changed considerably, giving rise to *L. peroffskeyana*. On the other hand, the ancestors of the latter may have been already differentiated in the early Tertiary, but somewhere else.

2. *L. PEROFFSKYANA* Regel in *Bull. Soc. Imp. Nat. Mosc.* (1857), n.1, 184, t.IV, f.20, 21, and in *Gartenfl.*, 6 (1857*), 11, t.186, f.23, 31, *ibid.* (1870), 227, t.660, (1875), 42 and (1876), 4, also in *Acta Hort. Petrop.*, 4 (1876), 295; Miq., *Prodr. Syst. Cycad.* (1861), 10, 22; A.D.C., *Prodr.*, 16, pt. 2 (1868), 547 (under *Genus dubium*).

Typification: The HOLOTYPE was a living plant cultivated in the Botanic Garden, St. Petersburg. From the description and figures there is no doubt of its identity.

Synonymy:

Macrozamia denisonii C. Moore & F. Muell. in F. Muell., *Fragm. Phytogr. Austral.*, 1 (1858), 41 [of the three syntypes the following may be taken as LECTOTYPE: "In vicinia fluminis Manning. Stephenson." NSW.40975, an old collection from Moore's time, but labelled only "Manning River", is almost certainly part of this. Moore (1884, p. 119) gives 1855 as the date of this collection].

Further synonymy is given by Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Description and Specimens: See Johnson in Anderson, *l.c.*

Distribution: Subtropical eastern Queensland and North Coast of New South Wales to the Manning River district, usually in hilly country in wet sclerophyll forest sometimes bordering on rainforest.

L. peroffskeyana† has been most generally known, especially in Queensland, as *Macrozamia denisonii*, but Regel's name has clear priority and undoubtedly belongs to

* Later than the first-cited reference. I have not seen the four *Gartenflora* references. They are quoted from Regel's second 1876 paper.

† The epithet has been spelt in various ways. Regel named it in honour of Count Peroffsky, an Imperial Russian Minister and benefactor of the St. Petersburg Botanic Garden.

the species. The distribution is scattered, small communities being found here and there in forested hilly country of the subtropical east coast. The plants are handsome and striking, but not as large as those of *L. hopei*; their maximum height appears to be about 7 m. Absurdly exaggerated claims of great individual age (to 10,000 years or more) for these plants have been made at tourist centres and in the popular Press. These estimates are usually attributed to C. J. Chamberlain, but I have found no such claim in any of Chamberlain's publications. His estimates of the ages of other cycad species, though perhaps a little high, are certainly not of this order. Plants of *L. peroffskyana* in the Sydney Botanic Gardens have attained a trunk height of 2 m. in less than a century. Since the plants grow only by apical increase of a single stem, and produce about the same number of fronds in each new crown, even the tallest individuals on this reckoning would be less than 500 years old.

Bentham (1873) included *L. hopei* in his concept of this species. Bailey (1902) distinguished the two, but used unreal differences in his key. He records *L. peroffskyana* only from south of Brisbane, but localities as far north as the Tropic of Capricorn are cited by Moore and Mueller, Miquel and other authors, though I have not seen this material. Schuster (1932) used the name *M. denisonii*, though citing the earlier *L. peroffskyana* in synonymy, and included *L. hopei* as a variety. The distinction between the two species of *Lepidozamia* seems quite clear (see above, p. 86).

II. MACROZAMIA Miq.

Miq., *Monogr. Cycad.* (1842), 35, also *Prodr. Syst. Cycad.* (1861), 8, 18, and in *Arch. Néerl.*, 3 (1868), 247, and *Verst. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 50 (excl. sect. *Lepidozamia*); A.D.C., *Prodr.*, 16, pt. 2 (1868), 535 (excl. *M. denisonii*); Benth., *Fl. Austral.*, 6 (1873), 250 (excl. *M. "perouskiana"*); Regel in *Acta Hort. Petrop.*, 4 (1876), 317; Schuster, *Pflanzenr.*, IV, i (1932), 86 (excl. sect. *Monoorientales = Lepidozamia*).*

Typification: Miquel originally accepted two supposed species in his new genus, which he named *M. spiralis* and *M. fraseri*. *M. fraseri* Miq. was very briefly described from imperfect material and cannot, as such, be the generic type. It is now known to be a synonym of the Western Australian species, *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn. The generic character was taken from material illustrated in drawings of Ferdinand Bauer, which was the whole basis of Miquel's description under *M. spiralis*. This material is now known also to belong to *M. riedlei*. However, the name *M. spiralis* (Salisb.) Miq. is nomenclaturally based on *Zamia spiralis* Salisb., cited by Miquel. The typification of this is discussed below (p. 103) under *M. spiralis*; it is a very different plant from *M. riedlei*. Miquel (1842, p. 37) was aware that Salisbury's plant may not have been the same as those he described, but saw no specimens. Under *M. spiralis* he also cited, but did not see, plants from Port Jackson previously described by R. Brown under "*Zamia spiralis* Salisb.", but which in fact belong to *M. communis* L. Johnson. Later, in *Verst. Meded. Koninkl. Akad.*, 15 (1863), 368, Miquel pointed out that Bauer's figures and hence his own description of *M. spiralis* pertained in fact to the same species as his *M. fraseri*. He then used "*M. spiralis*" for *M. communis* (with some confusion with plants later described under *M. miquelii* (F. Muell.) A.D.C.). Later authors used "*M. spiralis*" chiefly for either *M. communis* or *M. lucida* L. Johnson, but the name is herein (p. 103) restored to Salisbury's original species.

Hutchinson, in *Kew Bull.* (1924), 51, named "*M. spiralis*" (without author) as type species of *Macrozamia* Miq., but was unaware of the complicated circumstances and had made no detailed study of the genus. His selection is not binding. The International Code of Botanical Nomenclature (Lanjouw, 1956) lays down that the type of a generic name is a *species* (not a specimen nor, one may add, a specific name). Now a species consists of living organisms, past, present or future. Its nature must be elucidated by biological enquiry, and the circumscription of our concept of it is determined by taxonomic, not nomenclatural, considerations. Although the specific name *Macrozamia spiralis* (Salisb.) Miq. must be applied to a group of organisms including the plant

* Only important treatments purporting to cover the whole genus are cited.

described by Salisbury, this plant was certainly only in the vaguest way part of the concept in Miquel's mind when he described his new genus. On the contrary, he drew his description almost wholly from the plants represented in Bauer's plates.

Consequently I consider that the TYPE SPECIES of *Macrozamia* Miq. is the species to which Bauer's plants belong, whatever its name is held to be; in my treatment this is *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn.

By this typification we may preserve Miquel's sectional treatment, as far as it is applicable. True *M. spiralis* (Salisb.) Miq. belongs to section *Parazamia* (Miq.) A.D.C. (based on *Encephalartos* sect. *Parazamia* Miq., typified by *M. pauli-guilielmi* W. Hill and F. Muell.), while *M. riedlei* belongs to the section regarded by Miquel as typical: section *Macrozamia* of my treatment (*Encephalartos* sect. *Macrozamia* Miq., *Macrozamia* sect. *Genuinae* Miq.). If *M. spiralis* as fixed by Salisbury's type were taken as type species, Miquel's "typical" section would require a new name and his *Parazamia* would become *Macrozamia*.

It is regrettable that nomenclatural procedure demands so detailed an argument to settle permanently (one may hope) a matter of plain common sense.

Synonymy: There are no actual generic synonyms of *Macrozamia* when *Lepidozamia* Regel is excluded. Infrageneric names are listed below, under the two sections. The genus was included in *Encephalartos* by F. Mueller intermittently over many years (see refs. under the species), also briefly by Miquel, in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368. Before 1842, individual species were referred to *Zamia* or *Encephalartos*, and Mueller, *Fragm. Phytogr. Austral.*, 5 (1866), 172, stated: (translation) "I have reduced all the species of *Encephalartos* in the collections of the Melbourne museum subgenerically to *Zamia*." Despite this remark, he had continued to use *Encephalartos* (incl. *Macrozamia*) on the same page, and certainly did not formally establish *Encephalartos* in subgeneric rank under *Zamia*, as Schuster's (1932, p. 86) citation seems to indicate. In 1881 in his paper on *M. moorei* (q.v.) Mueller again expressed his view that *Macrozamia* was a "sub-generic group" of *Encephalartos*, if indeed both were not to be placed under *Zamia*, adding that "all genera are mere artificial groups to facilitate classification, and aid memory, while species in their true sense are originally created beings, which when perished . . . would require the godly might as much for their restoration as they did for their origination". This philosophy should be borne in mind when interpreting any pronouncement of Mueller's on classification or nomenclature.

More or less palm-like plants with a usually unbranched stem forming a subterranean caudex or a rather massive aerial trunk, clothed by the persistent leaf-bases, all parts more or less pubescent when very young, but glabrous (except petiole-bases) at maturity. Fronds few to numerous, simply pinnate (but the pinnae sometimes dichotomously divided), rhachis straight or twisted. Cataphylls present, angular-subulate, at first silky or woolly, finally often glabrescent. Base of petiole expanded, in most species silky or woolly-tomentose. Pinnae numerous in mature plants, spreading or secund, inserted near the edges of the rhachis towards the adaxial side, simple or once to thrice forked, straight or falcate; contracted and sometimes callously thickened at the base, stomata on lower or both surfaces. Cones of both sexes stalked, axillary among the fronds (with several cataphylls below and sometimes on the stalk), the spirally-arranged sporophylls glabrate (often glaucous) and spiniferous at the ends (spines sometimes almost obsolete on lower sporophylls). Male sporophylls with a broadly cuneate fertile region bearing the sporangia beneath in two separate to more or less confluent areas, and an upturned end terminated by an erect or spreading-erect spine, the latter sometimes very short on the lower sporophylls. Female sporophylls appearing peltate, with an angular-rounded stipes and a laterally expanded more or less terminally compressed end, the latter with a narrow transverse wing (continuation of the margins) terminated by a more or less erect short to long spine; the two ovules borne on the inward-facing margins ("inner surface") of the sporophyll-end; the sporophylls falling with the seeds attached by the outer fleshy red or yellow seed-coat, the inner seed-coat hard.

Chromosome number: $x = 9$. The number $2n = 18$ has been found in *M. miquelii*, *M. moorei* and material named "*M. tridentata*" (refs. in Darlington and Wylie, 1955), and also in *M. communis* (Brough and Taylor, 1940, as "*M. spiralis*"). Light (1924) records $n = 12$ for *M. riedlei* (as *M. fraseri*), but this early count is doubtful; if correct it suggests triploidy.

Endemic in Australia, with 14 species in the warm-temperate and subtropical regions, barely reaching the Tropic: 12 of them in eastern Australia (New South Wales 11, Queensland 5), 1 in Central Australia, 1 in south-western Australia. This excludes the quite distinct *Lepidozamia* (see above, p. 83), which most authors have included in the genus. The species grow mostly on nutritionally poor, frequently siliceous, soils in sclerophyll communities, in association with members of the old "Australian" floristic element. Most parts of the plants contain a toxic substance, *macrozamin* (Hurst, 1942; Webb, 1948; Gardner and Bennetts, 1956), and various species are held responsible for a form of stock poisoning known as "wobbles" (or miscalled "rickets"), especially common in cattle which can eat the tough fronds. The aborigines ate the starchy endosperm of the seeds after roasting and prolonged washing to remove the poison (Bailey, 1902; and various notes in herb. NSW). Several species have been cultivated as ornamentals.

As indicated above (p. 72), the taxonomy and especially the nomenclature of the genus have been quite extraordinarily confused and unstable.

Key to the Sections and Species.

Note: Juvenile plants of *Macrozamia* may differ considerably from the adult forms in details of the fronds; in particular the pinnae are usually toothed at the ends and the petioles are long and slender. The stomata of juvenile plants are confined to the lower pinna-surface. Only adult organs are described in the key and descriptions given here. Similarly, cone dimensions apply to mature cones (males at sporangial dehiscence, females at ripening of the seeds). *Petiole lengths do not include the woolly expanded base* and may be taken as the distance from the end of the tomentose portion to the lowest pinnae. The stomata are readily seen at a magnification of $\times 15-20$ diameters, or with practice at $\times 10$ diameters, especially in fresh material. To determine their presence or absence the upper pinna-surface should be compared with the lower, which, of course, always bears stomata.

1. Large plants with 15-150 fronds in the crown, aerial trunk present or absent, caudex 15-100 cm. diam. Fronds 50-300 cm. long; rhachis not strongly twisted, usually angled beneath (at least in petiolar portion) when dry, flat to angled and laterally 2-channelled (when dry) above, 6-30 mm. broad at lowest pinnae. Pinnae straight for most of their length, spreading, *nerves visible but narrow and not or scarcely raised on the lower surface when dry*; bases markedly callous on the anterior margin (\pm rugose when dry); the lowest pinnae usually progressively reduced and sometimes spine-like (not always so in *M. miquelii*). Mucilage canals present in the pinnae. ♀ cones 15-90 cm. long, 8-27 cm. diam., longest sporophyll spines 1-10 cm. long; seeds 2.5-8 cm. long. ♂ cones 15-50 (-60?) cm. long, longest sporophyll spines 1.5-5 cm. long i. Section *Macrozamia*.
2. Reduced spine-like pinnae extending almost to the base of the frond (spine-free petiole, excluding swollen base, 0-10 cm. long). Plants with massive trunks to 2-5 m. tall, 60-80 cm. diam. Fronds 150-300 cm. long with 150-250 pinnae. Rhachis 12-30 mm. broad at lowest pinnae. Stomata on both surfaces of pinnae. ♀ cones 40-90 cm. long, ♂ cones 30-45 cm. long. C. Queensland and N.S.W. Far N. Coast 1. *M. moorei*.
- 2.* Reduced pinnae not extending to near base of frond (petiole 12-60 cm.). Aerial trunk present or absent. Fronds 50-220 (-250?) cm. long, with 60-170 pinnae. Stomata on both surfaces of pinnae or on lower surface only. Cones various.
3. Stomata on both upper and lower surfaces of pinnae. Pinnae simple. West and Central Australian species.
4. Fronds not or scarcely glaucous. Seeds 3-5 (-6?) cm. long, 2-3.5 cm. thick. Spines of uppermost ♀ sporophylls 1.5-6 (or more?) cm. long, lower sporophylls usually with short broad spines. S.W. Australia 2. *M. riedlei*.
- 4.* Fronds markedly glaucous. Seeds 6-8 cm. long, 4-5.5 cm. thick. Spines of uppermost ♀ sporophylls ca. 1-2 cm. long, lower sporophylls almost spineless. Central Australia 3. *M. macdonnellii*.
- 3.* Either stomata on lower surface of pinnae only and pinnae simple or stomata on both surfaces and most pinnae forked. Eastern species.
5. Pinnae simple, stomata on lower surface only.
6. Pinnae thin and rather lax, easily bent, shining above, often rather crowded along the rhachis. Most sporophylls of ♀ and ♂ cones short-spined; longest spines (♀)

- 2-3½ cm., (♂) 1-2 (2½) cm. Most of the ♀ sporophyll-ends less than twice as broad as high; spines of ♂ sporophylls slender, 2-5 mm. broad at the base. Seeds 2.5-3.5 cm. long. Eastern parts of C. and S. Queensland and Far N. Coast (Richmond R.) of N.S.W. 4. *M. miquelii*.
- 6.* Pinnae thicker and more rigid, rather dull, often rather widely separated along the rhachis. Many sporophylls of ♀ and ♂ cones long-spined; longest spines (♀) 4-10 cm., (♂) 2-5 cm. Most of the ♀ sporophyll-ends at least twice as broad as high (excl. spine); spines of ♂ sporophylls 5-12 mm. broad at the base. Seeds 3-4.5 cm. long. Macleay River to Bega, also Goulburn River Valley, eastern N.S.W. . . . 5. *M. communis*.
- 5.* Most pinnae dichotomously once-divided. Stomata on both surfaces. Coonabarabran and country north of Liverpool Range, N.S.W. 6. *M. diplomera*.
- 1.* Rather small plants with 2-12 (rarely up to ca. 40 in *M. lucida*?) fronds in the crown, caudex almost or wholly subterranean, 5-30 cm. diam. (more in *M. platyrachis*?). Fronds 30-120 cm. long; rhachis straight or twisted, rounded or angular beneath, rounded to flat or concave above (sometimes with two lateral grooves), 3-18 mm. broad at lowest pinnae. Pinnae straight or falcate, spreading or erect, *nerves thick and prominent on the lower surface (especially when dry)*; bases not or only slightly callous on the anterior margin (not rugose when dry); the lowest pinnae usually not much reduced (sometimes somewhat so in spp. with secund pinnae or twisted rhachis). Mucilage canals absent from the pinnae. ♀ cones (10-)15-25 cm. long, 6-10 cm. diam., longest sporophyll-spines 0.5-4 (-5?) cm. long; seeds 2-3.5 cm. long. ♂ cones 10-25 cm. long, longest sporophyll-spines 0.2-1.5 cm. long ii. Section *Parazamia*.
7. Rhachis not or moderately spirally twisted (0-180°, rarely to 360° but if so petiole 20-40 cm. long or pinnae divided) though sometimes recurved near the end. Pinnae simple or divided.
8. Pinnae simple. Stomata on lower surface only.
9. Broadest pinnae 15-20 mm. broad, 15-18-nerved. Rhachis flat, 13-18 mm. broad at lowest pinnae. C. Queensland 7. *M. platyrachis*.
- 9.* Broadest pinnae 3-12 mm. broad, 5-11-nerved. Rhachis rounded or ± flat or concave above, 3-9 mm. broad at lowest pinnae.
10. Pinnae spreading in the living state. Rhachis scarcely to moderately (0-180°, rarely 360°) twisted; petiole rounded or flat above, 15-50 cm. long. Broadest pinnae 6-12 mm. broad, 12-35 cm. long, not or scarcely glaucous.
11. Pinnae glossy, ± falcate, *whitish at the base* when living, the longest ones 15-35 cm. long, 7-12 mm. broad. Petiole rounded, (20)25-50 cm. long. S. Queensland, N.S.W. (Far N. Coast) 8. *M. lucida*.
- 11.* Pinnae rather dull, straight to ± falcate, *pinkish to red or orange at the base* when living, the longest ones 12-25 cm. long, 5-10 mm. broad. Petiole rounded or subangular, (15)20-40 cm. long. N.S.W. (C. Coast to Goulburn R. Valley and Dunedoo) 9. *M. spiralis*.
- 10.* Pinnae secund, rising ± vertically from rhachis in living state. Rhachis not or slightly twisted, but recurved near the end; petiole concave above, 5-22 cm. long. broadest pinnae 3-8 mm. broad (8-20 cm. long), often ± glaucous. N.S.W. (C.W. Slopes) 10. *M. secunda*.
- 8.* Pinnae once to thrice dichotomously divided. Stomata on lower or both surfaces. N.W. Slopes of N.S.W.
12. Stomata present on both surfaces of pinnae. Pinnae once or twice divided, rather stiff, dull above, often ± glaucous beneath. Rhachis little if at all twisted (0°-90°-180°). N.S.W. (Warrumbungles, Pilliga Scrub and Warialda-Howell, on sandy soil) 11. *M. heteromera*.
- 12.* Stomata confined to lower surface of pinnae. Longest pinnae usually 2-3 times divided (if only once divided segments nevertheless very narrow), rather lax, dark green above, not glaucous. Rhachis usually twisted near the end (90°-180°-360°). N.S.W. (Nandewars and surrounding district, on stony hillsides) 12. *M. stenomera*.
- 7.* Rhachis strongly twisted (360° or much more, rarely less in depauperate short fronds of *M. pauli-guilielmi* ssp. *plurinervia* but if so then the petiole 5-15 cm. long). Pinnae simple (but sometimes toothed).
13. Broadest pinnae 3-7 mm. broad, 3-10-nerved, adult ones entire or closely 2-toothed at the apex. S. Queensland and N.S.W. (N. Tablelands, N.W. Slopes and Manning R.-Lake Macquarie) 13. *M. pauli-guilielmi*.
- 13.* Broadest pinnae 9-17 mm. broad, 10-13-nerved, adult ones 2-7-toothed at the apex. N.S.W. (N. Coast: Richmond R.-Macleay R.) 14. *M. fawcettii*.

i. Section MACROZAMIA.

Typification: As for the genus, the species now known as *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn.

Synonymy (infrageneric):

Encephalartos Lehm. sect. *Macrozamia* Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368 (this included only species of the section as here understood, exclusive of sect. *Parazamia* and of *Lepidozamia*. Type as for the genus *Macrozamia*).

Macrozamia Miq. sect. *Genuinae* Miq. in *Arch. Néerl.*, 3 (1868), 247, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 50 (absolutely equivalent to the above).

Macrozamia sect. *Polyorientales* Schuster, *Pflanzenr.*, IV, i (1932), 87 (in part, excluding several species. Nomenclaturally illegitimate since it includes the type of the earlier section *Parazamia* Miq., though not based on this. I select *M. moorei* F. Muell. as LECTOTYPE, since the other names included by Schuster are confused. Even should *M. moorei* be sectionally separated, Schuster's name remains rejected).

Macrozamia sect. *Polyorientales* Schuster subsect. *Attenuatae* Schuster, *l.c.* (for the greater part. I select *M. moorei* F. Muell. as LECTOTYPE).

Macrozamia sect. *Monoocidentales* Schuster, *l.c.* (this comprises only *M. riedlei* and *M. macdonnellii*, considered conspecific by Schuster, and distinguished sectionally by no tangible character from his sect. *Polyorientales*. It is nomenclaturally illegitimate since it is based on the type of the genus—see above, p. 87. Schuster nowhere refers to Miquel's earlier sectional names).

Pinnae predominantly straight and spreading, nerves visible but narrow and not or scarcely prominent on the lower surface when dry, apices always entire in adult fronds, bases markedly callous and (when dry) rugose on the anterior margin, mucilage canals present in the pinnae, the lowest pinnae usually progressively reduced.

Usually large plants with many large fronds, aerial trunk sometimes present and robust. Rhachis never strongly twisted (except in rare aberrant individuals), usually flattened above and angled beneath when dry. Cones usually large (females 15–90 cm. long, 8–30 cm. diam.; males 15–45 cm. long), sporophyll-spines short to long, always erect.

This is the more widespread section, having one species each in the south-west and the centre of the continent, as well as four in the east. The species show less evidence of reduction than those of sect. *Parazamia*, which suggests that sect. *Macrozamia* is the more primitive, or more conservative, of the two. Individuals of the various species, unlike those of section *Parazamia*, usually occur plentifully in fairly dense communities and may form quite an important and conspicuous part of the vegetation. Regeneration is vigorous in most places. In distribution the species show a replacement pattern without overlap, except in the case of *M. moorei* and *M. miquelii*, where the former is found both north-west and south of the latter's area, but not within it. Naturally-occurring hybrids are consequently unknown within the section. On the other hand the distribution of species of sect. *Macrozamia* frequently overlaps that of species of sect. *Parazamia*, and mixed stands occur in places. A few hybrids may be found, but the specific limits do not break down.

The six species of this section fall naturally into the following three groups: (a) the remarkable *M. moorei* alone, (b) the two vicarious western and central species *M. riedlei* and *M. macdonnellii*, (c) the three vicarious eastern species *M. miquelii*, *M. communis* and *M. diplomera*. Groups (b) and (c) may themselves be considered as a pair of vicarious "superspecies" (Text-figure 2).

1. M. MOOREI F. Muell. in *Chemist and Druggist, Australas. Suppl.*, 4 (March, 1881), 84.

Typification: "With certainty known from the mountainous regions of Queensland at the verge of the tropics", with a reference to its cultivation by Charles Moore in the Sydney Botanic Gardens, is the only information in the original publication, but in August, 1881 (see below) Mueller cited "In collibus praesertim altioribus lapidosis ad originem fluminis Noogo-River imprimis circum urbem [sic!] Springsure satis frequens; J. G. Macdonald; P. A. O'Shanesy". (I have not seen these SYNTYPES and therefore cannot name a lectotype, but the identity of the species is unmistakable from the description and locality.)

Synonymy:

Encephalartos moorei (F. Muell.) F. Muell., *Fragm. Phytogr. Austral.*, 11 (August, 1881), 125. In the preamble to his original publication of March, 1881, Mueller vacillated, as he had done for many years in various publications, regarding the generic recognition of *Macrozamia* as distinct from *Encephalartos*. The title of his paper referred to a "species of *Encephalartos*", and in his discussion he appeared to imply that *Macrozamia* was to be regarded as a subgenus of *Encephalartos*, if indeed both of these were not to be included in *Zamia*! However, although the preamble was equivocal, in the formal treatment the species was described under the binomial *Macrozamia moorei*, and in his later publication in August of the same year, when placing the species definitely under *Encephalartos*, Mueller cited *Macrozamia moorei* as a synonym,



Text-fig. 2.—Distribution of *Macrozamia* section *Macrozamia*: 1: *M. moorei*; 2: *M. riedlei*; 3: *M. macdonnellii*; 4: *M. miquelii*; 5: *M. communis*; 6: *M. diplomera*.

with full reference to its earlier publication. Clearly, Mueller did not really know whether or not he himself *accepted* his binomial *Macrozamia moorei* at the time of publication, and its validity under the I.C.B.N. depends on this. Since the case may be argued either way, I consider that *M. moorei* F. Muell. should be accepted as validly and legitimately published in March, 1881, thus preserving the established nomenclature and citation. The alternative is to reject *M. moorei* F. Muell., March, 1881, as invalid; the first valid publication would then be as *Encephalartos moorei* F. Muell., August, 1881, and the first valid publication under *Macrozamia* would be as *M. moorei* F. Muell. ex F. M. Bail., *Syn. Queensl. Flora* (1883), 501, which is not based on a reference to *Encephalartos moorei* F. Muell., but is to be treated as a new publication. A much more detailed nomenclatural discussion of this matter is possible, but, being devoid of biological significance, would be unprofitable. For further citations and misapplications see Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Description, specimens and further discussion: See Johnson in Anderson, *l.c.*

Chromosome number: $2n = 18$.

Distribution: Queensland and New South Wales: Two disjunct areas, in Central Queensland (Springsure-Carnarvon Range districts) and the Clarence River (Dalmorton) district of the North Coast of N. S. Wales, in dry sclerophyll forest or

in the ecotone between semi-wet sclerophyll forest and rainforest, on rather shallow, rocky or stony soils.

Apparently an old species now fragmented into two widely disjunct groups of populations, but within these still vigorous, *M. moorei* stands somewhat apart from the other species of the section, particularly in the long series of reduced pinnae extending almost to the frond-base, and in the large numbers of cones (especially males). Chamberlain (1913) was so impressed by the numerous lateral cones that he devoted a whole paper to this species and suggested a close relationship with the Mesozoic Bennettitales. However, the nature of the "strobilus" and its parts differs so greatly in Cycadales and Bennettitales that the relationship is now held to be rather a distant one. Certainly *Macrozamia* cannot be derived from anything like the Bennettitales.

The plants are massive and spectacular and of fairly rapid growth; individuals with trunks 2 m. tall and 60-70 cm. thick in the Sydney Botanic Gardens are less than 100 years old. Some apparent natural hybrids between *M. moorei* and *M. lucida* (of section *Parazamia*) are discussed in the forthcoming *Flora of N.S.W.*, part 1.

2. *M. RIEDELEI** (Fisch. ex Gaudich.) C. A. Gardn., *Enum. Pl. Austral. Occid.* (1930), 3; C. A. Gardn. in Gardn. and Bennetts, *Toxic Pl. W. Austral.* (1956), 6 (s. ampl.).

Basionym: *Cycas riedlei** Fisch. ex Gaudich. in Freycinet, *Voy. autour du Monde, Bot.* (1826), 434.

Typification: "In Novae Hollandiae orâ occidentali (Port du Roi George)." This is in herb. Paris. I have not seen it, but it was seen by Miquel, and from the locality there is no doubt of its identity.

Synonymy:

Macrozamia fraseri Miq., *Monogr. Cycad.* (1842), 37 [Schuster (1932) states that this is "sine descr.", but Miquel's description, brief as it is, is sufficient to validate the name]; Miq., *Prodr. Syst. Cycad.* (1861), 8, also in *Arch. Néerl.*, 3 (1868), 247, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 50; Benth., *Fl. Austral.*, 6 (1873), 252. Not *M. spiralis* (Salisb.) Miq. [var.] δ *fraseri* Regel in *Acta Hort. Petrop.*, 4 (1876), 318.

M. preissii Lehm., *Pugill.*, 8 (1844), 31, descr. (not seen) and in *Cat. Hort. Hamb.* (1842), nomen? (not seen); Heinzel in *Nov. Act. Acad.*, 21, i (1844), 203, t. 10-13 (not seen); Lehm., *Pl. Preiss.*, 1 (1845), 645; F. Muell., *Fragm. Phytogr. Austral.*, 1 (1858), 41, and various later references; A.D.C., *Prodr.*, 16, pt. 2 (1868), 525; Regel in *Acta Hort. Petrop.*, 4 (1876), 318; Schuster, *Pflanzenr.*, IV, i (1932), 101 (in part, excl. syn. *M. macdonnellii* and Central Australian citations).

Encephalartos preissii (Lehm.) F. Muell. in *Quart. Journ. Pharm. Soc. Vict.*, 2 (1859), 90 [this is validly published, but in the further reference given by Schuster (1932) to Miquel (1863) the name is mentioned only in synonymy of *E. fraseri*].

E. fraseri (Miq.) Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368.

E. oldfieldii Miq., *l.c.*, 370.

Macrozamia oldfieldii (Miq.) A.D.C., *Prodr.*, 16, pt. 2 (1868), 535; Miq. in *Arch. Néerl.*, 3 (1868), 250 [cited by Schuster from the separate as "Nouv. Matér. (1868) 58"]; Miq. in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 53. [Schuster (1932) gives this the first citation, as "Nieuw. Bijdr. Cycad. (1868) 53", but the paper thus entitled was published in the above-cited journal, the title-page of which is dated 1869; I can find no indication in it of an earlier date of publication of the paper, though this is possible. It matters little.]

* In publishing the combination, and consistently since, Gardner, who apparently did not consult the original, writes "*riedlei*" (all epithets here quoted with lower case initials though originally capitalized). Miquel (1868, 1869) and Schuster (1932) both cited "*riedleyi*"; and Regel (1876) gave "*riedeli*". The species was named for the French gardener Riedlé, and was correctly spelt "*riedlei*" by Gaudichaud. Though he used Fischer's herbarium name, Gaudichaud suspected that the plant's affinity was with *Zamia* rather than *Cycas*. The description is brief but sufficient.

*Encephalartos dyeri** F. Muell. in *Chemist and Druggist, Australas. Suppt.*, 3 (1885), 12.

*Macrozamia dyeri** (F. Muell.) C. A. Gardn., *Enum. Pl. Austral. Occid.* (1930), 3.

M. preissii Lehm. ssp. *dyeri*† (F. Muell.) Schuster, *Pflanzenr.*, IV, i (1932), 102.

Caudex sometimes mostly subterranean, but frequently forming a trunk 1-5 m. tall or said to be sometimes procumbent, 60-120 cm. diam. Fronds numerous (usually 50-100 or more?), at first erect, later spreading or drooping, up to 150-200 cm. long on mature plants; spine-free petiole (excluding the silky-woolly swollen base) 12-30 (or more?) cm. long, rhachis not markedly twisted, more or less flattened, 10-20 mm. broad at the lowest pinnae, flat to somewhat concave or convex above, often somewhat keeled distally, with two narrow lateral grooves (more marked when dry) decurrent from the bases of the pinnae, convex and usually subangular to angular beneath. Pinnae 100-150 (or more?), spreading, but the two ranks often inclined to each other, forwardly directed at an acute angle (the lowest least so), mostly rather crowded, but the lowest ones more distant, decidedly rigid, entire, straight, linear, the longest 20-35 cm. long, several of the lowest progressively reduced and spine-like, 6-11 (-15 in *dyeri* forms) mm. broad with 8-15 (-18 in *dyeri*) scarcely raised nerves beneath, gradually tapered to the pungent apex, contracted to the pale or somewhat reddish and anteriorly callous and (when dry) rugose base, green but not shining, with numerous stomata on both upper and lower surfaces. Cones stalked, in either sex 1-several(?) per plant, axillary among the fronds,* the base of the stalk surrounded by several spine-like, angular-subulate to strap-shaped cataphylls (pubescent or tomentose when young), sometimes with a few shorter decurrent cataphylls on the stalk itself. Male cones cylindrical, often somewhat curved when old, 20-40 (-60 in *dyeri*) cm. long, ca. 10 cm. diam. (sometimes more?); sporophylls cuneate to obovate-lanceolate, 3-5 (-6 acc. to Schuster) cm. long, ca. 1.5-2.5 cm. broad, the triangular to elongate upturned spines from almost obsolete to 1.5-5.5 cm. long (the longest near the apex of the cone). Female cones ovoid-cylindrical, 25-45 (or more?) cm. long, 15(?) -25 cm. diam., stalk ca. 12-20 (or more?) cm. long, to 3-4 (-5?) cm. thick; sporophylls ca. 5-8 (-10 acc. to Schuster) cm. long (stipes ca. 3-6 cm.), the expanded ends glaucous, 4.5-9 cm. wide, ca. 3-5 cm. high, the flattened erect spines increasing in length towards the apex of the cone, the lowest from almost obsolete to ca. 0.8 cm. and often lacerate, the uppermost from 1.5-6 (-10 acc. to Schuster, but doubtful) cm. long, broad-based; inner parts of the cone salmon-pink when fresh. Seeds 3-5 (-6?) cm. long, 2.5-3.5 cm. thick, outer coat bright red when ripe.

Chromosome number: $n = 12$, according to Light (1924), but this may well be a miscount, since it does not agree with related species ($n = 9$).

Distribution: Western Australia: South-western and southern coast region, from the Murchison River to east of Esperance, in dry and wet sclerophyll forest (or scrub) on sandy and lateritic soils.

Specimens examined: WESTERN AUSTRALIA: Bullsbrook area, 27 miles N.N.E. of Perth, Kennington, 31.v.1957 (NSW.42034); Armadale, J. M. Griffiths, viii.1900 (NSW.40660); Big Brook, M. Koch 1419, vi.19— (NSW.40662); Bow River, S. W. Jackson, xii.1912 (NSW.40661); Western Australia, J. B. Cleland, 1907 (NSW.40663); Western Australia, E. Brown, 1898 (NSW.40656).

M. riedlei exhibits considerable variation in size and habit, but if Gardner (in Gardner and Bennetts, 1956) is correct, all the Western Australian populations are to be regarded as conspecific. The only authentic material of *M. dyeri* which I have seen is a pair of collodion cuticular pulls from dorsal and ventral surfaces of a pinna of an apparent isotype ("Esperance Bay, W.A.") in herb. Kew, made available by the

* Included in the synonymy on the testimony of Gardner (1956). See discussion below.

† Gardner (1956) states that "the female has a solitary terminal central cone". Doubtless this is based on superficial observation; whatever the species, the cone (in individuals bearing but one) may appear terminal but on careful inspection is seen to be lateral. Again, it would be surprising if *M. riedlei* never bore more than a single cone, unlike its congeners.

kindness of Dr. R. Melville. These show stomata on both surfaces. The descriptions of *M. dyeri*, however, indicate that the pinnae are considerably broader than any which I have seen in available specimens of *M. riedlei*. Miss A. Baird (pers. comm.) indicates that *M. riedlei* varies greatly in stature in various parts of Western Australia and, as in *M. communis* in New South Wales, the development of the trunk above ground level tends to be greatest on shallow soils, in which the caudex cannot be pulled far below ground by the contractile roots. Gardner (*l.c.*) states that the largest forms occur towards the northern and eastern limits of its distribution.

While lacking personal field experience and sufficient herbarium materials of the Western Australian populations, I must follow Gardner in recognizing only a single species, though with reservations.

Both R. Brown (1810) and Miquel (1842) included material of this species under the names *Zamia spiralis*/*Macrozamia spiralis*. Bauer's figures reproduced by Miquel (*l.c.*, Pl. 4-5) actually represent *M. riedlei*, as Miquel himself (1863) later pointed out. This is discussed above under the typification of the genus, and below under *M. spiralis*. Schuster (1932) included *M. macdonnellii* under his "typical" *M. preissii* (= *M. riedlei*), though he gave *M. dyeri* subspecific rank. Bentham (1873) likewise included *M. macdonnellii* under *M. fraseri* (= *M. riedlei*). However, *M. macdonnellii* seems reasonably distinct and is certainly isolated.

Fronds of *M. riedlei* often appear very similar to those of *M. communis*, but the pinnae are generally even more rigid and may be distinguished by the presence of stomata on the upper surface.

3. *M. MACDONNELLI** (F. Muell. ex Miq.) A.D.C., *Prodr.*, 16, pt. 2 (1868), 537; Miq. in *Arch. Néerl.*, 3 (1868), 249, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 53; F. Muell., *Fragm. Phytogr. Austral.*, 9 (1875), 124 (and *ibid.*, 2 (1861), 179, nomen); Ewart and Davies, *Fl. Northern Territory* (1917), 19.

Basionym: *Encephalartos macdonnellii** F. Muell. ex Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 376.

Typification: "Nova Hollandia centralis, ad flumen Neales in Macdonnell-range, unde reportavit cel. peregrinator J. M. Stuart" (not seen, but of certain identity from the general locality and description. The present Neales River is a rarely-flowing stream in South Australia, debouching into Lake Eyre. There are certainly no *Macrozamia* species in this most arid region. Either there was some confusion as to the precise locality, or it was merely meant that the plant was collected at some time on the Neales River—Macdonnell Range stage in Stuart's epic expedition. The plant could not be missed in the Macdonnells).

Trunk usually developed above ground (the plants grow on shallow soils), 1-2 (-3) m. tall, but often more or less procumbent, 60-80 (or more?) cm. diam. Fronds numerous (50-100 or more), at first erect, later spreading or drooping, 150-220 cm. long on mature plants; spine-free petiole (excluding the silky-woolly expanded base) 12-25 (or more) cm. long; rhachis not markedly twisted, more or less flattened, 15-25 mm. broad at the lowest pinnae, flat to somewhat concave but usually more or less keeled above, with two narrow lateral grooves (more marked when dry) decurrent from the bases of the pinnae, convex and subangular to angular (when dry) beneath. Pinnae 120-170, spreading but the two ranks usually inclined to each other, forwardly directed at an acute angle, mostly rather crowded but the lowest usually 4-5 cm. apart, decidedly rigid, entire, straight, linear, the longest 20-30 cm. long, ca. 8-20 of the lowest progressively reduced and spine-like, 7-11 mm. broad with 8-15 scarcely-raised nerves

*By Miquel (1863, 1868, 1869), but not by Mueller or De Candolle, spelt "*macdonnellii*" but the single "n" is to be regarded as an unintentional error. Miquel correctly spelt "*Macdonnell-range*". F. Mueller (1875) is usually cited as the author of the valid combination under *Macrozamia*, but De Candolle definitely made it in 1868, though as a *species incerta*. De Candolle's treatment was published in mid-July, 1868, according to Stearn (1941); Miquel's paper in *Archives Néerlandaises* (1868) was probably published late in that year, although no month is indicated on the cover or title page of the part.

beneath, gradually tapered to the pungent apex, contracted to the pale anteriorly callous and (when dry) often somewhat rugose base, dull and (rhachis also) decidedly glaucous on both surfaces (especially when living), with numerous stomata on both upper and lower surfaces. Cones stalked, in either sex 1-several per plant, axillary among the fronds, the base of the stalk surrounded by several spine-like cataphylls, usually with a few shorter decurrent cataphylls on the stalk itself. Male cones cylindrical, often somewhat curved when old, 25-40 cm. long, ca. 8-10 cm. diam.; sporophylls cuneate-obovate, 3-4 cm. long, ca. 1.5-2 cm. broad, the expanded ends very glaucous and the triangular-acuminate to elongate upturned spines from obsolete on the lower sporophylls to 1.5-2.5 cm. long near the apex of the cone. Female cones ovoid-cylindrical, 40-50 cm. long, 20-27 cm. diam., stalk 12-20 (or more?) cm. long, to 4-5 cm. thick; sporophylls 7-10 cm. long (stipes ca. 5-7 cm.), the expanded ends glaucous, 8-12.5 cm. wide, ca. 4-6 cm. high, the spines almost or quite obsolete on the lower sporophylls, flattened and triangular to 1-2 cm. long near the apex of the cone. Seeds 6-8 cm. long, 4-5.3 cm. thick, outer coat bright orange-red when ripe.

Distribution: Northern Territory: Central Australia in the Macdonnell and associated parallel range systems, sometimes in sclerophyllous communities with *Eucalyptus* or rarely *Livistona*, but sometimes as scattered plants on almost bare rocky slopes with *Triodia* species.

Specimens examined: NORTHERN TERRITORY: Alice Springs, R. H. Pulleine, vii.1917 (NSW.40659); Standley Chasm, J. Garden and V. Lhuedé, vii.1954 (NSW.40657), photo; Standley Chasm, N. Forde 864, 23.v.1957, and 10.iii.1957 (NSW.41470); Standley Chasm, L. A. S. Johnson, x.1957 (NSW., male cone); Central Australia, R. Tate, 1894 (NSW. 40658). Also living material examined, Standley Chasm, L. A. S. Johnson, x.1957.

M. macdonnellii is clearly a relict species, closely related to *M. riedlei* but isolated from it by arid country and with sufficient consistently different characteristics to be given specific rank.

Bentham (1873), with only a fragment before him, could not distinguish it from *M. fraseri* (= *M. riedlei*), while Schuster (1932) placed it in the synonymy of his "typical" *M. preissii* (= *M. riedlei* excluding *M. dyeri*) without comment. The species is characterized by the glaucous fronds, the massive female cones (to almost 20 kgm. in weight) with most of the sporophyll-spines obsolete, and the huge seeds.

Popularly, *M. macdonnellii* has been much confused with the very restricted relict palm species *Livistona mariae*, with which it is associated at Palm Valley, but the *Macrozamia* is a much more widely distributed plant in Central Australia, found at times in very forbidding habitats, though always in the Macdonnell Range complex. The extraordinarily large seeds of this species may have evolved as a selective adaptation to the uncertain rainfall of the interior. Their great food reserves must serve to give seedlings a good start in life. Glaucous bloom is likewise most strongly developed in this species, again suggesting adaptive significance.

4. M. MIQUELI (F. Muell.) A.DC., *Prodr.*, 16, pt. 2 (1868), 535 (in part, as to lectotype); Miq. in *Arch. Néerl.*, 3 (1868), 248, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 51 (in part).

Basionym: *Encephalartos miquelii* F. Muell., *Fragm. Phytogr. Austral.*, 3 (1862), 38 (in part, as to lectotype).

Typification: "Ad ostium fluminis Richmond River; C. Moore. Ad sinum Moreton Bay; W. Hill. Ad flumen Fitzroy River sub circulo capricornu; A. Thozet." Mueller's original concept was strangely mixed; Moore's specimen belonged to the species later described as *M. fawcettii* C. Moore (sect. *Parozamia*), whereas Hill's and Thozet's represented the present most dissimilar species. The description was derived in part from each of these species and the confused concept survived by copying in later publications by A. De Candolle, Miquel and Mueller himself (see refs. in *Fl. N.S.W.*, pt. 1, in press) both under the name of *Macrozamia/Encephalartos miquelii* and the misapplied name *M. tridentata* (Willd.) Regel. It was never explicitly resolved, but

in time the name *M. miquelii* came to be applied (e.g. by Bentham, *Fl. Austral.*, 6 (1873), 253, and F. M. Bailey, *Queensl. Fl.*, 5 (1902), 1504) to the present species alone, whilst the other species has been generally known as *M. fawcettii*. Schuster's (1932) treatment is wholly confused and irrelevant in this connection.

The type folder in herb. MEL contains three sheets, as follows: (1) Rockhampton, Thozet (with old male cone). (2) Moreton Bay, collector not indicated (this includes female cone fragments in a packet, probably a later addition; the cone at least is not part of the type series since Mueller had no female material). (3) Richmond River, C. Moore (with seeds in a packet labelled in Mueller's hand: "*M. miquelii*. This represents the genuine species according to locality"). Of these, 1 and 2 are the present species and 3 is *M. fawcettii* C. Moore. I have no doubt that 1 is the original Thozet syntype indicated by Mueller as "Ad flumen Fitzroy River . . ."; the frond of 2 may be the Hill syntype, but the cone is not; the frond of 3 may or may not be the Moore syntype (which from the description must have belonged to *M. fawcettii*), but the seeds at least are a later collection. Mueller's annotation on 3 does not mean that he deliberately selected this element as lectotype; his concept always remained quite confused. Since Mueller's description applies in equal parts to both elements and the only definitely authentic syntype extant is Thozet's, which moreover includes male cone material mentioned in the original description, and since this specimen represents the species currently known as *M. miquelii*, I choose it (Rockhampton, Thozet MEL) as LECTOTYPE.

Synonymy, description and further discussion; see Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press). The synonymy and nomenclatural history, quite apart from the original confusion discussed above, are bewilderingly complex.

Chromosome number: $2n = 18$.

Distribution: Queensland and New South Wales: Central and southern coast districts of Queensland from Rockhampton southwards, and far North Coast of N. S. Wales (Upper Richmond River), in sclerophyll forest on poor sandy or stony soils.

Specimens examined: QUEENSLAND: Rockhampton, Thozet (MEL, LECTOTYPE); Berserker Range, Rockhampton, J. L. Boorman (N.S.W., seeds only); Fraser Island, per Queensland Forest Service, xii.1922 (TECH); Mount Perry, J. L. Boorman, viii. 1912 (NSW.40624, 40625); Moreton Bay [W. Hill?] (MEL); Queensland (N.S.W., cone only, old collection labelled *M. douglasii*, prob. from F. M. Bailey). NEW SOUTH WALES: In low flat ground between the Upper Richmond and Clarence Rivers, C. Moore, 1861 (NSW.40610, HOLOTYPE of *M. cylindrica* C. Moore). Also studied from living and preserved cultivated material.

M. miquelii, as here defined, includes *M. douglasii* W. Hill ex F. M. Bail. from Fraser Island and *M. mountperriensis* F. M. Bail. from Mt. Perry, inland from Bundaberg. These have been regarded, especially in Queensland (see Johnson in Anderson, *l.c.*, for references), as distinct from *M. miquelii*, while *M. cylindrica* C. Moore has been regarded as distinct in New South Wales, though it is little known outside cultivation. However, I can find no real discontinuity nor any greater variation within this series of populations than exists in *M. communis* in New South Wales or *M. riedlei* in Western Australia. *M. douglasii* represents luxuriant plants from the deep sands and wet climate of Fraser Island, and *M. mountperriensis* the other extreme of small plants from the more continental climate of Mt. Perry, while *M. miquelii* and *M. cylindrica* (between which there seems to be no difference at all) represent the more average forms from scattered localities in the coast districts. The differences in stature and in number of reduced basal pinnae, however, must be to some extent genetically determined, since cultivated plants preserve them to some degree. The same applies to local ecotypes of *M. communis* and *M. heteromera* cultivated in Sydney. On the other hand there is a clear morphological as well as geographic discontinuity between the populations of *M. miquelii* and *M. communis*, though they show parallel variation. This is discussed further by Johnson in Anderson, *l.c.* I know of no hybrids of *M. miquelii*. The species has been cultivated in Australia and overseas, and has a plethora of names in every conceivable rank (see Johnson, in press).

5. *M. COMMUNIS* L. Johnson, sp. nov.

Typification: About three miles west of Mossy Point, near Mogo, New South Wales, J. W. Vickery, iv.1958 (NSW.43071), female. HOLOTYPE.

Caudex plerumque subterraneus (per contractionem radicium seppultus) sed in solo minime profundo usque ad 1-2 m. altus, 30-60 cm. diametro. Frondes in corona usque ad 50-100 sed saepe pauciores, 70-200 cm. longae, petiolo (basi lanata expansa exclusa) 12-40 cm. longo, rhachi non torta (stirpibus insanis exceptis) plus minusve applanata, ad pinnas infimas 8-20 mm. lata, supra vel concava vel convexa aliquando carinata, sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa, infra subangulato-convexa. Pinae 70-130, patentes, angulo acuto prorsum directae, plurimae arctae sed infimae saepe distantes, quam illis *M. miquelii* crassiores rigidioresque, integrae, rectae, lineares, eae longissimae 16-35 cm. longae, 3-15 infimarum gradatim reductae spiniformesque, 4-12 mm. latae, infra vix prominule nervis 7-13 striatae, apicem pungentem versus sensim angustatae, basi pallida arcte contractae et in axillis callosae rugosaeque (in sicco), supra saturate virides haud vel vix nitentes, pagina inferiore sola stomatibus instructa. Coni feminei 1-6, masculi 1-10, axillares inter frondibus, basi axis conigeri cataphyllis spiniformibus (ad 18 cm. longis) instructa. Coni masculi cylindracei (vetustiores aliquando curvati) 20-45 cm. longi, 8-12 cm. diametro (5-8 cm. in stirpibus depauperatis), sporophyllis cuneatis vel obovato-cuneatis 2-4 cm. longis, 1.5-2.5 cm. latis, spinis planis erectis 0.1-5 cm. longis (longissimis 2-5 cm. versus apicem coni) basi 5-12 mm. latis. Coni feminei cylindracei, 20-45 cm. longi, 10-20 cm. diametro, in axibus 8-30 cm. longis 2-3 (-4?) cm. crassis gesti, sporophyllis 4-7 cm. longis (stipite 3-4.5 cm. incluso) parte terminali expansa glauca maturitate plerumque latitudine (3-8.5 cm.) quam altitudine (1.5-4.3 cm.) saltem duplo majore, spinis planis erectis, ad basin coni brevissimis (1-2.5 cm. longis) versus apicem longissimis (4-8 cm.), basi 8-20 mm. latis. Semina 3-4.5 cm. longa, 2-3 cm. crassa, integumentum parte exteriori carnosa miniata. Chromosomata somatica $2n = 18$.

Description (English), *specimens* and full *discussion*: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Coast and ranges from Macleay River to Bega and westward to the head of the Goulburn River, in dry sclerophyll forest, on sandy or stony soils.

This is the plant, familiar to every botanist who has worked in the Sydney district, which has been wrongly known in New South Wales as "*M. spiralis*"; it is not the species which has been called "*M. spiralis*" in Queensland (see below, under *M. spiralis* and *M. lucida*). Despite frequent references to it in the literature under this and other misapplied names (see Johnson, in Anderson, *l.c.*), it has never been described as a new species, hence the present description. The specific epithet reflects the abundance of this species in many parts of the Coast districts of New South Wales. *M. communis* shows a good deal of individual and some local variation in size of organs, but is clearly discontinuous in nature from related species of section *Macrozamia*. The Type is characteristic of the most luxuriant forms from the South Coast. Despite its occurrence in places near stands of certain species of section *Parazamia*, I have not yet found any evident hybridism either in the wild or in cultivated collections. Nevertheless, to judge by the behaviour of other species (e.g. *M. moorei*), hybrids are to be expected. *M. communis* is cultivated in gardens in Australia and overseas. Its well-known vernacular name is usually spelt "Burrawang", but today pronounced "Burrawong". For a discussion of the past nomenclatural confusion surrounding this species see Johnson in Anderson, *l.c.*

6. *M. DIPLOMERA* (F. Muell.) L. Johnson, stat. nov.

Basionym: *Encephalartos spiralis* (Salisb.) Lehm. var. *diplomera* F. Muell., *Fragm. Phytogr. Austral.*, 5 (1866), 172 (in part, as to lectotype, see below).

Typification: ". . . ab amico Carolo Moore in montibus Wambungle Mountains ad flumen Castlereaghii detectam." In point of fact these collections were made by

Moore's collector W. Carron, but Moore sent duplicates to Mueller. The type sheet is in herb. MEL labelled: Castlereagh River at the Wambungle [sic] mountains [New South Wales], [W.] Carron [before 1866]. This is a mixed collection: the sheet bears three pieces of fronds, of which two belong to the species here defined as *M. diplomera* (these I choose as LECTOTYPE) and one belongs to the species here defined as *M. heteromera* C. Moore (which was of similar mixed typification, see below). Mueller's description and epithet ("two-parted") clearly fit the former species better. The actual locality, of course, is the Warrumbungle Mountains, in the eastern sandstone foothills of which this species is found.

Synonymy: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Since Mueller's original description in varietal rank is very brief and rather informal (though valid), I now provide a new Latin description (for English description, see Johnson in Anderson, *l.c.*):

Caudex plerumque subterraneus, 20(?)–40 cm. diametro. Frondes in corona usque ad 50 (?), sed saepe pauciores, 60–120 cm. longae, petiolo (basi lanata expansa exclusa) 10–20 cm. longo; rhachi non torta, plus minusve applanata, ad pinnas infimas 8–12 mm. lata, supra concaviscula vel convexa (proxime saepe plus minusve carinata), sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa, infra subangulato-convexa. Pinnae 70–120, valde patentes, angulo acuto prorsum directae, plurimae arctae sed infimae 2–4 cm. distantes, rigidiusculae, omnes paucis apicalibus exceptis angulo acutissimo in segmentis duobus vix divergentibus dichotome divisae (plerumque versus basin pinnae sed in pinnis subapicalibus versus medium, rare segmento uno pinnarum nonnullarum infimarum ipso diviso vel sub apice unidentato), eae longissimae 15–20 (–25?) cm. longae, nonnullae infimarum gradatim abbreviatae spiniformesque, 5–10 mm. latae (segmentis 2.5–5 mm. latis), infra 6–13 nervis (in segmentis 3–7 nervis) vix prominule striatae, (pinnae segmentave) ad apicem pungentem sensim angustatae, basi pallida flavescentive constricta et in axillis callosae rugosaeque (in sicco, sinu furcae pinnarum etiam saepe callosae rugosiusculoque, supra virides non nitentes (in sicco saepe flavescentes), paginis utrisque stomatibus instructis. Coni non certe noti, probabiliter illis minoribus *M. communis* similes, axe configero femineo fide auctorum ferrugineo-tomentoso [cataphylla juniora in speciebus plurimis tomentosa sunt. L.J.].

Distribution: New South Wales: Southern part of North-west Slopes, around Coonabarabran and the eastern foothills of the Warrumbungle Mountains and east to the Mooki River, in dry sclerophyll forest on sandy or stony siliceous soils.

Specimens and further discussion: See Johnson in Anderson, *l.c.*

This species, of which cones are unfortunately unknown, is noteworthy for its divided pinnae. This character and the amphistomatic fronds clearly distinguish it from *M. communis*, the smaller inland forms of which it otherwise resembles. It is remarkable that its range corresponds in part with that of *M. heteromera*, which also has divided and amphistomatic pinnae, but which is as clearly a member of section *Parazamia* as *M. diplomera* is of section *Macrozamia*. Hitherto, most collectors and systematists have failed to distinguish *M. diplomera* from *M. heteromera*, usually including also a third species, *M. stenomera* (sect. *Parazamia*), which has divided but hypostomatic pinnae and is found to the north-east of this area. These facts of distribution suggest causal correlation of some kind: probably plants with divided pinnae possess some selective advantage, or at least are certainly not at a disadvantage, in the regional environment, but it is further possible that there has been introgressive gene-flow between populations belonging to the two rather diverse sections. A detailed study of these populations and their genetics should be of interest. In the field I have only once seen *M. diplomera*, in passing, and have been able to study *M. heteromera* only in areas where *M. diplomera* is absent. An apparent hybrid between the two was once grown in the Sydney Botanic Gardens from seed from the Coonabarabran district. The various distinctions between *M. diplomera* and *M. heteromera* are discussed by Johnson in Anderson, *l.c.*

ii. Section PARAZAMIA (Miq.) Miq.

In *Arch. Néerl.*, 3 (1868), 250, and in *Versl. Meded. Koninkl. Akad.*, ii, 3 (1869), 541; amplified hereunder.

Basionym: *Encephalartos* Lehm. sect. *Parazamia* Miq. in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 374.

Typification: Miquel (1863) included only *Encephalartos pauli-guilielmi* (W. Hill & F. Muell.) F. Muell. in his new section. The type species of *Macrozamia* sect. *Parazamia* is thus *M. pauli-guilielmi* W. Hill & F. Muell. The section as I conceive it includes the species correctly called *M. spiralis* (Salisb.) Miq. Hutchinson (1924) gives this binomial as type-species of *Macrozamia*, but, as argued above (p. 87), *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn. should be the generic type. The sectional name *Parazamia* may be used in the present circumscription only on this interpretation.

Synonymy (infrageneric):

Macrozamia sect. *Polyorientales* Schuster (nom. illegit.) subsect. *Acutae* Schuster, *Pflanzenr.*, IV, i (1932), 87 (I choose *M. pauli-guilielmi* W. Hill & F. Muell. as LECTOTYPE. This permanently disposes of the name. Schuster nowhere mentions Miquel's earlier sectional names).

Macrozamia sect. *Polyorientales* subsect. *Curvatae* Schuster, *l.c.* (I select *M. fawcettii* C. Moore as LECTOTYPE).

Pinnae usually more or less curved, spreading to erect (secund), nerves prominent on the lower surface especially when dry, apices entire to 2-7-toothed in adult fronds, bases slightly callous but never rugose, mucilage canals absent from the pinnae (present as always in the larger organs of the plant), the lowest pinnae not or only slightly, or one or two irregularly, reduced.

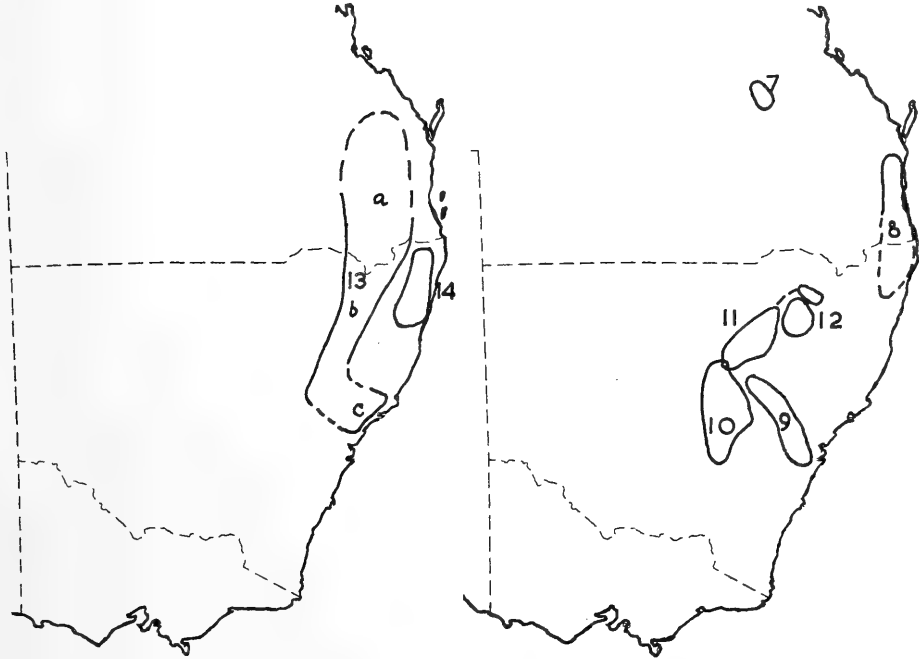
Small plants with few fronds, caudex wholly subterranean or only its crown protruding. Rhachis sometimes straight, but more often moderately to very strongly spirally twisted or strongly recurved or incurved near the tip, from rounded to flattened or even markedly concave above, rounded or less often somewhat angular beneath when dry. Cones small (females 10-25 cm. long, 6-10 cm. diam.; males 8-25 cm. long), sporophyll-spines short to medium (5 cm.), spreading to erect.

This very natural section is confined to eastern Australia, and its species show evidence of reduction and some degree of neoteny or carrying-over of semi-juvenile characteristics (prominent nerves, unreduced basal pinnae, toothed pinna-tips, lack of mucilage-canals in pinnae, rounded petioles, small caudices) into the adult state. Accordingly it is probably of relatively recent origin, that is to say, as an evolutionary line its adult character-complex has been evolved more recently than those characters preserved in and characteristic of sect. *Macrozamia*. Furthermore, speciation appears to be still in progress in sect. *Parazamia* (cf. the races of *M. pauli-guilielmi*) and some of the species are very closely allied. On the other hand the plants seem on the whole less successful than in sect. *Macrozamia*; the populations are diffuse, rarely forming close stands, though in such species as *M. heteromera* and *M. secunda* the total population is by no means small. Since the plants are scattered, small and relatively inconspicuous, and produce few cones at irregular intervals, they are frequently overlooked by collectors and good cone-material is lacking for some species. Since the cones seem to be very similar throughout the section, this is not such a taxonomic handicap as it may appear.

The species tend to show a replacement pattern (Text-figure 3), but this is not without overlap, though no two species of the section form mixed stands except marginally. Some marginal hybridism seems to occur between *M. secunda* and *M. heteromera*, *M. heteromera* and *M. stenomera*, *M. heteromera* and *M. pauli-guilielmi* ssp. *plurinervia*, and possibly between *M. secunda* and *M. spiralis*. In the case of the three subspecies of *M. pauli-guilielmi* there is a large-scale breakdown. Species of sect. *Parazamia* at times grow with or near species of sect. *Macrozamia* and hybrids may be found, as in the case of *M. lucida* and *M. moorei* at Dalmorton. Several apparent

chance inter-sectional hybrids have come up in the cycad beds in the Sydney Botanic Gardens. No chromosome numbers are recorded in this section.

One cannot arrange the eight species of the section neatly in subgroups, but certain of them do form rather close pairs or triplets; these are: (a) *M. lucida*-*M. spiralis*-*M. secunda* (the two end members differ markedly, but each is close to *M. spiralis*), (b) *M. heteromera*-*M. stenomera*, (c) *M. pauli-guilielmi*-*M. fawcettii*. Other cross-relationships are also evident, however, and *M. platyrachis* does not seem to fit in any one group better than another.



Text-fig. 3.—Distribution of *Macrozamia* section *Parazamia*: 7: *M. platyrachis*; 8: *M. lucida*; 9: *M. spiralis*; 10: *M. secunda*; 11: *M. heteromera*; 12: *M. stenomera*; 13: *M. pauli-guilielmi* (a: ssp. *pauli-guilielmi*, b: ssp. *plurinervia*, c: ssp. *flexuosa*); 14: *M. fawcettii*.

7. *M. PLATYRACHIS** F. M. Bail. in *Queensl. Agric. Journ.*, 3 (1898), 356, and in *Queensl. Flora*, 5 (1902), 1503 (as "*platyrachis*"); Schuster, *Pflanzenr.*, IV, i (1932), 99 ("*platyrachis*").

Typification: Range near Planet Downs, Queensland, H. C. Brock-Hollinshead, male, HOLOTYPE (a female cone was also sent). This is in herb. BRI. There is an ISOTYPE (vegetative) in NSW(40970).

Caudex mostly subterranean, to 60 cm. diam. according to Bailey, probably often less. Fronds few (to ca. 12?) in the crown, to ca. 100 cm. long, petiole ca. 15-25 cm. long excluding the expanded base (which Bailey describes as with "no woolly substance"); rhachis not or only moderately twisted (to ca. 180°?), 13-18 mm. broad at the lowest pinnae, flattened above with the two lateral furrows very shallow and obscure even when dry, convex and angular (at least when dry) beneath. Pinnae ca. 50 (sometimes more?), somewhat spreading-erect, more or less forwardly directed and twisted at the base, the upper ones fairly crowded but the lowest 2-3 cm. apart, rather stiff and very coriaceous, entire, from somewhat recurved-falcate to fairly

* The original spelling *platyrachis* should, I think, be retained. In 1902 and subsequently Bailey used *platyrhachis* but did not indicate this as a deliberate correction of an unintentional error. Neither form is particularly good Greek ("rrh-" would be best), but "-rachis" is acceptable latinized Greek.

straight, broad-linear, the longest 30-40 cm. long and the lowest ones not reduced, 12-20 mm. broad with *ca.* 15-18 rather prominent nerves beneath, somewhat tapered, but finally rather abruptly rounded to the mucronate apex, contracted to the somewhat paler, rather decurrent but not or scarcely callous base, green and somewhat glossy above, with stomata confined to the lower surface. Cones not examined; the following is from Bailey's data: Cones stalked, 1-several (at least in the males) per plant (presumably axillary amongst the fronds). Male cones cylindrical (probably immature ones measured), 7.5-10 cm. long, *ca.* 2.5 cm. diam., sporophyll-spines erect, slender, to 1 cm. long (prob. longer at times). Female cone more or less cylindrical, *ca.* 16 cm. long (*ca.* 8 cm. diam.?). Sporophyll-spines more or less erect, flattened, the longest (towards the apex of the cone) *ca.* 1.3 cm. long. Seeds *ca.* 2.5 cm. long, outer coat reddish ("reddish-brown" acc. to Bailey, these probably not fresh). [Doubtless cones and their parts vary a good deal in size, as in other species.]

Distribution: Queensland: Dryish (not arid) parts of Central Queensland (Planet Downs) in hilly country, doubtless in dry sclerophyll communities.

Specimens: See above, under Typification.

M. platyrachis is a poorly known but quite distinctive species. It is the most northerly member of section *Parazamia* and is readily recognized by its very broad, stiffly coriaceous pinnae and the broad rhachis which is flattened above and angular beneath. It does not show particular affinity with any one species, though clearly belonging to the section. Schuster (1932) grouped it with *M. fawcettii* because of its broad pinnae, but this is surely a case of convergence or parallel evolution in a single character; in other respects it does not much resemble *M. fawcettii*.

Bailey's statement that the petiole-bases lack woolly hairs needs confirmation; so does the collector's remark that the species does not cause "rickets" in stock.

8. *M. LUCIDA* L. Johnson, sp. nov.

Typification: Southern side of Ngungun, abt. 400 ft. alt., Glass House Mountains, Queensland, L. A. S. Johnson, 13.vi.1951 (NSW.40668), vegetative. HOLOTYPE. (Since no good material with cones was available, I have nominated as the type this specimen which I have seen living in the field.)

Caudex plerumque subterraneus, 10-20 (-30?) cm. diametro. Frondes in corona plerumque 2-15 (nonnunquam usque ad 40?), 80-110 cm. longae, petiolo (basi lanata expansa exclusa) 25-50 cm. longo; rhachis non torta, teretiuscula, ad pinnas infimas 3-7 mm. lata, supra saepissime rotundato-convexa (sed nonnunquam applanata vel proxime plus minusve medio subsulcata), sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa (in sicco), infra semper rotundato-convexa (haud angulata). Pinnae 50-100, patentes (seriebus duabus tamen non in eodem plano) et praesertim versus apices suos decurvatae, plurimae angulo acuto prorsum directae sed infimae cum rhachi angulum rectum saepe formantes, basi tortae, plurimae arctae sed infimae saepe 1.5-3 cm. distantes, integrae, pleraeque plus minusve recurvato-falcatae (sed versus apices suos aliquando prorsum curvatae), lineares, eae longissimae 15-35 cm. longae, infimae haud vel vix abbreviatae, 7-11 mm. latae, infra nervis prominentibus 5-11 striatae, apicem pungentem versus sensim angustatae, basi conspicue pallida callosiuscula sed non rugosa constrictae, supra nitentes virides, pagina inferiore sola stomatibus instructa. Coni maturi non visi, probabiliter illis *M. spiralis* similes; sporophyllis masculis usque ad 4 cm. longis, spinis brevibus. Conos ad *M. lucidam* probabiliter pertinentes, F. M. Bailey (1902) sequens nunc describo: Axis coniger usque ad 30 cm. longus. Coni masculi cylindracei, 15 cm. longi (vel longiores), ca. 4 cm. diametro, [immaturi? L.J.] spinis sporophyllorum infimorum obsolescentibus eis sporophyllorum apicalium usque ad 1.2 cm. longis. Coni feminei 15-20 cm. longi, 7.5-9 cm. diametro, sporophyllorum parte terminali ad 4 cm. lata et 2 cm. alta, spinis 0.6-5 cm. longis longissimis versus apicem coni dispositis. Semina ca. 2.5 cm. longa, ca. 2 cm. crassa, integumentum parte exteriori rubella.

Description (English) and *discussion* of misapplied names: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: Queensland and New South Wales: Southern Coast region of Queensland from Wide Bay to Moreton District, and Clarence River (N. Coast of N.S.W.).

Specimens examined: QUEENSLAND: Southern side of Ngungun, abt. 400 ft. alt., Glass House Mountains, L. A. S. Johnson, 13.vi.1951 (NSW.40668); Mt. Coonowrin, Glass House Mountains, ca. 300 ft., C. E. Hubbard 4112, 21.ix.1930 (BRI); Taylor's Range, near Brisbane, C. T. White, i.1912 (BRI); Palmwoods, C. T. White, 6.v.1907 (BRI); Enoggera Creek, F. M. Bailey, 7.i.1875 (BRI); Enoggera, C. T. White, vi.1919 (NSW.40699); Cedar Creek, near Brisbane, C. T. White 1961, 6.v.1923 (NSW.40671); Brisbane, J. L. Boorman, iv.1899 (NSW.40670). NEW SOUTH WALES: Three miles E. of Dalmorton, L. A. S. Johnson and E. F. Constable, vi.1957 (NSW.43069). Living and preserved cultivated material also examined.

This is the species which has been wrongly known in Queensland, but not in New South Wales, as *M. spiralis* (see below, under *M. spiralis*). Though related to the true *M. spiralis*, it clearly constitutes a quite distinct series of populations, and is readily distinguished in cultivation as well as in the wild. *M. lucida* is characterized by its long slender petioles, not or scarcely twisted rachis, and the curved, very glossy (whence the specific epithet) pinnae with sharply demarcated whitish but not very callous bases. Though it does not form dense stands it is widely spread in hilly country of the coast districts of southern Queensland, but in New South Wales only a single small stand is known as yet. It has been cultivated in the Sydney Botanic Gardens for many years and there maintains its distinctive appearance. For further treatment see the forthcoming *Flora of New South Wales*, part 1, where a probable hybrid population derived from *M. lucida* and the very different *M. moorei* is also discussed.

9. *M. SPIRALIS* (Salisb.) Miq., *Monogr. Cycad.* (1842), 36, as to basionym, excl. descr. and fig.; misapplied also by all later authors.

Basionym: *Zamia spiralis* Salisb., *Prodr. Stirp.* (1796), 401.

Typification: "Sponte nascentem juxta Port Jackson, locis umbris, legit Dav. Burton." As with most of Salisbury's types, no specimen of this appears to be extant. The correct application of the name must be established, if possible, from the description and other evidence. The description reads: "Z. foliolis 30-40 jugis, extrorsum falciformibus apice spinose 3-5 dentatis." "Petioli paululum spirales sunt." Together with the information on locality, habitat and collector quoted above, which was interpolated by Salisbury between the first and second descriptive sentences, this is the whole of the original information. The first author to do more than repeat Salisbury's description was R. Brown, *Prodr.* (1810), 348, who applied the name *Z. spiralis* to a mixture of the species now treated as *M. communis* L. Johnson and *M. riedlei* (Fisch. ex Gaudich.) C. A. Gardn., but expressed doubt whether these were conspecific. Miquel (1842), in making the new combination under *Macrozamia*, described only plants of *M. riedlei* (from figures of F. Bauer), but quoted R. Brown for the Port Jackson locality (representing *M. communis*), and, of course, his combination is nomenclaturally based on Salisbury's name, of which he had not seen the type. However, he remarked that Brown's description and Bauer's figures did not agree with Salisbury's description of dentate-tipped leaflets, and added "Quam ob rem credere posses, speciem ab his auctoribus recensitam a vera *Zamia spirali* Salisb. differre", with further remarks illustrating this doubt and also the confusion with the garden plants known as *Encephalartos tridentatus* and *E. pungens* (these were based, as *Zamia tridentata* Willd. and *Z. pungens* Ait., on young cultivated plants of supposed South African origin and of quite uncertain identity. Juvenile plants of *Macrozamia* and *Encephalartos* cannot be determined to the species).

Later, in *Versl. Meded. Koninkl. Akad.*, 15 (1863), 368-370, Miquel made it clear that Bauer's plates (from which his earlier description of *M. spiralis* had been taken) in fact depicted his *Encephalartos fraseri* (= *Macrozamia riedlei*) and went on to treat as "*Encephalartos spiralis* [Salisb.] Lehm." a mixture of *M. communis* and *M. miquelii*.

In a similar treatment, but under *Macrozamia* (Miquel, 1868, p. 249; 1869, p. 52), he again expressed doubt regarding Salisbury's plant.

Other authors have applied the name *M./E. spiralis* in various ways, but most generally to *M. communis* (e.g. Mueller, *passim*, Bentham, and such N. S. Wales authors as C. Moore, Maiden and Betche, Brough and Taylor. Full refs. in *Fl. N.S.W.*, Part 1, in press), though they often included one or more other species in their concept. Queensland botanists, following F. M. Bailey (esp. in *Queensl. Fl.*, 5 (1902), 1504), have used *M. spiralis* for the quite different species *M. lucida* L. Johnson.

Schuster, *Pflanzenr.*, IV, i (1932), 88, ignored priority and synonymized *M. spiralis** and *Z. spiralis** under his extraordinarily inclusive and confused concept of "*M. tridentata* (Willd.) Regel", based, of course, on the unidentifiable *Z. tridentata* Willd. (1806).

No one apart from Miquel (1842, 1869) seriously considered the original application of Salisbury's name. This we must now do.

Two species grow sufficiently close to Port Jackson to have been collected by David Burton before 1796. These are *M. communis* L. Johnson ("*M. spiralis*" of N.S.W. botanists) and the species hitherto known as *M. corallipes* Hook. f. While it would be convenient to retain the usage traditional in N. S. Wales (though not in Queensland), an honest application of the International Code of Botanical Nomenclature will not allow this.† In the absence of a material type, a name's application must be determined from the author's words and associated facts. Only when a reasonable degree of certainty is impossible does the Code permit a name to be dropped.

Juvenile fronds of all species have toothed pinnae, but Salisbury's description cannot apply to a wholly juvenile plant, since he mentions 30–40 pairs of pinnae. As in section *Macrozamia* generally, plants of *M. communis* old enough to have 60–80 pinnae in their fronds never have falciform pinnae spinosely 3–5-toothed at the apex, nor is the petiole (or rhachis) spiral (even "paululum"). On the other hand this description applies perfectly to many submature individuals of *M. corallipes* (sect. *Parazamia*). Consequently I have no doubt that Salisbury's plant was the latter species, for which the name *Macrozamia spiralis* (Salisb.) Miq., being nomenclaturally based on *Zamia spiralis* Salisb., must henceforth be used. The implications of this in the typification of the genus *Macrozamia* Miq. are discussed above (p. 87).

Synonymy, description and specimens: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press). The synonymy and history of misapplication are complex.

Distribution: New South Wales: North-east part of Central-western Slopes to Central Coast, from Dunedoo and the Goulburn River Valley to the lower Blue Mountains, Sydney and Waterfall districts, in dry or rarely semi-wet sclerophyll forest on poor, sandy or gravelly soils.

M. spiralis, as here defined, includes only those populations which would have been referred in the past to *M. corallipes* Hook. f. The plants are usually scattered and inconspicuous, with few fronds. The semi-juvenile fronds often seen, especially after fires, may be spirally twisted through 180° or more, and often have relatively few, widely-spaced pinnae with 2–several small teeth near their tips. Fronds of fully adult form, however, are little twisted and have more crowded pinnae usually simply mucronate at the tips. Occasionally *M. spiralis* grows close to stands of *M. communis*, but no hybrids are known. It overlaps *M. pauli-guilielmi* ssp. *plurinervia* in the Goulburn

* He cited both of these as "ex parte", which is meaningless for *Z. spiralis* Salisb., described from a single specimen. He nowhere indicated what he imagined the other part of this to be.

† Every responsible taxonomist, to say nothing of other botanists, must be disturbed by the number of such irritating corrections of ancient mistakes which the present rules of nomenclature make necessary, but the remedy cannot lie in individual botanists' refusal to obey the Code. In any case the nomenclature of *Macrozamia* has been so confused that a new point of departure should be welcome. I hope the present revision will satisfactorily supply this.

River Valley, but I have found no actual contact of populations. *M. spiralis* is replaced to the west by the closely allied *M. secunda*, and one or two inadequate specimens suggest that some interbreeding may occur, though I have seen no living intergrading plants.

It is important to remember that morphological studies (e.g. by Brough and Taylor, 1940) and chromosome counts under the name of *M. spiralis* apply in fact to *M. communis*.

10. *M. SECUNDA* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 120; Moore & Betche, *Handb. Fl. N.S.W.* (1893), 379, excl. var.?

Typification:* "Near Reedy Creek, east of Mudgee, where it was first found in 1858, but without fruit. Again found with only one old fruiting cone not far from Dubbo, by Rev. J. Milne Curran, in 1883. . . ." Only the former collection is extant, in herb. MEL, labelled: Reedy Creek, C. Moore, 1858. I therefore select it as LECTOTYPE.

Synonymy, description, specimens and discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Central-western Slopes and lower parts of Central Tablelands, from near Gilgandra to Grenfell and east to the Main Divide from Mudgee to Capertee, in dry sclerophyll forest on sandy or stony country.

M. secunda and *M. spiralis* may be regarded as a pair of vicarious species. The distinction seems sharp enough to justify specific rank. The concave petiole and stiff, usually narrow, second pinnae with very crowded nerves are characteristic. As in other species found in dry localities, the pinnae have much sclerenchymatous tissue and some glaucous bloom. Some hybridism with *M. heteromera* is evident where the species meet, as discussed by Johnson in Anderson, *l.c.* The name *M. secunda* var. *dichotoma* C. Moore & Betche, *Handb. Fl. N.S.W.* (1893), 379, probably applies to such a hybrid, but the type has been lost.

11. *M. HETEROMERA* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 122 (in part, as to lectotype and excl. var. *tenuifolia*); Moore & Betche, *Handb. Fl. N.S.W.* (1893), 380, in part.

Typification: "Among the Warrenbungle ranges and on the Castlereagh River country. Discovered in 1858; since collected near Rocky Glen, between Coonabarabran and Gunnedah." An old sheet dating from Moore's time, labelled "Warrumbungle Ranges", without collector's name, but probably collected by W. Carron or by Moore, is in NSW (40720). No specimen from Rocky Glen is extant. No original cone material has been preserved. I consider that NSW.40720 is the type sheet, but it bears a mixture, consisting of two pieces of frond belonging respectively to *M. heteromera* as here defined, and *M. diplomera* (F. Muell.) L. Johnson. Moore's description and comments covered both species, but specimens and cultivated plants later named by him chiefly belong to the former. Consequently I select as LECTOTYPE that part of NSW.40720 representing *M. heteromera* as herein defined. Both *M. diplomera* (see above, page 98) and *M. heteromera* are thus based on a mixture of the same two species, probably from duplicates from the same original collection, but selection of lectotypes in accordance with the emphasis of original descriptions or later usage allows both names to be used. The respective epithets ("two-parted", and "different" or "variably-parted") are particularly appropriate in their present application. Moore's total concept was extended by two varieties (see below).

Synonymy:

M. heteromera var. *glauca* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 122.

M. spiralis (Salisb.) Miq. var. *heteromera* (C. Moore) Maid. & Betche, *Census* (1916), 9, in part.

* Moore made no reference to *M. spiralis* (Salisb.) Miq. var. ? *secunda* Benth., *Fl. Austral.*, 6 (1873), 252, which is therefore not the basionym but an earlier synonym in a different rank. Maiden and Betche, *Census* (1916) 9, later made the homonymous varietal combination based on *M. secunda* C. Moore.

M. heteromera var. *tenuifolia* Schuster* forma *harmsii* Schuster, *Pflanzenr.*, IV, i (1932), 96.

Description, specimens and further discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1, in press. A specimen from Warialda, per Glenfield Veterinary Research Station, ix.1958 (NSW.46090) was collected too late for citation in the Flora.

Distribution: New South Wales: North-western Slopes, in the eastern and southern Pilliga Scrub from Narrabri to Coonabarabran and the foothills of the Warrumbungle Mountains, with an apparent outlier to the north-east near Warialda and Howell, in dry sclerophyll forest on siliceous soils.

M. heteromera resembles *M. stenomera* in its dichotomously divided pinnae, but these differ in the consistent presence of stomata on the upper surface. The degree of division varies considerably, both individually and locally, but is on the average less than that in *M. stenomera*. In cultivation, Moore's var. *glauca* preserves its characters of rather broad, once-divided, glaucous pinnae, but plants can be found showing every gradation in these characters and the *glauca* forms do not seem to show sufficient geographic or ecological cohesion to be treated as a subspecies. Var. *tenuifolia* C. Moore is *M. stenomera* (q.v.). The distinction from and possible hybridism with *M. diplomera* are dealt with above (p. 99). Some apparent hybrids with the adjacent *M. secunda* and *M. stenomera* are discussed by Johnson in Anderson (*l.c.*). Probable hybrids with *M. pauli-guilielmi* ssp. *plurinervia* also occur, near Warialda.

Note added 11th June, 1959.—A recent collection, from 19 miles east of Coonabarabran on Gunnedah road, W. Morris, v. 1959 (NSW.47164), has the pinnae quite undivided, and in general appearance resembles *M. spiralis*, but has the amphistomatic pinnae and short petiole (11 cm.) of *M. heteromera*. The locality is within the range of the latter species and about fifty miles north of the nearest known *M. spiralis*. The intervening areas may possibly reveal some intergradation between the two species.

12. *M. STENOMERA* L. Johnson, sp. nov.

Typification: Above Coryah Gap at 4500 ft., Nandewar Mountains, New South Wales, L. A. S. Johnson and E. F. Constable, xi.1954 (NSW.32204), vegetative. HOLOTYPE.

Synonymy: †

M. heteromera C. Moore var. *tenuifolia* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 122 (not *M. tenuifolia* Hort. ex Miq. in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 55, in synonym., nom. invalidum).

M. heteromera var. *tenuifolia* Schuster, *Pflanzenr.*, IV, i (1932), 96, nom. illegit., in part, excl. forma *harmsii* Schuster (this var. is described as new, not taken from C. Moore).

M. heteromera var. *dicranophylloides* Schuster, *l.c.*

Caudex plerumque subterraneus, ca. 8–15 cm. diametro. Frondes in corona paucae (ca. 2–10), 40–80 cm. longae, petiolo (basi lanata expansa exclusa) 7–15 cm. longo; rhachi plerumque praesertim apicem versus plus minusve torta (per 90°–360°) etiam plus minusve recurvata vel sinuosa, ad pinnas infimas (4–)5–9 mm. lata, supra proxime plana vel concavuscula vel nonnunquam aliquantulum carinata sed versus apicem rotundato-convexa, sulcis duobus lateralibus angustis e basibus pinnarum decurrentibus instructa (in sicco), infra plerumque rotundato-convexa. Pinnae 70–120, patentes (seriebus duabus tamen non in eodem plano) vel suberectae, plus minusve prorsum directae, basi tortae, plurimae arctae sed infimae 1.3–4 cm. distantes, quam illis *M.*

* See under *M. stenomera*, below.

† Since the synonyms are all in varietal rank and of confused past application, and since they were based on a specimen rather than a population-concept, I prefer (as the I.C.B.N. permits) to use a new epithet and a new type in describing the taxon in specific rank. This epithet may be legitimately retained in the rank of subspecies, should further knowledge show this to be more appropriate.

heteromerae laxiores, omnes (apicalibus aliquando exceptis) plerumque versus bases suas in segmentis angusto-linearibus plus minusve divergentibus 1-4-plo (pleraeqe 2-3-plo) dichotome divisae, longissimae 10-20 cm. longae, infimae haud vel vix abbreviatae nunquam spiniformes; segmentis primariis 2-4 mm. latis (secundariis tertiariisque 1-3 mm.) infra nervis prominentibus 4-6 (2-5 in segmentis secundariis tertiariisque) striatis, (segmentis ultimis) in apicem mucronatum vel aliquando bidentatum augustatis vel ultime abruptiuscule rotundatis, (pinnae) basi flavescenti aurantiacave callosiuscula sed non rugosa constrictae (callo in sinu furcarum pinnarum vel obsolete vel parvo), supra virides vix nitentes (sed quam illis *M. heteromerae* viridiores), infra non glaucae, pagina inferiore sola stomatibus instructa. Coni non certe noti, probabiliter illis *M. heteromerae* specierumque aliarum sectionis *Parazamiae* similes.

Description (English), *specimens* and further *discussion*: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: North-western Slopes and Northern Tablelands outlier in and around the Nandewar Mountains, in dry sclerophyll forest, on stony but not highly siliceous soils.

In the past these plants have not been distinguished from *M. heteromera*, but they appear to constitute a reasonably distinct group of populations which I have accordingly treated as a distinct species. Definitely matched cones are unfortunately lacking, but within section *Parazamia* these organs differ little from species to species and, though their collection is much needed, they probably have little bearing on the independent status of *M. stenomera*. The specific epithet refers to the characteristically narrow segments of the pinnae which, together with their usually higher degree of division, lack of glaucousness and especially lack of stomata on the upper surface, distinguish the species from *M. heteromera*. Spiral twisting of the fronds is also generally more pronounced in *M. stenomera*. The species grows on less siliceous soils than *M. heteromera*.

Specimens of apparent hybrids of *M. stenomera* with the adjacent *M. heteromera* are discussed by Johnson in Anderson, *l.c.*

13. *M. PAULI-GUILIELMI** W. Hill & F. Muell. in F. Muell., *Fragm. Phytogr. Austral.*, 1 (1859), 86.

Typification: "In vicinia sinus Moreton Bay rara. W. Hill" (MEL, not seen but unmistakable from the description).

As here defined this species comprises three geographic races, the extreme forms of which differ from each other quite as much as do several other population-groups treated in this revision as full species. However, in the latter cases the populations are effectively discontinuous (though some limited local interbreeding may occur), whereas the contiguous races of *M. pauli-guilielmi* show no such discontinuity but rather a clinal transition. Each of the three races, however, has decided characteristics of its own (preserved in cultivation under identical conditions) and occupies an area of distinct ecological character. Furthermore, the geographically intermediate race is by no means simply intermediate morphologically between the two terminal races, but is more extreme in certain features than either of them. We may reasonably infer either (a) that three populations have been effectively isolated in the past (later Tertiary and/or Pleistocene?), during which time they became genotypically and phenotypically differentiated, but that subsequent breakdown of isolation has led to extensive gene interchange in broad transitional contact zones, or (b) that differentiation has taken place under strong (ecological) selection pressure within a widespread, at least originally more or less panmictic population of high potential genetic

* Unlike such epithets as "*fawcettii*", here corrected according to the I.C.B.N. to "*fawcettii*", the epithet *pauli-guilielmi* is a direct Latin genitive (from "Paulus Guilielmus", i.e. Paul Wilhelm, Prince of Wurtemberg) and the terminal "i" should not be doubled. The clumsy epithet has been spelt in several ways (see *Fl. N.S.W.*, pt. 1) but the original orthography "*Pauli Guilielmi*" is not to be altered except by decapitalization and hyphenation, as authorized by the I.C.B.N.

variability, but without development of a fully effective breeding-barrier (genetic or spatial) between the population segments. (There is no evidence of effective introgression from any other species, another theoretically possible cause of intergrading geographic races.) In either case the three segments at the present time cannot be regarded as specifically distinct in nature, but each of them has sufficient cohesion and ecological and morphological distinctness to be treated as a subspecies.*

Full descriptions, synonymy and discussions of *M. pauli-guilielmi* and its three subspecies, and citation of New South Wales collections, will be found in the forthcoming *Flora of N.S.W.*, part 1. Only the following key, enumeration and necessary Latin diagnosis are given here.

1. Petiole much flattened, 5-15 cm. long. Pinnae lax, numerous (140-200), pale at base. Broadest pinnae 2-4 (-5) mm. broad, 3-5-nerved (odd ones rarely to 7). S. Queensland *a. ssp. pauli-guilielmi*.
- 1.* Petiole flattened to rounded, 5-30 cm. long, if flattened and less than 15 cm. long then broadest pinnae 4-7 mm. broad and 6-10-nerved and usually pinkish at the base.
 2. Petiole 5-20 (-25) cm. long, 5-11 mm. broad at lowest pinnae. Pinnae concave to convex, the broadest 4-7 mm. broad (10-30 cm. long), 6-10-nerved, often rather stiff, pinkish at the base when living. Extreme S. Queensland and N. Tablelands, N.W. Slopes and Upper Hunter Valley (N.S.W.) *b. ssp. plurinervia*.
 - 2.* Petiole 20-30 cm. long, 4-8 mm. broad at lowest pinnae. Pinnae concave, the broadest 3-5 mm. broad (17-30 cm. long), 5-6 (-7)-nerved, lax, pale at the base. Manning River-Lake Macquarie (N.S.W.) *c. ssp. flexuosa*.

a. ssp. PAULI-GUILIELMI.

Typification: As for the species.

Synonymy, description and further discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: Queensland: Southern areas, somewhat away from the coast, in the Districts of Burnett, Darling Downs and western portion of Moreton.

In the southernmost part of this range the subspecies shows clinal intergradation with *ssp. plurinervia*, and such intergrades extend into the far north of New South Wales, for instance near Acacia Creek. Plants of this subspecies have been cultivated a good deal, both in Australia and abroad.

b. ssp. PLURINERVIA L. Johnson, subsp. nov.

Typification: "Reedy Creek" Station, near Bonshaw, New South Wales, J. Leader, iv.1956 (NSW.40958), male. HOLOTYPE. (Female cone pieces are also associated with this sheet.)

Frondes (30-)40-90 cm. longae, petiolo (5-20, rare 25 cm. longo, basi expansa exclusa) cum rhachi supra applanato vel plus minusve rotundato vel aliquanto sulcato, infra angulato rotundatove, ad pinnas infimas 5-11 mm. lato, rhachi valde torta per revolutionibus una vel pluribus (vel in frondibus perbrevis plantarum depauperatarum per ca. 180°). Pinnae 50-150, arctae vel sparsiusculae, 10-30 cm. longae, rigidae vel laxiusculae, 4-7 mm. latae, 6-10-nerviae, aliquando plus minusve glaucae, basibus plerumque aurantiacis rubellisve, supra concavae vel planae etiam convexusculae. Coni plerumque glauci, feminei saepissime ovoidei spinis plerisque sporophyllorum patent erectis.

Description (English), specimens and further discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

* The category of *variety*, which many taxonomists still use to cover variations of diverse nature and of very unequal and frequently undefined biological and evolutionary significance (often not populations at all), usually conveys no more than that an author has chosen to name individuals differing in certain ways from the nomenclatural type, itself an object of no biological significance. *Subspecies*, on the contrary, though used by few taxonomic botanists in this country, has come in recent years to have a fairly definite meaning, at least to those whose interest is in evolutionary processes. This concept of an ecogeographic segment of a species has nothing in common with Schuster's (1932) virtually meaningless "subspecies" in *Macrozamia*.

Distribution: Queensland and New South Wales: Extreme south of Darling Downs District (Queensland) and lower parts of N. Tablelands, North-western Slopes and Upper Hunter Valley (New South Wales), in dry sclerophyll forest or woodland on stony slopes.

Intergrading forms to ssp. *pauli-guilielmi* are found in the extreme north of this region (see above). Hunter Valley populations show a clinal approach to ssp. *flexuosa*. Plants of the ssp. *plurinervia* series of populations have usually been referred to *M. flexuosa* or *M. pauli-guilielmi*. A full discussion is given in *Flora of N.S.W.*, part 1.

c. SSP. FLEXUOSA (C. Moore) L. Johnson, comb. et stat. nov.

Basionym: *Macrozamia flexuosa* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 121.

Typification: Moore says only “. . . grows plentifully between Raymond Terrace and Stroud”. There is only the following collection from Moore's time and this district in herb. NSW, and I consider it to be the HOLOTYPE: Limeburner's Creek, New South Wales, E. Betche, i.1883 (NSW.40951), vegetative, associated cones apparently lost.

Synonymy, specimens and further discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Southern part of North Coast and extreme north of Central Coast, from Bulladelah district to Lake Macquarie, in sclerophyll forest, on rather siliceous soils.

In some respects this race has more resemblance to the geographically remote ssp. *pauli-guilielmi* than to the contiguous ssp. *plurinervia*, although it differs markedly from ssp. *pauli-guilielmi* in the long, rounded petioles. As stated above, the southern populations referred to ssp. *plurinervia* exhibit clinal approach to ssp. *flexuosa*.

Submature plants of *M. spiralis* with rather twisted fronds have often been referred to *M. flexuosa*, but true *M. pauli-guilielmi* ssp. *flexuosa* is distinguished by its fronds being twisted through at least two complete revolutions and by its concave pinnae. No area of contact with *M. spiralis* is known, but the two may well meet in the Wollombi Creek-Macdonald River district.

14. *M. fawcettii* C. Moore in *Journ. Roy. Soc. N.S.W.*, 17 (1884), 120.

Typification: “On high ground on the upper part of the Richmond; discovered by C. Fawcett, Esq., P.[olice] M.[agistrate], . . . Only freshly-gathered leaves and old male cones have as yet been seen.” This is in herb. NSW, labelled: Upper Richmond River, New South Wales, C. Fawcett (NSW.40653), vegetative with male cone fragments. HOLOTYPE.

Synonymy, description, specimens and discussion: See Johnson in Anderson, *Flora of N.S.W.*, part 1 (in press).

Distribution: New South Wales: Farther North Coast and ranges, from Richmond River to Coff's Harbour, in dry or semi-wet sclerophyll forest on siliceous soils.

M. fawcettii, though closely related to *M. pauli-guilielmi*, the other species with twisted fronds, is isolated geographically and is clearly distinguished from all forms of *M. pauli-guilielmi* by its very broad, usually several-toothed pinnae. Whatever might happen if it were brought into contact with *M. pauli-guilielmi*, it is at the present time effectively isolated as a species. It overlaps *M. lucida* in distribution, but no contact has been observed.

The nomenclatural confusions which ensued from Mueller's association of specimens of *M. fawcettii* with the very different *M. miquelii* are discussed under the latter species and in the forthcoming *Flora of N.S.W.*, part 1.

III. BOWENIA Hook. ex Hook. f.

Hook. ex Hook. f.* in *Bot. Mag.*, 89 (1863), sub t.5398; *ibid.*, 98 (1872), sub t.6008; F. Muell., *Fragm. Phytogr. Austral.*, 5 (1866), 171; A.DC., *Prodr.*, 16, pt. 2 (1868),

* J. D. Hooker described the genus and species, but adopted names proposed though not published by W. J. Hooker, whom he again cited as author in 1872. Later authors, confused by this, have cited either “Hook.” or “Hook. f.” Under the I.C.B.N. the correct citation is as given above.

524; Miq. in *Arch. Néerl.*, 3 (1868), 254, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 57; Benth., *Fl. Austral.*, 6 (1873), 254; Regel in *Acta Hort. Petrop.*, 4 (1876), 316; F. M. Bail., *Queensl. Fl.*, 5 (1902), 1507; Chamberlain in *Bot. Gaz.*, 54 (1912), 419; Schuster, *Pflanzenr.*, IV, i (1932), 85.

Typification: *B. spectabilis* Hook. ex Hook. f. TYPE SPECIES (the sole original species).

Caudex subterranean, tuberous, naked, from the crown repeatedly producing one to numerous short, slender, more or less determinate frond- and cone-bearing branches (sometimes themselves branched); all parts more or less pilose or pubescent when young, but glabrescent (except petiole-bases, cataphylls and sporophylls) with maturity. Cataphylls short, flat, ovate-triangular, interspersed among the frond-bases. Fronds 1-several on each slender branch, long-petiolate; decomposed by pinnate (or at the end sometimes dichotomous) branching of the rhachis, the lowest branches sometimes approximate to appear quasi-palmate; rhachis somewhat curved but not twisted, base of petiole somewhat thickened, more or less hairy. Pinnules several to fairly numerous on each secondary rhachis (which is itself terminally expanded into a pinnule), spreading, inserted marginally but towards the adaxial side of the rhachis and more or less decurrent, not articulate, simple, entire or lacerate or toothed, obliquely ovate or lanceolate, contracted and more or less petiolulate at the base, with close quasi-parallel dichotomous venation, stomata confined to the lower surface. Cones of both sexes shortly stalked or subsessile, terminal on the short determinate branches, with the spirals (parastichies) of sporophylls so arranged that the sporophylls form vertical rows (orthostichies); sporophylls peltate with expanded oblate-hexagonal terminally-compressed spineless ends. Male sporophylls with a very short stipes, a broadly obovate-cuneate lamina the proximal half of which has two collateral fertile areas on the undersurface, and a more or less hexagonal end compressed to lie in the vertical plane. Female sporophylls with a fleshy stipes, the two ovules borne on the inward-facing margins ("inner surface") of the expanded hexagonal end. Seeds with a fleshy outer coat, inner seed-coat hard. Taproot tuberous, producing apogeotropic as well as normal roots.

Chromosome number: $x = 9$ (Darlington and Wylie, 1955).

Endemic in north-eastern Australia (Queensland), with two species, centred on the Cairns and Rockhampton districts respectively, in open spaces in rainforest and in eucalypt forest (Text-figure 4).

Bowenia is a very distinct genus among the Zamiaceae and has not been confused with any other. It possesses more advanced features than the other Australian genera and appears to be related to such American genera as *Zamia*, though some of the resemblances may be due to parallel evolution or convergence. Bentham's (1873) statement that it differs "from *Macrozamia* only in foliage and in the absence of the point to the cone-scales" is not true. The naked caudex, the system of short determinate branches, the terminal cone position, and the regular arrangement of the sporophylls are all very different from the characters of *Macrozamia*, to which *Bowenia* can be only very distantly related.

The decomposed fronds distinguish *Bowenia* from all other cycad genera. In some species of *Macrozamia* and at times in *Stangeria* the pinnae are dichotomously divided, but the rhachis itself is undivided, so that the fronds may be described as simply pinnate with forking pinnae. In *Bowenia* the rhachis itself branches.

The fronds are usually described as bipinnate, but Schuster (1932) refers to the branching as dichotomous. In *Bowenia* the frond at maturity may certainly be justly called bipinnate; there is a median rhachis (continuous with the petiole) bearing on each side two to five lateral secondary rhachides which in turn bear the final segments (pinnules) on either side. (The lowest laterals may arise at almost the same point due to arrested intercalary growth during development, but the arrangement is still pinnate.) Beyond the most distal lateral rhachis the median rhachis itself bears pinnules directly (in some cases it forks apparently dichotomously, each branch then

bearing pinnules). However, there is little difference between primary and secondary rhachides and the junctions tend to be fork-like, though the median branch is the larger and, unlike the lateral, continues on to branch again.

In the light of conditions in other plant groups, this can be regarded as a stage in the evolutionary development of a pinnate (or a kind of monopodial) branching from dichotomy by the process of "overtopping" (*Übergipfelung*). This process must be understood, however, in a phylogenetic and not an ontogenetic sense. The frond is a *determinate* branch-system with the whole of its ramifications established in the bud stage, and later simply expanded by intercalary growth and cell enlargement. It is not strictly comparable with a normal branch-system enlarging by apical growth, though probably evolutionarily descended from such a system, as indeed all the fronds



Text-fig. 4.—Distribution of *Bowenia*: 1: *B. spectabilis*; 2: *B. serrulata*.

(leaves) of the various pteropsid lines may be. Similar conditions can be seen in various living and extinct fern groups and in the extinct Pteridosperms, and the beginnings of the trend are evident even in some of the ancient Psilophytales.

So far as the *Bowenia* frond is concerned, the significant point is that the ramifying process is less stereotyped than in such groups as Angiosperms or Conifers, so that more or less modified dichotomy can occur in various parts of the branching system. The same applies to other cycads, but usually less strikingly. In *Bowenia* the capacity for dichotomy and for overtopping has made possible a particular kind of frond specialization apparently suited to the environment. *Bowenia* is not a primitive cycad, and we need not assume that the decompound frond has been continuously retained during its evolutionary history. It may well be a secondary acquisition, which would remain possible so long as the mechanism for unsteretyped branching was not lost.

Both species have been cultivated to some extent as ornamentals, but are rather tender even in the Sydney climate.

Key to the Species.

1. Pinnules entire or a few of them irregularly lacerate. Caudex elongate, with 1-5 frond-bearing branches. N.E. Queensland 1. *B. spectabilis*.
- 1.* Pinnules regularly serrate. Caudex subspherical, with 5-20 frond-bearing branches. Central eastern Queensland 2. *B. serrulata*.

1. *B. spectabilis* Hook. ex Hook. f. in *Bot. Mag.*, 89 (1863), sub t.5398; *ibid.*, 98 (1872), sub t.6008; F. Muell., *Fragm. Phytogr. Austral.*, 5 (1866), 171; A.D.C., *Prodr.*, 16, pt. 2 (1868), 524; Miq. in *Arch. Néerl.*, 3 (1868), 254, and in *Versl. Meded. Koninkl. Akad.*, ser. ii, 3 (1869), 57; Benth., *Fl. Austral.*, 6 (1873), 254; Regel in *Acta Hort. Petrop.*, 4 (1876), 316; F. M. Bail., *Queensl. Fl.*, 5 (1902), 1507, in part, excl. var.; Chamberlain in *Bot. Gaz.*, 54 (1912), 419; Domin in *Bibl. Bot.*, 20 (1915), 244; Schuster, *Pflanzenr.*, IV, i (1932), 85, in part, excl. var.

Typification: J. D. Hooker mentioned a specimen of *A. Cunningham's* from the Endeavour River, 1819, but stated that the description was made from a living plant with dried leaves and a male cone, from Rockingham Bay, sent by W. Hill to Kew in 1863. This material is thus the HOLOTYPE and is represented by *Bot. Mag.*, t.5398.

Caudex subterranean, 2-10 (or more?) cm. diam., elongate, passing into the elongate tuberous tap-root, its crown bearing (at any one time) 1-3 (-5) short slender frond- and cone-bearing branches. Fronds few (*ca.* 1-7), erect, with 4-10 more or less spreading branches (pinnae), to 100-200 cm. long (the first ones of a new series often smaller, from 40 cm.) and 100 cm. broad, somewhat pilose when young, but glabrescent with age; petiole *ca.* half the total length of the frond, slender (*ca.* 2-8 mm. thick), almost terete, but slightly channelled above, somewhat thickened and more or less villous at the base, sometimes also with shorter stiff hairs persistent throughout the proximal half; primary and secondary rhachides slender, slightly flattened but 1-2-channelled above and laterally ridged from the decurrent pinnule-bases, rounded to subangular beneath. Pinnules 7-30 on each pinna (also on the terminal unbranched portion of the primary rhachis), spreading, entire or a few with occasional coarse lacerations, rather thin and flexible, shining above, obliquely falcate-lanceolate (or more or less ovate on small fronds), 7-15 cm. long, 1.5-4 cm. broad, with numerous more or less parallel dichotomously-branched nerves visible on both surfaces but not prominent, tapered to the acute or often acuminate non-pungent apex, gradually contracted and finally more or less petiolulate at the slender decurrent base. Cones not seen mature, the following is partly derived from descriptions by other authors: Male cones shortly stalked, ovoid, to 5 cm. long and 2.5 cm. diam., sporophylls broadly obovate-cuneate with dilated, truncate, subhexagonal, more or less tomentose ends. Female cones sessile, oblong-globose and rounded at the apex, to *ca.* 10 cm. long (or longer?), 7-10 cm. diam.; sporophylls about 8-stichous, the expanded ends oblate-hexagonal (in the vertical plane), 3-5.5 cm. broad, *ca.* 1.5 cm. high, terminally more or less truncate-pyramidal with a central depression (said to be more or less tomentose but glabrescent in the immature example seen). Seeds to 3.2 cm. long, 1.8 cm. thick.

Chromosome number: $2n = 18$.

Distribution: Queensland: North-eastern coast and ranges from Cooktown to Rockingham Bay district, in the more open situations in and around rainforest.

Specimens examined: QUEENSLAND: Whyanbeel Creek, 7 miles north of Mossman, M. Tindale, 15.vii.1957 (NSW.42280); Cape Tribulation, W. W. Mason, i.1947 (NSW.40615); Yarrabah Mission, Trinity Bay near Cairns, P. R. Messmer, 16.vii.1952 (NSW.30535); Jordan's Creek, P. R. Messmer, 11.viii.1954 (NSW.30537); Babinda, W. W. Watts, vii.1913 (NSW.40618); Atherton district, per H. L. White, 1912 (NSW.40620); Malanda, C. T. White, i.1918 (NSW.40617); Geraldton, Johnstone River, S. W. Jackson, 1908 (NSW.40619); Rockingham Bay (NSW.40616).

The concept of *B. spectabilis* has been extended by some authors, including Schuster (1932), to include *B. serrulata*, but the latter differs in a number of characters and the two population-groups seem quite isolated (see below, under *B. serrulata*). According to Chamberlain (1912), *B. spectabilis* does not form dense stands like those of *B. serrulata*, and each plant produces fewer fronds. The species has been cultivated to some extent.

2. *B. serrulata* (W. Bull) Chamberlain in *Bot. Gaz.*, 54 (1912), 419.

Basionym: *B. spectabilis* Hook. ex Hook. f. [var.] *serrulata* W. Bull, *Catal.* (1878), 4, t.5.* [Chamberlain gave the citation "(André) Chamberlain, n. comb." and referred to *B. spectabilis* Hook. f. var. *serrulata* André, *Ill. Hort.*, 26 (1879), 184, t.366. However, André did not publish this as a new variety of his own; he cited it as "Hort. Angl." and his plate is identical with Bull's original, though he made no explicit reference to Bull. The same plate, with similar descriptions, and references to Bull's *Catalogue*, was reproduced also by T. Moore in *Florist and Pomologist* (July, 1878), 107, as "*Bowenia spectabilis serrulata*", as well as in *Gartenflora*, 27 (1878), 314, and in *Ill. Gartenz. Stuttgart*, 23 (1879), 99, t.15, as *B. spectabilis* var. *serrulata*. Since Bull's was the original valid publication of the variety from which the others were derived, it should be cited as the basionym. Despite the custom of citing the author of the variety in parentheses, the specific name *B. serrulata* dates, for purposes of priority, only from 1912.]

Typification: The description was taken from a living (vegetative) plant in Bull's collection in London; his plate must serve as HOLOTYPE. It unmistakably represents the present species.

Synonymy: *B. spectabilis* Hook. ex Hook. f. var. *serrata* F. M. Bail., *Syn. Queensl. Fl.* (1883), 501; *Queensl. Fl.*, 5 (1902), 1507.

In most respects similar to *B. spectabilis*, but differs as follows: Caudex subterranean, subspherical, to 20–25 cm. (or more) diam., with 5–20 short slender frond- and cone-bearing branches. Fronds (of well-developed plants) ca. 5–30, the pinnules sharply serrate (except in the lower $\frac{1}{4}$ – $\frac{1}{2}$) with rather pungent teeth 1–3 mm. long, sometimes also a few of them coarsely lacerate as (occasionally) in *B. spectabilis*. [There may be some difference in the cones, of which I have no material, but none is recorded.]

Chromosome number: $2n = 18$.

Distribution: Central eastern Queensland, in the vicinity of Rockhampton, in eucalypt (dry sclerophyll) forest.

Specimens examined: QUEENSLAND: Byfield, Busch, x.1916 (NSW.40621); Byfield, O. D. Evans, iv.1924 (SYD). Described also from cultivated material.

Though it has been treated by many authors, including the most recent monographer (Schuster, 1932), as a variety of *B. spectabilis*, *B. serrulata* differs consistently from the northern plants, as pointed out by Chamberlain (1912), in the serration of the pinnules (a condition quite distinct from the coarse laceration found in both species), the subspherical shape of the caudex and the more numerous frond-bearing branches. These characteristics are maintained in cultivation, given suitable conditions for full development (in pots, *B. serrulata* often grows poorly and produces few fronds). Furthermore, the populations are quite isolated in nature and occupy rather different ecological niches (unlike *B. spectabilis*, *B. serrulata* grows in rather dry sclerophyll forest and forms fairly dense and extensive stands). They thus agree with any reasonable concept of specific distinction, since each is now evolutionarily independent and differs materially from the other.

B. serrulata is sometimes grown in gardens and conservatories for its ornamental fronds.

INDEX OF NAMES.

Names accepted in this revision (Part II only) appear in SMALL CAPITALS, with reference to their numbers in the formal section (I, 1, etc.). Valid synonyms, in *italic*, are referred to their correct nomenclatural position (in roman) as determined by the identity of their types. Invalid *nomina nuda* and misapplications are not cited (for Schuster's misapplications see Table 1, p. 74). All epithets are decapitalized and terminations in "-i/-ii" are given in the

* I am indebted to Dr. R. Melville of the Royal Botanic Gardens, Kew, for copies of the descriptions in Bull's *Catalogue* and the Stuttgart *Gartenzeitung*. In *Index Londinensis* the entry in the latter publication is wrongly given as "*B. serrata*". In fact, it appeared as "*Bowenia spectabilis*, Hooker, var. *serrulata*". Previous to Bull's valid publication the trinomial appeared in *Gard. Chron.*, n.s., 8 (1877), 310, as a *nomen nudum*.

correct form as authorized by the I.C.B.N. (1956), irrespective of the original. Other misspellings are given in quotation marks.

BOWENIA Hook. ex Hook. f. (1863). III.

BOWENIA SERRULATA (W. Bull) Chamberlain (1912). III, 2.

B. SPECTABILIS Hook. ex Hook. f. (1863). III, 1.

B. spectabilis var. *serrata* F. M. Bail. (1883) = *B. serrulata*.

B. spectabilis [var.] *serrulata* W. Bull (1878) = *B. serrulata*.

Catakidozamia W. Hill (1865) = *Lepidozamia*.

Catakidozamia hopei W. Hill (1865) = *Lepidozamia hopei*.

Cycas riedlei Fisch. ex Gaudich. (1826) = *Macrozamia riedlei*.

Encephalartos sect. *Lepidozamia* (Regel) Miq. (1863) = *Lepidozamia*.

Encephalartos sect. *Macrozamia* Miq. (1863) = *Macrozamia* sect. *Macrozamia*.

Encephalartos sect. *Parazamia* Miq. (1863) = *Macrozamia* sect. *Parazamia*.

Encephalartos denisonii (C. Moore and F. Muell.) F. Muell (1859) = *Lepidozamia peroffskyana*.

E. douglasii F. Muell. (1883) = *Macrozamia miquelii*.

E. dyeri F. Muell. (1885) = *Macrozamia riedlei*.

E. fraseri (Miq.) Miq. (1863) = *Macrozamia riedlei*.

E. macdonnellii F. Muell. ex Miq. (1863), (*sphalm.* "*macdonelli*") = *Macrozamia macdonnellii*.

E. miquelii F. Muell. (1862) = *Macrozamia miquelii*.

E. moorei (F. Muell.) F. Muell. (August, 1881) = *Macrozamia moorei*.

E. oldfieldii Miq. (1863) = *Macrozamia riedlei*.

E. pauli-guilielmi (W. Hill and F. Muell.) F. Muell. (1859) = *Macrozamia pauli-guilielmi* ssp. *pauli-guilielmi*.

E. preissii (Lehm.) F. Muell. (1859) = *Macrozamia riedlei*.

E. spiralis (Salisb.) Lehm. (1834) = *Macrozamia spiralis*.

E. spiralis var. *diplomera* F. Muell. (1866) = *Macrozamia diplomera*.

E. spiralis var. *major* Miq. (1863) = *Macrozamia miquelii*.

LEPIDOZAMIA Regel (1857). I.

Lepidozamia denisonii (C. Moore and F. Muell.) Regel (1875) = *L. peroffskyana*.

LEPIDOZAMIA HOPEI Regel (1876). I, 1.

[*L. hopeites* (Cookson) L. Johnson (1959), *sp. foss.* See under I, 1.]

L. PEROFFSKYANA Regel (1857). I, 2.

MACROZAMIA Miq. (1842). II.

Macrozamia sect. *Genuinae* Miq. (1868), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Lepidozamia* (Regel) Miq. (1868) = *Lepidozamia*.

MACROZAMIA sect. MACROZAMIA. II, i.

Macrozamia sect. *Monooccidentales* Schuster (1932), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Monoorientales* Schuster (1932) *nom. illegit.* = *Lepidozamia*.

MACROZAMIA sect. PARAZAMIA (Miq.) Miq. (1868). II, ii.

Macrozamia sect. *Polyorientales* Schuster (1932), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Polyorientales* subsect. *Acutae* Schuster (1932) = *M.* sect. *Parazamia*.

Macrozamia sect. *Polyorientales* subsect. *Attenuatae* Schuster (1932), *nom. illegit.* = *M.* sect. *Macrozamia*.

Macrozamia sect. *Polyorientales* subsect. *Curvatae* Schuster (1932) = *M.* sect. *Parazamia*.

MACROZAMIA COMMUNIS L. Johnson (1959). II, 5.

M. corallipes Hook. f. (1872) = *M. spiralis*.

M. cylindrica C. Moore (1884) = *M. miquelii*.

M. denisonii C. Moore and F. Muell. (1858) = *Lepidozamia peroffskyana*.

M. denisonii var. *hopei* (W. Hill) Schuster (1932) = *Lepidozamia hopei*.

M. DIPLOMERA (F. Muell.) L. Johnson (1959). II, 6.

M. douglasii W. Hill ex F. M. Bail. (1883) = *M. miquelii*.

M. dyeri (F. Muell.) C. A. Gardn. (1930) = *M. riedlei*.

M. FAWCETTII C. Moore (1884). II, 14.

M. flexuosa C. Moore (1884) = *M. pauli-guilielmi* ssp. *flexuosa*.

M. fraseri Miq. (1842) = *M. riedlei*.

M. HETEROMERA C. Moore (1884). II, 11.

M. heteromera var. *dicranophylloides* Schuster (1932) = *M. stenomera*.

M. heteromera var. *glauca* C. Moore (1884) = *M. heteromera*.

M. heteromera var. *tenuifolia* C. Moore (1884) = *M. stenomera*.

M. heteromera var. *tenuifolia* Schuster (1932), *nom. illegit.* = *M. stenomera*.

M. heteromera var. *tenuifolia* f. *harmsii* Schuster (1932) = *M. heteromera*.

M. hopei W. Hill ex F. M. Bail. (1886) = *Lepidozamia hopei*.

[*M. hopeites* Cookson (1953), *sp. foss.* = *Lepidozamia hopeites*.]

M. LUCIDA L. Johnson (1959). II, 8.

M. MACDONNELLII (F. Muell. ex Miq.) A.D.C. (1868). II, 3.

M. mackenzii Hort. ex Mast. (1877) = *M. miquelii*.

M. macleayi Miq. (1868) = *M. miquelii*.

M. MIQUELII (F. Muell.) A.D.C. (1868). II, 4.

M. MOOREI F. Muell. (March, 1881). II, 1.

- M. mountperriensis* F. M. Bail. (1886) = *M. miquelii*.
M. oldfieldii (Miq.) A.D.C. (1868) = *M. riedlei*.
M. PAULI-GUILIELMI W. Hill and F. Muell. (1859). II, 13.
M. PAULI-GUILIELMI ssp. *FLEXUOSA* (C. Moore) L. Johnson (1959). II, 13c.
M. PAULI-GUILIELMI ssp. *PAULI-GUILIELMI*. II, 13a.
M. PAULI-GUILIELMI ssp. *PLURINERVA* L. Johnson (1959). II, 13b.
M. peroffskyana (Regel) Miq. (1868) = *Lepidozamia peroffskyana*.
M. PLATYRACHIS F. M. Bail. (1898). II, 7.
M. plumosa Hort. ex Mast. (May, 1875) = (probably) *M. pauli-guilielmi* ssp. *pauli-guilielmi*.
M. plumosa Hort. ex auct. anon. (June, 1875) = *M. pauli-guilielmi* ssp. *pauli-guilielmi*.
M. preissii Lehm. (1844) = *M. riedlei*.
M. preissii ssp. *dyeri* (F. Muell.) Schuster (1932) = *M. riedlei*.
M. RIEDLEI (Fisch. ex Gaudich.) C. A. Gardn. (1930), ("*riedlei*"). II, 2.
M. SECUNDA C. Moore (1884). II, 10.
M. secunda var. *dichotoma* C. Moore and Betche (1893) = (probably) *M. heteromera* × *M. secunda*.
M. SPIRALIS (Salisb.) Miq. (1842). II, 9.
M. spiralis var. *?corallipes* (Hook. f.) Benth. (1873) = *M. spiralis*.
M. spiralis var. *?cylindracea* Benth. (1873) = *M. pauli-guilielmi* (ssp.?).
M. spiralis var. *cylindrica* Regel (1876), *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *cylindrica* (C. Moore) Maid. and Betche (1916), *nom. illegit.* = *M. miquelii*.
M. spiralis var. *diplomera* (F. Muell.) A.D.C. (1868) = *M. diplomera*.
M. spiralis var. *?diplomera* F. Muell. ex Benth. (1873) = *M. diplomera*.
M. spiralis var. *eximia* Regel (1876) *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *fawcettii* (C. Moore) Maid. and Betche (1916) = *M. fawcettii*.
M. spiralis var. *flexuosa* (C. Moore) Maid. and Betche (1916) = *M. pauli-guilielmi* ssp. *flexuosa*.
M. spiralis var. *fraseri* Regel (1876), *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *heteromera* (C. Moore) Maid. and Betche (1916) = *M. heteromera*.
M. spiralis var. *hillii* Regel (1876), *nom. dub.* = *M. miquelii* or *M. communis*.
M. spiralis var. *?secunda* Benth. (1873) = *M. secunda*.
M. spiralis var. *secunda* (C. Moore) Maid. and Betche (1916) = *M. secunda*.
M. STENOMERA L. Johnson (1959). II, 12.
[*M. tridentata* (Willd.) Regel. See list of excluded and dubious names, below.]
M. tridentata ssp. *cylindrica* (C. Moore) Schuster (1932) = *M. miquelii*.
M. tridentata ssp. *cylindrica* var. *corallipes* (Hook. f.) Schuster (1932) = *M. spiralis*.
M. tridentata ssp. *cylindrica* var. *corallipes* f. *dielsii* Schuster (1932) = *M. spiralis*.
M. tridentata ssp. *cylindrica* var. *corallipes* f. *vavilovii* Schuster (1932), *nom. dub.* = *M. miquelii* or *M. communis*.
M. tridentata ssp. *cylindrica* var. *corallipes* f. *wallsendensis* Schuster (1932) = *M. communis*.
[*M. tridentata* ssp. *cylindrica* var. *pungens* (Ait.) Schuster (1932), *nom. dub.* (quoad typ.) = *Encephalartos* sp. ?]
M. tridentata ssp. *cylindrica* var. *pungens* f. *diplomera* (F. Muell.) Schuster (1932) = *M. diplomera*.
M. tridentata ssp. *cylindrica* var. *pungens* f. *hillii* Schuster (1932), *nom. dub.* = *M. miquelii* or *M. communis*.
M. tridentata ssp. *cylindrica* var. *secunda* (C. Moore) Schuster (1932) = *M. secunda*.
M. tridentata ssp. *mountperriensis* (F. M. Bail.) Schuster (1932), ("*mountperriensis*"), = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *douglasii* (F. Muell.) Schuster (1932) = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *mackenzii* (Hort. ex Mast.) Schuster (1932) = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *miquelii* (F. Muell.) Schuster (1932), *nom. illegit.* = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *miquelii* f. *milkaui* Schuster (1932), *nom. illegit.* = *M. miquelii*.
M. tridentata ssp. *mountperriensis* var. *miquelii* f. *oblongifolia* (Regel) Schuster (1932) = *M. miquelii*.
M. tridentata var. *oblongifolia* Regel (1876) = *M. miquelii*.
Zamia spiralis Salisb. (1796) = *Macrozamia spiralis*.

EXCLUDED AND DUBIOUS NAMES.

This list includes only names which are wholly dubious, possibly not being based on Australian plants at all. Names which can be placed to within a couple of species are included in the Index, above.

- Encephalartos pungens* (Ait.) Lehm., *nom. dub.* = *Encephalartos* sp.? See under II, 5 and 9.
E. tridentata (Willd.) Lehm., *nom. dub.* = *Macrozamia* or *Encephalartos* sp.? (juvenile). See under II, 4, 5 and 9.
Macrozamia tridentata (Willd.) Regel, *nom. dub.* (quoad basionym.) = *Macrozamia* or *Encephalartos* sp. (juvenile). See under II, 4, 5 and 9.

- M. tridentata* ssp. *cylindrica* var. *pungens* (Ait.) Schuster, *nom. dub.* (quoad basionym.) = *Encephalartos* sp.? See under II, 5 and 9.
Zamia pallida Salisb., *nom. dub.* = *Encephalartos* or *Macrozamia* sp.? (juvenile). See under II, 5.
Z. pungens Ait., *nom. dub.* = *Encephalartos* sp.? See under II, 5 and 9.
Z. tridentata Willd., *nom. dub.* = *Macrozamia* or *Encephalartos* sp.? (juvenile). See under II, 4, 5 and 9.

Acknowledgements.

My thanks are due to Mr. R. H. Anderson, Chief Botanist and Curator, National Herbarium, Royal Botanic Gardens, Sydney, for making this work possible, and to the past Directors of the Melbourne and Brisbane Herbaria for the opportunity to examine several specimens. Dr. Joyce Vickery has given generously of her time and experience in the discussion of some of the difficult matters of typification and nomenclature which abound in *Macrozamia*; responsibility for the decisions, however, rests with myself. Dr. R. Melville of Kew has been most helpful in sending me copies of obscure references. Miss D. P. Ragg, Librarian at the National Herbarium, has shown great patience and enterprise in obtaining many rare publications.

Dr. Isabel Cookson freely discussed with me her work on frond anatomy in *Macrozamia* and *Lepidozamia*, and some of her unpublished findings, though not specifically mentioned in this revision, have helped to influence and confirm my judgements. But for Mr. G. Chippendale, Botanist, Animal Industry Division, Alice Springs, I should not have been able to examine *Macrozamia macdonnellii* in the field. Mr. N. Forde had earlier sent me excellent material and photographs of this species. Finally, I thank all of my colleagues at the National Herbarium for co-operation in various ways, and particularly Mr. E. F. Constable, Official Collector, for his efforts and companionship in the field, especially in the re-discovery of the magnificent *M. moorei* in New South Wales.

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ROOT PARASITISM IN *ATKINSONIA LIGUSTRINA* (A. CUNN. EX F. MUELL.)
F. MUELL.

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(Fourteen Text-figures.)

[Read 29th April, 1959.]

Synopsis.

A brief survey is given of the terrestrial Loranthaceae. The structure of haustoria of *Atkinsonia ligustrina* (A. Cunn. ex F. Muell.) F. Muell. is described and compared with that found in some other phanerogamous root parasites.

INTRODUCTION.

The family Loranthaceae contains several hundred species, nearly all being parasitic shrubs growing on the branches of trees. Terrestrial species include *Nuytsia floribunda* R.Br., the Christmas tree of Western Australia, several South American species of *Gaiadendron* G. Don, *Loranthus terrestris* Hook. f. and *L. ligustrinus* Wall. in India, *L. buchneri* Engl. in Africa and *Atkinsonia ligustrina*, which occurs sporadically on dry rocky ridges in a restricted area of the Blue Mountains of New South Wales. Various authors, including Danser (1933), Moore and Betche (1893), Ruiz (1940) and Skene (1924), state that some or all of these terrestrial species are non-parasitic, though it should be remembered that with the older writers "non-parasitic" may merely mean "non-epiphytic". Hooker (1890) stated that *Loranthus ligustrinus* is "apparently terrestrial, a root parasite?", and referred to *L. terrestris* as follows: "always growing from the ground and hence probably a root parasite. Dr. Thomson and I gathered this plant at seven or eight localities and never found it attached to an aerial tree branch." Welwitsch (Hiern, 1900) found *L. buchneri* "growing parasitically on the roots of a Malvacea (probably a species of *Sida*), though at first sight terrestrial and not parasitical".

Herbert (1919) has shown that *Nuytsia floribunda* is a root parasite, as was indeed conjectured by Harvey in 1854 (Anonymous, 1869). It attacks a wide range of hosts, including both native and introduced species. The question whether the species of *Gaiadendron* are parasitic or not seems to have been little studied. Ruiz (1940) describes *Loranthus luteus*, presumably one of the species now referred to *Gaiadendron*, as a tree ten to twelve yards high, very beautiful on account of its abundance of yellow flowers, and not parasitic. MacBride (1937) cites in this genus two species referred to *Loranthus* by Ruiz and Pavón in 1802, and to *Phrygilanthus* in 1868 by Eichler. These species, *Gaiadendron ellipticum* (Ruiz et Pavón) Baehni ex MacBride and *G. lanceolatum* (Ruiz et Pavón) Baehni ex MacBride, he states to be "as far as is known, parasitic shrubs". *Gaiadendron*, on this interpretation, appears to contain both terrestrial and epiphytic species. One of the former, *G. punctatum* (Ruiz et Pavón) G. Don, described as a tree over 20 m. high, seems to be the largest of the known Loranthaceae. Finally, MacBride (1937) refers, rather cryptically, to *Phrygilanthus eugenioides* (H.B. et K.) Eichler (= *G. eugenioides* G. Don) as "half-parasitic on trees or growing independently". A personal communication from Dr. M. Cárdenas of Cochabamba, Bolivia, mentions this species as growing either in the soil or as a branch parasite.

Amyema scandens (Van Tieghem) Danser seems able to grow independently in the ground for a time before attacking a host plant. A specimen (McKee 2375) of this

species collected in New Caledonia had a stem two cm. in diameter, attached by many haustoria to the trunk of the host (a small tree of *Spermolepis gummifera* Brong. et Gris). Near ground level the parasitic stem became much thinner and separated from the host, entering the soil where it bore what appeared to be a poorly developed root system. The underground parts and the narrow stem immediately above them were dead, though still attached to the living parasitic stem higher up the stem of the host. *Amyema scandens* grows to a large plant climbing to the tops of tall trees, and in such cases may show no indication that it began life in the ground. Similar observations on this species, and on *Amylothea pyramidata* (Van Tieghem) Danser, have been recorded by other collectors in New Caledonia, e.g. Compton (Rendle, Baker and Moore, 1921: see description of *Loranthus glaucescens* S. Moore, a name treated by Danser (1936) as a synonym of *Amyema scandens*) and Virot (Guillaumin and Virot, 1953; Virot, 1956). It is of interest that these species seem capable of limited independent growth in the soil; they have not been adequately studied, but there is no evidence that they are ever root parasites. Later collectors have confirmed but hardly extended the following notes made by Balansa on the type specimen (Balansa 498) of *Neophyllum scandens* Van Tieghem (now *Amyema scandens* (Van Tieghem) Danser), which he collected in New Caledonia in 1869: "pourvue d'une tige ayant ses racines dans le sol même, elle grimpe au sommet des plus grands arbres, en implantant dans leur bois de distance en distance une racine qui égale souvent en grosseur la tige mère."

TAXONOMY AND NOMENCLATURE.

The species which is the subject of this paper has a somewhat involved synonymy. It was discovered by Allan Cunningham in 1817. He named it *Nuytsia ligustrina*, the name being first published by Lindley (1839), who, however, gave no description. The first description was that of Mueller (1861) who retained Cunningham's name, but later (Mueller, 1865), having received fruiting material, removed the species from *Nuytsia* and erected a new genus *Atkinsonia* for it, named after Miss L. Atkinson, who collected extensively in the Blue Mountains. To quote Mueller's own words: ". . . dicavi praeclarae Ludovicae Atkinson, cujus benignitate hanc et multas alias Neo-Cambriae plantas debeo." The genus has had a chequered history. Bentham and Hooker (1883) sank it in *Loranthus*, while Engler (1894) referred the single species to *Gaiadendron*. Later (Engler, 1897), he divided that genus into two sections: *Eugaiadendron*, containing the South American species, and *Atkinsonia* with one Australian species. Finally, Engler and Krause (1935) restored *Atkinsonia* as a separate genus, the distinguishing character being that in *Gaiadendron* the flowers are in racemes of triads and in *Atkinsonia* in simple triads. Two names cited by Jackson (1895), apparently as distinct, may refer to the present species. These are *Loranthus atkinsoniae* Benth. and *L. epigaeus* F. Muell. Mueller (1865) cites the latter as a synonym, but seems not to have published it; Danser (1933) cites it as *L. epigaeus* Jacks. The specific name *ligustrinus* is preoccupied in *Loranthus* by *L. ligustrinus* Wall., an Indian species. The present species is figured (as *L. atkinsoniae* Benth.) by Oliver (1880) and by Blakely (1922, Plate XXVIII). The only previously published investigation of its parasitism, except for a preliminary note (McKee, 1952) by one of the present authors, appears to be due to Blakely (1922), who examined the roots of several plants without finding haustoria.

DISTRIBUTION AND HOST RANGE.

The species is known only from the Blue Mountains of New South Wales, where it occurs sporadically, often on dry rocky ridges. It is not common, but is usually found in groups of from two to twenty plants. A suggestion that it occurs outside the Blue Mountains comes from Mueller (1860), who states that it "occurs in the Blue Mountains and is said to be found also on the north-eastern tributaries of the Darling". This suggests a northwards extension of the range of the species, but the phrase used is rather vague, as some of the headwaters of the Macquarie, which could be considered a "north-eastern tributary of the Darling", rise in the Blue Mountains, while other rivers

rising as far north as the Carnarvon Ranges in Queensland flow, occasionally at least, to the Darling. Specimens in the National Herbarium, Sydney, all come from the comparatively small area bounded by Linden, Mount Victoria and Mount Wilson, with one outlying locality at Marrangaroo. Material used in the present study came from Woodford and Linden.

A. ligustrina has been reported (McKee, 1952) to form haustoria on the roots of several hosts, including *Acacia intertexta* Sieb., *Platysace linearifolia* (Cav.) Norman (syn. *Trachymene linearis* Spreng.) and the narrow-leaved form of *Leptospermum attenuatum* Sm. Haustoria have also been observed on the roots of *Monotoca scoparia*

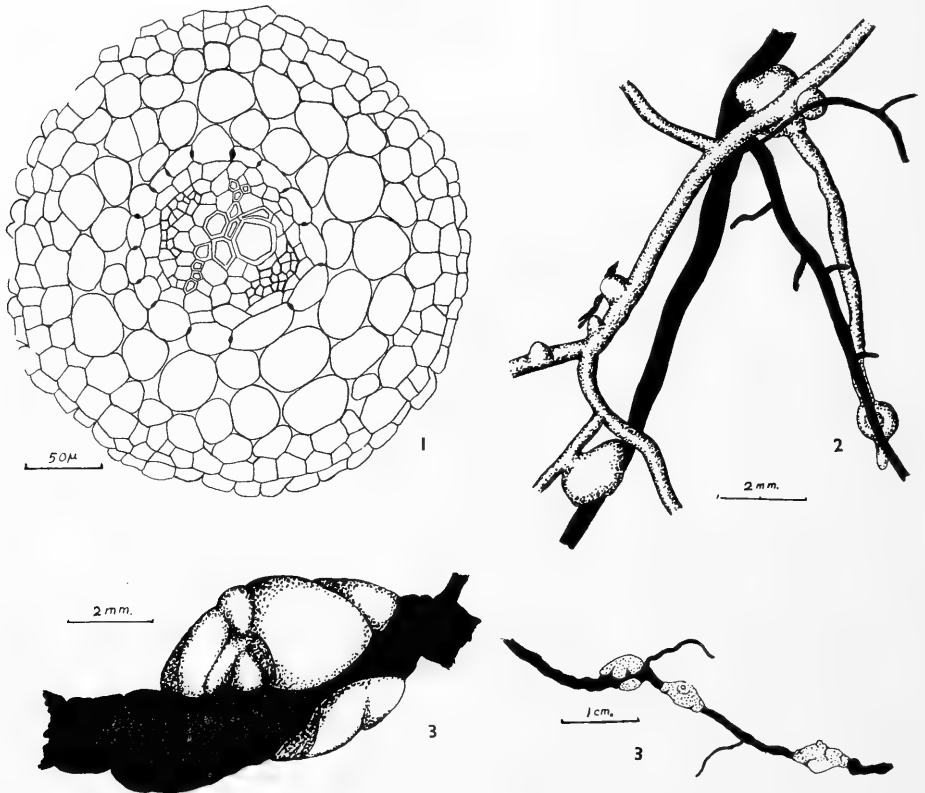


Fig. 1.—Cross-section of a root of *Atkinsonia*.

Fig. 2.—Young roots of *Atkinsonia* (stippled) showing branching and haustoria attacking the host (solid black).

Fig. 3.—An haustorium almost completely surrounding the host root.

R.Br. and *Caustis* sp. The haustoria examined in the present work were growing on the roots of *Acacia intertexta*, *Leptospermum attenuatum* and *Dillwynia ericifolia* Sm. No pronounced differences in behaviour were observed between haustoria on any of these hosts.

ROOT SYSTEM AND HAUSTORIA.

The late Dr. J. McLuckie made preliminary studies on the root system and haustoria of *A. ligustrina*, and raised seedlings which made considerable development in the absence of host plants. His seedlings, preparations and notes were unfortunately lost after his death in 1956. Seedlings were not studied during the present investigation, since a bush fire destroyed the above-ground parts of the plants from which our material was taken. The plants have since developed new shoots, but it will be some

time before they fruit again. For this reason the following account deals only with the root system and haustoria of established plants.

A. ligustrina is a shrub with a large number of leading shoots, growing to a height of about one metre. The root system is entirely subterranean, consisting of five or six fleshy primary roots which rapidly turn blue when damaged. Lateral roots, bearing the haustoria, are freely produced but short-lived. Thus the older primary roots are almost unbranched and bear numerous scars of fallen laterals. Young lateral roots are entirely devoid of root hairs, though Blakely (1922) recorded the presence of numerous root hairs on lateral roots of seedlings.

Internally, the structure of the root is comparable with that of other dicotyledons. The apical meristem consists of a small group of cells giving rise to the root tissue and also to a small root cap of about three rows of cells. Differentiation of vascular



Fig. 4.—Cross-section through union of haustorium (stippled) and host (*Leptospermum*). The solid black represents vascular tissue of the haustorium and the broken lines, zones of collapsed cells.

tissue tends to occur early, often less than 100μ from the tip. The mature root is diarch with a well-developed endodermis with distinct casparian bands (Fig. 1). Secondary growth takes place in the normal manner. Periderm is superficial and limited in extent. Branch roots arise in the usual endogenous manner in the pericycle opposite a protoxylem group.

Haustroria arise exogenously in the cortex of the root, their position being unrelated to the orientation of the parent root. They arise near the root tip, but their position is always lateral. They occur singly or in groups. It is possible that their development requires an external stimulus, perhaps proximity to a host root, but without seedlings this could not be investigated. The haustoria are often irregular in shape and may grow out some little distance before reaching a host root. The decayed remains of

numbers of young haustoria were found: these had presumably failed to make contact with a host.

When the host is reached, the haustorium flattens into a disc which attaches itself to the root (Fig. 2). This disc extends more or less evenly in all directions, wrapping itself round the host (Fig. 3). The disc may completely surround a small root, its originally separate parts joining with scarcely any line of division.

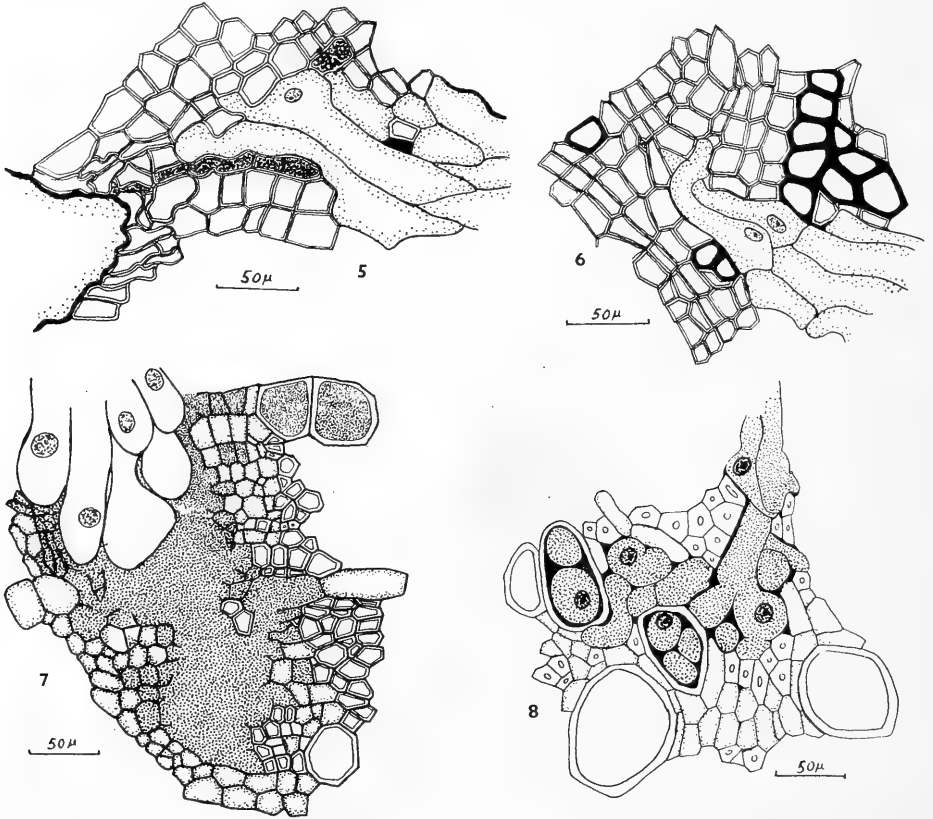


Fig. 5.—Cross-section of parasite union showing elongated cells of the haustorium (stippled) forcing apart the cells of the host xylem. The way in which the parenchyma ray cells have been pushed apart is particularly well shown. (Host *Acacia*.)

Fig. 6.—Cross-section of union of parasite and host, showing the elongated cells at the margin of the haustorium (stippled) which have forced apart the xylem cells of the host (*Acacia*).

Fig. 7.—Cross-section of part of an haustorium (cells left empty) growing through the region of the cambium of the host. In advance of the haustorium is a mass of yellowish material (dense stippling), and some of the same material can be seen in the vessels in the adjacent xylem. Many partly dissolved cells can be seen in the cambial region. (Host *Dillwynia*.)

Fig. 8.—Cross-section of host xylem and haustorium (stippled). In this older union the elongated cells at the margin of the haustorium are surrounded by yellowish material (shown black). Some elongated cells have entered the vessels of the host and grown along with them.

The disc at this stage has a central axis of meristematic tissue surrounded by vacuolated parenchyma. The cells on the attaching surface are elongated with dense contents and large nuclei. At an early stage a zone of collapsed cells appears, extending from the axis to the edges of the disc. Similar zones are found in the haustoria of other semi-parasites.

An outgrowth from the middle of the attached surface of the disc penetrates the host, partly dissolving, but chiefly forcing its way through the epidermis or cork into the cortex. Subsequent behaviour of the haustorium depends on the size of the host root. On a small root it may grow straight into the xylem, sometimes splitting the cylinder open. In a larger root, it may first extend tangentially in the host cortex, disrupting it to such an extent that groups of cortical cells may become embedded in the haustorial tissue. This process of radial growth and lateral expansion may be repeated in cortex, phloem, cambium and finally xylem, so that a complicated system of overlying discs on a central shaft is produced (Fig. 4). Finally the haustorium may grow radially right through the middle of the xylem cylinder.

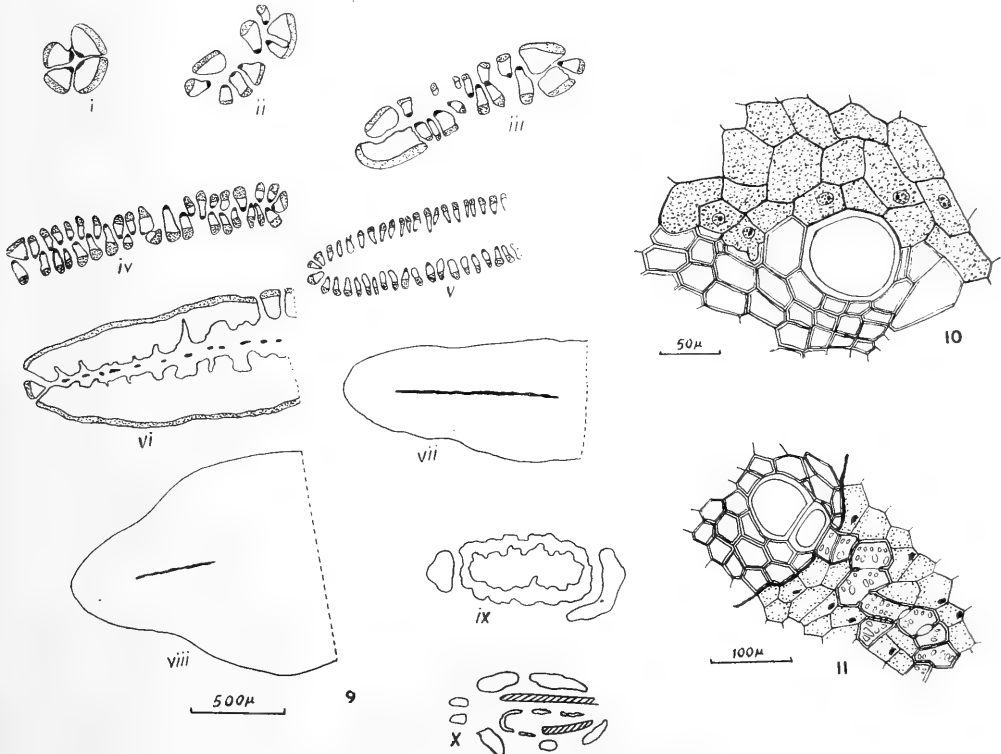


Fig. 9.—I-X. Cross-sections cut at successive levels in the haustorium to show the changes in orientation of the vascular tissue. See text for details. Phloem stippled, xylem clear, host xylem cross-hatched.

Fig. 10.—Xylem union between host and haustorium: young stage in which cells of the haustorium (stippled) are closely adpressed to the vessels of the host. (Host *Acacia*.)

Fig. 11.—Xylem union between host and haustorium: older stage in which the haustorial cell in contact with the host vessel has been differentiated into a xylem vessel segment which links up with the main vascular tissue of the haustorium. (Host *Acacia*.)

The advancing edges both of disc and shaft of the haustorium are composed of greatly elongated cells which have dense contents and large nuclei (Figs. 5, 6) and seem to force the opposing tissue apart. The cells are, nevertheless, quite plastic and in the xylem fit neatly into the gaps they have made (Fig. 5). In the phloem or cortex the cells reach their greatest size and are often embedded in masses of gummy material (Fig. 7). A similar gummy material is found in host xylem vessels near haustoria. It may result from a wound reaction by the host, or from the dissolving of host cells by the haustorium. Elongated haustorial cells sometimes grow inside vessels of the host. The margin of the haustorium is composed of glandular cells smaller than those just described, but also probably able to dissolve host tissue (Fig. 8).

The development of the vascular system of the haustorium begins near the parent root with two or four groups of xylem, each with an associated phloem group (Fig. 9). Within a few millimetres these groups break up to form a small irregular ring of open, collateral bundles as in *Dendrophthoë falcata* (Singh, 1954) and *Loranthus micranthus* (Menzies, 1954). At first the bundles tend to lie side by side with the relative positions of the xylem and phloem alternating in alternate bundles. Then the number of bundles increases and they become arranged in an ellipse. Further down (but still outside the host) the proportion of vascular tissue increases, the xylem consisting of a solid, somewhat squashed cylinder of cubical, reticulate vessels surrounded by what appears to be procambial or cambial tissue which differentiates into more xylem. No phloem was recognized at this level or below. Sections of the haustorium within the host plant show the xylem cylinder breaking up into a number of branches going out into the haustorial discs.

Connections between xylem of host and parasite are easily found round the margins of the haustoria inside the xylem. In early stages a meristematic cell of the haustorium

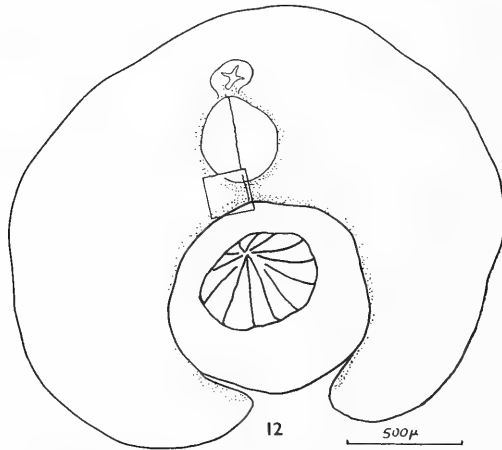


Fig. 12.—Section through host and parasite. No penetration of the host has yet taken place and a "gland" is a conspicuous feature of the haustorium. (Host *Leptospermum*.)

is closely appressed to a host vessel (Fig. 10). This cell later matures into a reticulate or pitted vessel which is continuous with the vascular system of the haustorium (Fig. 11). Zones of collapsed cells occur in all parts of the haustorium, but the conspicuous zones found round each xylem connection in *Loranthus micranthus* are absent in *Atkinsonia*.

The life of an haustorium appears to be relatively short. The haustoria found varied from a millimetre to a centimetre in diameter, but this variation appears to be related to size of root attacked rather than to age. They were all yellowish in colour and in all the vascular tissue had developed to approximately the same extent. Large woody haustoria with considerable secondary thickening, such as one sees in *Loranthus*, were not found. It seems probable that lateral roots and haustoria last only about a year and are then replaced by new ones.

HAUSTORIAL "GLANDS".

In *Santalum album*, *Cansjera rheedii* and *Otax scandens* (Barber, 1906) and also possibly in *Thesium* (Solms-Laubach, 1867-8), the haustorium appears to contain a "gland" secreting enzymes which function in the penetration of the host. A very similar structure has been found in the haustorium of *Atkinsonia*. The shape of this "gland" is shown in Figure 12. It first appears as two rows of elongated meristematic cells, those of one row abutting closely onto those of the other. As the "gland" becomes

older these cells become longer and longer and their contents begin to withdraw from contiguous walls. This continues until the "gland" consists of two rows of empty elongate cells surrounded by a very small-celled meristematic tissue (Fig. 13). Finally the elongated cells disappear altogether, leaving a cavity filled with red-staining amorphous material and fragments of cell and other débris. In *Atkinsonia* such "glands" were found only in haustorial discs which had not penetrated the host, but they were not found in all discs prior to penetration. No "glands" were found in older haustoria which had entered the host, nor was there any trace that a "gland" had ever been present. The "glands" appear to occupy the position taken up by the procambial tissue in haustoria which have penetrated the host. The orientation of the haustorial tissues round the "gland" also suggests that it is an abnormality following failure to penetrate the host rather than a transient feature of the normally developing haustorium. A possible sequence of events is that the penetration process grows out

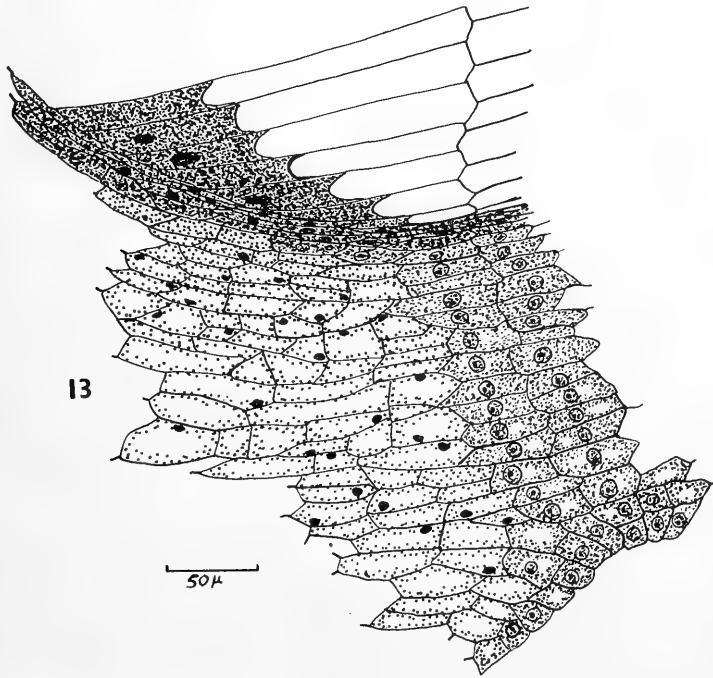


Fig. 13.—Detail of portion of Fig. 12 in the region of the "gland". The contents of the cells of the "gland" have contracted considerably. The tissues round the "gland" have dense contents and appear to have been considerably compressed. The density of the stippling indicates the density of the cell contents.

from the middle of the attachment disc, but, unable for some reason to penetrate the host, is forced back into the attachment disc and its elongated cells begin to digest one another. This would account for the pieces of débris, apparently not belonging to the haustorium itself, which are found within old "glands".

The structures figured by Barber (1906) for *Santalum album* show many similarities with those described above. Most of the "glands" he illustrates are in haustoria which have made little or no penetration, and he notes that the presence of a "gland" before penetration is not invariable. The peculiar structure he interprets as the "opening-up" of a "gland" would be more easily understood as a stage in "gland" formation on our interpretation. A similar example in a young haustorium of *Atkinsonia* has been found (Fig. 14): this could only be interpreted as the closing-up of a developing "gland". A difficulty encountered both with *Santalum* and *Atkinsonia* is that very few stages are found in which the haustorium is in the act of passing

through the cortex. This must be due to the fact that this stage is passed through very quickly.

McLuckie studied the haustoria of *Olax stricta* R.Br., a brief summary of his results being given by McLuckie and McKee (1954), and some observations on the same species were made in connection with the present work. *Olax* also shows a haustorial gland somewhat resembling those found in *Atkinsonia* and *Santalum*. Further investigation on a wider range of material is desirable to permit detailed comparison of the structures in *Olax* with those of the other two genera.

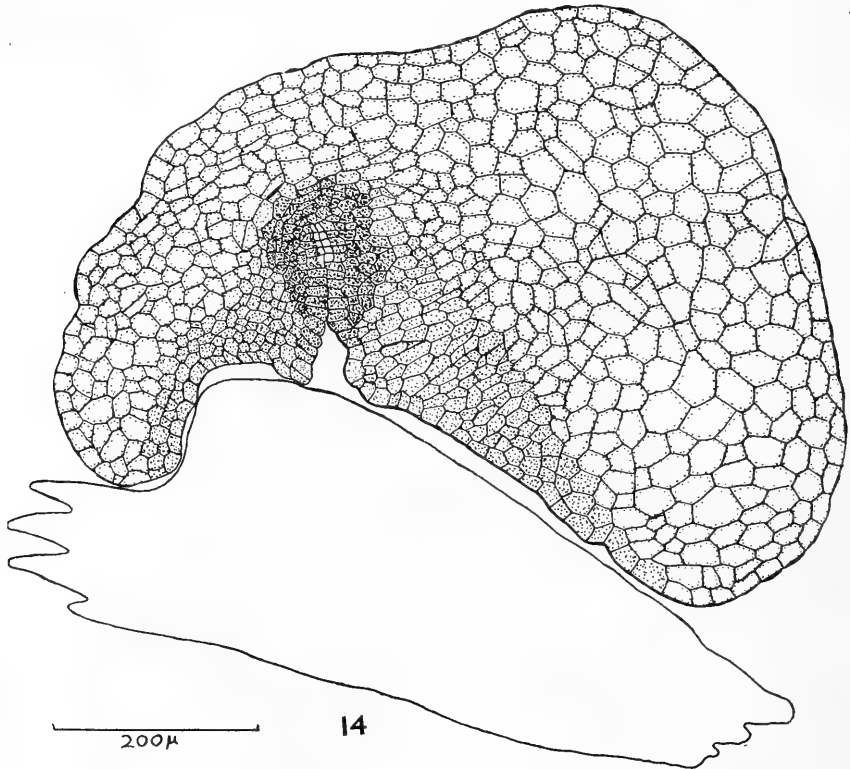


Fig. 14.—Young haustorium (stippled) in contact with the host.

No reference has been found to a "gland" of this type in aerial members of the Loranthaceae. It is interesting that a structure found in two families of root parasites should occur also in a root parasite belonging to a family composed predominantly of branch parasites.

Acknowledgements.

The authors wish to thank Miss I. Bowden, Woodford, N.S.W., for indicating the position of the plants which provided most of the material studied; the late Dr. J. McLuckie for encouragement and co-operation in the early stages of the work; and the following for helpful correspondence or discussion: Dr. S. T. Blake (Brisbane), Dr. M. Cárdenas (Cochabama, Bolivia), Prof. A. Guillaumin (Paris), Mr. L. A. S. Johnson (Sydney), Prof. D. Thoday (Bangor), Dr. R. Virot (Paris).

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DESCRIPTIONS OF TWO NEW SPECIES OF *CURIS* AND ONE NEW SPECIES OF
STIGMODERA (BUPRESTIDAE).

By C. M. DEUQUET.
(Three Text-figures.)

[Read 29th April, 1959.]

Synopsis.

Descriptions are given of two new species of *Curis* (*C. adamsi* and *C. zecki*) from Central Queensland, and of one species of *Stigmodera* (*Stig. zecki*) from Stanthorpe district, Southern Queensland.

CURIS ADAMSI, n. sp.

Elongate, rather flat, especially the prothorax.

Head bright green with fiery reflections, clypeus brilliant green. Pronotum purple-blue on disc area with narrow medial vitta varicolarous, green being the dominant shade, side margins a fiery coppery colour. Elytra dark bluish, with the base, lower part of suture from past middle to 4 mm. from apex and mesosternal side bright metallic green showing fiery coppery green reflections before their junction with the darker ground colour. Legs and antennae dark metallic blue. Underside: thoracic sternum fiery opalescent red, abdominal sternites purple.

Head, fairly deeply impressed between the eyes. *Pronotum* much depressed, apex nearly straight, strongly bulging at the middle, base very irregularly sinuate, posterior angles acute and slightly produced, sides unusually wide behind middle; disc with a wide depression terminated by a large basal fovea; and two shallow lateral depressions finely punctate, the punctation more apparent at the brightly illuminated sides. *Scutellum* dark blue, subcircular, hardly depressed in centre. *Elytra* notably depressed, narrower at shoulder than the broad prothorax, almost parallel till past middle, widening slightly before the apical convergence; apices separately and neatly rounded, the hind margins strongly serrated, the elytra noticeably shorter than the abdomen. Four costae are clearly seen on each elytron, the intervals coarsely and irregularly punctate, the surface of the elytra being decidedly rugose. *Underside* finely and closely punctate, with a sparse white pubescence. *Dimensions*: 16 to 18 by 5 to 6 mm.

Habitat: Edungalba, Central Queensland (E. E. Adams).

A strikingly beautiful species of which four examples kindly sent to me by Mr. E. Adams were examined. It is clearly distinct from previously described *Curis*, the nearest to it being *Curis aurifera* L. and G. and *Curis olivacea* Carter. It differs from both (1) by the almost total absence of any bright coloration on the discal line of its pronotum and on its basal pronotal fovea; (2) by the greater length, depth and width of this central pronotal depression; (3) by the colour pattern of its suture; (4) by its more largely exposed pygidium. From *Curis olivacea* it, moreover, differs by the coarser texture of its elytra.

Type in Coll. Adams; one paratype each to the Australian Museum, Sydney, and the author's collection.

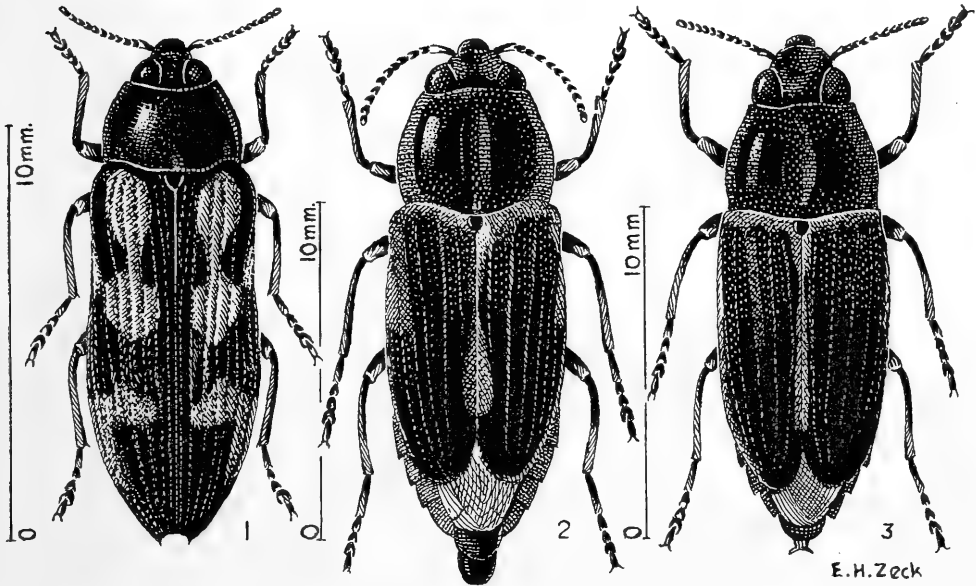
CURIS ZECKI, n. sp.

Oblong-ovate, somewhat attenuated at apex.

Head dark purplish blue, suffused with red gleams between the eyes; pronotum purplish blue with red reflections over the whole surface, but more so in the deep fovea at base; legs, antennae and underside dark metallic blue. Elytra purplish blue, the base, suture and sides bright green with golden red luminous radiations at their junction with the darker ground colour, this sutural fluorescence slightly interrupted

just past the base, widening a little past middle and coming to an end before the apex. Underside dark violet blue.

Head widely but shallowly impressed between the eyes, closely punctate. *Pronotum* apex and base bisinuate, the former strongly produced at middle, anterior angles acute, posterior sharply produced; disc with medial sulcus almost throughout, terminating with a deep and wide fovea at middle near base; finely and regularly punctate. *Scutellum* roundish, glossy, impunctate. *Elytra* wider than prothorax, shorter than body, slightly enlarged at shoulders, subparallel to past middle, thence tapering to apex; apices widely and separately rounded, margins neatly denticulate on apical part, disc irregularly punctate with three smooth costae, a considerable area of pygidium



exposed. *Underside* finely punctate, with a short cinereous pubescence. Dimensions: 15 × 5 mm.

Habitat: Edungalba, Central Queensland (E. E. Adams).

Type in Coll. Adams. One paratype each to the Australian Museum, Sydney, and to Mr. Zeck's and the author's collections.

This fine and clearly distinct species was discovered by Mr. E. Adams, an excellent and active entomologist from Central Queensland. Six examples are before me for examination. While showing some similarity to *Curis yalgoensis* Carter, it differs from it in (1) slightly smaller size, (2) colour of pronotum and elytra which is more florid in *yalgoensis*, (3) wider and deeper depression near base of pronotum, (4) different width of sutural fiery coloration, (5) wider apex, (6) pygidium more largely exposed.

In happy memory of a 40 years' sincere friendship I have given Emil Zeck's name to this rare insect.

STIGMODERA ZECKI, n. sp.

Ovata forma, paulum ad apices attenuata. Capite thoraceque aereo-viridibus, nitidis et punctulatis; elytris bronzeo-nigris, nitendibus, circum suturam majore aereis; maculis ternis flavis, apicis marginibus externis splendide sanguineis, punctato-striatis, pedibus viridi-aeneis; corpus subtus viridi-aeneum, dense albo pubescens.

Ovate, slightly attenuated behind.

Head fairly bright bronzy green; legs metallic bluish, antennae green; pronotum green with coppery gleams; elytra glossy dark blue with greenish reflections tinged

with bronze in the sutural area, with pale yellow markings as follows: female with two small roundish spots near the base almost above the shoulders, two slightly larger squarish ante-median ones situated behind the former, neither of these spots extending to the sides, a very small lateral one on the exterior margin situated about one-third of the entire length of the elytra from their base between the two previous spots and a straight anteapical fascia extending to the sides, but interrupted at suture and produced backwards along the margins down to within two mm. from the apex, this latero-produced part brightly sanguineous. With the male, the two roundish spots near the base are replaced by an oblique vitta produced downwards to meet and include the two medial spots.

Head excavated between the eyes, very closely punctate. *Pronotum* almost straight in front, strongly bisinuate at base, all angles acute, the posterior ones strongly produced, sides arcuately enlarged from apex to base, disc without medial line but showing a small basal fovea in front of the scutellum; fairly deep impressions at sides. *Scutellum* subcordate, centrally impressed. *Elytra* sharply widened behind shoulders and also past middle, fully attenuate behind, striate-punctate, the intervals more strongly raised on apical half, rounded and only minutely punctured; apex widely lunate, each elytron with wide oblique lunation and bispinose, the external spine more prominent, the sutural minute. *Underside* bronzy green, sternum with coppery tint, abdomen finely punctate, clothed with recumbent cinereous hair. Dimensions: $13 \times 4\frac{1}{2}$ mm.

Habitat: Stanthorpe district, Southern Queensland (A. Gemmell and E. Sutton).

Type in the Australian Museum, Sydney. Paratypes in E. Zeck, A. Gemmell, E. Sutton and the author's collections.

This pretty Buprest belongs to the interesting *producta* group which is confined to the eastern States of Australia, although the habitat of *Stigmodera producta* itself when described by Edw. Saunders 90 years ago was inaccurately given as Western Australia. Five examples are before me for examination. It is closely allied to *Stig. delta* Thomson, but differs as follows:

<i>Stig. delta</i> Thoms.	<i>Stig. zecki</i> , n. sp.
Average size: 14×5 mm.	$13 \times 4\frac{1}{2}$ mm.
Form more elongate.	Form more rotund.
Colour duller, less nitid.	More glossy, more glittering.
Pattern: The yellow colour of the basal vitta of the elytra nearly always reaches the margins.	It never does reach them, neither with males nor females.
Thin and smooth pronotal median line clearly visible.	Absence of pronotal median line.
Interstices more raised.	Interstices less prominent, surface of elytra smoother.
Marginal yellow stripe between the second and third leg wider and longer.	Marginal stripe thinner and shorter, almost invisible in some examples.
Sides greatly attenuated to the apex which terminates with minute oblique lunation.	Sides widely lunate with much longer external spine.

It may be mentioned that the yellow preapical fasciae and the dark blue preapical patches of *S. delta* and *S. zecki* are very different in shape and colour, and the backwards extension of the sanguineous margin also shows dissimilarities in width and length between these two species. Also that the ornamental design and coloration of the elytra of *S. zecki* is an almost exact replica of that of the dark variant of *S. delectabilis* Hope found in the Illawarra Coastal Range of N.S.W.

As a mark of appreciation of Mr. Emil Zeck's most valuable contribution to Australian entomology, it gives me great pleasure to name this new species after him.

NOTES ON AUSTRALIAN MOSQUITOES (DIPTERA, CULICIDAE). IV.

AÈDES ALBOANNULATUS COMPLEX IN VICTORIA.

By N. V. DOBROTOWSKY, Zoology Department, University of Melbourne.*

(Four Text-figures.)

[Read 29th April, 1958.]

Synopsis.

The present study has revealed that *Aë. alboannulatus* complex in Victoria consists of six forms. A comparative account of the biology and ecology of *Aë. queenslandis* and of the new forms is given. The taxonomic status of three forms is discussed. Adults of both sexes and the larvae of *Aë. rupestris*, n. sp., and *Aë. tubbutiensis*, n. sp., are described. An account is given of the variability of *Aë. queenslandis* (Strickl.) and notes on *Aë. alboannulatus* (Macq.) are added.

Most species of the *alboannulatus* group are distributed in the Oriental region and in the northern part of the Australian region. Only some species of *alboannulatus* s. str. subgroup (Knight and Marks, 1952) extend south into Victoria, South Australia and Tasmania. The two most common species of this subgroup, *Aë. alboannulatus* and *Aë. queenslandis*, have been previously recorded from Victoria (Edwards, 1924).

Aë. alboannulatus varies very little over its range of distribution and only one conspicuous variation, a yellowness of the apical part of the femora, has been found; this variety occurs in the western part of the Otway Ranges.

Aë. queenslandis, on the other hand, has been regarded as a highly variable species. A detailed study of specimens from Victoria has confirmed this opinion, but has also shown that the name *Aë. queenslandis* has, in the past, been applied to a complex of closely related forms. In addition to *Aë. queenslandis* four others can be recognized. Three of them have different geographical and/or ecological distribution and do not interbreed where their distribution overlap. Two are treated as species and are described below under the names *Aëdes rupestris* and *Aëdes tubbutiensis*; the third (Form A), which is undoubtedly a distinct species, will not be discussed here since it has already been reviewed, though not as yet named, by Lee, Dyce and O'Gower (1957). The fifth member of the complex, which will be referred to as the "yellow form", appears not to be reproductively isolated from *queenslandis* and will be treated as a variety of this species.

*Key to Victorian species of alboannulatus complex.**Adults.*

1. Tibiae and proboscis mottled with pale scales 2.
- Hind tibiae and proboscis black 3.
2. Scutum with patches of white scales. Femora with ochreous preapical ring, which may extend apically. Posterior pronotum with bronzy narrow scales dorsally. Venter white with median black spots *alboannulatus*.
- No patches of white scales on scutum. No preapical ring on femora. Posterior pronotum with pale goldish narrow scales dorsally *tubbutiensis*, n. sp.
3. Tibiae with white sub-basal ring form A.
- Tibiae without sub-basal ring 4.
4. Venter ochreous usually with scattered black scales *queenslandis*.
- Venter black with white lateral patches. Apical border of sternites always with broad black band *rupestris*, n. sp.

* 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.

Larvae.

1. Head setae 4, 5 and 6, almost in straight line. Prothoracic seta 1, 2-branched; 4, single; 5, 2-3-branched *rupestris*.
 - Head setae 4, 5 and 6, forming triangle. Prothoracic seta 5, single 2.
 2. Head setae 4, 5 and 6, forming almost a right angle, with setae 4 well in front of setae 5. Prothoracic seta 1, 2-branched; 4, single *alboannulatus*.
 - Head setae 4, 5 and 6, forming obtuse triangle with setae 4 slightly in front of or behind setae 5 3.
 3. Prothoracic seta 1, 2-branched; 4, 2-branched, rarely single *queenslandis*.
 - Prothoracic seta 1, single, rarely 2-branched on one side; 4, 2-3-branched *tubbutiensis*.

Distinguishing the larvae of *rupestris*, *alboannulatus* and *queenslandis* is not difficult, but the larvae of *tubbutiensis* are very similar morphologically to those of *queenslandis* and some cannot be identified with certainty.

AÈDES ALBOANNULATUS (Macquart).

Culex albo-annulatus Macquart, 1849, *Dipt. Exot.*, suppl. 4: 10.

Distinctive Characters: Adult. Vertex clothed with narrow curved bronze scales becoming white towards centre of vertex. Proboscis mottled. Scutum clothed with narrow, curved bronze scales and some patches of white scales. Posterior pronotum with narrow curved bronze scales dorsally. Femora with preapical band; femora and tibiae mottled. Sternites white scaled with median patch of black scales.

Description of Adult.

Female.—Head: Vertex clothed with narrow curved bronze scales except for small median area of white scales. Upright scales black; lateral scales broad and white except for large black patch in middle. Palpi black scaled with white scales on base of segments and on apex of last. Proboscis black scaled, mottled or pale scaled in middle. Scutum clothed with narrow curved bronze scales with some small areas of white scales; a patch of broad white scales just in front of scutellum. Anterior pronotum with narrow curved and elongate white scales and black bristles. Posterior pronotum with broad white scales below, broad black scales in middle and narrow bronze scales above; black area may have a few pale scales. Tergites black with incomplete white basal bands and lateral spots. Sternites white scaled with median and lateral apical black spots. Wing length: 5.0-7.5 mm. Upper fork cell 1.5-2.3 times as long as its stem. Legs: femora with preapical band or patch, which may join with knee spot. Tibiae mottled. Fore and mid tarsi with 2-3 white basal rings, hind tarsi with 4.

Male.—Palpi about as long as proboscis without labella; last two segments, and apex of shaft, with long, dark, silky hairs; a white spot at base of each segment. Proboscis less mottled than in female, sometimes only a few white scales. Upper fork cell 1.3 times as long as its stem. Tergites 2-7 with complete white basal bands; 2 may have only a patch of white scales; tergite 8 may be mottled. Sternites usually black with lateral white spots; white scales may predominate and black scales be reduced to patches in middle of segment and apical corners. Terminalia: very similar to terminalia of *queenslandis* and can be recognized only by the basal lobe of the coxite (Fig. 1, *a*) which has a row of about 20 setae instead of 10 as in *queenslandis*. Appendage of harpago not as expanded in middle as it is in *queenslandis*. Ninth tergite with prominent lobe bearing 2-5 strong setae.

Larva.—Head and siphon brown. Head about five-sevenths as long as broad. Antenna about half length of head, clothed with spicules; seta 1, 3-5-branched, arising at about half-way from base. Head seta 4, 4-5-branched; 5, 3-5-branched; 6, 2-4-branched; 7, 6-7-branched; 8, 1-2-branched; 9, 2-3-branched. Head setae 4, 5 and 6 arranged to form apices of almost right angle triangle (Fig. 1, *d, c*). Seta 4 medial to 5 and 6 and between them. Mentum with 9-12 lateral teeth. Prothoracic setae (Fig. 1, *b*): 1, 2-branched; 2, single, only slightly shorter than 1; 3, 4-5-branched, about three-quarters length of 2;

4, single, about as long as 3; 5 and 6, single; 7, 3-branched. Eighth abdominal segment: Pentad setae: 1, 3-5-branched; 3, 8-11-branched; 5, 4-6-branched; 2 and 4, single. Comb of large patch of fringed scales. Siphon index: 2.6-3.4, mean 2.9; seta 1, 6-7-branched. Pecten of 17-20 spines, each with 3-4 teeth at base, central ones the largest. Anal segment: saddle covering about half segment. Seta 1, single or 2-branched; 2, 5-8-branched; 3, single; 4, of 15 tufts. Anal papillae about as long as saddle, or shorter. Eggs (Fig. 1, *g*) black, narrow, slightly flattened ventrally, about 1.0-1.1 m. long with an index of about 4.

Biology: *Aë. alboannulatus* is a sylvan species. It occurs almost throughout Victoria, but has not been recorded in the Mallee. It breeds in ground pools and rock pools; the water is usually clear but may be more or less cloudy. *Aë. alboannulatus* usually avoids heavily shaded pools in dense forest, showing a preference for diffuse

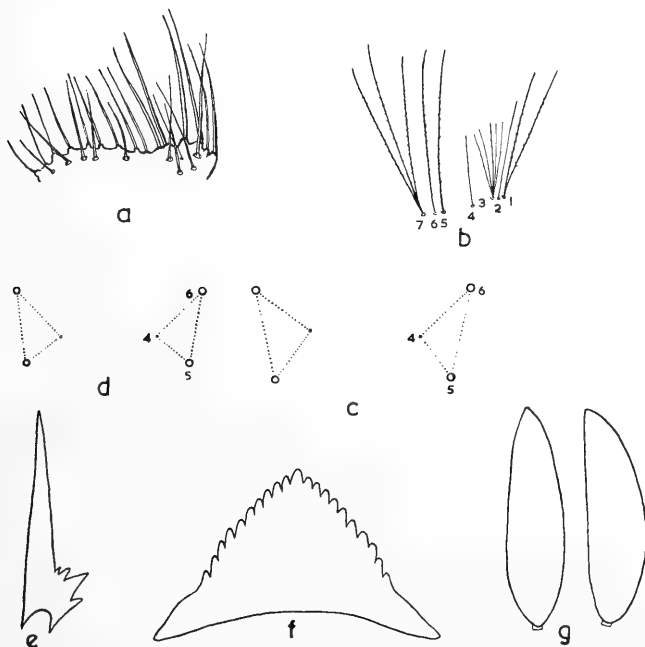


Fig. 1.—*Aedes alboannulatus* (Mocq.). Adult: *a*, basal lobe of coxite. Larva: *b*, prothoracic setae; *c* and *d*, bases of head setae 4, 5 and 6; *e*, pecten tooth; *f*, mentum; *g*, egg, plan and side view.

sunlight. On the Bogong High Plains, at an altitude of 5,400 ft., it was found during the summer to be breeding in ground pools fully exposed to the sun. In the flat country north of the Dividing Range it can use such pools only during the cooler months of the year, being confined during the summer to shaded gullies, backwaters and roadside ditches.

The spring generation of *alboannulatus* oviposits on the edges of pools many of which will dry during the summer; the eggs then remain dormant until autumn rains fill the pools again when most of the eggs hatch within 12 hours. Some larvae pupate and produce adults, early in August, but the majority do not pupate until the spring. In permanent water pools *alboannulatus* is able to breed all the year round.

Adults are always abundant during the spring, and commonly during the autumn in favourable places, but a prolonged dry summer may result in the drying out of pools which in normal years permit continuous breeding.

In Victoria *alboannulatus* is sometimes found breeding alone, but usually it is associated with *Aë. queenslandis*, *C. fergusonii* Taylor, *C. pipiens australicus* Dobr. and Drum., *Th. inconspicua* Lee and *A. annulipes* Walk.

Habits: The adults are vicious day-biting mosquitoes; they bite even during the winter at temperatures as low as 11°C.

AÉDES QUEENSLANDIS (Strickland).

Culicelsa queenslandis Strickland, 1911, *Entomologist*, 44, 179. *Culicelsa similis* Strickland, 1911, *ibid.*, 44, 132. *Culicada demansis* Strickland, 1911, *ibid.*, 44, 202. *Culicada cumpstoni* Taylor, 1914. *Trans. Ent. Soc. Lond.*, 1913, 692. *Culicada hybrida* Taylor, 1916. *PROC. LINN. SOC. N.S.W.*, 41, 568.

This is a rather variable species, and hence it is difficult to specify morphological traits which are common to all variants.

Distinctive Characters: Adult, Female.—Vertex with large or small area clothed with golden-yellow scales. Proboscis black scaled. Integument from light brown to dark brown. Thorax clothed with narrow light yellow or bronze scales; no patches of broad white scales in front of scutellum. Posterior pronotum with patch of broad white scales below, broad black scales in middle and goldish, narrow, curved scales above. Tarsi of fore and mid legs with two basal white bands, hind legs with four. Tergites black with incomplete yellowish basal bands, sometimes reduced to a few pale scales. Sternites clothed with ochreous scales; lateral apical spots of black scales, or of black scales and ochreous mixed.

Male.—Sternites black scaled with lateral elongate white spots; black apical part of sternites with some ochreous scales.

Larva.—Head setae 4, 5 and 6 arranged to form apices of a triangle; setae 4 lie between setae 5 and slightly in front of or slightly behind a line drawn through them. Prothoracic seta 1, 2-branched; 4, 2-branched or single, shorter than 3; 5, single.

Description of Adult.

Female.—Head: Vertex usually with large patch of golden yellow scales. In Tasmanian specimens this patch greatly reduced and all upright scales black. Proboscis black scaled. Thorax: Integument usually light brown, but dark brown in Tasmanian specimens. Scutum clothed with narrow curved golden yellow scales. Laterally, particularly in area near scutal angle, there is admixture of dark bronze scales. Scutum of Queensland specimens clothed with almost uniform goldish yellow scales; in Tasmanian specimens it is mainly clothed with dark bronze, almost black, scales, with yellowish bordering scales. Prescutellar area without broad scales. Anterior pronotum with yellowish narrow curved and elongate scales and bristles; in some specimens, particularly Tasmanian, bristles on dorsal part of anterior pronotum are dark, almost black. Posterior pronotum with patch of broad white scales below (yellowish in some Queensland specimens), broad black scales in middle and goldish yellow narrow curved scales above. South Australian and Tasmanian specimens have some pale broad scales in black middle area. Area of narrow yellowish scales reduced in some specimens to a line, but in others it extends downwards, reducing the black area. Pleura with usual patches of broad creamy scales and bristles. Wing length 3.2-5.4 mm. Upper fork-cell 2.3-3 times as long as its stem. Fore and mid femora black with mottling of yellowish scales, except for ventral side of basal two-thirds, which is pale scaled. Hind femur pale on basal half, black with yellowish mottling on apical half. In some specimens mottling increased towards end of femur and forms small or large ochreous preapical patch or ring; in some specimens apical part of femur is yellow. Tibiae black, pale scaled posteriorly, sometimes with streak anteriorly. In a few specimens hind tibia with inconspicuous or incomplete white ring at base. First 2 or 3 tarsal segments of fore and mid legs with white bands; tarsi of hind leg with 4 bands, some specimens with narrow fifth band. Band on segment 4 usually half length of segment, but in Queensland specimens it is only one-quarter-one-fifth of length of segment. Abdomen: Tergites black scaled with white lateral spots and incomplete yellowish basal band on tergites 2-6; in some specimens bands reduced to a few pale scales. Tergites 7-8 black or mottled with yellowish scales; in some specimens yellow

scales increased on tergites 6-8 replacing black scales. Sternites clothed with ochreous scales, with apical lateral black spots and usually mottling of black scales, the number of which sometimes exceeds yellow ones.

Male.—The male differs from the female as follows: Palpi black scaled, as long as proboscis without labella. Last two segments and apex of shaft with long dark hairs; segments 2-5 with patch of white scales. Torus brownish; flagellar segments pale, with dull silky verticillate hairs. Vertex clothed with narrow curved and upright yellowish scales. Thorax: Integument brown. Scutum clothed with yellow goldish scales with some admixture of dark bronze scales near area of scutal angle. Femur of fore leg black, mottled laterally and ventrally; femur of mid leg black mottled, pale scaled ventrally on basal half; femur of hind leg pale on basal two-thirds, apically black with few yellowish scales. Fore tarsi with 2 white rings, mid tarsi with 3, hind

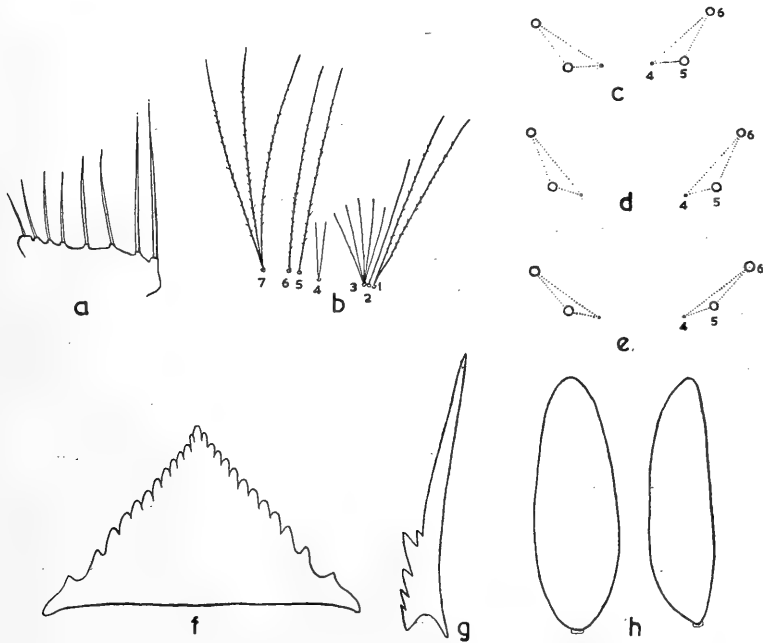


Fig. 2.—*Aedes queenslandis* (Strickl.). Adult: *a*, basal lobe of coxite. Larva: *b*, prothoracic setae; bases of head setae 4, 5 and 6 from: *c*, Queensland; *d*, Victoria; *e*, Tasmania; *f*, mentum; *g*, pecten tooth; *h*, egg, plan and side view.

tarsi with 4. Ring of segment 1 about one-fifth of segment. Tergites 2-6 with white basal bands, usually complete. Sternites black scaled with elongate lateral white patches not reaching apical border, and some yellowish scales scattered apically in black area. Terminalia: Coxite clothed basally with white scales and apically with black scales and golden bristles. Style about half length of coxite, narrowing to both ends, with 1-2 preapical setae, appendage slightly curved and about half length of style. Basal lobe of coxite narrow, transverse, with row of about 10 setae (Fig. 2, *a*). Harpago stout, with fine setae at base; appendage about as long as harpago, widened at middle and narrowing to end. Paraproct with single tooth and 5 fine setae. Ninth tergite with prominent lobe bearing 2-7 stout setae.

Variability of Males.—Scutal scales may be dark or light golden, with some admixture of dark bronze scales. In some specimens black scales occupy the greater part of the posterior pronotum. Upper fork-cell 1.4-1.7 times as long as stem. Sternites sometimes clothed with mixture of black, yellow and white scales in different proportions, or may have black median and lateral apical spots and white lateral spots.

YELLOW FORM.

This form differs from other variations in its general yellow colour, but, although typical specimens are quite distinct from the type form of *queenlandis*, there are intermediates.

The yellow form is characterized by: Lighter integument. Proboscis with a few pale scales on basal half. Torus yellow, darker on inner side. Broad scales on lower part of posterior pronotum yellowish. Fore and mid femora intensively mottled with yellowish scales, hind femora yellowish with mottling of black scales. Fore tibia pale below, black above—mid tibia mottled with yellowish scales; hind tibia black above and apically, elsewhere yellow. Tarsi of fore and mid legs with 3 banded segments, hind with 4; band on segment 4 about one-fourth length of segment. Bands on tergites in females, reduced to yellow patches or absent. Last 2-3 tergites clothed with ochreous scales. Sternites clothed with ochreous scales and a few scattered black ones; apical lateral spots black.

Larva.—Head and siphon light brown. Head about three-fourths as long as broad. Antenna about half length of head, clothed with spicules; seta 1, 4-6-branched, about half length of antenna and arising about halfway from base. Head seta 4, tiny, 4-6-branched; 5, 4-9-branched; 6, 3-5-branched; 7, 8-10-branched; 8, single; 9, 2-3-branched. Setae 4, 5 and 6 arranged to form apices of triangle; setae 4 lie between setae 5, slightly in front of, or slightly behind, a line drawn through them (Fig. 2, *c*, *d*, *e*). Mentum with 12-13 lateral teeth. Prothoracic setae (Fig. 2, *b*): 1, 2-branched; 2, single; 3, 5-10-branched, about three-fifths as long as 2; 4, small, 2-branched or single; 5 and 6, single; 7, 3-branched. Eighth abdominal segment; Pentad setae; 1, 4-6-branched; 3, 8-13-branched; 5, 4-9-branched; 2 and 4, single. Comb, large patch of fringed scales. Siphon index 3.1-3.7; seta 1, 8-9-branched. Pecten of 19-26 spines, each with 4-5 teeth at base. Anal segment: saddle covering about half segment. Seta 1, 1-2-branched; 2, 6-11-branched; 3, single, long; 4, of 13-16 tufts. Anal papillae about as long as saddle.

Eggs (Fig. 2, *h*) black, oval, slightly flattened ventrally and narrowing to the posterior end. They are about 1.0-1.1 mm. long with an index of 3.2-3.6.

Biology.—*Aë. queenlandis* is confined to woodlands. It breeds in swamps, ground and rock pools, dams, cavities in logs, and in artificial containers (tanks, tins, etc.), usually in shaded situations, since it requires water of relatively low temperature. It may make use of exposed shallow pools during the cooler months of the year, but in the summer can do so only at high altitudes; deep exposed pools are always more suitable.

In Victoria the temperature of the water in which *Aë. queenlandis* breeds has not been found to exceed 18°C., even during the summer, but in southern Queensland, where again shaded pools are preferred, the larvae may be able to tolerate higher temperatures; they have been collected (I. C. Yeo and H. Grening, 6.2.58) in pools exposed to the sun for several hours in which temperatures by mid-morning had reached 20°C.

The water may be clean or contain decaying leaves. In Victoria *queenlandis* sometimes breeds alone, but usually is found in association with *Th. inconspicua* Lee, *C. fergusonii* Tayl., *Aë. alboannulatus* Macq., and more rarely with *Th. littleri* Tayl., *A. stigmaticus* Skuse, *A. pseudostigmaticus* Dobr., *Aë. notoscriptus* Skuse, *Aë. rupestris* Dobr., *T. tasmaniensis* Strick., and with most of spring breeding *Aëdes* of the subgenus *Ochlerotatus*. During the coldest months development of larvae is slow, but a few pupae can be found almost throughout the winter. In the laboratory emergence of adults was observed at 10-11°C. *Aë. queenlandis* oviposits on moist soil or rock surfaces just above water level. The eggs cannot withstand severe desiccation, but in natural conditions, in forests, they remain viable throughout the summer and hatch after autumn rains fill the pools.

AËDES RUPESTRIS, n. sp.

Types.—The type series were bred from larvae collected at Lorne. All specimens have their associated larval and pupal skins. The holotype female, allotype male, 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: Adults.—Narrow curved scales on vertex goldish. Integument dark brown. Scutum with narrow dark golden and small areas of pale scales laterally. Scales in front of scutellum narrow. Femora mottled anteriorly. Proboscis and tibiae entirely black. Sternites black with white lateral patches. Apical border always with broad black band. Ninth tergite of male without prominent lobes. Larva: Head dark brown. Head setae 4, 5 and 6 with their bases about on a straight line. First and fifth prothoracic setae, 2-branched.

Holotype Female.—Head: Vertex with narrow curved decumbent scales, yellow goldish in centre. Upright forked scales yellow golden, becoming dark towards sides and neck. Lateral scales broad, flat and white except for central black patch. Torus black with patch of white scales; first flagellar segment of antenna pale at base with patch of white scales; other segments black. Palpi black scaled with patch of white scales on segment 2 and at base and apex of segment 3. Thorax: Integument dark brown. Scutum clothed with narrow dark golden scales, becoming pale around bare area, in front of wing roots, along border with posterior pronotum and anteriorly; admixture of black scales laterally. Scutellum pale scaled. Anterior pronotum with dark bristles, goldish curved narrow scales and broader elongate scales. Posterior pronotum with patches of broad white scales below, broad black scales in middle and narrow curved goldish scales above. Pleura with usual patches of broad white scales and pale bristles. Wing length: 4.2 mm. Upper fork-cell about twice the length of its stem. Stem of halteres pale; knob pale scaled except at tip and underneath, which are black scaled. Legs: Fore and mid femora mottled, pale ventrally on basal half; tarsal segments 1 and 2 with white bands, 3 with a few white scales at base. Hind femur pale ventrally on basal two-thirds, apical third black scaled with few white scales posteriorly. Hind tarsal segments banded, except last one. Band on segment 4 half length of segment. All legs with creamy knee spot and black tibia. Abdomen: Tergites black scaled. First tergite with apical patch of black scales; 2-5 with incomplete narrow white basal bands; 6 and 7 each with patch of pale scales. White lateral spots on all segments. Sternites black scaled with white lateral patches. Apical border of sternites always with complete broad black band.

Paratype Females.—The series of 11 paratype females does not show much variation. Length of wing varies from 3.6 to 4.3 mm. In some specimens tergite 1 has an apical patch of black scales mixed with a few white, 2 has a basal patch of white scales; 3-7 have complete, narrow bands. Sternites may be pale scaled with inconspicuous black scales, but apical black band is always conspicuous and complete.

Allotype Male.—This differs from the holotype as follows: Palpi black scaled, as long as proboscis without labella. Last two segments and apex of shaft with long dark hairs; 2-5 segments with patch of white scales. Torus black, flagellar segments pale, with dark silky verticillate hairs. Tarsi of fore and mid legs with 3 white basal bands, hind tarsi with 4. Wing length: 3.9 mm. Upper fork-cell 1.1 times length of stem. Abdomen: Tergite 1 with few dark and pale scales in middle, 2 with an incomplete basal band, 3-6 with basal bands joining white lateral spots, 7 with a few white scales at base, 8 with lateral white spots only. Sternites black with white elongate lateral spots not reaching apical edge. Terminalia: Coxite black scaled, with patch of white scales basally; laterally and sternally it bears long and some short setae. Style half length of coxite, narrowing sharply at mid length; 1-2 preapical setae; terminal appendage straight, about half length at style. Basal lobe of coxite narrow, transverse, with row of about 10 long setae along edge and several small ones on upper side. Harpago stout, with fine setae at base; appendage about as long as harpago, widened at middle and narrowing to end. Paraproct with single tooth and 2 very fine setae near tip. Ninth tergite without prominent lobe, a few fine short setae on inner side.

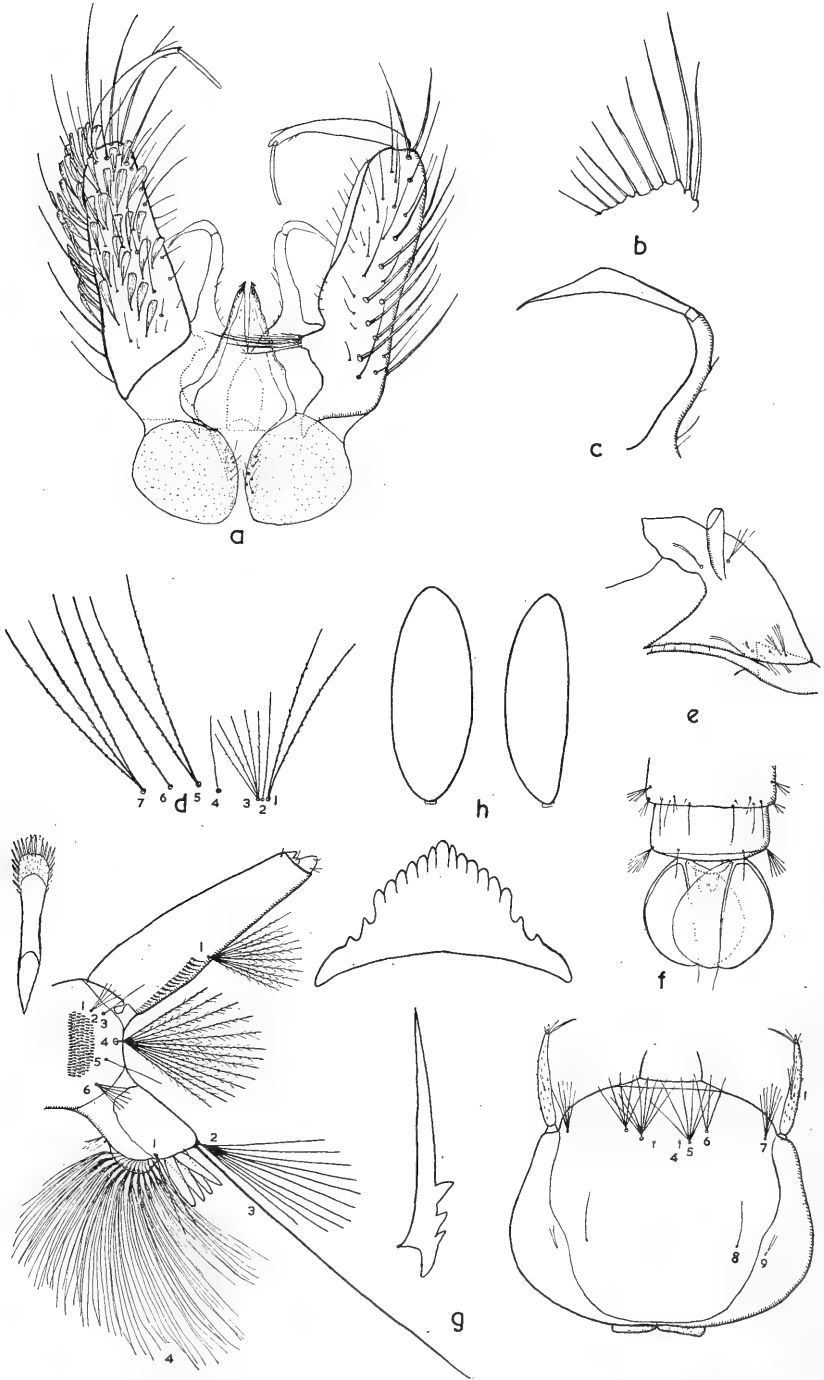


Fig. 3.—*Aedes rupestris*, n. sp. Adult: *a*, male terminalia; *b*, basal lobe of coxite; *c*, harpago. Larva: *d*, prothoracic setae; *g*, head, terminal segments and mentum. Pupa: *e*, part of cephalothorax; *f*, dorsal view of terminal abdominal segments; *h*, egg, plan and side view.

Paratype Males.—The series of 11 paratype males does not show much variation. The palpi of some specimens are slightly shorter than the proboscis. Some have only 2 tarsal bands on fore legs. Wing length: 3.6–3.9 mm. Sometimes tergite 7 has a complete basal band. White lateral spots on sternites are reduced in some specimens.

Larva (Fig. 3, *d, g*).—Head and siphon dark brown, body blackish. Head about four-fifths as long as broad. Antenna about two-fifths length of head, clothed with spicules, seta 1 with 2–4 branches, less than half length of antenna and arising at about two-fifths length from base. Head seta 4, tiny, 4–7-branched; 5, 5–7-branched; 6, 3–5-branched; 7, 5–10-branched; 8, single; 9, 2–3-branched. Setae 4, 5 and 6 with bases almost in a straight line. Mentum with 8–10 lateral teeth on each side. Prothoracic chaetotaxy: seta 1, 2-branched, long; 2, single, about three-fifths length of seta 1; 3, stellate, 5–11-branched and about half length of seta 1; 4, short, 1–2-branched; 5, long, 2–3-branched; 6, single, as long as 5; 7, 3-branched. Eighth abdominal segment: Pentad setae: 1, 3–4-branched; 3, 7–13-branched; 5, 5–7-branched; 2 and 4, single. Comb of about 150 fringed scales. Siphon stout, index 2.6–3.5, mean 2.9, seta 1, 6–10-branched. Pecten of 16–28 spines each with 2–3 teeth at base, the upper the largest. Anal segment: saddle covering more than half the segment. Seta 1, usually 2-branched, sometimes single; 2, 6–10-branched; 3, single, long; 4 of 14 tufts (one or two precratal). Anal papillae three-fifths to four-fifths length of saddle.

Eggs (Fig. 3, *h*) black, almost regular oval, flattened slightly on ventral side. They are about 1.0 mm. long with index 2.9–3.2.

Biology.—The breeding places of *Aë. rupestris* in Victoria are rock pools, in eucalypt forests, which are exposed to the sun. These are usually small and shallow with a thick layer of black mud and decayed leaves on the bottom. The water is brown, with a strong smell of decomposed eucalypt leaves. The temperature of the water in such pools rises during summer to about 30°C. at 1–2 p.m. In south Queensland the larvae of this species were collected, in large numbers, in two rock pools exposed to the sun; at 1–2 p.m. the temperature of water exceeded 37.5°C. (E. N. Marks, 19.11.57).

In some rock pools, particularly shallow ones with sloping edges, *Aë. rupestris* alone was found during the summer, but in these same pools, from late autumn to early spring, there were always some *queenslandis* larvae. In large and deep pools, with cleaner and cooler water, or with some vegetation, *queenslandis* was always more numerous than *rupestris* even during the summer. *Aë. alboannulatus* was found on several occasions in association with *rupestris*.

In south Queensland it was found in association also with *A. annulipes* Walk., *C. halifaxi* Theob. and *C. p. australicus* Dobr. and Drumm.

The eggs which remain dormant on the edges of dried pools hatch after being submerged by later rains. In the laboratory hatching of eggs was observed at temperatures in the range 9–14.5°C. At such low temperatures larvae developed only slowly, but eventually produced adults. Successful emergence of adults was observed in the laboratory at temperatures as low as 10°C.

Habits.—It is a day-biting mosquito, and is very common near its breeding sites; it ceases biting early in the winter when the temperature falls to 16–17°C.

Distribution.—Specimens have been bred from larvae collected at the following localities: VICTORIA: Franklin Riv. (6.3.53), Little Riv. and W. Tree Creek (north from Buchan, 17.1.56), Tubbut¹ (17.1.56), Nowa Nowa (4.12.57), all in Gippsland, Warburton (18.3.58), Lorne (1955–1958), Meredith (11.3.54), all collected by the author; Grampians (26.9.53) (A. Neboiss). S. QUEENSLAND: Upper Cedar Cr. (19.11.57, E. N. Marks), Lamington National Park (16.2.58, I. C. Yeo), Canungra (13.3.53), Nambour (25.4.45, J. L. Wassell), Somerset Dam (29.10.46, J. L. Wassell).

AËDES TUBBUTIENSIS, n. sp.

Types.—The type series was bred from larvae collected at Tubbut (E. Gippsland). All specimens have their associated larval and pupal skins. The holotype female, allotype male, six paratype males and six paratype females are in the collections of

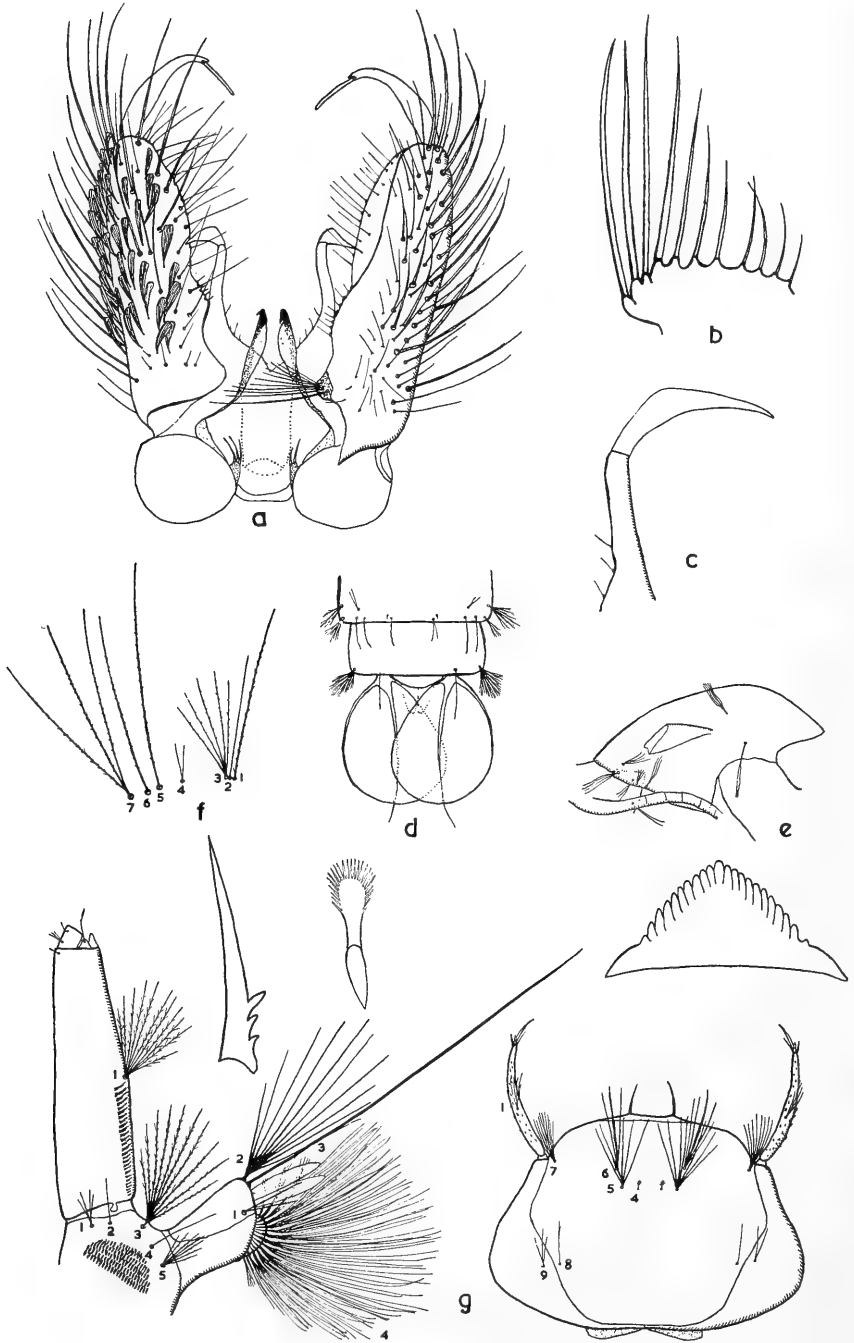


Fig. 4.—*Aedes tubbutiensis*, n. sp. Adult: *a*, male terminalia; *b*, basal lobe of coxite; *c*, harpago; Pupa: *d*, dorsal view of terminal abdominal segments; *e*, part of cephalothorax. Larva: *f*, prothoracic setae; *g*, head, terminal segments and mentum.

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.—Adult: Narrow curved scales on vertex pale. Proboscis mottled with white scales on basal two-thirds. Integument almost black. Scutum clothed with narrow dark bronze scales. Scales in front of scutellum narrow. Femora and tibiae mottled. Sternites white scaled with more or less conspicuous median black spot, or some mottling and apical lateral spots. Ninth tergite of male with prominent lobes and a few stout setae. Larva: Head dark brown. Head setae 4, 5 and 6 arranged to form apices of a triangle; setae 4 lie between setae 5 and slightly in front of line drawn through their bases. Prothoracic setae 1 and 4, single.

Holotype Female.—Head: Vertex with pale, narrow, curved scales. Upright forked scales pale in centre. Torus black with patch of white scales. First flagellar segment of antenna pale at base with patch of white scales; other segments black. Palpi black scaled with patch of white scales at base and at apex of segment 3; segments 2 and 3 with a few pale scales above. Proboscis black with mottling of white scales on basal two-thirds. Thorax: Integument almost black. Scutum clothed with narrow bronze and black scales, becoming pale around bare area near wing roots, on margins of scutum; two lateral pale patches near mid-length; scales in front of scutellum narrow. Scutellum pale scaled. Anterior pronotum with pale and black bristles, narrow curved, and elongate pale scales. Posterior pronotum with patch of broad white scales below, broad black scales in middle and narrow curved pale scales above; a few pale broad scales scattered in upper part of black area. Pleura with usual patches of broad white scales and pale bristles. Wing length: 5.6 mm. Upper fork-cell less than twice length of stem. Stem of halteres pale, knob pale scaled, except top and underneath, which are black scaled. Leg: Femora black scaled with white mottling; basal half pale scaled posteriorly. Knee spots yellowish. Tibiae black, mottled and with few white scales on base. Tarsal segments 1–2 of fore legs, 1–3 of mid legs and 1–4 of hind legs with basal white bands; bands on segment 4, half length of segment. Abdomen: Tergites black scaled. Tergite 1 with few pale and black scales in middle, 2–4 with incomplete basal white bands and lateral spots, 5–7 with bands joining lateral spots. Tergites 6–8 with scattered pale scales, increasing towards segment 8. Sternites white scaled with black mottling in middle and small apical, lateral spots.

Paratype Females.—The chief variations shown in a series of 11 females are: Size of pale spot on vertex may be reduced. Mottling of proboscis may be reduced to a few pale scales only. Mottling of hind tibia may be reduced. Basal bands on tergites may be reduced to small spots. Median black spot on sternites may be reduced; there may be only a few scattered black scales.

Allotype Male.—This differs from the holotype as follows: Proboscis black with occasional pale scales. Palpi about as long as proboscis including labella; last two segments and apex of shaft with long dark hairs. Patches of white scales on base of segments 2–5. Torus black; flagellar segments pale with dark silky verticillate hairs. Fore tarsi with 2, mid tarsi with 3 and hind tarsi with 4 basal white bands. Wing length: 4.0 mm. Upper fork-cell one and one-third times as long as its stem. Abdomen: Tergite 2 with narrow basal band, 3–6 with wide bands joining lateral spots. Sternites black scaled, with elongate, white lateral spots and a few white scales in middle of apical border. Terminalia (Fig. 4, a, b, c) of *Aë. tubbutiensis* is very similar to that of *Aë. queenslandis* and *Aë. rupestris*, but the styles are shorter—about one-third of the length of the coxite; first 4–5 setae of basal lobe about twice as long as those in *queenslandis*.

Paratype Males.—The chief variations shown in a series of 11 males are: Proboscis may be entirely black. The white lateral spots on the sternites may be small; white scales may extend from the lateral spots to the apical border and along it.

Larvae (Fig. 4, *f*, *g*).—Head and siphon dark brown; body blackish. Head about three-fourths as long as broad. Antenna about half length of head, clothed with spicules; seta 1, 4–5-branched, arising at about half-way from base. Head seta 4, tiny, 5–7-branched; 5, 5–7-branched; 6, 3–5-branched; 7, 7–10-branched; 8, single, rarely forked at apex; 9, 2–3-branched. Mentum with 10–12 lateral teeth on each side. Prothoracic chaetotaxy: seta 1 and 2 single; 3, 4–6-branched, as long as 2; 4, short, 2-branched; 5 and 6, single; 7, 3-branched. Eighth abdominal segment: seta 1, 4–5-branched; 3, 11–12-branched; 5, 6–7-branched; 2 and 4 single. Comb composed of large patch of fringed scales. Siphon index 3.1–3.7, mean 3.4; seta 1, 7–11-branched. Pecten of 20–30 spines, mean 25. Anal segment: saddle covering about half segment. Seta 1, single, may be 2-branched; 2, 6–12-branched; 3, single; 4 of 15–16 tufts. Anal papillae about as long as saddle.

Biology.—*Aë. tubbutiensis* breeds mainly in back water in creek beds and at times in rock pools more or less exposed to the sun. It avoids completely shaded pools (see Table 1).

TABLE 1.
The Habitats of Mosquito Larvae in Tubbut Area.

Date.	Habitat.	<i>Aë. tubbutiensis</i> .	<i>Aë. queenslandis</i> .	<i>Aë. rupestris</i> .	<i>Aë. alboannulatus</i> .	<i>Culex douglasi</i> .	<i>Anopheles stigmaticus</i> .	<i>A. annulipes</i> .
17.1.56	Little River, ground pool exposed to the sun ..	14	—	—	—	—	—	—
20.1.58	Tubbut, ground pool exposed to the sun ..	36	1	—	—	1	—	—
15.3.58	" " "	26	—	1	—	—	—	3
16.4.58	Snowy River, small grassy ground pool ..	2	1	1	—	—	—	2
16.5.58	Sandy Creek, shaded ground pool ..	2	23	—	1	—	31	—
"	Sandy Creek, rock pool, exposed to the sun, 50 yards further on ..	10	6	38	—	—	—	—
"	Dam Creek, ground pool, short period of direct sun	7	2	—	—	—	5	1
"	Dam Creek, rock pool, exposed to the sun ..	11	—	7	—	—	—	—

Habits.—Adults were not collected in nature and there is no information on their biting habits. It can be expected that it will bite man as readily as do other Victorian members of this complex.

Distribution.—All known breeding places are situated in the north-eastern corner of Gippsland, in wooded country at an elevation of about 1,000 feet. This area has an average rainfall of 25–30 inches.

AËDES sp. form A.

This unnamed form, belonging to the *alboannulatus* complex, which has a white ring on the tibiae (Lee, Dyce and O'Gower, 1957), was found breeding alone in a rock pool with clean water and exposed to dispersed sunlight at Tubbut (17.2.56). It was breeding also at Little River (17.2.56) in a rock pool exposed to the sun, with slightly murky water and decayed leaves on the bottom; in this pool the dominant species was *Aë. rupestris*.

THE STATUS OF MEMBERS OF THE COMPLEX.

Comparative studies of *queenslandis* and *rupestris* have shown that the two species differ in both their morphology and ecology. The ecological differences seem to be largely a matter of different temperature preferenda.

During 1955-58, a study was made of larval breeding sites of the two species in the rocky valley of the Erskine River, near Lorne. In this particular place the river widens, forming shallow rapids with numerous rocky pools. These pools provide permanent breeding sites for *rupestris* even during the summer when the water temperature may exceed 30°C.; it never makes use of the cooler pools in the surrounding forest. The forest pools, 100-200 yards away, are the permanent breeding places of *queenlandis*. This species also uses the exposed rock pools during the cooler months, but in summer its larvae are only occasionally found in them, and then in the deeper ones.

The problem of why *queenlandis* larvae should be practically absent from the exposed pools during the summer has been investigated by means of laboratory experiments.

Influence of water temperature on oviposition.—Blood-fed females of *queenlandis* and *rupestris* were placed in cages of six cubic feet capacity containing two dishes (7" × 10.5") of water with wicks of filter paper covering the sides and providing oviposition sites. In one experiment, the temperature of the water in one dish was 17-18°C., in the other 27°C.; in the second experiment the temperatures were 14-15°C. and 30°C. Air temperature in the cages was 17-22°C. (Table 2).

TABLE 2.
Number of Eggs Deposited in Water of Different Temperatures.

Species.	Temperature of Water.			
	17-18° C.	27° C.	14-15° C.	30° C.
<i>queenlandis</i>	—	—	563	0
<i>rupestris</i>	150	278	0	1347

From Table 2 it is evident that *queenlandis* would not normally deposit eggs on the edges of exposed rock pools during the summer; *rupestris*, on the contrary, would prefer these sites. Certainly in nature, during cold spells or cool evenings, when the temperature of water falls, *queenlandis* may deposit some eggs on the edges of the pools; these eggs, however, may be exposed to direct sunlight later on, and if there is no rain for some days the fall in water level may result in the eggs being subjected to desiccation.

Resistance of eggs of queenlandis and rupestris to desiccation.—Batches of 65 eggs of *queenlandis* and *rupestris* were placed on filter paper and exposed for different periods to a R.H. of 54-58% at a temperature of 20°C. In one experiment the eggs contained mature embryos, i.e., larvae ready to hatch; in a second experiment, immature embryos. After desiccation the filter paper bearing the eggs was immersed in water. The percentages hatching are shown in Table 3.

TABLE 3.
Ability of Eggs to Withstand Desiccation.

	Exposure.	Percentage Hatch.	
		<i>queenlandis</i> .	<i>rupestris</i> .
Mature embryo	2 days	1.5	95.4
Immature embryo	12 days	13.3	98.0

It is clear that the fully embryonated eggs of *queenlandis* are unable to withstand even a brief period of desiccation. This, indeed, was apparent after 24 hours, for within that period 61.6% of eggs had collapsed and others had opened. Of the *rupestris* eggs, on the other hand, only 4.6% collapsed and none opened. The higher survival of

queenslandis in the experiment using eggs with young embryos can be attributed to the fact that these eggs did not open; the embryos were thus protected to some extent from desiccation.

In another experiment 125 eggs of each species were placed on wicks of filter paper about half an inch above water level (17-18°C.). During the next three weeks 56% of *queenslandis* eggs hatched and the larvae were able to wriggle over the moist filter paper into the water; *rupestris* eggs did not hatch.

In nature, during the summer, the hatching of *queenslandis* eggs above water level could often be fatal for the emerging larvae, but with favourable meteorological conditions, some might succeed in making their way into receding rock pools. They would then be exposed to water temperatures of 30°C. or more, which would probably be unfavourable for their development.

Work on the thermal death points of larvae of these two species is in progress.

As mentioned earlier, the *alboannulatus* group is distributed in the tropics and subtropics, and there can be little doubt that *queenslandis* and *rupestris* had their origin in the north. Both are sylvan species, but, as emphasized above, they have different temperature requirements. *Aë. queenslandis* became adapted to cooler conditions, and, having dispersed southwards, presumably along the ranges, is an abundant mosquito in cooler parts of south-eastern Australia. *Aë. rupestris* has been less successful in the south. Suitable breeding sites, that is, rock pools exposed to the sun, are not common in Victorian ranges, and, while large local populations of *rupestris* may be found, the distribution of this species is very patchy.

It is clear then that the morphological differences between *queenslandis* and *rupestris* are accompanied by physiological and ecological differences. However, the decisive factor in determining taxonomic status is reproductive isolation. The *queenslandis* and *rupestris* are sympatric forms (the area of distribution of *rupestris* lies entirely within that of *queenslandis*), but the examination of hundreds of specimens of both forms, from all known Victorian localities, has not revealed any intermediates. It is evident that the two forms are reproductively isolated and that *rupestris* should be regarded as a distinct species.

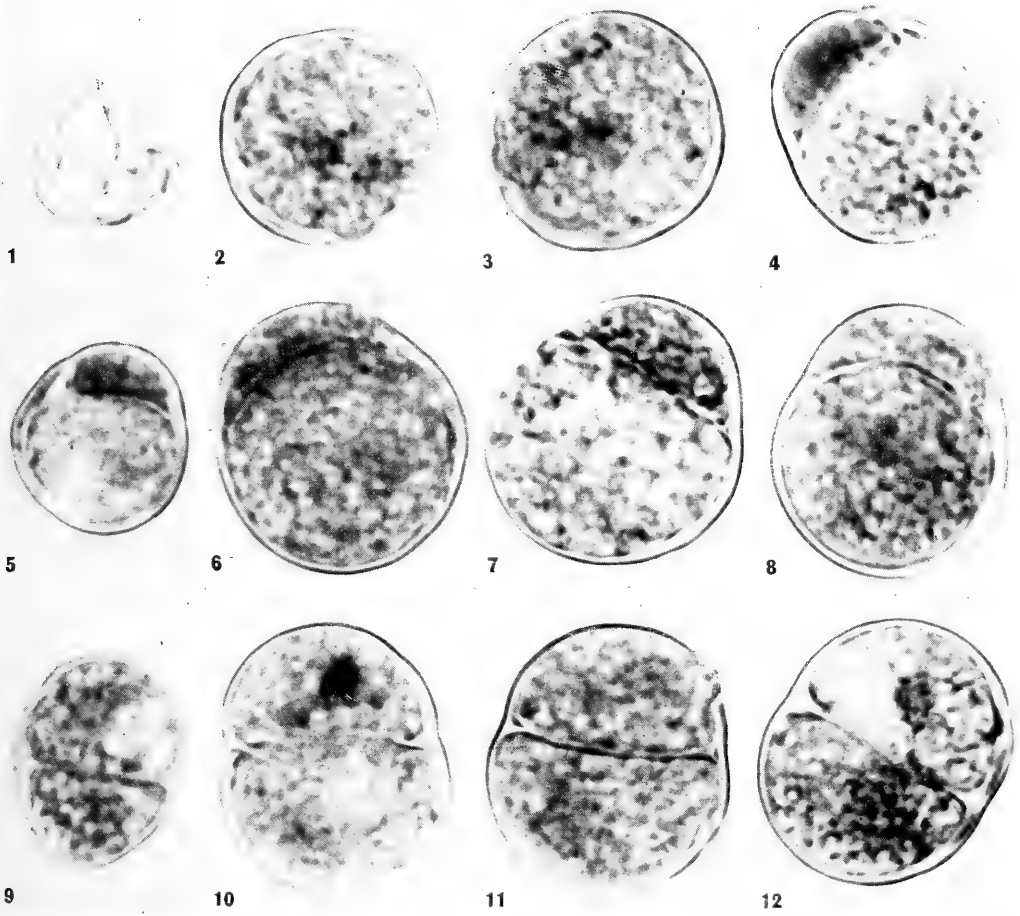
Both species bite man readily, but *rupestris* ceases to do so earlier in the year than *queenslandis*; early in June, when the temperature was 17°C., there were no biting *rupestris*, but *queenslandis* was scarcely less active than in the summer.

Aë. tubbutiensis, as far as we know, has a very restricted distribution; it has been recorded only in east Gippsland. *Aë. tubbutiensis* probably is more closely related to *queenslandis* than to the other species. Unfortunately, not much is known about the biology and ecology of this form, but it is apparent that it is more adaptable to higher temperatures than is *queenslandis*. *Aë. tubbutiensis* breeds mainly in ground pools, occasionally in rock pools, in the full sunlight or exposed to the sun for part of the day. Only once have adults of *tubbutiensis* (two females) been bred out from larvae collected from a shaded pool.

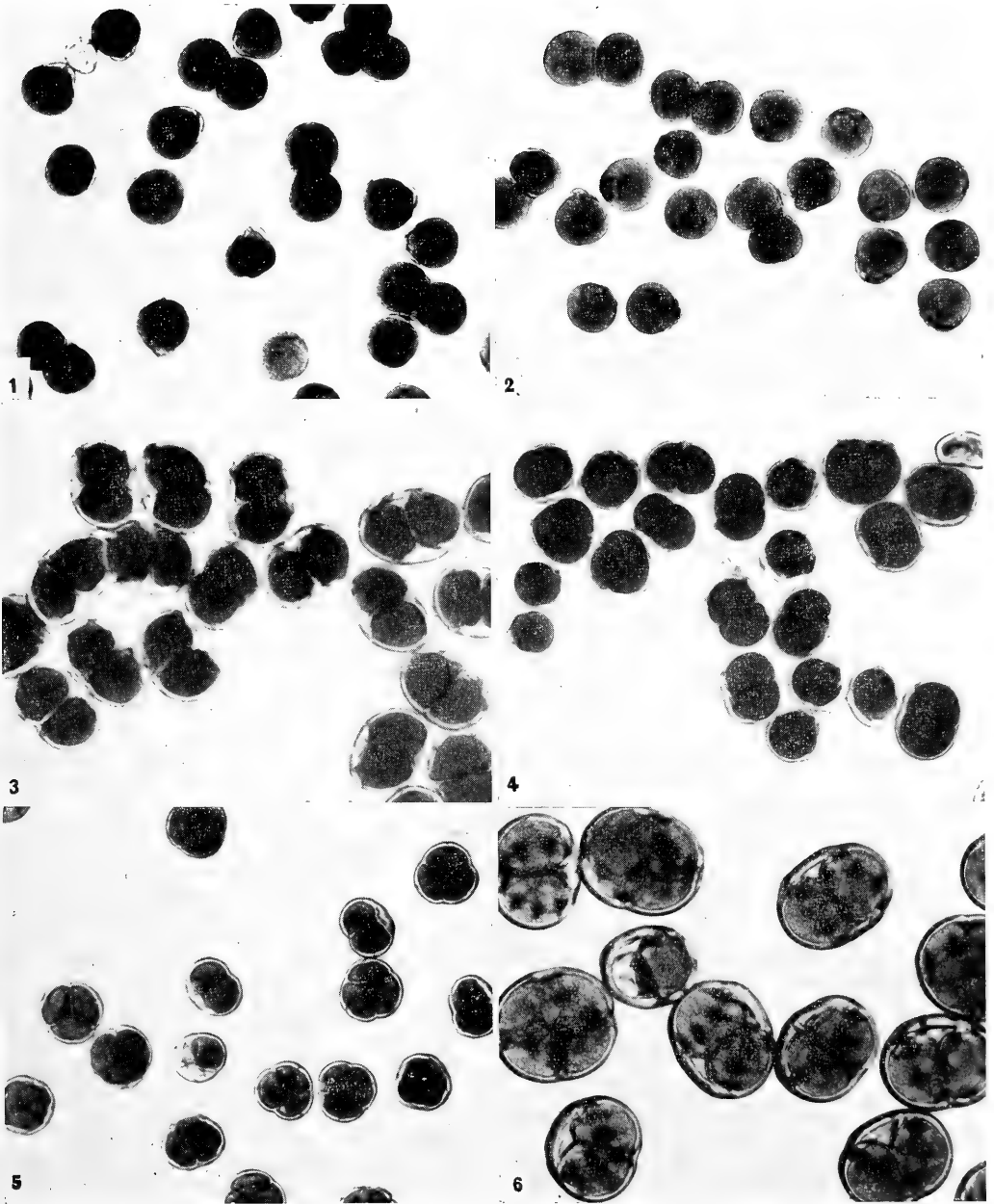
Examination of 121 adults and 70 correlated larval skins revealed only one female which could be regarded as an intermediate. Although *tubbutiensis* and *queenslandis* both vary considerably, there is not a continuous gradation between them.

If there were not reproductive isolation from *queenslandis*, intermediate forms should occur commonly. Mayr, Linsley and Usinger (1953) have stated, in relation to allopatric forms, "forms that hybridize only occasionally in the zone of contact are full species". The present author believes that this criterion can also be used for sympatric forms and thus can be applied in the case of *tubbutiensis*. As *tubbutiensis* is morphologically and ecologically distinct from *queenslandis* and reproductively isolated, it should be regarded as a separate species.

The yellow form of *queenslandis* merges into typical *queenslandis* and only extreme variants can be distinguished with certainty. The progeny of the females of the yellow

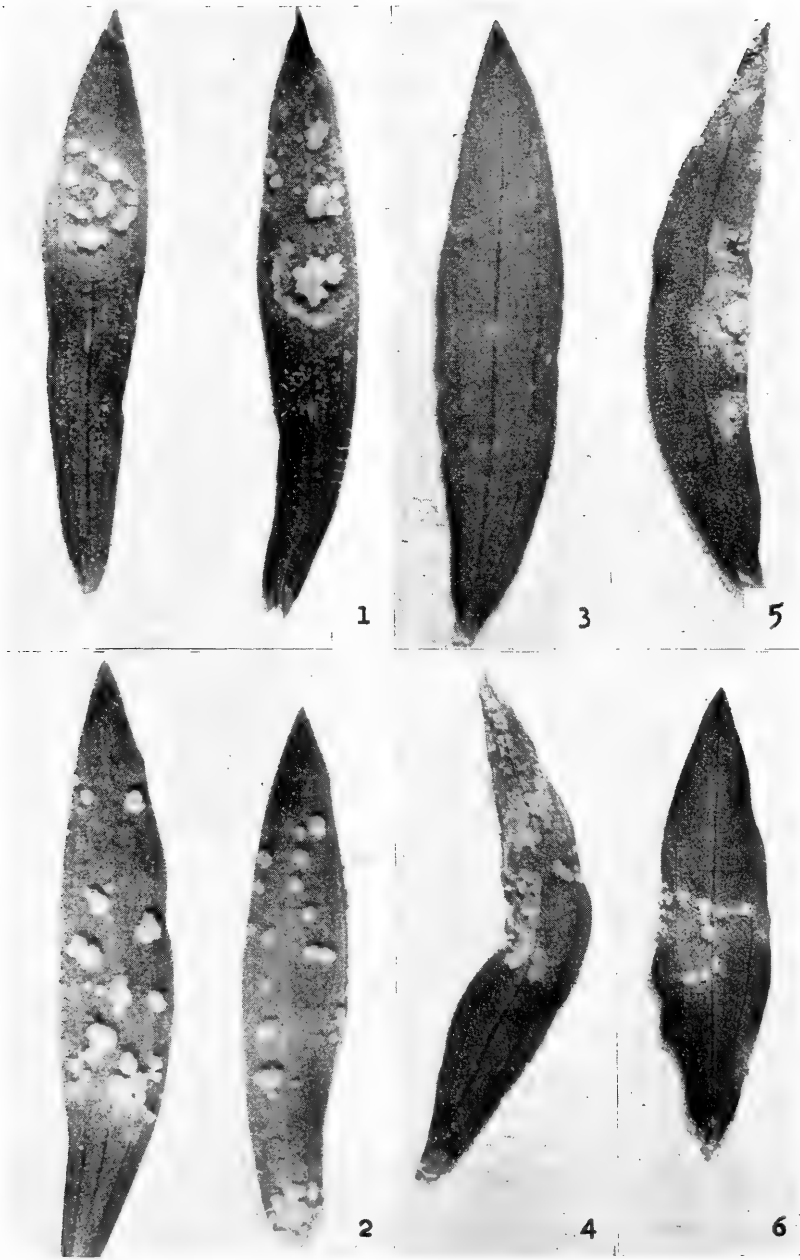


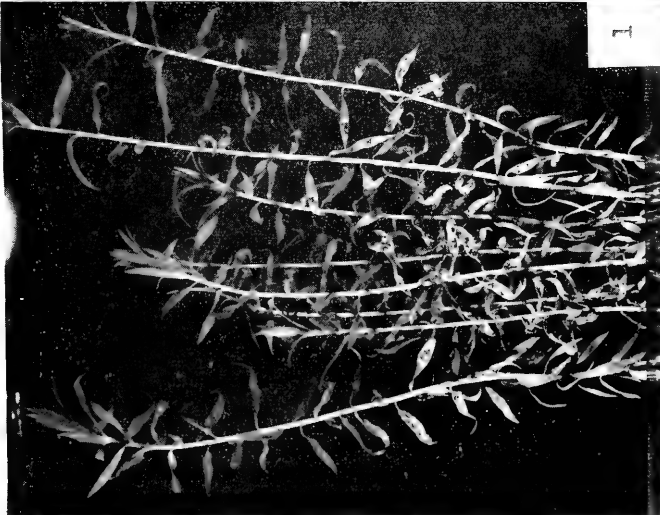
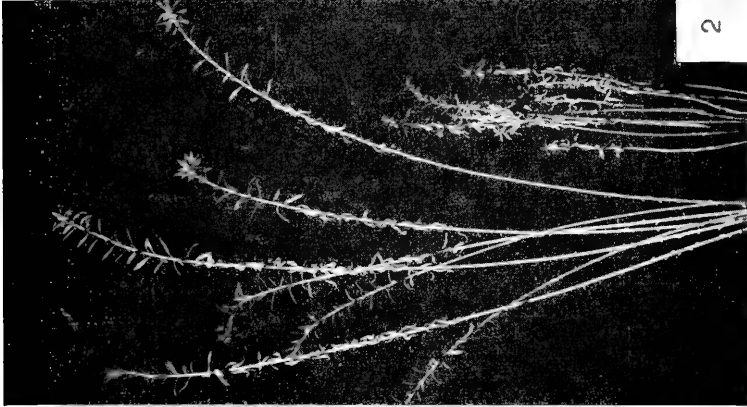
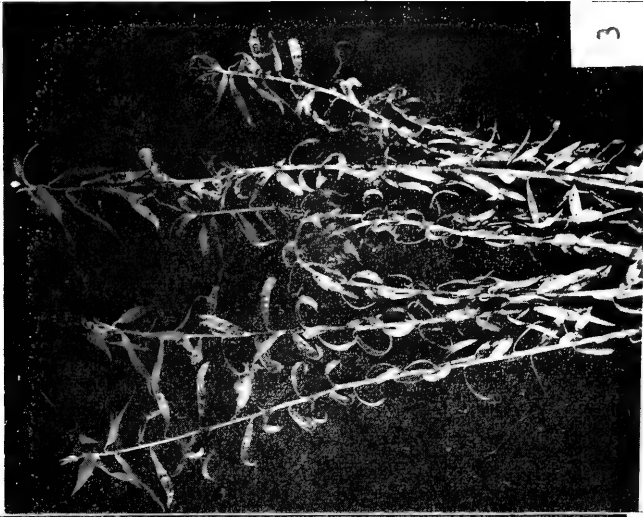
Breakdown of monad development in *Leucopogon virgatus*.



Variable tetrad pollen in *Astroloma* (1-3), *Acrotriche* (4), *Leucopogon* (5) and *Brachyloma* (6).









form are very variable; some are typical *yellow form*, others are indistinguishable from *queenslandis*. Apparently it is not reproductively isolated from *queenslandis* and as a sympatric form cannot be regarded as a distinct species.

Acknowledgements.

The author is grateful to Dr. F. H. Drummond for assistance in the preparation of the manuscript; he is also particularly indebted to Dr. E. N. Marks, University of Queensland, for helpful discussion and providing larval and adult material from Queensland, to Dr. P. F. Mattingly, British Museum, for comparison of specimens of *Aë. queenslandis* and *Aë. rupestris* from Victoria with the types of *C. queenslandis* Strickl. and *C. demansis* Strickl., and to Mr. Ernest Bass, Tubbut, for collecting larval material in the Tubbut area and to Mr. A. Neboiss, National Museum, Melbourne, for the gift of material.

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OBSERVATIONS ON THE ECOLOGY OF THE PHASMATID CTENOMORPHODES
TESSULATA (GRAY).

By P. HADLINGTON* and F. HOSCHKE.†

(Plates v-vi; two Text-figures.)

[Read 27th May, 1959.]

Synopsis.

The phasmatid, *Ctenomorphodes tessulata* (Gray, 1835) is a defoliator of trees in the coastal forests of northern New South Wales where it reached outbreak proportions during 1955-56. Its known range is from Colombatti State Forest, near Kempsey, New South Wales, to Goodwood, near Maryborough, in Queensland. Outbreaks have only been recorded from forests in New South Wales. *C. tessulata* is not host specific since it has attacked a wide range of species of the genera *Eucalyptus*, *Syncarpia*, *Acacia* and *Casuarina*.

Descriptions of adults and eggs, and a key to the nymphal instars are given. The life cycle in the field, laboratory observations and experiments are described. Investigations show that cleptid egg parasites and disease of the phasmatid eggs are regulating factors.

A similar stand composition occurs in all the areas of high phasmatid population. The effect of the defoliation on the management of forests is considered.

It is suggested that the occurrence of forest fires is followed by an increase in the numbers of *C. tessulata*. The probable effect of fire on the cleptid parasites is also discussed. There appears to be a correlation between the large fires of 1951-52 and the outbreak of *C. tessulata* in 1955-56.

INTRODUCTION.

Plagues of phasmatids have been recorded on the highlands of New South Wales over the past 75 years, and although it is likely that plagues occurred prior to 1880, this is the earliest date for which accurate records are available. The species concerned in these areas are *Podacanthus wilkinsoni* Macleay, 1881, and *Didymuria violescens* (Leach, 1814). More recently *Ctenomorphodes tessulata* (Gray) has been noted in large populations on the north coast of New South Wales. It is rather surprising that these have gone unrecorded, the first indication of their presence being extensive areas of defoliated forest trees. This can be partly attributed to the great diversity of form among the Phasmatidae and their resemblance to the vegetation upon which they feed.

A recent paper by Key (1957) on kentromorphic phases in the Phasmatidae has enabled the phase patterns to be correlated with the population densities in the three species reaching plague proportions.

The taxonomy and nomenclature of this and other species has been reviewed by Key (1957), and an application has been made to the International Commission on Zoological Nomenclature for the names to be added to the official lists of generic and specific names.

The descriptions of *C. tessulata* by Gray (1835), Westwood (1859) and Bates (1865) were based on a small number of museum specimens available at that time. Bates records that collections available to him bore the data, Moreton Bay, Australia. A single specimen in the collection of the Department of Agriculture and Stock, Brisbane, Queensland, was collected at Moreton Island in 1916. Collections have been made at Byron Bay and Richmond Range State Forest in New South Wales and a small infestation was recorded from Washpool State Forest in January 1955.

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Prior to 1956, *C. tessulata* had not been recorded as a pest, but has since caused defoliation of forest trees in three widely separated areas of north-eastern New South Wales. A feature of the outbreaks was that severe defoliation occurred during 1955-56 in all three areas. Nymphs and adults which were collected in these areas exhibited the pattern of the high-density phase. Single specimens of nymphs from Wedding Bells State Forest near Woolgoolga in November 1952, and adults of the same generation collected in February 1953 were described by Key as having a low density phase pattern. No further material from this forest was studied until January 1956, when defoliation occurred over approximately 100 acres and individual small trees of *Casuarina torulosa* carried as many as thirty-six phasmatids.

High populations were recorded from Toonumbar State Forest, near Kyogle, in January 1956, when a comparatively small area of forest was defoliated. Observations were not continued in this area as a fire occurred in December 1956. Widespread, but scattered, defoliation was observed on Tanban, Ingalba and Colombatti State Forests, near Kempsey, in February 1956. Defoliation in these State Forests was negligible during the 1956-57 summer, and it appears that the population is now at a very low level.

DISTRIBUTION AND HOSTS.

Label data on specimens from several sources* have been used as a basis for establishing the known distribution of *C. tessulata*. Specimens have been collected from Colombatti State Forest near Kempsey, N.S.W., to Goodwood, near Maryborough, Queensland, but distribution is probably more extensive.

The localities from which large numbers of *C. tessulata* have been observed vary in altitude from 200 feet to 2,000 feet, while single specimens have been taken mainly in coastal areas of altitudes less than 200 feet.

Very Low Density Populations: N.S.W.: Byron Bay; Queensland: Beechmont, Beerburum, Burleigh Heads, Goodwood, Landsborough, Nerang, Petrie and Moreton Island.

Low Density Populations: N.S.W.: Washpool and Richmond Range State Forests.

High Density Populations: N.S.W.: Toonumbar, Wedding Bells, Tanban, Ingalba and Colombatti State Forests.

Specimens at the Division of Entomology, C.S.I.R.O., Canberra, were examined by Dr. K. H. L. Key, who gave their respective phase patterns. This information has been related to the observations made in various outbreak areas in New South Wales and where accurate field data are available there is a correlation between the phase pattern and the abundance of the species.

Observations on host relationships have been made in Toonumbar, Wedding Bells and Tanban State Forests, the three main outbreak areas. The nymphal stages were often found on many tree species, but only the characteristic defoliation or act of feeding was taken as establishing a positive host record. Thus many possible hosts have been rejected on the basis of inadequate evidence of attack.

Field studies establish that the following tree species† normally provide food material for *C. tessulata*: *Syncarpia laurifolia* Ten., *Eucalyptus paniculata* Sm., *E. propinqua* Deane and Maiden, *E. gummifera* (Gaertn.) Hochr., *E. maculata* Hook., *E. resinifera* Sm., *E. punctata* DC., *E. triantha* Link, *E. pilularis* Sm., *Casuarina torulosa* Ait., *Acacia floribunda* (Vent.) Willd.

Specimens were reared in the laboratory by Key (1957) on *Acacia mollissima* Willd. and *Eucalyptus dives* Schauer. Adult phasmatids, collected from Tanban State Forest during January 1957, were held at Sydney and fed on locally available material of *Angophora costata* Domin, *Eucalyptus radiata* Sieb. and *Syncarpia laurifolia*. Some

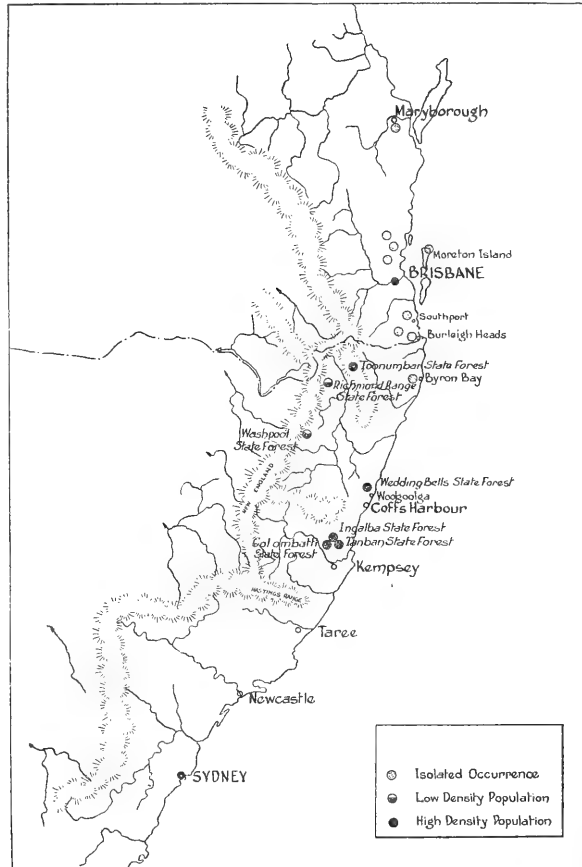
* Division of Entomology, C.S.I.R.O., Canberra; Department of Agriculture, N.S.W.; Department of Agriculture and Stock, Queensland; Forestry Commission of N.S.W.

† Identifications of trees in the field have been made by local field officers.

first instar nymphs which were collected in the field were reared entirely on *Syncarpia laurifolia* in the laboratory at Sydney.

These observations indicate that *C. tessulata* is not specific in its feeding habits as tree species of different genera, namely, *Syncarpia*, *Acacia*, *Casuarina* and *Eucalyptus*, have been attacked. It is probable that this phasmatid will feed on other species.

Other phasmatids which have occurred in high populations are more specific in their tastes, but *C. tessulata* has nevertheless exhibited selective feeding within the



Text-fig. 1.—Occurrences of *C. tessulata*.

genus *Eucalyptus*. *E. microcorys* was less preferred, for during 1956 it was observed that, while crowns of *E. microcorys* showed no defoliation which could be positively attributed to *C. tessulata*, those of *E. maculata* immediately adjacent were completely defoliated.

BIOLOGY AND DESCRIPTIONS.

During 1956 and 1957 intensive observations on *C. tessulata* were made in Tanban State Forest and in the laboratory at Sydney. Although Tanban State Forest is the southernmost of the three outbreak areas, and well separated from the others (Toonumbar and Wedding Bells State Forests), differences in the number of developmental stages of the insect between the three areas are considered unlikely to occur.

The data given hereunder, particularly in respect of the seasonal cycle, apply to material collected from Tanban State Forest. Investigations on Toonumbar or Wedding Bells State Forests have been confined to the collection of adult material and samples of litter from the forest floor.

(a) *Seasonal Cycle*: First instar nymphs were observed during late August and early September 1956, and most emergences had occurred before the end of September. Some fourth and fifth instar nymphs were collected during late September. These were always taken in areas having a north-easterly aspect, and it is presumed early hatching occurred in these situations. In general, only small variations in the proportion of the different instars were observed in the main population. The young nymphs ascended the trees near their hatching site and commenced to feed. Adults first appeared during December 1956, the males reaching maturity one or two weeks prior to the females. The adults of the high population recorded in January 1956 were not observed after February 1956, oviposition having occupied a period of 6-8 weeks.

Adults of the 1957 infestation did not survive more than a few weeks in the field, but many of those which were collected on 16th January 1957, and held in the laboratory, survived until May 1957.

(b) *Egg Studies*: Eggs were collected from forest litter during April 1956, immediately after the 1955-56 generation. Further samples were examined in December 1956 and April 1957, when it was anticipated that the 1956 hatchings had occurred. Litter samples were collected in April 1957, to assess oviposition of the 1956-57 generation. The results of these examinations are expressed in Table 1.

TABLE 1
Egg Dissections, Ctenomorphodes tessulata, Tanban State Forest.
Results expressed as percentages of total number of eggs collected.

Date of Collection.	Embryonic Development.	No Visible Development.	Parasitism.	Deterioration.	Empty Shells.
April, 1956	7.9	7.3	17.7	25.7	41.4
December, 1956 ..	0.8	2.5	7.4	34.5	54.8
April, 1957	0.0	0.0	5.8	27.0	67.2

Apparently some of the eggs laid in January and February 1956 hatched in August and September 1956, thus differing from those of *P. wilkinsoni* and *D. violescens* which usually hatch during the year following oviposition. A low percentage of eggs (2.5%) showed no development by December 1956, but these eggs appear to have deteriorated, or were parasitized later in the season. Some eggs laid by the specimens collected from Tanban State Forest in January 1957, and held at normal atmospheric conditions in Sydney, showed advanced embryonic development when examined in June 1957. Eggs of the same origin which were held in soil at 78°F. and at room temperature hatched during June and July of the same year. The embryonic period, including at least one diapause, may occupy eight months or even longer in the natural habitat. The glistening appearance which is characteristic of the freshly laid egg disappears during subsequent life of the egg when it is in soil, but no external signs such as colour changes have been noted which may indicate embryonic development.

A number of eggs from the 1956-57 generation were placed in moist soil. One batch was held at 76°F. while another was kept at room temperature and therefore subjected to diurnal variations. The latter yielded healthy first instar nymphs mainly early in the mornings (1.00 a.m.-6.00 a.m.) and only occasional hatchings took place at other times during the day. At 76°F. small and weakened first instar nymphs emerged only at irregular intervals. When transferred to plants and held at room temperature, they lived only a short time and were not observed to feed.

Once initiated the embryo develops very rapidly until it entirely occupies the chorion and it has proved difficult to obtain early developmental stages of the embryo. Of the eggs collected in April 1956, 7.7% were in an advanced stage until hatching took place in August and September 1956 (Table 1). The diurnal seasonal increase in temperatures appears to be an important stimulus to hatching, and there is evidence to suggest that the litter must be damp or wet before first instar nymphs can emerge satisfactorily.

Parthenogenesis has been recorded in the Phasmatodea by Salmon (1955) and other workers. Females of *C. tessulata* are able to produce eggs without fertilization and embryonic development and subsequent hatching occur in a proportion of these eggs.

(c) *Nymphs*: It has been determined by Key (1957) that there are six nymphal instars for the males and seven for the females. Results obtained with specimens collected at Tanban State Forest during 1956-57 agree with those obtained by Dr. K. H. L. Key working in Canberra on laboratory insects. The predominant instars collected at approximately weekly intervals are expressed in Table 2.

No overt gregariousness by the nymphs has been shown either in the field or the laboratory. The insects are most of the time in a resting state, even in dense populations. Specimens in the laboratory have been observed to feed more frequently during the day than the night, but temperature and other climatic factors probably determine times of feeding in the field. After some ecdyses the phasmatids feed on their exuviae, sometimes completely devouring them.

TABLE 2.
Tanban State Forest. Collection of Nymphs.

Date of Collection.	Predominant Instars.	Date of Collection.	Predominant Instars.
3.10.56	I and II	7.12.56	VI
26.10.56	III and IV	14.12.56	VI
2.11.56	III	21.12.56	VI
8.11.56	III and IV	28.12.56	VI, VII, A
16.11.56	IV	4. 1.57	VII, A
23.11.56	IV and V	11. 1.57	VII, A
30.11.56	VI	18. 1.57	A

(d) *Adults*: The nymphs reached maturity during the latter part of December 1956, in Tanban State Forest. First instar nymphs which had been collected from this State Forest in September 1956, and held under high density conditions at Sydney, became adults approximately one week earlier. Fifty adult males and females could be readily collected in the field during January 1957, but the insects had almost disappeared from the same area by 6th February 1957. During the previous year adults were present until the first week in March. Female specimens collected on 21st January 1957 were kept alive in the laboratory until June 1957, while males collected on the same date had all died by the end of April 1957. Adults of this species may live from 4 to 9 weeks in outbreak areas, but can be kept alive for at least five months in the Laboratory.

Observations made on Ingalba and Tanban State Forests in February 1956 and January 1957 indicate that the ratio of adult males to females is approximately 50:50, but in some sites females predominate. The ratio at emergence is not necessarily the same as that of the adults, for males become adults earlier, and they may die prior to the females.

Laboratory female specimens of *C. tessulata* laid from 300-900 eggs over a period of five months. The daily oviposition rate varied from 4 to 10 per female each day.

Copulation occurs soon after the adult stage is reached and approximately two weeks elapse before the females commence to lay. The males and females remain together for long periods and move around while feeding. Copulation occurs at irregular intervals, oviposition taking place between these acts. Neither adults, nor nymphs, exhibit any overt gregariousness.

The destructive potential of *C. tessulata* was compared with that of *P. wilkinsoni* and *D. violescens* by isolating two males in one cage and two females of the same species in another for all three species. Chewed off foliage and the faeces of these insects were collected, separated, oven-dried and weighed daily. The figures obtained were halved, to give a daily destruction rate of foliage for one specimen of each species. A

daily maximum and an average daily figure for fourteen days collection are given in Table 3.

The defaecation rates have not been interpreted statistically as insufficient material was available to design an experiment, with sufficient replications. It is apparent that *C. tessulata* is as destructive as either *P. wilkinsoni* or *D. violescens*, both in the quantity of food eaten and foliage otherwise destroyed. Extensive areas of forest have not been observed defoliated to the same extent as occurs with *P. wilkinsoni* and *D. violescens*, and this is partly explained by the adults of *C. tessulata* being comparatively short-lived in the outbreak areas. Phasmatids of the highlands are in the adult stage for approximately three months, while *C. tessulata* has not been observed six to eight weeks after maturity.

TABLE 3.
Comparison of Destructive Potential of Three Plague Phasmatids.
Results shown as grammes of oven-dry weight of material per insect per day.

Phasmatid.	Faeces.	Foliage.	Total.
<i>P. wilkinsoni</i> (male)			
Maximum	0.092	0.092	0.184
Average	0.054	0.044	0.098
<i>P. wilkinsoni</i> (female)			
Maximum	0.296	0.131	0.427
Average	0.188	0.066	0.254
<i>D. violescens</i> (male)			
Maximum	0.140	0.140	0.280
Average	0.084	0.023	0.107
<i>D. violescens</i> (female)			
Maximum	0.211	0.196	0.407
Average	0.156	0.062	0.218
<i>C. tessulata</i> (male)			
Maximum (1 day) ..	0.012	—	0.012
Average (1 day) ..	0.012	—	0.012
<i>C. tessulata</i> (female)			
Maximum	0.278	0.337	0.615
Average	0.176	0.111	0.287

It has been possible, in the case of the three plague phasmatids studied by Dr. K. H. L. Key, to correlate the high density phase pattern with most field outbreaks. This should enable entomologists to approximate the density of a population from which one or two specimens have been collected from the field. Large populations of immature phasmatids during the last ten years have not always been recorded until defoliation has become apparent in spite of the fact that single specimens have been collected and sent to entomologists for examination. Now, in the light of present knowledge, when nymphs show the medium to high density phase pattern, the population may warrant further investigation.

The following descriptions which are intended for use in the field will serve to distinguish *C. tessulata* from the other two species of injurious Australian phasmatids. They are based on fourteen males and twenty-three females in the collection of the Forestry Commission of New South Wales.

Male (Plate v, fig 1): Head bearing two large compound eyes and three ocelli. Antennae 26-segmented. Pronotum approximately 3 mm. long, surface uneven, narrower than head. Mesonotum approximately 13 mm. long, two rows of prominent dorsal tubercles numbering in all from 8 to 13, several slightly raised lateral tubercles, narrower than the pronotum. Metanotum approximately 7 mm. long, without tubercles, wider than mesonotum. Prothoracic legs bearing no spines, femora of mesothoracic legs carry spines along their length with two large spines at distal end. Spines evident along femora and tibiae of metathoracic legs and distal end of each. Tegmina brown, approximately 10 mm. long. Hindwings approximately 35 to 40 mm. long extend over fifth and sometimes part of sixth abdominal segments. Ten abdominal segments.

Genital lobes appear as enlargement on ventral surface of segments VIII and IX. Tenth segment modified to form claspers which bear spines. Cerci about $\frac{1}{8}$ inch long, leaf-like.

Female (Plate v, fig 2): Head bearing two large compound eyes and three ocelli. Antennae 25-28-segmented, shorter than those of male. Pronotum approximately 5 to 7 mm. long, no tubercles present, slightly narrower than head. Mesonotum 20 to 23 mm. long with two rows of dorsal tubercles and several lateral tubercles. Tubercles more prominently raised than in male. Metanotum 7 to 8 mm. long, non-tuberculate. Pronotum, mesonotum and metanotum of equal width. Prothoracic legs bearing spines along, and at distal end of femora. Mesothoracic legs with spines along femora and tibiae, as well as at distal end of these segments. Spines also present along and at distal extremities of femora and tibiae of metathoracic legs. Tegmina brown, approximately 13-15 mm. long. Hindwings 25 to 30 mm. long, apices extending almost to posterior margin of third abdominal segment. Ten abdominal segments. Operculum which covers genital valves arises from segment VIII, its apex extending beyond segment X and located between the cerci. Cerci about $\frac{1}{4}$ inch long, leaf-like.

General colour of the males and females light to dark brown.

The Egg: In the Phasmatoidea the egg may be regarded as a useful taxonomic accessory. Egg approximately 3 mm. long and 2 mm. in diameter at broadest point. Roughly elliptical in shape, somewhat wider in region of micropyle, distinctly flattened at both ends. When freshly laid, glistening black in appearance. Pale grey area extending over and around micropylar area. Smooth edged grey pigment appearing to overlie the black. Egg smooth, although microscopic examination shows it to be uneven. Black raised ridge in the shape of a Y surrounds the micropylar orifice at non-opercular end of egg.

Key to the Instars of C. tessulata.

Sex determination:

1. Operculum or minute furrow* on abdominal sternum VIII present female.
2. Operculum or minute furrow on abdominal sternum VIII absent male.

Male.

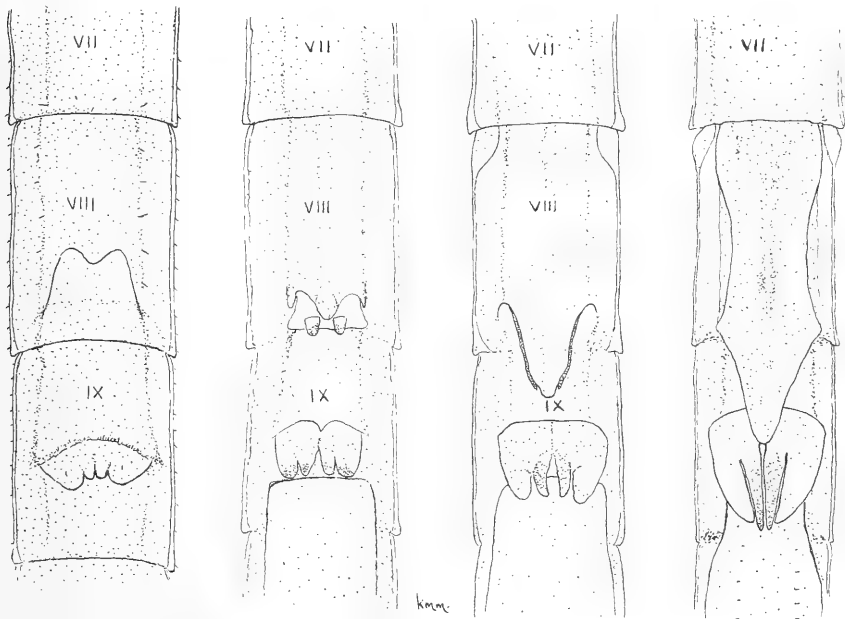
1. Lateral and dorsal mesothoracic tubercles not raised: wing rudiments not evident; antenna with 9 segments which are clearly separated, length approx. 12 mm. INSTAR 1.
Lateral and dorsal tubercles raised 2.
2. Dorsal tubercles not black: wing rudiments evident; antenna with 9 segments, several partially divided; length approx. 20 mm. INSTAR 2.
Dorsal tubercles black 3.
3. Apices of tegmen rudiments not extending over the metanotum: wing rudiments not in contact along their inner margin; antenna with about 18 distinct or partially divided segments; length approx. 30 mm. INSTAR 3.
Apices of tegmen rudiments extending over the metanotum 4.
4. Wing rudiments not in contact along their inner margins: antenna with about 19 distinct or partially divided segments; length approx. 40 mm. INSTAR 4.
Wing rudiments in contact along their inner margins 5.
5. Wing rudiments not extending to the posterior margin of abdominal segment 1: apices of tegmen rudiments do not reach the anterior margin of wing rudiments; antenna with about 22 segments; length approx. 55 mm. INSTAR 5.
Wing rudiments extending beyond the posterior margin of abdominal segment 1; apices of tegmen rudiments almost reaching the anterior margin of wing rudiments; antenna with about 24 segments; length approx. 70 mm. INSTAR 6.

Female.

1. Lateral and dorsal mesothoracic tubercles not raised: wing rudiments not evident; operculum present as a transverse furrow on sternum VIII; antenna with 9 distinct segments; length approx. 12 mm. INSTAR 1.
Lateral and dorsal mesothoracic tubercles raised 2.
2. Dorsal tubercles not black: operculum present as a pointed triangular projection on sternum VIII, Text-fig. 2; antenna with 9 segments, several of which are partially divided; length approx. 20 mm. INSTAR 2.
Dorsal tubercles black 3.

* Minute transverse furrow is present only in Instar 1, and live or recently killed material is necessary to see this structure.

3. Operculum not covering anterior genital valves on sternum VIII, Text-fig. 2: wing rudiments minute; antenna with about 18 distinct or partially divided segments; length approx. 30 mm. INSTAR 3.
Operculum covering or almost covering anterior genital valves on sternum VIII, Text-fig. 2 4.
4. Tegmen rudiments extending not more than half their length over anterior margin of metanotum; antenna with about 19 distinct or partially divided segments; length approx. 45 mm. INSTAR 4.
Tegmen rudiments extending more than half their length over anterior margin of metanotum 5.
5. Apex of operculum extending half-way along sternum IX, Text-fig. 2: and partly covering posterior genital valves; wing rudiments not in contact along their inner margins; tegmen rudiments separated along inner margin; antenna with about 22 segments; length approx. 55 mm. INSTAR 5.
Apex of operculum extending more than half-way along sternum IX 6.



Text-fig. 2.—Nymphal characteristics. From left: abdominal sterna of female instars.

6. Inner margins of wing rudiments not touching; operculum reaching posterior margin of segment IX, or almost reaching apices of posterior genital valve; wing rudiments extending almost to base of metacoxae. Tegmen rudiments extending at least half their length beyond anterior margin of metanotum; antenna with about 24 segments; length approx. 75 mm. INSTAR 6.
Inner margins of wing rudiments touch; operculum reaching to or beyond midpoint of segment X and exceeding apices of posterior genital valve; wing rudiments strongly tessellated, extending to base of metacoxae; apices of tegmen rudiments almost reaching anterior margin of wing rudiments. Antenna with about 26 segments; length approx. 110 mm. INSTAR 7.

MORTALITY FACTORS.

Several factors have caused, or have been suspected of causing, mortalities in the various stages of *C. tessulata*.

(a) *Temperature and Moisture*: The effects of weather in the field have not been studied, all observations being made on insects in the laboratory. Nymphs were at first difficult to rear, but when water was sprayed onto the leaves, the first instar phasmatids were observed to consume some of it and mortalities were reduced. When nymphs were held in jars with an adequate supply of food they were reared through

successive instars. A more successful method consisted of placing the recently hatched nymphs on young plants in nursery tubes, which were placed in a small container of moist soil, within a wire gauze cage approximately 24 in. \times 18 in. \times 18 in. The foliage was sprayed with water at least twice a day and the soil was watered on alternate days. Mortalities were low and nymphs were observed to feed during the third day. Key (1957) successfully reared the phasmatids from first instar nymphs by placing them in small wire mesh cages which were located over a container of water holding the leaves and covered with an inverted, loosely fitting plastic jar. An atomizer was used to spray the foliage twice a day during the early instars, and once a day during later instars.

Recently emerged nymphs apparently require moist conditions, which would be supplied as rain and dew in the field. Most emergences from eggs in the laboratory occurred during the early hours of the morning and their moisture requirements would probably be fulfilled by condensation. Moisture is apparently less critical during the later instars and in the adult stage, but prolonged dry conditions, particularly if accompanied by moderate to high temperatures, could cause high mortalities among the early instars.

First instar nymphs obtained from eggs held at 76°F. died a few days after being placed on food at temperatures of 55°F. to 65°F., but nymphs which hatched at temperatures of 55°F. to 65°F. and were placed with those hatched at 76°F. were reared successfully. Eggs held exposed under laboratory conditions of atmospheric humidity and temperature failed to hatch, while those kept in moist soil hatched normally. However, lack of moisture did not inhibit embryonic development, so that under dry conditions high mortalities would occur at hatching. Conditions such as these would not occur frequently under field conditions.

(b) *Food*: This species has been reared on *Syncarpia laurifolia*, *Acacia mollissima* and *Eucalyptus dives*, and a large percentage of the nymphs were reared to adults when any one of these host plants was used exclusively. In the field, recently emerged nymphs which ascend a tree, the foliage of which is not acceptable to them, may desiccate before a suitable host species is found.

(c) *Previous History of the Eggs*: Some eggs which were obtained from the 1955-56 generation showed no hatching although exposed to conditions which apparently stimulated hatching of the eggs obtained from the 1956-57 generation. Such factors as food requirements of the mature female, parthenogenesis and others which have not been elucidated, may affect the viability of the eggs.

(d) *Cannibalism*: Key (1957) records cannibalism as a possible mortality factor, and he states that chewed legs of recently moulted nymphs have been found in the rearing cages. When rearing specimens at Sydney, no cannibalism was noticed, but when ecdysis was completed, freshly emerged nymphs were observed to consume their exuviae and frequently the exuviae of others. This has been observed before ecdysis was completed; thus a nymph which has not shed the exuviae from its legs may possibly have them chewed off by another nymph. This could account, to some extent, for instances of limb regeneration frequently encountered in this species. Cannibalism is not considered to be a mortality factor of laboratory or field specimens, even though most mortalities of nymphs in the laboratory occurred at ecdysis.

(e) *Fire*: A large forest fire could be catastrophic to phasmatid populations, and it may destroy many insects and reduce their available food supply. A limited fire occurred on Toonumbar State Forest in December 1956, and insects which had emerged during the August or September may have been killed. This has been confirmed by observations since the fire.

(f) *Disease*: During mortality studies of *Podacanthus wilkinsoni*, Casimir and Edwards (1955—unpublished report, Forestry Commission N.S.W.) isolated a species of entomogenous fungus from nymphs and adults, but they state that this does not present sufficient evidence of pathogenicity. No instances of death attributable to pathogens have been determined, nor has it been possible to relate micro-organism activity with mortalities of *C. tessulata*. Nymphs have died when held at high humidities in the

laboratory and, some time after death, a fungal growth spread over the surface of their bodies. This fungus was considered to be a saprophytic type.

Dissections of eggs collected from the north coast outbreak areas showed a high mortality percentage from diseases of unknown origin (Table 1). Deterioration due to fungi, bacteria and physiological causes about which little is known at present has affected 25.7%, 34.5% and 27.0% of total eggs collected in April 1956, December 1956 and April 1957, respectively. From eggs of *C. tessulata* which showed deterioration, two fungi, *Verticillium* sp. and *Penicillium* sp.,* have been isolated. Both are commonly found in the soil and it is unlikely that they would be the primary cause of the deterioration.

(g) *Predators*: Insect predators have not been recorded attacking any stages of *C. tessulata*, although such attacks probably occur. Nymphs of the highland plague species have been attacked by *Harpobittacus* sp.† (Bittacidae-Mecoptera) in the Jenolan area.

Birds feed on phasmatids, but observations only include crows feeding on *D. violescens* and *P. wilkinsoni* in the highland areas. No doubt *C. tessulata* also falls prey to birds, although no instance of this has been observed. The resemblance of phasmatid eggs to seeds is rather striking, as can be seen from Plate vi.

Eggs of *C. tessulata* are shiny black and when freshly laid are easily discernible in the forest litter, but when the eggs lose their lustre, they become difficult to locate, as soil adheres to their surface. Quail have been active in Tanban State Forest during the latter part of the outbreak, and it is possible that there is some association between the activity of these birds and the reduction in the number of eggs.

(h) *Parasites*: Egg parasites of the genus *Myrmecomimesis* (Cleptidae-Chrysoidea) have been described by Riek (1955). The material examined by him was mainly obtained from the Jenolan area where plagues of *Didymuria violescens* and *Podacanthus wilkinsoni* were present. Eggs of *D. violescens* from Bago State Forest have yielded a total parasitism of up to 9% during 1954-55. During 1952, parasitism of *P. wilkinsoni* eggs averaged as much as 7% from several collecting sites on the Jenolan area.

The males of the several species of *Myrmecomimesis* found on the coast are winged while the females are wingless. Parasitized phasmatid eggs can be distinguished by the presence of small pits on the surface of the chorion, made by the female wasp when ovipositing. A small hole passes from at least one of these pits, through the vitelline membrane, causing the latter to become dark brown at the puncture. One egg may show several of these punctures, but only one parasite develops in each egg. Whether the pits are the result of exploratory efforts by the adult parasite in determining a suitable oviposition site or whether several parasites have actually oviposited in the egg has not been determined.

Phasmatid eggs which were laid during January and February 1956 were found to contain parasites when examined in April 1956. The parasite larva completely occupied the vitelline membrane indicating that development to this stage was comparatively rapid. The eggs were held in the laboratory until December 1956, when adult cleptid wasps emerged. Diapause may occur since the larvae remain in an advanced larval stage until November or December, although the phasmatid eggs are parasitized during January to April of the same year.

Attempts to induce parasitism by exposing *C. tessulata* eggs to *M. rubrifemur* under confined conditions were unsuccessful and a detailed study on the life cycle of *Myrmecomimesis* spp has not been made.

The specimens of *Loboscelidea* sp.‡ were obtained shortly after eggs and forest litter were received from Tanban State Forest in April 1956. No emergences occurred later

* Specimens examined by D. W. Edwards, Pathologist, Forestry Commission, N.S.W.

† Observations by L. Mors, Forester, Oberon, 1955.

‡ This species is being described by Mr. E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra.

in the year, as was the case with *Myrmecomimesis* spp. This indicates that certain differences exist between the life cycles of the two parasites. Since *Myrmecomimesis* sp. is more abundant than *Loboscelidea* sp., it is probable that the former would account for more parasitism.

Parasitism of *C. tessulata* eggs from the coast is given in Table 4. In addition, fluctuations in parasite numbers have been recorded for Tanban State Forest and these

TABLE 4.
Egg Dissection of April, 1956, Collection.
Expressed as percentages of total eggs collected.

State Forest.	Embryonic Development.	No Development.	Parasitism.	Deteriorated.	Empty Shells.
Toonumbar ..	19.4	13.2	20.6	21.4	25.4
Wedding Bells ..	2.0	1.9	12.4	21.2	62.5
Tanban	7.9	7.3	17.7	25.7	41.4
Ingalba	15.9	16.4	20.0	24.0	23.7
Colombatti ..	5.6	8.1	7.5	48.2	30.6

are expressed in Table 1. Parasitism of *C. tessulata* eggs is greater than that of either *P. wilkinsoni* or *D. violescens* in the highlands, and this has been verified by observations on the forest litter in Tanban State Forest in February 1956, when the parasites were active. At no time have the parasites been observed to be so abundant in the highland areas as to be apparent in the litter. The parasite which has occurred in all outbreak areas and in greatest abundance is *Myrmecomimesis rubrifemur* (Riek). The known occurrences of the other species are given in Table 5, but more extensive collections would probably have given a greater distribution of the species involved.

TABLE 5.
Occurrence of Cleptid* Parasites in Outbreak Areas.

Location.	Species.
Toonumbar State Forest	<i>Myrmecomimesis rubrifemur</i> (Riek).
Wedding Bells State Forest	<i>M. rubrifemur</i> (Riek).
Tanban State Forest	<i>M. rubrifemur</i> (Riek). <i>M. nigripedice</i> (Riek). <i>Loboscelidea</i> sp.
Ingalba State Forest	<i>M. rubrifemur</i> (Riek). <i>M. nigripedice</i> (Riek). <i>M. bispinosa</i> var. (Riek).

* Determinations by E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra.

DISCUSSION.

(a) Effect of Outbreaks on the Stand Composition and Forest Management.

The tree stand composition in all areas attacked by *C. tessulata* shows considerable similarity. Attack appears to be restricted to some of the drier type coastal hardwood forests of northern New South Wales.

A typical stand in which the attack occurs consists of *Eucalyptus punctata* (Grey Gum), *E. triantha* (White Mahogany), *E. paniculata* (Ironbark), *E. maculata* (Spotted Gum), *E. gummifera* (Red Bloodwood), *Syncarpia laurifolia* (Turpentine) and Stringybark. Always associated with attacked stands is an understory of *Casuarina torulosa* (Forest Oak), and *E. microcorys* (Tallowwood) is often associated with them. Other species which are occasionally found in attacked areas are *E. resinifera* (Red Mahogany), *E. umbellata* (Gaertn.) Domin (Red Gum), *E. saligna* (Blue Gum), *Tristania conferta*, R. Br. (Brush Box) and *Angophora* spp. (Wild Apple). The understory, particularly in the Kempsey area, consists mainly of Leguminosae. On Tanban State Forest, in the Kempsey district, phasmatids have attacked a stand of *E. pilularis* (Blackbutt), this

being associated with Grey Gum, Spotted Gum, White Mahogany, Ironbark, Stringybark and Turpentine. *E. pilularis* constituted more than 50% of the stand, and this is the only instance recorded where *C. tessulata* has attacked this species.

As *C. tessulata* has avoided *E. microcorys* in preference to other species of eucalypts, it was thought that this selectivity may have been accounted for on the basis of oil content of the leaves. A chemical examination of the leaves of favoured hosts and those of *E. microcorys* showed that the major oil constituents were very similar, and from these analyses both types of leaves should be equally acceptable. The minor constituents of the oils were not determined, and it is possible that these may account for the observed selectivity in the feeding habits.

Attack by *C. tessulata* in plague proportions has not yet been recorded as recurrent. The plagues during 1955-56 severely or completely defoliated areas of up to 100 acres. In 1956-57 the phasmatid population was less, and by the mid-summer of 1956-57 all of the trees attacked the previous season had recovered and recognition of the areas which had been severely affected the previous year was difficult. Severe attack on isolated areas without further heavy infestations the following season would be unlikely to have any serious or lasting effect on the trees, while repeated defoliations would either kill or retard the growth of the preferred species, and Tallowwood may be favoured as against the more susceptible species. The removal of cover would enable a greater degree of light to penetrate to the forest floor, thus releasing suppressed lignotubers. This again would be likely to favour the development of tallowwood stands rather than the more susceptible species.

The attacked stands contain only a small proportion of Tallowwood and it would be some time before it regenerated sufficiently to restock an area, particularly as the outbreak areas are of low site quality. When considering the merits of restocking with Tallowwood, it should be remembered that *C. tessulata* attacks many other valuable species.

(b) Influence of Forest Fires.

In 1951-52, fires burnt over large tracts of forest on the north coast, including those areas where outbreaks of *C. tessulata* were later to occur. The same areas were sometimes burnt more than once during the same season, particularly on Tanban State Forest. Although data have been available on the extent, intensity and date of occurrence of the fires, it was realized that the actual boundaries of the affected areas would be only approximate. For this reason the fire records have been related to phasmatid outbreaks only in a general manner.

Fires were recorded from Tanban, Ingalba and Colombatti State Forests and adjoining private property between 26th August 1951 and 4th January 1952, but in the six years since that time no extensive burns have occurred. Observations during the phasmatid plague of 1955-56 revealed that high populations were restricted to definite areas, whilst a low-density population existed throughout the rest of the regions. These high populations have occurred in most instances close to or within the limits of areas burnt in 1951-52.

Records of fires on Wedding Bells State Forest show that areas heavily infested by phasmatids in 1955-56 were burnt in 1951-52 during the period from 30th September to 26th October 1951, and local observations confirm these records. The phasmatid infestation of 1955-56 in Toonumbar State Forest was found to be present on a site which had not been burnt for at least eight years. A widespread fire did occur on 23rd September 1951, but this was some distance from the outbreak area. These fires varied in intensity from light ground fires to crown fires, and within a comparatively small area damage would have been caused to the crown of some trees whilst those in close proximity remained relatively untouched. The leaf litter is destroyed only by the hotter burns.

Nymphs of *C. tessulata* emerge in late August and early September when they ascend the trees, usually to the more tender terminal shoots. The egg parasites appear

to emerge mainly during December and February, when the eggs of *C. tessulata* are available for parasitism.

Fires which occur in the spring and early summer months may destroy the parasitized eggs of *C. tessulata* on the forest floor, and if the fire were not intense, it is likely that the developing nymphs present in the crowns of the trees would be unaffected. The eggs from this generation hatch the following spring; thus an increase in population could occur over the succeeding years. The figures of parasitism in Table 1 indicate that the cleptid parasites are important mortality factors and their destruction would remove their regulating influence on the phasmatid population, with a consequent rise in phasmatid numbers.

Records of fires on Ingalba, Tanban, Colombatti and Wedding Bells State Forests appear to be related to phasmatid plagues, although there are some areas in these State Forests which have been attacked by phasmatids without having been affected by fire.

The nymphal and mature phasmatids of the 1956-57 season disappeared prematurely from the outbreak areas, and this cannot be attributed to the activity of cleptid egg parasites which had greatly increased in number during the absence of fires. This points to the fact that at least one other major regulating factor, at present undetermined, was operating during the 1956-57 season. Climatic records for January and February 1957 do not suggest climate as the main factor, for adult phasmatids held in cages at Sydney lived many months. No dead phasmatids were collected from the forest litter, nor were any observed to exhibit moribund symptoms which may indicate disease.

Females of *C. tessulata* are flightless, and migration could not account for the decrease in population.

While fires may have had an influence by temporarily reducing the egg parasite population, it is also suggested that fires either in or near plague areas have had their influence on the bird population. This may have resulted in an increase in the population of *C. tessulata*, by the regulating factors being partly removed. The occurrence of a univoltine life cycle and the high egg laying potential of *C. tessulata* have probably enabled plagues to occur within four years of the fires.

After a period of five years high populations of *C. tessulata* are no longer present and it appears that there has been a return to a more stable environment. It will not be easy to test the hypothesis of predatism by birds without high populations of *C. tessulata*. As the practice of burning the litter on the forest floor in the spring and summer period may prolong phasmatid plagues by destroying the egg parasites, the relative merits of controlled burning should be considered in relation to plagues of *C. tessulata*. The effects of fires on the environment of a forest are not always fully realized.

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In the preparation of this paper the advice, particularly concerning taxonomy, of Dr. K. H. L. Key of the Division of Entomology, C.S.I.R.O., was frequently sought.

The senior author is indebted to his colleagues Mr. K. G. Campbell and Mr. K. M. Moore for their assistance in the egg dissection work and for their helpful criticism of the manuscript. The drawings of the female genitalia were also done by Mr. Moore.

The photos which form Plate v, figs. 1, 2 3 and Plate vi are by Mr. R. Moulton, Forestry Commission of New South Wales.

Mr. R. H. Luke of the Forestry Commission of New South Wales assisted in the correlation of fire and outbreaks, while Mr. F. R. Humphreys, also of the Forestry Commission of New South Wales, made the chemical analyses of the leaves of several host trees. Mrs. M. Casimir, Forestry Commission of New South Wales, has given advice from time to time during the investigations.

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EXPLANATION OF PLATES V-VI.

Plate v.

1. *Ctenomorphodes tessulata*. Adult male.
2. *Ctenomorphodes tessulata*. Adult female.
3. *Myrmecomimesis* sp. A parasite of Phasmatid eggs.
4. An outbreak area. Tanban State Forest, February, 1957. *E. maculata* with understorey of *C. torulosa*.

Plate vi.

Phasmatid eggs. Top row, left to right: *Ctenomorphodes tessulata* (Gray), *Ctenomorpha chronus* (Gray), *Podacanthus wilkinsoni* Macleay, *Podacanthus viridiroseus* (Gray), *Podacanthus typhon* Gray. Bottom row, left to right: *Didymuria violescens* (Leach), *Acrophylla titan* (Macleay), *Extatosoma tiaratum* (Macleay), *Tropidoderus childreni* (Gray).

AN ANNOTATED CATALOGUE OF DESCRIBED AUSTRALIAN TABANINAE
(DIPTERA, TABANIDAE).

By I. M. MACKERRAS, Queensland Institute of Medical Research, Brisbane.

(Nine Text-figures.)

[Read 27th May, 1959.]

Synopsis.

The described Australian species and subspecies of Tabaninae are arranged according to the modern classification of the subfamily, the numbers recognized as valid being: *Tabanus*, 20; *Paracanthocera*, 1; *Chalybosoma*, 2; *Cydistomyia*, 20; *Dasybasis*, 56. Six remain unrecognized, three are removed to other subfamilies, and nine are excluded as having been recorded wrongly from Australia. New synonymy:

In *Tabanus*: *queenslandii* Ferg. nec Ric. = *australicus* Tayl.; *geraldi* Tayl. = *concolor* Walk.; *aprepes* Tayl. = *townsvilli* Ric.; *diminutus* Walk. = *praepositus* Walk.; *nigritarsis* Tayl. = *dorso-bimaculatus* Macq.

In *Cydistomyia*: *postica* (Hardy nec Wied.) = *avida* (Big.); *sanguinaria* (Big.) = *nigropicta* (Macq.).

In *Dasybasis*: *darwinensis* (Tayl.) = *clavicallosa* (Ric.); *quadrata* (Tayl.) = *constans* (Walk.); *pseudopalpalis* Ferg. & Hill = *nemotuberculata* (Ric.); *adelaidae* (Ferg. & Hill) = *rufifrons* (Macq.); *bassii* (Ferg.) = *tasmanica* (Ferg.) = *neocirrus* (Ric.); *geraldtonensis* (Tayl.) = *regis-georgii* (Macq.); *regis-georgii* (auct. nec Macq.) = *spadix* (Tayl.); *pseudobasalis* (Tayl.) = *postica* (Wied.); *oraria* (English) = *macrophthalma* (Schin.); *acutipalpis* (auct. nec Macq.) = *exulans* (Erich.); *whitei* (Hardy) = *nepos* (Walk.) = *hebes* (Walk.); *gentilis imminutus* (Hardy) = *gentilis* (Erich.); *antecedens* (Walk., 1854 nec 1848) = *edentula* (Macq.); *flindersi* (Ferg.) = *antecedens* (Walk., 1848) = *gregaria* (Erich.); *brevidentata* (Macq.) = *fratercula* (Macq.) = *circumdata* (Walk.); *edentula* (auct. nec Macq.) = *abstersa* (Walk.) = *acutipalpis* (Macq.).

The subfamily Tabaninae is characterized by lacking functional ocelli and apical spurs on the hind tibiae, and by having the third antennal segment composed of a basal plate and four (occasionally three) terminal annuli, the style of the male hypopygium truncate, and the caudal ends of the spermathecal ducts of the female provided with mushroom-like expansions. It contains a large number of intergrading forms, which are exceedingly difficult to classify at both specific and supra-specific levels. I have recently been able to study the types of nearly all the Australian species, and the present paper is designed to clarify their synonymy, which had inevitably been obscure, as many of the crucial specimens had not been available to workers in Australia.

It will probably be a considerable time before a full revision of the subfamily can be completed, and the classification adopted here is, to some extent, tentative. The short definitions of the supra-specific divisions apply to Australian species only. They are intended primarily to indicate natural congeries of species, which may be raised or lowered in taxonomic status as subsequent investigations may indicate. Similarly, the species are arranged within the groups in a natural rather than alphabetical sequence, so that related forms can be compared. There are about 18 undescribed species (6 *Cydistomyia*, 12 *Dasybasis*) in the collections studied, but they do not affect the present discussion.

This work would not have been possible without helpful cooperation from a great many authorities. The type specimens in Australia were studied through the kindness of the Directors and Entomologists of the Queensland Museum, Brisbane, the Australian Museum, Sydney, the School of Public Health and Tropical Medicine, Sydney, the

Macleay Museum, Sydney, the National Museum, Melbourne, and the South Australian Museum, Adelaide. Mr. H. Oldroyd, of the British Museum (Natural History), compared many specimens with types, including the types of Erichson's species, which were borrowed for the purpose by Mr. H. F. Mattingly of the same institution. Mr. Oldroyd also provided facilities for me to work in his Department, as did Professor E. Séguy, of the Muséum National d'Histoire Naturelle, Paris. Professor Fritz Peus, of the Zoologisches Museum, Berlin, and Dr. Max Beier, of the Naturhistorisches Museum, Vienna, also compared specimens with types, and sent me types on loan when any difficulties of interpretation arose. To all of these I would express my most grateful thanks.

Species of which the types have been examined personally are indicated by an asterisk (*) in the body of the paper.†

Tribe TABANINI.

Basicosta covered with short, strong setulae, similar to those on the adjacent, swollen part of the costa (Mackerras, 1956, Fig. 6, C). This character seems to hold absolutely in the Australasian and Pacific faunas. The fronts of the females narrow towards the antennae, and their palpi are usually swollen at the base and taper to a relatively sharp point.

Genus TABANUS Linnaeus.

Type species: *Tabanus bovinus* Linn., Europe. No Australian synonyms.

This faunal element is of strictly Oriental origin, and none of the species can be separated from the widespread genus *Tabanus*, as it is at present recognized. The eyes are hairy (pattern not known) in *umbripennis*, bare in all the other species; conspicuously banded in *pallipennis*, *particaecus* and *ceylonicus*, bicoloured brown and green in *australicus*, concolorous green or brown in the remaining species.

The pallipennis Group.

Vein R_4 with strong appendix; frons of female relatively wide (index not more than 3); callus usually divided into two parts.

TABANUS PALLIPENNIS Macquart.

Tabanus pallipennis Macquart, 1846. *Dipt. exot.*, Suppl. 1, p. 32. Type ♀, from New Holland, not found in London or Paris.

**Tabanus rufinotatus* Bigot, 1892. *Mem. Soc. zool. Fr.*, 5, p. 673. Type ♀, from Australia, in the British Museum (Natural History).

**Tabanus elestëem* Summers, 1912. *Ann. Mag. nat. Hist.*, (8), 10, p. 224. Cotype ♀♀, from Darwin, N.T., in the British Museum (Natural History).

**Tabanus lineatus* Taylor, 1913. *Rpt. Aust. Inst. Trop. Med.* for 1911, p. 65. Type ♀, from Bowen, N.Q., in the School of Public Health and Tropical Medicine, Sydney. Not *T. lineatus* Fabricius, 1781 (= *giganteus* Degeer, 1776), Nearctic.

The type of *pallipennis* is evidently lost. It could not be found by Ricardo (1914), by Dr. P. Grenier, who searched for it in Paris for me last year, or by myself, in July-August, 1958. Under the circumstances, it is unfortunate that Hardy (1948) upset Ferguson and Hill's (1920) tentative identification of *pallipennis* as another species, and displaced the name *rufinotatus* under which this one was well known. *Tabanus designatus* Ricardo, 1913, from New Guinea, is an additional synonym.

Distribution.—Northern Territory; north and east coastal Queensland; north coastal New South Wales. Also New Guinea.

TABANUS PARTICAECUS Hardy.

Tabanus particaecus Hardy, 1948. *Proc. R. Soc. Qd.*, 58, p. 178. No type designated.

Hardy proposed *particaecus* as a "new name" for the species which he considered Ferguson and Hill (1920) had wrongly identified as *T. pallipennis* Macq. In order to

† The types of *Dasybasis gentilis* (Erichson) and *D. gregaria* (Erichson) were received from Professor Peus, and Mr. Oldroyd's interpretation of them confirmed, after this paper had gone to press.

avoid further confusion, I now propose to validate it by designating as lectotype a ♀ from the original bred series from Eidsvold, S.Q., referred to by Hardy, and now in the School of Public Health and Tropical Medicine, Sydney.

Distribution.—Southern Queensland; New South Wales, west of the Divide; north-western Victoria.

TABANUS UMBRIPENNIS Ricardo.

**Tabanus cinereus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 167. Type ♀, from Western Australia, in the British Museum (Natural History). Not *T. cinereus* Wiedemann, 1821, Neotropical.

Tabanus umbripennis Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 16, p. 283. Nom. nov. This species is, superficially, remarkably like the predominantly Holarctic genus *Hybomitra*.

Distribution.—South-western Western Australia.

The innotabilis Group.

Vein R_4 rarely with short appendix; frons of female relatively narrow (index more than 3); callus single, usually elongate.

(A) A black species, with shining subcallus and creamy white tarsi.

TABANUS CEYLONICUS Schiner.

Tabanus ceylonicus Schiner, 1868. *Reise Novara Dipt.*, p. 93. Type ♀, from Ceylon, in the Vienna Museum; a ♀ from Bramston Beach, N.Q., was sent to Dr. Beier, who reported that it agreed fully with the type.

**Tabanus kershawi* Ricardo, 1917. *Ann. Mag. nat. Hist.*, (8), 19, p. 221. Type ♀, from Claudie R., N.Q., in the National Museum, Melbourne.

The synonymy was known to Ferguson, but apparently not published until Oldroyd's (1949) revision of the Papuan species.

Distribution.—Widely in the Oriental region; north to the Philippine Is.; east to New Guinea, New Ireland and the Solomon Is.; and in north-eastern Queensland as far south as Innisfail.

(B) Species with a continuous, median, pale vitta on most or all abdominal tergites.

TABANUS QUEENSLANDII Ricardo.

**Tabanus queenslandii* Ricardo, 1914. *Ann. Mag. nat. Hist.*, (8), 14, p. 393. Type ♀, from N.E. Queensland, in the British Museum (Natural History).

**Tabanus walteri* Taylor, 1919. *PROC. LINN. SOC. N.S.W.*, 44, p. 48. Type ♀, from Hay, N.S.W., in the School of Public Health and Tropical Medicine, Sydney.

The name *queenslandii* has usually been applied to another species (*australicus*) which is common in Queensland; but the above synonymy was published by Taylor (1926), and subsequently confirmed by Oldroyd (*in lit.*) and by examination of the types.

Distribution.—Rare in north coastal Queensland; most specimens from western New South Wales.

TABANUS STRANGMANI Ricardo.

**Tabanus strangmannii* Ricardo, 1914. *Ann. Mag. nat. Hist.*, (8), 14, p. 393. Type ♂♀, from Darwin, N.T., in the British Museum (Natural History).

**Tabanus mastersi* Taylor, 1917. *PROC. LINN. SOC. N.S.W.*, 41, p. 754. Type ♀, from Bowen, N.Q., ♂ from Mackay, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

Miss Ricardo's name is now emended to *strangmani*, in accordance with the "Copenhagen Decisions". Taylor (1913) first misidentified the species as *gregarius* Erichson, but later named it and labelled types.

Distribution.—Northern Territory; eastern Queensland, from Moa I. to Eidsvold; western New South Wales (Moree).

TABANUS BREINLI Ferguson & Hill.

**Tabanus breinli* Ferguson and Hill, 1922. PROC. LINN. SOC. N.S.W., 47, p. 255. Type ♀, from Palm I., N.Q., in the School of Public Health and Tropical Medicine, Sydney.

Distribution.—North Queensland (Palm I. and adjacent coast).

TABANUS AUSTRALICUS Taylor.

**Tabanus australicus* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 53. Type ♀, from Brisbane, Q., in the Queensland Museum, Brisbane.

This species was misidentified as *queenslandii* by Ferguson (1920), and it has commonly been so labelled in Australian collections.

Distribution.—Northern Territory; Queensland, from Gulf of Carpentaria and Cairns to Brisbane.

TABANUS CONCOLOR Walker.

**Tabanus concolor* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 179. Type ♀, from New Holland, in the British Museum (Natural History).

Tabanus geraldii Taylor, 1920. *Proc. R. Soc. Vic.*, 32, p. 166. The type ♀, from Bathurst I., N.T., was stated to be in the collection of G. F. Hill, but it could not be found in Mr. Hill's lifetime, and must be presumed lost. I therefore select as neotype a ♀ in the School of Public Health and Tropical Medicine, Sydney, from Groote Eylandt, Northern Territory, N. B. Tindale, identified by Taylor and agreeing with his description.

T. concolor has not been recognized previously in Australian collections. The type is rather a small (13 mm.), faded specimen, but there is no doubt of its identity.

Distribution.—Northern Territory (Bathurst I., Groote Eylandt).

(C) Brown to greyish species, usually with an abdominal pattern of pale or dark triangles or spots.

TABANUS CINERESCENS Macleay.

Tabanus cinerescens W. S. Macleay, 1826. In: King's Narrative of a Survey of the Intertropical and Western Coasts of Australia, 2, p. 467. Mr. J. R. Henry searched the Macleay Collection in the University of Sydney for me, but could find no type specimen.

**Tabanus tetralineatus* Taylor, 1913. *Rpt. Aust. Inst. Trop. Med.* for 1911, p. 68. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

It is desirable to stabilize the name *cinerescens*, which is well established in the literature. I therefore select as neotype a ♀, from Katherine R., Northern Territory, Brown, in the School of Public Health and Tropical Medicine, Sydney. This specimen agrees with females in the British Museum, determined by E. E. Austen, who appears to have been the first modern worker (Austen, 1914) to recognize the species, and also with Ferguson's and Taylor's concept of it.

Distribution.—North-western Australia; Northern Territory.

TABANUS INNOTABILIS Walker.

**Tabanus innotabilis* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 177. Type ♀, from New Holland, in the British Museum (Natural History).

**Tabanus kurandae* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 58. Type ♀, from Kuranda, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

Miss Ricardo (1915a) wrongly listed *dorsobimaculatus* Macq. as a synonym of *innotabilis*, and was followed by Ferguson and Hill (1920) and Surcouf (1921). Taylor (1917a) misidentified specimens as *duplonotatus* Ric., and Ferguson and Hill (1920) corrected the error. *T. daruensis* Oldroyd, 1949, from New Guinea, is an additional synonym.

Distribution.—North-western Australia; Northern Territory; Queensland, from the Gulf of Carpentaria and the Torres Strait Is. down the east coast to Rockhampton. Also New Guinea, Solomon Is., Santa Cruz Is.

TABANUS DAVIDSONI Taylor.

**Tabanus davidsoni* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 65. Type ♀, from Mt. Tamborine, S.Q., in the School of Public Health and Tropical Medicine, Sydney.

This is the southern representative of *innotabilis*; I believe that it may be regarded as at least subspecifically distinct.

Distribution.—South coastal Queensland; north coastal New South Wales.

TABANUS PARVICALLOSUS Ricardo.

**Tabanus parvicollus* Ricardo, 1914. *Ann. Mag. nat. Hist.*, (8), 14, p. 394. Type ♀, from Moreton I., S.Q., in the British Museum (Natural History).

Distribution.—South-eastern Queensland; north coastal and inland New South Wales.

TABANUS TOWNSVILLI Ricardo.

**Tabanus townsvilli* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 281. Type ♀♂, from Townsville, N.Q., in the British Museum (Natural History). The original mislabelling noted by Ferguson and Hill (1922) has been corrected.

**Tabanus aprepes* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 56. Type ♀, from Kuranda, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

**Tabanus batchelori* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 58. Type ♀, from Batchelor, N.T., in the School of Public Health and Tropical Medicine, Sydney.

The synonymy of *aprepes* with *townsvilli* was suggested by Mr. Oldroyd, and confirmed when the type was examined.

Distribution.—Northern Territory; coastal and inland Queensland; coastal and inland New South Wales; south-western Western Australia (possibly a distinct race).

TABANUS NOTATUS Ricardo.

**Tabanus notatus* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 283. Type ♀, from Ching Do, N.Q., in the British Museum (Natural History).

This species is closely related to *T. lenticulatus* Oldr. of New Guinea.

Distribution.—North coastal Queensland, from Cape York to Mackay.

TABANUS SEQUENS Walker.

**Tabanus sequens* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 178. Type ♀, from Port Essington, N.T., in the British Museum (Natural History).

Distribution.—Northern Territory; east coastal Queensland, from Moa I. to Brisbane.

(D) Pale, unadorned species, with grey or fawn scutum, and predominantly yellowish abdomen.

TABANUS PRAEPOSITUS Walker.

**Tabanus praepositus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 158. Type ♀, from Port Essington, N.T., in the British Museum (Natural History).

**Tabanus diminutus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 183. Type ♀, from Port Essington, N.T., in the British Museum (Natural History).

**Tabanus obscurimaculatus* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 51. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

T. diminutus had not been recognized previously, but the type is in fair condition, and is clearly only a small specimen of *praepositus*; the description also agrees.

Distribution.—North-western Australia; Northern Territory; north Queensland (Moa I. and Lockhart R.).

TABANUS DORSOBIMACULATUS Macquart.

**Tabanus dorsobimaculatus* Macquart, 1850. *Dipt. exot.*, Suppl. 4, p. 29. Type ♀, from E. coast of New Holland, in the Paris Museum.

**Tabanus nigritarsis* Taylor, 1913. *Rpt. Aust. Inst. Trop. Med.* for 1911, p. 67. Type ♀, from Ching Do, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

Miss Ricardo (1915a) listed *dorsobimaculatus* as a synonym of *innotabilis*, but the type, which is in fair condition, is undoubtedly the same as *nigritarsis*, and the description also agrees better with *nigritarsis* than with *innotabilis*.

Distribution.—Northern Territory; north Queensland, from Cape York to Townsville.

TABANUS NIGRIMANUS Walker.

**Tabanus nigrimanus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 183. Type ♀, from Port Essington, N.T., in the British Museum (Natural History).

**Tabanus badius* Summers, 1912. *Ann. Mag. nat. Hist.*, (8), 10, p. 225. Two cotype ♀♀, from Darwin, N.T., in the British Museum (Natural History).

**Tabanus daphoenus* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 54. Type ♀, from near Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

Walker's type is in good condition, and the others agree with it. The species is poorly represented in Australian collections.

Distribution.—Northern Territory; north Queensland (Lockhart R.).

TABANUS OBSCURILINEATUS Taylor.

**Tabanus obscurilineatus* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 50. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

A small, yellow species, notable for its extremely small callus, but it shows no other resemblance to the predominantly Holarctic genus *Atylotus*.

Distribution.—North-western Australia; Northern Territory; north Queensland (Townsville).

Tribe DIACHLORINI.

Basicosta without strong setulae, contrasting with the costa (Mackerras, 1956, Fig. 6, B). Fronts of females usually diverging towards the antennae, occasionally parallel; their palpi usually slender, tapering gently to a rounded end.

Genus PARACANTHOCERA Enderlein.

Type species: *Acanthocera australis* Ric., Australia.

Antennae much longer than head, first segment three times as long as wide; slender, *Chrysops*-like species, with bulging, shining face, and conspicuous, brown pattern on wings. I had thought (These PROCEEDINGS, 82, p. 291) that this genus was a synonym of the earlier *Lissimas* End., but the type of the latter (**fenestratus* End., Celebes) proved to be a much less specialized insect.

PARACANTHOCERA AUSTRALIS (Ricardo).

**Acanthocera australis* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 16, p. 16. Type ♀, from Kuranda, N.Q., stated to be in the Berlin Museum, but the specimen in the British Museum (Natural History) is labelled as type.

Distribution.—North Queensland (Kuranda and Cairns district). A second species, **parallelus* (Walk.), is known from Batchian.

Genus CHALYBOSOMA Oldroyd.

Type species: *Tabanus metallicus* Ric., New Guinea.

Metallic blue-green, calliphorid-like flies, with subcallus, parafacials and face rather bare and shining.

CHALYBOSOMA CYANEA (Wiedemann).

Tabanus cyaneus Wiedemann, 1828. *Ausser. zweifl. Ins.*, 1, p. 152. Type ♀ in the Berlin Museum. Dr Peus has reported that a ♀ from south Queensland, sent to him for comparison, agreed perfectly with the type, which is labelled "Nov. Holl., Melly."

**Tabanus cyaneoviridis* Macquart, 1850. *Dipt. exot.*, Suppl. 4, p. 31. Type ♀, from "Tasmanie" (erroneous), in the Paris Museum.

Except for its metallic coloration, this species might be included with almost equal propriety in the genus *Cydistomyia*.

Distribution.—Central and south coastal Queensland; eastern New South Wales.

CHALYBOSOMA CASUARINAE English, Mackerras & Dyce.

**Chalybosoma casuarinae* English, Mackerras and Dyce, 1957. Proc. Linn. Soc. N.S.W., 82, p. 292. Holotype ♀, allotype ♂, morphotype larva, and pupal skins of types, from Merricumbene, N.S.W., in the Division of Entomology, C.S.I.R.O., Canberra.

A remarkable species, which breeds in rot-holes in *Casuarina* trees.

Distribution.—North and south coastal Queensland; south coastal New South Wales.

Genus CYDISTOMYIA Taylor.

Type species: *Cydistomyia doddi* Tayl. (= *albithorax* Ric.), New Guinea.

Smooth-bodied, non-metallic species; eyes bare in both sexes; vein R_1 without appendix; frons of female relatively narrow (index usually greater than 4).

CYDISTOMYIA TORRESI (Ferguson & Hill).

**Tabanus torresi* Ferguson and Hill, 1922. Proc. Linn. Soc. N.S.W., 47, p. 257. Type ♀, from Moa I., Torres Strait, in the School of Public Health and Tropical Medicine, Sydney.

This species belongs to the Papuan *laetus* group. It and *palmensis* form part of a recent intrusion from New Guinea.

Distribution.—Torres Strait Is.

CYDISTOMYIA PALMENSIS (Ferguson & Hill).

**Tabanus palmensis* Ferguson and Hill, 1922. Proc. Linn. Soc. N.S.W., 47, p. 256. Type ♀, from Palm I., N.Q., in the School of Public Health and Tropical Medicine, Sydney.

Distribution.—North Queensland, from Cairns to Townsville.

CYDISTOMYIA AVIDA (Bigot).

**Atylotus avidus* Bigot, 1892. Mem. Soc. zool. Fr., 5, p. 673. Type ♀, from Australia, in the British Museum (Natural History).

**Tabanus fuscipes* Taylor, 1913. Rpt. Aust. Inst. Trop. Med. for 1911, p. 62. Type ♀♂, from Magnetic I., N.Q., in the School of Public Health and Tropical Medicine, Sydney. Not *Tabanus fuscipes* Ricardo, 1908, Ethiopian.

Tabanus taylori Austen, 1914. Ann. Mag. nat. Hist., (8), 13, p. 265. Nom. nov.

Tabanus posticus Hardy, 1944, nec Wiedemann, 1828.

Hardy followed a suggestion by Ricardo (1915a), but the type of *posticus* has proved to be a *Dasybasis* of the *vetusta* group.

Distribution.—Coastal Queensland, from Palm I. (abundant) to Brisbane (rare).

CYDISTOMYIA NIGROPICTA (Macquart).

**Tabanus nigropictus* Macquart, 1855. Dipt. exot., Suppl. 5, p. 24. Type ♀, from "Inde" (erroneous), in the British Museum (Natural History).

**Atylotus sanguinarius* Bigot, 1892. Mem. Soc. zool. Fr., 5, p. 675. Type ♀, from Australia, in the British Museum (Natural History).

Miss Ricardo (1915a) pointed out that nothing like *nigropicta* was known from India, whereas it was close to, if not identical with, the Australian *sanguinaria*. Comparison of the types shows that they are conspecific.

Distribution.—South-eastern Queensland; north-eastern New South Wales.

CYDISTOMYIA PSEUDOARDENS (Taylor).

**Tabanus pseudoardens* Taylor, 1913. Rpt. Aust. Inst. Trop. Med. for 1911, p. 66. Type ♀, from Kuranda, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

A red-brown species, which is related to *C. lorentzi* (Ric.) in New Guinea and *hyperythrea* in south-eastern Australia.

Distribution.—North Queensland, from Cairns to Mt. Spec.

CYDISTOMYIA HYPERYTHREA (Bigot).

**Atylotus hyperythreus* Bigot, 1892. *Mem. Soc. zool. Fr.*, 5, p. 674. Type ♀, from Australia, in the British Museum (Natural History).

Distribution.—South Queensland (Mt. Tamborine); eastern New South Wales, from Dorrigo to Sydney.

CYDISTOMYIA DUPLONOTATA (Ricardo).

**Tabanus duplonotatus* Ricardo, 1914. *Ann. Mag. nat. Hist.*, (8), 14, p. 396. Type ♀, from S. Queensland, in the British Museum (Natural History).

Taylor (1917a) misidentified *innotabilis* as *duplonotatus*, and later (1917b, 1918) misidentified *duplonotatus* as *parvicallus*.

Distribution.—South-eastern Queensland; eastern New South Wales (Sydney).

CYDISTOMYIA LATICALLOSA (Ricardo).

**Tabanus laticallosus* Ricardo, 1914. *Ann. Mag. nat. Hist.*, (8), 14, p. 395. Type ♀, from Moreton I., S.Q., in the British Museum (Natural History).

**Tabanus rufoabdominalis* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 42, p. 525. Type ♀♂, from Stradbroke I., S.Q., in the Queensland Museum, Brisbane.

Distribution.—South coastal Queensland; north coastal New South Wales (Richmond R.).

CYDISTOMYIA LATICALLOSA var. HERONI (Ferguson).

**Tabanus heroni* Ferguson, 1921. *Rec. S. Aust. Mus.*, 1, p. 372. Type ♀, from Dorrigo, N.S.W., in the South Australian Museum, Adelaide.

The status of this form is puzzling. It seems to be consistently larger and more broadly built than *laticallosa*, and to link *laticallosa* with the normally very different *victoriensis*. I have used the old, vague term "var." to indicate lack of precise knowledge.

Distribution.—South Queensland (McPherson Range); northern New South Wales (Dorrigo plateau and adjacent coast).

CYDISTOMYIA DODDI (Taylor).

**Tabanus doddi* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 41, p. 758. Type ♀, from Kuranda, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

This species is not to be confused with the genotype, **Cydistomyia doddi* Taylor, 1919, which is restricted to New Guinea. Taylor (1913) originally recorded it as *abstersus* Walk., but described it and labelled a type, after Austin (1914) had pointed out the error. It is remarkable for having a long dorsal process on the third antennal segment, almost like *Dichelacera*. *C. doddi*, *magnetica*, *alternata* and *wentworthi* are best treated, either as distinct species, or as forming a north to south array of subspecies. The former arrangement is more convenient here.

Distribution.—North Queensland, from Kuranda to Townsville.

CYDISTOMYIA MAGNETICA (Ferguson & Hill).

**Tabanus alternatus* var. *magneticus* Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 258. Type ♀, from Magnetic I., N.Q., in the School of Public Health and Tropical Medicine, Sydney.

Distribution.—Coastal Queensland, from Magnetic I. to Rockhampton.

CYDISTOMYIA ALTERNATA (Ferguson & Hill).

**Tabanus limbatinevis* Macquart, 1850. *Dipt. exot.*, Suppl. 4, p. 29. Type ♀, from E. coast of New Holland, in the Paris Museum. Not *T. limbatinevis* Macquart, 1847 (see under "Excluded Species"). Macquart had evidently considered changing the later name, because he labelled the type in Paris "*T. fuscinevis* Macq., n. sp.", but that name had already been used for a Neotropical species.

Tabanus macquarti Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 277. *Nom. nov.* Not *T. macquarti* Schiner, 1868, Neotropical.

Tabanus alternatus Ferguson and Hill, 1922. PROC. LINN. SOC. N.S.W., 47, p. 258. Nom. nov.

Distribution.—South-eastern Queensland; north-eastern New South Wales.

CYDISTOMYIA WENTWORTHI (Ferguson & Hill).

**Tabanus wentworthi* Ferguson and Hill, 1922. PROC. LINN. SOC. N.S.W., 47, p. 259. Holotype ♀ from Leura, allotype ♂ from Blue Mts., N.S.W., in the Australian Museum, Sydney.

The frons index is slightly less than 4 in some specimens, but usually between 4 and 4.5.

Distribution.—New South Wales (Blue Mts.).

CYDISTOMYIA VICTORIENSIS (Ricardo).

**Tabanus victoriensis* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 275. Type ♀, from Dandenong Ranges, Victoria, in the British Museum (Natural History).

This is the southern and highland representative of the *doddi-wentworthi* series. Usually it is quite distinct, but some specimens vary towards *wentworthi*, and the frons index is also sometimes less than 4.

Distribution.—South Queensland (Mt. Tamborine and McPherson Range); highland and coastal New South Wales; Victoria.

The remaining six described species provisionally included in *Cydistomyia* are small (8–12 mm.), and of uncertain relationships. *C. silviformis* is fairly typical, but the *musgravi* complex may lead into the *microdonta* group of *Dasybasis*, and *brevior* and *griseicolor*, in different ways, into the *clavicallosa* group.

CYDISTOMYIA ATMOPHORA (Taylor).

**Tabanus atmophorus* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 59. Type ♀, from Kuranda, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

This may be no more than a northern subspecies of *musgravi*.

Distribution.—North Queensland, from Lockhart R. to Mackay.

CYDISTOMYIA MUSGRAVII (Taylor).

**Tabanus musgravi* Taylor, 1918. *Rec. Aust. Mus.*, 12, p. 64. Type ♀, from Underbank, N.S.W., in the Australian Museum, Sydney.

This species is remarkable in having a narrow green band across the eye of the female. The frons index is 3 to 4.

Distribution.—South-eastern Queensland, principally in the mountains; New South Wales, in high country from Dorrigo to the Blue Mts., and on the coast near Sydney.

CYDISTOMYIA RIVULARIS (Ferguson & Hill).

**Tabanus pygmaeus* Ferguson and Henry, 1920. PROC. LINN. SOC. N.S.W., 44, p. 842. Type ♀, from Kendall, N.S.W., in the Australian Museum, Sydney. Not *T. pygmaeus* Williston, 1887, Nearctic.

Tabanus rivularis Ferguson and Hill, 1922. PROC. LINN. SOC. N.S.W., 47, p. 264. Nom. nov.

This form is typically smaller than *musgravi* (about 10 mm., as against 11–12), and has a shorter callus and shorter, paler antennae; but there is considerable variation, and I doubt that it can be maintained as distinct.

Distribution.—South-eastern Queensland; north coastal New South Wales and Barrington Tops.

CYDISTOMYIA SILVIFORMIS (Taylor).

**Tabanus silviformis* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 62. Type ♀, from Stradbroke I., S.Q., in the Queensland Museum, Brisbane.

A small (8–10 mm.), brown species, with frons index 4 to 4.5 and banded abdomen. Known only from three females of type series.

Distribution.—South Queensland.

CYDISTOMYIA BREVIOR (Walker).

**Tabanus brevior* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 188. Type ♀, from Port Essington, N.T., in the British Museum (Natural History).

Tabanus marginatus var.B Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 189. ♀, from Port Essington, in the British Museum (Natural History). Miss Ricardo (1915a) recorded the synonymy. I did not see this specimen; the true **marginatus* (Walk.) is a *Mesomyia* (Chrysopinae).

**Tabanus anellosus* Summers, 1912. *Ann. Mag. nat. Hist.*, (8), 10, p. 226. Three cotype ♀♀, from Darwin, N.T., in the British Museum (Natural History).

**Tabanus australis* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 41, p. 757. Type ♀, from Stapleton, N.T., in the School of Public Health and Tropical Medicine, Sydney.

**Tabanus crypserythrus* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 60. Type ♂♂, from near Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

The enlarged upper facets of the eyes of the male are bare, and the frons index of the female is 4 to 4.5; but cell R_4 is wide, and vein R_4 more or less angulate, though without definite appendix.

Distribution.—Northern Territory.

CYDISTOMYIA GRISEICOLOR (Ferguson & Hill).

**Tabanus griseicolor* Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 262. Type ♀, from Hughenden, N.Q., in the School of Public Health and Tropical Medicine, Sydney.

A typical, small, greyish *Cydistomyia*, except for the wide frons, with an index of 2 to 2.5. Known only from four females.

Distribution.—North-western Queensland (Hughenden, Richmond).

Genus DASYBASIS Macquart.

Type species: *Dasybasis appendiculata* Macq., Australia.

Dolichapha Enderlein, 1930. Type species: *Tabanus gregarius* Erichs., Tasmania.

Non-metallic species, of varied habitus from smooth to relatively broad and hairy; eyes hairy, at least on the upper facets of the male; vein R_4 with appendix (except in the *microdonta* group); frons of female relatively wide (index usually less than 3).

This genus consists, partly of a clearly definable faunal element, and partly of a series of groups of uncertain affinities but seeming to find closer relationship here than elsewhere in the tribe. Some of these may require subgeneric recognition when the whole complex has been worked out. As the synonymy is complicated, it will be necessary to include brief definitions of the species to which the names are applied.

The microdonta Group.

Small to large (10–16 mm.), dark, parallel-sided species, distinguished by the combination of a smoothly curved vein R_4 , without appendix, and (usually) hairy eyes in both sexes. Males with eyes not markedly swollen and upper facets not conspicuously enlarged. Females with frons wide to moderately narrow (index 2 to 4.5); callus usually elongate and nearly full width of frons at base; terminal abdominal segments dorsoventrally compressed.

This small group of four species (two undescribed) is difficult to place. It could have evolved from the *victoriensis* and *musgravii* stocks of *Cydistomyia*; or it may represent the New Zealand subgenus *Dasybasis* (*Protodasyommia*) in Australia. It seems better, at the moment, to include it here.

DASYBASIS MICRODONTA (Macquart).

**Tabanus microdonta* Macquart, 1847. *Dipt. exot.*, Suppl. 2, p. 17. Type ♀, from Tasmania, in the British Museum (Natural History).

Tabanus wynyardensis Hardy, 1916. *Pap. Proc. R. Soc. Tas.* for 1916, p. 269. Location of the type ♂, from Wynyard, Tasmania, not known, but I have seen specimens from the type series.

A large (15–16 mm.), distinctive species, with wide frons (index 2·5 to 3) and relatively narrow callus.

Distribution.—Victoria; Tasmania.

DASYBASIS RAINBOWI (Taylor).

**Tabanus rainbowi* Taylor, 1918. *Rec. Aust. Mus.*, 12, p. 66. Type ♂, from King George Sound, W.A., in the Australian Museum, Sydney.

A small (11–12 mm.), undistinguished species, with relatively narrow frons (index 3·5 to 4·5). One of the new species (from Western Australia) is related; the other (from Mt. Kosciusko) is like a hairy *C. musgravii* with a wide frons (index 2 to 2·5).

Distribution.—South-western Western Australia.

The clavicallosa Group.

Small to medium-sized (8–13, occasionally 15 mm.), smooth, yellowish to greyish species, with unpatterned scutum, and abdominal pattern usually rather vague. Eyes of known males (five species) markedly swollen, with conspicuously enlarged, densely hairy, upper facets. Females with eyes bare; frons medium to rather narrow (index 2·5 to 4·5), parallel to slightly diverging; callus narrower than frons, often reduced, sometimes absent; terminal abdominal segments dorsoventrally compressed.

This is a predominantly northern group; but the presence of an appendix (often a long one) on *R.*, the hairy eyes of the male, the usually rather wide frons of the female (index 2·5 to 3 in ten of the species), and the evident relationship with the *oculata* group, suggest origin from *Dasybasis* rather than *Cydistomyia* stock. It extends into New Guinea (three species) and Bougainville (one species).

DASYBASIS GRISEOANNULATA (Taylor).

**Tabanus griseoannulatus* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 41, p. 756. Type ♀, from Brock's Ck., N.T., in the School of Public Health and Tropical Medicine, Sydney.

An obscure, greyish species, with unusually narrow frons (index 4·5); known only from a single female.

Distribution.—Northern Territory.

DASYBASIS ANGSTICALLUS (Ricardo).

**Tabanus angusticallus* Ricardo, 1917. *Ann. Mag. nat. Hist.*, (8), 19, p. 218. Type ♀, from Melville I., N.T., in the South Australian Museum, Adelaide.

A small (9–10 mm.), grey species, distinguished by the short, linear callus on the lower part of the relatively narrow frons (index 3 to 3·5).

Distribution.—Northern Territory.

DASYBASIS TRYPHERA (Taylor).

**Tabanus trypherus* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 41, p. 755. Type ♀, from near Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

A very small (8 mm.), greyish species, with relatively wide frons (index 2·5 to 3) and large, pear-shaped callus. Known only from two females, it may be an extreme variant of *clavicallosa*.

Distribution.—Northern Territory (Darwin).

DASYBASIS CLAVICALLOSA (Ricardo).

**Tabanus clavicallosus* Ricardo, 1917 (Feb.). *Ann. Mag. nat. Hist.*, (8), 19, p. 219. Type ♀, from Milson I., N.S.W., in the British Museum (Natural History).

**Tabanus darwinensis* Taylor, 1917 (Apr.). *Proc. Linn. Soc. N.S.W.*, 41, p. 758. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

**Tabanus griseus* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 55. Type ♀, from Brisbane, Q., in the Queensland Museum, Brisbane.

A small (9–12 mm.), grey species, with frons index 2.5 to 3, and pear-shaped callus; eyes of ♀ with just perceptible hairs. Ferguson and Hill (1922) established the synonymy of *griseus*; the type of *darwinensis* almost completely lacks the normal paler banding on the abdominal tergites, but is otherwise identical.

Distribution.—Northern Territory (Darwin); coastal Queensland (Townsville, Brisbane); coastal New South Wales (Newcastle to National Park south of Sydney). Though the species is not uncommon, its distribution seems to be patchy.

DASYBASIS CLAVICALLOSA BANKSIENSIS (Ferguson & Hill).

**Tabanus clavicallosus* var. *banksiensis* Ferguson and Hill, 1922. PROC. LINN. SOC. N.S.W., 47, p. 262. Type ♀, from Moa (Banks) I., Torres Strait, in the National Museum, Melbourne.

This form may prove to be a distinct species, when sufficient specimens are available for study.

Distribution.—Northern Territory (Melville I.); north Queensland (Moa I.). Also New Guinea.

DASYBASIS NEOGERMANICA (Ricardo).

**Tabanus neogermanicus* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 283. Type ♀, from Darwin, N.T., in the British Museum (Natural History).

**Tabanus fugitivus* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 61. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

**Tabanus hilli* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 64. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

One of the larger species of the group (11–14 mm.); yellowish-brown, with frons index 2.5 to 3, long, narrow callus, and well-defined abdominal bands.

Distribution.—North-western Australia; Northern Territory.

DASYBASIS GERMANICA (Ricardo).

**Tabanus germanicus* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 282. Type ♀, from Cairns, N.Q., in the British Museum (Natural History).

A small (7–11 mm.), variable, fawn and brown to yellowish-brown species, with wide third antennal segment, frons index 2.5 to 3.5, pear-shaped callus, and deep brown to blackish fore femora.

Distribution.—Northern Territory; eastern Queensland, from Torres Strait Is. (Saibai, Moa) and Cape York to Gladstone. Also New Guinea.

DASYBASIS CONSTANS (Walker).

**Tabanus constans* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 186. Type ♀, from New Holland, in the British Museum (Natural History).

**Tabanus quadratus* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 52. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

**Tabanus minor* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 64. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney. Not *T. minor* Macquart, 1850, Neotropical.

Tabanus minusculus Ferguson and Hill, 1920. PROC. LINN. SOC. N.S.W., 45, p. 466. Nom. nov. Not *T. minusculus* Hine, 1907, Nearctic.

Tabanus palmerstoni Ferguson and Hill, 1922. PROC. LINN. SOC. N.S.W., 47, p. 263. Nom. nov.

A small (7–11 mm.), greyish fawn, rather variable species, with frons index 2.5 to 3, callus usually oval and tapering to a point above, entirely yellowish antennae and femora, and banded abdomen. The synonymy of *minor* was established by Taylor (1926) on the authority of Austen; *quadratus* differs only in having the frons usually a little wider, and the callus oblong rather than oval.

Distribution.—North-western Australia; Northern Territory.

DASYBASIS PARVA (Taylor).

**Tabanus parvus* Taylor, 1913. *Rpt. Aust. Inst. Trop. Med.* for 1911, p. 69. Type ♀, from Darwin, N.T., in the School of Public Health and Tropical Medicine, Sydney.

D. parva, *neopalpalis* and *pseudocallosa* are small (8–10 mm.), obscure, yellowish species, of which only a few specimens are known. The frons index of *parva* is 3·5, and the callus is light brown, wedge-shaped.

Distribution.—Northern Territory.

DASYBASIS NEOPALPALIS (Ferguson & Hill).

**Tabanus palpalis* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 66. Type ♀, from Batchelor, N.T., in the School of Public Health and Tropical Medicine, Sydney. Not *T. palpalis* Ricardo, 1911, Oriental.

Tabanus neopalpalis Ferguson and Hill, 1920. *Proc. Linn. Soc. N.S.W.*, 45, p. 465. *Nom. nov.*

Frons index 2·5 to 3; callus dark brown, small, rounded.

Distribution.—Northern Territory.

DASYBASIS PSEUDOCALLOSA (Ferguson & Hill).

**Tabanus pseudocallosus* Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 254. Type ♀, from Darwin, N.T., in the National Museum, Melbourne.

Frons index 2·5; callus light yellow, triangular, resting on the shining yellow subcallus; costal cell brown.

Distribution.—Northern Territory; north Queensland.

DASYBASIS NEMOTUBERCULATA (Ricardo).

**Tabanus nemotuberculatus* Ricardo, 1914. *Ann. Mag. nat. Hist.*, (8), 14, p. 388. Type ♀, from Cape York, N.Q., in the British Museum (Natural History).

Tabanus pseudopalpalis Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 252. The type ♀ was stated to be in Mr. Hill's collection, but it cannot now be found. I therefore designate as neotype the remaining ♀ of the type series, from Batchelor, N.T., G. F. Hill, No. 1405, now in the collection of the School of Public Health and Tropical Medicine, Sydney. This may be the original type, unlabelled; but one cannot be sure, because the field observation numbers included series taken at the same time and place.

A small (10–11 mm.), slender, yellow-brown species, with rather narrow frons (index 3 to 3·5), only a variable indication of a light yellow callus, the costal cell yellow or brown, and the radial cells sometimes darkened also. Northern Territory specimens (*pseudopalpalis*) have a wider antennal plate and less darkened wings than those from Queensland (*nemotuberculata*), and subspecific separation may ultimately be desirable.

Distribution.—Northern Territory; north Queensland (both sides of Cape York Peninsula).

DASYBASIS SPATIOSA (Ricardo).

**Tabanus spatiosus* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 288. Type ♀, from Stannary Hills, N.Q., in the British Museum (Natural History).

Distinguished from *nemotuberculata* by being somewhat longer (11–12 mm.) and paler, with a somewhat wider frons (index 2·5 to 3), and a more definite, brown callus.

Distribution.—North Queensland.

DASYBASIS NEMOPUNCTATA (Ricardo).

**Tabanus nemopunctatus* Ricardo, 1914. *Ann. Mag. nat. Hist.*, (8), 14, p. 388. Type ♀, from Dunk I., N.Q., in the British Museum (Natural History).

**Tabanus aurihirtus* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 15, p. 290. Type ♀♂, from Townsville, N.Q., in the British Museum (Natural History).

**Tabanus hackeri* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 42, p. 522. Type ♀, from Bribe I., S.Q., in the Queensland Museum, Brisbane.

A larger (10–15 mm.), stouter species than the preceding; pale grey to yellow, with rather vague or no abdominal pattern; frons index 3 to 4; no callus. Taylor (1919) misidentified a specimen from Stradbroke I. as *spatiosa*. Yellow specimens may be mistaken for *vespiformis*, but can be recognized by the flat terminal abdominal segments.

Distribution.—East coast, from Cape York to northern New South Wales (apparently strictly littoral).

DASYBASIS OCHREOFLAVA (Ferguson & Henry).

**Tabanus ochreoflavus* Ferguson and Henry, 1920. *Proc. Linn. Soc. N.S.W.*, 44, p. 845. Type ♀, from Kendall, N.S.W., in the Australian Museum, Sydney.

A medium-sized (11–14 mm.), relatively robust species, distinguished from *nemopunctata* by darker general colour, more definitely banded abdomen, and well-defined, narrow, brown callus.

Distribution.—South Queensland (Moreton I.); northern New South Wales (Kendall).

The oculata Group.

Differs from the *clavicallosa* group principally in having the eyes hairy in both sexes, the frons of the female usually wider (index 2 to 3), the general coloration more brownish, and scutum and abdomen with more definite pattern. The eyes of the known males (seven species) are usually not markedly swollen, nor with the upper facets conspicuously enlarged. Terminal abdominal segments of females dorsoventrally compressed, except *regis-georgii*, in which they are markedly narrowed.

The distribution is essentially southern, only *oculata* and *spadix* extending into north Queensland.

DASYBASIS RUFIFRONS (Macquart).

**Tabanus rufifrons* Macquart, 1855. *Dipt. exot.*, Suppl. 5, p. 28. Type ♀, from New Adelaide, N. Holland, in the British Museum (Natural History).

**Tabanus meridionalis* Ferguson, 1921. *Rec. S. Aust. Mus.*, 1, p. 376. Type ♀, from Adelaide, South Australia, in the South Australian Museum, Adelaide. Not *T. meridionalis* Thunberg, 1827, from unknown country.

Tabanus adalaidae Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 264. *Nom. nov.*

A pale, but patterned species, with an indefinite, light yellow callus. Macquart's type is somewhat greasy, which has made the frons seem reddish, but there is no doubt of its identity. Miss Ricardo (1917) misidentified this species as *postponens*.

Distribution.—South Australia.

DASYBASIS NEOCIRRUS (Ricardo).

**Tabanus neocirrus* Ricardo, 1917. *Ann. Mag. nat. Hist.*, (8), 19, p. 223. Type ♀ (not so labelled), from Swansea, Tasmania, in the British Museum (Natural History).

**Tabanus tasmanicus* Ferguson, 1921. *Proc. R. Soc. Vic.*, 33, p. 20. Type ♀, from Dunally, Tasmania, in the Australian Museum, Sydney.

**Tabanus bassii* Ferguson, 1921. *Proc. R. Soc. Vic.*, 33, p. 22. Type ♀, from Wilson's Promontory, Victoria, in the National Museum, Melbourne.

A small-medium (10–13 mm.), variable, greyish species with medium frons (index about 3), small, club- or pear-shaped callus, and banded abdomen. There is no doubt that the type of *neocirrus* was mis-labelled, as pointed out by Ferguson (1921a) and Hardy (1934). The specimen in the British Museum agrees with Miss Ricardo's description, and is from her stated type locality; the one in the South Australian Museum, labelled as the type, is from South Australia, is evidently her second specimen, and is not conspecific with the first. The three types differ appreciably from one another, but I believe that they all fall within the range of variation of the species.

Distribution.—Coastal New South Wales, south of Sydney; Victoria; Flinders I.; Tasmania.

DASYBASIS NEOBASALIS (Taylor).

**Tabanus basalis* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 182. Type ♀, from New Holland, in the British Museum (Natural History). Not *T. basalis* Macquart, 1838, Oriental.

Tabanus neobasalis Taylor, 1918. *Rec. Aust. Mus.*, 12, p. 67. Nom. nov.

A relatively robust (11–14 mm.), fawn-brown species, with distinctive abdominal pattern, medium frons (index 2.5 to 3), relatively wide, heart-shaped callus, and wide antennal plate.

Distribution.—South Queensland (Eukey); mountain and coastal districts of New South Wales; Victoria. There is also a complex of related forms, some of which may require specific recognition, from Victoria, Tasmania and Western Australia.

DASYBASIS OCVLATA (Ricardo).

**Tabanus pusillus* Macquart, 1855. *Dipt. exot.*, Suppl. 5, p. 29. Type ♀, from Sydney, N. Holland, in the British Museum (Natural History). Not *T. pusillus* Macquart, 1838, China.

Tabanus oculatus Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 16, p. 276. Nom. nov.

**Tabanus kendallensis* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 68. Type ♀, from Kendall, N.S.W., in the School of Public Health and Tropical Medicine, Sydney.

Distinguished from *neobasalis* by generally smaller size (10 mm.), somewhat wider frons (index 2.5), smaller, more rounded callus, and narrower antennal plate. I would have been doubtful of the value of these characters, but Miss English has informed me that the pupae also differ significantly.

Distribution.—Eastern Queensland, from Cairns to the McPherson Range; coastal and mountain districts of New South Wales, from the Queensland border to Canberra.

DASYBASIS POSTPONENS (Walker).

**Tabanus postponens* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 179. Type ♀, from New Holland, in the British Museum (Natural History).

A small-medium (10–12 mm.), nondescript, brown species, with banded abdomen; like a small *acutipalpis*, but immediately distinguishable by the somewhat wider frons (index 2.5 to 3), and narrowly oval callus with short extension.

Distribution.—Coastal New South Wales, from Kendall to Nowra. There are what may be variants in South Australia and Western Australia, but their status is uncertain.

DASYBASIS DIXONI (Ferguson).

**Tabanus dixoni* Ferguson, 1921. *Proc. R. Soc. Vic.*, 33, p. 23. Type ♀, from Lake Hattah, Victoria, in the National Museum, Melbourne.

A small-medium (10–12 mm.), fairly brightly patterned species, with a wider frons than *postponens* (index 2 to 2.5) and a markedly narrower callus than *spadix*. Specimens from South Australia were identified as *regis-georgii* (Ric. nec Macq.) by Miss Ricardo (1917).

Distribution.—Victoria; South Australia; south-western Western Australia.

DASYBASIS SPADIX (Taylor).

**Tabanus spadix* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 41, p. 761. Type ♀, from Sydney, N.S.W., in the School of Public Health and Tropical Medicine, Sydney.

**Tabanus brisbanensis* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 42, p. 526. Type ♀, from Brisbane, S.Q., in the Queensland Museum, Brisbane.

Tabanus regis-georgii Ricardo, 1915, and subsequent authors, nec Macquart.

A small (9–11 mm.), compact, brightly patterned species, with wide frons (index 2) and large, heart-shaped callus. It was wrongly identified by Miss Ricardo (1915b) as *regis-georgii*, and Australian workers have universally followed her determination, in spite of the fact that it is not known from Western Australia (see comment by Ferguson and Hill, 1920, p. 466).

Distribution.—Eastern Queensland, from Cairns to Stradbroke I.; coastal New South Wales; Victoria (Mallacoota Inlet).

DASYBASIS SPADIX DIEMANENSIS (Ferguson).

**Tabanus diemanensis* Ferguson, 1921. *Proc. R. Soc. Vic.*, 33, p. 25. Type ♀ and allotype ♂, from Bream Ck., Tasmania, in the Australian Museum, Sydney.

This form has a slightly narrower frons and smaller callus than the mainland race, and the upper facets of the eyes of the male are only slightly enlarged over a relatively small area. It seems better to treat it as a subspecies than a full species. Taylor (1919) misidentified it as *brisbanensis*.

Distribution.—Victoria; Tasmania; one ♀ from South Australia may belong here.

DASYBASIS REGIS-GEORGII (Macquart).

**Tabanus regis-georgii* Macquart, 1838. *Dipt. exot.*, 1 (i), p. 132. Type ♀, from King George Sound, W.A., in the Paris Museum.

**Tabanus geraldtonensis* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 70. Type ♀, from Geraldton, W.A., in the School of Public Health and Tropical Medicine, Sydney.

A distinctive species, not only by the abdominal pattern, but by having the terminal segments of the female compressed, and the eyes of the male distinctly swollen, with considerably enlarged upper facets, suggesting relationship with the *macrophthalma* group. Macquart's specimen is old, rather wasted, and has only a label "Roi Georg.", but there is little doubt that it is the type; it is certainly the same species as Taylor's.

Distribution.—South-western Western Australia.

The vetusta Group.

Nearly concolorous, grey to yellowish, medium-sized to large (11–17 mm.) species. Eyes of males usually markedly swollen and with upper facets conspicuously enlarged, densely hairy. Females with eyes hairy in southern species, bare in northern ones; frons moderately wide (index 2.5 to 3), nearly parallel, with small callus or none; terminal segments of abdomen laterally compressed, producing a tent-like appearance of the cerci in end view (Text-fig. 1).

This is a very distinctive group of six (two undescribed), coastal, sand-haunting species, which may merit higher taxonomic status, but its precise relationship to the *macrophthalma* group has still to be defined.

DASYBASIS CAESIA (Walker).

**Tabanus caesius* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 180. Type ♀, from unknown country, in the British Museum (Natural History).

Tabanus leucopterus van der Wulp, 1868. *Tijdschr. Ent.*, 11, p. 98. Type ♀, from Aru Is., in the Rijksmuseum Nat. Hist., Leyden.

**Tabanus griseohirtus* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 41, p. 753. Type ♀, from Melville I., N.T., in the School of Public Health and Tropical Medicine, Sydney.

A grey species, with the eyes of the female bare, frons index 2.5, and no callus. The synonymy of *leucopterus* was established by Oldroyd (1949).

Distribution.—North-western Australia, including Montebello I.; Northern Territory; Torres Strait Is. (Murray, Moa, Thursday); north Queensland, from Cape York to Townsville. Also New Guinea and Aru Is.

DASYBASIS VETUSTA (Walker).

**Tabanus vetustus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 179. Type ♀, from Swan R., W.A., in the British Museum (Natural History).

An almost uniformly grey to yellowish-grey species, with eyes of the female hairy, frons index 2.5, and a small, dark callus.

Distribution.—The typical race is restricted to south-western Western Australia and South Australia. Specimens from Victoria and Tasmania belong to a distinct subspecies with entirely dark third antennal segment.

DASYBASIS VESPIFORMIS (Ferguson & Henry).

**Tabanus vespiiformis* Ferguson and Henry, 1920. *Proc. Linn. Soc. N.S.W.*, 44, p. 840. Type ♀, from Kendall, N.S.W., in the Australian Museum, Sydney.

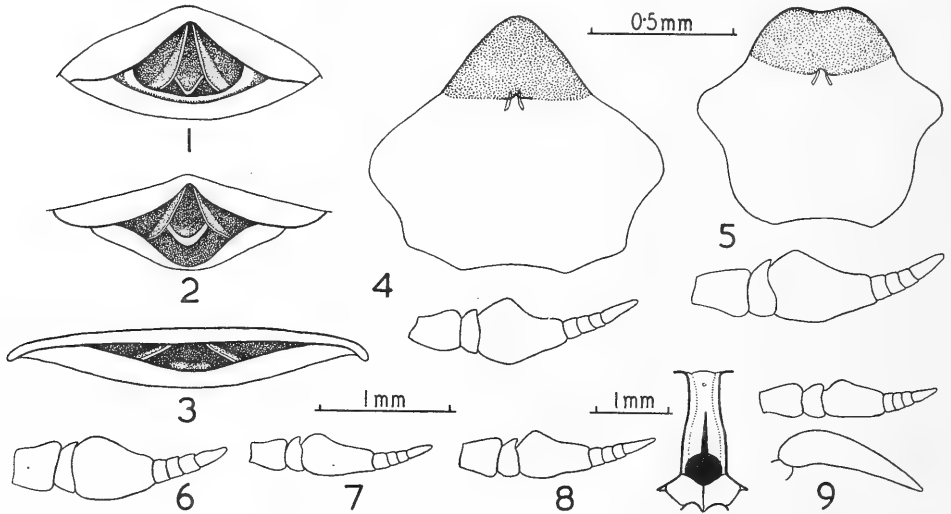
A large (15–17 mm.), yellow species, with frons index 3, and only vague indications of a callus. The type specimen was damaged, and neither the name nor the original description gives a true impression of the species.

Distribution.—Coastal New South Wales, from Kendall to National Park, south of Sydney.

DASYBASIS POSTICA (Wiedemann).

**Tabanus posticus* Wiedemann, 1828. *Ausser. zweifl. Ins.*, 1, p. 152. Type ♀, from Australasia, in the Berlin Museum.

**Tabanus pseudobasalis* Taylor, 1918. *Rec. Aust. Mus.*, 12, p. 68. Type ♀, from King George Sound, W.A., in the Australian Museum, Sydney.



Text-figs. 1-9.

1: End view of abdomen of *Dasybasis vetusta* (Walk.), ♀ from Western Australia. 2: Same of *D. hebes* (Walk.), ♀ from Tasmania. 3: Same of *D. circumdata* (Walk.), ♀ from Canberra. 4: Eighth sternite and antenna of *D. hebes*, ♀ from S. Queensland. 5: Same of *D. circumdata*, ♀ from Dorrig plateau. 6: Antenna of *Dasybasis exulans* (Erich.), ♀ from Tasmania. 7: Antenna of *D. acutipalpis* (Macq.), ♀ from Victoria agreeing with type of *abstersa* (Walk.). 8: Same of typical ♀ from Tasmania. 9: Frons, antenna and palp of *D. tasmaniensis* (White), paratype ♀. Scales: top, for eighth sternites; lower left, for abdomens, antennae and palp; lower right, for frons.

A medium-sized (11–14 mm.), plump, unadorned species, with olive scutum and yellow abdomen. The possibility that this species might be *postica* had not been considered until the type was received for study.

Distribution.—South-western Western Australia; South Australia.

Both the new species are robust and yellowish, like *vespiformis*. One, with eyes bare in the female, is from north-western Australia; the other, with eyes hairy in both sexes, is from south coastal New South Wales and Victoria.

The macrophthalma Group.

Robust (13–16 mm.), rather flat-bodied, grey or brown species, with well-developed scutal and abdominal patterns. Eyes densely hairy in both sexes; more or less swollen and with moderately to conspicuously enlarged upper facets in the males. Females with wide (index 2 to 3), almost parallel frons; callus usually full width of frons and restricted to its lower half; terminal abdominal segments narrowed, cerci tent-like, eighth sternite either small or pointed apically (Text-fig. 2).

There are eight Australian species (three undescribed) in this group, and they have a rather characteristic appearance, which is contributed to by a deep subcallus and

smoothly bulging parafacials and face in the females; in most species, too, the antennae are black, contrasting with the wide expanse of whitish tomentum below them. It is difficult to decide how far the characters they share with the *vetusta* group are expressions of relationship or of common adaptation to life in a sandy environment. On the one hand, they are reinforced by common, distinctive features in the known pupae (Miss English, personal communication); but, on the other hand, the adults of *exulans* and its immediate allies seem to lead rather towards the *appendiculata* group.

Three species are known outside Australia, one from New Guinea, one from the Admiralty to the Santa Cruz Is., and one from New Caledonia and Loyalty Is. The eyes are bare in the females, but otherwise they are very like *macrophthalma*.

DASYBASIS MACROPHTHALMA (Schiner).

**Tabanus macrophthalmus* Schiner, 1868. *Reise Novara Dipt.*, p. 83. Type ♂, from Sydney, N.S.W., in the Vienna Museum.

**Tabanus orarius* English, 1949. *Proc. Linn. Soc. N.S.W.*, 74, p. 154. Holotype ♀, allotype ♀, morphotype larval and pupal skins, from Narooma, N.S.W., in the Macleay Museum, University of Sydney.

A distinctive, grey species, which breeds in the sand of ocean beaches. The type from Vienna is labelled "*megalops*" and "Sydney". It agrees perfectly with the description of *macrophthalma*, down to individual details, such as the retracted abdomen, and there is no *megalops* in the *Novara* Diptera, so there is no doubt that it is the specimen described. It also agrees perfectly with recent males of *oraria*.

Distribution.—South coastal New South Wales.

DASYBASIS ALBOHIRTIPES (Ferguson).

**Tabanus albohirtipes* Ferguson, 1921. *Rec. S. Aust. Mus.*, 1, p. 377. Type ♀, from South Australia, in the South Australian Museum, Adelaide.

A brownish-grey species, which falls naturally between *macrophthalma* and *cirrus*.

Distribution.—South Australia; south-western Western Australia. There is also a related, undescribed species in Western Australia.

DASYBASIS CIRRUS (Ricardo).

**Tabanus cirrus* Ricardo, 1917. *Ann. Mag. nat. Hist.*, (8), 19, p. 222. Type ♀, from Milson I., N.S.W., in the British Museum (Natural History).

**Tabanus robustus* Taylor, 1919. *Proc. Linn. Soc. N.S.W.*, 44, p. 69. Type ♀, from Brisbane, Q., in the Queensland Museum, Brisbane.

A large (16 mm.), dark greyish-brown species, with characteristic drop-shaped callus.

Distribution.—East coastal, from Palm I. in north Queensland to the Hawkesbury R. in New South Wales.

DASYBASIS EXULANS (Erichson).

**Tabanus exulans* Erichson, 1842. *Arch. Naturges.*, (1), 8, p. 270. Type ♀, from Tasmania, in the Berlin Museum.

Tabanus circumdatus var. White, 1915, *nec* Walker.

Tabanus acutipalpis auct. *nec* Macquart.

This robust (15–16 mm.), dark, southern species was wrongly identified as *acutipalpis* by Ricardo (1915*b*), Ferguson (1921*a*, 1921*b*) and Hardy (1934, 1939, 1948). The antennal plate is angulate dorsally in the type, but more usually rounded as in Text-figure 6. The eighth sternite is small, and more concave distally than in *circumdatus* (Text-fig. 5).

Distribution.—Eastern New South Wales (chiefly montane); Victoria; Tasmania.

DASYBASIS HEBES (Walker).

**Tabanus hebes* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 159. Type ♀, from unknown locality, in the British Museum (Natural History).

**Tabanus nepos* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 181. Type ♀, from unknown locality, in the British Museum (Natural History).

Tabanus circumdatus White, 1915, *nec* Walker; also other authors in part (records from Tasmania and most, if not all, from South Queensland; others probably represent a mixture, with this species in the minority).

Tabanus whitei Hardy, 1939. PROC. LINN. SOC. N.S.W., 64, p. 44. Proposed as a "new name" for *Tabanus circumdatus* White, 1915, *nec* Walker, 1848, and no type indicated. In order to fix its identity, I therefore select as lectotype a ♀ in the School of Public Health and Tropical Medicine, Sydney, from Mangalore, Tasmania, 18.i.1914, A. White, labelled "*T. circumdatus* Walk." in White's handwriting.

A slightly smaller (13–15 mm.), duller species than the preceding; antennal plate almost as wide, but with sharp dorsal angle; most easily recognized by its distinctive eighth sternite (Text-figs. 2, 4).

The types of *hebes* and *nepos* are large (15 mm.), brown females, with clearly visible, pointed eighth sternites. A female from Eidsvold, south Queensland, returned to Ferguson by Austen as agreeing with the type of *circumdatus*, agrees very well with these two, but not so well with the type of *circumdatus*. The type labels are very small, and it seems possible that Austen may have mistaken the specimen he picked out for comparison.

Distribution.—South-eastern Queensland; eastern New South Wales; Victoria; Tasmania; South Australia; south-western Western Australia.

The trilinealis Group.

Differs from the *appendiculata* group only in the females having bare eyes and relatively narrow fronts (index 3 to 4); otherwise they closely resemble *circumdatus* and its allies. No males are known.

DASYBASIS TRILINEALIS (Ferguson & Henry).

**Tabanus trilinealis* Ferguson and Henry, 1920. PROC. LINN. SOC. N.S.W., 44, p. 841. Type ♀, from Kendall, N.S.W., in the Australian Museum, Sydney.

An ornate species, with sharply defined scutal vittae, and almost confluent median abdominal triangles.

Distribution.—South-eastern Queensland; north coastal New South Wales to Sydney.

DASYBASIS KEWENSIS (Ferguson & Henry).

**Tabanus kewensis* Ferguson and Henry, 1920. PROC. LINN. SOC. N.S.W., 44, p. 843. Type ♀, from near Kendall, N.S.W., in the Australian Museum, Sydney.

Resembles a rather dark *circumdatus*.

Distribution.—South-east Queensland (Nerang); north coastal New South Wales to Sydney.

DASYBASIS EIDSVOLDENSIS (Taylor).

**Tabanus eidsvoldensis* Taylor, 1919. PROC. LINN. SOC. N.S.W., 44, p. 49. Type ♀, from Eidsvold, S.Q., in the School of Public Health and Tropical Medicine, Sydney.

Extremely like *acutipalpis*, except for bare eyes and wider antennal plate.

Distribution.—South-eastern Queensland.

DASYBASIS MILSONIS (Ricardo).

**Tabanus milsonis* Ricardo, 1917. *Ann. Mag. nat. Hist.*, (8), 19, p. 220. Type ♀, from Milson I., N.S.W., in the British Museum (Natural History).

Larger (15 mm.) and more robust than the other members of the group, and with hairs on the eyes just perceptible at $\times 15$.

Distribution.—Northern New South Wales, from Narrabri to Hawkesbury R.

The appendiculata Group.

Small to fairly large (10–15 mm.), usually dark, compact, hairy species, with fairly well-defined scutal and abdominal patterns. Eyes densely hairy in both sexes; varying in males from unenlarged, with entirely small facets, to somewhat swollen, with moderately enlarged upper facets. Females with frons very wide to medium (index 1.5 to 3, rarely 3.5), markedly diverging to nearly parallel; callus nearly always full

width of frons at base, often with median extension; face usually truncate, and separated from parafacials by a clearly defined suture on each side (cf. *macrophthalma* group); terminal segments of abdomen dorsoventrally compressed (Text-fig. 3).

This group is essentially southern, not being known north of Eidsvold in south Queensland. Its nearest relatives are in southern South America and South Africa. Hardy (1948) separated the first four species, with very wide, strongly diverging frons, as the subgenus *Dasybasis* sens. strict., from the remainder, which he included in the subgenus *Dolichapha* Enderlein. It seems to me that the respective genotypes merely represent one end and about the middle of a continuous series in which any division is purely arbitrary. The group, as now defined, is sufficiently compact to stand as a single unit.

DASYBASIS APPENDICULATA Macquart.

**Dasybasis appendiculata* Macquart, 1847. *Dipt. exot.*, Suppl. 2, p. 25. Type ♂♀, from New Holland, in the British Museum (Natural History). The ♂ bears Macquart's "n. gen., n. sp." label, and must be regarded as the holotype.

A small, hairy, blackish species; with very wide, strongly diverging frons (index 1.5 to 1.8); transverse callus, with short median extension; slender, blackish antennal plate, which is gently curved dorsally; and spotted wings; the only member of the group with the eyes banded in life (cf. *Cydistomyia musgravii*). The antennal style usually has four annuli, but they are often obscure, and it was described as three-annulate by Macquart, which led Enderlein (1922) to include *Dasybasis* in the Haematopotini.

Females can be divided into two, fairly distinct variants. One, represented by the type female and two recent females from Victoria, is smaller (9–10 mm.), with almost the whole frons and subcallus shiny, and extensive shiny black areas on the parafacials and face. The other, much commoner, usually somewhat larger (10–12 mm.) race has the shiny areas limited to the callus and variably on the upper part of the subcallus, but the parafacials and face entirely tomentose; it tends to merge with the still larger (12–13 mm.) *froggatti* in southern New South Wales. Males have the parafacials and face tomentose, and can be distinguished only by size, slight differences in coloration and general appearance, and association with the females. The type male agrees best with males that were taken in company with the two Victorian females mentioned above, and it is to the rarer, southern race, therefore, that the name should be strictly applied.

Distribution.—New South Wales, from Mudgee to southern highlands (common race); Victoria (both races).

DASYBASIS FROGGATTI (Ricardo):

**Tabanus froggatti* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 16, p. 285. Type ♀, from S. coast of N.S.W., in the British Museum (Natural History).

Distinguished from the commoner race of *appendiculata* only by generally larger size, more robust build, somewhat narrower frons (index 2), and more extensively darkened tibiae. There are intermediates, particularly at Canberra, and I doubt that specific separation can be maintained.

Distribution.—New South Wales (Lismore, south coast, southern highlands); the only species that is abundant above the tree-line on Mt. Kosciusko.

DASYBASIS GENTILIS (Erichson).

Tabanus gentilis Erichson, 1842. *Arch. Naturges.*, (1), 8, p. 271. Type ♀, from Tasmania, in the Berlin Museum, 1842, compared with specimens from Australia by Mr. H. Oldroyd.

Tabanus gentilis imminutus Hardy, 1948. *Proc. R. Soc. Qd.*, 58, p. 171. No type nor definite type locality indicated.

A brightly marked, brown species, with wide frons (index 1.8 to 2) relatively wide, red-brown antennal plate, brown legs, and conspicuously spotted wings. The antennal character relied on by Hardy to distinguish the mainland race varies considerably in both mainland and Tasmanian specimens.

Distribution.—Mountains of New South Wales, from the Dorrigo plateau to Kiandra; Victoria; Tasmania.

DASYBASIS NEOLATIFRONS (Ferguson & Hill).

**Tabanus latifrons* Ferguson, 1921. *Proc. R. Soc. Vic.*, 33, p. 19. Type ♀♂, from Cradle Mt., Tasmania, in the Australian Museum, Sydney. Not *T. latifrons* Zetterstedt, 1842. Palaearctic.

Tabanus neolatifrons Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 264. *Nom. nov.*

A distinctive, medium-sized (12–13 mm.), black species, with frons index 2 to 2.5, antennal plate moderately wide and rounded dorsally, grey, unspotted wings, and small median white spots on abdominal tergites.

Distribution.—Flinders I.; Tasmania.

DASYBASIS IMPERFECTA (Walker).

**Tabanus imperfectus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 179. Type ♀, from New Holland, in the British Museum (Natural History). The label "New South Wales, ex col. Saunders" is a later addition.

A small (10 mm.), slender, black species, with greyish-white hairs on the eyes (a distinguishing feature of this and the next species), medium, diverging frons (index 2.5 to 3), slender, gently curved antennal plate, and narrow pale apical bands on abdominal tergites. It was correctly identified by White (1915) and Ferguson (1921*a*, 1921*b*), but not by Hardy (1952).

Distribution.—Tasmania.

DASYBASIS EDENTULA (Macquart).

**Tabanus edentulus* Macquart, 1846. *Dipt. exot.*, Suppl. 1, p. 34. Type ♀, from Tasmania, in the Paris Museum.

**Tabanus antecedens* Walker, 1854. *List Dipt. Brit. Mus.*, 5, Suppl. 1, p. 253. Type ♀, from Tasmania, in the British Museum (Natural History). Not *T. antecedens* Walker, 1848, ♂ (see under *gregaria*).

A black species, with white hairs on eyes, and narrow, pale bands on abdominal tergites. Distinguished from *imperfecta* by larger size (12–14 mm.), more parallel-sided frons, usually somewhat different callus, and wider antennal plate. It is quite easy to separate the two series, even with a hand-lens ($\times 8$), and I have no doubt that they are specifically distinct.

Macquart's name has been used by different authors for two different species. This proved to be due to the fact that, alone among his species that I have studied, he attached "n. sp." labels to two specimens. One, in the Paris Museum, agrees with his description and his statement that the specimen was in "Muséum", and I select it as lectotype in order to remove any doubt. It is now headless, but it is accompanied by a perfect specimen with the same collector's or accession number ("73 44"), and both are undoubtedly the species at present under consideration. This type is evidently the specimen referred to by Ferguson (1921*b*), when he suggested the synonymy accepted here. White (1915) and Ricardo (1915*b*) correctly identified the *antecedens* of 1854, but not *edentula*. Hardy (1934, 1939, not 1948) accepted Ferguson's suggested identification.

The second "type" specimen is in the British Museum, and it does not agree with Macquart's description. It is from the Bigot collection, is labelled "Van Dieman", and is a medium-sized (12.5 mm.), smooth, brown species, identical, I believe, with Tasmanian specimens of *acutipalpis*. It provided the basis for the name "*edentulus*" being attached to the common, smaller, brown Tasmanian species by White (1915), Ricardo (1915*b*), Taylor (1917*b*, 1918), Ferguson and Henry (1920), and Ferguson (1921*a*, 1921*b* in part).

Finally, Hardy (1948) synonymized *antecedens* Walker, 1854, with *flindersi* Ferg., which it does not at all resemble.

Distribution.—Tasmania.

DASYBASIS GEMELLA (Walker).

**Pangonia gemella* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 139. Type ♀, from Western Australia, in the British Museum (Natural History).

This species had not been recognized, except that Ferguson had left an ms. note that it was a tabanine with hairy eyes, and there are two females correctly identified in the Australian Museum. It proved to be a not uncommon, western species, with a broad, strongly angled antennal plate, like *gregaria*, but with a wide frons (index 1·8 to 2) and the wings spotted as in *appendiculata*.

Distribution.—South-western Western Australia.

DASYBASIS GREGARIA (Erichson).

Tabanus gregarius Erichson, 1842. *Arch. Naturges.*, (1), 8, p. 271. Type ♀, from Tasmania, in the Berlin Museum; examined by Mr. Oldroyd, and a specimen returned by him as agreeing with it.

**Tabanus antecedens* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 178. Type ♂, from New Holland, in the British Museum (Natural History). Not *T. antecedens* Walker, 1854 (see under *edentula*).

**Tabanus flindersi* Ferguson, 1921. *Rec. S. Aust. Mus.*, 1, p. 374. Type ♀, from Flinders I., Bass Strait, in the South Australian Museum, Adelaide.

A medium-sized (12–13 mm.), strongly built, dark brown species, characterized by a broad, blackish antennal plate with prominent, rectangular dorsal angle; frons index about 2·5; wings suffused with brown anteriorly and variably along the veins in southern specimens, more or less uniformly greyish in northern ones.

The identity of *gregaria* had been obscure, until Mr. Oldroyd returned a typical southern *flindersi* as agreeing with the type. Walker's 1848 type of *antecedens* has lost the antennae; it is dark, thickset, with the upper facets of the eyes moderately enlarged but not sharply differentiated from the lower, and the hairs on face and parafacials predominantly brown. It is difficult to identify precisely, but it agrees distinctly better with males of *gregaria* from coastal New South Wales than with males of *indefinita* from the same area.

Distribution.—Coastal New South Wales, from Woy Woy to Jervis Bay; Tasmania; possibly also South Australia.

DASYBASIS MORETONENSIS (Ferguson & Hill).

**Tabanus confusus* Taylor, 1917. *Proc. Linn. Soc. N.S.W.*, 42, p. 523. Type ♀, from Brisbane, S.Q., in the Queensland Museum, Brisbane. Not *T. confusus* Walker, 1848, Nearctic.

Tabanus moretonensis Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 264. *Nom. nov.*

The northern representative of *gregaria*, from which it differs in being smaller, smoother, with clearer wings, and the upper facets of the eyes of the males larger and more definitely marked off from the lower. It might be better treated as a subspecies than as a full species.

Distribution.—South-eastern Queensland.

DASYBASIS DUBIOSA (Ricardo).

**Tabanus dubiosa* Ricardo, 1915. *Ann. Mag. nat. Hist.*, (8), 16, p. 284. Type ♀, from Burnett R., S.Q., in the British Museum (Natural History).

A small-medium (10–13 mm.), compact, smooth, black species; frons index 3 to 3·5; antennal plate wide, with well-defined dorsal angle; wings clear; pale abdominal pattern well defined, with large median triangles on the tergites.

Distribution.—South-eastern Queensland.

DASYBASIS DUBIOSA INDEFINITA (Taylor).

**Tabanus indefinitus* Taylor, 1918. *Rec. Aust. Mus.*, 12, p. 68. Type ♀, from Nepean R., N.S.W., in the Australian Museum, Sydney.

More hairy and more thickset than the northern race, usually more brown in general colour, and with smaller median and lateral triangles on the abdominal tergites. Hardy (1952) sank both *dubiosa* and *indefinita* under *imperfecta*, which he misidentified. As Queensland specimens can be distinguished even from the darkest ones from New South Wales, I feel that subspecific separation of the first two is justified, with *imperfecta* quite distinct.

Distribution.—South Queensland (Stanthorpe, Eukey); New South Wales, from the Dorrigo plateau to Canberra, and on the coast south of Sydney.

DASYBASIS HOBARTIENSIS (White).

**Tabanus hobartiensis* White, 1915. *Pap. Proc. R. Soc. Tas.* for 1915, p. 13. Type ♀, from Hobart, Tasmania, in the British Museum (Natural History).

A small (11 mm.), compact, brown species; apparently the Tasmanian representative of *indefinita*, from which it is distinguished by smaller size, paler hairs on eyes, somewhat wider frons (index 2.5), and antennal plate with rounded dorsal angle. Possibly it should be treated as a third subspecies in the complex.

Distribution.—Tasmania.

DASYBASIS TASMANIENSIS (White).

**Tabanus tasmaniensis* White, 1915. *Pap. Proc. R. Soc. Tas.* for 1915, p. 8. Type ♀, from Bagdad, Tasmania, in the British Museum (Natural History).

This species has not been identified correctly in Australia, Ferguson (1921*b*) giving the name to a small, black species close to (or a variant of) *imperfecta*, and Hardy (1934) treating it as a synonym of *gregaria*. It is apparently rare, because I brought the paratype female (from the same place and date as the type) back with me, and have not been able to match it exactly among 394 specimens of Tasmanian *Dasybasis* available for review. It is very close to *hobartiensis*, differing only in larger size (12 mm.), narrower frons (index 3), somewhat differently shaped callus, which is slightly narrower than the frons at the base (Text-fig. 9), narrower antennal plate, and brown suffusion of the wings anteriorly and narrowly along the veins. However, the two specimens of *tasmaniensis* do stand out when placed alongside specimens of *hobartiensis*, and I think that they probably represent a distinct species.

Distribution.—Tasmania.

DASYBASIS CIRCUMDATA (Walker).

**Tabanus circumdatus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 185. Type ♀, from unknown country, in the British Museum (Natural History).

**Tabanus fraterculus* Macquart, 1850. *Dipt. exot.*, Suppl. 4, p. 30. Type ♀, from "Tasmanie" (erroneous), in the Paris Museum.

**Tabanus brevidentatus* Macquart, 1855. *Dipt. exot.*, Suppl. 5, p. 28. Type ♀, from Sydney, N. Holland, in the British Museum (Natural History).

All three types are in poor condition (that of *circumdata* has had the head gummed on, and has lost the third antennal segment and the apical four segments of the abdomen), but they seem to me to agree better with the larger, common, eastern mainland species, than with either of the others that resemble it. In spite of White's and Austen's earlier determinations, I cannot associate *circumdata* satisfactorily with the species now identified as *hebes*.

This species is about the same size as *hebes*, but is distinguished from it by usually darker colour (melanic forms are frequent, especially in the mountains), more truncate face, better defined facial sutures, and especially by the shape of the eighth sternite (Text-fig. 5). Since returning to Australia, I have found that the terminal segments can be revealed without appreciable damage to the specimen, by simply chipping away the free parts of the seventh tergite and sternite with a fine pin, working inwards from each side to avoid risk of damaging the underlying structures.

Distribution.—Eastern New South Wales; Victoria; with possible extensions to south Queensland, South Australia and Western Australia; not known from Tasmania.

DASYBASIS ACUTIPALPIS (Macquart).

**Tabanus acutipalpis* Macquart, 1838. *Dipt. exot.*, 1. (i), p. 131. Type ♀, from King I., "Océanie" (at least latter erroneous), in the Paris Museum.

**Tabanus abstersus* Walker, 1850. *Insecta Saund. Dipt.*, 1, p. 58. Type ♀, from New South Wales, in the British Museum (Natural History).

Tabanus edentulus White, 1915, and other authors, *nec* Macquart (see under *edentula*).

There are three females in Paris identified by Macquart, the type being labelled "Nouv. Holl., Durville" (the description gives "De l'île King, dans l'Océanie. M. Durville. Muséum"), and there is also a female "cotype" in the British Museum labelled "Tasmanie". All four seemed to be conspecific, but I had difficulty in identifying them, until Professor Séguéy very kindly sent me the series from Paris for more detailed study. The type proved to have a wide eighth sternite, like Text-figure 5, and to agree also in external characters with the smaller of the two, common, brown Tasmanian species, although the antennal plate was a little wider than is shown in Text-figure 8.

Mainland specimens, to which the name *abstersa* strictly applies, may represent a distinct race, and are usually distinguishable from *circumdata* by smaller size (10–12 mm.), slightly different frons, and narrower antennal plate, with more rounded dorsal angle (Text-fig. 7); melanism is equally common. I am inclined, at present, to think that *circumdata* and *acutipalpis* are separate, variable species, with overlapping phenotypes, but they may completely fuse.

Distribution.—All States, from south-eastern Queensland to Tasmania and south-western Western Australia.

DASYBASIS INNOTATA (Ferguson & Henry).

**Tabanus innotatus* Ferguson and Henry, 1920. *Proc. Linn. Soc. N.S.W.*, 44, p. 847. Type ♀, from Kendall, N.S.W., in the Australian Museum, Sydney.

A distinctive, slaty black, long-bodied (14–15 mm.) species, with moderately wide frons (index 2.5 to 3), blackish antennae, grey pleura, black legs, quite dark grey wings, and a row of small, white, median spots on the abdominal tergites.

Distribution.—Coastal New South Wales, from Kendall to Moruya. There is a closely related species (or subspecies) in Western Australia.

DASYBASIS MILSONIENSIS (Ferguson & Hill).

**Tabanus milsoni* Taylor, 1917 (Apr.). *Proc. Linn. Soc. N.S.W.*, 41, p. 760. Type ♀, from Milson I., N.S.W., in the School of Public Health and Tropical Medicine, Sydney. Not *T. milsonis* Ricardo, 1917 (Feb.), from same type locality (see under *trilinealis* group).

Tabanus milsoniensis Ferguson and Hill, 1922. *Proc. Linn. Soc. N.S.W.*, 47, p. 265. *Nom. nov.*

A small (10 mm.), obscure, greyish-brown species, with medium frons (index 3), short, wide, strongly angulate, orange-brown antennal plate, and well-defined pale median triangles on the abdominal tergites.

Distribution.—Coastal New South Wales, from Milson I. to Sydney.

There are also three small, greyish, undescribed species in this group. One is represented by the mislabelled "type" of *neocirrus* (Ric.) and other specimens from South and Western Australia; the second is from the same States; and the third is from western New South Wales.

UNIDENTIFIED SPECIES.

The types of the following species cannot be traced, and no one has been able to identify them satisfactorily from the descriptions. It may be noted that none of the types of Macquart's 1846 species which were recorded as from the collections of the Marquis Spinola and of Guérin and Reiche have been found in Paris or London. These include *Pangonia singularis*, *Pangonia bicolor* and *Tabanus pallipennis*, as well as those listed below.

Tabanus brevivitta Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 157. ♂. "New Holland. From Mr. Gould's collection."

Tabanus funebris Macquart, 1846. *Dipt. exot.*, Suppl. 1, p. 33. ♀. "De la Nouvelle-Hollande. MM. Reiche et Guérin."

Tabanus nigriventris Macquart, 1846. *Dipt. exot.*, Suppl. 1, p. 34. ♀. "De l'île Sidney. Collection de M. le Marquis Spinola."

Tabanus propinquus Macquart, 1855. *Dipt. exot.*, Suppl. 5, p. 27. ♀. "De la Nouvelle-Hollande. Sydney. M. Bigot." The type should be in the British Museum, but there is only a specimen labelled "*propinquus* ♂" in Bigot's handwriting. It has lost its head and half the abdomen, and Mr. Oldroyd thinks that "what is left of it looks uncommonly like an African *T. ustus*."

Tabanus remotus Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 177. ♀. "New Holland. Presented by the Haslar Hospital."

Tabanus sidneyensis Macquart, 1846. *Dipt. exot.*, Suppl. 1, p. 33. "De l'île Sidney. Collection de M. le Marquis Spinola."

EXCLUDED SPECIES.

Three, previously unrecognized, Australian species belong to other subfamilies.

Tabanus bifasciatus Macquart, 1834. *Hist. nat. Ins.*, Dipt., 1, p. 201. Believed to be a synonym of *Scaptia* (*Scaptia*) *guttata* (Don.), Pangoniinae.

**Tabanus erraticus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 189. Is a species of *Ectenopsis* (*Ectenopsis*), Pangoniinae, from Western Australia; does not displace any currently used name.

**Tabanus lunulatus* Bigot, 1892. *Mem. Soc. zool. Fr.*, 5, p. 688. Is a species of *Mesomyia* (*Vepriella*), Chrysopinae, replacing **insularis* (Ric.).

The following species are excluded from the Australian list.

**Atylotus claripennis* Bigot, 1892. *Mem. Soc. zool. Fr.*, 5, p. 675. Type ♀, from "Australie", in the British Museum (Natural History). Neotropical; replaces *Tabanus hookeri* Knab (Fairchild, 1956).

**Holcopsis fenestratus* Enderlein, 1925. *Mitt. zool. Mus. Berl.*, 11, p. 372. Type ♀, doubtfully from "S.W. Australia", in the Berlin Museum. Unlike any known element in Australian fauna; possibly Neotropical.

**Stibasoma hemiptera* Surcouf, 1912. *Bull. Mus. Hist. nat. Paris*, ann. 1912, (2), p. 62. Type ♀, from "Nov. Holl.", ex col. Bigot, in the Paris Museum. Neotropical; probably *Dasychela* (Fairchild, 1956).

**Tabanus leucophilus* Walker, 1848. *List Dipt. Brit. Mus.*, 1, p. 154. Type ♀, from "New Holland", in the British Museum (Natural History). Belongs to a distinctive group of southern Palaearctic (desert) species of *Tabanus*, but could not be matched exactly in the British Museum collection.

**Tabanus limbatinevris* Macquart, 1847. *Dipt. exot.*, Suppl. 2, p. 16. Type ♀, "De la Tasmanie. M. Bigot", in the British Museum (Natural History). (Not *T. limbatinevris* Macquart, 1850—see under *Cydistomyia alternata*.) A synonym of the Nearctic *Tabanus abdominalis* Fabricius, by comparison with named specimens; synonymy suggested, and concurred in, by Dr. C. B. Philip.

**Tabanus rubricallosus* Ricardo, 1914, New Caledonia. Recorded by Hardy (1948) from New South Wales; misidentification of *Dasybasis macrophthalma* (Schiner).

Tabanus serus Walker, 1862, Ceram. Recorded by Summers (1912) from Northern Territory; misidentification of *Tabanus dorsobimaculatus* Macquart.

**Tabanus similis* Macquart, 1850. *Dipt. exot.*, Suppl. 4, p. 31. Type ♀, "De la Tasmanie. M. Bigot", in the British Museum (Natural History). Agrees with the Nearctic **Tabanus lineola scutellaris* Walker, by comparison of types by Dr. C. B. Philip and I.M.M.

Tabanus spoliatus Walker, 1860, Celebes. Taylor (1918) noted that Miss Ricardo had identified a male in the Australian Museum as *T. spoliatus*. Hardy (1948) pointed out that the specimen was really *Tabanus parvicallus* Ricardo.

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OBSERVATIONS ON SOME AUSTRALIAN FOREST INSECTS.

4. XYLEBORUS TRUNCATUS ERICHSON 1842 (COLEOPTERA: SCOLYTIDAE) ASSOCIATED WITH DYING EUCALYPTUS SALIGNA SMITH (SYDNEY BLUE-GUM).

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

(Plate vii; three Text-figures.)

[Read 27th May, 1959.]

Summary.

Numerous deaths of trees of *E. saligna* Smith on State Forests and private property, with consequent economic loss, have recently caused concern to Forestry officers and landholders.

Investigations into the causes of these deaths and the association of attack by *Xyleborus truncatus* Erichson with brown staining in the wood of dying trees are described.

Biology, hosts and distribution of the insect are given and typical damage is described and figured.

Results of assessments of the quantity of commercial timber destroyed in two areas of greatest tree-mortality are included; the areas are mapped and their locations are given.

The factors apparently contributing to attack by *X. truncatus* and deaths of trees are discussed.

INTRODUCTION.

Eucalyptus saligna Smith (Sydney blue-gum) occurring on State Forests and private property in coastal areas of New South Wales was reported as dying during the period 1949 to 1958, the increasing number of deaths reaching economic significance toward the end of that period. Throughout that time, psyllids of the genus *Spondylaspis* (Hemiptera: Psyllidae) were occurring in plagues and causing severe defoliation and debilitation of several *Eucalyptus* species.

Attention was first drawn to this problem on private property in the Gosford-Wyong area by Mr. P. C. Hely, at that time District Entomologist, Department of Agriculture, Gosford, who reported that many local residents were blaming *Manorina melanophrys* Latham (bell-birds) for the general debilitation of blue-gums in the area. Hely suggested that psyllids of the genus *Spondylaspis* were more likely to be the cause (unpublished report, 1950). An investigation of the food of the bell-birds was made by Campbell and Moore (1956).

During the years 1953 to 1956 single, scattered, dying trees were observed in many areas, and the deaths of *E. saligna* on State Forests and private property were beginning to cause concern to Forestry officers and owners of private property. By this time the psyllids had attained plague proportions on trees in numerous gullies, on slopes, and on the flats, and had caused partial or complete defoliation continually for some years.

The initial association of *Xyleborus truncatus* Er. (Pl. vii, 1b, 1c) with a dark brown staining in the timber of a dying tree was observed during May 1954 at Lisarow, N.S.W. The foliage of an *Angophora intermedia* De Candolle (rough-barked apple) about twenty feet in height, was observed to be brown and apparently dead, and a colony of the beetle was present in the trunk of the tree at approximately six feet above ground level. Dark brown staining of the wood above and below this colony was extensive, and no other evidence of the possible cause of death was observed. *A. intermedia* is not known to be a host of *Spondylaspis* spp.

SELECTION OF STUDY AREAS.

Investigations to determine the causes of tree mortalities were begun by the writer during November 1956 at Ourimbah State Forest No. 290, where an area of forest

approximately two miles in length and five to ten chains in width, extending along the centre of a north-easterly slope, was severely infested with *Spondylia* spp., and on property of Mr. J. Catt of Lisarow. A study of the biology and ecology of the psyllids which was made in those areas will form the subject of a separate paper.

When a wood-boring beetle was invariably found in association with the debilitated trees, many other areas of forest were also examined where the psyllids were present in large numbers and deaths of *E. saligna* were occurring.

When selecting areas for intensive examination, those where logging had occurred during the previous ten years were regarded as unsatisfactory for the purpose, because the healthier, larger and better quality trees suitable for economic utilization had been removed. Those remaining were generally deformed or affected by insect attack (mainly by Lepidoptera, Coleoptera or Isoptera), decomposition of the wood where mechanical injury had occurred, or fungi.

The numerous effects of fire in a stand of timber are not completely understood, and because these may have introduced unknown variables during investigations, areas where fire had occurred within the previous ten years were also considered unsuitable.

A gully was selected at Lisarow on the opposite side of the creek to the area assessed and shown in Text-figure 1, where a stand of large and previously vigorous *E. saligna* trees occurred and where there had been no logging or fire after 1945. The gully extended approximately north and south, with a northerly aspect, the timber-stand composition on its slopes being principally of *E. pilularis* J. E. Smith (blackbutt), *E. paniculata* J. E. Smith (grey iron-bark), *Syncarpia laurifolia* Tenore (turpentine), *A. intermedia*, *E. saligna* and *E. acmenioides* Schauer (white mahogany), with the two latter species predominating. From the central area of the slopes and extending to the creek, palms, brush-woods and vines formed a moderate to dense cover beneath these species. This area had been severely attacked by *Spondylia* sp. for at least eight years prior to these investigations.

METHODS OF STUDY.

Twelve trees of *E. saligna* which appeared almost dead were selected for observations on the association of their probable deaths with some cause other than the psyllid attack. The twelve trees examined varied in height from thirty to ninety feet, and in diameter at breast-height-over-bark from seven to fifteen inches. The trunks were apparently free from injury or insect attack, and the trees had previously made vigorous, straight growth. Each tree was felled and cut into various lengths, which were then examined for evidence of any agent which may have contributed to the tree's debility. Attack by *Spondylia* sp. and *X. truncatus* was found to occur on each tree.

There does not appear to be a precise definition of a "dying", "almost dead" or "dead" tree, and it was necessary to establish a practical classification of tree condition for the purpose of this study. This was formulated by the writer after two years of observations on most of the Gosford-Wyong area, which included approximately 150 separate areas where the psyllids occurred in large populations and trees of *E. saligna* were in various stages of debilitation. From this survey it was assumed that the majority of trees bearing dead branches, and with relatively few epicormics, would die, and this was considered to be a practical basis for these investigations.

RESULTS OF INVESTIGATIONS AND DESCRIPTION OF DAMAGE.

In all areas examined where *X. truncatus* occurred and damage by the psyllids was severe, trees were found to be in various stages of debility. Some showing vigorous regrowth of crowns appeared healthy; others carried one or more dead branches with variable amounts of foliage or some epicormics on the trunk or branches, while other trees had died.

Many trees severely affected by the psyllids were attacked by *X. truncatus*, and in these, variable degrees of dark brown staining of the timber occurred contiguous to the hole made by the beetle. This staining extended in a strip of variable width, from the

entrance hole and along the sapwood for varying distances toward both the bases and the crowns of the trees. In a number of instances it was found to have penetrated the truewood.

Early stages of attack were denoted by a dark brown stain approximately one-quarter of an inch in width on the surface of the sapwood, extending above and below the hole for from two to six inches. In the later stages, this stain had spread along the sapwood and truewood, principally below the holes, becoming paler brown in colour as it extended down the trunk, and the bark covering the stained area had eventually cracked and died.

In trees assumed to be almost dead, the stain covered by the dead and dying bark sometimes reached to ground-level. The earlier stages showed little or no cracked bark. The cracking of the bark always began contiguous to and beneath the scolytid hole, spreading downwards.

In some of the less debilitated trees attack by *X. truncatus* was not always found. Attack in a tree was usually indicated by the presence of one or more dead lower branches, with little or no crown foliage, or with epicormics on the trunk or branches.

During the preliminary investigation of severely debilitated trees, extensive brown staining of the wood tissues was associated with scolytid attack in four areas of forest which were in some instances as far as twelve miles apart. Live or dead beetles of *X. truncatus*, or its colony chambers, were found in fourteen of the sixteen trees inspected throughout these areas. In the other two trees staining was associated with borer holes (probably those of this scolytid), but these did not contain beetles or larvae.

The association of *X. truncatus* attack with brown staining and the probable death of a tree was consistently established in almost every tree out of a total of approximately 60 examined thereafter.

The founding of a colony of *X. truncatus* is not necessary for staining of the timber to become evident, or for the death of a tree; a single hole, sometimes containing a dead beetle only, was at times sufficient to produce the condition. Initial attack on a tree by *X. truncatus* was usually found in the dead or dying lower branches of the tree-crown, and occurred either high or low in the trunk only when a tree was apparently considerably debilitated.

Trees on which the crown or epicormic growth appeared vigorous and healthy as though recovering from psyllid attack, and those considered nearest to death, showed attack by *X. truncatus*. Some trees were apparently able to withstand a single attack, although others showing a single attack had died.

Attack by *X. truncatus* with consequent death of trees sometimes occurs where the psyllids have played no part in their debilitation, although prolonged attack by *Spondyliaspis* sp., or damage by other agencies, apparently reduces the vitality of trees, causing them to become susceptible to attack by *X. truncatus*.

OTHER SPECIES OF WOOD-BORING COLEOPTERA.

Additional wood-boring beetles observed attacking debilitated *E. saligna* are as follows:

ANOBIIDAE: *Derophtilinus granicollis* Lea.

BOSTRYCHIDAE: *Xylion cylindricus* Macl., *X. collaris* Er., *Xylopsocus gibbicollis* Macl.

BRENTHIDAE: *Cyphagogus bipunctatus* Senna.

PLATYPODIDAE: *Platypus australis* Froggatt.

SCOLYTIDAE: *Xyleborus compressus* Lea, *X. pseudoangustatus* Schedl, *X. solidus* Eichh.

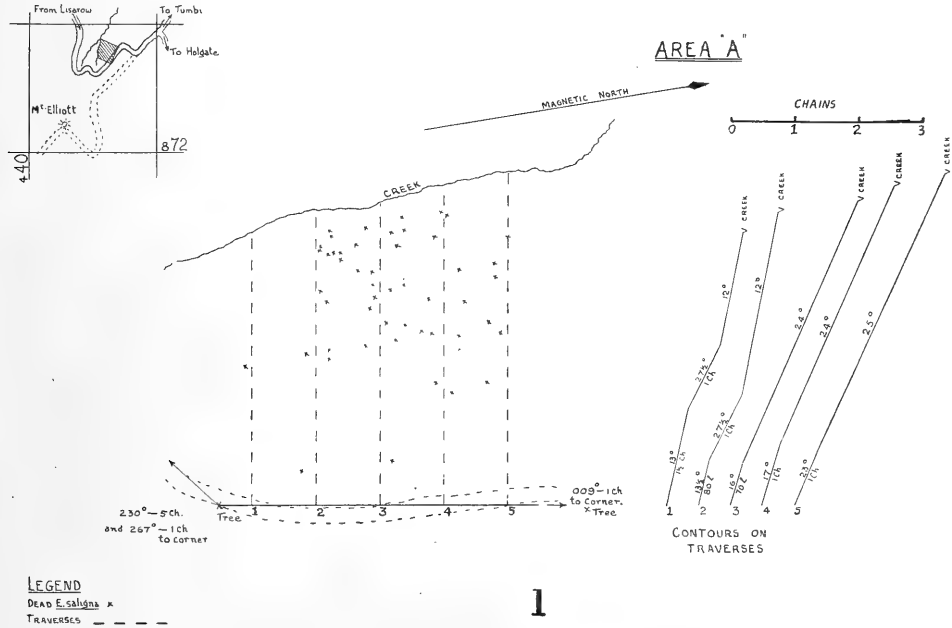
In the trees examined, attack by *X. truncatus* always preceded any evidence of attack by these other species.

LOSS OF COMMERCIAL TIMBER.

To determine the amount of commercial quality timber represented by the *E. saligna* killed on two areas of forest, one hundred percent. assessments were made of 2.4 acres on the property of Mr. J. Catt at Lisarow (area "A", Text-fig. 1), and 1.05 acres on Ourimbah State Forest (area "B", Text-fig. 2). The locations of these areas on the Gosford-Norahville military sheet, Zone 8, are shown as insets on the respective figures.

From the surveyed baselines of each of the assessed areas traverses at 90° and at one chain intervals were made. Trees within one half-chain on either side of these traverses were assessed, and marked to obviate duplication of assessment.

On area "A" 92 trees were measured and assessed for the quantity of commercial timber which they represented. Fifty-one trees (55%) were classified as dead (of this number 19.6% were assessed as "expected to die" because of the extent of their debility



Text-fig. 1.—Area "A" of assessed *E. saligna*, on property of Mr. J. Catt, Lisarow, N.S.W. Location 440,600 east, 872,750 north.

when examined). The amount of commercial timber represented by the fifty-one trees was 9,409 super feet hoppus (58% of the total s.f. hoppus of *E. saligna* on the area), and that by the trees classified as "living", 6,813 s.f. hoppus.

On area "B" 69 trees were assessed. Forty-one trees (59%) were classified as dead (this figure included 24% assessed as "expected to die"). The timber represented by the forty-one trees totalled 16,156 s.f. hoppus (64.9% of the total s.f. hoppus of *E. saligna* on the area), and that by the trees classified as "living", 8,724 s.f. hoppus.

Totals for both of the assessments:

Dead trees:	92 (57%)	25,565 s.f. hoppus.
Living trees:	69 (43%)	15,537 s.f. hoppus.
Grand total:	161 trees	41,102 s.f. hoppus.

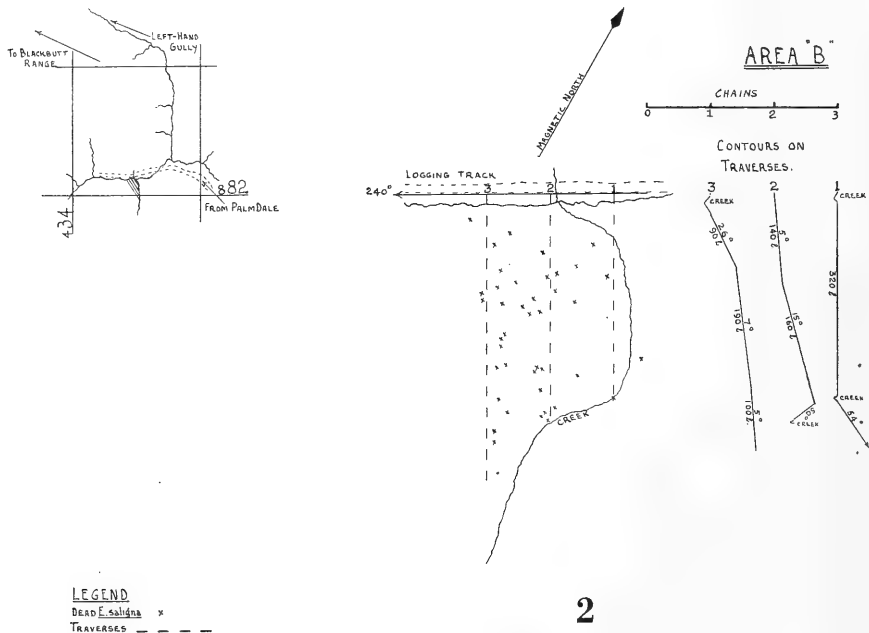
Volumes of timber derived from these assessments are based on Forestry Commission Recovery Tables for *Eucalyptus grandis* (flooded gum), Pine Creek S.F. (a closely allied species), which were considered adequate, as tables for *E. saligna* were not available. These figures are indicative of the loss of commercial timber in areas where the incidence of mortalities was greatest.

DISTRIBUTION.

X. truncatus is widely distributed. The original description by Erichson (1842) is based on a specimen from Van Diemen's Land. A specimen from Armidale, N.S.W., was described by Lea (1893), who also gave South Australia and Tasmania as localities. Specimens were collected at Forbes and Ourimbah in New South Wales, and also in Victoria by Froggatt (1926). Brimblecombe (1953) records its occurrence in Queensland. It has been collected at Wentworth Falls, Kincumber and Wyong, N.S.W., by the writer.

HOSTS.

Froggatt (1926) recorded *E. saligna* and *E. camaldulensis* Dehn. (river red-gum) as hosts. *E. acmenioides*, *E. maculata* Hook. (spotted gum) and *E. citriodora* Hook. (lemon-scented gum) have been recorded by Brimblecombe (1953). *A. intermedia*, *E.*



2

Text-fig. 2.—Area "B" of assessed *E. saligna* on Ourimbah State Forest No. 290, Forestry District of Newcastle, sub-district of Wyong. Location 434,500 east, 882,075 north.

propinqua Deane & Maid. (grey-gum) and *E. piperita* Smith (peppermint) are recorded by the writer.

From the distribution of *X. truncatus* it is assumed that a wide range of *Eucalyptus* spp. would be attacked.

BIOLOGY.

Biology of this species is recorded by Froggatt and Brimblecombe.

Approximately sixty trees of *E. saligna* in the eight to twenty-five years age-group were felled in the Gosford-Wyong area during 1957 and 1958 and the following observations made.

X. truncatus has been found only in standing trees. The colony-chambers (Pl. vii, 1a) are found in the truewood as deep as two inches within the branches or the trunk, the narrowest portion of the chamber being above the entrance tunnel. The colony-chambers, which vary in size, are approximately 2 mm. wide, 5 mm. in height, with a basal length of 4 mm., their size probably depending on the number of larvae reared in them. The walls of the chambers or the holes are sometimes stained a brown to black

colour which spreads into the sapwood or truewood above and below them. The staining may be seen above and below the galleries in the figure. There may be no typical chamber such as that figured, but only a more or less horizontal hole from the outside of the trunk or limb, and which may contain adults, pupae or larvae.

One colony contained 13 larvae, most of which were in the last instar, and only the base of the colony-chamber was stained. Some live colonies were found in apparently dead and dry branches, although it was more usual to find them in timber which still contained sap.

Froggatt and Brimblecombe refer to attack occurring in damaged areas on trees, where sapwood had been exposed. In each of the instances observed during these investigations, attack occurred through the previously undamaged, smooth bark of *E. saligna* and *E. propinqua* or the rough bark of *A. intermedia*.

The association of *X. truncatus* with dying trees has not previously been reported, although Froggatt recorded that the exposed area of wood surrounding the point of attack turned brown and died.

Oviposition apparently occurs over many months in the one colony, for larvae of most instars, pupae and adults occur together during most months of the year. During these investigations oviposition occurred from October to May, and during the latter month a cluster of approximately 15 eggs was found in a colony-chamber containing larvae and pupae. This suggests that the one colony-chamber may be utilized for the rearing of more than one generation of beetles.

Beetles may bore into either a limb or tree-trunk and die without founding a colony or without evident staining of the timber. Some apparently killed by sap-flow or gum-flow were found in the entrance holes.

The parent beetle appears to attend a colony for some months, and some have been found in entrance holes around the external edge of which a white, powdery substance (probably the excreta of the larvae, or excess fungal growth) had been removed from the gallery. A single exit hole is constructed from the end of the colony-chamber opposite to the entrance hole made by the parent when founding the colony.

The life cycle occupies approximately three months in the warmer weather, and six months or more for the overwintering generation. Emergences of adults from a colony may occur from September to about May, while pale coloured adults, together with last instar larvae, were taken during July. It is presumed that adults would not have emerged from the tree until the following spring.

No parasites of *X. truncatus* were found during these investigations.

Adult bees of *Hylaeus aralis* Kll. (Colletidae: Hylaeinae) were reared from gallery-chambers. Their larvae overwinter in thin skin-like cells in the galleries.

DESCRIPTIONS.

The adults, 2.5 mm. to 3 mm. in length, may be identified by the truncate elytra, a feature which is apparently confined to this one species of the Australian Scolytidae. They superficially resemble species of the Bostrychidae, in which family this feature is comparatively common, and Lea (1893) initially placed *X. truncatus* in that family.

The taxonomy of *X. truncatus* has been referred to by Brimblecombe (1953).

Larva.—There is apparently no previous description of a last instar larva of *X. truncatus*, although Froggatt figured a larva without designating to it any particular instar. Last instar (Text-fig. 3): Length approximately 3.5 mm. to 3.8 mm. Head-capsule pale cream with mouthparts varying from tan-colour to dark brown; remainder of larva opaque white; cylindrical; the exoskeleton more or less covered with microsetae which are visible at high magnifications; apodous; arcuate, with the abdomen prominently deflexed from about the fourth abdominal segment, so that the distal segments are often at an angle of about 90° to the proximal segments; pseudopods present on each thoracic segment; tenth abdominal segment small, and consisting of little more than the anal aperture; the dorsal aspect of each segment except abdominal

segments nine and ten is divided transversely to form an anterior and a posterior protuberance approximately equal in length.

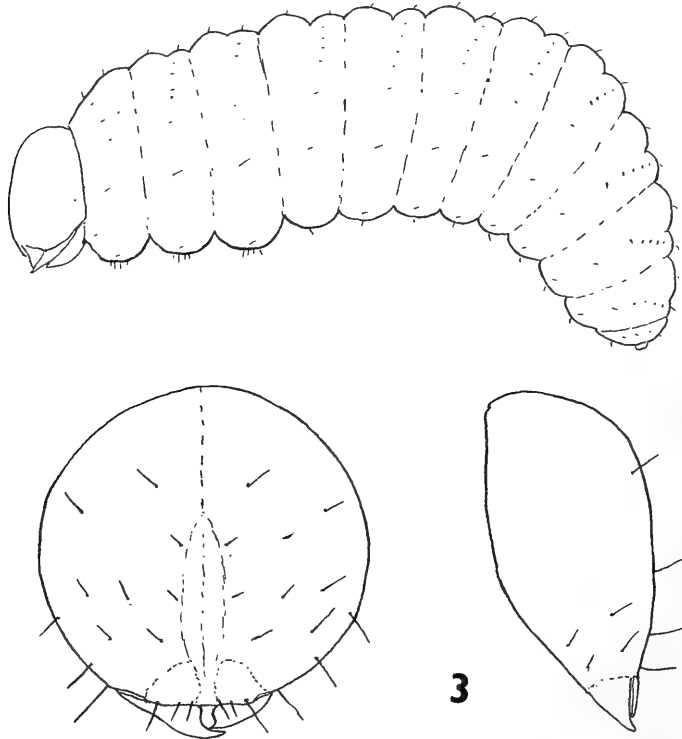
Setal arrangement on the head-capsule and body-segments is shown in Text-figure 3.

Pupa.—The pupa, about 3 mm. in length, is at first white, later becoming yellow, then pale brown prior to the emergence of the adult.

DISCUSSION.

The cause of deaths of *E. saligna* was not determined, and these observations present a basis for further investigations.

Species of the Scolytidae are known to be vectors of Dutch elm disease, with consequent deaths of trees, in forests of Europe and America (Collins *et al.*, 1936;



Text-fig. 3.—Setal arrangement on body-segments and head-capsule of last instar larva of *X. truncatus*.

Parker *et al.*, 1941), and it is suggested that *X. truncatus* is similarly associated with some pathogen or toxic agent capable of causing tree mortalities. It is most unlikely that the limited damage caused by these beetles would be the direct cause of death.

Certain weather conditions or physiological conditions of trees may be essential for optimum effect of the mortality factor which is not necessarily associated with psyllid or scolytid attack.

The considerable number of dead and dying trees occurring in areas of large psyllid populations and where *X. truncatus* attack occurred was generally associated with debilitation of trees apparently due to, or accentuated by, persistent psyllid attack. However, the *A. intermedia* attacked by *X. truncatus* was not debilitated by psyllids, which suggests that site-favourability may be a factor contributing to debilitation, and thus inducing attack by *X. truncatus*. This may be the principal factor operating in all instances.

From an examination of meteorological records supplied by the Narara Citrus Experiment Station, it is evident that the reports of large populations of psyllids together with debilitation of *E. saligna* correspond with the years of abnormal rainfall experienced from 1949 to 1956. The average annual rainfall for that period was 69.29 inches. Rainfall exceeded 86 inches for each of two years and exceeded 72 inches each year for a further three years during those eight years.

For comparison, the average annual rainfall for the years 1935 to 1941 was 37.16 inches for the seven-year period, while the average annual rainfall for the intervening seven years of 1942 to 1948 (45.06 inches) approached the normal figures for precipitation on the area, which for the 41 years from 1917 to 1957 averaged 49.83 inches per annum.

At present an analysis of factors contributing to deaths of the trees is hypothetical, but the hypothesis considered most tenable is that the abnormal rainfall adversely affected the physiology of *Eucalyptus* and other species generally, making them susceptible to heavy attack by psyllids.

It appears that moderate temperatures together with high relative humidity favour a large increase in psyllid population in the areas studied (probably through conditions unfavourable to their natural parasites), causing the progressive debilitation of the trees and culminating in a greater susceptibility to attack by *X. truncatus*.

Observations on these factors are being continued.

Acknowledgements.

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EXPLANATION OF PLATE VII.

1a. Colony-chambers of *X. truncatus* (Scolytidae) in *E. saligna* with associated staining of the timber. 1b. Adult beetle of *X. truncatus* (lateral view). 1c. Adult beetle of *X. truncatus* (dorsal view).

Photographs by D. Rose.

THE GENUS *CONOSTYLIS* R.BR.

I. LEAF ANATOMY.

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(Twenty-five Text-figures.)

[Read 24th June, 1959.]

Synopsis.

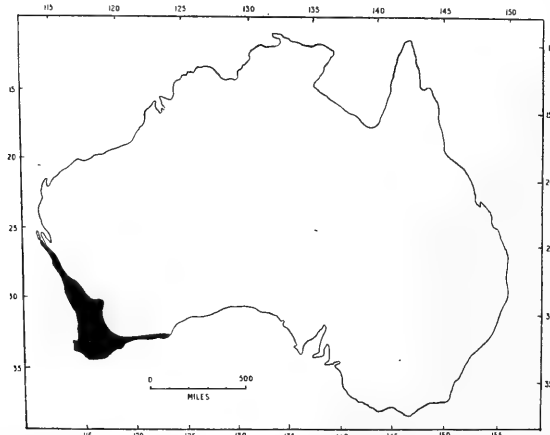
Anatomical features of the leaves of selected species of *Conostylis* are described and illustrated and their systematic and ecological significance discussed briefly.

INTRODUCTION.

Occurrence and Habit.

The genus *Conostylis* is restricted to a small area in south-western Australia where it is a conspicuous member of the Liliiflorae in all but the wettest vegetation communities.

In habit, there is extreme diversity between the different species. All are perennials and many have a strong capacity for vegetative reproduction which may be by means of stolons, rhizomes or a method of growth referred to by Bentham (1873) as proliferous branching. The habit may therefore be prostrate and spreading, caespitose



Text-fig. 1.—Distribution of the genus *Conostylis*. The occurrence within this area of the species dealt with in the present paper is indicated in Table 2.

or almost shrubby, some plants attaining a height of 50–60 cm. There is nearly always a large amount of sclerenchyma in the leaves, stems and roots, and a number of species bear harsh spines on the leaf margins. The flowers and flowering scapes of practically all species bear a dense, woolly tomentum of branched trichomes.

Materials and Methods.

The data presented have been derived from foliar cross sections prepared largely from fresh material fixed in the field, although some species have, of necessity, been studied from herbarium material; in the latter case leaves were boiled in water for a few minutes before being sectioned. Measurements on specimens, part of the leaves of which were fixed fresh, while the remainder was thoroughly pressed and dried, showed that the maximum shrinkage likely in dried herbarium material was of the

order of 10% (linear measurement) compared with fresh specimens. On boiling for a few minutes the original size was restored.

Difficulties were encountered in attempts to microtome this material, probably due to the extremely fibrous nature of the leaves of most species. Satisfactory hand sections were obtained and were stained with safranin and fast green (Johansen, 1940) and made permanent.

Camera lucida drawings were employed throughout.

GENERAL STRUCTURE.

The chief feature of taxonomic importance is the disposition of sclerenchymatous tissue in the vicinity of the vascular bundles. By considering, in addition, lignification of the epidermal cell walls, presence or absence of tannin-containing cells, occurrence of large subepidermal cavities, leaf shape and the occurrence of surface hairs and protuberances, it has been possible to identify the twelve species dealt with here.

A developmental feature of interest lies in the origin of the two surfaces of the lamina. Although exhibiting, in cross section, a structure similar to that of an isobilateral leaf, such as is found in species of *Eremophila* or *Eucalyptus*, the disposition of the conducting tissues in the mature leaf of *Conostylis* has resulted from the ontological fusion of the two halves of the plicate sheathing base (Text-fig. 24). By this process the adaxial surface has been highly reduced and the two lateral surfaces of the mature part of the leaf are each abaxial. Arber (1925) has described this phenomenon in *Romulea*, *Galaxia* and some other monocotyledonous genera.

Because almost the entire leaf surface is abaxial, some difficulty arises in describing the orientation of structures within the leaves. For the purpose of this study the terms upper or lower are abandoned in referring to the leaf surfaces; instead, structures in the vicinity of either epidermis will be referred to as *outer*, while by the *inner* part of the leaf will be meant the region near the imaginary line of fusion of the two halves of the lamina.

HISTOLOGY.

Epidermis.

Typical cells are more or less isodiametric, having a diameter of 20–30 μ ; the largest observed were about 80 μ in diameter. The cell walls are commonly heavily lignified and are often tangentially compressed (Text-fig. 12), but sometimes are thin and parenchymatous.

The thickening material appears to be lignocellulose, said to be a "relatively infrequent component of epidermal walls" (Linsbauer, quoted by Esau, 1953). Several species show stratification in the walls (Text-fig. 14). Pit pairs are frequently seen, particularly on the inner tangential and the radial walls. The cuticle is commonly 1–2 μ thick. Stomata are usually neither deeply sunken nor exserted; exceptions are mentioned specifically below.

The determination of stomatal frequency from the examination of leaf-reconstructions from cross sections might prove easier than from surface counts which, in this genus, are hampered by the presence of hairs and ridges on the leaf surface in some species. Measurements of stomatal frequency and size of guard cells are of interest in the case of *C. setigera*, which is thought to be a polyploid derivative of *C. setosa* (Green, 1958).

Multicellular trichomes arise from the laminar epidermis of some species, while in others marginal spines or setae consist of fibrous outgrowths of the epidermis. The leaf blade trichomes are of the branched candelabra type (Esau, 1953) (Text-fig. 2), while the marginal spines or setae may be minutely branched on the upper side or entire.

Palisade.

In the present paper the term *palisade* is used to denote the principal (and usually palisade-like) photosynthetic tissue of the mesophyll. The term *storage parenchyma*

TABLE I.*

	Number Examined.	Typical Locality.	Other Localities.	Cuticle Thickness. (μ)	Epidermal Cells.	Palisade Cells.		Storage Parenchyma Cells.
						Radial.	Tangential.	
1. <i>C. stylitoides</i>	2	North of Geraldton.	East of Geraldton.	—	15	30	12	45
3. <i>C. candidans</i>	4	Nedlands.	Rottnest Island.	—	15-20	30	15	35
4. <i>C. setosa</i>	2	National Park.	Kalamunda.	1	10	40	10	40-50
5. <i>C. androstemma</i>	3	Kalamunda.	—	1.7	45×15	45	15	70
6. <i>C. petrophaloides</i>	1	Newdegate.	—	2.5	80×20	30	10	40-80
7. <i>C. vaginata</i>	2	North of Hopetoun.	Near Hopetoun.	4	30×15	50	15	20-80
8. <i>C. setigera</i>	4	King's Park.	Medina.	1.2	14	38	12	45
9. <i>C. juncea</i>	3	Bassendean.	Applecross.	2.3	15-20	34-45	15	30-60
10. <i>C. beatiana</i>	2	Esperance.	—	2	20	30	10	30-100
11. <i>C. caricina</i>	4	Near Toodyay.	—	2.3	60×30	50	10	70-80
12. <i>C. aculeata</i>	11	East of Geraldton.	North of Geraldton, Darling Range, South-west.	3.5	10	30	12	20-30

* All dimensions are of average cell diameters in μ . For cells showing considerable variation from the mean the extreme range is shown; for cells which are markedly anisodiametric in transverse section the radial and tangential diameters are joined by the sign x.

is used to refer to the remaining tissue of the mesophyll, exclusive of the vascular tissue. It may or may not contain chloroplasts and is only rarely spongy.

The palisade consists typically of 2 layers of cells about $15 \times 7\mu$, occurring directly beneath the epidermis on both sides of the leaf. It may be in the form of a continuous band around the leaf or it may be interrupted by girder-like masses of sclerenchyma surrounding the vascular bundles and extending on the outside to the epidermis. In *C. aculeata*, whose leaves are characteristically of the interrupted type in the mature state, inspection of soft vigorous regrowth following a fire revealed an uninterrupted palisade.

In one species, *C. juncea*, large subepidermal parenchymatous cells have been observed within the palisade. These cells are ovoid in both cross section and longitudinal section, are much larger than the palisade cells, and have occurred regularly in all leaves examined (Text-fig. 18).

The cells of the palisade are thin-walled and the tissue may either be sharply demarcated from or merge indistinctly into the storage parenchyma.

Storage Parenchyma.

The storage cells are usually more or less isodiametric with slightly thickened walls and the intercellular spaces inconspicuous. Sometimes the storage parenchyma appears spongy with small, regular intercellular spaces (Text-fig. 18).

Chloroplasts are found usually in diminished numbers toward the inside of the leaf, but rarely are almost as dense as in the palisade (Text-fig. 4). Cells with darkly-staining contents, presumably phlobaphene, an oxidation product of tannins (Johansen, 1940), occur prominently in the storage parenchyma and sometimes in the palisade (Text-fig. 20 and 25). These cells appear pale to dark brown in unstained sections and almost black with safranin and fast green; their presence appears characteristic of five species (Table 2).

Vascular Tissue.

Almost without exception, the most striking feature of the vascular bundles is the occurrence of large areas of sclerenchyma associated with the conducting tissues. In many cases the conducting elements are completely surrounded by a *mestom* sheath (Schwendener, quoted by Esau, 1953); sometimes the fibres immediately adjacent to the phloem have a distinctive appearance (smaller lumen and differential stainability).

Often the *mestom* sheath is in turn surrounded by a prominent parenchymatous sheath which may be entire or broken where the phloem fibres extend outward to join the epidermis (Text-fig. 6 and 12 resp.).

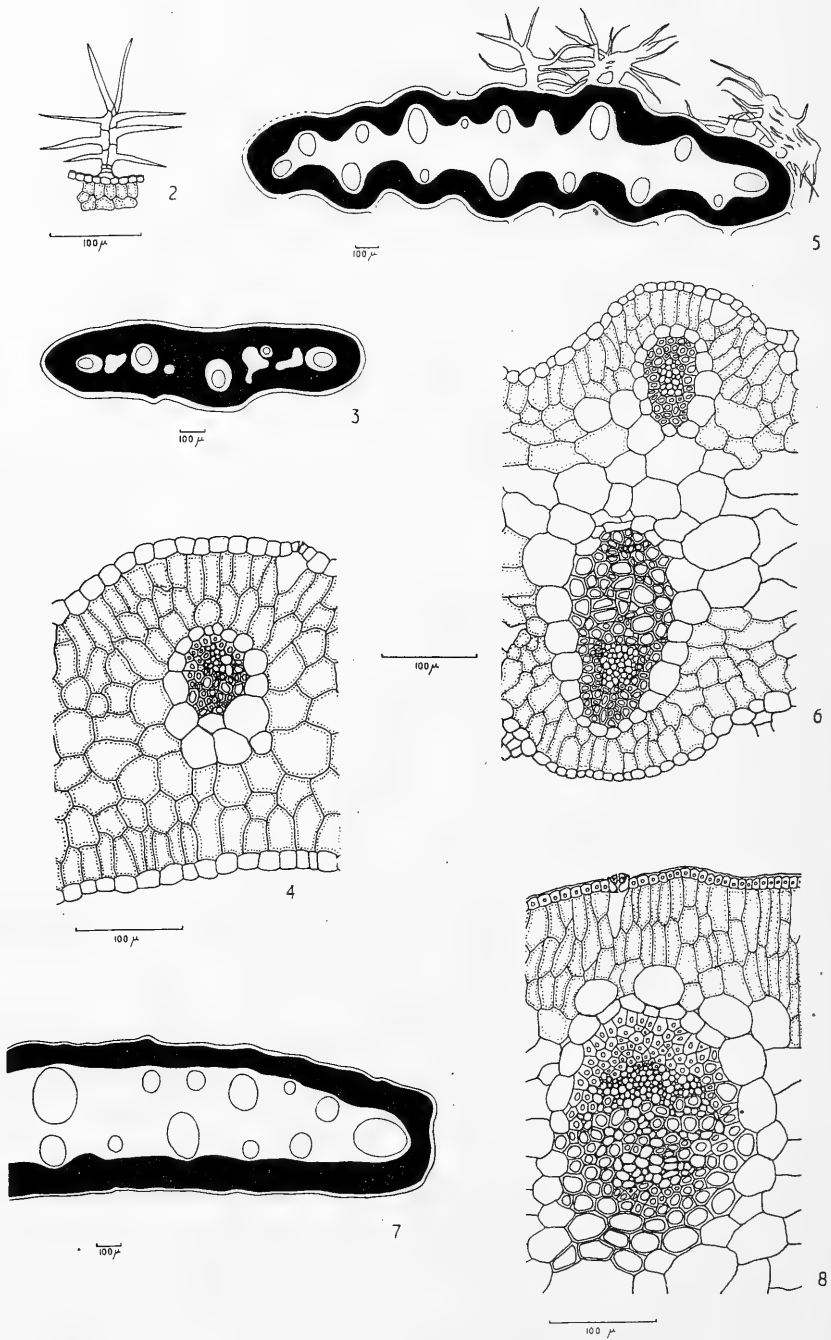
The cells of the xylem and phloem call for no special comment. Phloem has been observed clearly in sections cut from herbarium specimens more than fifty years old, its preservation evidently being due to the protection of the fibrous sheath.

The vascular bundles occur in two rows in the flat leaves, often with larger and smaller bundles alternating (Text-fig. 5). As a result of the developmental fusion of the sheathing leaf base, the bundles are oriented with the phloem toward the outside. In one species, *C. aculeata*, the larger bundles are united in pairs in the girder-like mass of sclerenchyma (Text-fig. 25), while in another, *C. setigera*, three bundles are commonly united within a mass of sclerenchyma which does not reach the epidermis (Text-fig. 16).

SPECIFIC ANATOMICAL DESCRIPTIONS.

In the following descriptions, twelve species have been chosen as being representative of the main types of anatomical structure observed in the genus. The names of other species whose anatomy is essentially similar are appended to each description. The arrangement is approximately in order of increasing degrees of xeromorphism, as inferred from the disposition of the sclerenchyma, presence of tannin cells, leaf tomentum and form and other minor characters (Table 1).

The descriptions are based on single preparations, chosen as typical of the species as a result of the examination of leaves from as many localities as possible. In most



Text-fig. 2-8.—In the low-power diagrams the palisade is shown in black and the vascular bundles in outline. 2, *C. candidans*, a small but otherwise typical example of a candelabra-type trichome; 3-4, *C. stylidioides*; 5-6, *C. candidans*; 7-8, *C. setosa*.

cases leaves from 3 or 4 localities throughout the range were examined in conjunction with the particular leaf described below, but in some cases only one specimen was available; the details are set out in Table 1. The dimensions of component cells found to be most variable are shown, with measurements from a typical preparation.

1. *CONOSTYLIS STYLLIODES* F. Muell. (Text-fig. 3-4.)

This species is almost alone in the genus in its paucity of the xeromorphic characters so common in most other species, although a loose tomentum can occur on the leaf surface in plants from some parts of the range (notably to the west of Geraldton). The remarkable absence of lignification is reflected in the flaccid nature of the leaves.

Epidermal cells are thin-walled and isodiametric; the stomata, if anything, are slightly exerted. The palisade merges indistinctly into the storage parenchyma. The number of chloroplasts in the storage parenchyma is scarcely less than in the palisade, except for an ill-defined zone of central cells which contain no chloroplasts. The vascular bundles are scarcely strengthened, the inner sclerenchymatous sheath being reduced to very few (5-8) fibres in most cases. The cells of the parenchymatous sheath are slightly more regular than those of the storage parenchyma and contain no chloroplasts. *C. prolifera* Benth., *C. racemosa* Benth.

2. *CONOSTYLIS SEORSIFLORA* F. Muell.

Similar to the above, except for the presence, in the single specimen examined, of lignified walls in the epidermal cells immediately adjacent to the vascular bundles. The remainder of the epidermis is parenchymatous.

3. *CONOSTYLIS CANDICANS* Endl. (Text-fig. 5-6.)

A prominent anatomical feature of the leaves is the presence of large, multicellular, branched trichomes arising from the epidermis. These give the leaf its characteristic mealy appearance in surface view.

Epidermal cell walls are unligified and the cells are more or less isodiametric; from the epidermis arise numerous candelabra-type trichomes similar to those occurring on the scape and perianth of most species (Text-fig. 2). These consist of a central axis of 4 longitudinal series of cells; the lower 1-2 layers bear no projections, but the 3-4 above bear aciculate protuberances in each of 4 directions, approximately at right angles to the axis. The phloem is capped by 3-4 layers of fibres which occasionally become produced outward to the epidermis, interrupting the palisade. A parenchymatous outer sheath occurs prominently. *C. dealbata* Lindl.

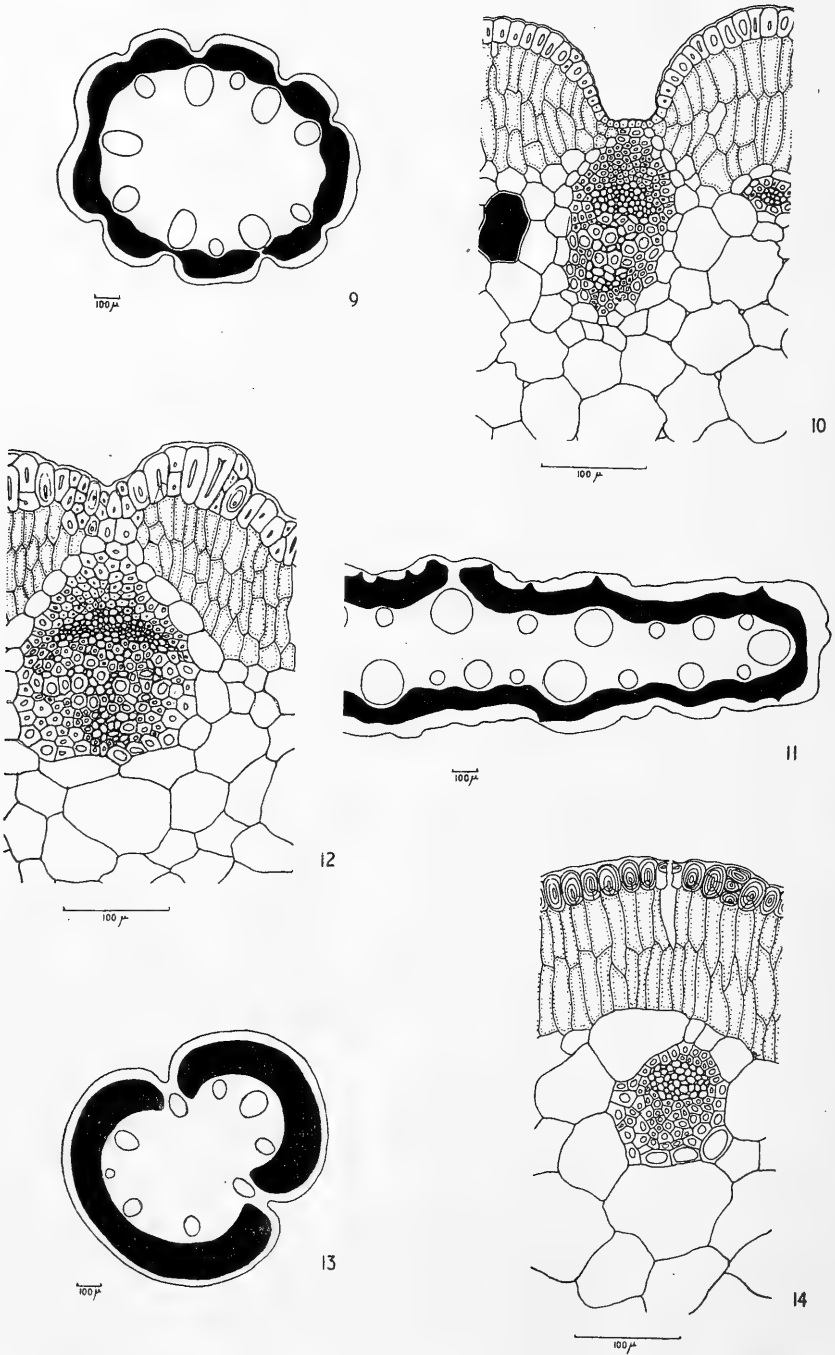
4. *CONOSTYLIS SETOSA* Lindl. (Text-fig. 7-8.)

No single outstanding feature characterizes this species. The leaf is more rectangular in section than in other species, the palisade is uninterrupted and pairs of bundles occasionally may be more or less united by the fusion of their fibrous sheaths on the inside.

The epidermis consists of isodiametric cells having lignified walls and a small lumen. The palisade is continuous and clearly demarcated from the storage parenchyma whose cells may be more or less spongy, with very few chloroplasts. The vascular bundles are each surrounded by a fibrous sheath, in turn surrounded by a parenchymatous sheath, except in the rare cases when the fibrous sheaths of two opposite bundles coalesce.

5. *CONOSTYLIS ANDROSTEMMA* (Lindl.) F. Muell. (Text-fig. 9-10.)

Leaves of this species are more or less circular in section with deep, longitudinal grooves. By comparing Text-figures 9 and 21 it may be seen that such grooves may occur opposite (i.e., on the same radius) or between the major bundles, in different species. Further observations will be necessary to confirm the taxonomic value of this character, which appears uniform in the species examined. The sole exception



Text-fig. 9-14.—9-10, *C. androstemma*; 11-12, *C. petrophiloides*; 13-14, *C. vaginata*.

occurs in an undescribed subspecies of *C. androstemma*, geographically removed from the typical subspecies here described and illustrated, in which the grooves of the single specimen examined were between the major bundles. Tannin cells occur in the storage parenchyma.

Epidermal cells are anisodiametric, with walls heavily lignified. In some places the space normally occupied by one epidermal cell is occupied by two or three, one above the other. This condition will be referred to by the term *multiple epidermal cells*; in no way does it refer to a hypodermal layer, being restricted to the occurrence of multiple cells in an otherwise single-layered tissue (Text-fig. 10, 12, 14, 18, etc.). The palisade tissue merges into the storage parenchyma whose cells do not appear spongy in spite of small regular intercellular spaces. Many storage cells adjacent to the palisade may contain deposits of tannin; one section showed 11 tannin-containing cells in the outer storage parenchyma. The usual fibrous and parenchymatous sheaths surround the bundles, the latter less prominently than in many other species. The fibrous sheath of the larger, alternate bundles often penetrates the palisade to join the epidermis.

6. CONOSTYLIS PETROPHILOIDES F. Muell. ex Benth. (Text-fig. 11-12.)

A particularly heavily lignified epidermis occurs in this species. Striations, multiple cells and pits are characteristic. The palisade is practically continuous.

The epidermal cells are markedly anisodiametric, being greatly compressed tangentially. The cell walls are lignified, striated and pitted and the cells contain, as a rule, a small compressed lumen. Multiple cells are very common. Stomata are slightly exerted. The palisade lies in a practically continuous band and is clearly demarcated from the adjoining tissues. The storage parenchyma cells do not appear spongy and do not contain chloroplasts. The conducting tissues are immediately surrounded by several layers of fibres, in turn surrounded by a parenchymatous sheath which is rarely broken.

7. CONOSTYLIS VAGINATA Endl. (Text-fig. 13-14.)

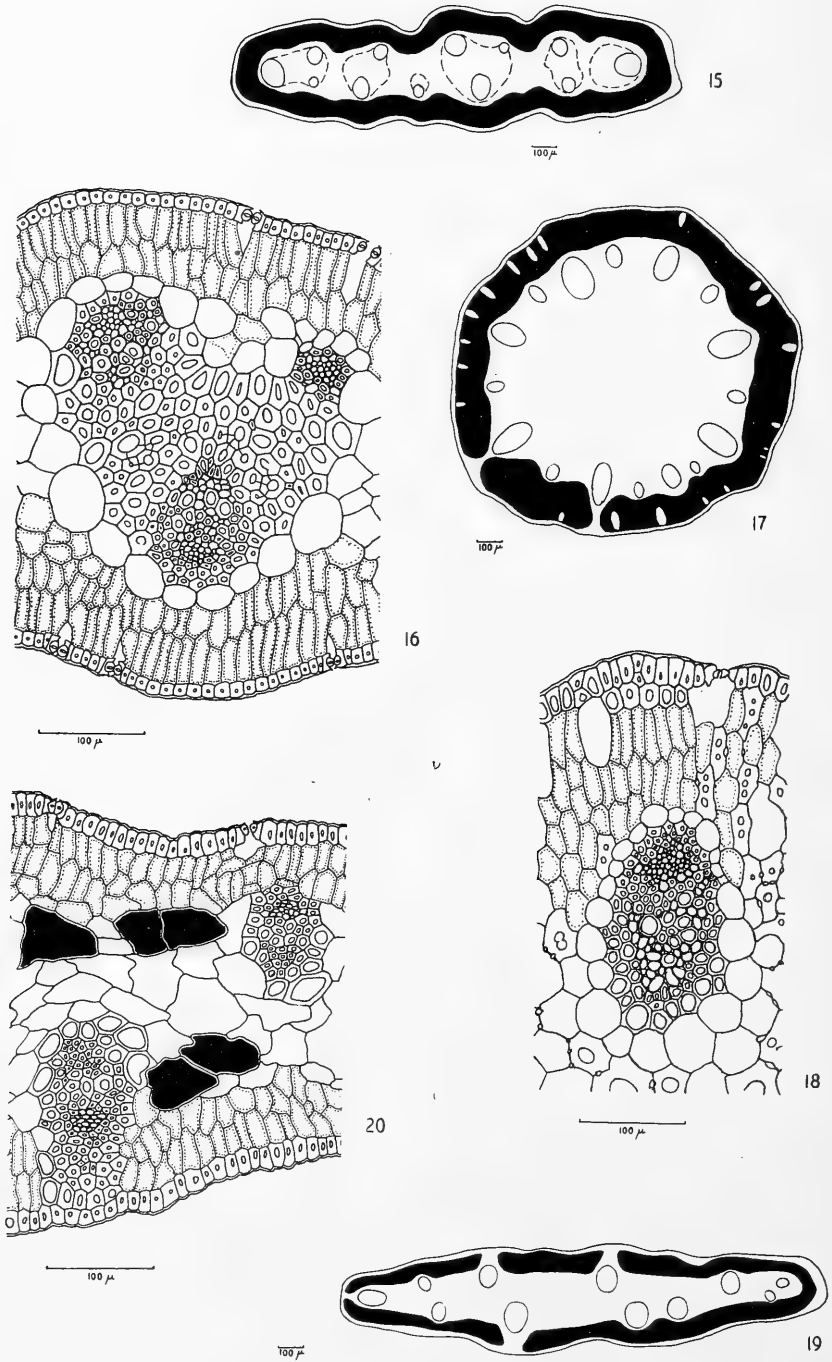
The leaves are more or less circular in section and the palisade is often in a continuous band. When the palisade is interrupted, the epidermis is deeply grooved at the point of interruption (Text-fig. 13). Epidermal cell walls are heavily lignified, striate and pitted, and multiple cells occur infrequently.

Epidermal cells are anisodiametric with occasional multiple cells. The walls are heavily lignified, with prominent striations and pits on the inner tangential and radial walls. The palisade forms a very regular band, sharply distinct from the storage parenchyma which contains no chloroplasts. The vascular bundles are each surrounded by a fibrous and a parenchymatous sheath, the latter not well defined and occasionally broken by the fibrous sheath when it is produced outward to the epidermis.

8. CONOSTYLIS SETIGERA R.Br. (Text-fig. 15-16.)

A large area of fibres often encloses three vascular bundles and the palisade is always continuous. These features produce an appearance in this species (and its relatives, *C. melanopogon* and *C. psyllium*) quite unlike that in any other species in the genus.

Epidermal cells are small and isodiametric with the walls heavily lignified. The palisade is regular and continuous and the storage parenchyma, small in extent, contains chloroplasts. Each fibrous bundle sheath encloses, typically, three vascular bundles; the sheath is usually one cell thick on the outside of the bundles, but the whole of the more or less triangular region within the three bundles consists of a mass of fibres. Pit pairs occur in the walls of many of these cells. The individual bundles are smaller than in many other species. A prominent parenchymatous sheath surrounds each group of three bundles and its fibrous matrix. *C. melanopogon* Endl., *C. psyllium* Endl.



Text-fig. 15-20.—15-16, *C. setigera*; 17-18, *C. juncea*; 19-20, *C. bealiana*.

9. *CONOSTYLIS JUNCEA* Endl. (Text-fig. 17-18.)

This species is distinguished by the presence of large subepidermal cells bearing a superficial resemblance to substomatal chambers. The storage parenchyma cells have intercellular spaces which give this tissue an appearance unlike that of any other species examined.

Epidermal cells are anisodiametric with occasional multiple cells, and the cell walls are heavily lignified. The palisade contains prominent subepidermal cells which are ovoid in both transverse and longitudinal section; however, the reliability of this as a taxonomic character cannot be estimated until the exact nature and constancy of the cells is known. They occur irregularly around the leaf, 20 being counted in one typical section. The palisade for the most part is continuous, but is usually interrupted at one or two places by the outward extension of the fibrous bundle sheath; it merges into the storage parenchyma, the cells of which resemble somewhat the typical spongy mesophyll found in the leaves of many genera, e.g., *Lilium*. Small regular intercellular spaces may be seen both in section and surface view of the cell walls. The vascular bundles are each surrounded by a fibrous sheath which may protrude through the outer, enclosing parenchymatous sheath, to join the epidermis.

C. involucrata Endl.—Note: Flat-leaved forms of *C. juncea*, placed under *C. involucrata* by Bentham (1873), cannot be maintained as a separate species, since terete and flat leaves occur frequently on a single plant. The anatomical structure of the flat leaves retains the spongy parenchyma and the subepidermal cells described above, although the general pattern resembles a flat-leaf type such as *C. bealiana* (Text-fig. 19-20).

10. *CONOSTYLIS BEALIANA* F. Muell. (Text-fig. 19-20.)

Many prominent tannin-containing cells occur in the storage parenchyma of the leaves of this species. The palisade is well defined and interrupted by many of the fibrous bundle sheaths which extend to the epidermis.

Epidermal cells are isodiametric with heavily lignified walls. The palisade consists typically of 2 cell layers which are sharply distinct from the storage parenchyma. The storage cells contain no chloroplasts; they are irregular in shape in the only specimens examined, but there is no reason to believe that this is due to distortion arising from the preparation of the herbarium specimens used, since this appearance was not seen in other species where comparison between living and herbarium material was possible. The outermost cells of the storage parenchyma are frequently very large and contain tannin-like deposits; no chloroplasts occur in this tissue. The vascular bundles are surrounded by a fibrous sheath which often penetrates the surrounding parenchymatous sheath to join the epidermis.

11. *CONOSTYLIS CARICINA* Lindl. (Text-fig. 21-22.)

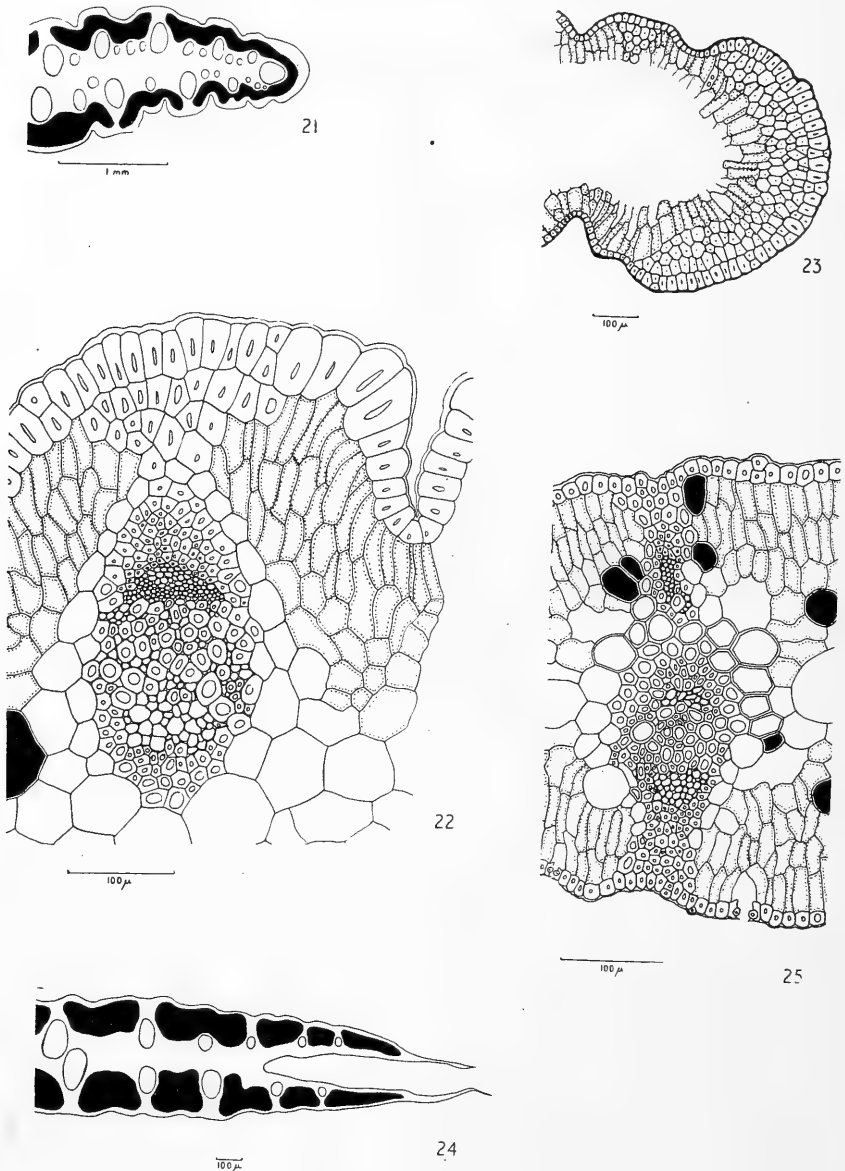
The leaves are characterized by their large cross sectional area, the presence of tannin cells in the storage parenchyma and an extremely heavily thickened epidermis.

Epidermal cells are tangentially compressed, larger than in all other species, with heavily lignified walls; multiple cells occur infrequently. Stomata are confined to grooves in the epidermis. The palisade is deeper and consists of more layers of cells than in the other species; it occurs in a well-defined layer merging into the storage parenchyma. Tannin cells occur infrequently in the outer cell layers of the storage parenchyma. The vascular bundles are each surrounded by a fibrous sheath which, in many bundles, penetrates the parenchymatous sheath, interrupting the palisade, to join the epidermis.

12. *CONOSTYLIS ACULEATA* R.Br. (Text-fig. 23-25.)

The most prominent feature of the leaves of this species is the occurrence of girder-like masses of sclerenchyma, across the whole width of the section, from epidermis to epidermis, enclosing usually two vascular bundles. Several layers of heavily lignified hypodermal fibres occur at the margins.

Epidermal cells are isodiametric with heavily lignified walls; the epidermis is frequently undulate with grooves occurring between the vascular girders (see discussion under *C. androstemma*) or the epidermis may be more or less flat. At the margins



Text-fig. 21-25.—21-22, *C. caricina*; 23, Hypodermal fibres in a form of *C. aculeata*; 24-25, *C. aculeata*, the low power diagram showing the plicate sheath near the base of the leaf.

occur several to many layers of hypodermal fibres (Text-fig. 23). It is upon this last character that the species *C. bromelioides* is based; in this species the thickening is sufficiently heavy to be conspicuous exomorphically. The palisade is much dissected by the vascular girders; it merges into the storage parenchyma, cells of which contain chloroplasts and frequently tannin. The parenchymatous bundle sheath is reduced to a single layer of cells on each side of the fibrous girder. The girder structure is developed most strongly in certain related species such as *C. robusta* and *C. bracteata*;

in all cases it represents the coalescence of two fibrous bundle sheaths when the bundles are heavily strengthened and occur directly opposite one another. *C. breviscapa* R.Br., *C. bracteata* Lindl., *C. bromelioides* Endl., *C. preissii* Endl., *C. harperiana* W. V. Fitzg., *C. teretiusscula* F. Muell., *C. spinuligera* F. Muell. ex Benth., *C. serrulata* R.Br., *C. laxiflora* Benth., *C. cymosa* F. Muell. ex Benth., *C. phathyrantha* Diels.

DISCUSSION.

Ecology and Geographical Distribution.

Attempts to correlate anatomical features of the leaves of *Conostylis* species with geographical and ecological ranges have proved disappointing. Table 2 shows that when the species are arranged according to the degree of development of xeromorphic characters the leaf anatomy does not reflect the influence of the present environment. Of the two species which never occur on sand (*C. setosa* and *C. caricina*) no characters

TABLE 2.

	Epidermal Cell Walls Lignified.	Palisade Interrupted.	Bundles United.	Tannin Cells Present.	Terete Leaves.	Laminar Trichomes.	Soil Types.*	Distribution.†	Annual Average Rainfall (cm.)
1. <i>C. styliidioides</i> ..	-	-	-	-	-	-	S-C	CW-NW	25-50
2. <i>C. seorsiflora</i> ..	+	-	-	-	-	-	S	S-SE	50-75
3. <i>C. candicans</i> ..	-	-	-	-	-	+++	S-C	CW-NW	25-100
4. <i>C. setosa</i> ..	+	-	-	-	-	-	C	CW	100
5. <i>C. androstemma</i> ..	+	±	-	+	+	-	S	CW	37
6. <i>C. petrophiloides</i> ..	+	±	-	-	-	-	S	C-SE	25-50
7. <i>C. vaginata</i> ..	+++	±	-	-	+	-	S	S-SE	45-50
8. <i>C. setigera</i> ..	+	-	+++	-	-	-	S-C	S-SW-CW	75-100
9. <i>C. juncea</i> ..	++	±	-	±	±	-	S	CW	75-100
10. <i>C. bealiana</i> ..	+	++	-	+++	-	-	S	SE	50-75
11. <i>C. caricina</i> ..	+++	+	-	++	-	-	C	CW	100-110
12. <i>C. aculeata</i> ..	++	+++	++	+	-	-	S-C	NW-CW-SW-S	30-125

* S=sand, siliceous or calcareous; C=clay, including lateritic soils.

† Refers to the following broad areas in the South-West Vegetation Province: C=central, NW=north-west, CW=central-west, SW=south-west, S=south, SE=south-east.

of the foliar anatomy separate them from other groups of species. Of the remaining species examined the following grow commonly in sandy situations, but have been recorded also in clayey soils: *C. styliidioides*, *C. candicans*, *C. setigera* and *C. aculeata*; once again, no anatomical character or group of characters separates these out as a group. The same situation exists with regard to geographical distribution and rainfall. Anatomical characters are therefore genetically controlled and are not modified to any great extent by the environment.

Systematics.

In many cases anatomical characters have proved closely correlated with those determining systematic affinity. This is to be expected, since the exomorphic characters employed in determining species boundaries frequently reflect some internal anatomical feature. The following groups of species, shown as being anatomically related in the foregoing descriptions, are recognized by Bentham (1873) as being closely related on exomorphic characters:

1. *C. styliidioides*, *C. prolifera*, *C. racemosa*.
2. *C. candicans*, *C. dealbata*.
3. *C. setigera*, *C. melanopogon*, *C. psyllium*.
4. *C. juncea*, *C. involuocrata*.
5. *C. aculeata*, *C. bracteata*, *C. bromelioides*, *C. preissii*, *C. spinuligera*, *C. serrulata*, *C. laxiflora*, *C. cymosa*.

Key to the Species examined, based on Anatomical Characters.

1. Palisade continuous.
 2. Vascular bundles united in small groups by the bundle sheaths 8. *C. setigera*.
 - 2.* Vascular bundles discrete.
 3. Epidermal cell walls thickened and lignified.
 4. Leaves terete.
 5. Tannin cells occurring in the mesophyll.
 6. Epidermis \pm smooth; prominent subepidermal cells in the palisade 9. *C. juncea*.
 - 6.* Epidermis undulate; subepidermal cells absent 5. *C. androstemma*.
 - 5.* Tannin cells absent 7. *C. vaginata*.
 - 4.* Leaves flat.
 7. Prominent subepidermal cells in the palisade; leaves often \pm terete .. 9. *C. juncea*.
 - 7.* Palisade of chlorenchyma cells only.
 8. Margins notably square in section; subepidermal fibres absent 4. *C. setosa*.
 - 8.* Margins rounded; prominent rows of subepidermal fibres 6. *C. petrophiloides*.
 - 3.* Epidermal cell walls thin and mostly parenchymatous.
 9. Epidermal cells adjacent to vascular bundles lignified, otherwise parenchymatous 2. *C. seorsiflora*.
 - 9.* Epidermal cells entirely parenchymatous.
 10. Epidermis bearing a heavy grey tomentum of branched trichomes 3. *C. candidans*.
 - 10.* Trichomes sparse or absent on leaf surface 1. *C. styliidioides*.
- 1.* Palisade interrupted by an extension of the fibrous bundle sheaths, commonly of alternate bundles.
 11. Alternate pairs of vascular bundles united in a sclerenchymatous girder passing across the section from epidermis to epidermis 12. *C. aculeata*.
 - 11.* Vascular bundles discrete.
 12. Leaves terete.
 13. Epidermis smooth; prominent subepidermal cells in the palisade 9. *C. juncea*.
 - 13.* Epidermis undulate or grooved.
 14. Epidermis with grooves adjacent to alternate vascular bundles 5. *C. androstemma*.
 - 14.* Epidermis with one or two grooves only, adjacent to fibrous interruptions of palisade 7. *C. vaginata*.
 - 12.* Leaves flat.
 15. Tannin cells occurring in the mesophyll.
 16. Epidermal cells \pm isodiametric; palisade of 2 cell layers 10. *C. bealiana*.
 - 16.* Epidermal cells tangentially compressed; epidermis of 3 cell layers 11. *C. caricina*.
 - 15.* Tannin cells absent.
 17. Prominent subepidermal cells in the palisade 9. *C. juncea*.
 - 17.* Palisade of chlorenchyma cells only 6. *C. petrophiloides*.

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SOMATIC HYBRIDIZATION BETWEEN PUCCINIA GRAMINIS VAR. TRITICI AND
PUCCINIA GRAMINIS VAR. SECALIS.

By I. A. WATSON and N. H. LUIG, The University of Sydney.

[Read 24th June, 1959.]

Synopsis.

Somatic hybrids between *Puccinia graminis* var. *tritici* and *P. graminis* var. *secalis* have been obtained under glasshouse conditions. Their pathogenic properties combine those of their parental strains. It is suggested that somatic hybridization between the two varieties of *P. graminis* may play a role in the origin of new strains of wheat stem rust in the field.

It has now been well established that when certain selected cultures of *Puccinia graminis* Pers. var. *tritici* (Eriks. and E. Henn.) are mixed in the uredial stage on plants of the appropriate graminaceous host, hybridization will readily occur (Watson, 1957; Watson and Luig, 1958). It has been shown that under Australian field conditions certain pathogenic strains of *P. graminis* var. *tritici* could have arisen as somatic hybrids between previously existing strains (Watson & Luig, 1958). Since *P. graminis* var. *secalis* is widespread throughout Tasmania and was found from widely separated areas of the eastern Wheat Belt of Australia in 1958, the possibility of somatic hybrids occurring between this organism and *P. graminis* var. *tritici* has been studied. It is well known (Stakman *et al.*, 1930) that these two varieties of *P. graminis* will hybridize sexually on the barberry.

TABLE 1.

Reaction Types of Twelve Wheat Varieties, Rye and Agropyron repens to Parental Strains of P. graminis and Two Hybrids between Them.

Variety.	Parents.		Hybrids.	
	Red <i>P. graminis</i> var. <i>secalis</i> 57241.	Orange <i>P. graminis</i> var. <i>tritici</i> NR 2.	M9-a.	M10-a.
Little Club	:1, 2-	4	3 ^c	3 ^{c+}
Marquis	;	3+	:2 [≡]	x, 2++
Reliance	0	3+	0	0
Kota	0;	3	0;	0;
Arnautka	0;	0;	0;	0;
Kubanka	0;	X	0;	0;
Acme	0;	0;	0;	0;
Einkorn	:1-	3+	3- ^c	3-
Vernal	;	3+	:1+	3
Khapli	0;	;	0;	0;
Yalta (Sr 11, Sr 12)	;	3+	3	:1,2 [≡]
Morocco W1103 ..	:1	3+	:1	3+
Black Winter Rye ..	1+,2,3+	:1=	1,2,3+	1,2,3+
<i>Agropyron repens</i> ..	2	0;	0;	0;

Using single spore cultures of red *P. graminis* var. *secalis* (accession number 57241; from Gosford, N.S.W.) and orange NR-2 (Watson, 1957) and adopting the same crossing procedures as previously outlined (Watson, 1957), two different somatic hybrids were obtained from several mixtures. The reactions of these hybrids on varieties of Table 1 which have been stable over several generations are clearly distinguished from those of any existing Australian strain of *P. graminis*. M9-a, for

example, which attacks Yalta is avirulent on Morocco, usually a very susceptible variety. Emmer is susceptible to M10-a, but Kota resistant, and we have not previously found that combination in any one strain. Moreover, both strains, although they do not produce a very susceptible reaction on Black Winter Rye, are more virulent on rye than are the parental strain NR-2 and other strains of *P. graminis* var. *tritici*. *Agropyron repens*, which is susceptible to *P. graminis* var. *secalis*, is resistant to both strains M9-a and M10-a and Little Club is not fully susceptible to either. Hence the two hybrids may be considered more or less intermediate in their parasitic properties between those of their parental varieties of *P. graminis*.

DISCUSSION.

There is considerable significance in these results from the point of view of breeding for stem rust resistance. Since from this cross a hybrid was derived having virulence on Vernal Emmer there seems no reason why such intervarietal crosses would not produce hybrids capable of rendering ineffective other genes now used as sources of rust resistance. In this regard *P. graminis* var. *secalis* must be considered as an avirulent strain of *P. graminis* var. *tritici*.

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DIPTERA OF KATOOMBA. PART 3.
STRATIOMYIIDAE AND TACHINIDAE.

By G. H. HARDY.

[Read 24th June, 1959.]

Synopsis.

Synonymy is recorded and four species that have not previously been found in New South Wales are given under Stratiomyiidae. Characters and synonymy are discussed for some variable Australian Tachinidae and include three specific names in genus *Actia*, four generic synonyms under *Aprotheca*, which include seven specific names placed as synonyms, and six names are excluded from the generic conception adopted. Keys are given to aid in identifying the species of *Odontomyia*, *Actia* and *Aprotheca*.

STRATIOMYIIDAE.

Foreword.—Previous records from the Blue Mountains of New South Wales are *Metoponia gemina* Hardy, from Leura, *Ophiodesma flavipennis* Macq., Blackheath, and *Odontomyia opertanea* White, recorded in Hardy 1920, 1932 and 1938. A record of a species of *Chiromyza* from Blackheath is mentioned in Hardy 1924, but no more specimens have been found.

Eye coloration.—Taxonomists take advantage of the colour patterns in the eyes of Diptera wherever this feature occurs, and use it as an aid towards specific isolation. Occasionally the pattern is found to be unstable, but conforming in its variation within a sequence of development that reaches a maximum that is the typical form for the species. Some recorded colour patterns are given in Hardy 1938 and 1939, and in the latter paper, the scheme adopted for describing the patterns is given. More of these colour patterns are recorded below.

References.—Earlier papers give references to species and those are not repeated below, only subsequent references being added here.

BOREOIDES SUBULATUS Hardy.

Hardy, 1920, *Proc. Linn. Soc. N.S.W.*, 45: 540; 1924, 49: 364. Kershaw, 1926, *Vict. Nat.*, 43: 159.

Hab.—Leura: 12 April 1953. This species is stated to infest a garden regularly every autumn, and some specimens and eggs were transferred to my garden at Katoomba, but failed to become established.

ACTINA BREVIHIRTATA Hardy.

Hardy, 1932, *Proc. Roy. Soc. Qland*, 44: 42.

Hab.—Katoomba; 31 males, 30 females. The earliest date in any year is 22nd September 1955, and the last 27th March 1958. Many specimens were on an old compost heap that was covered by a dense growth of a weed (*Ranunculus*) during January 1959.

Described from Queensland, this record is the first from New South Wales.

ACTINA INCISURALIS Macq.

Hardy, *Proc. Roy. Soc. Tasm.*, 1920, pp. 40-1; 1932, *Proc. Linn. Soc. N.S.W.*, 43: 53-4. Fuller, 1934, *Proc. Linn. Soc. N.S.W.*, 59: 190-6.

Hab.—Katoomba; this common species is occasionally seen.

NEOEXAIRETA SPINGERA Wiedemann.

Hardy, *Proc. Roy. Soc. Tasm.*, 1920, pp. 42-3; 1939, *Proc. Linn. Soc. N.S.W.*, 64: 37. Malloch, 1928, *Proc. Linn. Soc. N.S.W.*, 53: 361-2.

Hab.—Katoomba; very abundant.

DAMAROMYIA NITENS Hardy.

Hardy, 1931, *Ann. Mag. Nat. Hist.* (10), 8: 125.

Hab.—Katoomba; 1 male, 1 female, 20th and 19th November 1953 respectively.

On the male the eyes were reflecting red-green, and the female had in addition a red bar at antennal level.

DAMAROMYIA TASMANICA Kertesz.

Hardy, 1931, *Ann. Mag. Nat. Hist.* (10), 8: 125-6. James, 1950, *Proc. Ent. Soc. Washington*, 52: 312-5.

Hab.—Katoomba; 1 female, 19 November 1957.

DAMAROMYIA CLIVOSA Hardy.

Hardy, 1931, *Ann. Mag. Nat. Hist.* (10), 8: 128.

Hab.—Katoomba; 1 male, 8 January 1958; 1 female, 2 February 1959. Known previously from Brisbane to Sydney, the present record at over 3000 feet suggests that the species will be found widely distributed southwards into Victoria.

Normally this species has the scutellum raised 30° to the plane of the thorax. Contrary to a prior statement (Hardy, 1950) within this genus the scutellum does articulate, rising and falling with the wing motion. The tests were made with the flat type of scutellum, and now these two specimens were tested for the raised scutellum. In both cases tests showed a considerable stiffness existed, especially on this female, and it became necessary to depress the scutellum; then the wing action became apparent.

ACANTHASARGUS PALUSTRIS White.

Hardy, *Proc. Roy. Soc. Tasm.*, 1920, p. 48.

Hab.—Katoomba; 8 males, 4 females, November to January during the years 1951 to 1959. Described from Tasmania, this record is the first from the mainland of Australia.

When alive the eyes showed, in accord with age at time of capture, red-green reflections that developed red above antennal level and entirely green below, thence green above also, leaving a red bar just above antennal level. A silvery sheen of the abdomen on the male is seen from the front and side views.

ACANTHASARGUS FLAVIPES Hardy.

Hardy, 1932, *Proc. Roy. Soc. Qland*, 44: 48-9.

Hab.—Katoomba; 1 male, 23 December 1955. Described from Queensland, this record is the first from New South Wales.

OPHIODESMA FLAVIPALPIS Macq.

Hardy, 1932, *Proc. Roy. Soc. Qland*, 44: 44.

Hab.—Katoomba; 4 males, 2 females and several others of inferior condition. September to November, 1957 and 1958.

One male had two red bars below and one above antennal level, and above these was a blotch mixed red and green, each reflecting strongly in accord with the direction of light. A female had a red blotch both above and below the two central bars, and the red area on a third specimen was reduced to two bars both above and below antennal level. These differ considerably from eye markings of the allied species *O. innoda* Hardy 1932.

Genus ODONTOMYIA Meigen.

So variable are the characters of two common Australian species, that it proved impossible to discover features that may distinguish between some forms given specific names. There is a trend in any single breeding area to yield a definite variant which may be an ecological form, but long series collected over wide areas are found to have characters grading from one described form to another. White (1916) recognized

these four, but separated *carinifacies* on colour marks and the style of the antennae being attenuated, stating the species appears to be scarce. The attenuated antennal style is an abnormality sometimes found on both sexes in a long series collected from a single area. It has been found from Tasmania to New South Wales, and probably is commonest in colder regions of these States.

Key to species of Odontomyia.

1. Scutellar spines curved to become upwardly directed 2.
- Scutellar spines straight, lying horizontally in continuity with the scutellum 3.
2. Scutellar spines arising subapically from beneath the scutellum *opertanea* White.
- Scutellar spines arising from the apical margin of the scutellum *scutellata* Macq.
3. Abdomen with the dorsal area black with green or yellow side spots varying in size; when large they are generally confluent at the lateral margin *hunteri* Macleay.
- Abdomen with dorsal area black centrally, with a lateral green or yellow border, varying in width *decipiens* Guérin.

ODONTOMYIA DECIPENS Guérin.

Oxycera decipiens Guérin 1838. Hardy, 1938, PROC. LINN. SOC. N.S.W., 63: 70.

Synonymy.—*amyris* Walker 1849, *annulipes* Macquart 1849, *ialmenus* Walk. 1849, *kirchneri* Jaennick 1867, *marginella* Macq. 1849, *pectoralis* Thomson 1869, *picea* Walk. 1850, *regisgeorgii* Macq. 1838, *rufifacies* Macq. 1849, *stylata* Macq. 1847, *subdentata* Macq. 1849.

O. pallida Hill, 1919, PROC. LINN. SOC. N.S.W., 44: 456, is a new synonym.

Hab.—Although widely distributed over coastal and lowland areas of Australia, this species is unknown from the mountains of New South Wales.

Hobart; 1 female, 8 January 1955, had its eye colour reflecting red and green with a red bar at antennal level, and not quite reaching the posterior border of the eye. Above this bar the red dominated, and below it the green had the stronger reflections.

ODONTOMYIA HUNTERI Macleay.

Stratiomys hunteri Macleay 1830. *Odontomyia hunteri* Hardy 1938, PROC. LINN. SOC. N.S.W., 63: 72.

Synonymy.—*Carinifacies* Macq. 1849, including var. *grandimaculata* and var. *minima* Hardy 1920, *laterimaculata* Macq. 1849, *stricta* Erichson 1842, and *sidneyensis* Schiner 1868.

O. obscura Hill, 1919, PROC. LINN. SOC. N.S.W., 44: 457, is a new synonym.

Hab.—Katoomba; 3 males, 22nd, 27th and 28th December 1955. The last, on one antenna only, had the style attenuated as on White's specimen of *carinifacies*. 2 females December 1949 and 9th November 1950, also a series of both sexes which are inferior in condition.

Tasmania; Hobart, 7th and 11th January 1955. The male has a red bar which was below antennal level near the face, and it sloped upwards. The female has a purple bar at antennal level and a large purple blotch above on the otherwise green eye. Eight other males and one female were captured in the same month, and all specimens are typical *laterimaculata* of White's interpretation.

ODONTOMYIA SCUTELLATA Macq.

Hardy, 1938, PROC. LINN. SOC. N.S.W., 63: 72.

Hab.—Katoomba; 1 male, December 1949.

References (Stratiomyiidae).

- FULLER, 1934.—PROC. LINN. SOC. N.S.W., 59: 190-6.
 HARDY, 1920.—*Proc. Roy. Soc. Tasmania*, pp. 33-64.
 ———, 1920.—PROC. LINN. SOC. N.S.W., 45: 532-542.
 ———, 1924.—*Idem*, 49: 360-370.
 ———, 1931.—*Ann. Mag. Nat. Hist.* (10), 8: 120-9.
 ———, 1932.—*Proc. Roy. Soc. Queensland*, 43: 50-5; 44: 41-9.
 ———, 1938.—PROC. LINN. SOC. N.S.W., 63: 70-4.
 ———, 1939.—*Idem*, 64: 34-40.

- HARDY, 1950.—*Ent. mon. Mag.*, 86: 230.
 HILL, 1919.—*Proc. Linn. Soc. N.S.W.*, 44: 458-462.
 JAMES, 1950.—*Proc. Ent. Soc. Washington*, 52: 312-5.
 KERSHAW, 1926.—*Vict. Nat.*, 43: 159-160.
 MALLOCH, 1928.—*Proc. Linn. Soc. N.S.W.*, 53: 361-5.

TACHINIDAE.

Foreword.—The two genera *Actia* and *Aprotheca* are parasites of Lepidoptera that were becoming of interest to economic entomology, and the endeavour to unravel the complicated features in literature concerning them was first undertaken by me when holding the Walter and Eliza Hall Fellowship in economic biology at the Queensland University (1922-34). The work was continued later, extending into the period of my retirement to the Blue Mountains of New South Wales. The experience gained from field observation on these flies, under two quite different climatic conditions, has permitted a better understanding of the genera than had been acquired before. There remains now only the confirmation, or otherwise, of identity by comparison with surviving types of the Australian Linnaemyiini in European collections, and that were described by very early authors; apparently none were described by them belonging to genus *Actia*. The synonymy given below appears to be an accurate interpretation of conclusions reached during recent researches on these genera.

Tribe ACTIINAE.

During recent years, the trend has been to amalgamate various Calyprate families into one family unit, Tachinidae, and to divide the complex formed into divisions that do not follow the traditional classification. These and other proposed classifications for the family can be regarded as tentative efforts to improve the taxonomy of the Diptera, efforts that ultimately may achieve an advancement, but at present the schemes become too elaborate in their effect to render the phylogeny of the Calypratae on a satisfactory plan. In these notes Tachinidae is a name retained in the original sense, and in this grouping it becomes divisible into three easily identified parts.

The subfamily Phasiinae has the broadly visible sternites of the abdomen; the Dexiinae has the aedeagus of the male divided into two articulating parts, the second of which is very long and slender, and finally the Tachininae incorporates the remaining genera and is divisible into tribes. All three are separated from other Calyprates that may have the strongly upturned vein M_1 , by the postscutellum which bulges below the scutellum without the concavity between them, a concavity such as seen on Calliphoridae and Sarcophagidae. The two following tribes belong to the Tachininae; the Linnaemyiini has some genera with minute palpi and, according to Malloch, only one genus of Actini occurs in Australia, and is based largely on vestiture. Vestiture is an unsatisfactory feature to use because of variability within species and leads either to assembling species into complex units or to forming monotypical genera and subgenera to accommodate the less usual forms. Already the use of it has led to much synonymy needing clarification by the aid of field observation and breeding.

Genus ACTIA Desvoidy.

Between 1929 and 1936, J. R. Malloch had recorded 14 specific names for about 70 specimens of the genus *Actia*. The characters used in antennal proportions, chaetotaxy and other features, are proving to be so variable on some species that it becomes necessary to seek new methods for determining the specific limits. It had been found necessary to reduce two of his names to synonymy under *A. darwini* Mall. (Hardy, 1938), a species that occurs abundantly around Brisbane, and below three more names are similarly reduced under *fergusoni* Bezzi, which species is abundant in Katoomba.

The surprising feature in the synonymy is *A. eucosmae* Bezzi, which proves to be an aborted female specimen of *A. fergusoni*, occurring in about 3% of known specimens.

The following list gives the number of specimens in parentheses that were studied by Malloch.

A. fergusoni Bezzi 1923, ♂ (12, both sexes mentioned by Malloch); *eucosmae* Bezzi 1926, ♀ (2, = *fergusoni*, aborted form); *valida* Curran 1927, ♂, ♀ (2); *norma* Mall. 1929,

♂, ♀ (25); *darwini* 1929, ♂, ♀ (5); *invalida* ♂, ♀ and sp. ♀, 1930 (7 + 1, = *fergusoni*); *baldwini* ♂ (1); *lata* ♂ (1); *parviseta* ♂ (2); *brevis* ♂ (1 or ?2, in the Ferguson collection one female is marked allotype, but no record is given for this, = *darwini*); *nigritula* ♀ (4); *argentifrons* ♂ (1); *plebia* ♂, ♀ (7); *quadriseta* 1936, ♀ (1, = *darwini*).

Key to species of Actia.

1. With fissicorn third antennal segment on male only 2.
With normal antennae on both sexes 3.
2. Upper branch of third antennal segment on male with forked subbranches. 4 posterior postsutural dorsocentral bristles *baldwini* Mall.
Upper branch of the third antennal segment simple, and second segment of the arista elongate on both sexes. Normally with 4 postsutural dorsocentral bristles, but sometimes only three are apparent. Abdomen brown on male and on female normally black with segmentations brown and white. They vary towards the first two segments on the female, being largely brown, and ventrally the amount of brown varies too. Always the abdomen is slightly shining *fergusoni* Bezzi.
3. Main radial vein bare, only the radial sector is setulose 4.
Both branches of the radial field setulose 6.
4. With 4 posterior dorsocentral bristles. Abdomen black *parviseta* Mall.
With 3 posterior dorsocentral bristles. Abdomen yellowish-brown, varying to quite dark .. 5.
5. Anal vein complete *norma* Mall.
Anal vein incomplete *lata* Mall.
6. With 3 posterior dorsocentral bristles. Largely yellowish species *darwini* Mall.
With 4 posterior dorsocentrals 7.
7. Abdomen all black on female (male unknown) *nigritula* Mall.
Abdomen yellowish at sides *angustifrons* and *plebia* Mall.

ACTIA FERGUSONI Bezzi.

Schizotachina fergusonii Bezzi, 1923, PROC. LINN. SOC. N.S.W., 48: 157, fig. 8; Townsend, 1926, *Philippine J. Sci.*, 29: 542 (*Schizoceromyia*); Malloch, 1929, PROC. LINN. SOC. N.S.W., 54: 116, and 1930, *ibid.*, 55: 304, fig. 32A. *Actia eucosmae* Bezzi, 1926, *Ann. Mag. Nat. Hist.* (9), 17: 239; Malloch, 1929, PROC. LINN. SOC. N.S.W., 54: 116, and 1930, *ibid.*, 55: 307. *Actia valida* Curran, 1927, *Ent. Mitt. Berlin*, 16: 356 (*Schizactina*); Malloch, 1930, PROC. LINN. SOC. N.S.W., 55: 305. *Actia invalida* Malloch, 1930, PROC. LINN. SOC. N.S.W., 55: 305, fig. 32B. *Actia* sp. Malloch, 1930, PROC. LINN. SOC. N.S.W., 55: 305.

New synonymy.—The description of *A. eucosmae* agrees with those abortive female specimens of *fergusoni* that have the wing venation incomplete, leaving the upper branch of the median field short. Similarly the position of the median cross-vein, relative to the radial-median cross-vein, varies in the species and normally is placed halfway between *r-m.* cross-vein and the bend of the upper median vein, and may extend beyond that.

Chaetotaxy, as used by Malloch, varies too much to be of specific value, and similarly species cannot be isolated on the proportions of segments in the arista. *A. valida* Curran and *A. invalida* Malloch can therefore be regarded as being synonyms only.

When handling some freshly caught specimens in Brisbane, the end of the arista on one specimen gradually broke away in pieces, leaving a shorter and shorter remnant of the third segment. This suggested that the reduction on specimens may be due to wear taking place, but this shortening has not been repeated on test with Katoomba specimens. The length of the second segment of the arista varies too, and there is quite a complex of relative lengths in these two segments.

Hab.—Katoomba; numerous specimens, mainly females, collected over the years 1952–1959, during the months from September 8th to May 17. The last date includes an aborted female specimen agreeing with *eucosmae* Bezzi, and another of these is dated 18th April, both in the year 1954. About 3% of known female specimens are found to be aborted to more or less the same degree.

ACTIA NORMA Malloch.

Malloch, 1929, PROC. LINN. SOC. N.S.W., 54: 116; 1930, *ibid.*, 55: 307, fig. 33.

Hab.—Katoomba; occurring from early June (11th), but rare until September–December, and then becomes less plentiful to early February (3rd).

Some recorded characters are inconstant, and it is possible that *A. lata* Mall. may prove to be conspecific.

ACTIA PARVISETA Mall.

Malloch, 1930, PROC. LINN. SOC. N.S.W., 55: 308; Hardy, 1938, *Proc. Roy. Soc. Qland.*, 49: 68.

Hab.—Katoomba; 2 females, the allotype and paratype ♀, 5 January 1959. The species was based on two males, and in accord with key characters, these two female specimens can be regarded as only conspecific. They are black specimens with very little brown, varying in position and amount on legs of the two sides on one specimen, but the other has entirely black legs. The white pulverulent covering on the abdomen gives a very slight whitish reflection, but forms a dense complete line of white at the abdominal segmentations. In general appearance the species comes nearest to *fergusoni*, but has a distinctly greater dorsal arch in its outline from head to abdominal tip, and it was distinguishable thereby when seen in the field.

Tribe LINNAEMYIINI.

Taxonomy.—The species of this discussion differ from other Tachininae by having minute palpi. The typical genus *Linnaemyia* has frontal-orbital bristles on the male, the parafacials and eyes hairy, and the third antennal segment is about twice as long as the second. In these characters *O. flavipennis* Macq. (= *similis* Walk.) agrees; however, the species has been placed as genotype of both *Amphibolosia* Surcouf and *Ballardia* Curran.

It is usual to regard this species and *M. brevigaster* Macq. as being congeneric, the latter name being quoted as genotype of *Chaetophthalmus* Brauer and Berg., but an error was made in assuming that the genotype had frontal-orbital bristles on the male *brevigaster*, misleading some subsequent authors.

All proposed genera concerned with the synonymy given here are monotypical, and when a series of genera are each based upon a single species, all in one zoological region, the fact suggests that the treatment given has been very faulty. It is advisable to amalgamate the generic conceptions of doubtful validity, and make a new approach to the problem of specific identities.

There are two common species belonging to the tribe widely spread in eastern Australia, and these are very variable in characters. The following names in sequence of publication refer to these two species and the description of one other suggests that three species occur:

M. brevigaster Macq. 1846 (♂) and *M. bicolor* Macq. 1848 (♀) are sexes of one. *A. rufipes* Macq. 1849 (♂ & ♀) has not been recognized again. *O. flavipennis* Macq. 1949 (♀), *O. nudistylum* Macq. 1854 (♀), *T. similis* Walk. 1956 (♂), *B. pallipes* Curran 1927 (♂) and *C. biseriatus* Mall. 1930 (♂) form the third.

In addition, in 1929 Malloch identified specimens, giving Macquart's two first names to forms that did not agree, placing them under different genera.

M. brevigaster Macq. ♂ has insufficient data in its description to determine its identity alone, but the figure given for the conspecific *M. bicolor* ♀ shows the dark colour of the abdomen very wide and applicable only to forms without frontal-orbitals on the male. Macquart's description of *M. vittatus* ♂ (p. 150), which is a *Cuphocera*, is described with frontal-orbitals (deux soies près du bord internes des yeux), showing that Macquart noted this character when present on males, and this followed immediately after the description of *brevigaster* ♂ (p. 159) wherein the character is not mentioned. Obviously it was absent.

One main difference gathered from literature lies in the very wide and the narrower summit of the head. The very wide case is recorded for *flavipennis* and *nudistylum*, both are females, and the male of the former is in agreement with the definition of *Chaetophthalmus* as originally but faultily defined. According to Austen, the holotype

of *Tachina similis* Walker conforms, as does also a paratype of *pallipes* Curran. The male of *biseriatus* Mall., in its description, is the same species.

Habits.—Several hundreds of freshly caught adult specimens have been examined over the years 1922–1958, but only three pupae have been discovered by me. These pupae were clustered together in the soil without host remains, and from them females emerged (5 May 1957). The adults which mainly frequent the ground, low herbage and flowering shrubs, get trapped at windows, and they look very like *Calliphora* subgen. *Proekon*, or, as in one case, subgenus *Neopollenia*. They may be found every month of the year, sometimes in enormous numbers, becoming the dominant Tachinid fly of a district for a short time. In the colder localities they are found from early Spring to late Autumn.

GENUS APROTHECA Macq.

Aprothea Macquart 1849, *Dipt. Exot.*, suppl. 4: 175; Brauer & Bergenstamm 1891, *Denk. Akad. Wiss. Wien*, 58: 408, 444: 1893, *ibid.*, 60: 224. *Chaetophthalmus* Brauer & Bergenstamm 1891, *l.c.*, 58: 383; 1893, *ibid.*, 60: 145. *Amphibolosia* Surcouf 1914, *Nouv. Arch. Mus. Paris*, 6: 109. *Ballardia* Curran 1927, *Bull. Ent. Res. London*, 18: 166. *Apalpus* Malloch 1929, *Proc. Linn. Soc. N.S.W.*, 54: 318.

Synonymy.—Although the genotype of *Aprothea* remains unrecognized in Australian collections, its general position in taxonomy remains without doubt. From other Australian forms it differs by the absence of the appendix in the radial field of the wing. Though usually present, the appendix is found to atrophy and hence becomes unreliable as a generic character.

Under *Chaetophthalmus* only two names are given in Brauer and Bergenstamm (1891–3), namely, *Micropalpus brevigaster* and *M. bicolor*, respectively the male and female of one species.

Amphibolosia Surcouf, with genotype *Ochromyia flavipennis* Macq., is the form with an extra wide frons, and frontal-orbital bristles on the male.

Ballardia Curran has the same genotype under the name *pallipes*.

Apalpus Malloch, based on one female specimen, has an outstanding bristle in the parafacial region. Where chaetotaxy is found differing so widely even within a species this character cannot be regarded as of generic value. The description is based on a unique female, yet the figure is labelled male. The sternopleurals are stated to be 1:1 or 1:1:1, possibly differing on the two sides of the specimen. The inner series of frontal bristles is said to extend almost to the eye, but illustrated otherwise on the figure.

Key to species of *Aprothea*.

1. Male with frontal-orbital bristles. Both sexes with summit of head wider than eye-width. (Subgen. *Amphibolosia*.) *similis* Walker.
Male without frontal orbital bristles. Both sexes with summit of head less wide than eye-width. (Subgen. *Aprothea*.) 2.
2. At least female with an outstanding parafacial bristle. (Male unknown.) Western Australian *dorsalis* Malloch.
Without such parafacial bristle 3.
3. Abdominal stripe normally occupying much of the tergites dorsally, but not extending far along apical margins of the segments *brevigaster* Malloch.
Abdominal stripe narrow, but extending into bands along the margins of three tergites
..... *rufipes* Macquart.

Aprothea rufipes Macq. (1849, p. 176) apparently is not recognizable from description, and possibly was from Sydney, not Tasmania as recorded. The description comes very near to *A. brevigaster* Macq. and may prove to be a variation of it.

A. dorsalis Malloch (1929, p. 318) is described as having a narrow frons, and it is assumed here that, when found, the frons of the male will be similarly narrow and will be without the frontal-orbital bristles.

APROTHECA BREVIGASTER Macq.

Micropalpus brevigaster Macquart 1846, *Dipt. Exot.*, suppl. 1: 149; Schiner 1868, *Reise Novara, Dipt.*, 2: 330; Hardy 1938, *Proc. Roy. Soc. Qland.*, 49: 68 (*Chaetophthalmus*). *Micropalpus bicolor* Macquart 1848, *Dipt. Exot.*, suppl. 3: 44; Brauer 1898, *Sitz. Acad. Wiss. Wien*, 107: 495 (*Chaetophthalmus*); Hardy 1938, *Proc. Roy. Soc. Qland.*, 49: 68. ? *Nemoroea brevigaster* Macquart 1849, *Dipt. Exot.*, suppl. 4: 183. ? *Linnaemyia bicolor* Malloch 1929, *Proc. Linn. Soc. N.S.W.*, 54: 317.

Synonymy.—Malloch attached the first name to a specimen from North Queensland which had frontal-orbital bristles on the male, and this certainly is an error. The female from Barrington Tops (N.S.W.) has been discovered at Katoomba and may prove to be a variant of *brevigaster*. The ground-colour of the abdomen sometimes showing below the pulverulent overlay suggests this, and in general appearance it looks like subgenus *Neopollenia* (*Calliphora*) due to that overlay. Moreover the small series from Katoomba (1 ♂, 6 ♀) shows a graduating density of overlay. Also, some quite normal looking specimens of *brevigaster* have a slight overlay of the same colour, seen when viewed from the rear, making the abdomen look brown, and so far no specimens showing a denser covering than that have been found.

Those specimens under *Nemoroea* added to the original series by Macquart are recorded with long palpi and hence cannot be congeneric.

Hab.—Katoomba; abundant from November to January, but in the 1957-8 season they were not as plentiful as in previous years.

APROTHECA SIMILIS Walker.

Ochromyia flavipennis Macquart 1849, *Dipt. Exot.*, suppl. 4: 245; Surcouf 1914, *Nouv. Arch. Mus. Paris*, 6: 110, pl. 5, fig. 5 (*Amphibolosia*), name preoccupied. ? *Ochromyia nudistylum* Macquart 1854, *Dipt. Exot.*, suppl. 5: 131; Bigot 1877, *Ann. Soc. Ent. France*, 7: 260; Brauer 1899, *Sitz. Acad. Wiss. Wien*, 108: 517 (*Chaetophthalmus*); Surcouf 1914, *Nouv. Arch. Mus. Paris*, (5) 6: 116; Hardy 1938, *Proc. Roy. Soc. Qland.*, 49: 68 (*Amphibolosia*). *Tachina similis* Walker 1856, *Ins. Saund. Dipt.*, 2: 266; Austen 1907, *Ann. Mag. Nat. Hist.* (7), 19: 332 (*Chaetophthalmus*). *Ballardia pallipes* Curran 1927, *Bull. Ent. Res. London*, 18: 166; Hardy 1938, *Proc. Roy. Soc. Qland.*, 49: 68 (*Amphibolosia*). *Chaetophthalmus biserialis* Malloch 1930, *Proc. Linn. Soc. N.S.W.*, 55: 311.

Synonymy.—The specimens are so abundant and variable, the characters grading from one form to another, and no differences detected in the male terminalia, that only one species is possible under the five names. There may be a doubt concerning the name *nudistylum*, originally described from Adelaide and placed as a synonym of *brevigaster* with doubt.

A more certain identification is *Tachina similis* Walk. which was based on a male with the frontal-orbital bristles.

The sternites of this species may have two rows of strong bristles, one row each on the two apical ones, but the character is a variable one, with bristles decreasing in number and often absent on the penultimate sternite, and thus the form *biserialis* Mall., based on a single specimen, becomes congeneric.

Hab.—Katoomba. Found nearly every month of the year, chiefly in Spring and Summer. 31 August and 1 April are first and last normal dates of occurrence, but in addition two females occurred on the wing on the 4th and 9th June 1957; also a male on 17 June 1958.

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SOME EAST AUSTRALIAN SEA-GRASS COMMUNITIES.

By E. J. FERGUSON WOOD.*

(Two Text-figures.)

[Read 24th June, 1959.]

Synopsis.

The common sea-grasses in the estuaries of south-east Australia are *Posidonia* spp (probably two species), *Ruppia maritima*, *Halophila ovalis*, *Zostera capricorni*, *Z. muelleri*, and *Z. tasmanica*. In *Z. muelleri* there are fewer anthers than in the other two species, which may be distinguished by the spathes.

In the estuarine environment, *Ruppia* grows in water of lower salinity than the other grasses, *Halophila* grows in deep, muddy water, but may be found growing sparsely in the shallows, *Posidonia* normally grows on sandy slopes, but may occur in shallow waters, while *Zostera* grows best on shallow flats with a mud bottom, though the mud may be overlain by sand. *Z. muelleri* grows near the shore, in shallow water, from Queensland into eastern Victoria and possibly further west, *Z. capricorni* grows from about Noosa in Queensland to Lake Tuross in New South Wales, and *Z. tasmanica* from Tuross south.

Swans cause great depredations on *Zostera* beds by digging up and eating the stolons and young shoots; these depredations may be semi-permanent or permanent, depending on the water movement over the flats.

INTRODUCTION.

The taxonomy of Australian sea-grasses has been dealt with by several workers, but no ecological studies have been made. This paper deals briefly with the taxonomy of the common sea-grasses of south-east Australia and records field observations. Numerous attempts have been made to cultivate *Zostera* and *Posidonia* under aquarium conditions. Even with the simulation of natural conditions, including tidal action, the plants have not lived for more than a few months. Sections of the bottom with the plants undisturbed were transferred to plastic tanks in running water, but even under those conditions the plants grew for only three months, flowered, and died. They did not regenerate from the stolons nor did the seeds mature. Owing to these failures, it has not been possible to confirm field observations by laboratory experiment.

PREVIOUS STUDIES.

Bentham (1877) listed from Australia 7 genera of marine grasses, including the following species: *Ruppia maritima* L., *Posidonia australis* Hook., *Zostera nana* Roth., *Z. tasmanica* G. v. Mart., *Cymadocea antarctica* (Labill.) Endl., *C. ciliata* (Forsk.) Ehr., *C. serrulata* Aschers., *C. isoetifolia* Aschers., *Lepilaena australis* Drumm., *L. cylindrocarpa* Benth., *L. preissi* F. Muell., *Naiaa major* All., *N. tenuifolia* R. Brown, *Halophila ovalis* Hook., and *H. spinulosa* Benth. None of Bentham's records were from New South Wales.

Ostenfeld (1929) gave a more recent list, and some further localities. He listed *Cymadocea angustata* Ost., *C. antarctica* (Labill.) Endl., *C. ciliata* (Forsk.) Ehr., *C. isoetifolia* Aschers., *C. rotundata*? (Ehr.) Aschers. and Schweinf., *C. serrulata* (R. Br.) Aschers., *Diplanthera uninervis* (Forsk.), all from Western Australia or Queensland; *Posidonia australis* Hook. from southern Tasmania, and Western Australia north to Carnarvon; *Zostera capricorni* Aschers. from Queensland, Port Jackson, Long Reef, Botany Bay, and Harwood Island in New South Wales; and *Z. muelleri* Irmisch from Port Phillip and Point Lonsdale in Victoria, Victor Harbour and Port Pirie in South Australia, Tasman Peninsula, D'Entrecasteaux Channel, Port Esperance, and Southport in Tasmania. *Halophila decipiens* Ost. is recorded from Sydney Harbour; *H. ovalis*

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(R. Br.) Hook. from Port Jackson in New South Wales, Pialba to Cape York in Queensland, Geraldton, Swan River, and Rottnest Island in Western Australia, Victoria, and Tasmania; and *H. spinulosa* (R. Br.) Aschers. from Pialba and Moreton Bay in Queensland.

Thalassia hemprichi (Ehr.) Aschers. was collected from Port Dennison and Murray Island in Queensland, and *Enhalus acroides* (L. fil.) Steud. from Thursday Island and Cape York.

TAXONOMY.

Genus HALOPHILA Thou.

Submerged marine herbs. Flowers unisexual, solitary, within a pair of herbaceous bracts. Male flower: perianth of 3 segments; 3 anthers, sessile, alternating with segments, erect, two-celled, cells opening outward; pollen confervoid. Female flowers: no perianth, single ovary tapering into a filiform style with a short stigma, either single or divided into 3 to 5 filiform segments. Several ovules, erect, attached to sides of cavity. Fruits membranous, opening irregularly. Seeds nearly globular, with thin testa, rather loose. Embryo erect with thick radicular base nearly the shape of the seed, distinct plumula and an involute or spiral cotyledonous end, both nearly immersed in a terminal groove. Leaves in pairs, apparently opposite, sessile or petiolate, the petioles frequently enclosed at base in 2 broad, scarious, white or hyaline scales. Floral bracts axillary, sessile, or males pedicillate.

Bentham states (1877, p. 182) that the genus is confined to the Indian and West Pacific Oceans and the Mediterranean Sea. *H. ovalis* is the common species of the genus in the environment considered in this paper.

HALOPHILA OVALIS Hooker.

Stems creeping and rooting under water, emitting at each node 2 broad, thin, colourless, hyaline scales 2 or 3 lines in diameter. Within these scales lie a pair of leaves with long slender petioles and a herbaceous lamina varying from oval and less than half an inch long to oblong-elliptical and 2 to 2½ in. long, very thin, penniveined, with a broad central nerve and very fine lateral, oblique veins; margin quite entire. Involucres or double spathes enclosing flowers ovate, sessile within scales. Male flowers on pedicel emerging from involucre, females sessile within it.

Genus RUPPIA L.

Normally subsaline aquatic plant with slender, much-branched stems, and linear-filiform leaves. Flowers hermaphrodite, in a spike enclosed when young in the sheathing bases of the floral leaves. Perianth absent. Anthers 2, each with 2 distinct cells (described sometimes as 4 one-celled anthers), the cells opening outwards. Pollen grains narrow-oblong, slightly curved with ends somewhat dilated. Four carpels, at first sessile, but soon protruded on long stalks, each with a pendulous ovule and terminating in a short style or broad, almost sessile, stigma. Fruiting carpels ovoid or pear-shaped, often oblique, obtuse or more or less produced into a slightly curved beak.

Bentham (1877), from whom the above description was taken, considers that there is only one species which exhibits considerable variation, but not in diagnostic characters. The material collected during the present investigation agrees closely with his description of *R. maritima*.

RUPPIA MARITIMA L.

Stems and leaves submerged, filiform, the leaves often very long; barren leaves alternate, slightly dilated at base. Leaves crowded in a tuft, dilated at base into thin, almost scarious sheaths, closely imbricate and completely enclosing the young spike, which soon emerges on a (short or long) spirally coiled pedicel, bringing it to the surface of the water. Flowers 2-6, sessile, at first close together, later often distant. Anthers less than half line long. Carpels at the time of flowering are not exceeding

anthers, but immediately after flowering anthers fall away, and stalks of carpels lengthen by as much as half an inch to an inch or more. Ripe carpels one line or more in length.

Genus *POSIDONIA* König.

Marine submerged plants. Flowers hermaphrodite, or the terminal one of each spike male or semi-abortive. Perianth absent. Anthers 3 to 6, consisting of a broad, almost fleshy connective, with 2 short dorsal cells at base, separated by the broad, thick centre. Ovary of one sessile carpel, with 1 erect ovule, terminating in 2, 3, or more short stigmatic lobes. Fruit indehiscent, the pericarp thick and fleshy or succulent. Seed adnate to one side of cavity; embryo erect, straight, with a rather large plumule in a terminal groove. The base of the stem is covered with filamentous remains of old

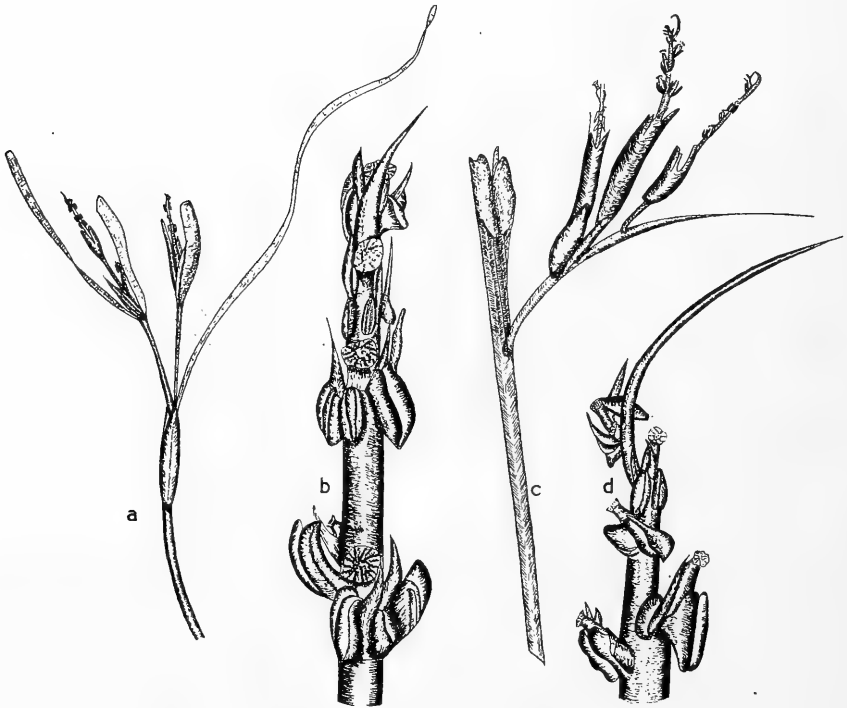


Fig. 1.—Floral differences in *Posidonia*: *a*, Merimbula form—showing arrangement of anthers, and *b*, showing fertile shoot. *c*, Port Hacking form—showing arrangement of anthers, and *d*, showing fertile shoot. Drawn by L. Crosby.

leaf-sheaths. Leaves often very long, breaking off transversely from the persistent sheathing base. Scape leafless below inflorescence, bearing at end several spikes, each in axis of a short, floral leaf, the peduncle enclosed at the base of 2 sheathing bracts, each flower subtended by a small bract and two bracteoles.

The genus is at present being revised by Dr. Melville at Kew, but there appear to be two forms on the east Australian coast, one collected from Merimbula and having 6 anthers per pistil and a long slender leaf (Fig. 1, *a* and *b*), the other from Port Hacking, having 3 anthers and a shorter thicker leaf (Fig. 1, *c* and *d*). The arrangement of the spadices is also somewhat different as the figures show.

Genus *ZOSTERA* L.

Marine submerged plants. Flowers unisexual, males and females in alternate rows on the membranous rachis of the spike enclosed in the sheathing base of the floral leaf. Perianth absent. Male flowers of a single, ovate, laterally attached, one-celled anther;

pollen confervoid. Female flowers of a single carpel, gourd-shaped, laterally attached near apex, and produced above attachment into a filiform two-branched style. Fruit an indehiscent nutlet. Embryo with deep, longitudinal groove forming 2 valves which fold over the long, curved, linear cotyledonous end. Creeping rhizome, emitting short stems with long, narrow, grass-like leaves separated from their narrow sheathing bases by a transverse line. Peduncles axillary or terminal, bearing a single spike completely enclosed in the more or less dilated but continuous sheathing base of the floral leaf or spathe, which otherwise resembles the stem-leaves. Rachis of spike broad and thin, with margins folded inward and bearing flowers and fruits only on inner surface.



Fig. 2.—Differences of *Zostera* species: a, Anthers of *Z. capricorni* (*Z. tasmanica* is similar); b, Anthers of *Z. muelleri*; c, Fertile shoot of *Z. capricorni*; d, Fertile shoot of *Z. muelleri*; e, Sterile shoot of *Z. capricorni*; f, Sterile shoot of *Z. muelleri*; g, Fertile shoot of *Z. tasmanica*. Drawn by L. Crosby.

Setchell (1933) divided *Zostera* into 3 sections, *Alega*, which has not been recorded from the Southern Hemisphere, *Zosterella* and *Heterozostera*, both of which have southern representatives. He points out that there is considerable confusion with regard to the type material from Australia and New Zealand.

There appear to be three species of *Zostera* represented in east Australian waters corresponding to *Z. capricorni* Ascherson, *Z. muelleri* Irmisch (both in the *Zosterella* section) and *Z. tasmanica* (*Heterozostera*).

Setchell divides these species on the leaf venation, shape of leaf apex and the retinacula (bracts ? arising within the elevated margin of the spathe), though the *Heterozostera* section has other characteristics. However, the examination of several hundred specimens shows considerable variation in the shape of the leaf apex and in the leaf venation, thus reducing the usefulness of these criteria for diagnosis of the species concerned. This variation can be discerned in leaves from one bed, and even from individual plants. Examination of material collected from various parts of Port Hacking, Lake Macquarie and Lake Illawarra showed that in *Zostera capricorni*, 20 per cent. of the uninjured leaf tips were evenly rounded, 23 per cent. regularly truncate,

15 per cent. irregularly truncate, and 42 per cent. regularly or irregularly notched. In *Z. muelleri*, 15 per cent. were evenly rounded, 27 per cent. regularly and 13 per cent. irregularly, truncate, while 45 per cent. were notched. The denticulation of the leaf tips also varied considerably; this may be due to injury rather than to specific differences, especially as the majority of leaves examined had obviously been damaged, the whole tip being missing.

However, a separation of the species can be made using the number and arrangement of the anthers. In *Z. tasmanica* and *Z. capricorni*, the anthers are arranged in two closely packed rows (Fig. 2, a), while in *Z. muelleri* they are alternate and somewhat spaced (Fig. 2, b). *Z. tasmanica* has 20-24 anthers per inflorescence, *Z. capricorni* 13-20, and *Z. muelleri* 10-11. The length of the fertile shoot is not very useful for separating *Z. muelleri* from *Z. capricorni*, as both are long relative to the plant (Fig. 2, c and d). *Z. muelleri* can be distinguished in the field from *Z. capricorni* by the fact that the leaves of the former are smaller and narrower. A sample from Lake Macquarie of 300 leaves of each species gave mean dimensions of: *Z. muelleri*, 30 × 2 mm., and *Z. capricorni*, 55 × 4.5 mm., though many samples of the latter from other areas would have a far greater length, and leaves up to 1 metre long have been observed at Stewart's Point, Crookhaven and other places. *Zosterella* and *Heterozostera* are separated by the situation of the stem bundles and fibre strands, and by the stem and spathes. In *Zosterella* the rhizomes have one lateral bundle on each flank and fibre strands in the inner portion of the cortical layer, the stems are horizontal, with very short vertical branches, and the spathes are very slightly swollen but conspicuous. In *Heterozostera*, i.e., in *Z. tasmanica*, there are multiple vascular bundles in the internodes, the fibre strands are just beneath the epidermis, the vertical stems are often long (up to 30 cm.), and the spathes markedly swollen, and sessile, being almost or quite shielded by the sheath of the leaf below (Fig. 2, g). The floral branches of the *Heterozostera* are very hard to find in the field (cf. Fig. 2, f and g), whereas the long, well differentiated, fertile branches of the *Zosterella* section are easy to see (Fig. 2, c, d, e).

The differences between the three Australian species are summarized thus:

<i>Z. muelleri</i> .	<i>Z. capricorni</i> .	<i>Z. tasmanica</i> .
Anthers 10-11, alternate.	Anthers 13-20, in 2 packed rows.	Anthers 20-24, in 2 packed rows.
Leaves up to c. 30 × 2 mm.	Leaves from 45-100 × 4.5 mm.	Leaves from 45-100 × 5 mm.
One lateral bundle on each side of internode.	One lateral bundle on each side of internode.	Multiple bundles in internodes.
Fibres in inner cortex.	Fibres in inner cortex.	Fibres near epidermis.
Spathe obvious, not swollen.	Spathe obvious, not swollen.	Spathe inconspicuous, swollen.
Fertile stem longer than barren stem.	Fertile stem longer than barren stem.	Fertile stem similar to barren stem.

ECOLOGICAL RELATIONSHIPS.

Because the east coast of Australia is characterized by a large number of shallow coastal lagoons and meandering river estuaries, the sea-grass associations become ecologically and economically important. Within the estuaries they form large areas which are associated with inshore fisheries and oyster culture. They occur in micro-biologically active areas, the roots being in reducing zones while the leaves are in oxidized water which, under active photosynthesis, is oxygen-saturated.

The grasses found on the east coast are, in rising order of importance, *Halophila*, *Ruppia*, *Posidonia* and *Zostera*. *Cymadocea*, which occurs in large beds, and washes ashore to form banks up to 6 feet deep and many feet wide in the Bunbury-Busselton area of Western Australia, is unimportant on the east coast.

(a) *Halophila*.

Halophila is relatively unimportant in the estuaries of eastern Australia, except in some relatively deep, still, muddy areas, often below 20 ft., such as Bundabah (Port

Stephens), Merimbula Lake, and deeper parts of Lake Macquarie. In these places it is usually dominant or associated with red algae such as *Gracilaria* sp. Where it occurs in shallow water it is sparse to subdominant, e.g., Little Swan Bay (Port Stephens) and Gunnamatta flats (Port Hacking). It is then associated with *Zostera* or, less often, *Posidonia*, together with numerous red algae such as *Gracilaria*, *Laurencia*, *Gigartina*, *Polysiphonia* and *Ceramium*, and the brown *Ectocarpus*. *Halophila* appears to be associated with reduced, sulphide-containing muds. The Lake Macquarie muds where *Halophila* was found had Eh values of -50 to -100 mV, and the same limits were observed in the *Halophila* regions in Port Hacking. While *Halophila* is usually found in areas of lower chlorinity, from 18 to 19.0‰, it can also occur, as it does in Port Hacking, in water of normal chlorinity, from 19.5 to 20‰. Illumination in the deeper regions of growth was of the order of 5 to 10 per cent. of surface values.

(b) *Ruppia*.

Ruppia, often called "swan grass", is usually associated in the east coast estuaries, with water of lower chlorinity, from about 16‰ as in Swan Bay (Port Stephens) to almost potable water, as at Killarney (George's Basin) and upper Lake Conjola. In these cases it is dominant. In other cases, e.g., Galgabba Flats in Lake Macquarie and at the western end of Merimbula Lake, *Ruppia* is associated with *Zostera* where the chlorinity is 17.5-19.5‰. On Galgabba flats and Lake Erraring, in Lake Macquarie, *Zostera* was dominant until a large flock of swans invaded the area and removed most of the *Zostera*, leaving the *Ruppia*. (In both Merimbula and Lake Macquarie, heavy freshes may cause stratification and a temporary lowering of the chlorinity to about 5‰ which may favour the growth of *Ruppia*.) The Eh of the muds on which *Ruppia* grows is usually negative, though at Killarney the surface was oxidized, but a very strong sulphate reduction was going on a centimetre below. *Ruppia* normally has few epiphytes, although at times it does become covered with a mat of *Ectocarpus*, or filamentous blue-green algae, diatoms (chiefly *Synedra ulna*) being relatively sparse. *Ruppia* flowers in the summer, from November through to February, but seedlings have been observed only at a lagoon near Shell Harbour, New South Wales, and at Paynesville in Gippsland, Victoria. *Ruppia* has not been found in water much more than 6 feet deep at mean low water, and appears to require good illumination, and little current.

(c) *Posidonia*.

More than one species of *Posidonia* has been recognized in Australian waters, but the taxonomy of the genus is still doubtful. *Posidonia* has its greatest development in the South Australian gulfs and on the west coast of that State. There, the growth is so abundant that numerous attempts have been made to use the fibre commercially (Winterbottom, 1917). On the east coast of Australia, however, *Posidonia* is of interest merely as forming a community in the sea-grass association, where it normally occurs in waters from about 6 feet below mean low water to between 20 and 30 feet. Here it is characteristic of sloping, sandy shores, where the bottom has a positive Eh extending for several centimetres in depth, the water is clear, and turbidity slight, e.g., in Lake Macquarie, Cabbage Tree (Port Hacking), Weeney and Quibray Bays, and on the northern slope of Towra Point in Botany Bay. At Merimbula, the *Posidonia* occurs as the dominant form on shallow tidal flats between the causeway and the entrance to Merimbula Lake where the Eh is about +250mV. At times it is found associated with *Zostera*, e.g., on the Belmont flats (Lake Macquarie), and with *Zostera* and *Ruppia*, e.g., in the shallows of Merimbula Lake. In such cases it does not appear very healthy. *Posidonia* has not been found in exposed waters on the east coast.

Posidonia usually has a number of epiphytes on the leaves, e.g., diatoms, red algae (*Melobesia*, *Ceramium*, *Polysiphonia*, *Laurencia*), brown algae (*Ectocarpus*, *Colpomenia*), the green algae (*Vaucheria*, *Enteromorpha* and *Chaetomorpha*), and blue-green algae (*Oscillatoria*, *Lyngbya*). In addition, the ciliate, *Vorticella*, the tube-worm, *Spirorbis*, and encrusting bryozoa are numerous. The epiphytic diatoms are less

important than on the adjacent *Zostera* but, in general, the same species occur and consist of stipitate forms including *Licmophora*, *Navicula*, *Skeletonema*, *Plagiogramma*, *Melosira*, *Grammatophora*, *Cocconeis* and *Amphipleura*.

Though *Posidonia* is normally the dominant form, the community usually contains a number of algae, including *Sargassum*, *Gigartina*, *Gracilaria*, and a very large number of species of red algae, *Dictyota*, often *Cystophyllum* (at Wallis Lake), *Codium tomentosum* and *C. lucasi*, various Caulerpas.

The leaves of *Posidonia* contain a nitrogen-containing reducing substance, volatile in steam, which reduces cadmium or lead acetate to the metal, but differs in odour from that contained in *Zostera* (Wood, 1953).

(d) *Zostera*.

Of the sea-grass communities, the *Zostera* community is most important both ecologically and commercially. In Europe, Japan, America and Australia, this plant is associated with the growth of crustacea and other larvae, oysters, and other molluscs, and is of general occurrence in estuaries in temperate waters. The "wasting disease" of this plant in Europe and America, and the consequent failure of various fisheries in these countries, showed how close the relation was between the plant and the animal life of the estuary (Renn, 1936).

Zostera grows in water which is marine in character, and has a chlorinity of the order of 18-19‰, though it may, at times, encroach into less saline waters. It grows from low tide mark to a depth of about 20 feet and appears to require good illumination, as it does not do well in turbid water. The depth to which it grows seems to depend on turbidity. The grass can persist in the presence of currents of several knots, as in the channel entrances to Lake Macquarie and Sussex Inlet. *Zostera* has been found growing on bottoms with Eh values of +180 (Lake Macquarie, in gravel) to -150 mV (Maianbar, in sand and reduced with abundant H₂S (0.2n)), and where the pH varies between 5.5 in the mud to 9.3 in the water on sunny days near midday.

The plants have been found with their root hairs in actual contact with particles of hydrotroilite (FeSH(OH)). *Zostera* normally has its root system in a reducing environment and produces organic reducing substances (Wood, 1953); it seems probable that its metabolism is adapted to such environments. The reducing substances occur in the epidermis of the leaves and stolon, and in the leaf gland cells. They are associated with a pigment which is possibly a digalloyl.

The *Zostera* community is rich with plant and animal life. The microbial groups in the mud consist of bacteria of the sulphur cycle, including *Desulphovibrio*, *Thiobacillus* sp., *Th. denitrificans*, *Chromatium*, *Chlorobium*, large numbers of heterotrophs, including anaerobes, a few naviculoid diatoms, flagellates, and ciliates, including anaerobic *Colpidium*, *Euplotes*, and rhizopods. The epiphytes are very numerous and include a very large assemblage of diatoms, *Ectocarpus*, *Ceramium*, *Polysiphonia*, *Oscillatoria*, *Lyngbya*, and other blue-green algae, while the protozoan *Vorticella*, and the serpulid *Spirorbis* are common, e.g., in the channel at Lake Macquarie. The epiphytes serve as food for mullets and other phytophagous fish, the gastropod *Pyrazus* etc., and the *Zostera* itself is consumed, and apparently digested, by the nudibranch *Aplysia*, and the garfish (*Reporhampus ardelio*).

Zostera flowers and fruits in the summer, from November to the end of March, and flowering occurs in patches, at times small and localized, and at times large and widespread. Although a careful watch was kept for several years, no seeds or juvenile plants were observed except at Paynesville in Victoria, hence it would appear that propagation is very largely vegetative. *Zostera muelleri* occurs mainly in shallow water (low water line to about 5 feet) and *Z. capricorni* in deeper water (from 2 feet below low water to below 20 feet). However, the two species may be interspersed. Soon after flowering, most or all of the aerial shoots die off, and only the stolons, which are subterranean, and a few residual shoots or stools remain. Thus, in autumn, a *Zostera* flat may seem completely bare of weed. The dead leaves either wash out into deeper water or ashore, where they form high banks which rot slowly. Cellulose

digestion of the cell walls is very slow, and no cellulose digesting bacteria were isolated from Lake Macquarie. However, Imai *et al.* (1951) have shown that the decaying *Zostera* serves to harbour and nourish a number of microorganisms including heterotrophic bacteria and colourless flagellates. These authors found that, in Japanese waters, one of these flagellates, *Monas* sp., serves as the food of the larval oyster (*Ostrea gigas*), and that the spawning of this oyster coincides with the death of the *Zostera* in Matsushima Bay and Mangoku Inlet. The spawning of the Australian oyster has not been definitely correlated with the death of *Zostera*, but occurs between December and March when the *Zostera* is declining, so the same relation may hold in Australian estuaries. Living *Zostera* harbours a number of microplankton and phytoplankton as well as zooplankton organisms and small fish. Diatoms such as *Coscinodiscus*, *Biddulphia*, and dinoflagellates such as *Exuviaella*, *Gymnodinium*, *Prorocentrum*, are common in the community, and so are various crustaceans, e.g., Copepods, Mysids, Caprellids, which, no doubt, attract the fish into the community, where they also find shelter from their enemies.

Swans may cause great depredations in the *Zostera* beds. In the cases observed large areas were denuded, and this may be assumed to have had repercussions on the fishing potential of the areas. Swan faeces were examined and found to consist entirely of *Zostera*, mainly stolons, the leaves being torn off and allowed to float away. Another effect of this denudation by swans is that the bottom is no longer held in place by the *Zostera* stolons, and may be moved about by currents and winds, thus becoming oxidized and so unfit for future growth of the plant. This has happened over a large portion of the Goodwin Sands, Mallacoota, on the "proclaimed" areas of Lake Illawarra and in Lake Erraring, an offshoot of Lake Macquarie.

The larger organisms associated with *Zostera* include a number of algae, e.g., *Enteromorpha prolifera*, *Chaetomorpha*, *Microdictyon*, *Colpomenia*, *Cystophyllum*, *Codium*, *Caulerpa*, *Dictyota*, etc., and some of these during spring or autumn may form a felt which covers the *Zostera*, and may produce anaerobiosis below it. With these felts are *Ectocarpus*, various filamentous red algae, and diatoms, as well as the microplankton. Such felts at last float off and may cause a nuisance on the estuary or on the beaches, and by fouling nets and lines, making it impossible to fish.

In the Gippsland Lakes, the *Zostera* beds are said to have been denuded by crabs which invaded the lakes after the opening of the entrance, but it is difficult to know at this stage whether the crabs, or changes in lake level and salinity due to deforestation, were the real cause of this denudation. *Zostera* is the most abundant sea-grass in south-eastern Australian estuaries. At Stewart's Point, it covers the old bed of the Macleay River for about 15 miles in water from 0 to 6 feet deep. Here, the old mouth of the river just south of Grassy Head has been closed for many years, and there is little or no water movement. The sea-grass persists in water which, in the summer, becomes too hot to walk in, and which kills *Gracilaria* and other algae. There is a similar occurrence of *Zostera* in the Crookhaven River, near Greenwell Point. In the channels of Lake Macquarie, Queen's Lake (Camden Haven), Maianbar, and Sussex Inlet, *Zostera* also covers most of the bottom, but in these cases there is a strong current of several knots. Sussex Inlet flows into George's Basin and, in the vicinity of the drop-over, as in Lake Macquarie, the *Zostera* is replaced by *Posidonia*, almost the reverse of the situation at Merimbula. In Port Stephens and Botany Bay, the dominant sea-grass on the southern shore is *Posidonia*, which extends up the estuary to Salamander Bay in the former and to Towra Point in the latter. *Zostera* is dominant on the northern shores of these estuaries. In Port Hacking, *Zostera* is dominant on both shores, except on the side of the channel near the Marine Laboratory. During the last 20 years, especially in more recent years, *Posidonia* has extended from the northern slope of the channel in Port Hacking, and has grown onto the flats, replacing *Zostera*. This may be due to the effect of man, in altering the environment by dredging, digging the flat for worms, etc., and suggests that *Posidonia* is less responsive to changes in environment than *Zostera*.

Zostera has also been observed in the unprotected Bate Bay and off Tathra, and may occur in 20 to 30 feet on sandy-mud bottom in other places. Estuarine *Zostera* is bright green when young, but later turns purple-brown owing to the development of accessory pigments while the stolons become woody. The oceanic *Zostera*, on the other hand, remains green throughout the summer, and the stolons remain succulent.

Zostera capricorni and *Z. muelleri* were found from Moreton Bay to Tuross Lake (Turlinjah), and *Z. tasmanica* from Tuross southwards. *Z. tasmanica* and, to a lesser extent, *Z. muelleri* were found at Merimbula, Mallacoota, and in the Gippsland Lakes.

The areas used for culture of the Australian oyster, *Crassostrea commercialis*, are closely associated with the *Zostera* beds, the distribution being practically that of *Z. capricorni*, though some areas are suited for spatting and others for fattening, and the *Zostera* community does not give a clue in this matter. There is no doubt, however, that the biological activity, especially that of the sulphur cycle, which occurs in the *Zostera* community plays an important part in supplying the microorganisms which the oyster requires as food and in the release of phosphate, nitrogen compounds, etc.

Acknowledgements.

Thanks are due to officers of this Division, including Prof. L. G. M. Baas Becking, for some of the data used in this paper and for helpful discussions, to Mr. L. H. Crosby for collecting material and drawing the diagrams, and Messrs. Rochford and Spencer for hydrological data.

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THE EFFECTS OF INORGANIC SALTS ON DIVIDING CELLS.

By MARY M. HINDMARSH, School of Biological Sciences, University of New South Wales.*

(Plate viii; two Text-figures.)

[Read 24th June, 1959.]

Synopsis.

Onion root tips treated with certain inorganic salts showed abnormal cell division and a reduction in the number of dividing cells with time. The addition of a low concentration of other salts to the medium neutralized the effect of the single inorganic salt. This inhibition of the cell division process seems to be due to ion unbalance in the external solution, rather than the specific effect of any inorganic ion.

INTRODUCTION.

A wide variety of organic substances is known to produce abnormalities in mitosis in both plant and animal cells, and the effects of some inorganic salts on the cell division process have also been described. In 1945 Levan, who treated onion root tips with a number of inorganic salts, mostly nitrates, found that solutions of the salts of 27 different metals produced cytological changes in the cells of the meristem. Galinsky (1949) reported the inhibition of cell division in the same material, by solutions of Na_2HPO_4 , NaHPO_4 , and KH_2PO_4 . He attributed the observed abnormalities to the presence of the phosphate and compared them to the effects produced by colchicine and acenaphthene. Using chick cells in tissue culture, Hughes (1952) found that abnormal tonicity upset cell division by suppressing spindle formation and producing blocked metaphase. This raises the possibility that cytological abnormalities in the presence of inorganic salts may be due to an ion unbalance in the solution, rather than to a specific effect of any inorganic ion. When a phosphate buffer was used to control the pH in some experiments with onion seedling roots (Hindmarsh, 1953), it was noticed that abnormal mitoses were produced in the root meristems, and experiments were designed to find whether this was caused by the phosphate or by the univalent ions in the solution.

MATERIALS AND METHODS.

Onion seeds were surface sterilized in a saturated solution of bleaching powder for 5 to 10 minutes, set out in sterilized petri dishes on filter paper moistened with culture solution and incubated for 7 days at 22°C. The culture solution was KNO_3 0.0025M, $\text{Ca}(\text{NO}_3)_2$ 0.0025M, MgSO_4 0.001M, and KH_2PO_4 0.0005M (Hoagland and Broyer, 1936) at a pH of 5.3.

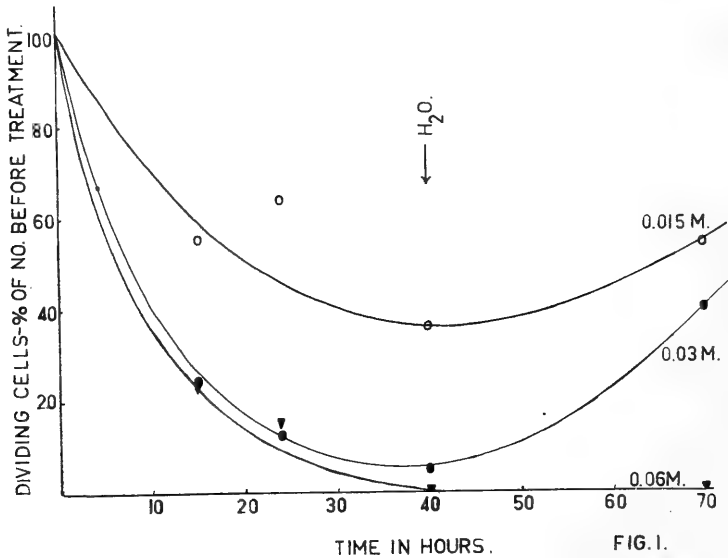
Preliminary examinations of the relationship between root length and the number of dividing cells in the root tips were made to find the least variable material for cytological investigation. Counts of dividing cells showed that seedlings with roots from 6.0 to 11.0 mm. after 6 to 7 days proved less variable than shorter or longer roots. The over-all mean for four experiments was 290.5 for 74 roots, and the pooled standard deviation within these four groups (calculated from the mean of each group) was 67.7.

Roots were treated by floating seedlings on 20 c.c. of the test solution in 150 c.c. Erlenmeyer flasks. All the solutions were autoclaved without any appreciable change in pH. The few seedlings which sank during the course of an experiment were discarded.

* This work was done during the tenure of a Linnean Macleay Fellowship at the Botany School, University of Sydney.

Root tips were fixed in acetic alcohol and stained in 1.0% aceto-orcein. To count the number of dividing cells in each stage of division, roots were heated in acidified aceto-orcein stain and the meristematic region stained more deeply than the remainder of the root. This deeply stained tip was removed just behind the meristematic zone, and cut into 4 pieces in fresh 1.0% stain. These pieces were squashed into a single cell layer by pressure on the coverslip and division stages scored during a systematic examination of the whole slide.

The buffer solution was a mixture of 2 parts $\text{Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O}$ (23.9g/l), and 8 parts KH_2PO_4 (9.07g/l) with a final concentration of 0.06M and a pH of 6.2. Roots were treated with 0.06M KCl, 0.06M, 0.03M, and 0.015M phosphate, and with each solution combined with Hoagland's culture solution. Controls were grown in the culture solution.



RESULTS.

a. *The effect of the buffer solution.* There was no evidence of any chromosome fragmentation with this treatment, but other cytological abnormalities were produced. The number of dividing cells in root tips was reduced by all concentrations indicating

TABLE 1.

Time in Hours.	Phosphate Concentration.		
	0.015M.	0.03M.	0.06M.
15	Numerous normal dividing cells.	Fewer divisions than normal. Chromosomes short and thick, otherwise normal.	Blocked metaphase. Few anaphase—all irregular.
24	Mainly normal. Few blocked metaphase.	Few divisions, some normal, some blocked.	Very few divisions, all abnormal. No anaphase and telophase.
40	Mainly normal. Some cells have short, thick chromosomes. Few blocked metaphase.	Most cells resting nuclei, but some roots have few prophase and blocked metaphase.	All roots have only interphase nuclei.
40+30 in water	All normal dividing cells.	All normal dividing cells.	All interphase nuclei.

that the onset of the cell division process was prevented (Text-fig. 1). The spindle mechanism was also affected and cytological abnormalities varied with the concentration of the phosphate buffer and time (Table 1).

The first observed effects were shortening, thickening of chromosomes in otherwise normal metaphase and anaphase stages, followed by irregular metaphase and anaphase stages with some chromosomes left off the metaphase plate or lagging at anaphase. Finally all early stages were affected as they were unable to pass metaphase; blocked metaphase occurred instead of normal metaphase plate formation (Pl. viii, A and B). Some binucleate cells formed, but these were rare, suggesting that there is little effect on cells which were in anaphase and telophase at the time of treatment.

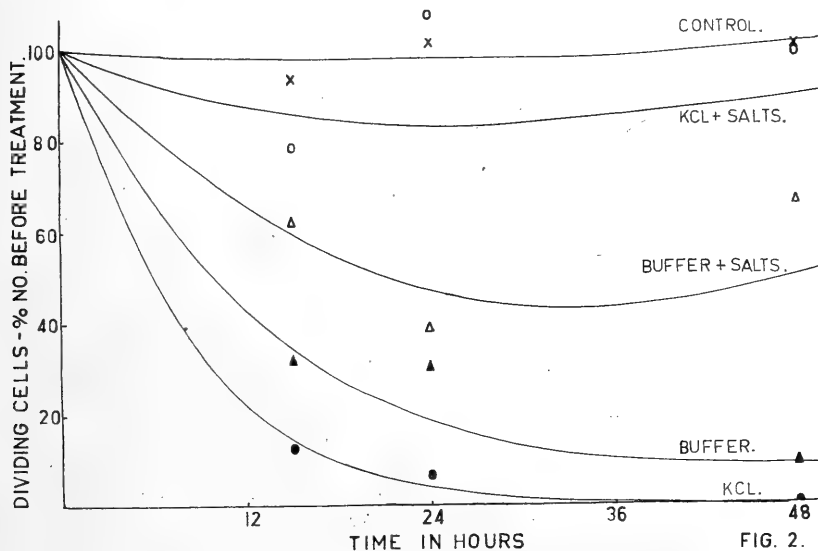


FIG. 2.

The cells of roots returned to water or culture solution after treatment with 0.06M phosphate buffer for 40 hours did not begin division even after 30 hours. Most cells appeared to be quite healthy, but some were pycnotic. The roots remained white and turgid and were apparently still alive. There was no "stickiness" of chromosomes such as was observed during treatment with nitrophenols (Levan and Tjio, 1948; Hindmarsh, 1951). After shorter treatment at 0.06M and after treatment with lower concentrations the roots recovered in water or mineral solution and commenced normal division.

In roots treated with 0.06M phosphate buffer and mineral solution together, no cytological abnormalities were observed. All stages of normal mitosis were found in these roots, but there was a gradual reduction in the number of dividing cells with time (Pl. viii, F). This reduction was not as great as with phosphate buffer alone (Text-fig. 2).

b. The effect of a single salt solution. The entry of cells into cell division was affected more by 0.06M KCl than by the same concentration of phosphate buffer (Text-fig. 2). KCl solution also produced extra contraction of the chromosomes in metaphase and anaphase stages, and a few blocked metaphase stages at 15 hours (Pl. viii, C, D and E). The addition of a culture solution to the KCl solution reduced the effect on the number of dividing cells (Text-fig. 2), and in roots so treated the chromosomes as well as the division process were perfectly normal (Pl. viii, G).

DISCUSSION.

The results of these experiments show that the ionic composition of external solution can influence the course of the cell division process.

Chemical inhibition of the mitotic cycle can occur in one of three ways. Some chemicals inhibit or destroy the spindle mechanism, leading to the formation of blocked metaphase, abnormal anaphase and telophase in the early stages of treatment, and ultimately to the complete absence of anaphase and telophase, and to polyploidy, e.g., colchicine. A second group has a similar effect, but also prevents the onset of prophase leading to a reduction in the number of dividing cells with time, and as each cell goes through only one cycle during treatment there is no polyploidy, e.g., sulphanilamide. A third group causes chromosome breakage, e.g., nitrogen mustards.

The cytological abnormalities produced in these experiments are similar to those of the second group of chemicals. A sodium-potassium phosphate buffer produced spindle abnormalities in meristematic cells, only in the absence of other salts. Both the phosphate buffer alone, and the buffer with mineral salts added, reduce the number of dividing cells by preventing the entry into prophase, but this effect is greater with the buffer solution only. The spindle mechanism was inhibited by the buffer alone, but not by the combined solution. Similar effects were obtained with KCl solution, which has less effect on the spindle mechanism and more effect on the interphase to prophase stage of the cycle. Again, the addition of a culture solution with a low concentration of divalent as well as monovalent ions allowed the division process to continue in a normal manner and reduced the effect on the number of dividing cells.

An analogous phenomenon is known in root growth in culture solutions. It is generally agreed that there must be a suitable balance of the various ions in a solution, to maintain normal plant growth. The toxic action of a single salt such as KCl is reduced by the addition of quite low concentrations of a divalent salt. Antagonism, the influence of one ion in preventing the toxic symptoms due to another ion alone, is well known, but imperfectly understood. The best known example in plants, the antagonism of Ca or K by the other ion, presumably occurs because the presence of K or Ca alone in solution results in structural disorganization of the cytoplasm. In these experiments the ion unbalance in the external solution affects the cell division process, as the cytological abnormalities produced by both the phosphate buffer and the KCl were neutralized at least in part by the addition of low concentrations of other salts to the solution. This suggests that the cytological abnormalities may be the indirect result of physiological changes in the cells, and are not due to the specific effect of any inorganic ion. This inhibition of the cell division process may be one factor which contributes to the inhibition of root growth in an unbalanced solution.

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* Seen in abstract only.

EXPLANATION OF PLATE VIII.

A-B: Blocked metaphase in sodium-potassium phosphate buffer. C-E: Abnormal metaphase and anaphase in KCl. F: Normal cell division in phosphate buffer + culture solution. G: Normal cell division in KCl + culture solution.

THE REPRODUCTION AND EARLY LIFE HISTORY OF THE GASTROPOD
CYMATILESTA SPENGLERI (PERRY) (FAM. CYMATIDAE).

By D. T. ANDERSON, University of Sydney.

(Communicated by Miss I. Bennett.)

(Plate ix; 17 Text-figures.)

[Read 29th July, 1959.]

Synopsis.

C. spengleri shows clear sexual dimorphism. Pairing occurs in the spring, and the female produces a characteristic egg mass. Early development through a yolky veliger to metamorphosis takes place within the egg mass, with escape of the young to a free-living benthic existence at 16 days. The pattern of reproduction and early life history is typical for a mesogastropod prosobranch.

INTRODUCTION.

Many workers have made contributions to our knowledge of the life histories of prosobranch gastropods, and the details that have emerged have been clearly summarized by Lebour (1937) and Thorson (1946, 1950). The majority of investigations, however, have been of European and American species and the life histories of the tropical and subtropical marine prosobranchs, especially those of the eastern Pacific, remain largely unrecorded. Many of the families occurring in this region are represented in the molluscan fauna of the eastern Australian seaboard, among them the Cymatidae (triton shells). The following account of the early life history of *Cymatilesta spengleri* is the first for a member of this family.

SEX DIFFERENCE AND SPAWNING HABITS.

C. spengleri is typical of the smaller cymatids, an average adult specimen measuring 4-5 inches in length. Like all prosobranchs, the species is dioecious, and a degree of sexual dimorphism is evident in addition to the presence of the penis in the male. The female is slightly the larger, with a thicker and less sharply conical spire and a much thicker rim to the mouth of the shell. Adults of both sexes are found in considerable numbers near the low water mark on rocky shores in the vicinity of Sydney. Breeding takes place in the spring (October-November), the animals being found associated in pairs at this time, and egg masses are attached to shaded rock faces just above the extreme low level of spring tides. The extent of the sublittoral range of the species and the possibility of sublittoral breeding are undecided, but an indication of a more than littoral distribution is given by the preponderance of fully grown adults on the shore. As will be seen below, the species has no planktonic larval stage and hatches as an almost complete miniature adult. Stages of growth leading to the adult must take place mainly in sublittoral waters, and it may even be that the later migration of adults to the shore is a breeding migration.

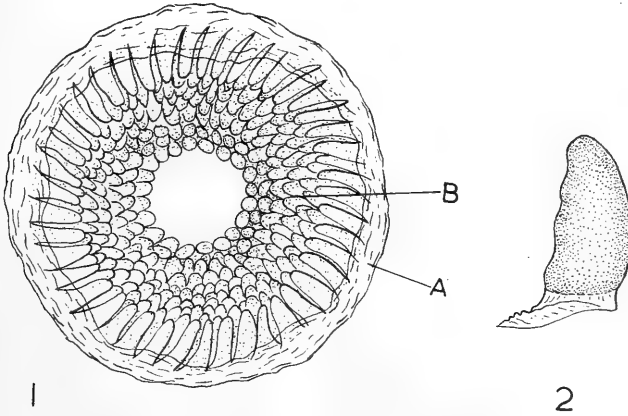
Copulation has not been observed in *C. spengleri*, but must considerably precede spawning by the female, since egg laying occurs in isolation. On November 11, 1958, Miss I. Bennett, of the Zoology Department, University of Sydney, and myself, while collecting at Long Reef, Collaroy, north of Sydney, found in addition to several egg masses suspected to be of this species, a female in process of spawning an identical egg mass. Both egg mass and parent are shown in Plate ix.

THE EGG MASS.

When complete, the egg mass (Pl. ix, A, B; Text-fig. 1) is circular in outline, cup-shaped, and glued to the rock by its flat base. It consists of a spiral of conical egg capsules, beginning in the centre of the mass with the capsules vertically placed and

continuing outwards and upwards until the capsules at the rim of the cup are horizontally placed. The outer surface of the mass is made up of a series of thin, horny, overlapping, transparent plates, with the close-packed capsules firmly attached to their inner surfaces.

The female fashions the egg mass within the mouth of the shell, and the diameter of the two correspond. The region of greatest height of the mass is formed at the anterior rim of the shell, the opposite lowest region lying under the first coil of the visceral spire. The mode of construction of the mass is not yet clear, but the individual egg capsules are extruded from the mantle cavity already fully formed. The horny plates must therefore be produced and glued together and the capsules attached to



Text-fig. 1, 2. *Cymatilesta spengleri*: 1. Egg mass, natural size. 2. Egg capsule, $\times 2$. A, horny plates of surface layer; B, egg capsule.

them by a means accessory to the genital system. Each of the several hundred egg capsules is a horny, transparent, flattened, blunt ended cone curving outwards at the base (Text-fig. 2). Within it is a clear jelly in which lie several hundred eggs, each creamy white in colour, but imparting to the whole egg mass a delicate pale orange tint.

METHODS.

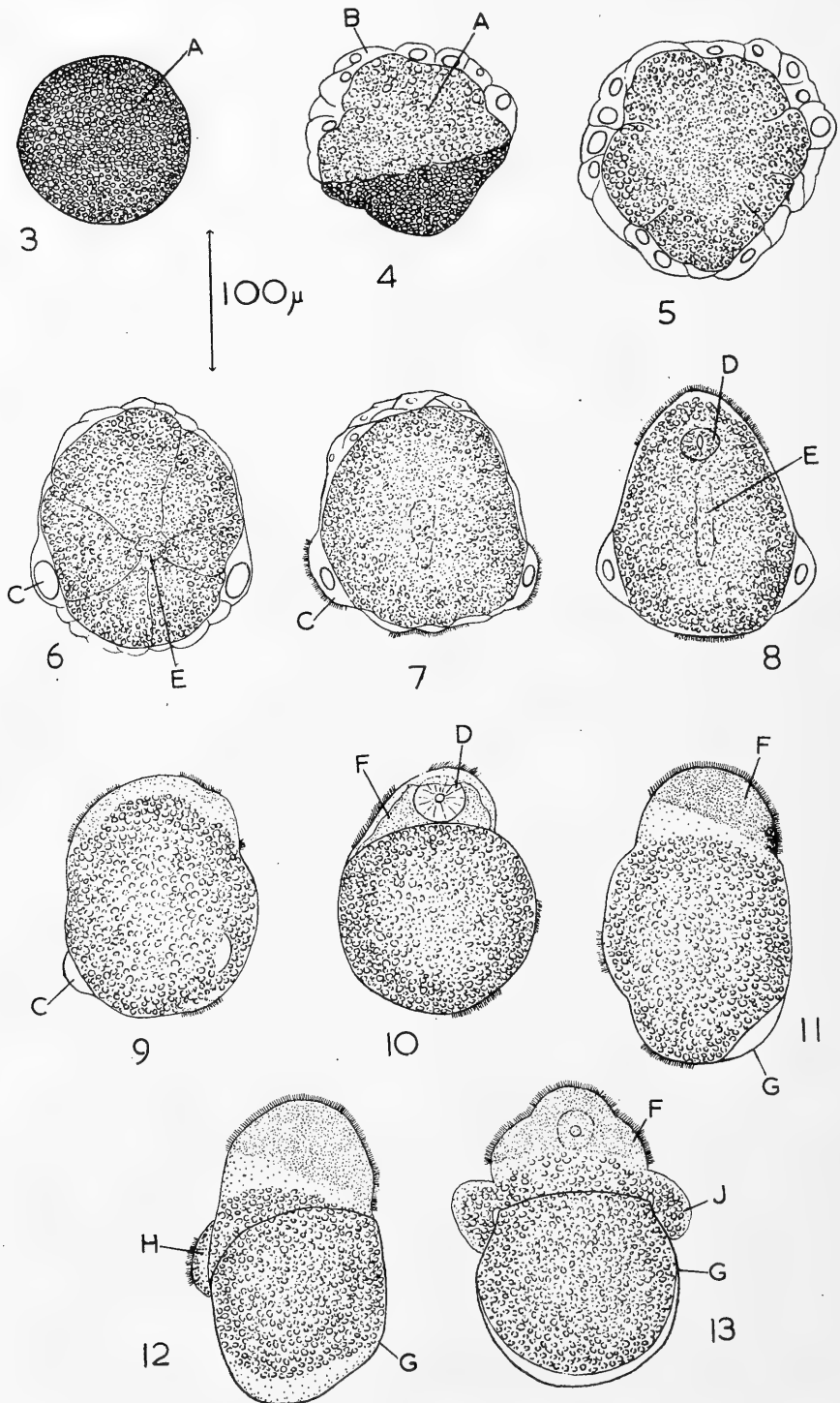
The newly spawned egg mass was maintained in a bowl of clean sea water in the laboratory. With constant aeration and a change of sea water every three days, the embryos within the egg capsules developed steadily, feeding on yolk reserves, for 16 days, when hatching took place. It did not prove possible to culture the hatched embryo further, but by this time they had almost completed metamorphosis and were benthic in habit.

At intervals during the 16-day period, capsules were removed from the mass and slit open to release embryos for observation alive. Camera lucida drawings were made of specimens narcotized with 10% alcohol, magnesium chloride proving ineffective at normal narcotic concentration.

EXTERNAL FEATURES OF DEVELOPMENT.

The fertilized egg of *C. spengleri* is opaque, spherical, 120μ in diameter, creamy white in colour, and covered by a very thin egg membrane closely adherent to the egg (Text-fig. 3). Before cleavage begins the membrane disappears, and the cleavage blastomeres are only loosely held together in the early cleavage stages. The egg is very yolky, large yolk globules being uniformly distributed throughout the cytoplasm.

The first two cleavages are almost equal, but the third is very unequal, giving a quartette of small micromeres at the animal pole and four large yolky macromeres at the vegetal pole. Cleavage follows the normal spiral pattern, but all the micromeres



Text-fig. 3-13. *Cymatilesta spengleri*: 3. Fertilized egg. 4. 5 hr. blastula, lateral view. 5. 14 hr. gastrula, lateral view. 6. Early trochophore, 17 hr., dorsal view. 7. Trochophore, 20 hr., dorsal view. 8. Trochophore, 24 hr., ventral view. 9. Early veliger, 36 hr., dorsal view. 10. Veliger, 2½ days, dorsal view. 11. Veliger, 3½ days, ventral view. 12. Veliger, 6 days, dorsal view. 13. Veliger, 8 days, dorsal view.

A, yolk; B, micromeres; C, lateral ciliated cells; D, stomodaeum; E, archenteron; F, oral hood; G, shell; H, foot; J, yolk masses.

are small, the major part of the yolk residing in the four vegetal pole macromeres. A solid blastula with a cap of animal pole micromeres is found about five hours after first cleavage.

Gastrulation proceeds wholly by epiboly, the micromeres multiplying and spreading over the macromeres (Text-fig. 4), at first equally on all sides, but later more rapidly dorsally and posteriorly, so that eventual closure of the blastopore takes place mid-ventrally from behind forwards, the anterior end of the blastopore remaining open as the future mouth. By the time gastrulation is complete the large yolky (endoderm) cells have begun to increase in number and the embryo shows some increase in size, though still retaining a spherical shape (Text-fig. 5). At this stage it is about 14 hours old.

During the next three hours the embryo elongates along the antero-posterior axis and becomes ovoid, pointed anteriorly and blunt posteriorly (Text-fig. 6). The superficial layer of yolk-free cells remains very thin, while the endoderm cells are further increased in number and can now be seen to surround a central space, the archenteron. On either side at the widest part of the embryo one of the superficial cells becomes enlarged and projects above the general surface, showing a large clear nucleus. By the time the embryo is 20 hours old these cells have become ciliated, and a further area of short cilia has appeared at the posterior end (Text-fig. 7). At the anterior end multiplication of the superficial cells is beginning, giving a layer more than one cell thick. The embryo now corresponds to a trochophore in which, associated with the presence of yolk, the larval organs are largely suppressed.

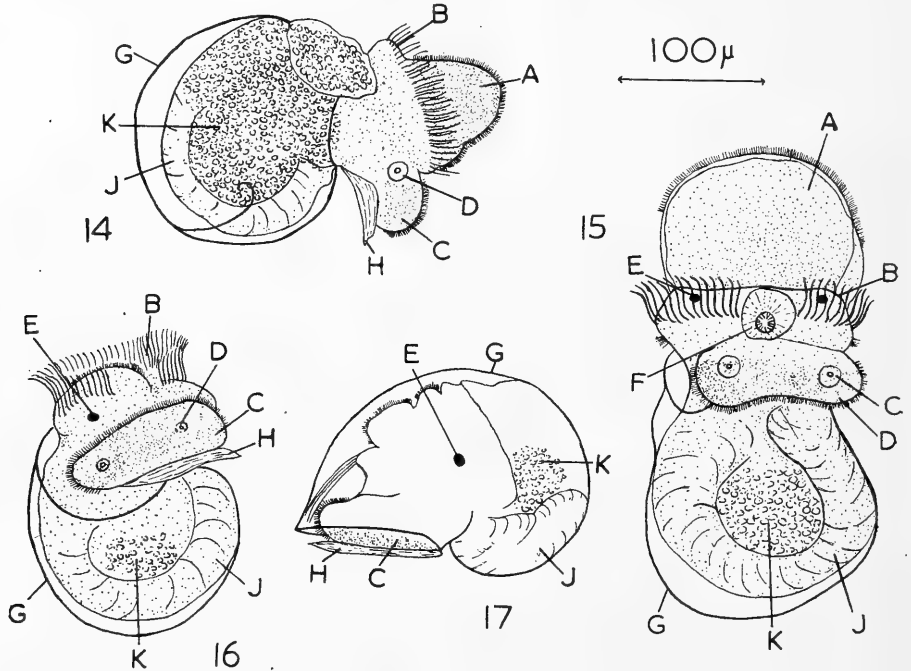
With further development the outline of the trochophore becomes better defined, the anterior end becoming more pointed. The cilia on the large lateral cells disappear, but by 24 hours a new ciliated area is present at the anterior end (Text-fig. 8). The outline of a cylindrical stomodaeum can also be seen, while the archenteron now shows as a central cylindrical space running along the antero-posterior axis, at right angles to the stomodaeum.

In the succeeding 36 hours (Text-fig. 9, 10) very little increase in size takes place, but the shape of the embryo changes in various ways. The main mass of the body containing the yolky endoderm becomes spherical and sharply demarcated from the anterior ciliated region, which broadens as a flattened oral hood overlying the stomodaeum and bearing short cilia on its convex upper (dorsal) surface. The cilia beat vigorously, driving a current backwards over the body, but cause no movement through the jelly at this stage. Neither is there any muscular movement. The posterior patch of cilia is displaced towards the left as a result of asymmetrical growth of the body, and a further patch develops laterally on the same side. The significance of these cilia is obscure.

The embryo now begins to increase in length, in size of the oral hood and in clarity of definition of the stomodaeum, which now has a ciliated lumen (Text-fig. 11). The remainder of the body remains opaque and yolky, obscuring the internal changes taking place. The $3\frac{1}{2}$ -day embryo, however, shows one new surface feature in the presence of a small cap shell at the posterior end of the body, towards the right side, secreted by an ectodermal thickening, the shell gland.

During the next three days, with little further increase in the size of the embryo, the shell spreads anteriorly over the dorsal surface and also downwards over the posterior end of the embryo as a broad cap (Text-fig. 12). The posterior and lateral cilia disappear, while a posterior fold of the body surface immediately underlying the shell marks the first origin of the mantle cavity. Mid-ventrally a transverse ciliated protuberance grows out, the rudiment of the future foot. The embryo is now clearly divided into head anterior to the shell, foot ventrally, and visceral hump covered by the shell. The yolk still obscures details of internal structure, but it is at this stage that the first muscular movement begins, a twisting of the posterior end of the visceral hump forwards and outwards towards the right, preliminary to torsion.

By the time the embryo is eight days old torsion of the visceral hump is complete (Text-fig. 13). The region joining the visceral hump to the head and foot narrows and behind it the hump becomes globular and shows the differentiating gut coiling posteriorly, then dorsally, over it. The shell also attains a globular form, with a wide mouth from which the head and foot project. Withdrawal into the shell is not possible at this stage. The oral hood is by this time deeply convex and differentiated into a narrower anterior and broader posterior part, heralding the formation of the velum. The foot increases in size as a transverse antero-posteriorly flattened projection covered on the anterior face and edges by numerous short cilia. The posterior face of the foot bears a small thin operculum. Embedded in the base of the foot on either side



Text-fig. 14-17. *Cymatilesta spengleri*: 14. Veliger, 9 days, lateral view. 15. Veliger, 10 days, ventral view. 16. Metamorphosing veliger, 16 days, ventral view. 17. Metamorphosing veliger, 16 days, lateral view, showing withdrawal into shell.

A, oral hood; B, velum; C, foot; D, otocyst; E, eye; F, stomodaeum; G, shell; H, operculum; J, intestine; K, yolk.

is a spherical, hollow otocyst containing a small, round, refractile otolith. The foot and head are now almost devoid of yolk, and the embryo appears at this stage to extrude yolk masses enclosed in a thin layer of cytoplasm from either side just anterior to the shell margin. The reason for this is not clear.

Growth and differentiation proceed rapidly over the next two days (Text-fig. 14, 15). The yolk gradually disappears in the visceral hump, with accompanying differentiation of the viscera, especially of the coiled gut, which now shows peristalsis. The shell, showing clear evidence of spiral form, enlarges and widens at the mouth, and a columella muscle faintly visible on the left side of the visceral hump in the living embryo is able to effect partial withdrawal of both head and foot into it. The foot becomes broader and its operculum larger and thicker. In the head, the anterior part of the oral hood becomes greatly enlarged and covered with short cilia dorsally, while the posterior part broadens and grows ventrally towards the stomodaeum, forming a circular rim on which are borne the long, strongly beating cilia of the velum. The velar cilia beat backwards, with typical propulsive and recovery strokes, and also in a

clockwise direction viewed from the anterior end, in such a way that metachronal waves of beating pass successively round the velar rim. The total effect of the cilia on the head is to drive the embryo forward through the jelly, and observation of an egg mass at this time gives the impression of vigorous activity.

Within the velar rim and around the stomodaeum, rudiments of the adult head are now beginning to become organized, and a pair of black eyespots is especially conspicuous on either side of this part of the head. No obvious response to unidirectional light is detectable, however, in embryos of this age.

The velum enlarges further on the twelfth day and projects as two lateral lobes from the sides of the head. Following this, a period of four days supervenes during which there are no gross changes in external form, though a gradual diminution in the remaining yolk in the visceral mass and an increase in muscular movement of all parts of the embryo indicate continuing histogenesis. The sixteenth day of development, however, yields the onset of a new period in the life history with retrogression of the "larval" organs of the embryo and hatching from the capsule. The anterior part of the oral hood is rapidly resorbed, together with the large lateral lobes of the velum, so that the head becomes bilobed and compact, with the two eyespots anteriorly and a tight velar ring around its margin (Text-fig. 16). With this change, the entire anterior end can now be withdrawn into the shell and the mouth of the shell closed by the operculum (Text-fig. 17). Locomotion is still brought about by the velar cilia, but these now beat not continuously but in coordinated short bursts, stopping and starting together. At about this time the capsule wall breaks down at the free end, apparently as a result of putrefaction, and the embryos escape rapidly from the jelly into the surrounding sea water. They are benthic in habit from the start, the ratio between the power of the reduced velum and the size of the body being too low to allow swimming except very close to the substratum. Crawling and active feeding presumably soon follow.

DISCUSSION.

The summary of information on the life histories of British prosobranchs given by Lebour (1937) provides a background against which the life history of *C. spengleri* can be viewed. It is characteristic of the mesogastropod prosobranchs that their eggs are laid in thick-walled protective capsules filled with a gelatinous, usually nutritive medium in which the eggs float. Each egg has a very thin egg membrane which disappears early in development, and follows a course of development through spiral cleavage to a well-developed veliger larva. In these respects *C. spengleri* is typical of its group. Lebour clearly shows, however, and Thorson (1946) amply confirms, that hatching from the capsule may vary even within closely related species from the veliger stage, followed by a long planktotrophic life, to the fully metamorphosed stage, followed by a crawling benthic existence. *C. spengleri*, typical of species with a heavily yolked egg, approximates to the latter condition; but it cannot be assumed that other cymatids will have life histories lacking a planktonic stage.

Acknowledgements.

I should like to thank Miss I. Bennett for advice on the collection of material and for the photographs of Plate ix, A, B, Professor P. D. F. Murray for the photograph of Plate ix, C, and Mr. W. H. I. Dawbin for discussion of the paper in manuscript.

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EXPLANATION OF PLATE IX.

A, B. *Cymatilesta spengleri*. Female and egg mass ($\times \frac{1}{2}$). C. *Cymatilesta spengleri*. Veligers, 11 days.

A NEW MITE PARASITE (*HARPYRHYNCHUS*) FROM THE ROSELLE PARAKEET
(TROMBIDIFORMES, ACARI).

By R. F. LAWRENCE, Natal Museum, Pietermaritzburg, South Africa.

(Communicated by Dr. A. R. Woodhill.)

(Two Text-figures.)

[Read 29th July, 1959.]

Synopsis.

A new species of avian skin parasite, *Harpyrhynchus rosellacinus*, belonging to the order of Trombidiform mites, is described. The mite was taken from a cyst in the skin of the roselle parakeet and is the first *Harpyrhynchus* to be described from an indigenous Australian bird.

INTRODUCTION.

During 1958 Dr. Marc André, of the École pratique des Hautes Études, Ministère de l'Éducation Nationale, Paris, sent me a number of avian parasites from the Trouessart Collection; among them was a good series of mounted specimens of a new species of *Harpyrhynchus* from the roselle parakeet *Platycercus eximius*. This appears to be the first indigenous representative of the genus from Australia and as such is of some interest, also in view of the fact that in general it differs very little from the various species of the genus found in Europe and Africa while resembling two of these in some detail. The slides were labelled *Sarcoborus* (a synonym for *Harpyrhynchus*) *crista-galli* Berlese & Trouessart, which is obviously a slip, as the *Harpyrhynchus crista-galli* described by these two authors (1889, p. 139) from the African speckled Coly, *Colius striatus*, has a quite different and very characteristic appearance; it has recently been figured and redescribed by Lawrence (1959, fig. 1).

I am greatly indebted to Dr. Marc André for allowing me to describe this new form. The Holotype slide and the bulk of the material have been returned to the collection of which Dr. André is in charge, while a paratype slide will be deposited in each of the following institutions: The Australian Museum, Sydney, Australia, and the Natal Museum, Pietermaritzburg, South Africa.

Family HARPYRHYNCHIDAE Dubinin.

Genus HARPYRHYNCHUS Mégnin.

HARPYRHYNCHUS ROSELLACINUS, n. sp. (Figs. 1, 2).

Material: A mounted series of 33 adult females and 11 larvae on 13 slides, taken from a cyst in the skin of the parakeet *Platycercus eximius* at Sydney (no further data), in the collection Trouessart.

Holotype: One slide with 4 adult females. *Paratypes*: Three slides with 5, 2 and 1 adult females respectively.

Dorsal surface as in Figure 1a, dorsal shield clearly defined, a little longer than wide, with two setae situated just within its anterior border, these a little longer than the pair laterally and a little posteriorly to the peritremes, and subequal to the lateral setae between the insertion of legs I and II. Lateral margin between legs II and III with two similar setae situated close to each other, the one on the edge of the body, the other (a little in advance of it) inserted on the dorsal surface. All these setae with fine accessory hairlike serrations, a little stronger in the two last-named setae, all the remaining setae of the body and legs simple.

Ventral surface as in Figure 2 (of a larger paratype ♀), the setae arranged as in Figure 2, rising from large circular disc-like areas; posterior margin of body in the middle with a short slender seta on each side of the anal opening, very near the margin but definitely inserted on the ventral surface.

Pedipalps as in Figure 1c, seen from above, enlarged, from below as in Figure 2; dorsal surface with 3 large serrate hairs, the anterior one thickest and with about 18 tooth-like serrations arranged in a regular row on its dorsal margin, these modified hairs situated well in anterior third of the dorsal swelling; in addition a stout simple



Fig. 1. *Harpyrhynchus rosellacinus*, n. sp., ♀. a, dorsal surface (holotype); b, leg I in dorsal view ♀ (paratype); c, pedipalp in dorsal view enlarged (paratype).

seta rising from near the middle point of the pedipalp and laterally to the centre, this seta unusually long, easily surpassing the peritremal openings on each side; basal segment of pedipalp with 2 conspicuous setae on its ventral surface (Figure 2).

Legs: Leg III with 2 or 3, IV with only 2 very short rounded segments; III with 4 or 5 long terminal setae (5 probably the correct number) of which 3 are considerably thicker and longer than the two others; leg IV with 3 terminal setae, 2 being long and thick (Fig. 1a, 2). The thickest seta of tarsus III a little stouter than the thickest of

tarsus IV, the length of these two setae subequal and about equal to the total length of body. In Figure 1a the anterior legs of the holotype are bent over and downwards so that their apices are obscured; Figure 1b of another adult female shows leg I seen from above in full extension.

Dimensions: Length and width of holotype ♀ (mouth-parts included), 310 μ and 264 μ respectively; of a larger paratype ♀, 370 μ and 278 μ .

Larva: Round, wider than long, with only three pairs of well-developed legs, the two anterior ones with relatively much longer setae than in the adult, but with similar

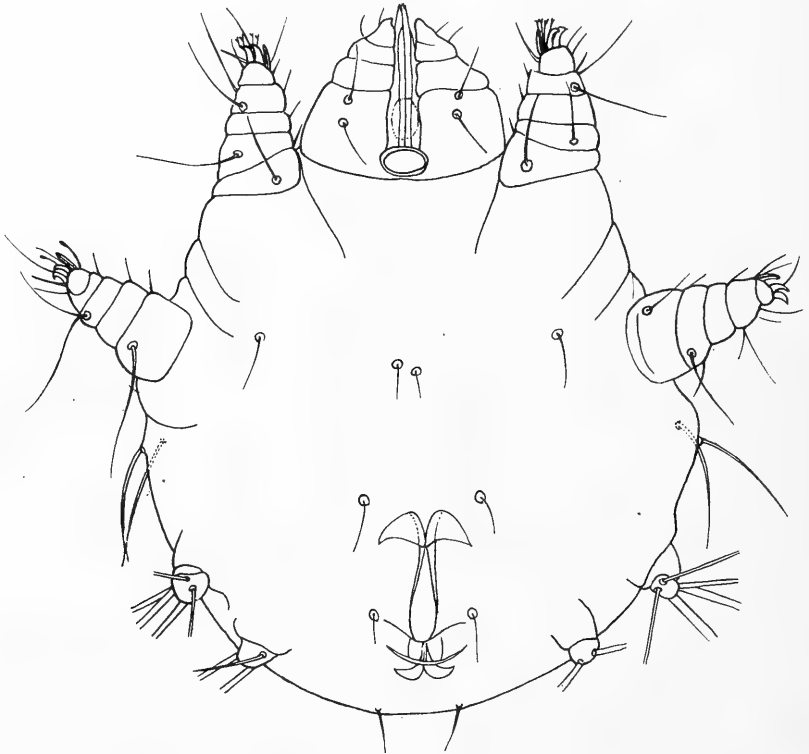


Fig. 2. *Harpyrhynchus rosellacinus* n. sp. Ventral surface of a paratype ♀.

claws and other terminal structures; leg III with 2 or 3 short, rounded segments, the apical one with three setae of different lengths, the second longest much exceeding the longest setae of the anterior legs, the longest about 1½ times the total body length.

Dorsal plate well defined, pedipalp well developed, with 3 modified hairs dorsally similar to those of adult, but no long simple seta posterior to these.

Dimensions: Total length and width of body, 120 μ and 127 μ respectively; longest seta of leg III, 209 μ .

No nymphs or male specimens are represented in the material before me. A number of encapsulated eggs are mounted with adult females on some of the slides; long setae and appendages at various stages of development can be seen through the capsules of the eggs which seem to be embedded in a structureless colloidal substance, possibly the contents of the cyst.

Affinities: The parasite resembles two species of *Harpyrhynchus* more closely than any others, *nidulans* Mégnin and *tracheatus* Fritsch. In having the dorsal setae provided with fine, almost invisible serrations, it resembles *nidulans* rather than *tracheatus*, but differs from it in the modified dorsal hairs of the palp being much

more heterogeneous in size and provided with stronger, more numerous and more regular serrations; the long smooth seta behind these hairs is either absent in *nidulans* or situated on the lateral surface; furthermore, the arrangement of the ventral setae of the abdomen is quite different in the two species and the number of long terminal setae on legs III and IV is also different, these being respectively 6-8 and 5-6 according to the illustrations of Fritsch for *nidulans*, 1954, fig. 1 (5-7 and 4 respectively according to the figures given by Dubinin, 1957, p. 97-99, figs. 23 and 25, for the same species).

From *tracheatus* it differs in the smooth dorsal seta of the pedipalp enlargement being much longer and situated further posteriorly, reaching beyond the peritreme, while in *tracheatus* it falls far short of it. The dorsal shield is comparatively wider and the setal pattern of the ventral surface is different from that of *tracheatus*, but the number of long terminal setae for legs III and IV is the same.

Taking all these characters into consideration, *rosellacinus* appears to resemble *tracheatus* more closely than any of the hitherto described forms, but is distinct from it; *tracheatus* was taken by Fritsch from a host belonging to a very different order of birds since it was found on the common buzzard of Europe, *Buteo buteo*.

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FLORAL STRUCTURE AND ANATOMY IN THE FAMILY GOODENIACEAE
DUMORT.

By R. C. CAROLIN, University of Sydney.

(Forty-five Text-figures.)

[Read 29th July, 1959.]

Synopsis.

The floral anatomy of most genera in this family has been examined. It is concluded that the ovary of the Goodeniaceae is 4-carpellary, although various reductions and fusions obscure this. The ovary is fairly constant in form; a basal 2-locular zone, a medial unilocular zone and an uppermost 2-locular zone, the latter two being sterile. The relative sizes of these zones give the appearance of partial or complete 1-locular or 2-locular conditions. Solidification of one loculus may also give an apparently 1-locular condition. The inferior condition of the ovary may, in general, be considered to have arisen by fairly superficial mass growth, i.e., by fusion of the outer floral parts to the ovary. The evolution within the family is considered in the light of these investigations. It is noted that floral form alone hardly indicates a Campanulaceae origin.

INTRODUCTION.

The use of vascular patterns as a guide to structure has been a controversial technique. The crux of the problem appears to be the lack of knowledge of the fundamental cause of the initiation of a vascular strand. Puri (1951), Douglas (1944, 1957), and Eames and Macdaniels (1947) have summarized the arguments in favour of the conservative nature of vascular patterns. It is not intended to reiterate these arguments, suffice it to say that they appear reasonable. These patterns are controlled by the genotype of the plant and, because of their relative constancy, it can be assumed that the genetic systems responsible for them are well "buffered" against interference from the environment. The numerous cases of vascular strands pointing to the assumed positions of aborted organs implies that this genetic system is "conservative", i.e., new floral forms are superimposed on the previous vascular structures. Thus the vascular pattern of the flower can be used as a guide to changes in genotype, i.e., phylogeny.

Colozza (1907, 1908) has described the vegetative anatomy and Brough (1927) examined the ontogeny of the flower of a single species. Saunders (1939) gives some data on a few genera; this is not complete and the interpretation is coloured by the theory of carpel polymorphism. This theory is considered to be an unnecessary complication.

MATERIAL AND METHODS.

Mature flowers and often young fruits were embedded in wax in the usual manner using chloroform as the wax solvent. Both transverse and longitudinal sections were cut at a thickness of 15 μ . The sections were stained with crystal violet and counterstained with erythrosin. In most cases fresh material was fixed in formalin-acetic-alcohol. In a few cases herbarium specimens were soaked in warm detergent before embedding in wax. The results are presented as diagrams in the main; only a few of the drawings of the serial sections have been reproduced here. In view of the fact that a number of species are known to show variability in their floral vascular patterns (Hall, 1956) a number of specimens (between 5 and 15) were examined for each species. The nomenclature of the vascular strands is that used by Eames and Macdaniels (1947).

OBSERVATIONS.

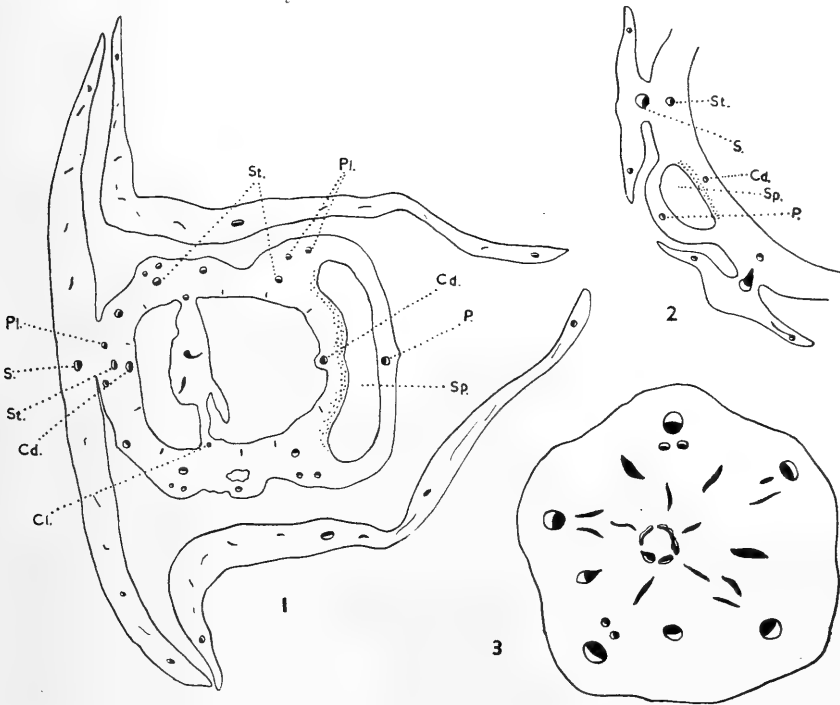
The carpels appear to be considerably modified and the loculi walls are probably formed by several carpels. The term pseudocarpel is therefore used in this presentation of the results to include the walls of each loculus and the corresponding part of the septum (see below).

The point of reference for the genus may be taken as *Velleia* with a superior ovary and semi-epigynous stamens. This genus will be described rather more fully and the others compared with it.

VELLEIA Smith.

There are two main floral types within the genus, those with five sepals and those with three.

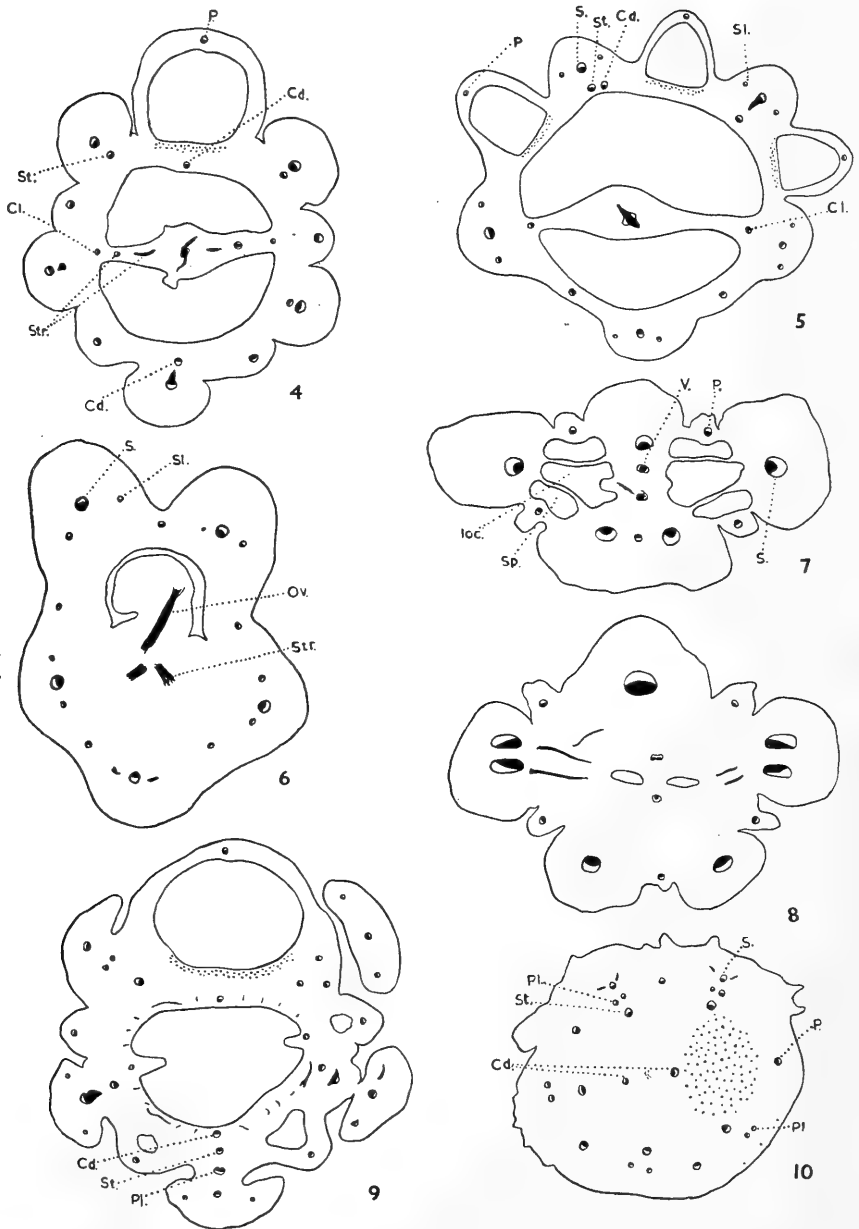
V. paradoxa R.Br. has five sepals. The first vascular strands which diverge from the central stele of the receptacle are on the sepal radii; almost immediately above these the strands on the petal radii also diverge and these latter almost immediately branch into three. The two lateral members of each group unite with the strands on the sepal radii, one on either side, whilst the central strand continues on into the petals without further change. Five further bundles diverge from the central stele on the



Text-figures 1-3.

1. *Velleia lyrata*, t.s. of lower flower. 2. *Goodenia scapigera*, part of pseudo-ovary. 3. *Goodenia decurrens*, t.s. of receptacle showing vascular strands before their fusion.

sepal radii (presumably the staminal bundles) which unite with those already on these radii (Fig. 3). The vascular elements remaining in the central stele resolve into four or five strands which further unite into two strands diverging outwards and a single strand in the centre. Those diverging outwards (pseudocarpellary dorsal bundles) are on the post-ant. axis, the posterior one uniting with the posterior strand on the sepal radius and the anterior one doubling backwards into the spur. The outer floral whorls themselves are fused to the ovary at the base; the sepals become free first, except for the posterior one which remains united to the ovary for some considerable distance. In the lower quarter of the flower the petal lateral, staminal and post-pseudocarpellary dorsal bundles all diverge from the appropriate strand on the sepal radii, which latter passes into the sepal itself where it branches into three. The petals diverge somewhat higher up as a complete tube (Fig. 1, 2) into which the petal strands pass. Still higher the stamens diverge, also supplied by their own vascular



Text-figures 4-10.

4. *Goodenia decurrens*, t.s. of lower part of pseudo-ovary. 5. *Anthotium rubriflorum*, t.s. of pseudo-ovary. 6. *Dampiera stricta*, t.s. of pseudo-ovary at level of ovular insertion. 7. *Leschenaultia biloba*, t.s. of pseudo-ovary. 8. *Leschenaultia biloba*, t.s. of ovary dome. 9. *Goodenia decurrens*, t.s. of upper part of pseudo-ovary. 10. *Scaevola albida*, t.s. of ovary dome.

S, sepal main; Sl, sepal lateral; P, petal main; Pl, petal lateral; St, stamen; Cd, Ps-carp. dorsal; Cl, Ps-carp. lateral; V, Placental; Sp, spur or space.

supply (Fig. 3, 31). This fusion of the various vascular supplies and their subsequent separation from each other is illustrated in Figure 40, although in this case the separation occurs lower in the flower than in *Goodenia*. The anterior petal is drawn out into a spur whilst the anterior wall of the ovary is nectiferous. The remnants of the central stele pass into the placentae as an irregular bundle. Very low down two bundles pass out from it along the septum and take up a position at the junction of septum and ovary wall (ps.-carp. lat. bundles). The central bundle progresses up into the septum and branches of it supply the ovules. In addition two further sterile bundles pass out on either side towards the ovary wall and there fuse with the pseudo-carpellary lateral bundles (see Fig. 4). The remaining vascular tissues are entirely used up in supplying the uppermost ovules.

The ovary represents the standard Goodeniaceous type, the general form of which is repeated throughout the family. In the lowest part the ovary is divided by a single septum with an axile placenta (Fig. 1, 4). About halfway up the ovary a split appears in the axis, thus giving a semblance to parietal placentation (see Fig. 9). Very few ovules, or none at all, are inserted in this region; they are mainly found in the lowermost zone. Just below the ovary summit the inturned edges of the pseudocarpels meet once again, regenerating the apparently bilocular condition. Thus there is a lowermost "bilocular" zone, a medial "unilocular" zone and an uppermost "bilocular" zone (Fig. 31).

The style is supplied by the pseudocarpellary dorsal and lateral bundles which do not, however, pass into the style unchanged. They bifurcate as shown in Figure 11, and these branches fuse as indicated to give the condition of four bundles as shown in Figures 12 to 15. These four bundles are arranged over the loculi, none over the junction of septum and ovary wall as would be expected if the loculi represented individual carpels. Immediately below the indusium these bundles undergo a series of bifurcations to form a ring of vascular tissue.

V. lyrata R.Br.—This species has three sepals, but otherwise is very similar to the previous species. The lateral sepals are united to their anterior lateral partners and the vascular supply of these compound sepals still retains some degree of separateness (Fig. 1).

V. montana Hook. f.—Essentially the same as the preceding species.

SYMPHYOBASIS.

S. macroplectra (F. Muell.) Krause.—Unfortunately no material of this interesting monospecific genus was available. It would appear to be similar to *Velleia* except that the corolla and stamens are virtually epigynous, whereas the sepals are almost entirely hypogynous, i.e., the ovary is superior.

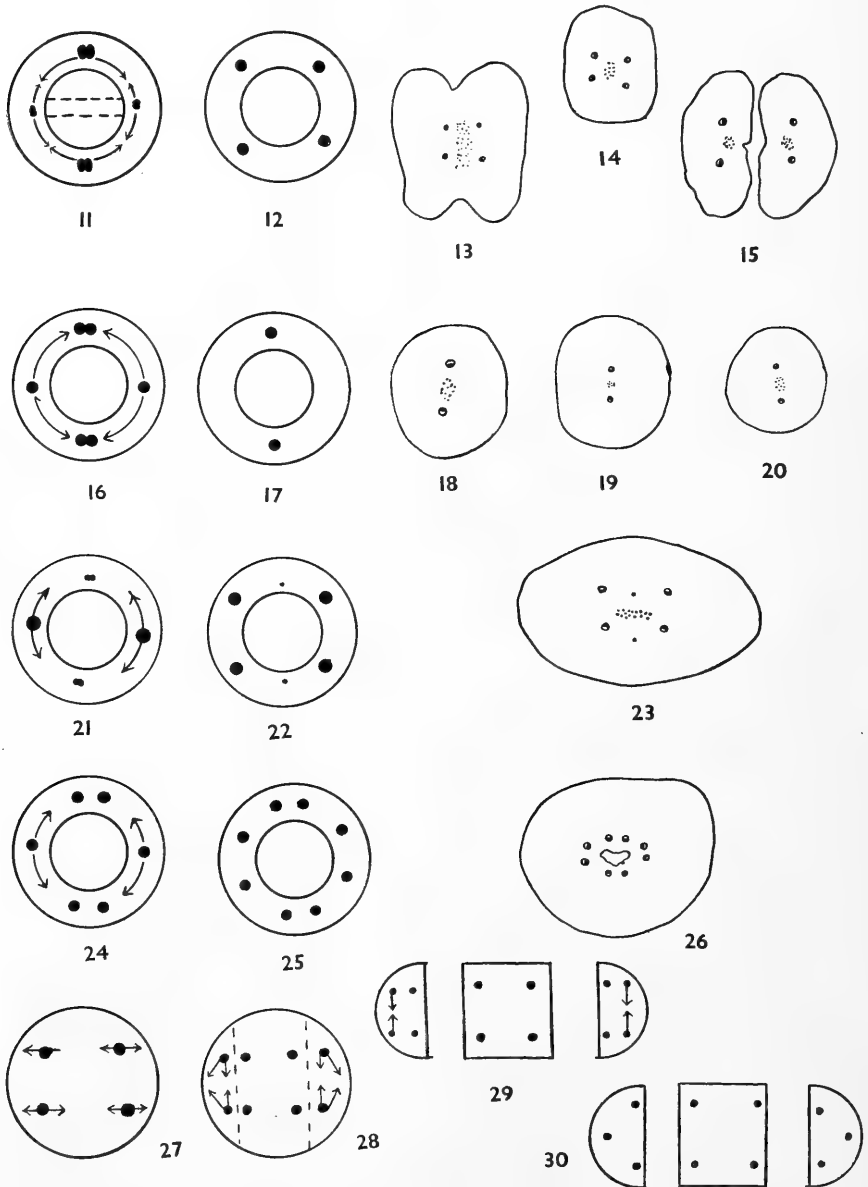
GOODENIA.

G. decurrens R.Br.—The basic plan is similar to that found in *Velleia paradoxa*. The sepals and other outer floral whorls separate from the ovary wall at a much higher level and the condensation of the vascular system is correspondingly increased (Fig. 4, 9, 32). The ribs on the floral tube each contain a bundle which divides at the point at which the rib diverges from the ovary wall as a sepal, into six as shown in Figure 40, although the bundle supplying the stamens may diverge somewhat lower (Fig. 4). These bundles are: sepal main, two sepal lateral, petal laterals and staminal. In addition the posterior bundle on the sepal radius gives rise to one of the pseudo-carpellary dorsal bundles (Fig. 40). These ribs have a different texture, and in some other species a different indumentum, from the grooves between them. The texture and the indumentum correspond exactly to that of the sepals which are formed by the separation of these ribs from the pseudo-ovary wall. The grooves are supplied with single bundles which pass directly into the petals as petal main bundles. The anterior pseudo-carpellary dorsal bundle diverges from the bundle on the anterior petal radius at a low level in the pseudo-ovary wall and is separated from the ovary wall

proper by a spur or pocket (Fig. 4, 9, 32). In other respects the vascular pattern is similar to *Velleia* (also see Fig. 14, 40).

G. ovata Sm. and *G. bellidifolia* Sm. showed only minor differences.

G. heterophylla Sm.—In this species the sepals do not diverge from the pseudo-ovary wall until very close to the summit of the ovary and there is a corresponding condensation of the vascular tissue.



Text-figures 11-30.

11, 12. Derivation of stylar vasculature in 4-strand styles. 13. *Velleia paradoxa*, style. 14. *Goodenia bellidifolia*, style. 15. *Goodenia pusilliflora*, style. 16, 17. Derivation of stylar vasculature in two strand styles (except *Brunonia*). 18. *Dampiera stricta*, style. 19. *Scaevola hookeri*, style. 20. *Anthotium rubriflorum*, style. 21, 22, 23. Stylar vasculature of *Scaevola ramosissima*. 24, 25, 26. Stylar vasculature of *Leschenaultia*. 27, 28, 29, 30. Vasculature of stylar branches in *Calogyne pilosa*. Varying levels in style; 27 lowest, 30 highest.

G. pusilliflora F. Muell.—Although agreeing with *G. decurrens* in most respects, the only specimens of this species which were examined had 2-fid styles. This branching reached almost to the base of the style and the cleft was at right angles to the ovary septum, each branch containing two vascular strands (Fig. 15) which have been formed in the same way as in *G. decurrens*.

G. paniculata Sm.—This species is a member of the Section *Pluriseratim* Benth. or *Amphichila* DC. The floral construction is similar to that of the other species described except that the ovules are inserted in a number of rows on the placentae instead of in two rows.

G. scapigera R.Br.—This species is a member of the section *Monochila* Benth. Once again it differs from the other species examined in minor details only, the most interesting being the attachment of the ribs (sepals) to the pseudo-ovary wall (Fig. 2). This attachment is by a narrow strip of tissue only; the whole inner surface of the sepaline rib is not adherent to the rest of the pseudo-ovary wall as in the previous species.

CALOGYNE.

C. berardiana (Gaudich.) F. Muell.—The floral structure of this species resembles that of the *Goodenias* very closely. The distinctive character is considered to be the 2-fid style, the structure of which is exactly similar to that of *G. pusilliflora* (see above).

C. pilosa R.Br.—This species differs from the *Goodenias* only in the presence of a 3-fid style. This branching occurs quite close to the indusium, the vascular supply of the branches being supplied by branches from the four standard bundles in the manner indicated in Figures 27-30. From these diagrams it is obvious that the stylar condition bears little relationship to that found in the previous species or to the carpellary condition of the ovary.

SELLIERA.

S. radicans Cav.—This genus has essentially the same floral structure as that found in the *Goodenias*. The sepaline ribs, however, are not evident as such and the pseudo-carpellary dorsal bundles separate from the corresponding outer bundles (see Figure 40) very low in the pseudo-ovary wall. The spur is reduced to a small anterior pocket.

VERREAUXIA.

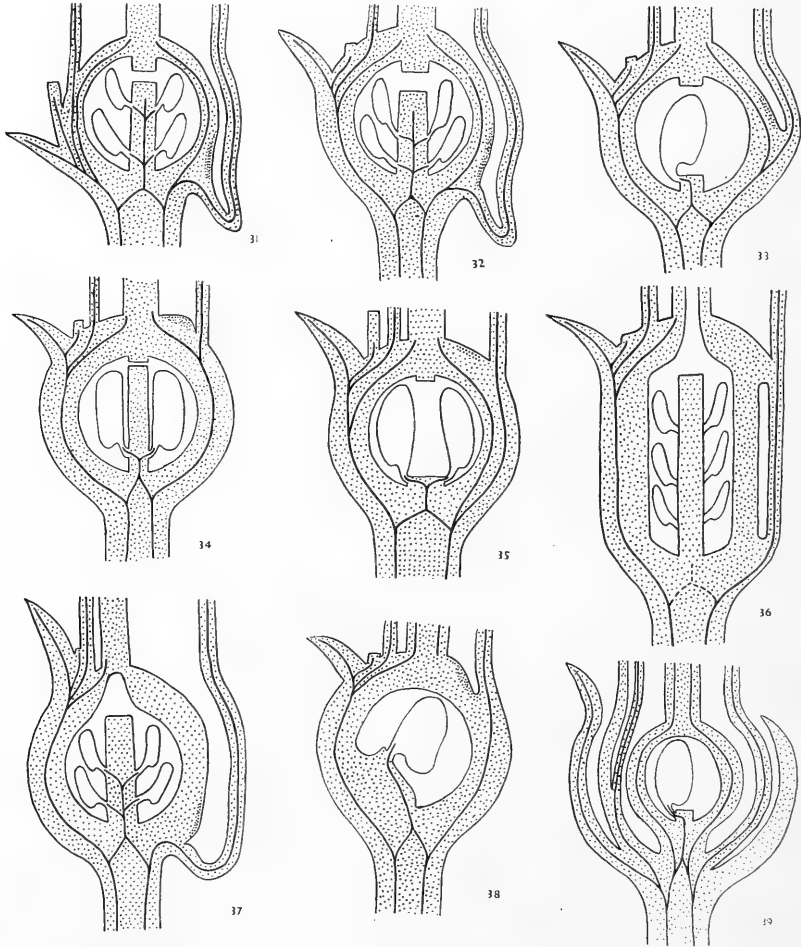
V. reinwardtii (de Vriese) Benth. The structure of the pseudo-ovary wall is essentially the same as that of the *Goodenias* (Fig. 33) and the derivation of the vascular supply of the separate organs is the same (see Fig. 40). The main difference is to be found in the ovary itself which is usually described as 1-locular with a solitary ovule. In fact the standard ovary form is present, but the lowermost "bilocular" zone and the uppermost "bilocular" zone are very small. The ovule is inserted in the posterior position on the short, lower septum. The sterile septal bundles do not occur, but otherwise the vascular pattern is similar to that found in the *Goodenias* (Fig. 33, 45).

SCAEVOLA.

Three main types of ovary are found in this genus as described by Krause (1912): (i) "bilocular" with one ovule per loculus; (ii) "unilocular" with two ovules in the loculus; (iii) "unilocular" with one ovule in the loculus.

S. albida Sm.—This species has type (ii) ovary, but once again it is found that the structure is really that of the generalized type as found in the previous genera. The basal "bilocular" zone is considerably reduced and one ovule is inserted on either side of the short septum. Immediately beneath the style the "bilocular" condition is regenerated. Ten bundles diverge from the central receptacular stele almost at the same time. These pass outwards into the pseudo-ovary wall unaltered. There are no ribs on the outside of this wall. Five of them on the sepal radii behave in the same way as those in the same position in *Goodenia*, the other five on the petal radii likewise

(Fig. 40, 10). There is, however, no spur and the anterior pseudocarpellary bundle diverges from the corresponding petal bundle at the summit of the ovary and not before (see Fig. 34). After the ten main bundles have diverged from the central stele the remnants resolve into a single bundle with irregular patches of phloem around a central xylem core. Below the septum, i.e., in the receptacle, this bundle branches into three, two passing outwards to the junction of septum and ovary wall (pseudocarpellary laterals) and the central one continuing into the placenta and supplying the ovules (Fig. 34).



Text-figures 31-39. Longitudinal diagrammatic sections of pseudo-ovary.

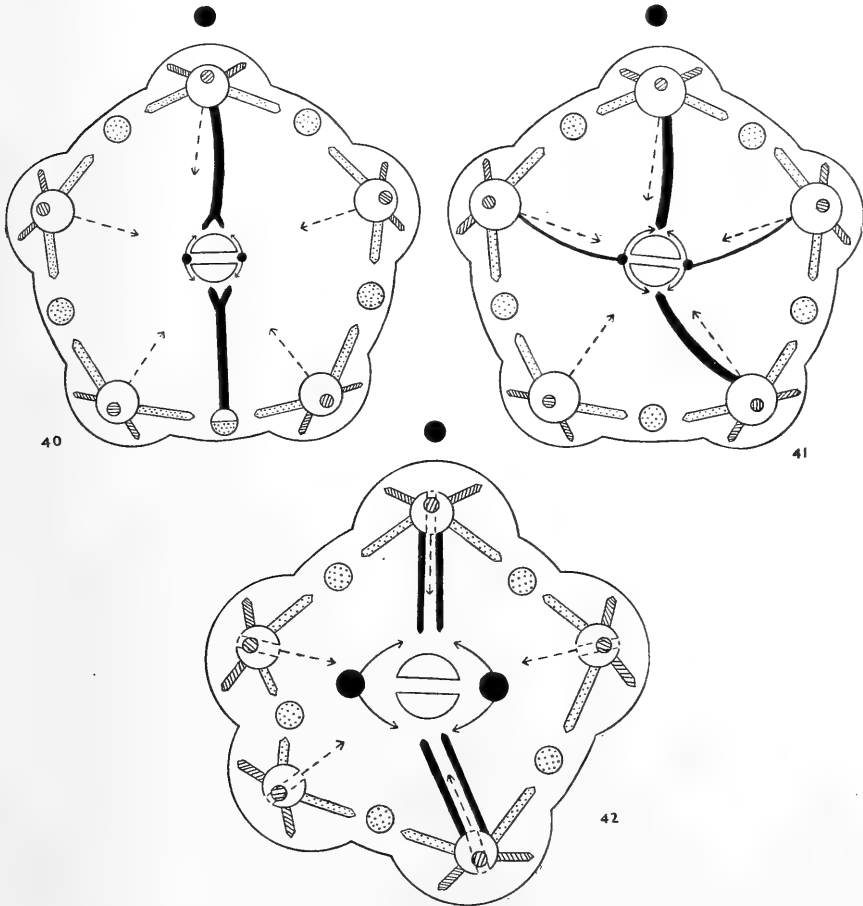
31, *Velleia*; 32, *Goodenia*; 33, *Verreauxia*; 34, *Scaevola (spinescens)*; 35, *Diaspisis*; 36, *Leschenaultia*; 37, *Anthotium*; 38, *Dampiera*; 39, *Brunonia*.

S. spinescens R.Br.—This species has type (i) ovary. Apart from the presence of an unvascularized septum extending almost to the top of the ovary there is little difference between this and the preceding species. The basal "bilocular" zone is thus very large whilst the medial "unilocular" zone is very small (Fig. 34, 45).

S. hookeri F. Muell.—Similar to the previous species, but the style contains two vascular bundles derived as shown in Figures 16, 17 and 18.

S. ramosissima (Sm.) Krause.—This species displays a number of differences from the patterns described for the previous ones. Generally the structure is the same as that found in *S. spinescens*, but the derivation of some of the vascular bundles at the ovary

dome is different. The sepal lateral bundles actually diverge from the bundles on the petal radii, a condition found nowhere else in the family so far. The pseudocarpellary dorsal bundles are very weak and when they reach the base of the style they do not bifurcate; the lateral bundles do, however, and the resultant bundles remain free. This produces a six-strand condition in the style of this species (Fig. 21-23).



Text-figures 40-42. Derivation of vascular bundles at the ovary dome.

40. *Goodenia* group. 41. *Dampiera* group (in *Anthotium* the ps.-carp. lateral are united to a sepal bundle). 42. *Leschenaultia*. // // // Sepal Traces, . . . Petal Traces, — — — Stamen Traces, ● Carpel Traces.

S. fasciculata Benth. and *S. helmsii* Pritzel.—These species have type (iii) ovary. Their floral structure is more comparable to that of *Verreauxia*. Not only is the structure of the ovary the same, but a spur is present containing the nectary which is not situated on the top of the ovary as in the other *Scaevolas*.

DIASPASIS.

D. filifolia R.Br.—The only species described to date in this genus. The floral structure is similar to that of *S. albida*. No ribs are present on the surface of the pseudo-ovary and there is no pocket or spur containing a nectary. The styler supply is derived in the same way as that of *S. hookeri*. The anterior pseudocarpellary dorsal bundle is free for the greater part of the pseudo-ovary wall (Fig. 35).

LESCHENAULTIA.

L. biloba Lindl.—Externally the pseudo-ovary has four ribs, one of which is larger than the others and is shallowly grooved. Ten bundles diverge from the receptacular stele almost at the same level, three of these passing into the smaller ribs, four into the grooves between them and three into the large rib. This large rib appears to be the result of the confluence of two ribs and the groove between. If this is accepted the derivation of the vascular supply of the various floral organs at the ovary summit is similar to that found in the preceding species with the exception of the stylar supply (Fig. 7, 8, 36, 42). The bundles on the sepal radii very often become split into two (Fig. 7); this division is closed up again before the divergence of the bundles at the ovary dome except for the pseudocarpellary dorsals. These diverge from the posterior and an anterior lateral bundle on sepal radii, as double structures (Fig. 7, 42). They remain separate, passing on into the style as distinct bundles. The bifurcations of the lateral bundles provide eight separate strands in the style (Fig. 24–26). The remains of the receptacular stele resolve into two bundles which pass laterally and remain at the junction of the septum and ovary wall. These are the placental supply (Fig. 8) and apparently also represent the pseudocarpellary laterals of the other genera as they continue on above the level of ovular insertion and bifurcate at the base of the style (see above). The ovary does not quite correspond to the generalized form. The “bilocular” zone is well developed and the ovules are inserted in it; just beneath the style the septum splits and a “unilocular” condition is found, which continues on into the style, and there is no uppermost “bilocular” zone. The style is hollow and even open to the exterior via the indusium. Another very peculiar condition is evident in the pseudo-ovary wall. A definite space is present opposite the four bundles on petal radii contained within the grooves. This space separates the tissue surrounding the bundle from the (?) ovary wall proper. The space does not communicate with the exterior at all as it is closed over above; there is no question of its being nectiferous (Fig. 7, 8, 36).

L. linearoides DC., *L. divaricata* F. Muell., and *L. formosa* R.Br. are essentially the same as the preceding species.

ANTHOTIUM.

A. rubriflorum F. Muell.—The derivation of the vascular supply in the receptacle is similar to that found in the Goodenias. The placental supply is a single strand which provides pseudocarpellary laterals whilst still in the receptacle. There are five ribs on the wall of the pseudo-ovary and three deep spurs on the anterior petal radii (Fig. 5) and two much smaller ones on the posterior petal radii. The derivation of the vascular supplies from the bundles of the pseudo-ovary wall is similar to that of *Leschenaultia*. The main difference is to be found in the ovary supply. One pseudocarpellary dorsal diverges from the posterior sepal bundle close to the ovary summit, the other diverges from one of the anterior-lateral sepal bundles low in the pseudo-ovary wall and for the greater length of this latter it is free (Fig. 7). The staminal bundles also diverge from the corresponding sepal bundles, low in the pseudo-ovary wall. The two pseudocarpellary dorsals fuse with the bifurcations of the pseudocarpellary laterals to produce a two-strand condition in the style (Fig. 16, 17, 20). It should also be noted that the bundles on the sepal radii in the pseudo-ovary wall do not split, nor are the pseudocarpellary dorsals double as in *Leschenaultia*.

DAMPIERA.

With regard to floral structure there are two main types within this genus: (i) “bilocular” ovary with one ovule per loculus, (ii) “unilocular” ovary with a solitary ovule. Unfortunately no satisfactory material of the former was obtainable.

D. stricta R.Br.—This species is a member of the latter group. In spite of the term “unilocular” usually applied to this ovary it shows the generalized form, although considerably modified basally. The posterior pseudocarpel is solid (Fig. 6, 38, 45) for most of the basal zone. Immediately above the insertion of the single, anterior ovule,

this pseudocarpel becomes hollow and then the septum aborts, leaving the "unilocular" condition. Just beneath the style the "bilocular" condition is regenerated. There are five ribs on the wall of the pseudo-ovary, each rib corresponding to a sepal. Within these ribs, moreover, there are three vascular bundles, a main one and two lateral ones which are derived from the former low down. The main one divides at the ovary dome to give rise to the staminal strand and two petal laterals each. The posterior and one of the anterior lateral ones further give rise to the two pseudocarpellary dorsals (Fig. 41, 45). There are small nectiferous pockets opposite the grooves, which latter also contain a bundle outside the pocket, which passes directly into the petal. Brough is in error when he states that the nectaries are opposite the stamens. The derivation of the main bundles of the pseudo-ovary wall within the receptacle is similar to that seen in *Scaevola*. The remnants of this stele resolve into a single strand also as in *Scaevola* which passes upwards into the placenta. At the point of ovular insertion this bundle divides into three, one bundle to the ovule and the other two passing outwards to fuse with the posterior lateral bundles on the sepal radii (Fig. 6, 45). These, presumably, are the pseudocarpellary laterals. Evidence is provided for this by the distribution of vascular bundles to the stylar base; in addition to the pseudocarpellary bundles mentioned above the two posterior-lateral sepal bundles distribute a strand each to the base of the style. These strands bifurcate and fuse with the other two as indicated in Figures 16, 17, 41, giving a two-strand structure to the style (Fig. 20).

The insertion of the ovule and abortion of the solid pseudocarpel take place so close to the base that an impression of basal insertion is conveyed.

D. spicigera Benth.—Generally very similar to the preceding species, but the solid pseudocarpel is continued further up the wall of the ovary conveying the impression of lateral insertion. This is characteristic of the section *Linschotenia*.

D. purpurea R.Br.—Similar to *D. stricta*. The petal lateral bundles are free for the greater length of the pseudo-ovary wall and lie beside the sepal laterals in the rather obscure sepaline ribs.

BRUNONIA.

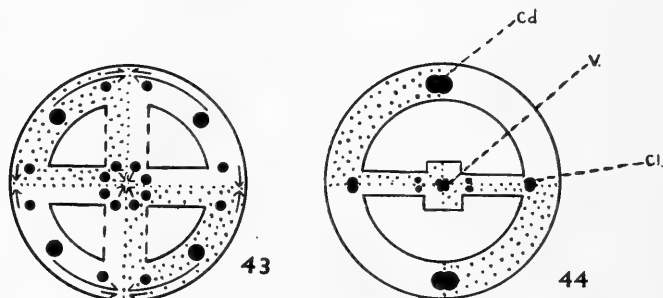
B. australis R.Br.—This species has a superior ovary and hypogynous, epipetalous stamens. Sepal, petal and stamen strands are all derived separately from the receptacular stele and do not fuse. The carpellary supply consists of two dorsals which diverge next, anteriorly and posteriorly, and the single strand resolution of the remnants in the septum. This latter passes directly into the ovule. The style is supplied directly by the dorsal strands without further division or fusion. The style is therefore two-stranded, although different in derivation from any of the other two-strand styles found in this family. The ovary shows a basal "bilocular" zone with the solitary ovule inserted on the short septum. There is no uppermost "bilocular" zone and most of the ovary is aseptate (Fig. 39, 45).

DISCUSSION AND CONCLUSIONS.

These results are summarized in diagrammatic form in Figures 31-42 and 44 which can be used as a basis for discussion.

The structure of the individual floral whorls follows the general pattern found in the Angiosperms with the exception of the ovary. Sepals and petals are, in the more primitive forms, supplied by a single bundle which divides into three, one main and two laterals. This is somewhat obscured, due to vascular condensation in the more advanced genera, but is clear in *Velleia*. In almost all genera examined the ovary can be divided into the three zones mentioned under *Velleia*. It is in vasculature of the ovary that a rather peculiar situation is found. The presence of sterile strands in the placental septum has to be explained, and the fact that the stylar vascular supply is not in the position that one would expect if the locules corresponded to carpels is also anomalous. Nevertheless, the situation can be explained in terms of the classical theory provided that the locules are considered to be derived from two carpels and not one.

The ancestral form of the Goodeniaceae is postulated to have had four carpels in the four lateral positions, each with five vascular strands, a dorsal, two laterals and two ventrals (Fig. 42). Concomitant with the abortion of the septa on the anterior-posterior axis there have been fusions of the vascular bundles as shown in Figure 43. This gives the four-strand condition of the *Velleia* ovary with a central placental supply; the two bundles from the original lateral septa, however, are sterile and diverge as the sterile septal bundles (Fig. 44). At the base of the style the vascular supply rearranges so that the four ancestral carpels are represented by one single strand each (Fig. 11, 12) in some forms or by varying numbers of strands in others (Fig. 21-25). Thus it is postulated that the pseudocarpellary dorsal bundles are, in fact, double or quadruple bundles, a conclusion supported by their bifurcation at the base of the style



Text-figure 43. 4-locular ancestral ovary showing fusions of vascular bundles (in the phylogenetic sense) to produce the Goodeniaceous ovary.

Text-figure 44. Ovary of Goodeniaceae, basic type.

and possibly by their twinned nature in *Leschenaultia* (although in this latter case it may be simply a reflection of the double nature of their parent bundles). It is considered that the ovary of this family has achieved a bilocular condition by fusion of carpels two by two and subsequent condensation of their vasculations rather than by simple abortion. Further development within the family has occurred by the acquisition of a virtually unilocular condition (along at least two different lines), reduction in ovular number and further condensation in the vasculature.

Before considering the relationships of the various genera it may be profitable to consider the question of the inferior ovary in the family. This question really involves much more than can be dealt with satisfactorily here. Puri (1952) has thrown some doubt on the usefulness of the vascular pattern in determining the nature of the pseudo-ovary wall. Douglas has attempted to counter this, but does not appear to have invalidated Puri's arguments entirely. Both of these workers have useful, although different, ways of looking at the same problem. It seems that the ovary of the Goodeniaceae becomes inferior by virtue of fusion of the outer floral whorls to the ovary wall (in the phylogenetic sense) which is here defined as due to relatively superficial mass growth in the ontogenetic sense. The similarity of the structure of the ribs on the pseudo-ovary wall and the sepals which continue them has been remarked upon in connection with *Goodenia*. The resemblance is even more striking in the case of *Dampiera stricta* where both ribs and sepals contain many sclereids, but the petals and the receptacle do not, and the ribs contain the same vascular pattern as the sepals. The presence of a single spur in those genera allied to *Goodenia* and several spurs in *Anthotium* also indicate that superficial zonal growth only is involved, otherwise the position of the spur would be closer to the ovary summit and one could probably expect some inversion of vasculature in this region. Likewise the spaces in the pseudo-ovary wall of *Leschenaultia* are most easily interpreted as incomplete fusion of the petals to the ovary wall, possibly a number of closed spurs. The ribs of the pseudo-ovary of *Goodenia scapigera* likewise are most easily interpreted as incomplete fusion of the sepals to the inner floral whorls. Lastly there is the phylogenetic sequence from *Velleia* through *Symphobasis* to *Goodenia* which is most easily interpreted as increasing

fusion of floral whorls or increasingly early onset of coalescence of growth areas in ontogeny. There is no internal evidence with respect to *Selliera*, *Scaevola* or *Diaspasis*, but it is reasonable to suggest that the inferior ovary in the case of this family has arisen by superficial zonal growth, although there is the possibility that this growth zone may move into the inner parts of the receptacle as evolution progresses. The difference between the two theories postulated to explain the floral tube and the pseudo-ovary wall becomes smaller when it is considered in this light.

Four main lines of development in the family may be distinguished. *Brunonia* stands somewhat apart and, indeed, has been elevated into a monotypic family. The hypogynous position of the stamens and the very reduced nature of the ovary, separate it from other genera. The former condition may be looked upon as primitive, whereas the latter may be considerably advanced. The different nature of the style vasculature has been remarked upon above. Primulaceae and Gentianaceae have both been mentioned as possible ancestors for this genus, but the generalized structure conforms fairly well with that of the rest of the family.

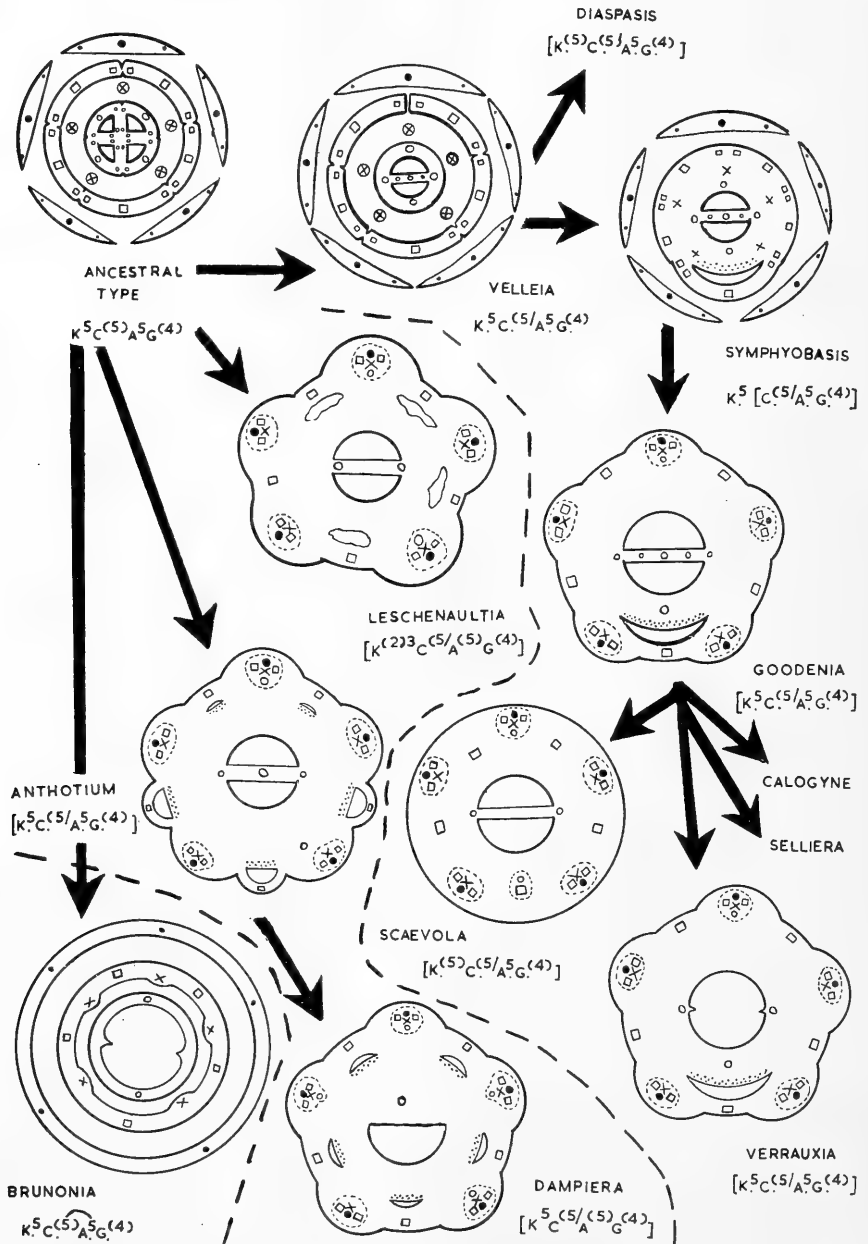
Velleia shows a certain amount of fusion between floral whorls at the base of the flower, the inner floral parts being united to the ovary to a higher level than the outer ones. This fusion is carried still higher in the flower in *Symphyobasis*, and in *Goodenia* the sepals are fused often almost to the ovary dome. *Calogyne* is a differentiate from *Goodenia* with divided indusia. *Selliera* is also a differentiate from *Goodenia*, distinguished on the fruit and corolla. *Pentaptilon* and *Catosperma* may be representatives of this line with pendulous ovules. In some species of *Goodenia* the number of ovules is reduced to two and in *Verreauxia* to one with a concomitant increase in the size of the "unilocular" medial zone of the ovary (see Fig. 31-33, 45). The presence and position of the single spur and the derivation of the pseudocarpellary dorsals from posterior sepal and anterior petal strands are also characteristic of this group. *Scaevola* is also considered to be a member of this group in which the spur has been lost. The vascular pattern is still essentially the same except in the case of *S. ramosissima*, although the condensation of the vasculature is particularly noticeable. There is no separate derivation of petal laterals and staminal strands from the receptacular stele as in the other members of the *Goodenia* group, and the bundles only separate at the ovary dome. Thus *Scaevola*, in general, exhibits more complete and presumably more efficient fusion than the rest of the group. *Leschenaultia* tends to stand even further apart from the rest of the family than *Brunonia*. The vasculature is, in many instances, quite different from any other member, as has been indicated above. The derivation of the pseudocarpellary dorsals and the presence of three large, closed spurs may indicate a relationship with the next group, but in other respects, notably the hollow style and the structure of the indusium (Carolin, unpub.), it is even more divergent.

Anthotium and *Dampiera* have much in common and are quite different from the other groups. The derivation of the pseudocarpellary dorsals and the presence of several spurs distinguish them from the *Goodenia* group, and the ribs on the pseudo-ovary wall and the placental supply separate them from *Leschenaultia*, in addition to the more orthodox characters. *Anthotium* shows considerable fusion between whorls, but the vasculatures of the different organs tend to remain more or less separate, at least in the upper part of the pseudo-ovary (Fig. 45, 37). In *Dampiera* the ovular number and the size of spurs are reduced. In addition, the condensation of the vascular supply is more evident than in *Anthotium* (Fig. 45, 38), and the ovary becomes "unilocular" by reduction of the basal "bilocular" zone and solidification of one "loculus".

It is evident that the scheme of affinities put forward by Krause (1912) has to be considerably modified in the light of this investigation.

Extrapolating these characters, an ancestral form can be suggested (Fig. 45). It was presumably pentamerous except for the gynoeceum which consisted of four united carpels; the petals were united into a tube as in *Brunonia* and the sepals were free. From this, *Brunonia* has developed by the reduction of the ovary (possibly in the same manner as the other genera, although equally possibly by simple abortion of two

carpels). The other genera have developed after a slit appeared in the corolla and further development has been along the usual lines of ovular reduction, gradual increase in union between floral parts and condensation of their vascular systems. On these



Text-figure 45. Phylogeny of floral types in the Goodeniaceae.

● Sepal Traces; □ Petal Traces; × Stamen Traces; ○ Carpel Traces.

results it is impossible to suggest any relationships between this family and any other modern groups. The pollinating mechanism would appear to be the connecting link between Goodeniaceae and Campanulaceae, and it is hoped to make this the subject of a separate paper.

If these phylogenetic schemes bear examination from other quarters, the family, in the wide sense, may be divided into the following subfamilial groups: (i) GOODENIA group: *Velleia*, *Symphyobasis*, *Goodenia*, *Calogyne*, *Selliera*, *Verreauxia*, *Diaspasis*, *Scaevola* (*Pentaptilon* and *Catosperma*); (ii) LESCHENAULTIA group: *Leschenaultia*; (iii) DAMPIERA group: *Anthotium*, *Dampiera*; (iv) BRUNONIA group: *Brunonia*. Cytological evidence (Martin, Peacock, Carolin, all unpub.; Jackson, 1958) and other morphological observations all tend to support this conclusion.

These results also suggest that certain generic limits may need revision. *Calogyne berardiana*, as it differs so little from Goodenias and as its style can no longer be considered to be characteristic, should probably be returned to *Goodenia*. *Scaevola fasciculata* and *S. helmsii* should probably be referred to *Verreauxia*.

Acknowledgements.

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IRON DEFICIENCY IN *EUCALYPTUS DIVES* SCHAUER.

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(Communicated by Professor L. D. Pryor.)

[Read 29th July, 1959.]

Synopsis.

A chlorosis in *Eucalyptus dives* Schauer growing at Ginninderra, A.C.T., was observed during the spring of 1956 when rainfall was excessive and soils became waterlogged. It disappeared when the soils dried out and did not reappear in 1957 or 1958 when rainfall was below normal.

Treating affected leaves with iron compounds reduced the intensity of the chlorosis.

Spectrographic analyses of chlorotic foliage in 1956 and healthy foliage in both 1956 and 1957 showed that the iron content of various portions taken from chlorotic branches was generally lower than that of corresponding parts of healthy branches from both 1956 and 1957 samples.

INTRODUCTION.

Eucalyptus dives Schauer is widespread in Australia, grows readily on poor soils and dry ridges (Ewart, 1930) and is not ordinarily found in poorly drained situations (C. W. E. Moore, private communication).

Pryor (1956) reported that this species was one of a relatively small group (Renantherae) of Eucalypts that readily developed chlorosis if grown in steam sterilized soil but was healthy in the same soil unsterilized. He concluded that this chlorosis was due to the absence of mycorrhiza on the roots following sterilization of the soil.

During the late winter of 1956, chlorotic foliage was observed on a number of adult trees of *E. dives* growing at Ginninderra in the Australian Capital Territory. The affected leaves were the younger ones occurring mostly on the northern and north-western sides of the trees.

The rainfall at Ginninderra in 1956 was nearly twice the normal amount of approximately 24" p.a. and soils were waterlogged during the winter. Many species of trees in the Australian Capital Territory suffered from excessive wetness and some died.

EXPERIMENTAL PROCEDURE.

During the spring of 1956, chlorotic leaves on an affected tree were matched for colour, labelled, and six at random were dipped into a solution of ferric potassium ethylene-diamine tetra acetate (0.2 ppm iron) containing a small amount of Tween-20 spreader.

A number of chlorotic leaves were detached, six were partly immersed in distilled water and six in a solution of ferrous sulphate (0.04 ppm iron) in petrie dishes in the laboratory.

Six branches bearing normal and six having chlorotic leaves were detached from trees and separated into current seasonal growth and previous seasonal growth as indicated by the colour and development of the main stem. The older portion was further subdivided into leaves and peduncles.

In 1957 no chlorotic leaves were evident and branches were taken at random during the spring when the trees were at the same growth stage as those sampled in 1956. These were separated into bulk fractions as in the previous year.

The samples were analysed spectrographically, standards for the analyses being prepared by adding known amounts of the elements under analysis to portions of a composite sample of dry matter. Sulphated ash of the samples and standards were

packed into cavities in graphite electrodes and arced at 15 amps d.c., the lower ash-filled electrode being the anode. The spectrograph used was a Hilger Large Quartz instrument set at the wave-length range 2450–3500 Å, the plates were Ilford Thin Film Half-tone and development was effected using ID13 developer. Analysis line intensities were computed from line densities measured on a Hilger non-recording microphotometer. The coefficient of variation associated with this method of analysis is about $\pm 10\%$ for a single determination. The estimates of concentration of the elements sought were made on the means of triplicate spectrographic determinations on each ash sample.

RESULTS.

Four weeks after treatment with Fe-K-EDTA the chlorotic leaves on the trees had developed green patches of colour in places where injury to the cuticle had occurred from various causes. The untreated leaves with similar injury to the cuticle remained chlorotic.

TABLE 1.

Content of Iron, Manganese and the Iron/Manganese Ratio in the Dry Matter of Healthy and Chlorotic Foliage of Eucalyptus dives Schauer from Ginninderra, A.C.T.

Sample.	Fe. (P.p.m.)	Mn. (P.p.m.)	Fe/Mn Ratio.
<i>A. Current seasonal growth.</i>			
1956 (wet year):			
{ Healthy foliage	95	620	0.156
{ Chlorotic foliage	45	870	0.053
1957 (dry year):			
Healthy foliage	70	449	0.156
<i>B. Previous seasonal growth.</i>			
1956 (wet year):			
{ Healthy leaves	85	627	0.135
{ Chlorotic leaves	40	404	0.099
{ Healthy peduncles	85	449	0.189
{ Chlorotic peduncles	62	888	0.070
1957 (dry year):			
Healthy leaves	155	745	0.208
Healthy peduncles	175	790	0.221

In the laboratory, the leaves immersed in the solution of ferrous sulphate became greener after about 10 days, the mid-ribs darkened and numerous dark spots developed near their apices. Those immersed in water did not change colour or develop spots.

Table 1 gives the results of spectrographic determination of the iron content of various portions taken from chlorotic and healthy branches. It will be noted that it was lower in chlorotic samples taken in 1956 than in healthy samples taken in both 1956 and 1957.

As it is known that reduced uptake of iron under waterlogged conditions is often associated with excessive uptake of manganese (Twyman, 1946), the manganese concentrations were also determined and these figures are included in Table 1.

DISCUSSION.

Since the analyses showed that the unhealthy parts were lower in iron than the corresponding healthy ones, and the treatment of the chlorotic foliage with iron compounds caused greening to occur, it is evident that the trees were suffering from an iron chlorosis in 1956 (Karschon, 1956).

As Leeper (1935) has shown that the availability of soil manganese can be greatly increased during a wet season it is to be expected that in 1956 trees in the Australian Capital Territory had a greater opportunity for taking up an excessive amount of manganese than usual.

Smith and Specht (1953) have shown that a reduction in the Fe/Mn ratio is characteristic of iron chlorosis induced by an excessive uptake of manganese. The

ratios given in Table 1 are not inconsistent with this, but it should be noted that the manganese concentration was not in every case higher in chlorotic than in healthy foliage.

McCool (1935) has shown that manganese induced iron chlorosis is more severe in high light intensity and Wiederspahn (1957) showed that these symptoms in apples developed first on the better lighted sides of the trees. Since the iron chlorosis observed in *E. dives* at Ginninderra occurred on the northern and north-western sides of the trees, it, also, was probably dependent on incident light intensity.

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POLLEN TETRAD SEGREGATION IN *ASTROLOMA PINIFOLIUM* AND IN
ACROTRICHE FASCICULIFLORA.

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(Four Text-figures.)

[Read 26th August, 1959.]

Synopsis.

An analysis is made of tetrad segregation in the two species on the bases of three hypotheses—indépendence, the operation of cytoplasmic competition, and a relationship to the two divisions of meiosis. It is concluded that both cytoplasmic and meiotic conditions may contribute to the behaviour. There is also a significant contribution by environmental factors, and a precise partition of the effects of the environment, the cytoplasm, and the nucleus, is not yet possible.

INTRODUCTION.

Pollen tetrad segregation, in which some or all of the pollen grains in a tetrad are aborted, has been recorded in twelve species of the Styphelieae (Smith-White, 1959). From a consideration of the patterns of pollen development found in other species of the tribe, it has been inferred that this tetrad segregation must have originated on several occasions and that these origins have been dependent upon a prior evolutionary history of monad-type pollen development and cytoplasmic polarity in pollen mother cells. In fact, it is inferred that within the Styphelieae there has been preadaptation to the establishment of pollen tetrad segregation.

It is reasonable to expect that the characteristics of such behaviour might reflect its causation. An analysis of the frequencies of the five possible kinds of pollen tetrad—nullads, monads, dyads, triads and full tetrads—may contribute to an understanding of the mechanisms involved. Unfortunately, the tetrahedral arrangement of the pollen grains in the tetrads, and the distortion due to the differential growth of good and aborting grains, prevent the recognition of the planes of the first and second meiotic divisions. Analysis must be made on the basis of unordered tetrads.

In this paper an analysis has been attempted of data for two species, *Astroloma pinifolium* Benth. and *Acrotriche fasciculiflora* Benth.

Ast. pinifolium occurs in coastal districts of eastern Australia, extending from southern Queensland to eastern Tasmania. In this distribution it shows several major disjunctions, and it usually occurs in small isolated local populations in each region. Still more isolated populations are found in the Warialda district of north-west New South Wales and in the Grampians of south-western Victoria. The pattern of distribution suggests that the species is old and relict. Material studied in this paper was obtained from the east coastal region, from Sydney to Evans Head. Data from Grampians plants are presented for comparison and contrast.

Acr. fasciculiflora is found only in south-eastern South Australia, its range extending from the Adelaide Hills and Mt. Lofty Ranges to Kangaroo Island. The material studied was collected in Long Gully, Belair National Park.

THE DATA.

Observed frequencies of tetrad types for a representative selection of plants of the two species are given in Tables 1 and 2. Table 3 summarizes the analysis according to two hypotheses for 57 plants of *Ast. pinifolium*. Tables 4 and 5 present data and analysis for within-plant variation for two selected plants of *Ast. pinifolium*.

The data given for each plant in Tables 1 and 2 are composite in that they were obtained from two or more flowers and 10 or more anthers. There is significant variation between flowers and between anthers within plants, which is illustrated by the data given in Tables 4 and 5, and by the graph in Text-figure 3.

TABLE 1.
Astroloma pinifolium.
Tetrad Segregation Data.

Plant and Hypothesis.	Tetrad Type Proportions. % × 100.					N.	(p+q) or (x+y+z).	χ ² .
	r ₀ .	r ₁ .	r ₂ .	r ₃ .	r ₄ .			
R57/8 ..	7673	1790	484	52	1	9595	0·927+0·073	378·2
I ..	7384	2326	273	15	0			
III ..	7658	1808	485	44	5			
LP57/4 ..	7183	2347	415	54	0	4651	0·8751+0·1033+0·0216	0·49
I ..	7056	2571	351	21	0			
III ..	7174	2338	444	41	2			
W54/6 ..	6011	3151	750	83	5	5878	0·847+0·138+0·015	2·2
I ..	5916	3319	698	65	2			
III ..	6006	3147	753	89	5			
R57/5 ..	4982	3538	1262	208	9	4468	0·877+0·123	12·3
I ..	4746	3888	1195	163	8			
III ..	4970	3596	1214	204	16			
TG57/4 ..	4065	4182	1488	243	22	8785	0·705+0·255+0·040	2·7
I ..	4116	4091	1524	253	16			
III ..	4116	4091	1524	253	16			
LP53/3 ..	3998	3728	1866	374	34	8022	0·801+0·199	5·2
I ..	3797	4160	1709	312	21			
III ..	3969	3780	1782	420	49			
TG57/2 ..	3157	4204	2116	482	41	9595	0·642+0·318+0·040	5·2
I ..	3145	4219	2122	472	40			
III ..	3165	4204	2114	477	41			
O55/2 ..	2914	4313	2301	451	21	6088	0·785+0·215	63·1
I ..	3015	4215	2210	515	45			
III ..	2884	4435	2243	413	25			
R57/6 ..	2874	4138	2321	603	63	15284	0·63+0·30+0·07	11·5
I ..	2820	4199	2345	582	54			
III ..	2862	4119	2338	616	64			
W54/5 ..	2659	4332	2504	475	30	3603	0·741+0·259	18·3
I ..	2809	4198	2353	586	55			
III ..	2601	4386	2461	516	36			
TG57/1 ..	2743	3983	2659	580	35	9254	0·537+0·413+0·050	5·5
I ..	2695	4182	2433	629	61			
III ..	2695	4182	2433	629	61			
W54/2 ..	2459	4354	2665	501	21	3753	0·7287+0·2713	6·8
I ..	2658	4175	2460	644	63			
III ..	2401	4410	2613	540	36			
W54/1 ..	2559	4276	2501	625	39	3314	0·535+0·385+0·080	0·8
I ..	2643	4173	2470	650	64			
III ..	2500	4300	2549	602	49			
TG57/5 ..	2970	3472	2635	833	90	8923	0·51+0·43+0·06	2·5
I ..	2541	4152	2544	693	71			
III ..	3025	3740	2366	748	121			
O55/1 ..	2005	3980	3027	906	81	1721	0·7205+0·2795	42·9
I ..	2052	3987	2906	941	114			
III ..	1980	4049	2960	910	100			
A53/1 ..	2079	3513	3495	857	56	11322	0·519+0·403+0·078	42·9
I ..	1991	3959	2951	978	121			
III ..	1998	3996	2946	948	112			
W54/9 ..	1619	3972	3277	1054	78	3463	0·445+0·455+0·100	1·1
I ..	1785	3845	3105	1141	150			
III ..	1600	4016	3304	984	96			
O57/6 ..	1078	4260	3988	635	39	9001	0·400+0·502+0·098	3·1
I ..	1709	3796	3160	1170	162			
III ..	1156	4114	4029	665	30			
O57/1 ..	1199	3712	3649	1286	154	9424	0·304+0·605+0·055	12·6
I ..	1419	3572	3372	1414	223			
III ..	1225	3710	3649	1272	144			

Localities: A, Audley. R, LP, La Perouse and Malabar. O, Oatley. E, Evans Head. TG, Tea Gardens. W, Warrah. Gr, Grampians.

TABLE 1.—Continued.
Astroloma pinifolium.—Continued.
 Tetrad Segregation Data.—Continued.

Plant and Hypothesis.	Tetrad Type Proportions. % × 100.					N.	(p+q) or (x+y+z).	χ ² .
	r ₀ .	r ₁ .	r ₂ .	r ₃ .	r ₄ .			
E51/2 ..	454	3128	4876	1424	118	1608		
I ..	957	<i>3086</i>	<i>3644</i>	1913	377		0·5594+0·4406	136·4
III ..	484	2948	4968	1474	121		0·22+0·67+0·11	2·55
O57/5 ..	940	2464	3698	2351	547	6466		
I ..	742	2719	3736	2280	522		0·522+0·478	52·1
III ..	841	2668	3566	2300	625		0·29+0·46+0·25	26·5
O55/8 ..	3169	4260	2191	351	29	2392		
I ..	3249	<i>4218</i>	<i>2053</i>	444	36		0·755+0·245	13·0
III ..	3136	4368	2081	390	25		0·56+0·39+0·05	3·1
R57/11 ..	3630	3918	1974	434	43	9098		
I ..	<i>3452</i>	4206	2107	<i>390</i>	36		0·7665+0·2335	39·5
III ..	3600	3960	1929	462	49		0·60+0·35+0·07	3·8
GR58/1007 ..	3028	5946	1026	0	0	2758	q=0·200	
Gr58/1005 ..	1229	7149	1614	4	4	2571	q=0·260	
Gr58/1008 ..	660	1657	7579	33	71	2408	q=0·430	
Gr58/1001 ..	431	2082	7416	5	66	1974	q=0·430	

Localities: A, Audley. R, LP, La Perouse and Malabar. O, Oatley, E, Evans Head. TG, Tea Gardens. W, Warrah. Gr, Grampians.

For hypothesis I (independence) expected frequencies are given in *italics* where they are below observed frequencies.

In the collection of the data, the greatest possible care has been taken to avoid biologically meaningless sources of error. In slide preparation, anthers were dissected in a drop of stain-mountant on the slide under binocular magnification, to remove at least 90% of the pollen. The drop of mountant used was limited so that no exudation occurred at the edges of the cover slips, which might lead to a loss of the small nullads. Finally, within-slide sampling error has been avoided in most cases by scanning the whole area of each slide. In the data given for the Grampians plants of *Ast. pinifolium* a sectorial sampling method was used.

THE ANALYSIS.

Three different hypotheses have been examined. These are: (I) The survival or death of any microspore is independent of the fates of its three sister microspores in the same tetrad. (II) There is competition for survival between the four microspores in each tetrad. (III) The fates of the four microspores in each tetrad are related to the meiotic divisions.

I. *The hypothesis of independence.*

With independence, the observed frequencies of the five classes of tetrad should conform to the terms of the binomial (p+q)⁴, where q is the prospect that any microspore will survive, and p (=1-q) is its prospect of abortion.

Writing a₀...a₄ for the observed frequencies of the five tetrad types, their summation being N, the total sample, and r₀...r₄ for the corresponding proportions, summing to unity, the observed value of q is

$$q = \frac{4a_4 + 3a_3 + 2a_2 + a_1}{4N}$$

Using values of q obtained directly from the data, expected frequencies e₀...e₄, based on the hypothesis of independence, have been calculated. Comparison of the observations with the expected frequencies (Hypothesis I) are presented in Tables 1, 2 and 3. Only one-quarter of the plants of eastern *Ast. pinifolium* show an acceptable fit to the hypothesis. The distributions of tetrad-type frequencies in the Grampians

plants are remote from the binomial form, and in *Acrotriche fasciculiflora*, all thirteen plants examined show an unsatisfactory fit.

The hypothesis of independence does not provide a generally satisfactory explanation of the segregation behaviour in either species. In the eastern *A. pinifolium*, however, it seems probable that the causes of tetrad segregation are occasionally capable of simulating independence.

TABLE 2.
Acrotriche fasciculiflora.
Tetrad Segregation Data.

Plant and Hypothesis.	Tetrad Type Proportions. % × 100.					N.	Parameters (p+a) or (x+y+z).	χ^2 .
	r ₀ .	r ₁ .	r ₂ .	r ₃ .	r ₄ .			
54/11	9603	332	62	3	0	3378		
I	9544	448	8	0	0		0.9884+0.0116	213.8
III	9604	333	62	1	0		0.980+0.017+0.003	0.03
54/12	9012	739	244	5	0	4008		
I	8813	1132	54	1	0		0.9689+0.0311	318.9
III	9025	722	242	9	0		0.950+0.038+0.012	0.05
54/8	1824	4368	3231	561	16	1891		
I	2214	4055	2784	850	97		0.686+0.314	59.8
III	1806	4420	3172	572	30		0.425+0.520+0.055	1.68
54/9	1331	4429	3775	459	6	1778		
I	1967	3947	2969	993	124		0.666+0.334	158.1
III	1369	4403	3799	417	12		0.370+0.595+0.035	0.76
54/7	1010	4657	3872	461	0	2278		
I	1841	3878	3064	1076	142		0.655+0.345	276.4
III	1156	4250	4144	438	12		0.34+0.625+0.035	17.2
54/1	1349	3678	4074	888	11	2602		
I	1646	3753	3208	1212	174		0.637+0.363	120.0
III	1122	4087	4090	671	30		0.335+0.610+0.055	43.8
54/3	974	4273	3980	773	0	1294		
I	1636	3746	3216	1227	176		0.636+0.364	104.2
III	1069	4009	4150	736	36		0.327+0.613+0.060	4.2
54/4	833	4395	4155	616	0	1752		
I	1638	3746	3216	1227	176		0.636+0.364	214.9
III	973	4012	4415	579	20		0.312+0.643+0.045	12.7
54/2	822	4183	4300	655	40	2979		
I	1546	3678	3282	1302	196		0.627+0.373	348.1
III	961	3968	4406	640	25		0.31+0.64+0.05	13.1
54/5	784	4067	4579	606	0	2326		
I	1516	3654	3303	1327	200		0.624+0.376	345.3
III	824	3846	4736	577	18		0.287+0.670+0.043	5.9
54/10	677	3862	4602	854	5	2084		
I	1375	3533	3402	1456	234		0.609+0.391	267.2
III	784	3752	4769	670	25		0.28+0.67+0.05	12.6
54/13	600	4122	4277	966	35	1999		
I	1349	3498	3403	1471	239		0.607+0.393	218.7
III	812	3733	4732	786	36		0.285+0.655+0.060	32.7
54/6	409	3232	5274	1067	18	1640		
I	1086	3223	3587	1775	329		0.574+0.426	278.1
III	484	3168	5448	864	36		0.22+0.72+0.06	10.8

Contingencies :

Total, $\chi^2=798.1$ (excluding 54/11 and 54/12).

Between plants, $\chi^2=542.5$.

Within plants, $\chi^2=255.6$.

Within plant data not presented in table.

All sets of data are from counts of two flowers.

(The full tetrad classes, being generally very small, have been grouped with the triad classes for the calculation of the contingency χ^2 , leaving a total of 22 degrees of freedom.)

II. The hypothesis of competition.

There are many reasons for the inference that cytoplasmic gradients may constitute the primary system of control in pollen development in the Styphelieae (Smith-White, l.c.). It is possible that the frequent occurrence of tetrad segregation in the tribe is

dependent upon cytoplasmic differentiation. Such a system would necessarily involve competition between sister microspores for cytoplasmic necessities. The occurrence of a competition effect, however, would not exclude a nuclear or even a chromosomal mechanism.

Competition between sister microspores would cause deviations from the theoretical frequencies calculated on the basis of independence. Such competition may be either positive or negative.

Negative competition or assistance would occur if, when some microspores survive, others in the same tetrad have an increased prospect of survival. A similar situation would exist if the death of a microspore increased the prospect of death of other

TABLE 3.
Maximum Likelihood Approximations to Independence and to the Trinomial Square Form.
East Coast Populations of *Astroloma pinifolium*.

Hypothesis.	Population.	Number of Plants showing χ^2 Values Equivalent to Probabilities of							Total Plants.
		<0.01	0.01-0.05	0.05-0.10	0.10-0.50	0.50-0.90	0.90-0.95	0.95-1.0	
I. Independence ($p+q$) ⁴	Oatley ..	13	—	—	3	1	2	2	21
	Warrah ..	7	—	1	—	—	—	—	8
	Evans Head	6	—	—	—	—	—	—	6
	Malabar ..	11	3	—	2	2	—	—	18
	Tea Gardens ..	2	—	—	1	—	—	1	4
	Totals ..	39	3	1	6	3	2	3	57
III. Trinomial square ($x+y+z$) ²	Oatley ..	3	3	—	4	6	2	3	21
	Warrah ..	—	—	—	2	5	1	—	8
	Evans Head	—	—	—	3	2	1	—	6
	Malabar ..	1	3	—	3	6	3	2	18
	Tea Gardens ..	2	—	—	1	—	—	1	4
	Totals ..	6	6	0	13	19	7	6	57

members of the tetrad. Just this effect has been observed in an unusual strain of *Petunia* studied by Levan (1942). It leads to an excess of nullads and full tetrads, and a deficiency of the other classes, compared with independence. Levan infers that dying pollen grains produce toxic degenerative substances which have adverse effects on the other members of the tetrad.

Conversely, positive competition implies that where some microspores develop, others in the same tetrad are at a disadvantage—necessary substances may be in limited supply, and may have non-uniform distribution within the mother cell.

Comparison of the data in Table 1 with binomial expectancy shows that in eastern *Ast. pinifolium*, in those plants where the data do not fit the hypothesis of independence, there is no consistent surplus or deficiency in the dyad and monad classes as compared with the binomial expectancy. There is no consistent indication of either positive or negative competition within tetrads.

In the data for *Acr. fasciculiflora* given in Table 2, however, all thirteen plants showed a marked excess of dyads over binomial expectancy, nine plants show an excess of monads, and all other classes in all plants, with the minor exception of nullads in plant 54/12, are deficient. The consistency of the thirteen sets of data suggests very strongly that competition between microspores does operate, and further analysis is justified.

If q_1 and p_1 , respectively, represent the prospects that a first microspore will survive or abort, and if q_2 , q_3 , q_4 and p_2 , p_3 , p_4 are the prospects for survival or abortion of a second microspore following the survival of a first, of a third following the survival of two, and of the fourth following the survival of the other three, the theoretical

frequencies of the five tetrad categories will be:

$$e_0 = p_1^4$$

$$e_1 = q_1 (p_1^3 + p_1^2 p_2 + p_1 p_2^2 + p_2^3)$$

$$e_2 = q_1 q_2 (p_1^2 + p_2^2 + p_3^2 + p_1 p_2 + p_1 p_3 + p_2 p_3)$$

$$e_3 = q_1 q_2 q_3 (p_1 + p_2 + p_3 + p_4)$$

$$e_4 = q_1 q_2 q_3 q_4$$

The values q_1 , q_2 , q_3 and q_4 can be related such that

$$q_2 = f_1 q_1, \quad q_3 = f_2 q_2, \quad q_4 = f_3 q_3$$

$$\text{and } f_2 = a f_1, \quad f_3 = c a f_2 = c a^2 f_1.$$

Dropping the subscript to f_1 ,

$$q_2 = f q_1, \quad q_3 = a f^2 q_1, \quad q_4 = c a^3 f^3 q_1.$$

In this formulation, there are four parameters, q_1 , f , a and c , and the last three measure or determine the increasing severity of competition between first and second, second and third, and third and fourth microspores. Since there are at most four degrees of freedom in any set of data, statistical testing of the formulation is not possible. However, values for the parameters have been calculated for eleven sets of data from Table 2 (excluding plants 54/11 and 54/12). The following five sets are representative:

Plant	q	f	a	c
54/8367	.841	.958	.133
54/7436	.648	.650	.0077
54/1394	.951	.562	.0133
54/3441	.718	.794	.0000
54/6550	.732	.582	.0588

It will be noted that a is of the same order of size as f ; it may be slightly larger, or substantially smaller. The parameter c is very small, but lower values of c are not necessarily associated with low values of a or f . Competition acting against the third microspore is scarcely greater than that acting against the second, but that operating against a fourth microspore is very severe.

The very sharp increase in competitive effect operating against the survival of all four microspores, which is indicated by this analysis, suggests that competition does not conform to a simple pattern. It is consistent, however, with the operation of a cytoplasmic gradient (Text-figure 1A, B). If there is a gradient distribution of necessary cytoplasmic substances (stippling) and also variation in total amount, and if the plane of the first meiotic division tends to lie along this gradient, varying from position (a) to position (b) with a mean at (m), competitive effects consistent with those observed could result. It is perhaps significant that in *Astroloma* and in many other species of the Styphelieae the spindle of the first meiotic division is eccentric and laterally displaced (Text-figure 1C) and may be across a cytoplasmic gradient.

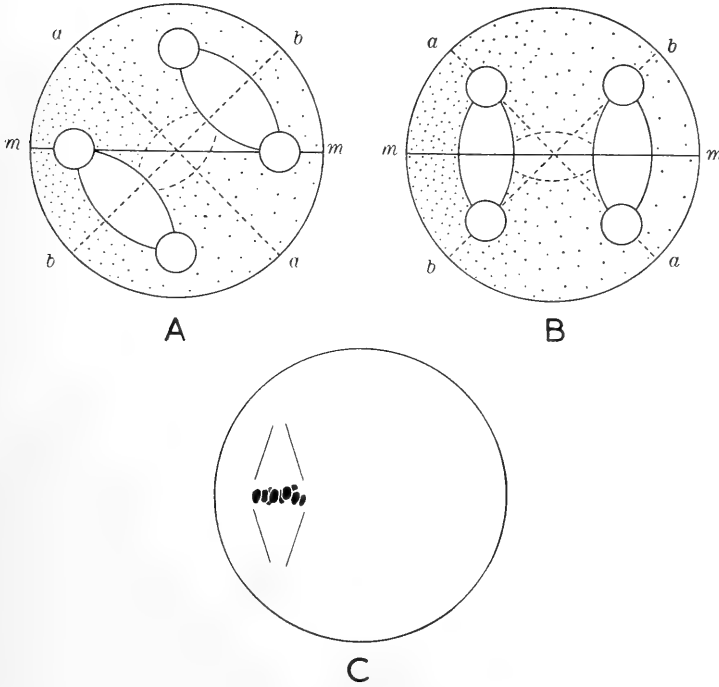
III. The hypothesis of meiotic dependence.

This hypothesis assumes that the tetrad segregations are related to and dependent upon the conditions of meiosis. Martin and Peacock (1959, pp. 272-278) have examined tetrad segregation in several species of *Leschenaultia* (Goodeniaceae). They find that, consequent upon low chiasma frequency and terminal chiasma localization, there is an appreciable frequency of univalents at first metaphase in pollen mother cells; loss and misdivision of univalents is responsible for some, but probably not all, of the observed pollen grain death.

In the Styphelieae it is not possible to recognize the plane of the first division in the mature pollen tetrads. This plane, however, may still be considered to divide the pollen mother cell (PMC) into two half-mother cells ($\frac{1}{2}$ MCs). Each $\frac{1}{2}$ MC would then be capable of yielding one of three possible results—neither, one only, or both its daughter microspores might survive. The prospects of these three possible results will be designated by the symbols x , y and z respectively.

With independence, there would arise the identities $x = p^2$; $y = 2pq$; $z = q^2$; and $(x + y + z)^2 = (p + q)^4$.

Independence, however, might operate between, but not within, half-mother cells and the tetrad-type frequencies would then fit the expansion of the trinomial $(x + y + z)^2$. This relationship, which will be referred to as the "trinomial square", is illustrated in Text-figure 2. Recognition of the plane of the first division, if possible, would permit the separation of the terms y^2 and $2xy$ in the theoretical frequency of dyads. This hypothesis of independence between $\frac{1}{2}$ MCs is hypothesis III in Tables 1, 2 and 3.



Text-figure 1.—The effect of competition in a cytoplasmic gradient. The gradient is represented by stippling. Variation in total supply of the gradient substances is not indicated. The orientation of the division spindles varies, with a mode as in B. Orientation as in A would yield monads or triads, according to the quantitative supply of gradient substance. Orientation as in B would yield dyads rather than monads. Cf. text. In C, the spindle eccentricity characteristic of the family is illustrated.

In order to test the data in Tables 1, 2 and 3 against the hypothesis, maximum likelihood estimates of x , y and z have been approximated, using a method of iteration described by Kempthorne (1957, pages 172-177), the iteration being repeated only until a satisfactory χ^2 value was obtained, or until it became obvious that a satisfactory χ^2 value was unobtainable. In many of the sets of data, the initial estimates, obtained from the equations

$$y = \sqrt{2r_0 + r_1 + r_2 - 2\sqrt{r_0}}, \quad x = \frac{r_1}{2y_1}, \quad z = 1 - x - y$$

have given acceptable χ^2 values, and no further iteration has been carried out.

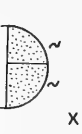





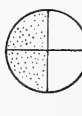

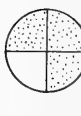
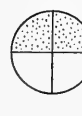


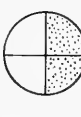


The observed frequency distributions obtained for eastern *Ast. pinifolium* are surprisingly consistent with this third hypothesis (Tables 1, 3). By contrast, the tetrad-type distributions obtained for the Grampians population of the species are remote from the form, and it must be inferred that the direct causes of segregation are quite different.

In *Acr. fasciculiflora*, four plants among thirteen give an excellent fit to the hypothesis, two show a barely acceptable fit, and seven show a very bad fit.

Within-Plant Variation.

Significant variation occurs between flowers within plants in probably all plants of both species. Intraplant variation, however, generally seems to be of lesser degree than interplant variation, and this feature is clearly shown by Text-figure 3. In Table 2,

THE TRINOMIAL SQUARE FORM

Text-figure 2.—The trinomial square form.

x , y and z are the prospects for the three possible results from a $\frac{1}{2}$ MC. With independence, the whole tetrad result becomes $(x + y + z)^2$.

the contingency χ^2 value for within-plant variation is only one-half that for between-plant variation, for equal degrees of freedom.

In Tables 4 and 5, data from individual flowers and anthers are given for two plants of *Ast. pinifolium* and are sufficient to illustrate the characteristics of intraplant variation. These two plants have been selected as representative of plants showing good and bad fit, respectively, to the trinomial square form.

In both plants there is significant variation, even between the five anthers of a single flower. In R57/6 (Table 4), the grand totals, flower totals, and individual anther sets, with one exception, all conform to trinomial squares. In A53/1, the data for flower 1 show an acceptable fit, but the other flowers do not, and the fit of the grand-total distributions is very bad.

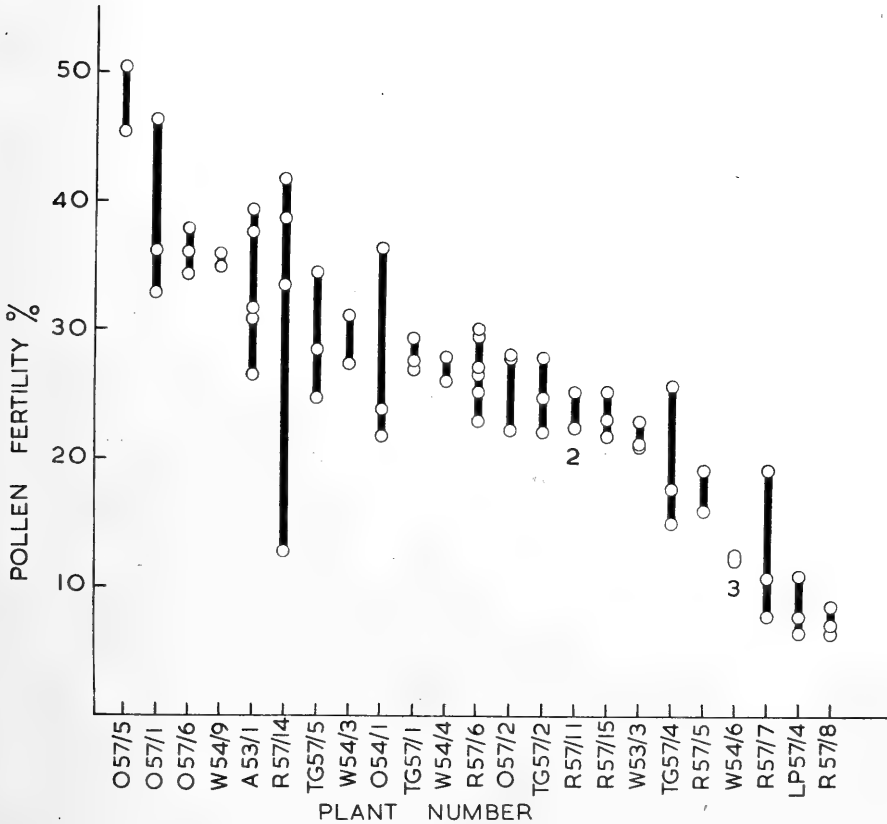
The data in Table 4 show two features which deserve comment. The first is that χ^2 values tend to be either very low, corresponding to probabilities above 0.5, or very high with probabilities below 0.01. The distribution of χ^2 values does not appear to be normal. The second feature is that, although the individual anther distributions all fit trinomial squares, they are significantly different, and yet the grand total distribution conforms to a "mean" trinomial square. It can be shown algebraically that the means of the individual terms of two different trinomial squares cannot be themselves the terms of a trinomial square. This contradiction in the data has not been resolved.

Intraplant variation in tetrad segregation is generally at a significant level, and must mean that the behaviour is subject to environmental modification. Interplant variation, however, is generally greater in degree, and this fact suggests that there are both genetical and environmental components involved. The existence of the

environmental effect, however, makes the interpretation of interplant variation difficult and hazardous.

The Meaning of the Trinomial Square Form.

The consistency of the fit to the trinomial square hypothesis in plants of eastern *Ast. pinifolium* must have significance in relation to the causes of tetrad segregation. This form has several implications which relate it to the conditions of meiosis (Text-figure 2).



Text-figure 3.—Variation in pollen fertility within and between plants. *Astroloma pinifolium*.

The values plotted are the q values for total microspore survival, each determination being from the five anthers of a flower. It is suggested that both genetic and environmental components affect pollen fertility.

The values x , y and z represent the prospects that neither, one only, or both the microspores derived from a second division $\frac{1}{2}$ MC shall survive. It is clear that to give the trinomial square form:

(i) The events leading to microspore failure or survival are operative or effective during the second division of meiosis.

(ii) The two $\frac{1}{2}$ MCs of each PMC must have similar prospects.

(iii) These prospects in the two $\frac{1}{2}$ MCs must be independent.

(iv) From (ii) and (iii) it follows that the first meiotic division must be strictly equational, both in chromosomal segregations or abnormal chromosome behaviour, and

in cytoplasmic differentiation. In particular, the cytoplasmic polarity present during the first division in *Leucopogon juniperinus*, which is demonstrated by the non-random segregation of univalents (Smith-white, 1948), and which is generally involved in the monad-type of pollen development in the Styphelieae (Smith-White, 1955, 1959), must be absent, or must be delayed, at least, until after the beginning of the second divisions.

TABLE 4.
Variation in Tetrad Segregation Within and Between Flowers.
Plant R57/6.

Flower.	Anther.	Tetrad Type Proportions. % × 100.					N.	q.	(x+y+z).	χ^2 .	P.
		r ₀ .	r ₁ .	r ₂ .	r ₃ .	r ₄ .					
1	1	457	412	118	13	0	608	0.172	0.676+0.304+0.020	0.15	0.98
	2	290	458	219	31	2	576	0.247	0.538+0.426+0.036	0.10	0.99
	3	279	435	243	41	2	581	0.263	0.528+0.412+0.060	0.60	0.8
	4	287	399	241	66	7	544	0.277	0.54+0.37+0.09	0.19	0.98
	5	248	403	246	87	16	549	0.306	0.50+0.40+0.10	2.21	0.7
Totals	..	315	421	212	47	5	2858	0.252	0.562+0.375+0.063	1.16	0.85
2	1	339	356	246	59	0	675	0.256	0.52+0.40+0.08	19.1	0.001
	2	282	439	229	43	7	674	0.264	0.52+0.40+0.08	6.7	0.15
	3	272	431	221	69	5	605	0.276	0.52+0.41+0.07	2.4	0.5
	4	259	436	242	48	15	665	0.281	0.50+0.40+0.10	10.9	0.03
	5	256	423	246	72	3	601	0.286	0.51+0.42+0.07	1.85	0.75
Totals	..	283	416	237	58	6	3220	0.272	0.532+0.391+0.077	0.44	0.97
3	1	328	407	223	38	4	445	0.246	0.573+0.355+0.072	1.96	0.7
	2	295	423	231	49	2	529	0.260	0.55+0.39+0.06	1.11	0.8
	3	231	419	257	85	8	611	0.305	0.481+0.436+0.083	2.09	0.6
	4	222	413	274	82	9	559	0.311	0.47+0.44+0.09	0.11	0.99
	5	123	434	317	113	13	602	0.365	0.38+0.50+0.02	7.65	0.07
Totals	..	233	420	262	76	8	2746	0.301	0.483+0.435+0.082	1.67	0.7
Grand totals		278	419	237	60	6	8824	0.275	0.530+0.395+0.075	1.36	0.85

(Full tetrad classes have been grouped with triad classes.)

Contingencies: Total, $\chi^2=346.3$. 42 d.f.

Between flowers $\chi^2=71.3$. Heterogenous.

Contribution to total χ^2 by anthers 1—1 and 3—5=251.2.

The trinomial square form of frequency distribution does not necessarily imply but it does suggest that chromosomal or genetical segregations are involved. It is possible to devise model systems which are capable of giving this form. The conditions necessary are:

(i) There must be a substantial degree of chiasma localization, such that definite chromosome segments are always distal to the first chiasma, and always proximal to a second chiasma if such is formed. These segments will always show second division segregation and, like the differential segments of an *Oenothera* system, will be excluded from crossing over, and so protected from breakdown (Text-figure 4).

(ii) These segments, on different chromosomes, must carry all genes, or chromosome blocks, concerned in the tetrad segregation.

(iii) There must be at least two gene or chromosome block systems, A/a, B/b, . . . and A'/a', B'/b', . . . which may be either alternate or duplicate to each other in action. Each system must include two or more complementary genes or blocks, and all must be independent of one another in segregation.

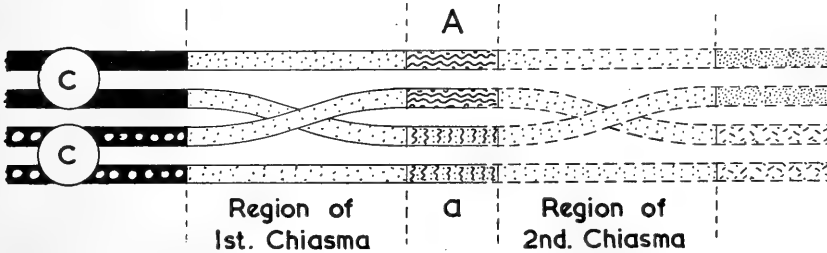
The minimum system possible is A/a B/b A'/a' B'/b' which would give

A B and A' B' systems duplicate, $(.125 + .625 + .250)^2$.

A B and A' B' alternate, $(.250 + .625 + .125)^2$.

A system A/a B/b C/c A'/a' B'/b' C'/c' would permit a wider range of trinomial squares.

Such an hypothesis of two gene or chromosome block systems is permitted by the apparent secondary polyploid constitutions of *Astroloma pinifolium* ($n=7, x=4$) and of *Acrotriche fasciculiflora* ($n=9$. Smith-White, 1955). However, the hypothesis would



Text-figure 4.—Diagram of a bivalent with chiasma localization.

Segments outside the chiasma regions are isolated from crossing over. The region distal to the first chiasma region would show regular reduction at second anaphase.

not seem to permit the degree of intraplant and environmental variation which has been described, unless it were associated with a very considerable effect of environment on chiasma frequency and chiasma localization.

Chromosome fragmentation is known to occur as a characteristic feature of meiosis in pollen mother cells of eastern *Ast. pinifolium*, and will be described in another paper. This abnormal meiotic behaviour may be associated with a system of chromosome

TABLE 5.
Variation in Tetrad Segregation Within and Between Flowers.
Astroloma pinifolium. Plant A53/1.

Flower.	Anther.	Tetrad-type Proportions.					N.	q.	Parameters (xyx).	χ^2 .	P.
		r_0 .	r_1 .	r_2 .	r_3 .	r_4 .					
1	1	332	395	239	33	0	461	0.242	0.54+0.41+0.05	6.1	0.10
	2	247	468	254	31	0	460	0.267	0.50+0.46+0.04	0.6	0.85
	3	254	448	270	28	0	496	0.268	0.51+0.45+0.04	2.9	0.40
	4	266	442	266	26	0	421	0.269	0.51+0.45+0.04	2.8	0.40
	5	231	453	265	49	2	433	0.282	0.50+0.45+0.05	1.0	0.80
Totals ..		267	441	259	33	0	2271	0.265	0.51+0.45+0.04	5.7	0.15
2	1	202	326	385	82	6	491	0.341	0.405+0.515+0.080	18.5	0.001
	2	185	322	368	118	6	475	0.360	0.39+0.52+0.09	14.5	0.004
	3	178	301	363	148	11	535	0.379	0.39+0.52+0.09	17.7	0.001
	4	134	308	429	124	5	396	0.390	0.32+0.58+0.10	9.0	0.01
	5	120	277	450	143	10	476	0.412	0.31+0.57+0.12	14.2	0.01
Totals ..		165	307	397	123	8	2373	0.376	0.343+0.550+0.107	82.9	0.000
3	1	140	315	381	149	15	549	0.363	0.35+0.52+0.13	7.6	0.10
	2	151	336	401	101	11	456	0.371	0.36+0.53+0.11	7.34	0.10
	3	135	336	405	172	10	398	0.386	0.36+0.53+0.11	4.78	0.30
	4	119	330	385	152	15	455	0.404	0.34+0.55+0.11	6.4	0.15
	5	102	303	458	131	7	413	0.409	0.32+0.58+0.10	9.1	0.01
Totals ..		129	323	403	133	12	2271	0.393	0.34+0.55+0.11	26.4	0.001
Grand totals		187	356	354	97	7	6915	0.345	0.38+0.53+0.09	130.1	0.000

Contingency : Total χ^2 .. 533.4. Heterogenous.
 Between flowers 439.3. Heterogenous.
 Within flowers 94.1. Heterogenous.

segregation similar to the model just described. Fragmentation does not occur in Grampians *Ast. pinifolium* or in *Acrotriche fasciculiflora*, and it must therefore constitute an additional complication rather than a primary cause of pollen tetrad segregation in the Styphelieae.

SUMMARY AND CONCLUSIONS.

An analysis of pollen tetrad segregation in *Astroloma pinifolium* and *Acrotriche fasciculiflora* has been attempted.

In eastern *Ast. pinifolium*, segregations generally fit a trinomial square form, and occasionally fit the hypothesis of independence. Tetrad segregations in a population of the same species from south-west Victoria (Grampians) are very different.

In *Acrotriche fasciculiflora*, segregations occasionally fit the trinomial square form, but more often show significant departures from this form.

The trinomial square form of tetrad frequency distribution requires strict equationality of the first meiotic division, and independence between the two second divisions in each mother cell, and a genetic or even chromosomal mechanism may be involved.

Deviations from the trinomial square form could be determined by loss of strict equationality of the first division. In the case of genetic or chromosomal mechanisms this would require a shift in regions of chiasma localization.

Consistent departures from expectations based on independence in *Acrotriche fasciculiflora* suggest that cytoplasmic conditions may be in part responsible for pollen death within tetrads. In particular, a gradient distribution of cytoplasmic substances may be involved.

Highly significant and very substantial intraplant variation in tetrad type frequencies occur, showing the behaviour to be sensitive to environmental modification. Until environmental effects can be evaluated, attempts to explain interplant and interpopulation differences are hazardous. Acceptable model systems must permit substantial environmental modification.

It is possible that both chromosomal and cytoplasmic systems operate as partial causes of segregation behaviour in the Styphelieae.

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POLLEN TETRAD PATTERNS IN *LESCHENAULTIA*.By P. G. MARTIN¹ and W. J. PEACOCK.²

(Plate x.)

[Read 26th August, 1959.]

Synopsis.

Mature pollen grains of *Leschenaultia* remain associated in tetrads. In eleven collections from both wild and cultivated plants of three species, aborted pollen grains, varying in frequency from 7% to 53%, have been observed. All combinations of good and aborted grains in a tetrad were present in every collection. Univalent formation at meiosis has been observed. An hypothesis relating univalent distribution and pollen abortion patterns is presented. This, almost certainly, accounts for a large proportion of pollen abortion, but there may be other contributory causes.

INTRODUCTION.

The genus *Leschenaultia* R.Br. is different from other genera of the family Goodeniaceae in that the mature pollen grains remain in tetrads. This is uncommon, but not rare, among Angiosperms, but, whereas there is a tetrahedral arrangement of pollen grains in most such genera, in *Leschenaultia* there is a rhomboidal arrangement in a single plane. Mature pollen of *Leschenaultia* was stained with a cytoplasmic stain and it was observed that there was always a proportion of unstained, aborted pollen grains. Within tetrads every possible combination of stained and unstained pollen was observed, viz:

Full tetrads ..	4 stained
Triads	3 stained, 1 aborted
Dyads A	2 stained, 2 aborted, the latter being adjacent
Dyads O	2 stained, 2 aborted, the latter being opposite
Monads	1 stained, 3 aborted.
Nullads	4 aborted

These are illustrated in Plate x, figs. 1 and 2.

This paper is concerned with observations of the frequencies of the different types and a consideration of hypotheses to explain the observations.

MATERIALS AND METHODS.

Samples of mature pollen from plants of *L. formosa* R.Br. and *L. linarioides* DC. were collected by Mr. D. E. Symon in their native habitat in Western Australia. Most observations were carried out on plants of *L. formosa* and *L. biloba* Lindl. grown in cultivation. The samples of *L. linarioides* and *L. formosa* collected in their native habitat were diploid ($2n = 18$). Among cultivated plants of both *L. formosa* and *L. biloba*, diploids ($2n = 18$) and tetraploids were found. All the observations reported refer to diploid plants. It is worth recording that, whereas nearly all pollen produced by the tetraploid *L. formosa* plant aborted, the tetraploid *L. biloba* plant produced approximately 70% "fertile" (i.e. normally stained) pollen.

For mature pollen observations, buds were collected just before anther dehiscence and, after opening the corolla, fixed in acetic-alcohol (1:3). Anthers were dissected in a dextrin-sorbitol fluid similar to that described by Zirkle (1940) in which acid fuchsin replaced carmine. Aborted pollen grains were quite colourless and those assumed to be fertile stained bright red so that there was no doubt in distinguishing them. Little

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pollen was lost in mounting and tetrads were rarely broken or lying on their sides. All tetrads on a slide were counted and it is thought that errors in counting were negligible.

For observations of meiosis, buds were fixed in acetic-alcohol (1:3) and subsequently stored in 70% alcohol. Following hydration, buds were hydrolysed for five minutes in N HCl at 60°C. and then squashed in 2% synthetic orcein (G. T. Gurr, London) in 60% acetic acid. The pre-treatment with HCl not only improves the stain but helps separate the pollen mother cells, which otherwise tend to adhere to the tapetum. Alternatively an aceto-carmin squash technique was used without previous hydrolysis.

RESULTS.

1. Observations on Pollen Grains.

Frequencies of the different types of tetrads and the frequencies of aborted pollen grains are shown in Table 1.

TABLE 1.
Frequencies of Tetrad Types in Various Collections.

Species.	Plant and Collection.	Sample Size.	Full Tetrads.	Triads.	Dyads A.	Dyads O.	Monads.	Nullads.	Tetrads with at Least One Aborted Pollen Grain.	Percentage Aborted Pollen Grains.
<i>L. linarioides</i> ..	Wild plant 1	1,652	0·815	0·073	0·064	0·012	0·027	0·009	0·185	12·1
<i>L. biloba</i> ..	Cultivated plant 1, Collection 1	297	0·094	0·189	0·306	0·037	0·239	0·135	0·906	53·3
	Cultivated plant 1, Collection 2	349	0·185	0·421	0·248	0·058	0·072	0·016	0·815	40·3
	Cultivated plant 1, Collection 3	2,345	0·554	0·258	0·116	0·013	0·027	0·032	0·446	18·1
<i>L. formosa</i> ..	Wild plant 1	1,405	0·809	0·122	0·037	0·009	0·008	0·015	0·191	7·4
	Cultivated plant 1 ..	970	0·911	0·041	0·022	0·014	0·003	0·009	0·089	3·9
	Cultivated plant 2 ..	1,658	0·589	0·293	0·078	0·014	0·013	0·013	0·411	14·2
	Cultivated plant 3 ..	703	0·341	0·404	0·159	0·033	0·037	0·026	0·659	24·7
	Cultivated plant 4 ..	934	0·358	0·442	0·140	0·023	0·022	0·015	0·642	27·4
	Cultivated plant 5, Collection 1	933	0·250	0·399	0·260	0·024	0·044	0·023	0·750	29·6
	Cultivated plant 5, Collection 2	811	0·361	0·430	0·136	0·023	0·035	0·015	0·639	22·8

Although there is considerable variation in their frequencies, abortion patterns are similar in all three species whether collected in cultivation or the native state. Thus the underlying causes of abortion may be similar in all three species and must be present in the native state.

The great variability between the three different collections from the one plant of *L. biloba* suggests that the environment has an important effect. This is confirmed by the two collections from the fifth cultivated plant of *L. formosa*. These were statistically different (χ^2 for heterogeneity = 51·818 with 3 degrees of freedom. $P < \cdot 001$).

However, within a bud the contents of anthers are not heterogeneous. The individual counts for the five anthers from the one bud of *L. formosa* wild plant 1 are shown in Table 2.

This result has been confirmed using buds from *L. formosa* cultivated plants 3, 4 and 5, the probabilities derived from the contingency χ^2 s being 10–20%, 10–20% and 60–70% respectively.

These data may be summarized as showing that there may be a large variation between buds on the same plant, but that the anthers within a bud are homogeneous.

The large variation within a plant made it difficult to correlate observations on meiosis and on pollen grains. In the absence of facilities for growing plants under constant environmental conditions, collections of meiotic material of *L. biloba* were

made and other buds, of similar length and presumably at the same stage, were marked for later pollen grain studies. Only one pair of collections was successful at both stages. The pollen grain counts are shown in Table 3. The three buds were not heterogeneous, which lends support to the assumption that they were at the same stage when marked.

In some tetrads one or more small aborted microcytes were observed (Plate x, fig. 3).

TABLE 2.
Numbers of Tetrad Types in One Bud of L. formosa (Wild Plant 1).

Anther.	Full Tetrads.	Triads.	Dyads A.	Dyads O.	Monads.	Nullads.	Total.
1	239	41	10	2	2	3	297
2	219	38	7	3	1	2	270
3	219	35	16	0	2	8	280
4	225	27	14	7	4	5	282
5	234	31	5	1	2	3	276
Total	1,136	172	52	13	11	21	1,405

χ^2 heterogeneity = 19.836 with 12 degrees of freedom * $0.10 > P > 0.05$.

* Dyads O, Monads and Nullads were grouped into one class.

TABLE 3.
Numbers of Tetrad Types in Three Buds of L. biloba (Plant 1, Collection 3) Judged to have been at the Same Stage of Development.

Bud.	Full Tetrads.	Triads.	Dyads A.	Dyads O.	Monads.	Nullads.	Total.
1	465	247	103	14	27	26	882
2	439	185	78	8	14	21	745
3	396	172	90	9	22	29	718
Total	1,300	604	271	31	63	76	2,345

χ^2 heterogeneity = 13.233 with 10 degrees of freedom $0.20 < P < 0.30$.

2. Observations on Pollen Mother Cells.

In all three species the diploid complement of chromosomes was 18. Detailed studies of meiosis were confined to *L. formosa* and *L. biloba*. Prophase stages were difficult to observe. At metaphase I, a large proportion of bivalents was seen to have a single terminalized chiasma (Plate x, fig. 4). In *L. biloba* the chiasma frequency in one sample was 9.85 ± 0.95 and in a sample from *L. formosa* 11.55 ± 0.3 .

Univalents were frequently observed at metaphase I, anaphase I and early telophase I (Plate x, fig. 5). The frequencies for *L. biloba* (cultivated from plant 1) are shown in Table 4.

Of 780 cells scored, 100 contained univalents, 98 cells with one pair and two cells with two pairs. Similar observations in three collections from *L. formosa* showed univalents to be present in 10.6%, 17.4% and 11.4% of pollen mother cells respectively.

Collection 3 in Table 4 corresponds to the pollen grain data shown in Table 3, i.e. the buds in Table 3 were judged to have been undergoing meiosis at the same time as Collection 3, Table 5, was made. The important point to be noticed is that, whereas univalents appeared in only 23% of pollen mother cells, aborted pollen grains appeared in 44.6% of tetrads.

Although frequencies have not been estimated, laggards have also been observed at telophase II (Plate x, fig. 6). It was also observed in cells at the second division of meiosis that spindles were always parallel and never crossed. An important implication of this is that, in a dyad-O tetrad, a stained and an aborted cell must be sister cells

from the same second division spindle. When each spindle gives rise to one stained and one aborted pollen grain, usually equal numbers of dyad-A and dyad-O tetrads should result. Dyad-A, but not dyad-O, tetrads could also result from some polar inequality at the first division of meiosis.

TABLE 4.
*Number of Pollen Mother Cells of L. biloba Containing Univalents at Metaphase I—
 Telophase I.*

Collection.	Cells with Univalents.	Total Cells.	Percentage of Cells with Univalents.
Collection 1—			
Bud 1	27*	273	10
Bud 2	18	161	11
Collection 2	20*	195	10
Collection 3	35	151	23
Total	100	780	—

* Includes one cell with four univalents.

DISCUSSION.

The data in Tables 1, 2 and 3 show that, when buds, from one plant, at different stages of development were studied, the tetrad patterns were heterogeneous. However, when buds at approximately the same stage of development were studied, the tetrad patterns were not heterogeneous. Because anthers in a bud also were homogeneous it is deduced that the environment of the plant is important in determining the frequency of pollen abortion.

One simple hypothesis which should be considered to account for the abortion patterns observed is that abortion was caused by a randomly occurring event. If this were so, the frequencies of the different patterns should have followed a binomial distribution. Thus in the data shown in Table 2, the frequency of aborted grains was $\frac{414}{5620} = .744$. The expansion of $(.9256 + .0744)^4$ should give the expectations in the different classes of tetrads. These are as follows.

	Full Tetrads.	Triads.	Dyads.	Monads.	Nullads.
Expected	1030.4	332.2	40.2	2.1	Very small
Observed	1136	172	65	11	21

Also the frequency of adjacent dyads should have been twice that of opposite dyads. The observations were 52:13. There were significant departures from both expectations and these were also shown by all other data. On its own, at least, this hypothesis must be discarded.

The high frequency of univalents observed at meiosis suggests that pollen abortion might be explained by their distribution. The low frequency of cells with more than one pair of univalents (observed twice in 780 cells) suggests that an hypothesis could be formulated taking account only of cells with one pair of univalents.

Let p be the frequency of formation of one pair of univalents; i.e. 1-p is the frequency of non-formation of univalents. Any one univalent may have one of three fates, i.e.:

- (1) Be included undivided at one pole at anaphase I. Let the frequency of this be x.

(2) Be lost, i.e. not included at either pole at anaphase I. Let the frequency of this be y .

(3) Divide at anaphase I, one chromatid going towards each pole. Let the frequency of this be z .

Misdivision may be included with loss since the result would be the same. Thus $x + y + z = 1$ Equation 1.

When a univalent divides, an individual chromatid may be lost, either before telophase I or during the second meiotic division. Let the frequency of this, for any one chromatid, be w .

Using these parameters, the frequencies of the different tetrad types have been worked out and are shown in Tables 5 and 6. Table 5 is based on the additional hypothesis that deficiency only leads to abortion, i.e. disomic pollen grains are viable. Table 6 is based on the alternative hypothesis that any unbalance leads to abortion.

The six equations derived from either table, together with Equation 1, could, in theory, be solved by the method of maximum likelihood (Mather, 1951, page 47) for any particular set of data. The task is, however, formidable and has not been achieved.

TABLE 5.

Tetrad Types Resulting from Distribution of Univalents on the Hypothesis that Only Deficiency Leads to Abortion. For further explanation, see text. To distinguish the two poles, they are called N and S. For brevity, "full tetrads" are shown as "tetrads".

	1st univalent \ 2nd univalent	Lost.	Included Whole.		Divided and Included.			Frequency.	
			N.	S.	N & S.	N.	S.		Nil.
	Lost	Nullad	Dyad A	Dyad A	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Monad	Monad	Nullad	y
Included whole	N	Dyad A	Dyad A	Tetrad	Triad	Dyad A	Triad	Dyad A	$\frac{x}{2}$
	S	Dyad A	Tetrad	Dyad A	Triad	Triad	Dyad A	Dyad A	$\frac{x}{2}$
Divided and included	N & S	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Triad	Triad	$\frac{1}{2}$ Tetrad $\frac{1}{2}$ Triad $\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Triad $\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Triad $\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	zw^2
	N	Monad	Dyad A	Triad	$\frac{1}{2}$ Triad $\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Monad	$zw(1-w)$
	S	Monad	Triad	Dyad A	$\frac{1}{2}$ Triad $\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Monad $\frac{1}{2}$ Dyad A	Monad	$zw(1-w)$
	Nil	Nullad	Dyad A	Dyad A	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Monad	Monad	Nullad	$z(1-w)^2$
Frequency	y	$\frac{x}{2}$	$\frac{x}{2}$	zw^2	$zw(1-w)$	$zw(1-w)$	$z(1-w)^2$		

Total frequencies :

- Full tetrads = $(1-p) + p(\frac{1}{2}x^2 + \frac{1}{2}z^2w^4)$.
- Triads = $pzw[2x + zw^2(2 - 1\frac{1}{2}w)]$.
- Dyads A = $pz[2y + 2z(1-w) + \frac{1}{2}x] + pzw^2\{y + z[\frac{1}{2}w^2 + (1-w)(3-2w)]\}$.
- Dyads O = $pzw^2[y + \frac{1}{2}zw^2 + z(1-w)(2-w)]$.
- Monads = $pzw(1-w)[4y + z(1-w)(4-3w)]$.
- Nullads = $py^2 + pz(1-w)^2[2y + z(1-w)^2]$.

If it were done the whole univalent hypothesis and the alternative subsidiary hypotheses could be tested.

Observations of univalents at meiosis I, of laggards at meiosis II and of microcytes within spores showing abortion patterns support the univalent hypothesis. Microcytes presumably form around the univalents. The frequency of tetrads containing one or more aborted spores should be less than the frequency of pollen mother cells containing univalents because a full tetrad may be formed even when univalents are present at meiosis (Tables 5 and 6). In the observation reported here, the frequency of tetrads containing one or more aborted spores ranged from 9% to 90% with a mean of 52%;

TABLE 6.

Tetrad Types Resulting from Distribution of Univalents on the Hypothesis that any Unbalance Leads to Abortion. For further explanation, see text. To distinguish the two poles, they are called N and S. For brevity, "full tetrads" are shown as "tetrads".

	1st univalent	2nd univalent	Included Whole.		Divided and Included.			Frequency.	
			Lost.	N.	S.	N & S.	N.		S.
	Lost	Nullad	Dyad A	Dyad A	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Monad	Monad	Nullad	y
Included whole	N	Dyad A	Nullad	Tetrad	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Monad	Triad	Dyad A	$\frac{x}{2}$
	S	Dyad A	Tetrad	Nullad	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Triad	Monad	Dyad A	$\frac{x}{2}$
Divided and included	N & S	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{3}{4}$ Tetrad $\frac{1}{4}$ Nullad $\frac{1}{2}$ Dyad A	$\frac{1}{2}$ Monad $\frac{1}{2}$ Triad	$\frac{1}{2}$ Triad $\frac{1}{2}$ Monad	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	zw ²
	N	Monad	Monad	Triad	$\frac{1}{2}$ Monad $\frac{1}{2}$ Triad	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Nullad	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Monad	zw(1-w)
	S	Monad	Triad	Monad	$\frac{1}{2}$ Triad $\frac{1}{2}$ Monad	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Nullad	Monad	zw(1-w)
	Nil	Nullad	Dyad A	Dyad A	$\frac{1}{2}$ Dyad A $\frac{1}{2}$ Dyad O	Monad	Monad	Nullad	z(1-w) ²
Frequency	y	$\frac{x}{2}$	$\frac{x}{2}$	zw ²	zw(1-w)	zw(1-w)	z(1-w) ²		

Total frequencies:

$$\begin{aligned} \text{Full tetrads} &= (1-p) + p(\frac{1}{2}x^2 + \frac{1}{2}z^2w^4). \\ \text{Triads} &= 2pzw(1-w)(x+zw^2). \\ \text{Dyads A} &= pzw^2\{x+y+z(\frac{1}{2}w^2+3(1-w)^2)\} + 2px\{y+z(1-w)^2\}. \\ \text{Dyads O} &= pzw^2\{x+y+2z(1-w)^2\}. \\ \text{Monads} &= 2pzw(1-w)\{x+2y+z[w^2+2(1-w)^2]\}. \\ \text{Nullads} &= pz(1-w)^2\{2y+z[w^2+(1-w)^2]\} + p(y^2 + \frac{1}{2}zw^2 + \frac{1}{2}x^2). \end{aligned}$$

the frequency of pollen mother cells containing univalents ranged from 10% to 23% with a mean of 13%. Although there is a considerable difference between these mean values, this cannot be taken as disproof of the univalent hypothesis because of the great variability and the overlapping distributions. Moreover, with one exception, there was no direct correlation between the two sorts of observations. In the one set of data in which an attempt was made to estimate frequencies of tetrad types which could be correlated with meiotic observations, tetrads with aborted spores were twice as frequent as pollen mother cells with univalents. This suggests that univalent distribution alone

can account for only part of the observed abortion, but it is not a rigorous enough test to exclude its accounting for all abortion.

If univalent distribution cannot account for all abortion, there must be other causes co-existing, e.g., abortion due to randomly occurring events would increase the frequency of triads and dyads, but would make less difference to the frequencies of monads and nullads. A further hypothesis which should be mentioned is that proposed, for some species (e.g., *Astroloma pinifolium*) of the Epacridaceae by Smith-White in a paper in this Part of these PROCEEDINGS (pp. 259-270). If, at meiosis, the segregation of cytoplasmic and/or chromosomal factors is equational at the first division but reductional at the second, such as to cause abortion at both poles, one pole or neither in each half mother cell in the ratio $x:y:z$, then the different tetrad types can be derived from the trinomial $(x + y + z)^2$. Because univalent distribution is responsible, almost certainly, for a large proportion of abortion, no attempt has been made to apply the trinomial hypothesis alone. It is mentioned as a possible co-existing cause of abortion, although it is considered unlikely to be operating because terminal localization of chiasmata causes reduction at the first meiotic division for most chromosomal material.

It is not apparent how a rather high proportion of inviable gametes persists in these species. Presumably this selective disadvantage is outweighed by some contingent advantage. For example, the terminal localization of a single chiasma may preserve intact different combinations of genes, the presence of which is advantageous to a local population of species. The chance failure of formation of this chiasma would result in univalents and relative infertility. Possibly the disadvantage of this is not as great as the advantage of terminal localization of a single chiasma. This may be particularly true where there is always some fertile pollen and pollination is very efficient as it may be in *Leschenaultia* with its elaborate indusium for collecting and holding pollen.

Acknowledgements.

We would like to thank Dr. S. Smith-White for valuable advice and criticism. One of us (W.J.P.) carried out this work while holding a C.S.I.R.O. post-graduate studentship.

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EXPLANATION OF PLATE X.

Fig. 1. Camera lucida drawings of the various types of tetrads in *Leschenaultia formosa*. Top (left to right): full tetrad, triad, dyad O; bottom (left to right): nullad, dyad O, monad, dyad A. $\times 200$.

Fig. 2. *Leschenaultia formosa*. Pollen tetrads stained with acid fuchsin showing full tetrads, triad, dyad A and monad. $\times 100$.

Fig. 3. *Leschenaultia biloba*. Pollen tetrads showing full tetrads, dyad O and dyad A, with one microcyte. $\times 100$.

Fig. 4. *Leschenaultia biloba*. Pollen mother cells at metaphase I. In the majority of bivalents there is a single, terminally localized chiasma. Aceto-orcein; $\times 830$.

Fig. 5. *Leschenaultia biloba*. Pollen mother cell at telophase I, showing two univalents. Aceto-orcein; $\times 830$.

Fig. 6. *Leschenaultia formosa*. Pollen mother cell at telophase II showing laggards. Aceto-carmine; $\times 830$.

SEED COAT ANATOMY AND TAXONOMY IN *EUCALYPTUS*. II.*

By E. GAUBA and L. D. PRYOR.

(With Plates xi-xiii; Text-figures 20-39.)

[Read 26th August, 1959.]

Synopsis.

Blakely's Series Eudesmiae of the Section Macrantherae comprises 12 species of which 11 have been examined. Except the Subseries Leptospermae their seeds are of hemitropous structure, bifacial, the dorsal side uniform, the ventral side containing chalaza (with the vascular system), hilum and micropyle. There is an immediate transition of the conducting tissue from the placenta to the chalaza, that is to say without the formation of a raphe. The inner epidermis of the outer integument is a crystal epithelium par excellence, the inner integument is suberized, the inner cuticle very tender and smooth (or with inconspicuous projections).

Apart from these common features the separate species often display considerable differences not only in morphological aspects (seed smooth, ribbed or winged) but particularly with regard to the anatomy of epidermis, hilum, micropyle etc., suggesting some necessary rearrangement within the Eudesmiae or even a transfer of some species to other groups of the Macrantherae (or the reverse).

The Subseries Leptospermae (*E. tenuipes* and *E. curtisii*) exhibits—as far as the testa structure is concerned—no relation to the hemitropous Eudesmiae. The seeds are anatropous with a typical raphe, hence with a different relative position of chalaza, hilum and micropyle and a different vascularization. The crystal epithelium is missing, the inner cuticle rather conspicuous and with relatively prominent ribs. There is no doubt from the complete uniformity in testa structure that these two species are very close relatives and sharply demarcated from the remainder of the Eudesmiae.

Section MACRANTHERAE. Series EUDESMIAE (Benth.) Blakely.

INTRODUCTION.

Of the twelve species listed by Blakely in the Series Eudesmiae the seed of the following eleven were examined.

(1) Subseries Fasciculares: *E. erythrocorys*, *E. tetragona*, *E. eudesmoides*, *E. ebbanoensis*.

Subseries E fasciculares: *E. odontocarpa*, *E. tetrodonta*.

Subseries Holocalyces: *E. virata*, *E. similis*, *E. baileyana*.

Their seeds are of hemitropous structure and we distinguish between the ventral side (with chalaza and its vascular system, hilum and micropyle) and the uniform dorsal side.

(2) Subseries Leptospermae: *E. tenuipes* and *E. curtisii*.

Their seeds are of anatropous origin and we may distinguish between a raphe side (with chalaza and raphe bundle) and a uniform raphe-free side. Hilum and micropyle lie side by side at the basal end of the seed.

The following explains the lettering in the Text-figures and Plates: *cd*, clinging disc; *ch*, chalaza; *cot*, cotyledons; *cr*, crystal epithelium; *ec*, embryo cuticle; *end*, endosperm; *h*, hilum; *hy*, hypocotyl; *ic*, inner cuticle; *ie*, inner epidermis; *ii*, inner integument; *lc*, lignified cells; *m*, micropyle; *mu*, mucilage; *nr*, nucellus remnants; *oc*, outer cuticle; *oe*, outer epidermis; *oi*, outer integument; *rm*, root meristem; *vb*, vascular bundle.

In the following the different parts of the testa are described together with some remarks on the nucellus, endosperm and embryo.

OUTER INTEGUMENT.

Originally a transitory storage tissue supplying the growing seed with food material, it undergoes during maturation various alterations in contents and structure of its cells. The final stage which is discussed here is that reached in ripe abscised seed.

* See Part I, PROC. LINN. SOC. N.S.W., 1958, 83, Part 1: 20-32.

Outer Epidermis.

The somewhat tabular cells are polygonal in surface view and more or less isodiametric (Fig. 20, 21), the only exception being *E. erythrocorys* where most of the cells are elongated parallel with the surface (Fig. 22). The outer walls are thin, giving cellulose reaction (*E. eudesmoides*, *E. baileyana*, *E. similis*), or thick and lignified (*E. erythrocorys*) or have mucilage as secondary wall deposits (*E. tetragona*, *E. ebbanoensis*). The mucilaginous cells of *E. odontocarpa* are of particular interest because of the complex structure of the outer wall. The smaller cells have a mucilaginous layer beneath a thin outer wall of cellulose, outlined against the lumen by a tender cellulose membrane (Fig. 23*a*). In the large bulging cells there is next to the lumen a thick, lignified and pitted membrane (Fig. 23*b*). In some instances this membrane was seen embedded within the mucilage of which the inner layer showed traces of pits continuous with those of the lignified membrane (Fig. 23*c*). This suggests that a formerly solid wall underwent *pro parte* a subsequent mucilaginous modification. In *E. tenuipes* and *E. curtisii* not only all epidermal cells have membrane mucilage but also many cells of the integumentary parenchyma (Fig. 24). The mucilage is impregnated with brown tannin-like substances. After their removal with Eau de Javelle it stains blue with chloriodide of zinc. Cuprammonia stains for a short while light blue, whereupon, swelling rapidly, the mucilage exhibits striking lamellations before being dissolved.

Phlobaphene deposits in epidermis cells are a regular feature in the anatropous Eudesmiae (*E. tenuipes*, *E. curtisii*), recalling the anatropous Renantherae.

Where the outer walls are thin they have collapsed in ripe seed and are more or less appressed to the inner walls rendering the surface minutely pitted (*E. baileyana*, *E. similis*). On the other hand a gregarious occurrence of thick-walled bulging cells causes the wrinkled appearance (*E. odontocarpa*). In *E. tetradonta* the sometimes warty surface is due to groups of lignified cells elongated perpendicularly to it.

The cuticle covering this epidermis is well preserved in *E. erythrocorys* and *E. tenuipes*, but in *E. baileyana* the usual stains and reagents failed to reveal its presence. In some sections of *E. eudesmoides* (and some other species) the cuticle was seen as an unbroken line, in others only in fragments, more or less detached from the epidermis, or, if not entirely missing, merely as a dotted line. Of course, the ovule always has a perfect cuticle which during maturation to seed may become disorganized or even completely resorbed. A loosening of its contact with the epidermis may also occur so that sectioning followed by treatment with reagents may tear off and wash away what remained of it.

Inner Epidermis.

This epidermis is, in all seeds of hemitropous structure, a typical crystal epithelium, each cell containing one large and a few smaller crystals of monoclinic calcium oxalate monohydrate. Crystalline granules (crystal-sand) are also often present, sometimes also elongated crystals (styloids).

The most common well-developed crystals are six or eight-faced, more rarely ten-faced. Professor Machatschki* (in litt.) gives the following indices which we reproduce with his sketches (Text-fig. 25).

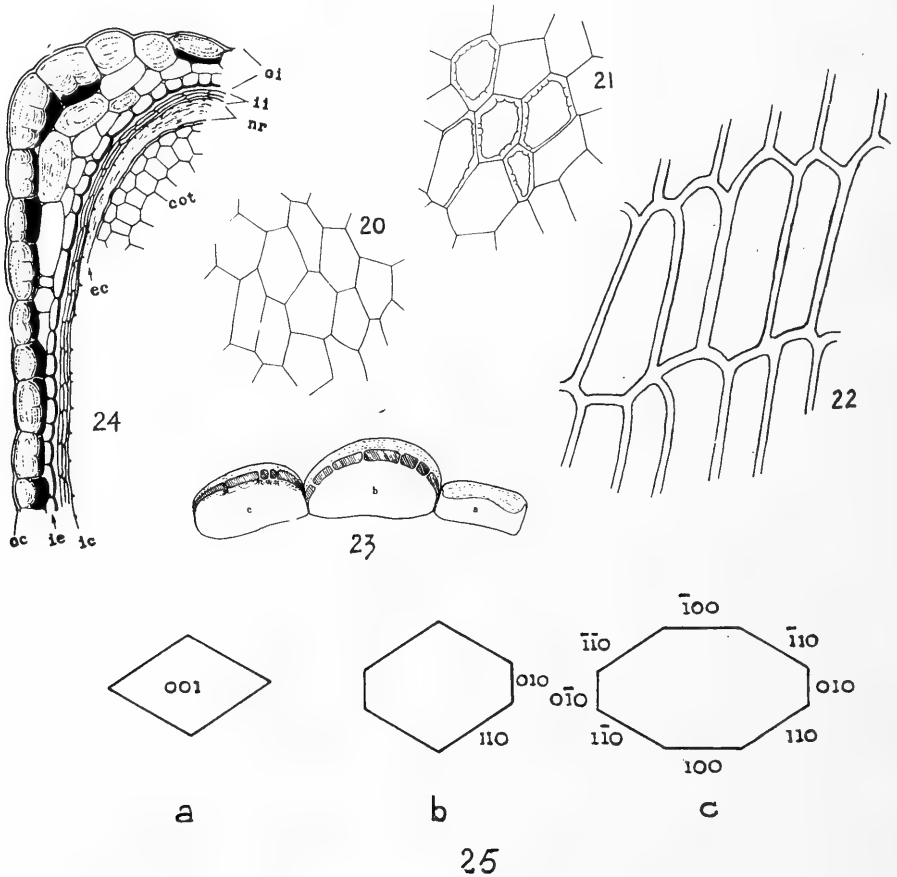
Hence we may infer that Figure 25*a* is a combination of the prism (110) and the basal pinacoid (001), Figure 25*b* shows an additional clinopinacoid (010) and finally the ten-faced crystal in Figure 25*c* also the orthopinacoid (100).

The larger crystals are encased within cellulose sheaths which, after dissolving the crystals, imitate so precisely their outline that only with a polarization microscope are these structures recognized as merely empty forms.

* We are greatly indebted to Prof. Dr. F. Machatschki, Director of the Institute of Mineralogy at the University of Vienna, for the examination of crystals in the seed coat of *E. eudesmoides*.

The cells are closely packed, their morphologic outer walls thick, constricting the lumen to such extent that there remains very little room to accommodate the crystals (Fig. 28, 32). This may explain their tabular habit parallel to the basal pinacoid (001).

As part of the integument which develops from a more or less circular rim at the base of the future nucellus the crystal layer of the mature seed exhibits at its base a circular, elliptic or oval gap, the "window in the crystal armour"—a very appropriate designation.



Text-fig. 20-24.—20-22, surface view of the dorsal epidermis, 100 \times . 20, *E. baileyana*; 21, *E. tetradonta*, showing a group of sclerified cells; 22, *E. erythrocorys*. 23-24, mucilaginous epidermis cells. 23a-c, *E. odontocarpa*, three types of outer wall modifications, 160 \times ; 24, *E. tenuipes*, transv. sect. through an edge of seed. Mucilage dotted, phlobaphenes black, 250 \times .

Text-fig. 25a-c.—*E. eudesmoides*, oxalate crystals of the inner epidermis (Crystal epithelium) of the outer integument.

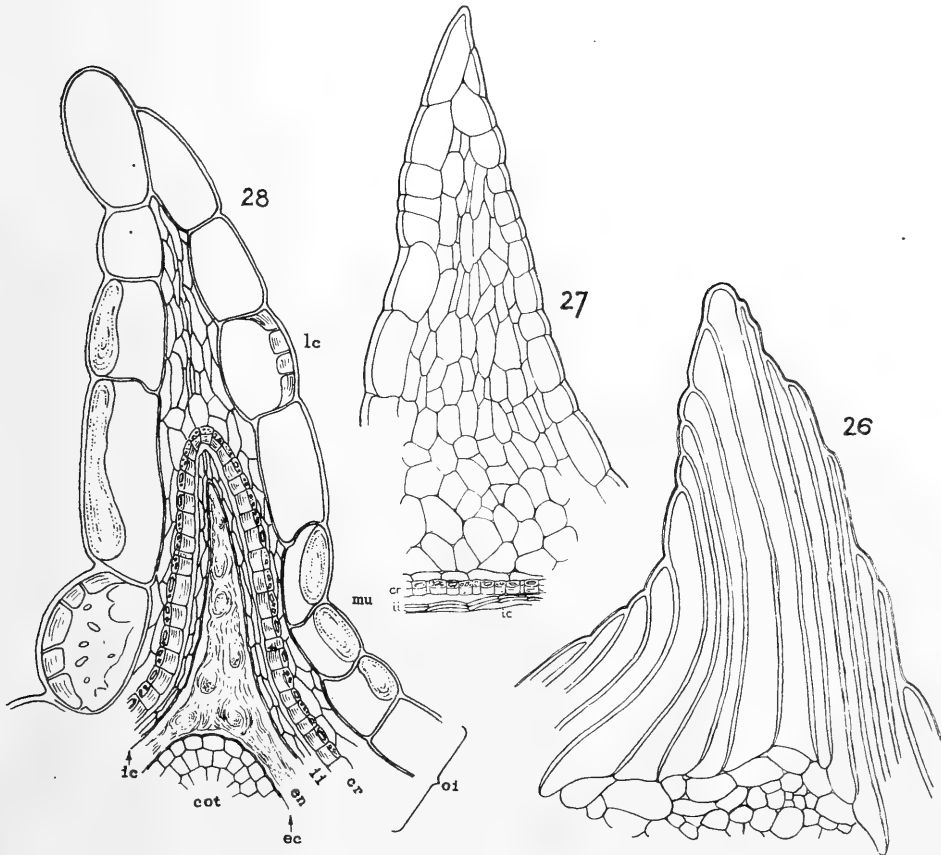
The cells of this epidermis are crystal-bearing to its very fringe (*E. tetragona*, *E. eudesmoides*, *E. baileyana*) or some rows bordering the "window" are empty (*E. odontocarpa*) and moreover both empty and suberized in *E. erythrocorys* and *E. ebbanoensis*. The border is more or less smooth or as in *E. similis* jagged (Fig. 35b, c).

This striking crystal epithelium in hemitropous seed is missing in the anatroplus Subseries of Leptospermae (*E. tenuipes* and *E. curtisii*). Crystals occur here, too, but only dispersed in the hilar and chalazal region and along the raphe, the cells having

only slightly thickened outer walls (Fig. 24 *ie*). The far greater part of the inner epidermis has no crystals.

Integumentary Parenchyma.

The parenchymatous tissue between the two epidermal layers and originating from them is always multi-layered on the ventral or raphe side. From here the number of layers gradually decreases towards the opposite side where it is reduced to a few (*E. erythrocorys*, *E. tetragona*) or to a single, often interrupted one (as in most of the species), and sometimes even missing (*E. baileyana*, *E. virata*). A greater amount of this parenchyma is also found in wings (Fig. 27, 28) and in the costae.



Text-fig. 26-28.—Transv. sect. through ridges and wings. 26, *E. erythrocorys*, ridge, 50×; 27, *E. tetragona*, wing, 130×; 28, *E. odontocarpa*, wing, 250×.

The homogeneity of this tissue is often disturbed by the occurrence of cells—single or in groups—with different contents or wall structure. Crystal idioblasts are for instance very frequent in the ventral side of *E. ebbanoensis*, with crystals partly embedded in the uneven wall thickenings (Pl. xi, fig. 5*b*), in the micropylar region of *E. erythrocorys* (Pl. xi, fig. 1*a*), in wings of *E. tetragona*, etc. Sclereid idioblasts are not infrequent in *E. erythrocorys*, in *E. tetradonta* adjacent to the inner epidermis and in *E. ebbanoensis* among suberized cells below the hilum (Pl. xi, fig. 5*b*). In *E. erythrocorys* suberized cells along the bundle branches were observed. Mucilaginous cells occur in *E. tenuipes* (Fig. 24) and *E. curtisii*. Phlobaphene deposits are often seen (*E. tetradonta*, *E. tetragona*) and impregnation of all walls with tannins, including those of both epidermal layers, is the rule. Because of this the seed coat is of dark (brown to black) appearance.

INNER INTEGUMENT.

This is always two-layered and suberized. The cells are tabular, without inter-cellular spaces, empty and very often completely obliterated. Like the outer integument it embraces with its circular base the chalaza. This is true also of its inner cuticle which is always present though not as conspicuous as in the Renantherae.* However, the median cuticle, separating the two integuments and present in the ovule, is missing in mature seeds. Only in *E. tetradonta* were some fragments of it seen.

RIDGES AND WINGS.

The seeds of *E. baileyana*, *E. similis*, *E. lirata* and *E. ebbanoensis* have a smooth surface, that is to say their testa is not expanded into ridges or wings.

The angular seeds of *E. erythrocorys* have prominent ridges built up by epidermis cells exceedingly elongated at right angle to the surface (Fig. 26). The ridges in *E. tetradonta* are of similar structure.

E. tetragona has wings, the broadest among the Eudesmieae, though scarcely exceeding 1½ mm. in width. The cross section through the circumferential wing reveals that the outer epidermis and parenchyma of the outer integument are the constituent parts (Fig. 27).

E. eudesmoides and *E. odontocarpa* have a circumferential membranous wing separating the ventral side from the dorsal. This delicate and narrow expansion has nevertheless a complex structure as both integuments and endosperm tissue (or in the vicinity of the chalaza, nucellar tissue) participate in its build up. The presence of the thick-walled crystal layer confers some mechanical protection which in *E. odontocarpa* is increased by lignification of some epidermal cells (Fig. 28). During germination the wing at the root pole is neatly split by the pressure of the swelling clinging disc, whereupon the hypocotyl emerges between the wing halves. Therefore the role of the clinging disc is not only to fix the germinating seed to the substratum, but as it expands by growth to burst the testa first of all.

HILUM.

After the shedding of the seed an elliptical, more or less discernible scar, the hilum, marks the abscission region. In hemitropous species it is located on the ventral side, overlapping partly the chalaza, though sometimes but to a very small extent (*E. eudesmoides*). However, the vascular bundle always has direct access to the chalaza. Therefore, there is no "raphe" so characteristic of the anatropous seed (*E. tenuipes* and *E. curtisii*).

In *E. baileyana*, *E. tetragona*, *E. eudesmoides* and *E. similis* the hilum is bordered by thin-walled peripherally elongated cells forming a sort of parenchymatous sheath (Fig. 29, 30). In *E. erythrocorys* the hilum is sharply circumscribed by a rim of sclereids (Fig. 31).

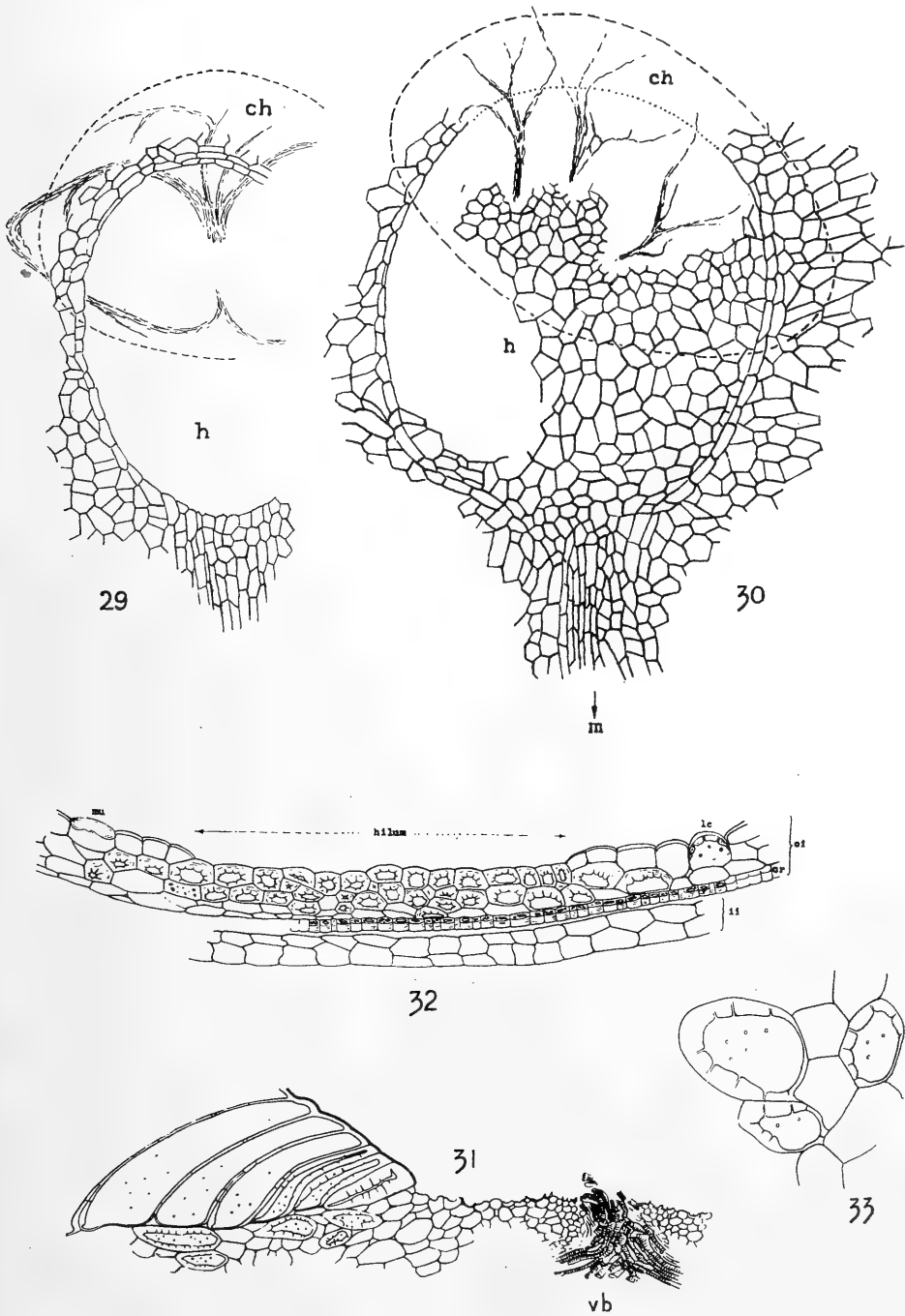
The surface of the hilum is flat or a shallow depression (*E. baileyana*, *E. eudesmoides*, etc.) or convex and shield-like (*E. ebbanoensis*, Pl. xi, fig. 5b).

Three types of cicatrization of the hilum were observed:

(1) Desiccation, shrinkage and collapse of the exposed cells, giving the hilum a pulverulent appearance, as for instance in *E. tetragona*, *E. eudesmoides*, *E. similis*, *E. erythrocorys* (Fig. 31). There is no suberization of the exposed cells and even cutinization was not traceable. Therefore, this is a very primitive type of wound healing.

(2) In *E. odontocarpa* the hilar scar is sealed by sclereids with lignified walls impregnated with tannins. These sclereids are either closely packed (Pl. xii, fig. 1) or dispersed in groups, and belong not only to the uppermost layer but also to the subjacent tissue (Fig. 32). It must be pointed out, however, that the sclerification seldom extends over the entire hilum, but is mostly restricted to that part which lies

* In some instances where this cuticle was very delicate and the usual stains were not adequate we used successfully a Rosanilin solution discoloured with SO₂.



Text-fig. 29-33 (hilar structures).—29-30, surface view of the hilum (*h*) overlapping the chalaza (*ch*). Some tissue partly removed to show the extent of the chalaza (broken line) and the vascularization. 29, *E. baileyana*, 50 \times ; 30, *E. tetragona*, 65 \times , three bundle strands enter separately into the chalaza. The arrow points in the direction of the micropyle *m*. 31-32, trans. sect. through the hilum. 31, *E. erythrocorys*, 100 \times . A rim of macrosclereids surrounds the hilum in which a vascular bundle (*vb*) enters; 32, *E. odontocarpa*, 160 \times . The hilum is sealed by sclereids (metaplasia by sclerification). 33, *E. erythrocorys*, surface view of the hilum with dispersed sclereids, 200 \times .

outside the chalaza (Pl. xii, fig. 1). Thus the portion overlapping the chalaza was often seen without sclerification but sometimes bordered by a more or less complete rim of thick-walled cells. This form of cicatrization represents, at least partially, a case of metaplasia* by sclerification and wall impregnation by antiseptic substances.

Sclereids with lignified uneven wall thickenings can be seen also in the hilum of *E. erythrocorys* where they occur singly or in groups, variably dispersed among thin-walled cells (Fig. 33). Their occurrence is too scanty to be of any value for the protection of the scar, but unequal tensions in such a heterogeneous tissue may facilitate the final separation of the seed.

(3) The most perfect case of metaplasia, that is by suberization, is exhibited in *E. ebbanoensis* where all surface cells of the hilum are suberized and completely filled with solid phlobaphenes extremely resistant to acids and bases. Suberized cells occur also in the underlying layers of the hilar cushion, intermixed with crystal- and sclereid-idioblasts (Pl. xi, fig. 5a-b). This is a remarkable case because Netolitzky, who critically revised the entire literature on Angiosperm seeds (about 1,100 papers), states that hitherto (1926) no suberization has been observed on the hilum. Hintringer (1927), who examined 80 species of 9 families, confirms Netolitzky's statement.

It is worth mentioning that the agents stimulating the formation of sclereids (*E. odontocarpa*) or inducing suberization (*E. ebbanoensis*) bring about the same metaplastic changes in some epidermis cells adjacent to the hilum (Pl. xi, fig. 5a). Analogy can be drawn with the traumatic stimulus of wound hormones in tissues not directly affected by injuries.

In the hilum of *E. similis* suberization is confined to a few cells surrounding the entrance of the bundles into the chalaza.

As we are concerned only with the hilar structure of the mature abscised seed the mechanism of its separation from the placenta and the time of the metaplastic wall modifications are not discussed. This would require ontogenetic investigations. But it seems quite certain that the metaplasia precedes the abscission.

Finally, the break in the vascular bundle occurs in the transition region between placenta and hilum where short tracheids have been preformed (Fig. 31). The somewhat protruding bundle stubs can be located on the hilum of many species.

CHALAZA.

The crystal layer, the suberized inner integument and the inner cuticle form together at their base a "window" which embraces and delimits laterally in a spectacular way the inner part of the chalaza. The outer part (above the window) passes imperceptibly into the parenchyma of the outer integument.

Two features characterize the chalaza: (1) The presence of a suberized tissue, the so-called "chalaza cork", in mature seed closing the gap and filled with dark coloured phlobaphenes. Thus, in some instances the chalaza is externally discernible without optical aid as a dark spot, in particular in those cases where these deposits are confined not only to the suberized part but occur throughout the whole chalaza. (2) The presence of the conducting tissue above the suberized zone.

As in the Renantherae the nucellus tissue† can participate in a variable amount in the formation of the chalaza cork. In *E. baileyana* and *E. tetragona* it originates almost entirely from the nucellus, in *E. odontocarpa* it is chiefly the true chalaza parenchyma of which the inner part undergoes the suberization. *E. tetradonta* is exceptional in having no chalaza cork.

* The term "metaplasia" was introduced into plant anatomy by Küster (1903) to designate progressive changes in histological character other than by cell growth or division. In our case these changes concern chiefly a sclerification or a suberization to form a protective cicatrice over the abscission region.

† In sections through the chalaza an imaginary line closing the gap in the inner cuticle defines neatly the chalaza from the nucellus.

VASCULARIZATION.

The vascular supply to floral parts has received a great deal of attention in recent years. It has been suggested that the vascular bundles of an organ are more conservative than its external form and therefore they may contribute to the solution of phylogenetic and taxonomic problems. A critical review of the whole literature—*pro* and *contra*—was given by V. Puri (1951).

In the *Eudesmiae* with anatropous seed the vascular bundle is brought up from the hilum to the chalaza through the raphe (Fig. 34*a, b*).

In the *Eudesmiae* with hemitropous seed the conducting tissue enters directly from the placenta into the chalaza. In some species the number of strands penetrating the seed is not constant. In *E. tetragona* we saw one to three (Pl. xiii, fig. 2 and Text-fig. 30), in *E. similis* (Fig. 35*a, b, c*) up to four strands entering separately into the chalaza. A variable number can be seen also in *E. erythrocorys*, whereas in *E. eudesmoides* (Pl. xii, fig. 2), *E. ebbanoensis*, *E. baileyana* (Pl. xiii, fig. 1) and *E. lirata* (Fig. 36*a, b*) we observed always one single strand.

The bundle entrance never lies in the centre of the hilum but always close to its upper border. From here the bundle spreads immediately into several branches (*E. odontocarpa*, Pl. xii, fig. 1) or the ramification starts at a short distance from its entrance (*E. baileyana*, Fig. 29 and Pl. xiii, fig. 1; *E. tetradonta*, Fig. 37*a, b*).

The whole venation system seldom lies within the chalaza, most frequently some of the stronger branches penetrate somewhat the parenchyma of the outer integument but without taking an intra-integumentary course.

In *E. odontocarpa* the nearly straight branches spread palmately in the chalaza (Pl. xii, fig. 1), whereas in other species they are curved in varying degrees, displaying, especially the outer ones, an arctuous course along the chalaza border, as for instance in *E. baileyana* (Pl. xiii, fig. 1). Even abrupt angular turns can be observed (Fig. 35).

The bundles are amphicribal, the tracheary elements being only tracheids with helically thickened walls. Veins and veinlets terminate either freely with a single or double file of tracheids, or some of the branches may merge at their tips, as for instance in *E. baileyana* (Fig. 29) or *E. similis* (Fig. 35). The latter has sometimes transverse anastomoses interconnecting main strands (Fig. 35*c*).

Considered as a whole the vascular supply is very poor in *E. tetragona* (Pl. xiii, fig. 2), whereas in *E. erythrocorys* it displays a high degree of ramification and, by merging of the branchlet endings, a reticulate venation.

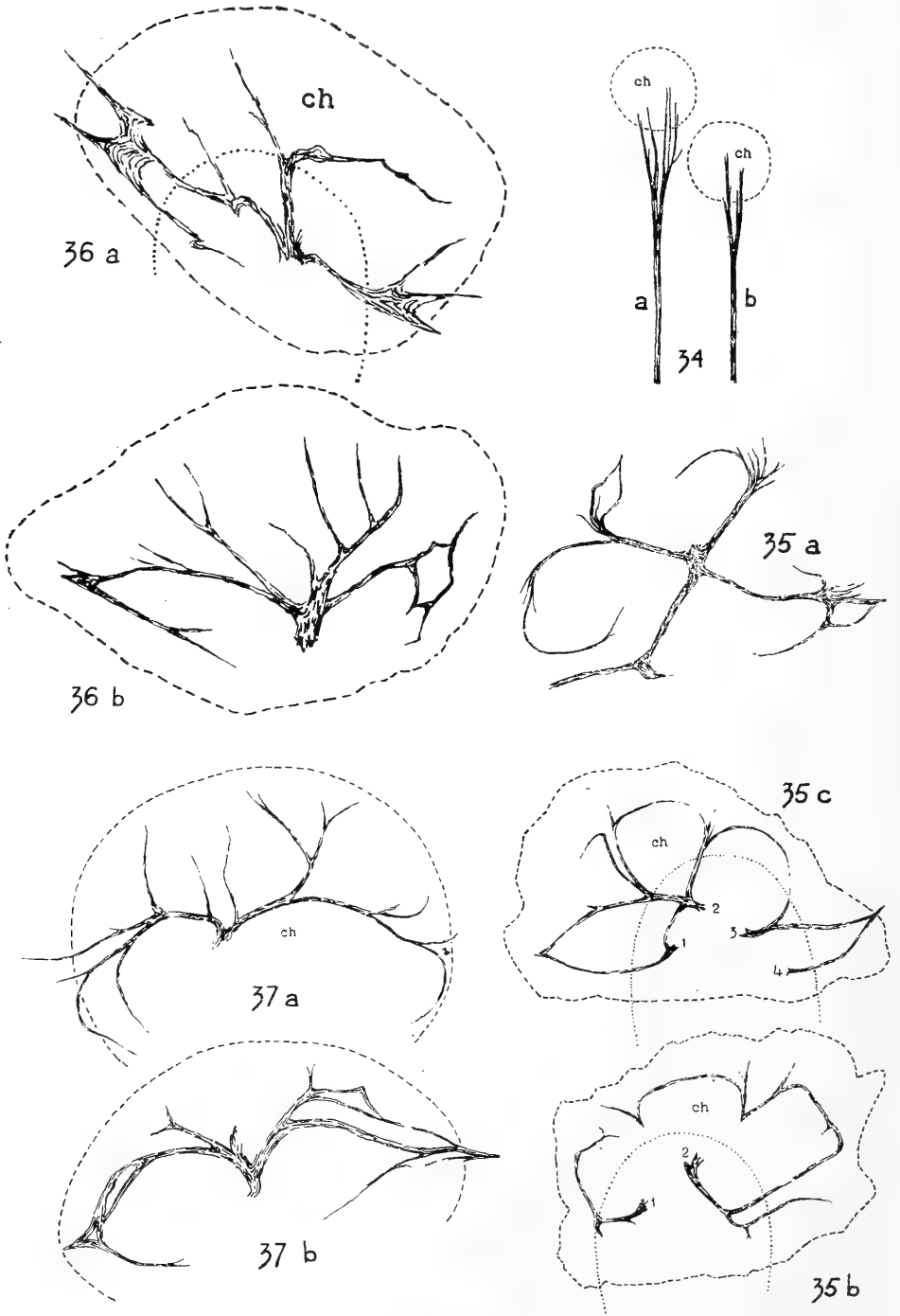
The venation patterns as shown here for hemitropous seeds exhibit a relatively wide range of variation within this small Series, even allowing for the variations within the same species. Thus at first glance it seems doubtful whether any taxonomic conclusion can be reached at this stage before the investigation is extended to the remaining hemitropous Macrantherae.

MICROPYLE.

Its approximate position in hemitropous seeds is given by prolongation of the hilar axis towards the root pole. On this line it can be discerned externally, sometimes even with the unaided eye, as a small tubercle or callosity (*E. odontocarpa*, Fig. 38*a*; *E. baileyana*), or it is hidden between ridges (*E. erythrocorys*, *E. tetradonta*) or wings (*E. tetragona*).

Inner and outer integument participate in its build-up, forming respectively the endostome and exostome. Due to the uniformity of the inner integument the endostome is of a relatively simple structure, whereas the exostome is bounded by three anatomically different parts (outer epidermis, integumentary parenchyma, crystal layer), of which each can contribute in various degrees to its formation. Thus, the micropyle as a whole exhibits in some species a very complex structure.

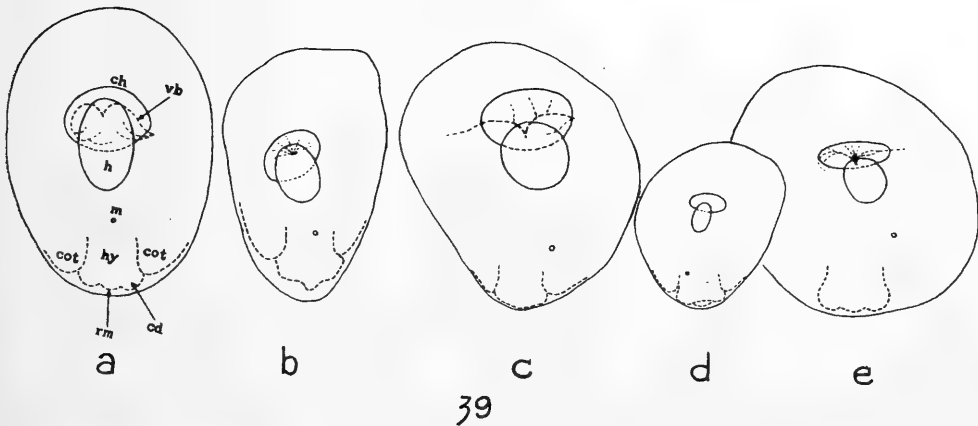
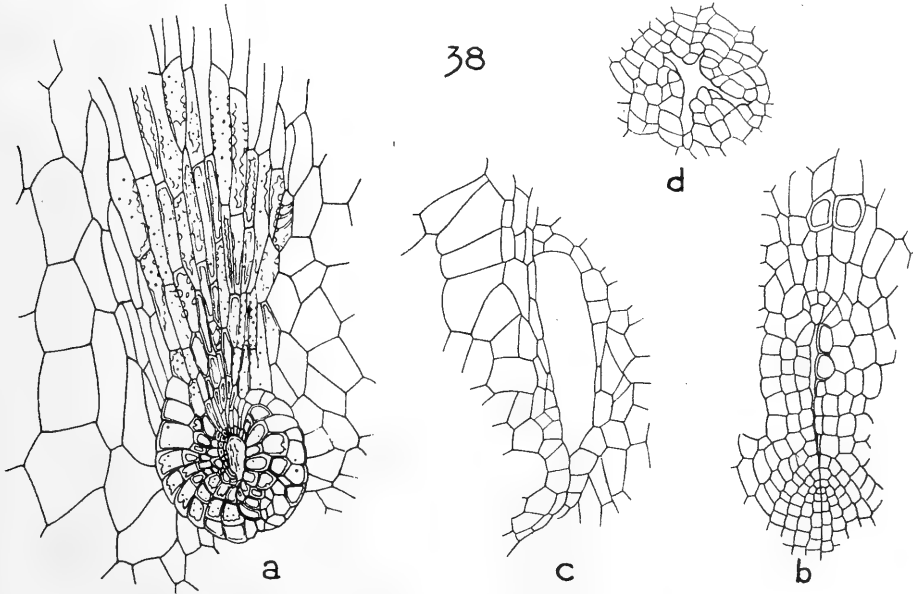
Reports upon the micropyle structure of mature seeds in general are rather scarce, owing probably to technical difficulties in obtaining suitable preparations. We have found the best way is to isolate in the micropylar region the inner cuticle, inner



Text-fig. 34-37.—Vascularization patterns. 34, anatropous species (Leptospermae). 34a, *E. tenuipes*, 85x; 34b, *E. curtisii*, 96x. 35-37, hemitropous species. 35a-c, *E. similis*, 45x (a with one, b with two, c with four separately entering bundle strands); 36a-b, *E. lirata*, 96x; 37a-b, *E. tetradonta*, 45x.
 (Broken line: chalaza extent; dotted line: hilum.)

integument, crystal layer and outer epidermis and to examine separately these layers in surface and side view.

Without claiming completeness some of our observations are illustrated in Text-figure 38 and on Plate xi. Variations, sometimes considerable, are frequent within the



Text-fig. 38a-d.—Variations of the micropylar structure in *E. odontocarpa*, ca. 160x. a, surface view; b, c, exostome aperture in the (isolated) outer epidermis; d, endostome aperture (d was lying beneath c).

Text-fig. 39a-e.—Seed diagrams showing on the ventral side the relative position of chalaza (ch) with the vascular bundle (vb), the hilum (h), the micropyle (m), the hypocotyl (hy) with root meristem (rm) and clinging disc (cd), and the cotyledons (cot). ca. 9x.

a, *E. baileyana*; b, *E. odontocarpa*; c, *E. tetradonta*; d, *E. ebbanoensis*; e, *E. eudesmoides*.

same species, especially with regard to the aperture of the micropyle. This is understandable if we bear in mind that the integuments have to keep pace with the increase in volume of the growing embryo, but there are differences in the rate of their growth which determine the final shape and size of the aperture in the integuments respectively in their different layers. On the seed surface for instance the micropyle may appear

as a circular or irregular opening (Pl. xi, fig. 2a), as a narrow or gaping slit (Fig. 38b, c), or it may be closed by contact or overlapping of its margins.

In separating the different layers in the micropylar region we first remove the endosperm which vaults gently into the suberized endostome (Pl. xi, fig. 1a) and is rich in oil and proteins. The inner cuticle is said in general to be apparently missing beneath the micropyle. But in *E. tenuipes* we could isolate it as a tender membrane with rib-like projections simulating a cellular structure (Pl. xi, fig. 3b).

The inner integument penetrates as a small or elongated hump (Pl. xi, fig. 1c, 2b), open or closed on the top, or as a two-lipped projection (the lips parted or firmly appressed) more or less deep into the exostome. In hemitropous seeds the inner limit of the exostome is well defined by the crystal layer which can be more or less vaulted, closed or with an open slit, the bounding cells of which are frequently devoid of crystals (Pl. xi, fig. 4b). We remember that in some species a crystal-free border of the crystal epithelium surrounds the chalaza.

In the exostome of *E. tetragona* the crystal layer is elongated into a tube or a horn-like protuberance which in *E. erythrocorys* can be up to 1 mm. long terminating just beneath the outer epidermis through which a capillary canal leads outwards (Pl. xi, fig. 1a). But in some instances we saw this "crystal horn" either as a blunt cone (Pl. xi, fig. 1b) or attenuated into a fine point and covered with integumentary parenchyma protruding freely between the epidermis cells.

It was said (Netolitzky, p. 38) that the disappearance of the cuticle lining the inner walls of the micropyle seems to be the rule. But in some species we saw it either well preserved (Pl. xi, fig. 1a, 2a, 4b) or in fragments (Pl. xi, fig. 4a).

RELATIVE POSITION OF CHALAZA, HILUM, MICROPYLE AND HYPOCOTYL.

In the hemitropous Eudesmieae the arrangement of these parts on the ventral side of the seed is illustrated by Figure 39. As can be seen, only in *E. baileyana* (Pl. xii, fig. 1; Text-fig. 39a) are they lying on the median line and symmetrical with it. In the other species they show considerable dislocations. Often the chalaza is turned away from the median and the hilum placed obliquely to it. As already mentioned, the position of the hilum determines always that of the micropyle: it lies on the prolongation of the longitudinal hilum axis towards the root pole.* The position of the hypocotyl with the apical root meristem indicates—and germination tests confirm—that it does not emerge through the micropyle.

In the anotropous Eudesmieae the disposition of those parts follows the Renantherae pattern (see Part I, Fig. 12); the chalaza lies on the raphe side just below the top. Hilum, micropyle and hypocotyl tip are at the basal end of the seed.

NUCELLUS, ENDOSPERM AND EMBRYO.

Remnants of the nucellus tissue, the cells empty and obliterated, are always present in variable amounts and extent and line the inner face of the testa. The endosperm remnants enveloping the embryo are better preserved. Their thick-walled cells are still rich in proteins.

Nucellus or endosperm (or both) project into the embryo folds between cotyledons and hypocotyl, thus showing ridges on the inner face. They may even penetrate into the wings (Fig. 28). The greatest amount is always found beneath the chalaza.

Generally, in the anotropous Eudesmieae the nucellus lines the whole inner face of the testa while the endosperm is restricted to the chalazal and micropylar region. In the hemitropous Eudesmieae the inverse relationship exists: the endosperm can be isolated as an unbroken layer enveloping the whole embryo whilst the nucellus is confined chiefly to the ventral side of the seed.

* This direction is anatomically well marked by elongated rectangular epidermis cells leading from the base of the hilum to the micropyle (Text-fig. 29, 30; Pl. xi, fig. 5a; Pl. xii, fig. 1). Only a histogenetic investigation would reveal what significance has to be attributed to this constant feature.

The embryo, covered by a semi-solid cuticle, consists of the two cotyledons folded in a complicated way and bent down along the hypocotyl. Root and shoot are still at a primordial stage, that is, as apical meristems occupying the two poles of the hypocotyl which alone represents the embryo axis.

The reserve materials stored in the embryo are oil droplets and aleurone grains, the latter enclosing cluster crystals of calcium oxalate and globoids.

To exhibit the oxalate crystals it is advisable to remove successively the oil, proteins and globoids, whereupon they are clearly seen (up to 8 or more per cell). After treatment with HCl they disappear by formation of soluble CaCl_2 , whereas cautious addition of sulphuric acid converts them on the spot into clusters of needle-shaped crystals of calcium sulphate.

The distribution of the cluster crystals of calcium oxalate in the embryo cotyledons is also worthy of note. In *E. erythrocorys*, *E. tetragona*, *E. eudesmoides*, *E. ebbanoensis* and *E. odontocarpa* they occur in all parts of the mesophyll, whereas in *E. baileyana* and *E. similis* the palisade tissue is devoid of them, though in the latter clusters in a few palisades can occasionally be observed. In *E. curtisii* and *E. tenuipes* (as well as in *Tristania conferta*) they seem to be missing altogether.

In Angophoras (*A. intermedia*, *A. costata*, *A. cordifolia*) they are confined to the upper epidermis, each cell containing one large druse or having instead a single crystal (tetragonal bipyramid?). Such crystals can be observed occasionally also among cluster crystals of *E. baileyana*, but here they are rare.

The globoids are generally of globular shape, but irregular form: even vermicular (*E. erythrocorys*) can be encountered frequently.

IS THE SERIES EUDESMAE A NATURAL GROUP?

It is necessary to consider separately the Subseries with anatropous and hemitropous seeds in the light of the above results.

The two anatropous species, *E. tenuipes* and *E. curtisii*, agree completely in all anatomical details with each other, in spite of the quite different shape of their seeds. In *E. curtisii* they are very slender, "somewhat similar to those of *Tristania conferta* R.Br., and quite distinct from any other species of *Eucalyptus*". In *E. tenuipes* they are "D-shaped to oblique pyramidal" (Blakely, 1930). Thus, they are "leptosperm" in *E. curtisii* only, but of a "renantherous" type in *E. tenuipes*. Nevertheless they are undoubtedly close relatives, but the designation "Leptospermae" for this Subseries is inappropriate as it covers only one of the two species.

Among the hemitropous species the members of the Subseries Holocalyces: *E. baileyana*, *E. similis* and *E. lirata** seem also to form a natural group. Blake (*loc. cit.*, p. 335) mentioned that similarities of some vegetative and floral characters "suggest that *E. similis*, *E. baileyana* (and presumably *E. lirata*), *E. phoenicea* and *E. miniata* are better grouped together". We shall comment on this proposal after having investigated the Series Miniatae.

In the Subseries Efasciculares the seeds of its two species, *E. odontocarpa* and *E. tetradonta*, have little in common both anatomically and morphologically, and to unite them in a group on seed characters alone appears impossible. *E. odontocarpa* has thin, flat, somewhat concave-convex seeds, carinate on the back, and with a circumferential wing which, though tender and narrow, has nevertheless a very complex structure (Fig. 28). The surface is wrinkled due to bulging mucilaginous epidermis cells, and the hilum sclerified (Pl. xii, fig. 1). In *E. tetradonta* the seeds are angular-orbicular in outline and are depressed and rather thick, costate with the ribs built up by macrosclereids, the surface often warty due to groups of lignified cells perpendicularly elongated to it. There is no trace of sclerification in the hilum. Among the

* Of *E. lirata* we had two seeds only (from the type specimen) for examination so that not all structural details could be investigated.

hemitropous Eudesmieae *E. odontocarpa* is the only species with a straight, palmately branched chalaza bundle (Pl. xii, fig. 1), whereas in *E. tetradonta* the branches have an arctuous course (Fig. 37). On the other hand, *E. tetradonta* is the only species in the Eudesmieae without any suberization in the chalaza region. Müller (Eucalyptographia, Dec. I) reports that "*E. tetradonta* has no immediate close affinity to any of its congeners, except to *E. odontocarpa* . . .", and Blakely (Key, p. 70) says that "the two species are thrown together by the morphosis of the buds and fruits, but differing widely in habit". Blake (*loc. cit.*, p. 335), commenting on Blakely's Eudesmieae, is cautious when suggesting that this Series "should perhaps be limited to *E. tetragona*, *E. odontocarpa*, *E. erythrocorys*, *E. eudesmoides*, and perhaps *E. tetradonta*".

A still greater diversity is encountered in the Fasciculares, comprising *E. erythrocorys*, *E. tetragona*, *E. eudesmoides* and *E. ebbanoensis*. *E. erythrocorys* has solid ribs formed by strongly elongated, thick walled, lignified epidermis cells, unique among the Eudesmieae (Fig. 22, 26). *E. tetragona* and *E. eudesmoides* have winged seeds, those of *E. ebbanoensis* are without any testa expansion. Thus, purely externally they all display a very different aspect. Among the Eudesmieae *E. erythrocorys* is the only species with the rim of macrosclereids surrounding the hilum (Fig. 31) and with the most complicated reticular venation which in *E. tetragona* is very poor and simple (Pl. xiii, fig. 2). Unique among all Eucalypts so far examined, and to our knowledge perhaps the Angiosperms hitherto investigated, is the suberization of the hilum in *E. ebbanoensis* (Pl. xi, fig. 5). The micropyle structure of *E. erythrocorys* and *E. tetragona* is also unusual. The crystal epithelium is elongated into a tube or horn-like protuberance, sometimes extended up to the outer epidermis (Pl. xi, fig. 1a), or even terminating freely between the epidermis cells (Pl. xi, fig. 1b).

We have stressed here only some of the more striking differences in morphological and anatomical seed characters of species allotted by Blakely to four Subseries and these united into the Series Eudesmieae. In the light of the above evidence the question arises as to which facts induced Blakely to make this classification. He considers (Key, p. 68) the Eudesmieae as "closely allied to Angophora particularly in the opposite character of the leaves, toothed calyx, texture of some of the fruits, and in the morphology of the seeds".

So far as the phyllotaxis and the calyx teeth are concerned, none of these characters is constant throughout the whole Series.

E. ebbanoensis, *E. similis* and *E. baileyana* are quoted as having alternate leaves. In *E. tetragona*, *E. tetradonta*, *E. lirata*, *E. tenuipes* and *E. curtisii* opposite and alternate leaves occur.

With regard to the calyx teeth Blakely's designation of the Subseries "Holocalyces" expresses their lack in this group.

In view of the great variety of seed types in the Eudesmieae it is difficult to understand Blakely's hint at the morphological similarity of Angophora and Eucalyptus seed. Taking for instance the very different seeds of *E. erythrocorys*, *E. tetragona*, *E. ebbanoensis*, *E. baileyana*, *E. curtisii* or *E. tenuipes*; none resembles at all seeds of *Angophora intermedia*, *A. costata* or *A. cordifolia*. A cursory glance at the anatomical structure of these Angophoras reveals a type of epidermis not seen in any Eudesmieae (thin-walled palisade-like cells rich in tannins), the inner integument completely or partially resorbed and not suberized, the oxalate druses of the cotyledons confined to the upper epidermis, etc.

Surprisingly, a comparison of *Eucalyptus curtisii* with *Tristania conferta* (both with anatropous seeds) reveals a perfect uniformity not only in all morphological details—as already pointed out by Blakely (Key, p. 72)—but also in the anatomical testa structure.

At this stage of our investigations further speculation about the affinity of species is not justified.

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EXPLANATION OF PLATES XI-XIII.

Plate xi.

(Cork tissue and cuticles brown.)

1-4: Micropylar structures. 1a-c, *E. erythrocorys*: 1a, longit. sect. (semi-diagrammatic), 45×; 1b, "crystal cone" protruding between epidermis cells (semi-diagrammatic), 45×; 1c, endostome from 1a, 125×. 2a-b, *E. ebbanoensis*, 330×: 2a, micropylar aperture in the outer epidermis; 2b, endostome (open). 3a-b, *E. tenuipes*, surface view, 250×: 3a, endostome (closed); 3b, inner cuticle beneath the endostome. 4a-b, *E. eudesmoides*, surface view, 250×: 4a, micropylar slit in the outer integument; 4b, micropylar slit in the crystal epithelium. 5a-b, *E. ebbanoensis*, hilum, 160×: 5a, surface view; 5b, trans. sect.

Plate xii.

Vascularization patterns (photomicrographs).

1: *E. odontocarpa*, ca. 100×. ch, chalaza; h, hilum; m, micropyle. 2: *E. eudesmoides*, ca. 100×.

Plate xiii.

Vascularization patterns (photomicrographs).

1: *E. baileyana*, ca. 100×. 2: *E. tetragona*, ca. 90×.

EXPERIMENTAL CROSSING OF *Aedes (Stegomyia) aegypti* Linnaeus and
Aedes (Stegomyia) albopictus Skuse (Diptera, Culicidae).

By A. R. Woodhill, Department of Zoology, University of Sydney, Sydney.

(Plate xiv.)

[Read 26th August, 1959.]

Synopsis.

Experimental crossings were made between various strains of *A. aegypti* and *A. albopictus*. Out of a total of 49,649 eggs deposited all were sterile, with the exception of one egg which gave rise to a male adult which showed thoracic markings combining the characters of the parent species.

INTRODUCTION.

This cross was first attempted by Toumanoff in 1937 and since then by various workers; the results of these experiments have been fully discussed by Kitzmiller (1953) and by Mattingly (1956) and a complete list of references will be found in their papers. The results obtained by various authors may be briefly summarized as follows: in all cases where fertile progeny was obtained the reciprocal cross was sterile, while the F_1 progeny and succeeding generations all completely resembled the female parent with the exception of one female in Toumanoff's and one male from a back cross in Bonnet's experiments which resembled the male parent. In some crosses the fertile progeny were produced by using *A. aegypti* as the female parent and in others by using *A. albopictus* as the female. Other workers again found complete sterility in both reciprocal crosses. In view of these contradictory results the author carried out a series of experiments during the period 1955-1959, the results of which are presented in this paper.

METHODS.

Standard laboratory colonies of various strains of *A. aegypti* and *A. albopictus* were maintained and eggs from these were used to obtain adults for the crossing experiments. Single pupae were isolated in tubes and the resulting adults were checked twice for species and sex before being liberated in the cages. Mass matings were made, with the numbers of males and females per cage varying from approximately 100 to 250. In all experiments examinations were made of spermathecae of small samples of females for the presence of living spermatozoa. Eggs from the matings were deposited on rough textured white filter papers placed in small dishes of water, and these were kept wet for 48 hours to allow the embryos to develop and were then dried out slowly and kept at 80°F. and 90% relative humidity for 7 days before being counted and immersed in water; they were then kept in water to observe hatching for at least 10 days before being discarded. Small quantities of dried yeast and ground rat biscuits were added to the water, as it has been suggested that some organic pollution stimulates hatching, although this has not been the author's experience. The adults were kept in nylon marquisette cages 12" × 10" × 10", were given raisins, sugar solution and fruit, and offered blood feeds three times weekly. The breeding work was carried out in a warm room at 80°F. and 75% to 80% relative humidity with natural daylight, including some hours of direct sunlight.

Eggs from the standard colonies treated as described above were 100% fertile. After the eggs from any particular culture or cross were handled, all glassware, instruments and bench surfaces were sterilized by heat treatment and the hands of the author thoroughly washed in very hot water. All cages were sterilized by dry heat before being used. These methods were also applied at all times to the handling of standard colonies.

The work was carried out entirely by the author with the exception of counting the eggs, which was carried out by an assistant who maintained the same precautions.

RESULTS.

During the period 1955-1957 crosses were attempted between *A. aegypti* from Mornington Island, Queensland (Q.), and two strains of *A. albopictus*, one from the Philippines (P.) and the other from Singapore (S.). Specimens of the strain of *A. aegypti* used were submitted to P. F. Mattingly, who stated that they were mainly var. *queenlandensis* with a few dark enough to be considered as the type form (see Mattingly, 1957).

The details of the experiments are shown in Table 1.

TABLE 1.

Experiment Number.	Date.	Number of Mosquitoes, Sex and Species.	Number of Blood Feeds.	Number of Eggs Deposited.	Number of Eggs Hatched.	♀♀ Examined for Living Sperms.	
						Number Positive.	Number Negative.
1	June, 1955	254♀ alb. (P) × 245♂ aeg. (Q).	370	177	0	3	22
		250♀ aeg. (Q) × 260♂ alb. (P).	660	6,538	0	12	13
2	June, 1956	122♀ alb. (S) × 133♂ aeg. (Q).	210	1,676	1	4	6
		100♀ aeg. (Q) × 105♂ alb. (S).	220	349	0	1	9
3	July, 1957	182♀ alb. (P) × 241♂ aeg. (Q).	285	1,565	0	1	9
		186♀ aeg. (Q) × 246♂ alb. (P).	560	1,089	0	0	10
4	Sept., 1957	180♀ alb. (S) × 216♂ aeg. (Q).	305	837	0	1	19
		180♀ aeg. (Q) × 243♂ alb. (S).	435	8,757	0	0	20
				20,988			

Copulation was observed frequently in all crosses and in most cases living spermatozoa were observed in at least some of the females. The females fed freely, but the number of eggs deposited did not always correspond with the number of blood feeds taken. The number of females examined for living spermatozoa was too small to allow of any correlation between these figures and the number of eggs deposited. It will be seen that out of a total of 20,988 eggs, only one was fertile. This was bred through to the adult stage and resulted in a male specimen which was completely intermediate in dorsal thoracic markings between *A. aegypti* and *A. albopictus* (see Plate xiv). The genitalia of this specimen were submitted to P. F. Mattingly, who considers that they resemble *A. albopictus* with some slight modification in the direction of *A. aegypti*.

The most recent report of successful crosses between *A. aegypti* and *A. albopictus* is that by Bonnet in Hawaii in 1950. It was thought that the failure to repeat the results of previous experiments may have been due to the presence of different strains of the species used. Accordingly eggs of both species were obtained from Hawaii (H.), and the results of a series of crosses made with these during 1958-1959 are shown in Table 2.

TABLE 2.

Experiment Number.	Date.	Number of Mosquitoes, Sex and Species.	Number of Blood Feeds.	Number of Eggs Deposited.	Number of Eggs Hatched.	♀♀ Examined for Living Sperms.	
						Number Positive.	Number Negative.
1	Oct., 1958	106♀ alb. (H) × 127♂ aeg. (H).	172	3,169	0	5	5
		128♀ aeg. (H) × 182♂ alb. (H).	432	13,326	0	3	7
2	Feb., 1959	143♀ alb. (H) × 188♂ aeg. (H).	151	3,227	0	12	8
		140♀ aeg. (H) × 194♂ alb. (H).	495	8,939	0	6	14
				28,661			

As before, frequent copulation was observed in all crosses and at least some of the females showed living spermatozoa in the spermathecae. In this series *A. aegypti* fed much more freely than *A. albopictus*, and this showed a distinct correlation with the number of eggs deposited. It will be seen that of a total of 28,661 eggs deposited all were completely sterile.

DISCUSSION.

The experiments outlined above were carried out on a much larger scale than those made by previous workers and all possible precautions were taken to avoid contamination of cultures by stray eggs. Two different strains of *A. aegypti* were used and three different strains of *A. albopictus*, though not in all the possible combinations. It is surprising therefore that the results of previous workers could not be confirmed. This leads to consideration of the possibility that previous results may have been due to the contamination of cultures by stray eggs accidentally introduced. As the eggs of these species remain viable in the dry state for several months there is an ever present danger, when various cultures are being bred in the same laboratory, that eggs may adhere to instruments, glassware or the hands of the operator or fall onto bench surfaces and be accidentally picked up again. The whole position is very puzzling and must remain open for the time being. It is hoped to obtain further strains of both species and to repeat the experiments with these.

Acknowledgements.

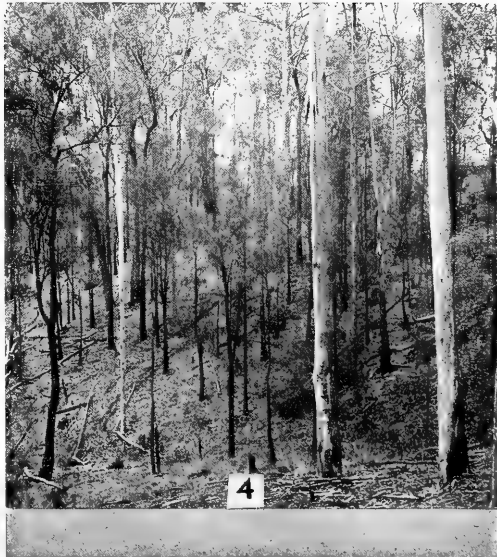
The author wishes to thank Mr. P. F. Mattingly for examining specimens of *A. aegypti* and the genitalia of the hybrid and for his continued interest in the work, Dr. L. E. Rozeboom, Dr. D. H. Colless, Mr. P. Y. Nakagawa and Dr. Elmo Hardy for forwarding eggs of various species, and Miss E. Hahn and Mr. R. Barnard for assistance. The latter was responsible for breeding through the single hybrid while the author was in hospital.

References.

- KITZMILLER, J. B., 1953.—Mosquito Genetics and Cytogenetics. *Separata da Rev. Bras. de Malariol. e D. Trop.*, Vol. 5, No. 4: 285-359.
- MATTINGLY, P. F., 1956.—Species Hybrids in Mosquitoes. *Trans. Roy. Ent. Soc. London*, 108, Pt. 2: 21-36.
- MATTINGLY, P. F., 1957.—Genetical Aspects of the *Aedes aegypti* Problem. *Ann. Trop. Med. and Parasit.*, 51, No. 4: 392-408.

EXPLANATION OF PLATE XIV.

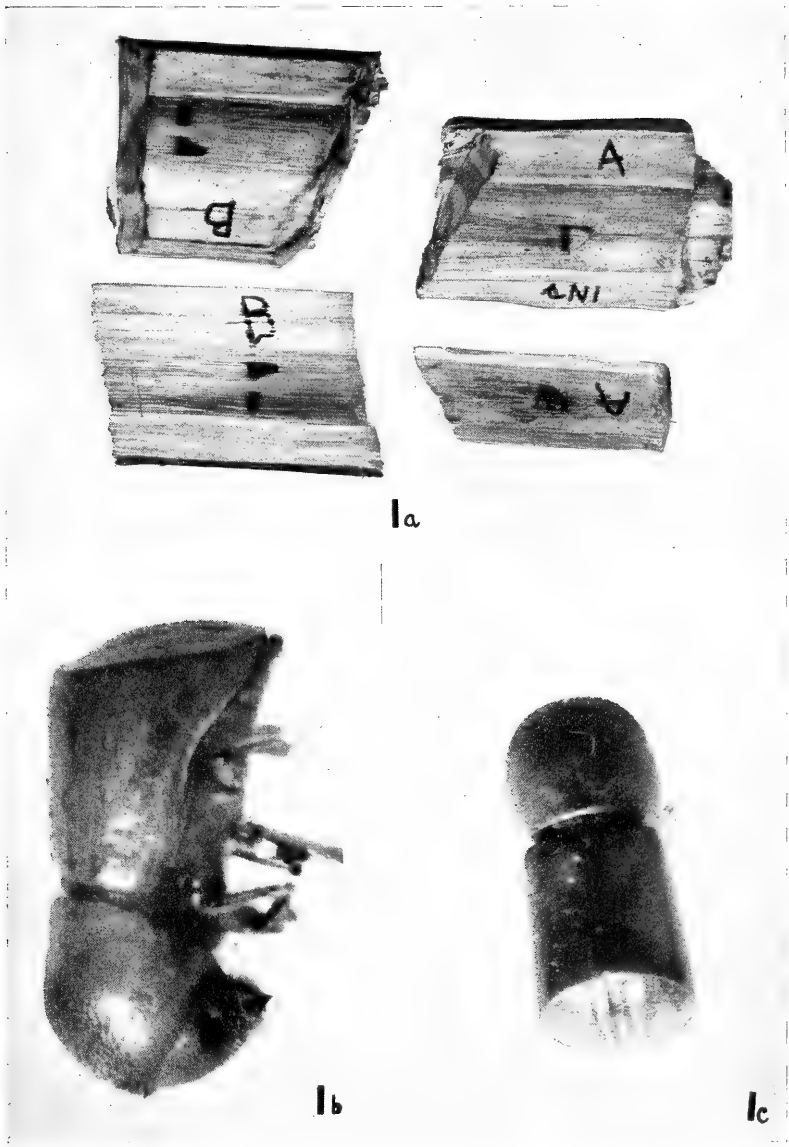
Adult male showing combination of characters of *A. aegypti* and *A. albopictus*.



1, 2, *Ctenomorphodes tessulata*. 3, *Myrmecomimesis* sp.

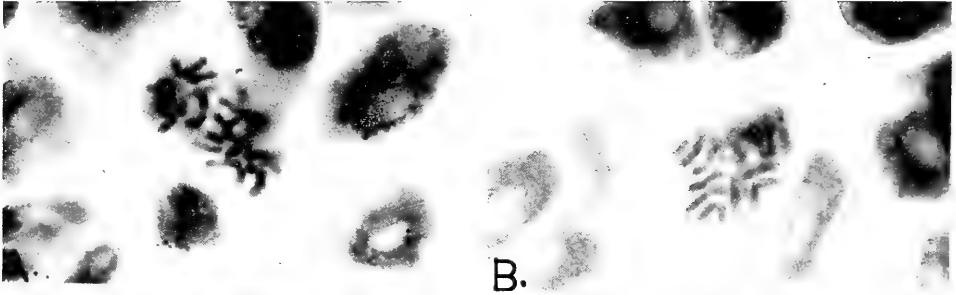


Phasmatid eggs.

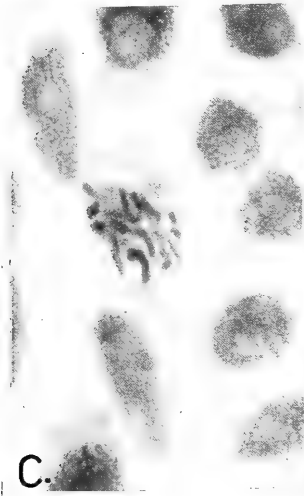


Xyleborus truncatus.





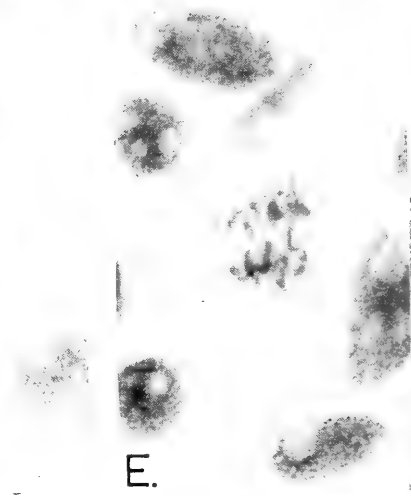
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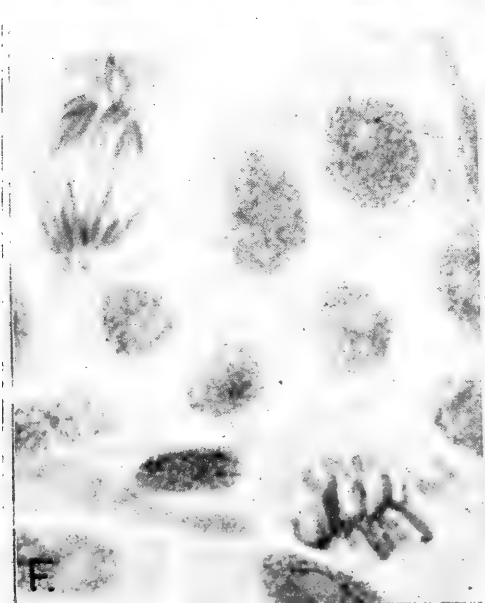
C.



D.

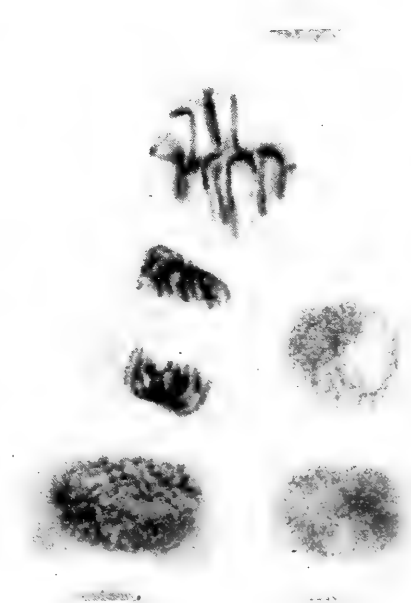


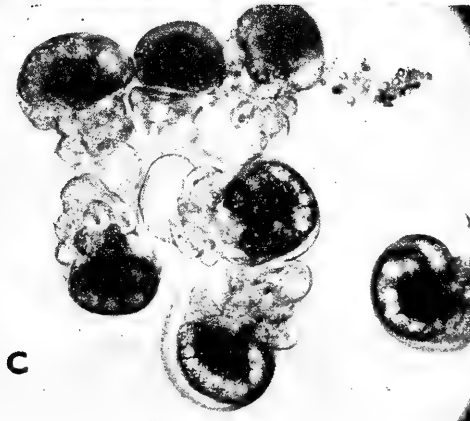
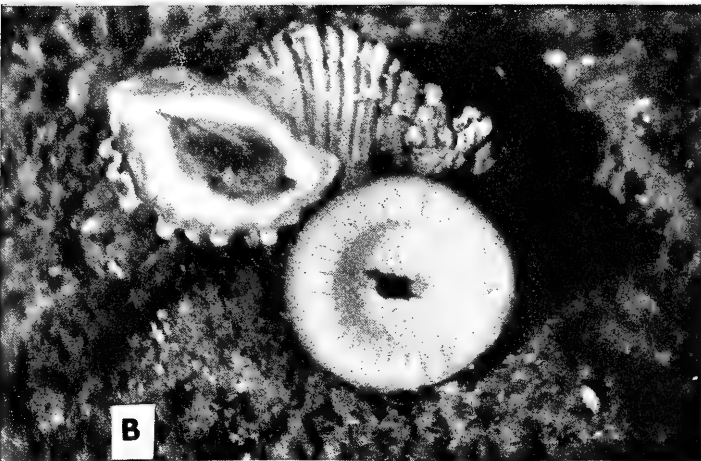
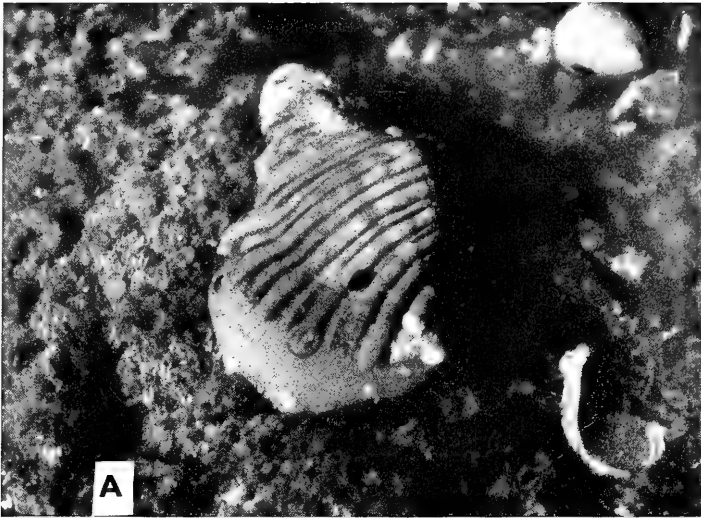
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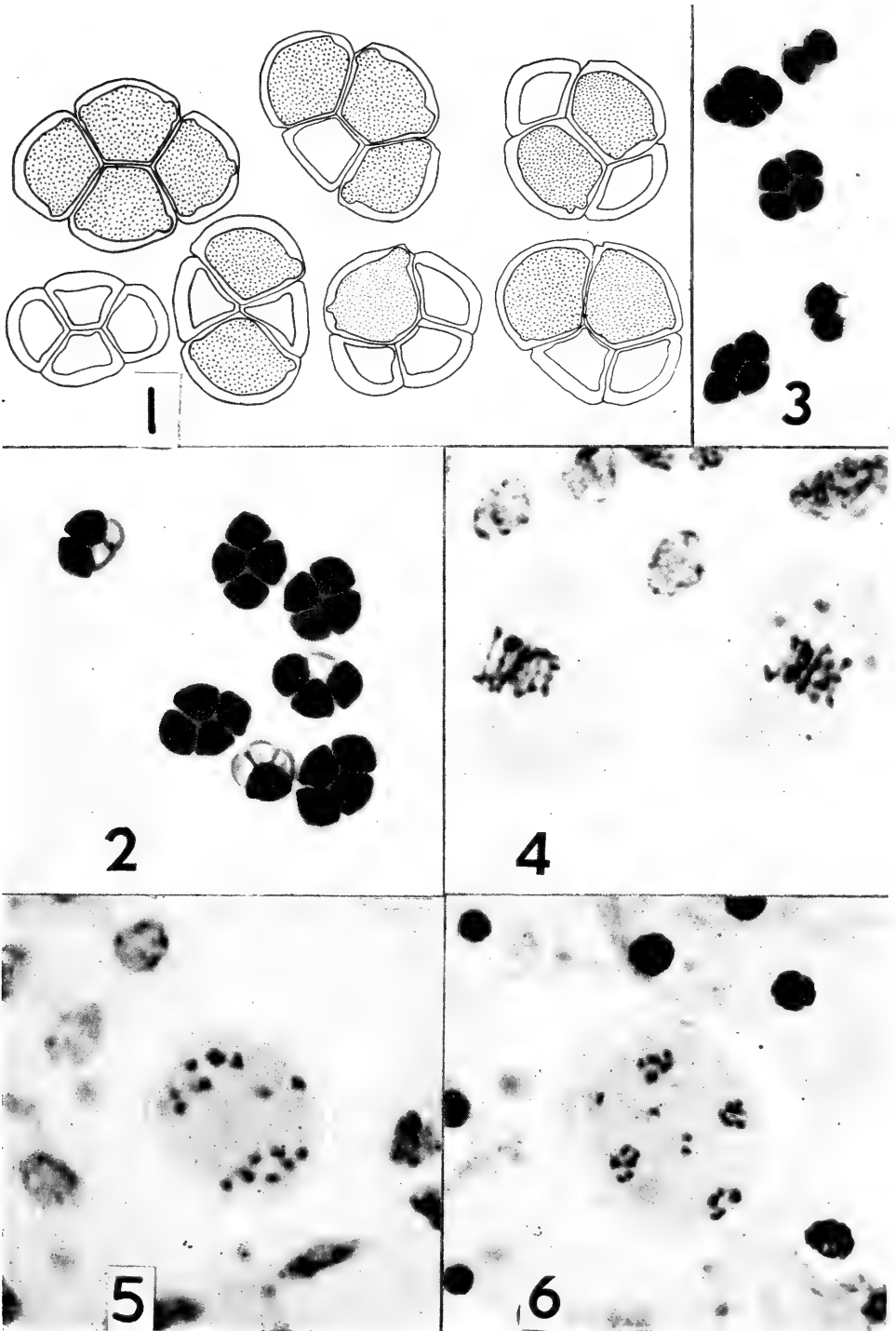
F.

G.

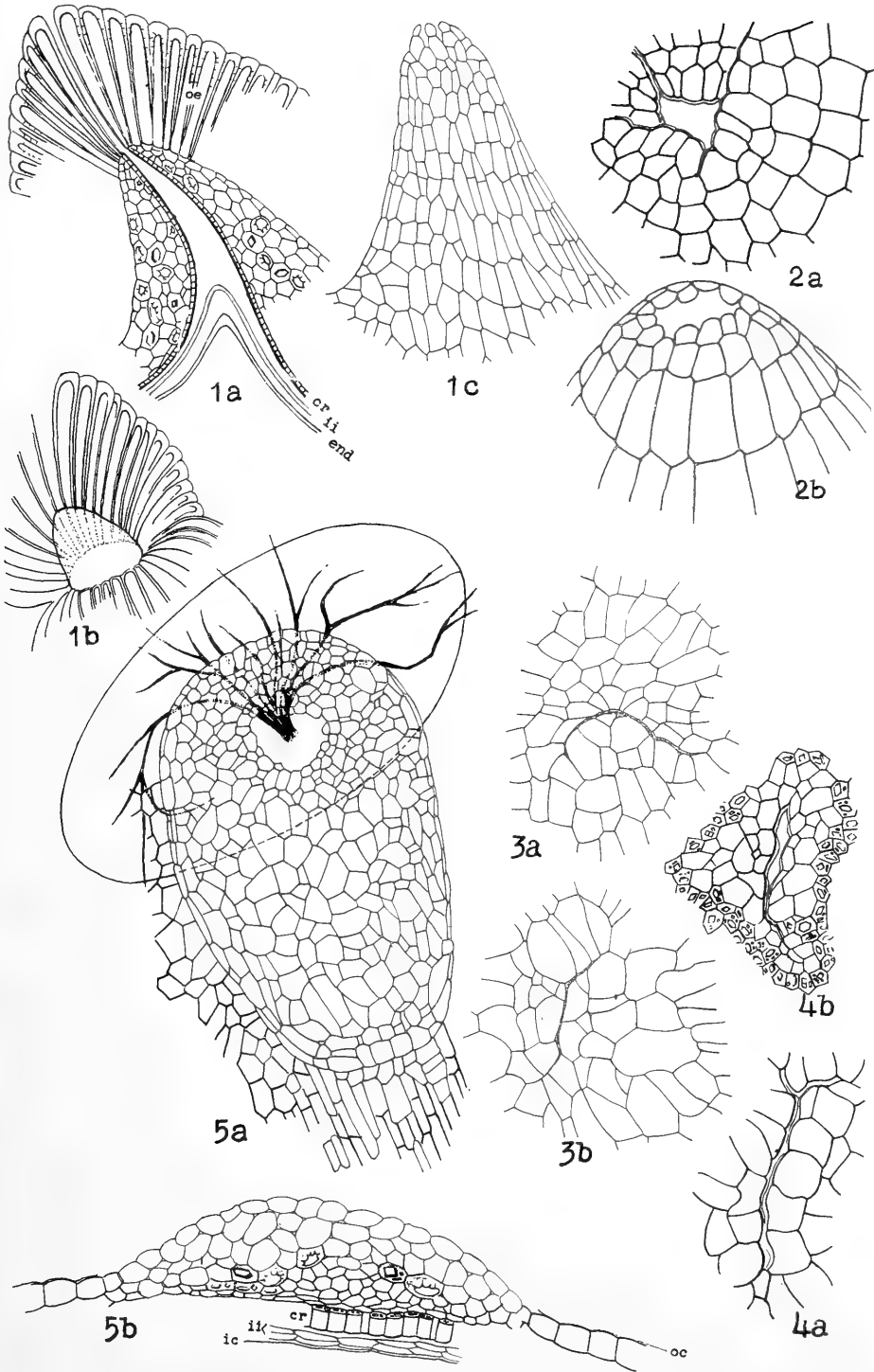


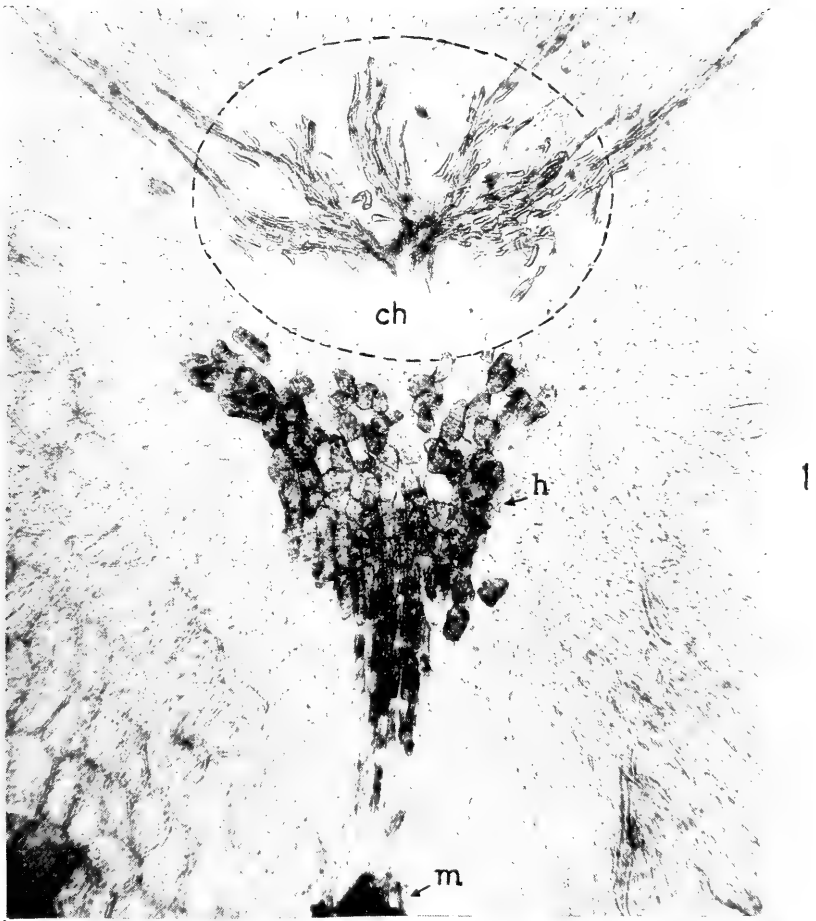


Cymatilesta spengleri. A, B. Female and egg mass. C. Veligers, 11 days.

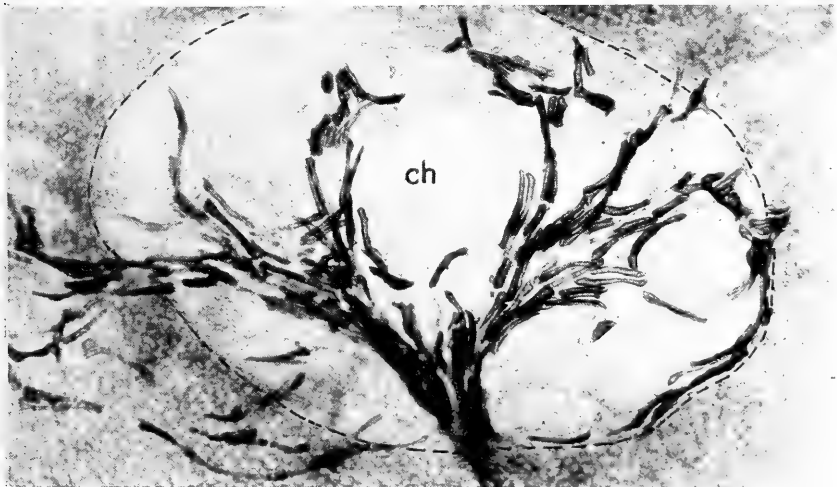


Pollen tetrads in *Leschenaultia*.





1



2

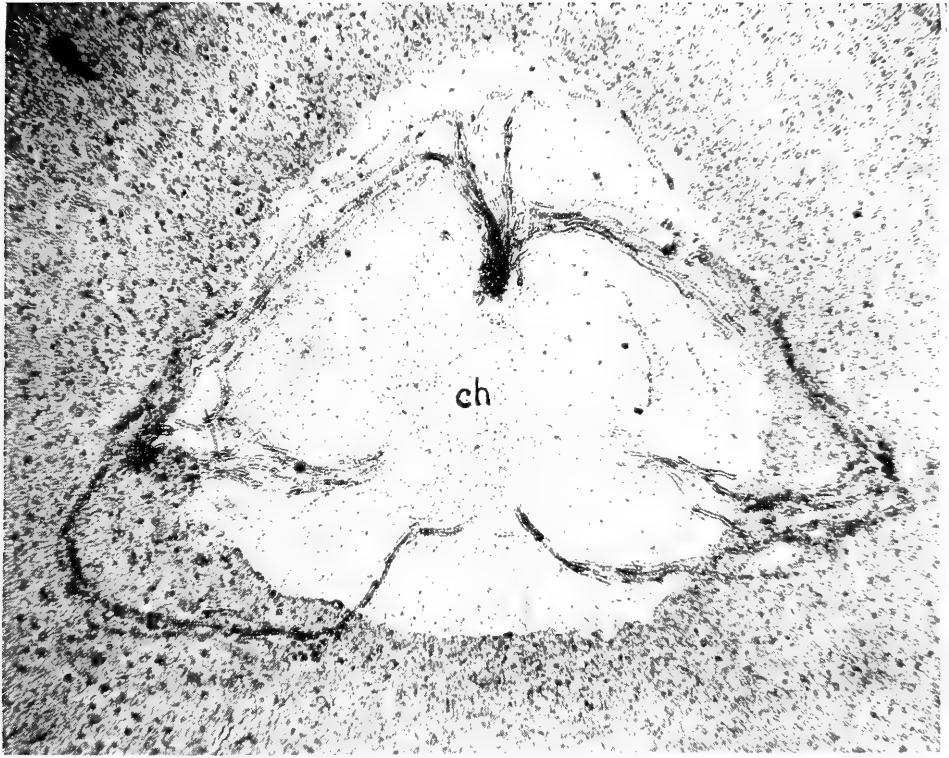


fig. 1

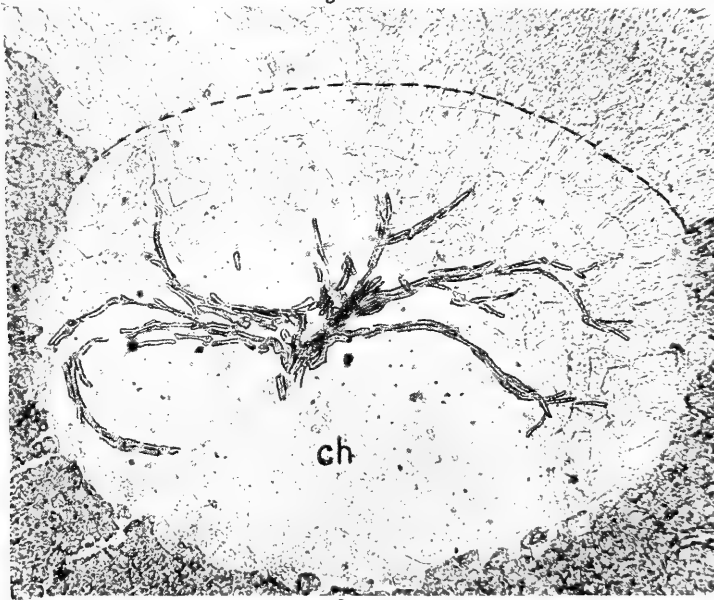
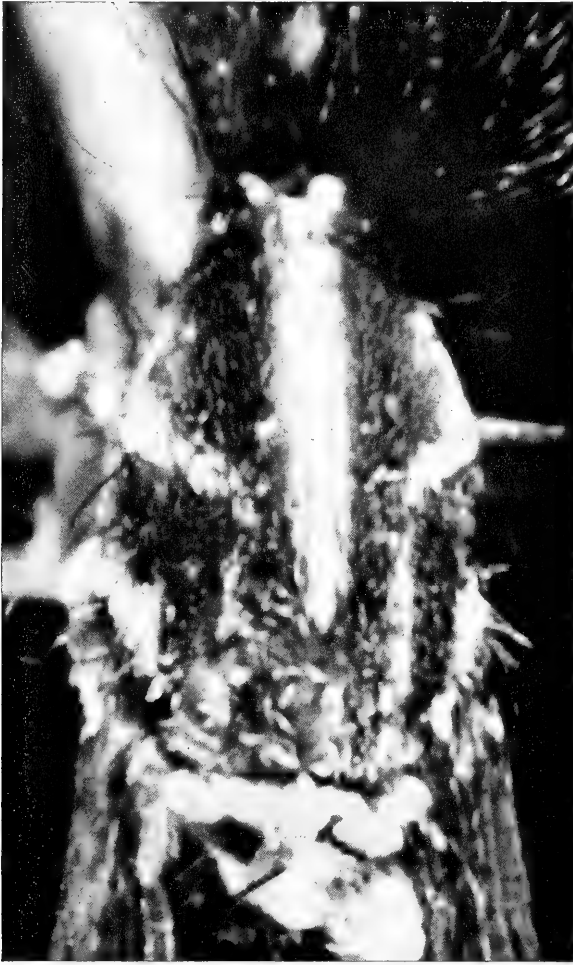


fig. 2



Adult male showing combination of characters of *Aedes aegypti* and *Aë. albopictus*.

RANUNCULUS LAPPACEUS AND ALLIED SPECIES OF THE AUSTRALIAN
MAINLAND.

I. TAXONOMY.

By BARBARA G. BRIGGS, Department of Botany, University of Sydney.
(Plate xv; Ninety-one Text-figures.)

[Read 30th September, 1959.]

Synopsis.

The species of the *R. lappaceus* group which occur on the Australian mainland are considered in the light of morphological and experimental data. *R. colonorum* Endl., previously reduced to synonymy under *R. lappaceus* Sm., is recognized. The following taxa are described for the first time: *R. pachycarpus*, *R. eichleranus*, *R. victoriensis*, *R. muelleri* Benth. var. *brevicaulis*, *R. clivicola*, *R. niphophilus* and *R. productus*. The chromosome number has been determined for the majority of species; in all those studied $2n = 16$. Distribution maps are given for all species except those which have very restricted ranges. A key is provided to the Australian species of the group, including those limited to Tasmania.

INTRODUCTION.

In the treatment of *Ranunculus* in the *Flora Australiensis*, Bentham grouped together a number of previously described species. *R. colonorum* Endl. and *R. discolor* Steud. were placed in synonymy under *R. lappaceus* Sm. and a number of other species reduced to varietal rank. Melville (1955) considered that many of these taxa merit specific status. The species recognized by Melville include: *R. pimpinellifolius* Hook., *R. scapigerus* Hook., and *R. nanus* Hook. which had been reduced by Bentham to varietal rank under *R. lappaceus*; *R. pascuinus* (Hook. f.) Melville which was originally described as a variety of *R. lappaceus*; *R. triplodontus* (Hook. f.) Melville which Bentham had equated to *R. lappaceus* var. *nanus* Benth; and also *R. concinnus* (Hook. f.) Melville and *R. decurvus* (Hook. f.) Melville which are based on varieties of *R. scapigerus* Hook. Many of these species are limited to Tasmania and are not dealt with in the present study. Melville also clarified problems of typification and gave detailed descriptions of other species of the group.

There remain a number of described species not included in Melville's study and several undefined taxa which are described here for the first time.

This taxonomic study has been carried out in conjunction with a study of hybridization between many species of the group. The results of the latter study will be reported separately; however, in all cases where such information was available these results have been considered in determining the taxonomic policy adopted.

The abbreviations used for the names of Herbaria are those recommended by Lanjouw and Stafleu (1956).

In the descriptions mean values are given for highly variable dimensions and are placed in brackets between the figures indicating the extreme values observed.

The shape of the achenes is indicated by three measurements of the body of the achene, excluding the beak. The terms used are indicated in Fig. 16.

Illustrations: Except where otherwise stated, the following magnifications have been used: leaves $\times 1$; sepals $\times 5$; petals $\times 4$; nectaries $\times 9$; achenes $\times 9$.

Characteristics of the R. lappaceus group: The members of the *R. lappaceus* group differ from most of those of the *R. sessiliflorus* group (Melville, 1956; Eichler, 1957) in lacking tubercles or bristles on the achenes, and also in having simple or branched flowering-stems arising from a rootstock or from stolons, not from an erect leafy stem. *R. rivularis* Banks et Sol. and allied species (Melville, 1955, described as species 14-19)

differ from those of the *R. lappaceus* group in having elliptical petals and long stolons. These features are not found together in any of the species of the *R. lappaceus* group. In addition most of the species allied to *R. rivularis* may be distinguished by achenes with a slender incurved beak, a form rarely found in members of the *R. lappaceus* group. *R. anemoneus* F. v. Muell. and *R. gunnianus* Hook. are distinguished by their thick creeping rootstocks and their distinctive leaf-shapes, *R. anemoneus* having orbicular laminae with numerous overlapping lobes, whereas *R. gunnianus* has laminae pinnately divided into terete segments.

The members of the group appear to be closely allied, but definition of the systematic status of the group must be left until a more complete treatment of the genus is provided.

Key to the Australian Species of the Ranunculus lappaceus Group.

The species described in the present study are numbered in sequence; the remaining Tasmanian species are described by Melville (1955).

1. Sepals reflexed.
2. Achene beak less than 1 mm. long, strongly recurved *R. plebeius* (5).
- 2.* Achene beak more than 1 mm. long, straight or arching with a recurved tip.
3. Petals obovate-cuneate, achenes compressed and more than 2 mm. dorsiventrally
..... *R. colonorum* (4).
- 3.* Petals elliptic to obovate, achenes lenticular and less than 2 mm. dorsiventrally
..... *R. scapigerus* (6).
- 1.* Sepals spreading.
4. Achenes almost globular *R. pachycarpus* (2).
- 4* Achenes lenticular.
5. Nectary-lobe cuneate or obovate.
6. Achene beak slender, erect or arching, recoiled at the tip; achenes more than 1.5 mm. long; roots fibrous *R. lappaceus* (1).
- 6* Achene beak stout and strongly recurved; achenes less than 1.5 mm. long; roots \pm tuberous *R. robertsonii* (3).
- 5* Nectary-lobe semi-orbicular, oblong, triangular or absent.
7. Petals obovate-cuneate or broad-obovate.
8. Petals white; spreading by stolons *R. millanii* (16).
- 8* Petals yellow; no stolons developed.
9. Achenes compressed, stems mostly branching, with 2-4 flowers *R. clivicola* (13).
- 9* Achenes lenticular, flowering stems mostly simple.
10. Petals 6-(10)-14; lamina divided into linear-lanceolate lobes; leaves hirsute with spreading hairs *R. dissectifolius* (12).
- 10* Petals 5, rarely 6-8; leaf segments broad or if linear-lanceolate covered with appressed hairs.
11. Nectary-lobe oblong or semi-orbicular.
12. Petioles covered with spreading hairs *R. graniticolus* (8).
- 12.* Petioles covered with short appressed hairs.
13. Leaves ternate with segments ternately or biternately-lobed, lobes linear-lanceolate *R. etchleranus* (9).
- 13* Leaves simple or divided into elliptic or lanceolate lobes.
14. Leaves simple with deep incisions near the apex, or ternately or biternately dissected or lobed, lobes lanceolate to broad lanceolate *R. victoriensis* (10).
- 14.* Leaves simple and entire or deeply incised near the base, or pinnately dissected with the lateral lobes elliptic and entire *R. pascuinus*.
- 11.* Nectary-lobe triangular or absent.
15. Leaves simple and entire or dentate, the laminae hirsute on the upper surface
..... *R. muelleri* (11).
16. Hairs on margins of laminae appressed, flowering stems exceeding leaves, laminae shorter than petioles *R. muelleri* var. *muelleri*.
- 16.* Hairs on margins and upper surfaces of laminae spreading, flowering stems usually shorter than leaves and petioles shorter than laminae
..... *R. muelleri* var. *brevicaulis*.
- 15* Leaves ternately or pinnately dissected.
17. Leaf segments deeply divided into lanceolate lobes; carpels 30-80
..... *R. niphophilus* (14).
- 17* Leaf segments entire or trilobed; carpels 15-20 *R. nanus*.
- 7* Petals elliptic to narrow-obovate.
18. Leaves linear or divided into linear segments *R. setaceus*.
- 18* Leaves or leaf segments elliptic to ovate.
19. Leaves simple or ternately dissected or lobed.

20. Petals obovate-oblong, pale yellow starch-free zone c. $\frac{1}{2}$ of petal length .. *R. nanus*.
 20* Petals tapering to a claw below, pale yellow starch-free zone c. $\frac{2}{3}$ of petal length
 *R. triplodontus*.
 19* Leaves pinnate.
 21. Nectary with a distinct lobe.
 22. Nectary-lobe triangular; petals golden-yellow *R. pimpinellifolius* (7).
 22* Nectary-lobe semi-orbicular; petals pale yellow *R. productus* (15).
 21* Nectary with a thickened bracket but no distinct lobe.
 23. Lateral leaf segments overlapping terminal segment; petals elliptic .. *R. concinnus*.
 23* Lateral leaf segments distant from terminal segment; petals linear to narrow-
 elliptic *R. decurvus*.

DESCRIPTION OF SPECIES.

(1) *RANUNCULUS LAPPACEUS* Sm. in Rees Cycl., 29 (no. 61), 1819. (Text-figs. 1, 5-10.)

Perennial herb with fibrous roots. *Flowering stems* simple or branched with 2-10 flowers, 4-(35)-70 cm. tall, hirsute with hairs long and spreading below but short and appressed above, or the whole stem with either spreading or appressed hairs. *Leaves* mostly basal, hirsute; petioles with appressed or spreading hairs, laminae with appressed hairs: basal leaves with petioles 2-(10)-30 cm. long, basally flattened, membranous toward the margin at the base; laminae ovate to deltoid in outline 12-(45)-80 mm. long and about as broad, ternately or biternately dissected or lobed with dentate segments, when ternate the terminal petiolules to 3 cm. long and the lateral ones to 1 cm. long, lobes lanceolate and usually acute: lower cauline leaves similar to basal leaves; upper cauline leaves sessile or petiolate and usually ternately lobed, approaching the uppermost lobed or entire and linear sessile bracts. *Flowers* 15-(30)-40 mm. diam. *Sepals* 5, green, spreading, concave, elliptic, 4-(7)-10 mm. long, 2-5 mm. broad, apex obtuse and hooded, 3 primary veins forking from the base, abaxial surface hirsute with spreading hairs, usually membranous and glabrous toward the margin. *Petals* 5, golden-yellow, obovate-cuneate, 7-(12)-17 mm. long, 6-(10)-13 mm. broad, obtuse or truncate, starch-free zone $\frac{1}{4}$ - $\frac{1}{3}$ petal length, 3 primary veins forking from the base; nectary 0.5-2.5 mm. from base; nectary lobe cuneate, 0.7-(1.2)-2.4 mm. long and usually slightly broader, attached laterally to petal for $\frac{1}{3}$ - $\frac{2}{3}$ of its length. *Stamens* 40-(70)-110. *Carpels* 20-(30)-50, flat, ovate; style 1-1.5 mm. long, straight, with a recoiled tip. *Achenes* in a globular head 6-9 mm. diam.; lenticular, obovate-cuneate, 1.7-3.5 mm. long, 1.3-2.8 mm. dorsiventrally, 0.7-1.2 mm. laterally, margin narrowly ridged, lateral faces smooth or dimpled, shouldered and slightly rugose below the beak; beak slender, 0.8-(1.2)-1.8 mm. long, arched with a recoiled tip. *Fruiting receptacle* 3-5 mm. long, 0.7-1.2 mm. diam., staminal zone glabrous, achene zone elliptic and hirsute.

Chromosome number: $2n = 16$. Voucher specimens: Snowy Mountains Highway, 6 ml. S.E. of Yarrangobilly Village, B. G. Briggs, 20.2.1957 (SYD); Oakdale, B. G. Briggs, II.1957 (SYD). Also Curtis (1948).

Range: Eastern Australia, including Tasmania; New Zealand.

Ecological distribution: Grassland and sclerophyll forest up to 5,000 ft. altitude.

Holotype: Port Jackson, Dr. White. Smith's Herbarium (LINN.).

Unrecognized varieties: The following varieties are not recognized as they are based on minor characters and lie within the continuous variation range of the species:

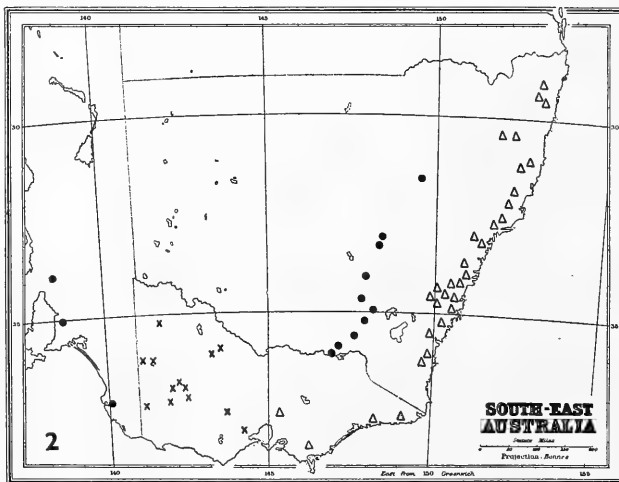
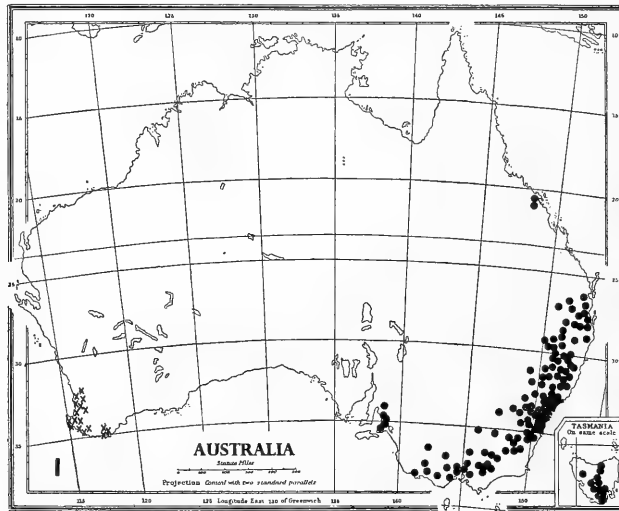
R. lappaceus Sm. var. β *obtusatus* DC. *Regni Vegetabilis*, 1: 286. *Holotype*: Port Jackson, Mus. de Paris (P, Photo SYD.). There is some uncertainty as the specimen at Paris was originally labelled by De Candolle as "*R. australis* var β DC" and the label has since been altered, possibly by Desfontaines, to "*R. lappaceus* var β DC et Spach".

R. lappaceus Sm. var. *pubescens* DC. *Regni Vegetabilis*, 1: 286. *Holotype*: New Holland 1821. Mus. de Paris (G-DC, Photo SYD).

R. lappaceus Sm. var. β *latilobus* Hook. f. *Fl. Tas.* 1: 6. 1855. *Holotype*: Woolnorth, Tas. Gunn. no. 633 (K. Photo CANB!). No type is specified for the variety, but Gunn numbers 90 and 633 are cited after the specific description. Melville (1955) concludes that no. 633 belongs to this variety.

Specimens examined:

QUEENSLAND: Strathdichie North, Proserpine, K. Macpherson, no. 2 (BRI 001135); Strathdichie, nr. Proserpine, Rev. N. Michael, no. 1117 (BRI 001134); Dalrymple Heights, M. S. Clemens, 1947 (BRI 010093, BRI 001136); Top of the Bersaker Ra., Rockhampton, Baniman (MEL); Gympie, Dr. F. H. Kenny, 5.1.1907 (BRI 001172); Kumbia Rd., Kingaroy, Rev. N. Michael, 23.11.1947 (BRI 010100); Plains of the Condamine, L. Leichhardt (NSW 44872); Bunya Mountains, C. T. White, October 1919 (BRI 001133); Burpengary, S. L. Everist and L. Pedley, 31.9.50 (BRI 001168); near Brisbane, Hernie (MEL); Sunnybank Cemetery Reserve, Brisbane, C. E. Hubbard, 11.7.1930, no. 3304 (BRI 001137); Laidley Creek, L. Watkins (BRI 001174); Eight-Mile Plains near Brisbane, C. T. White, 19 October, 1918



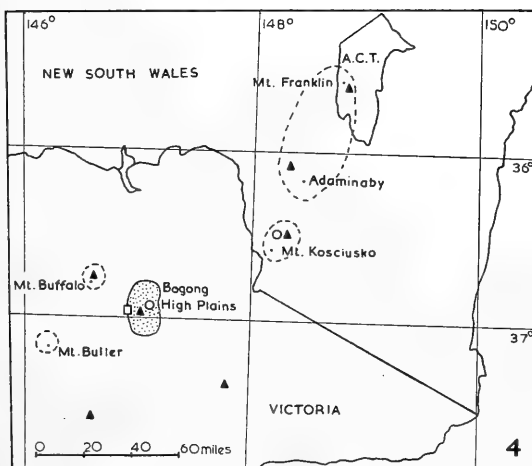
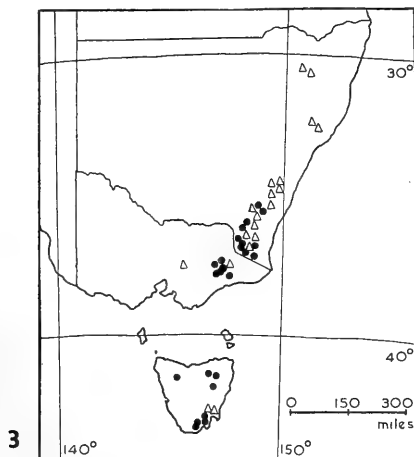
Text-fig. 1.—Distribution of *R. lappaceus* Sm. ● and *R. colonorum* Hügel in End. ×.

Text-fig. 2.—Distribution of *R. pachycarpus* B. G. Briggs ●, *R. robertsonii* Benth. × and *R. plebeius* R.Br. ex DC. △.

(NSW 44871); Base of Mt. Gravatt, C. T. White, 11.7.1930, no. 6855 (BRI 001170); Ramsay Downs, Mrs. J. Marquis (BRI 001176); Ramsay Downs, F. M. Bailey (NSW 44873); Warrill View, I. F. Swan, Aug. 1955 (BRI 010002); Oxenford, C. E. Hubbard, 17.8.30, no. 3671 (BRI 031166); Cunningham's Gap, C. T. White, 19.7.1930, no. 6898 (BRI 001171); Canungra, C. T. White, May 1917 (BRI 001129); between Booningbar and Burleigh Heads, C. T. White, Sept. 1912 (BRI 001102); Bapaume-Poziers Rd., K. N. Shea, 23 October, 1956, no. S43 (BRI 005786); Stanthorpe, H. Wright, Nov. 1916 (BRI 001128).

NEW SOUTH WALES: The divisions of the State are those of Anderson (1932).

North Coast: Lismore district, A. E. Fiford, 17.10.1950 (NSW 44914); Girard State Forest, 3 ml. W. of Drake, E. F. Constable, 28 Apr. 1956 (NSW 38472); Watts Crk. Dalmorton, E. F. Constable, 28.10.1952 (NSW 24353); Macleay R., Dr. B. (MEL); Hastings R., Dr. B.K.C. (MEL); Kendall, F. M. Bailey, Sept. 1932 (NSW 27089); Taree, B. G. Briggs, 23.10.1956 (SYD); Gloucester Buckets, J. H. Maiden, 9.1897 (NSW 44917); 20 ml. S. of Gloucester, B. G. Briggs, 25.10.1956 (SYD); Mayer's Flat to Bungwahl, L. A. S. Johnson, 13.X.1953 (NSW 26415); Buladelah, B. G. Briggs, 24.10.1956 (SYD); Wallsend, J. L. Boorman, 10.1899 (NSW 44920); Newcastle, L. Leichhardt (NSW 44921); Putty, B. G. Briggs, 25.10.1956 (SYD).



Text-fig. 3.—South-east Australia showing distribution of *R. scapigerus* Hook. ● and *R. pimpinellifolius* Hook. △.

Text-fig. 4.—Southern New South Wales and Eastern Victoria showing distribution of *R. graniticolus* Melville (dotted lines), *R. eichleranus* B. G. Briggs □, *R. victoriensis* B. G. Briggs (stippled) and *R. millanii* F. v. Muell. ▲.

Central Coast: Wyongah, 6 ml. N. of Wyong, E. F. Constable, 13th Sep. 1954 (NSW 30965); Hawkesbury Agricultural College, Richmond, W. M. Carne, 20.10.1911 (NSW 44961); Galston, J. H. Maiden and J. L. Boorman, 6.1905 (NSW 44958); Wahoonga, W. A. Dixon, Nov. 03, no. 47 (NSW 44954); Port Jackson, Rev. Dr. Woolfs (MEL); Concord West, O. D. Evans, 1929 (SYD); Ashfield, J. H. Maiden, 18.9.91 (NSW 44955); Rookwood, E. Cheel, 27.8.1898 (NSW 44963); Hurstville, J. H. Camfield, 10.99 (NSW 27087); Penshurst, E. Cheel, Oct. 1900 (NSW 44964); Penshurst, J. H. Camfield, 10.1895 (NSW 44962); Kogarah dist., J. H. Camfield, 8.1900 (NSW 27088); near Oatley's, E. Betche, 2.9.1886 (NSW 44960); Macquarie Fields, Georges R., J. L. Boorman, 8.1914 (NSW 44957).

South Coast: Island off Cabbage Tree Point Jervis Bay, F. A. Rodway, Oct. 1920, no. 55 (NSW 44927); Huskisson Jervis Bay, F. A. Rodway, Sept. 25 (NSW 44929), 28.8.1930 (NSW 44928); Conjola, W. Heron 1898, no. 57 (NSW 44926); 6 ml. N. of Bateman's Bay, B. G. Briggs, 3.2.1956 (SYD); Bega, J. J. Fletcher, No. 88 (NSW 44930); Twofold Bay, Sept. '60 (MEL).

Northern Tablelands: Wallangarra, J. L. Boorman, 11.1906 (NSW 27079); 10 ml. N. of Tenterfield, B. G. Briggs, 18.10.1956 (SYD); Tenterfield, B. G. Briggs, 18.10.1956 (SYD); Emmaville, J. L. Boorman, 10.01 (NSW 44850); Glen Innes, F. H. Kenny, Nov. 1901 (BRI 001173); Inverell Rd. and Frasers Creek, J. L. Boorman, 9.1901 (NSW 27078); Ben Lomond, J. H. Maiden, 12.99 (NSW 44849); Coryah Gap, Nandewar Ranges, L. A. S. Johnson and E. F. Constable, 6 Nov. 1954 (NSW 44846); Biscuit Creek, c. 7 ml. N.W. of Ebor on Guyra Rd., J. Vickery, 10.1.1958 (NSW 44845); Guy Fawkes near Ebor, B. G. Briggs, 20.10.1956 (SYD); Bundarra-Uralla Road, G. L. Davis, 13.11.49, Herb. F. A. Rodway, no. 15116 (NSW 44847); New England, C.W.L. (MEL); Armidale, Perrot, 1871 (MEL); University (Armidale), G. L. Davis, 19.10.1954 (AD 95809048); Thomas' Lagoon near Armidale, G. L. Davis, 28.12.1953 (AD 95809049), 11 ml. S.W. of Armidale, B. G. Briggs, 19.10.1956 (SYD); Walcha Road, E. Betche, 26.10.1886 (NSW 44841); Yarrowitch, nr. Walcha, B. G. Briggs, 22.10.1956 (SYD); Walcha Road, E. Betche, 26.10.1886 (NSW 44841); Goonoo Forest, G. W. Althofer, 1947 (NSW 44953); Barrington Tops, 5100 ft. alt., J. L. Boorman, 12.1915 (NSW 44848); Barrington Tops, L. Fraser and J. Vickery, 7.1.1934 (NSW 44844); Barrington Tops, R. Carolin, 13.4.58, no. 493 (SYD); Allyn River to Barrington Tops, Mary Fuller, 1.1928 (SYD).

Central Tablelands: Orange, P. Althofer, 5.1946, no. 78 (NSW 44857); Perth, near Eathurst, J. L. Boorman, 3.1901 (NSW 44856); Blayney, J. L. Boorman, 12.1907 (NSW 44858); Mt. Coricudgy, 25 ml. E. of Rylstone, L. A. S. Johnson, 28.10.1951 (NSW 44860); Ilford, near Mudgee, B. G. Briggs, 18.10.1956 (SYD); 10 ml. N. of Oberon on Tarana road, J. Garden, 10.11.1952 (NSW 4486); S. of Hampton, J. Garden, 12.11.1952 (NSW 27081); Oberon, J. Garden, 10.11.1952 (NSW 27080); Jenolan Caves, W. F. Blakely, 10.99 (NSW 44854); Abercrombie Caves, K. Mair, 20.10.1951 (NSW 17861); Mt. Werong, L. A. S. Johnson and E. Constable, 23.10.1951 (NSW 44859); Mt. Werong-Ruby Creek, L. A. S. Johnson and E. Constable, 23.10.1951 (NSW 17680); Alpine, near Bargo, B. G. Briggs, 6.10.1957 (SYD); Mittagong, L. A. S. Johnson, 15.11.1949 (NSW 44853); 3 ml. from Bowral on Kangaloon Road, L. A. S. Johnson, 15.4.1951 (NSW 27082); Burrawang, J. J. Fletcher, 11 Nov. 88 (NSW 44855).

Southern Tablelands: Hoskingtown-Braidwood, C. W. E. Moore, 19.11.1952, no. 2089 (NSW 27084); Captains Flat to Braidwood, C. W. E. Moore, 4.11.1952, no. 1980 (NSW 44868); Mt. Franklin, A.C.T., B. G. Briggs, 10.1957 (SYD); near Mt. Gingera, A.C.T., B. G. Briggs, 10.1957 (SYD); 14 ml. N. of Kiandra, B. G. Briggs, 20.2.1957 (SYD); Laurel Hill, north of Tumberumba, E. J. McBarron, 27.12.1948, no. 2851 (NSW 44864); 7½ ml. N. of Tumberumba, B. Briggs, 1.1956 (NSW 44865); Tumberumba, W. Bull (MEL); T₂ track, Tumut R. valley near Cabramurra, M. Mueller, 25.11.55, no. 3039A (NSW 44862); Upper Tumut R., J. C. Newman, 19.12.1952 (NSW 44863); Kancoban, B. G. Briggs, 20.12.1955 (SYD); Thredbo River, Mt. Kosciusko, J. H. Maiden and W. Forsyth, January 1899 (NSW 27083).

Western Slopes: Mt. Russell, E. Breakwell, Nov. 1914 (NSW 44936); Inverell, Adelaide Chapman, Sept. 1912 (SYD); Howell, J. H. Maiden and J. L. Boorman, 8.1905 (NSW 44940); Head of Gwydir River (MEL); Tamworth, J. L. Boorman, 9.1907 (NSW 44938); Warrumbungle ranges, W. Forsyth, Oct. 1901, no. 10 (NSW 44939); 3 ml. N. of Wallabadah, R. H. Goode, 11.11.1954, no. 101 (NSW 44937); Blandford nr. Murrurundi, H. M. R. Rupp, 2.10.1944 (NSW 44919), 10.1947 (NSW 44918); Woolooma, Mt. Buttress, Scene, A. L. White, 11.1904 (NSW 44946); Gulgong, J. H. Maiden and J. L. Boorman, April 1901 (NSW 44950); Gulgong, J. L. Boorman, 9.1916 (NSW 44951); Cedar Creek, Widdin Valley, S. of Widdin, E.F., 2 Sept. 1957 (NSW 44793); Euchareena, G. W. Althofer, 1917 (NSW 44945); Molong, J. L. Boorman, 11.1906 (BRI 001131); Bowman Park near Cudal, W. F. Blakely, 10.1906 (NSW 44949); Cowra, J. Beattie, 6.11.1915, no. 48 (NSW 44944); Rockview Station, Old Junee, A. Chislett, 13.11.1942 (NSW 27091); between Uriarra and Taemar, C. W. E. Moore, 3.11.1952, no. 1967 (NSW 27086).

Plains: Euabalong, J. L. Boorman, 5.1906 (NSW 27090); Yanco, H. Wenzel, 8.12 (NSW 44941); Bara, via Hay, Miss E. Officer, 1.1904 (NSW 44942).

VICTORIA: Wimmera, Dallachy (MEL); Upper Murray, C. F. French Jr., 1886 (MEL); Wangaratta (MEL); Tamleigh, Goulburn Valley, J. Minchin, 1886 (MEL); Mitta Mitta, S. F. Clinton, Oct. 1916 (MEL); Wedderburn, W.W.W., no. 1257 c. 10.1918 (MEL); Feathertop (MEL); nr. Dibbins Hut, Mt. Hotham, B. G. Briggs, 28.12.1955 (SYD); Dinner Plain, Hotham-Omeo Road, B. Briggs, 1.1956 (NSW 44904, SYD); Peacock Spur, Mansfield to Whitfield Rd., B. Briggs, 1.1956 (NSW 44903); Cobboras Mountains (MEL); near Seymour, Mrs. F. M. Reader, 9.11.1902 (MEL); along Silverband Rd., Grampians, T. and J. White, 2.11.1953 (NSW 44897); Kilmore, Rev. J. W. Dwyer, 10.1918 (NSW 44892); Dalesford, R. Wallace, 6.1879 (MEL); Creswick, Whan, no. 191 (MEL); Victoria Valley, Grampians,

R. Melville, 28.10.1952, no. 1819 (AD 95724028, NSW 44902); Dunkeld, S. Fisher, 1871 (MEL); Upper Yarra, C. Walter, Aug. 1892 (NSW 44891); Shipton, Rev. Wm. T. Whan (NSW 44894, 44895, 44896), 1863 (NSW 44890); Werribee, Fullager (MEL); You Yangs, C. Walker, 8.1900, pro parte (MEL); Hawkesdale, H. B. Williamson, Nov. 1901 (NSW 44893); Mouth of Gleneig R., W. Allitt (MEL).

SOUTH AUSTRALIA: Sevenhills, Flinder's Ranges, Herb. J. M. Black, 22.11.1933 (AD 95729049); Montacute, J. B. Cleland, 21.10.44 (AD 95828051); Mt. Lofty Ranges, creek 1 mile above Magill, J. B. Cleland, Herb. J. M. Black, 15.11.1943 (AD 95729050); Horsnell's Gully, J. B. Cleland, 13.11.43 (AD 95828055); Mt. Lofty Ra., near Summertown, E. S. Booth, 20.10.1956, no. 25 (AD 95729052); National Park, Belair, Herb. J. M. Black, 15.12.16 (AD 95729047); Mt. Lofty, J. B. Cleland, 18.9.20 (AD 95828054); Mt. Lofty Ranges, J. Addison (BRI 001103); Macclesfield, Blandourky, 1850 (MEL); Back Valley off Inman Valley, J. B. Cleland, 25.10.36 (AD 95729053), ex. Herb. J. M. Black (AD 95729048); Lucindale S.E., E. H. Ising, 29 Oct. 1934 (AD 95729054); Pt. Douglas, north of Cape Northumberland, J. B. Cleland, 12.41 (AD 95828052).

TASMANIA: Launceston, near Hobart Town Rd., ex herb. S. C. Hannaford, November 1865 (NSW 44885); Perth, 97 (MEL); Waratah, A. H. S. Lucas, Dec. 1924 (NSW 44880); St. Marys, E. Rees, Oct. 1929 (HO); 11 ml. S. of Breona, B. G. Briggs, 16.1.1958 (SYD); Penstock, A. V. Giblin, Xmas 1929 (HO); 62 ml. from Queenstown on Lyell Highway, B. G. Briggs, 17.1.1958 (SYD); 1 ml. W. of Dee R., Lyell Highway, L. A. S. Johnson, 19.1.1949 (NSW 44882); Victoria Valley, F. A. Rodway, 12.1917 (NSW 44875); R. Jordan, F. A. Rodway, Nov. '98, no. 51 (NSW 44877); Hobart, A. H. S. Lucas, Nov. 1923 (NSW 44879); Hobart Town, Hannaford no. 3 (MEL); near Hobart Town, Dr. Mueller, Xmas 1870 (NSW 27061); Hobart Waterworks, F. A. Rodway, Oct. '98 no. 50 (NSW 44876); Sandy Bay, Hobart, F. A. Rodway, Nov. '98 no. 38 (NSW 44878); Blackman's Bay, N. of Murdunna, R. Melville, 17.12.1952, no. 2447 (AD 95724037, BRI 100003, MEL, NSW 44887); Mt. Nelson, E. Rodway, December 1929 (HO).

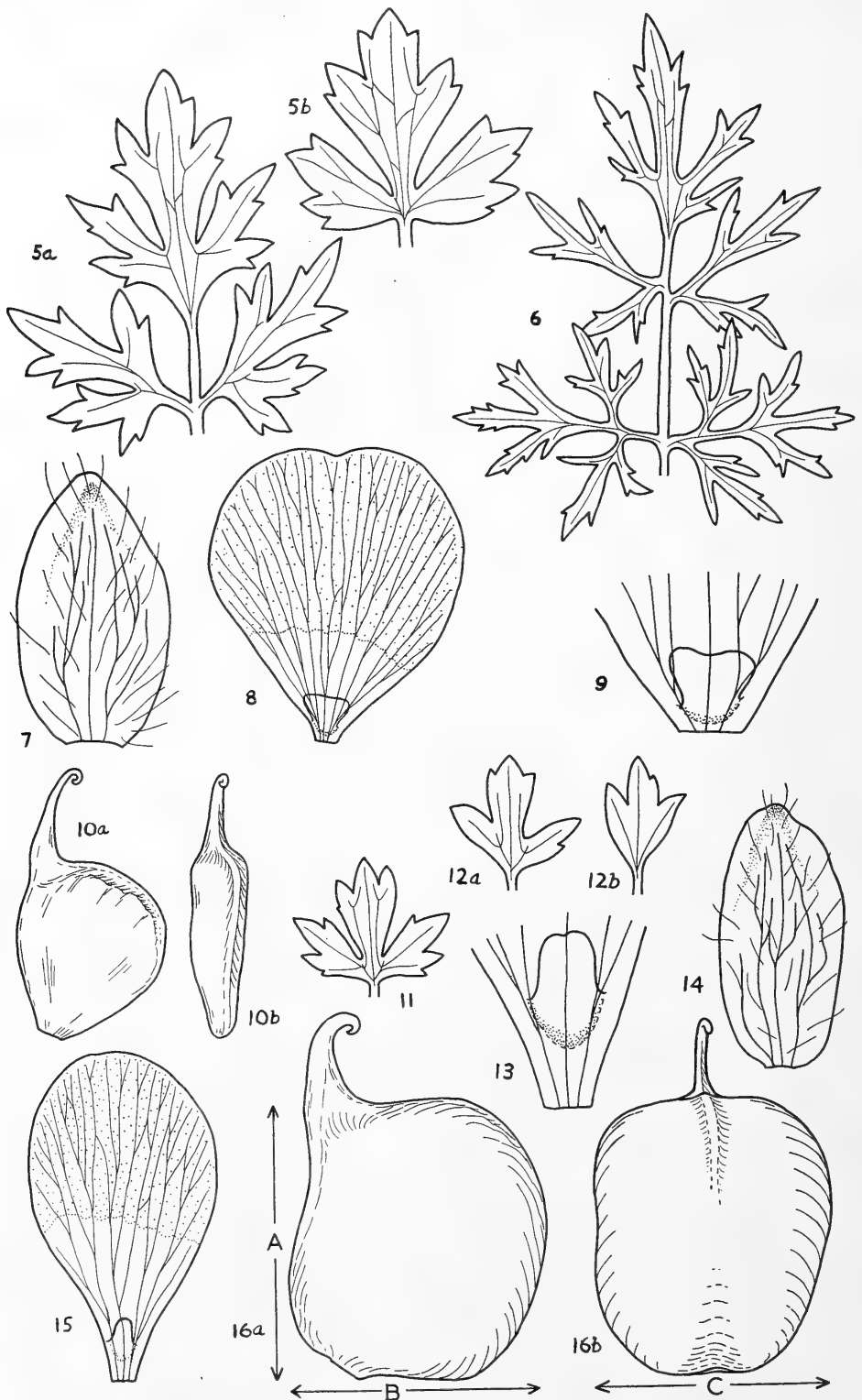
New Zealand specimens differ from the typical Australian material and several named varieties are limited to New Zealand.

Within Australia there is considerable variation between local populations in leaf-dissection, indumentum and degree of branching of flowering stems. This variation shows no distinct correlation with habitat trends. Plants from Tenterfield to Ebor on the Northern Tablelands of New South Wales, from Corryong to Omeo in the Victorian Alps and from Tasmania usually have leaves ternately-lobed rather than ternate. The most finely dissected leaves were found from Taree to Buladelah on the North Coast, N.S.W., and from Tumut to Mansfield on the tableland tract of Southern New South Wales and Victoria. The plants from the last-mentioned region also show slightly tuberous roots and a low average carpel number. None of these variants appear to merit taxonomic recognition as all intergrade fully with the typical form.

(2) *RANUNCULUS PACHYCARPUS*, sp. nov. (Text-fig. 2, 11-16.)

Herbae pilis longis plerumque sub-appressis obtectae. Caules floriferi simplices vel ramosi et plerumque foliati. Folia radicalia vel simplicia et dentata vel ternolobata vel ternata. Sepala patentia. Petala aureo-flava, obovato-cuneata. Lobi nectariorum cuneati. Achenia glabra prope globosa rostris tenuibus rectis sed prope apicibus recurvatis praedita.

Herb with slightly tuberous roots. *Flowering stems* 6-(15)-40 cm. tall, simple or branched with up to 5 flowers; covered with long spreading hairs below, but short appressed ones above. *Leaves* mainly basal, hirsute with soft sub-appressed hairs 1-2 mm. long: basal leaves with petioles 1-(4)-12 cm. long, basally flattened, membraneous toward the margin at the base; laminae ovate to elliptic in outline, 8-(17)-45 mm. long with breadth approximately equal to length, coarsely dentate with 3-7 teeth or ternately dissected or lobed with segments lobed or dentate, lobes broad to narrow lanceolate and acute, when ternate the terminal petiolule to 1 cm. long and the lateral ones to 5 mm. long; cauline leaves usually present; lower cauline leaves usually petiolate and similar in form to the basal leaves; upper leaves sessile, approaching the uppermost sessile and lobed or entire bracts. *Flowers* 13-28 mm. diam. *Sepals* 5, concave, spreading ovate-cuneate, 2.5-7 mm. long, 1.5-4 mm. broad, hooded at the apex with a thickened subterminal beak, 3-5 primary veins usually forking from the base, abaxial surface covered with long spreading hairs, glabrous and membraneous towards the margin.



Text-figs. 5-10.—*R. lappaceus* Sm. 5-6, Leaves; 7, Sepal; 8, Petal; 9, Nectary; 10a, b, Achene, lateral and dorsal views. 5a, 5b, 7-10 from Putty, N.S.W., 6 from Buladelah, N.S.W.

Text-figs. 11-16.—*R. pachycarpus* B. G. Briggs. 11-12, Leaves; 13, Nectary; 14, Sepal; 15, Petal; 16a, b, Achene $\times 6$, lateral and dorsal views. 11, 13-16 from isotypes, 12 from Bumberry, N.S.W. Achene measurements, fig. 16: A = length, B = dorsiventral measurement, C = lateral measurement.

Petals 5, golden-yellow, obovate-cuneate, 6–15 mm. long, 3–10 mm. broad, obtuse or truncate or emarginate, starch-free zone $\frac{1}{4}$ – $\frac{1}{2}$ of petal length, 3 primary veins usually branching from base; nectary 0.2–1.0 mm. from base, nectary-lobe oblong or cuneate, 1–2 mm. long, 0.7–1.3 mm. broad, truncate or emarginate, attached laterally to petal for c. $\frac{1}{2}$ of its length. *Stamens* 25–45. *Carpels* 15–30; glabrous, ovate; style slender 1–2 mm. long, straight with a recurved tip. *Achenes* in a globular or elliptic head 7–11 mm. long; globular or obovate-cuneate and plump, pericarp very thick, 2.5–5 mm. long, 2–3.5 mm. dorsiventrally, 2–3.5 mm. laterally, lateral faces smooth, often with a shallow dorsal groove; beak 1.5–2 mm. long, recurved or straight with a recurved tip. *Fruiting receptacle* 5–8 mm. long, 0.8–1 mm. diam.; staminal zone glabrous, achene zone elliptical to terete and hirsute with short fine hairs.

Range: Western slopes of New South Wales, eastern South Australia.

Holotype: Northern slopes of Mt. Brown, c. 22 km. east of Pt. Augusta, South Australia. Growing among rocks. P. G. Wilson, 20.x.1958, no. 622 (AD 95912009). *Isotypes*: AD, NSW, K, P, US.

Specimens examined:

NEW SOUTH WALES: Goonoo forest, also Harvey Ra., G. W. Althofer, 1947 (NSW 44953); Bumberry, E. F. Constable, 4.10.1951 (NSW 44947); Cookamidgera, E. F. Constable, 22.9.1947 (NSW 4906); Mirool, G. V. Scamell, 24.8.27 (SYD); Temora, Rev. J. W. Dwyer, 8.1915, no. 540 (NSW 44948); Junee, Rev. J. W. Dwyer, 9.1915, no. 595 (NSW 44931); Wagga, R. Helms, 6.1900 (NSW 27092); Holbrook, E. J. McBarron, 28.9.47, no. 1095 (SYD); Culcairn, E. J. McBarron, 1.9.1949, no. 3503 (SYD); Albury, Monument Hill, E. J. McBarron, 4.9.48, no. 1948 (SYD).

SOUTH AUSTRALIA: Burra Burra (MEL); Verfus Guichen Bay, Dec. 1848 (MEL); Third Creek, Jan. 10 1848, Dr. Mueller (MEL).

(3) *RANUNCULUS ROBERTSONII* Benth. *Fl. Aust.*, 1:10.1863. (Text-figs. 2, 17–21.)

Perennial herb. *Roots* tuberous, fleshy and 1–3 mm. diam. at base, usually tapering abruptly to filiform and 0.1–0.5 mm. diam. *Flowering stems* 1–(10)–25 cm. high, simple or branching with 2–3 flowers. *Leaves* mostly basal; petioles and lower surfaces of laminae densely covered with short antrorse-appressed hairs, upper surfaces of laminae with scattered hairs or rarely glabrous: basal leaves with petioles 1–(7)–9 cm. long, membranous towards the margin at the base; laminae ovate to deltoid in outline, 12–(15)–25 mm. long, 8–(15)–22 mm. broad, deeply ternately or biternately lobed or, more usually, pinnately dissected into 3–9 segments and the segments deeply lobed, terminal petiolules to 10 mm. long, lateral petiolules to 5 mm. long, lobes acute and lanceolate to narrow-linear: cauline leaves usually present; the lower ones sessile or petiolate with laminae similar to those of basal leaves; upper leaves sessile and trifid. *Flowers* 13–26 mm. diam. *Sepals* 5, green, spreading, concave, broad-lanceolate to ovate, 3–5.5 mm. long, 1.5–3 mm. broad, apex hooded, 3 primary veins forking from the base, abaxial surface hirsute with short hairs or rarely glabrous, margins membranous and glabrous. *Petals* 5, golden-yellow, ovate-cuneate, 8–14 mm. long, 4.5–8 mm. broad, usually emarginate or rarely obtuse or truncate, starch-free zone $\frac{1}{2}$ of petal length, 3 primary veins branching at or below the nectary; nectary 0.2–0.5 mm. above base of petal; nectary-lobe cuneate, 1.5–2 mm. long, 0.8–1.2 mm. broad, truncate or emarginate, attached laterally to petal for $\frac{1}{2}$ – $\frac{3}{4}$ of its length. *Stamens* 30–35. *Carpels* 15–35; glabrous, flat, ovate; style 0.8–1.2 mm. long, straight with a recurved tip. *Achenes* in a globular or elliptical head, 3–5 mm. long: lenticular, semi-orbicular, 1.1–1.5 mm. long, 1–1.3 mm. dorsiventrally, 0.6–0.9 mm. laterally, margins narrowly keeled, lateral faces irregularly dimpled; beak slender, 0.9–1.2 mm. long, straight with a recurved tip. *Fruiting receptacle* 2–3 mm. long, 0.5–0.7 mm. diam.; staminal zone glabrous, achene zone hirsute and terete to narrow elliptic.

Chromosome number: $2n=16$. Voucher specimen: Near Mirrantawa, Grampians, VIC. B. G. Briggs, 17.8.1958 (SYD).

Range: Western Victoria.

Ecological distribution: Grassland and forest areas.

Typification: Two collections were cited by Bentham: East Bank of the Glenelg River, Nangela Vale, Robertson (K, photo. CANB, SYD, duplicate MEL!); Forest land near Glenelg River, Robertson (K, photo. CANB, SYD, duplicate MEL!). Both collections agree fully with the original description. The material in the Kew Herbarium from Nangela Vale is chosen as the lectotype.

Lectotype: East bank of the Glenelg River, Nangela Vale, Robertson (K, isolectotype MEL).

Specimens examined:

VICTORIA: N.W. of L. Albacutya, C. French, 9.87 (MEL); Loddon (MEL); Charlton, W. W. Watts, 10.1917, no. 732 (NSW 44889); Donald, Dr. Curdie (MEL); 3 ml. W. of Kaniva, R. Melville, 15.9.1952, no. 870 (MEL, NSW 44901); Fyan's Lake, Bellellen nr. Stawell, R. Melville, 2.11.1952, no. 1942 (MEL, NSW 44900); Moora Moora Reservoir, Grampians, T. and J. Whaite, 26.10.1953, no. 1506 (NSW 44899); near Ararat, C. Green (MEL); Salt Creek, Poolaigelo nr. Dergholm, J. Willis, 8.9.1949 (MEL); Creswick, Whan, no. 190 (MEL); near Melton, F. M. Reader (MEL); You Yangs, C. Walter, 1900, pro parte (MEL).

The most finely dissected leaves are found on plants from the Grampians, Victoria. Elsewhere the leaves often have broad segments similar to those of *R. lappaceus* Sm. The small plump achenes of *R. robertsonii* seem to be the most reliable feature characterizing the species.

(4) RANUNCULUS COLONORUM Endl. *Enumeratio Plantarum*: 1.1837 (Text-figs. 1, 22-26.)

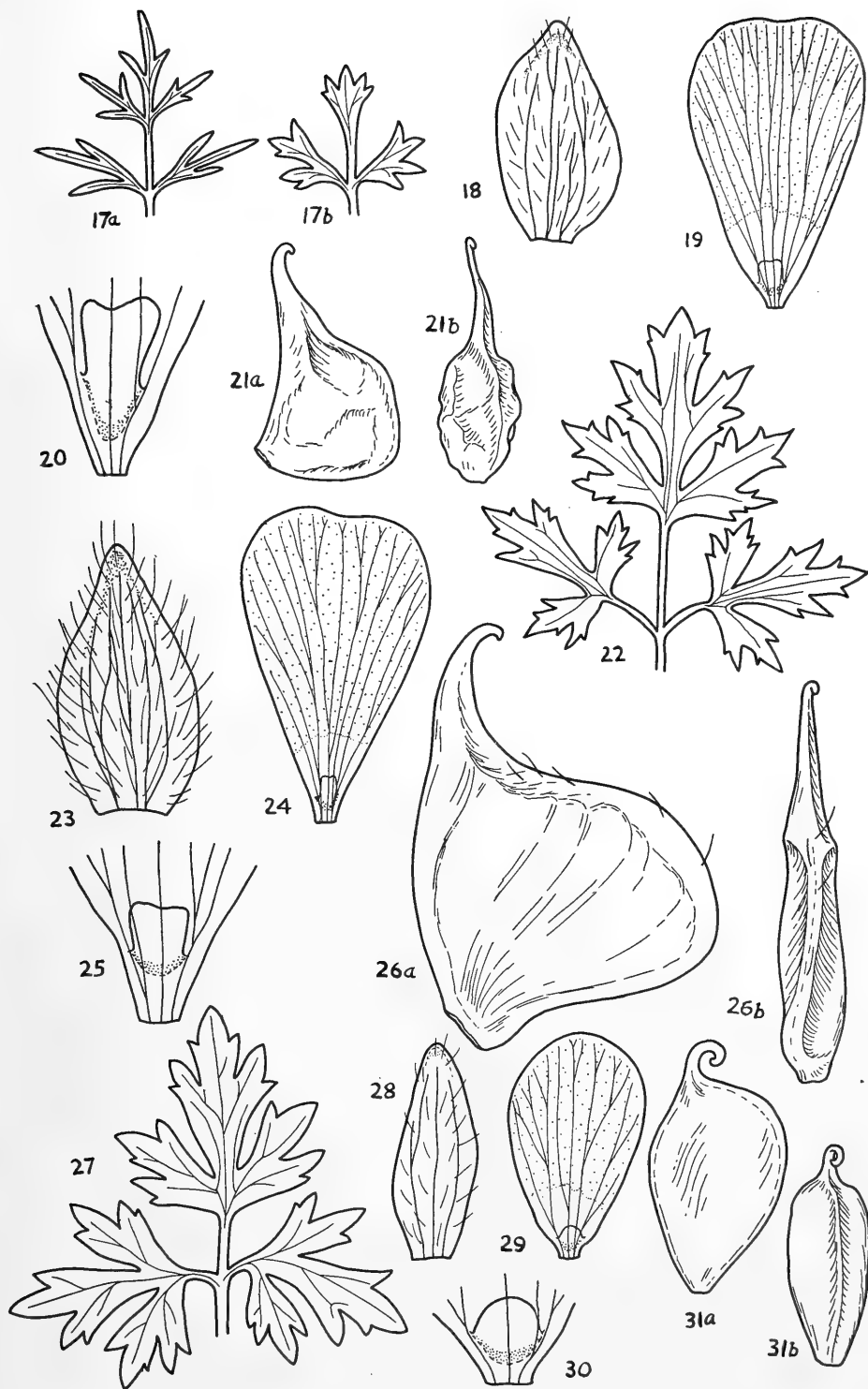
Synonym: *Ranunculus discolor* Steud. in Lehman *Plantae Preissianae*, 1:263.1844.

Perennial herb with fibrous roots. *Flowering stems* branched with 2-8 flowers, 20-60 cm. tall, covered with long spreading hairs below and short appressed ones above. *Leaves* hirsute; petioles with long spreading hairs, laminae with short appressed hairs on upper surface but spreading ones below: basal leaves with petioles 8-20 cm. long, basally flattened, membranous toward the margin at the base; laminae ovate in outline, 35-80 mm. long and about as broad, ternate with segments ternately-lobed and coarsely dentate, terminal petiolules 7-25 mm. long and lateral ones 2-14 mm. long: lower cauline leaves similar to basal leaves; upper cauline leaves sessile or petiolate, ternately lobed with dentate segments, approaching the uppermost lobed or entire and linear-lanceolate sessile bracts. *Flowers* 16-(22)-40 mm. diam. *Sepals* 5, becoming reflexed, ovate to ovate-cuneate, 2.5-5 mm. long, 1.5-2.5 mm. broad, 3 primary veins branching from near the base, abaxial surface covered with long spreading hairs, glabrous and membranous toward the margin. *Petals* 5, golden-yellow, obovate-cuneate, 9-(12)-20 mm. long and 5-14 mm. broad, obtuse or truncate, starch-free zone $\frac{1}{4}$ of petal length, 3 primary veins forking from the base; nectary 0.3-0.5 mm. from base; nectary lobe cuneate or oblong, 0.7-1.5 mm. long, attached laterally to petal for $\frac{1}{4}$ to all of its length. *Stamens* 40-60. *Carpels* 20-45; flat, ovate, with a few fine hairs on dorsal ridge; style straight or arching with a recurved tip. *Achenes* in a globular head 6-11 mm. diam.; compressed, obovate to obovate-cuneate, 2-4 mm. dorsiventrally, 0.6-0.9 mm. laterally, marginal ridges prominent, lateral faces smooth or ridged over the position of the seed, shouldered and slightly rugose below the beak; beak slender, 1.5-(2.2)-3 mm. long, arched or recurved. *Fruiting receptacle* 3-4 mm. long, 0.8-1.5 mm. diam.; staminal zone glabrous, achene zone elliptic and hirsute with short fine hairs.

Range: Southern Western Australia.

Holotype: Swan River, Hügel. The specimen was in the Vienna Herbarium, but has been destroyed. Inquiries at the following herbaria, BR, CGE, K, MEL, have failed to locate any isotype material. The original description is clear and detailed, and it is therefore not considered necessary to erect a neotype at present.

The holotype of *R. discolor* Steud., in districtu Perth, Preiss no. 1347, 23rd Sept., 1839, has not been located. It was probably at Hamburg and was lost during the war. Isotype material (MEL!) agrees fully with the original description of *R. colonorum* Endl.



Text-figs. 17-21.—*R. robertsonii* Benth. 17, Leaves; 18, Sepal; 19, Petal; 20, Nectary; 21a, b, Achene, lateral and dorsal views. 17-20 from near Mirrantawa, Grampians, Vic., 21 from Charlton, Vic.

Text-figs. 22-26.—*R. colonorum* Endl. 22, Leaf; 23, Sepal; 24, Petal; 25, Nectary; 26a, b, Achene, lateral and dorsal views. 22 from Serpentine, W.A., 23-26 from Woodman's Point, nr. Cooger, W.A.

Text-figs. 27-31.—*R. plebeius* R.Br. ex DC. 27, Leaf; 28, Sepal; 29, Petal; 30, Nectary; 31a, b, Achene, lateral and dorsal views. From near Bemboka, N.S.W.

Specimens examined:

Millewa, J. Burton Cleland, 10.1908 (NSW 44909); Mundaring, Dr. J. Burton Cleland (NSW 44913); Greenmount, R. Helms, 23.9.1899 (NSW 44906); Greenmount, A. H. Hamilton, 20.9.1902, no. 193 (NSW 44908); Claremont, C. A. Gardner, 13 Sept. 1920, Herb. Forests Dept. no. 735 (PERTH); Swan River, F.v.M. Nov. 1877 (MEL); Swan River, Miss J. Sewell, 1858 (MEL); Swan River, 1888 (MEL); Swan River, A. Helmrich (MEL); Woodman's Point, nr. Cooger, C. A. Gardner, 26 Oct. 1942 (PERTH); Pinjarrah, S.W. Railway, R. Helms, 23.9.97 (PERTH); Busselton, A. and E. Pries, 1870 (MEL); Yallingup, J. H. Maiden, Oct. 1909 (N.S.W. 44907); Blackwood River, Mrs. McHard, 1893 (MEL); Blackwood R. 125 (MEL); Blackwood R., Hester, 1875 (MEL); near Karri Dale, P. Walcott, Dec. 1867 (MEL); Manjimup, R. D. Royce, 31 Oct. 1946, no. 1355 (MEL); Warren's River, Perrot Walcott, 1872 (MEL); Upper Hay River, Mary Warburton, 1870 (MEL); Lake Wagin, N. of King George's Sound, Miss M. Cronin, 1890 (MEL); K.G. Sound, J. R. Muir (MEL); W.A., P. Walcott (MEL); W.A. Forest Dept., 2.1901 (NSW 44911); Walcliff, Miss Russell (MEL); Serpentine, M. Fitzgerald, Sept. 1901 (NSW 44905); Jardanup, Miss Knox-Peden, 3.1919, no. 45 (NSW 44910); Bow River, S. W. Jackson, 11.1912 (NSW 44912).

(5) RANUNCULUS PLEBEIUS R.Br. ex D.C. *Syst. Veg.*, I:288.1817. (Text-figs. 2, 27-31.)

Perennial herb with fibrous roots. *Flowering stems* 8-(30)-80 cm. high, branched with 2-(4)-16 flowers, hirsute, hairs long and spreading below, but short and appressed above. *Leaves* mainly basal, hirsute; hairs long and spreading on petioles, short and usually appressed on laminae: basal leaves with petioles 3-(12)-28 cm. long, basally flattened, glabrous and membranous towards the margin at the base; laminae ovate to deltoid in outline, 1-(4)-7 cm. long and often slightly broader, ternate or rarely ternately-lobed, segments ternately-lobed and acute, segments of ternate leaves ovate in outline with terminal petiolules to 10 mm. long and lateral ones to 8 mm. long: lower cauline leaves similar to basal leaves; upper leaves often sessile, ternately-lobed to entire, approaching the occasional uppermost entire and linear or dentate bracts. *Flowers* 7-(12)-16 mm. diam. *Sepals* 5, green, reflexed, ovate-cuneate to elliptic, 2.5-5 mm. long, 1-2 mm. broad, obtuse with a subterminal thickened beak, 3 principal veins forking above, hirsute on the abaxial surface with appressed or spreading hairs, membranous and usually glabrous toward the margin. *Petals* 5, golden-yellow, obovate to elliptic, 5-10 mm. long, 2.5-3.5 mm. broad, obtuse, starch-free zone $\frac{1}{4}$ - $\frac{1}{2}$ of petal length, 1-3 primary veins forking at or below nectary; nectary 0.3-0.7 mm. above base of petal; nectary-lobe ovate to elliptic, 0.5-1 mm. long, attached laterally to petal for $\frac{1}{2}$ of its length. *Stamens* 9-25. *Carpels* 25-(40)-60; flat, ovate, glabrous or with a few stout hairs on the dorsal ridge and lateral faces; style straight with a recoiled tip. *Achenes* in a globular head 6-8 mm. diam.; lenticular obovate to obovate-cuneate, 1.8-2.8 mm. long, 1.3-2 mm. dorsiventrally, 0.7-1 mm. laterally, slightly shouldered and rugose below the beak, margins narrowly ridged, lateral faces smooth; beak slender, strongly recurved, 0.7-1 mm. long. *Fruiting receptacle* 4-5 mm. long, 0.7-2 mm. diam.; staminal zone glabrous, achene zone elliptic and sparingly hirsute.

Chromosome number: $2n=16$. Voucher specimen: Bemboka, B. G. Briggs, 2.2.1956 (SYD).

Range: Eastern Australia.

Ecological distribution: Damp situations in forest areas on coast and tablelands, usually below 3,000 ft. altitude.

Holotype: In paludos prope Kingstown, R. Brown, Oct.-Nov., 1804, no. 5253 (BM, photo. SYD!).

Specimens examined:

QUEENSLAND: Condamine 403 (MEL); Mr. Archer's waterholes, Dr. Leichhardt, 23rd Nov. 43 (NSW 44780).

NEW SOUTH WALES: Koreelah Peak to White Swamp, J. H. Maiden, 12.1907 (NSW 44770); Copmanhurst, Rev. Rupp, 11.09 (NSW 44782); Grafton, R. J. Flynn, 13.11.1953 (NSW 27070); New England, A. Norton (BRI 001140); Oara R., J. L. Boorman, 11.'12 (NSW 27067); Beilsdown Creek, Dorrigo Forest Reserve, J. H. Maiden, 12.93 (NSW 44768); Stony Creek, Telegraph Point to Wauchope, H. and B. Gray (NSW 46149); Manning River, E. Cheel, 12.1899 (NSW 44769); Gloucester to Krumbach, N. C. Ford, 7.1.1958 (NSW 44787); Cessnock,

Paton and Derricott, 4.3.1957 (NSW 44789); Avoca, J. Blackmore, 10.4.1950 (NSW 27069); Cattai Creek, O.D.E., 11.39 (SYD); Gordon, A. Hamilton, 12.2.1899 (NSW 44771); St. Marys, O. D. Evans, 12.25 (SYD); Rockdale, J. H. Camfield, 8.6.1901 (NSW 27073), 3.1.1903 (NSW 44774), 14.3.1903 (NSW 27068); Kogarah, J. H. Camfield, 11.99 (NSW 27074); Bulli, E.B., 12.1890 (NSW 44783); Bulli, L. Johnson, 1875 (MEL); Mittagong, W. A. Dixon, 2.18 (NSW 27071); Welby to Bowral, E. J. Strugnell, 23.3.1955 (NSW 44791); Kiama, J. H. Camfield, 12.99 (MEL, NSW 44773); Southern slopes of the Barren Ground, nr. Berry, H. Salasso, 8.3.1954 (NSW 27075); Paddy's River, Goulburn-Sydney Rd., E. F. Constable, 25 Jan. 1956 (NSW 36701); Barrengarry Pass, O. D. Evans, 3.6.1925 (SYD); Mt. Cambewarra, Nowra, E. F. Constable, 7.12.1950 (NSW 16320); Beaumont, Cambewarra Ra., F. A. Rodway, 7 Dec. 1933, no. 1220 (NSW 44775); Between Bomaderry and Cambewarra, H. Salasso, 12.3.1955, no. 1315 (NSW 44786); Tarago, J. L. Boorman, 11.1911 (NSW 44777); Monga or Sugar-loaf Mt., near Braidwood, J. L. Boorman, 3.1909 (NSW 44784); Termeil to Bateman's Bay, F. A. Rodway, 1.1924, no. 460 (NSW 44772); Snowball, 44 ml. S'th of Braidwood, F. A. Rodway, 3.2.1946 (NSW 44785); Hopping Joe Creek, E. of Cann River-Bombala Road, R. Melville, 13.1.1953, no. 2868 (BRI 010004, MEL, NSW 44788).

VICTORIA: Snowy River, Dr. M. (MEL); near Seymour, Mrs. F. M. Reader, 9.11.1902 (MEL); between Bemm and Combinbah Rivers, W. A. Sayer, 1887 (MEL); towards the Moe swamps, April 1853 (MEL).

In some of the plants from Narooma to Brown Mountain on the South Coast, N.S.W., the petals are replaced by sepal-like structures. These structures resemble the sepals in size and texture and are hirsute on the abaxial surface, but usually have only one primary vein branching from near the base. In all other features these plants are typical of the species. The following collections contain both normal plants and such aberrant individuals: Nunnock R., 5 m. W. of Bemboka, B. G. Briggs, 2.2.1956 (SYD); near Bega, B. G. Briggs, 2.2.1956 (SYD).

(6) *RANUNCULUS SCAPIGERUS* Hook. *Journ. Bot.*, 1:244.1834. (Text-figs. 3, 32-37.)

Synonym: *R. lappaceus* Sm. var. *scapigerus* Benth.

Perennial herb with fibrous roots. *Flowering stems* 2.5-(20)-60 cm. tall, simple or branched with 2-4 flowers, hirsute with hairs spreading below and appressed above. *Leaves* mostly basal, covered with long spreading hairs on the petioles and short appressed ones on the laminae: basal leaves with petioles 1-(8)-15 cm. long, basally flattened, membranous toward the margin at the base; laminae ovate in outline, 7-(25)-60 mm. long and as broad or slightly broader, usually ternately or biternately lobed, rarely ternate with terminal petiolule to 1 cm. long and lateral ones to 5 mm. long and the segments with obtuse lobes: cauline leaves often present; lower ones similar to basal leaves; upper ones often sessile, ternately lobed to entire, approaching the uppermost linear to lanceolate and usually sessile bracts. *Flowers* 8-(14)-16 mm. diam. *Sepals* 5, green, reflexed, elliptic, 5-7 mm. long, 2-3 mm. broad, obtuse, hooded at apex with a subterminal thickened beak, 3 principal veins forking above, abaxial surface hirsute with spreading hairs, usually membranous and glabrous toward the margin. *Petals* 5, golden-yellow, usually tinged with purple on abaxial surface, elliptic to obovate, 6-9 mm. long, 2-5 mm. broad, obtuse, starch-free zone $\frac{1}{3}$ - $\frac{1}{2}$ of length, 3 principal veins forking at nectary; nectary 0.3-0.7 mm. above base of petal; nectary-lobe ovate or broad-oblong, 0.3-1 mm. long, 0.4-0.5 mm. broad, attached laterally to petal for $\frac{1}{3}$ - $\frac{1}{2}$ of its length. *Stamens* 15-35. *Carpels* 20-(30)-50; flat, ovate, usually with a few stiff hairs on the dorsal ridge and lateral faces; style straight with a recoiled tip. *Achenes* in a globular head 5-8 mm. diam.; obovate-cuneate, lenticular, 1.7-3 mm. long, 1.2-2 mm. dorsiventrally, 0.6-1 mm. laterally, rugose and slightly shouldered below the beak, marginal ridges distinct, lateral faces smooth; beak slender, 1.2-2 mm. long, straight with a recoiled tip. *Fruiting receptacle* 2-4 mm. long, 0.7-2 mm. diam.; staminal zone glabrous, achene zone hirsute and elliptic.

Chromosome number: $2n=16$. Voucher specimen: Daner's Gap, Mt. Kosciusko, B. G. Briggs, 5.1.1959 (SYD).

Range: Southern New South Wales, Victoria, Tasmania.

Ecological distribution: Grassland and forest areas. On the mainland it occurs mainly between 3,000 and 5,000 ft. altitude, but in Tasmania it extends to lower altitudes.

Holotype: Tasmania, Gunn, no. 229, 1833 (K, photo. CANB!).

Unrecognized variety: *R. scapigerus* Hook. var. *foliosus* Melville, Kew Bull 1955: 197. *Holotype*: On the grassy banks of a rivulet in a gully N. of Wilfred's Hill, Mt. Buffalo Plateau, R. Melville, 1.1.1953, no. 2684 (K, isotype MEL! NSW!).

This variety is characterized by branched flowering-stems with cauline leaves trifid, trilobed or ternate. Both varieties are common in Tasmania, but most mainland specimens which I have examined belong to var. *foliosus*. In Tasmanian material there is a complete gradation between the varieties and both are present in many collections. The nature of the cauline leaves and the extent of stem branching are closely related in development and can scarcely be considered as separate features. Considering the limited nature of the characters separating the varieties and the continuity of variation within the species, the maintenance of the two varieties does not seem justified.

Specimens examined:

NEW SOUTH WALES: N.W. of Cotter Trig, A.C.T., N. C. Ford, 16.1.1954 (NSW 27076); Coree-Queanbeyan, R. H. Cambage, 9.12.1911, no. 3280 (NSW 44776), 10.12.1911, no. 3239 (NSW 27077); 12 ml. N. of Rules Point, B. G. Briggs, 20.2.1957 (SYD); Snowy Mts. Highway, 6 ml. S.E. of Yarrangobilly Village, B. G. Briggs, 20.2.1957 (SYD); Happy Jack's Corge near junction with Tumut River, M. Mueller, 28.11.54, no. 2587A (NSW 44767); Daner's Gap, Kosciusko area, B. G. Briggs, 5.1.1959 (SYD); Plains of Heaven track, Mt. Kosciusko area, J. Garden, 9.1.1956 (NSW 44790); Hannel's Spur, Kosciusko area, B. G. Briggs, 11.1.1959 (SYD); Thredbo Ski Village, nr. Mt. Kosciusko, B. G. Briggs, 7.1.1959 (SYD); The Pilot Lookout, Jindabyne-Geehi Rd., B. G. Briggs, 15.1.1956 (SYD); Top of Brown Mountain nr. Bega, B. G. Briggs, 2.2.1956 (SYD).

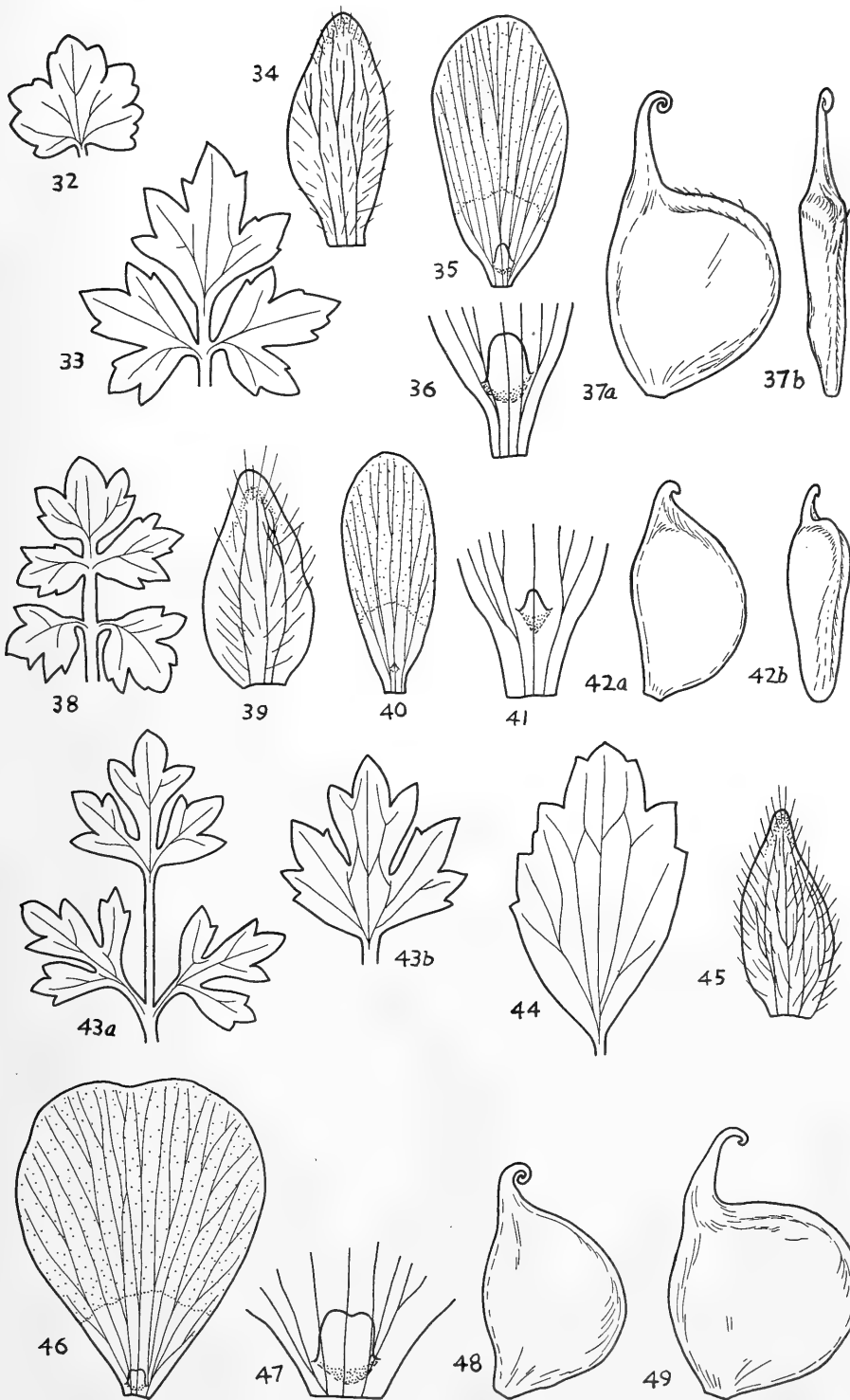
VICTORIA: Dividing Ranges, C. Walker, Nov. 1898 (NSW 44778); Hohman's Gap, Tawonga to Bogong Plains, B. G. Briggs, 24.12.1955 (SYD); Falls Creek, nr. Bogong High Plains, B. G. Briggs, 24.12.1955 (SYD); Mt. Lock nr. Mt. Hotham, B. G. Briggs, 31.xii.1952 (NSW 44898); Mt. Hotham, A. J. Tadge, Dec. 1914 (MEL); Mt. St. Bernard, nr. Mt. Hotham, B. G. Briggs, 2.1.1956 (SYD); Red Jacket Creek, Gargurevich, 1874 (MEL); Gippsland, Howitt, 1882 (MEL); Sources of the Brodribb R., E. Merrah, XI.1887 (MEL); Dandenong Ranges, C. Walker, Nov. 1897 (NSW 44779); Sherbrooke Forest, Dandenong Ranges, J. H. Willis, 10.1.1950 (MEL); Yarra, C. Walter (MEL).

TASMANIA: Herb. W. H. Archer (NSW 27060); H. and S. Hills no. 1066 (MEL); Mt. Arthur, Sullivan and Contes, 1886, no. 85 (MEL); Mt. Barrow, H. M. Rupp, Jan. 1922, no. 88 (NSW 27062); Mt. Barrow, M. Tindale, 17.12.1954 (NSW 44678); Waratah, A. H. S. Lucas, Dec. 1924 (NSW 27065); ascent of St. Paul's Dome, Nov. 1849 (MEL); Mt. Wellington, A. H. S. Lucas, Jan. 1901 (NSW 27064); Mt. Wellington, L. Rodway, Dec. 97 (NSW 27063); Mt. Wellington, F. A. Rodway, Jan. 1901, no. 49 (NSW 27059), Dec. 98, no. 48 (NSW 27058); Mt. Wellington, E. Rodway, Dec. 1929 (HO); Mt. Wellington, R. Melville, 10.12.1952, no. 2270A (NSW 44679), no. 2270B (MEL, NSW 44680); Hobart, Herb. S. C. Hannaford, 12.1870 (NSW 27061); Hobart, F. A. Rodway, Dec. 98, no. 48 (NSW 27058); Lady's Bay nr. Southport, Dec. 1855 (MEL).

(7) RANUNCULUS PIMPINELLIFOLIUS. Hook. *Journ. Bot.*, I:243.1834. (Text-figs. 3, 38-42.)

Synonym: *Ranunculus lappaceus* Sm. var. *pimpinellifolius* Benth. *Fl. Aust.*, I: 12.1863.

Perennial herb with fibrous roots. *Stems*: sometimes with short erect stems bearing a cluster of leaves and flowering stems; flowering stems erect or spreading, 2-(10)-25 cm. tall, simple or occasionally branched with 2-5 flowers, hirsute with long hairs spreading below and appressed above. *Leaves* mostly basal, hirsute with long spreading hairs, upper surface of laminae sometimes glabrous or nearly so; basal leaves with petioles 1-(8)-13 cm. long, basally flattened, membraneous towards the margin and almost glabrous at the base; laminae ovate or elliptic in outline, 5-(18)-30 mm. long, 5-(11)-25 mm. broad, pinnately divided into 3-5 segments, terminal segment ternately or biternately-lobed, lateral segments with petiolules 3-4 mm. long, segments ovate or obovate, ternately lobed and coarsely dentate: cauline leaves often present; lower cauline leaves similar to basal leaves; upper leaves sessile or shortly petiolate, ternately lobed or entire and linear-lanceolate. *Flowers* 5-(10)-15 mm. diam. *Sepals* 5, green, spreading, concave, elliptic to ovate, 2.5-6 mm. long, 1.5-2 mm. broad, hooded at apex with a subterminal thickened beak, 3 primary veins, forking from the base,



Text-figs. 32-37.—*R. scapigerus* Hook. 32-33, Leaves; 34, Sepal; 35, Petal; 36, Nectary; 37a, b, Achene, lateral and dorsal views. 32 from Mt. Wellington, Tas., 33-37 from Hannel's Spur, Kosciusko area, N.S.W.

Text-figs. 38-42.—*R. pimpinellifolius* Hook. 38, Leaf; 39, Sepal; 40, Petal $\times 5$; 41, Nectary; 42a, b, Achene, lateral and dorsal views. From Piper's Creek, Kosciusko area, N.S.W.

Text-figs. 43-49.—*R. graniticotus* Melville. 43-44, Leaves; 45, Sepal $\times 4$; 46, Petal; 47, Nectary; 48-49, Achenes. 43, 45-48 from Guthrie's Creek, Kosciusko area, N.S.W., 44 from Kiandra, N.S.W., 49 from Mt. Buller, Vic.

abaxial surface hirsute with spreading hairs, usually glabrous and membranous towards the margin. *Petals* 5—rarely 8, golden-yellow, elliptic to obovate-cuneate, 4–9 mm. long, 1.5–3.5 mm. broad, starch-free zone $\frac{1}{3}$ – $\frac{1}{2}$ of petal length, 3 primary veins forking from the base; nectary 1–2 mm. above base of petal in a shallow pocket terminating a thickened ridge; nectary-lobe triangular, to 0.5 mm. long. *Stamens* 20–35. *Carpels* 8–(25)–40; flat, semi-orbicular; style stout and straight with a recurved tip. *Achenes* in a globular head 4–6 mm. diam.; lenticular, semi-orbicular, 2–2.8 mm. long, 1.5–2 mm. dorsiventrally, 0.6–0.8 mm. laterally, marginal ridges obscure, lateral faces smooth, tapering gradually into a stout recurved beak 0.5–1 mm. long. *Fruiting receptacle* 1.5–4 mm. long, 0.5–1.5 mm. diam.; staminal zone hirsute or glabrous; achene zone hirsute and elliptic to ovate.

Chromosome number: $2n=16$. Voucher specimen: Piper's Gap, Mt. Kosciusko, B. G. Briggs, 10.1.1959 (SYD).

Range: Eastern New South Wales, Victoria, Tasmania.

Ecological distribution: Swamps and wet grassland in tableland and sub-alpine situations, usually from 2,500 to 6,000 ft. altitude.

Holotype: Growing with *R. lappaceus* (Gunn no. 90), R. Gunn (K).

Unrecognized varieties: *R. pimpinellifolius* var. *a glabrior* Hook. f. in *Hook. Journ. Bot.*, 2:401.1840. Based on the same type as the species. *R. pimpinellifolius* var. *vestitus* Hook., *Icones Plantarum*, 3: Pl. 260, 1839. Holotype: Abundant on the edge of a stream called Blackman's River near Hobart Town, Tas. R. Gunn. (K, photo., CANB!) This variety is not recognized as it differs from the type only in minor characters, which grade imperceptibly into those of the typical form.

J. D. Hooker at first (1840) recognized *R. pimpinellifolius*, but later (1855) reduced it to synonymy under *R. hirtus* Banks et Sol. ex DC.; Rodway (1903) equated it to *R. scapigerus*, to which he gave varietal rank under *R. lappaceus*.

Specimens examined:

NEW SOUTH WALES: Guy Fawkes, J. L. Boorman, 12.1909 (NSW 44749); Guy Fawkes Creek Gorge, R. Carolin, 17.11.57, no. 428 (SYD); Barwick R., Armidale-Pt. Lookout Rd., B. G. Briggs, 20.8.1956 (SYD); Barrington Tops, L. R. Fraser, J. W. Vickery, 7.1.1934 (SYD); Erumlow Creek, Barrington Tops, L. A. S. Johnson, 1.xii.1954 (NSW 44751); Oberon, J. Garden, 10.11.1952 (NSW 44753), 11.11.1952 (NSW 44754); Oberon district, J. Vickery, 6.10.1952 (NSW 44755); Jenolan Caves, W. F. Blakely, 11.99 (NSW 44757); Colong-Yerranderie, R. H. Cabbage, 5.12.1911, no. 3217 (NSW 44756); Taralga, E. Cheel, 12.12.1919 (NSW 44745); Mt. Gingera, C. W. E. Moore, 17.12.1953 (NSW 44746); Mt. Gingera, M. Tindale, 16.1.1954 (NSW 44747); Queanbeyan River, between Jerangle and Captains Flat, J. Garden, 12.1.1956 (NSW 44760); Kiandra, J. Thompson, 20.1.1958 (NSW 44744); Happy Jack's Plain, 15 ml. south of Kiandra, J. Thompson, 18.1.1958 (NSW 44742); Toolong Ra., 12 ml. south of Kiandra, J. Thompson, 20.1.1958 (NSW 44743); Kybean, R. H. Cabbage, no. 2122 (SYD), 5.11.1908, no. 2022 (NSW 44761); Lower slopes of Mt. Kosciusko, A. T. Hotchkiss, 1.1.1954 (NSW 44763); Rennix Gap, Kosciusko area, B. G. Briggs, 16.1.1957 (SYD); Plains of Heaven track, Mt. Kosciusko area, J. Garden, 9.1.1956 (NSW 44758); Junction of Wragge's and Piper's Creeks, Mt. Kosciusko, J. Garden, 9.1.1956 (NSW 44759); Piper's Creek, Kosciusko area, B. G. Briggs, 16.1.1957 (SYD); Piper's Gap, C. W. E. Moore, 2.2.1953, no. 2859 (NSW 44762); Perisher Gap, Kosciusko area, B. G. Briggs, 16.1.1957 (SYD); Between Charlotte Pass and Snowy River, Mt. Kosciusko, H. J. Eichler, 5.2.1957, no. 13653 (AD 5748012); Kosciusko 5000', J. McL. and A.H.K.P., 1.25 (SYD); Thredbo Ski Village, near Mt. Kosciusko, B. G. Briggs, 7.1.1959 (SYD).

VICTORIA: Strathbogie per H. B. Williamson, 1902, no. 980 (MEL, NSW 44748); Omeo, Dr. M., Dec. 54 (MEL).

TASMANIA: Pontville on the Jordan, W. W. Spicer, '18 (MEL); Blackman's River, Herb. Gunn, no. 635, pro parte (HO); Formosa, ex Herb. Gunn, no. 635 (HO, NSW 44764); ex Herb. W. H. Archer (NSW 44765, 44766).

(8) *RANUNCULUS GRANITICOLUS* Melville. *Kew Bull.*, 1955: 205–206. (Text-figs. 4, 43–49.)

Perennial herb with fibrous roots. *Flowering stems* 2–(12)–40 cm. long, usually simple, rarely branched with 2–3 flowers, hirsute with hairs spreading or sometimes appressed above. *Leaves* mostly basal, hirsute; petioles with long spreading hairs and

laminae with short appressed ones: basal leaves with petioles 1-(7)-25 cm. long, basally flattened, membraneous toward the margin at the base; laminae ovate to elliptic in outline, 1-(3)-4 cm. long, length 1-3 times breadth, simple with the margin coarsely dentate, or ternately or biternately dissected or lobed with dentate segments, when ternate the segments ovate in outline with acute lanceolate lobes and with the terminal petiolule to 15 mm. long and the lateral ones to 5 mm. long; rarely a few inner leaves entire and linear-lanceolate: cauline leaves often present; sessile or petiolate, entire and linear-lanceolate or ternately dissected or lobed. Flowers 10-(15)-36 mm. diam. *Sepals* 5, green, spreading, concave, ovate-cuneate or elliptic, 3-7 mm. long, 1.5-4 mm. broad, usually hooded at apex, 3 to rarely 5 primary veins forking from the base, abaxial surface covered with spreading hairs, membraneous and glabrous towards the margin. *Petals* 5 to rarely 8, golden yellow, abaxial surface sometimes tinged with purple, obovate-cuneate, 6-(10)-20 mm. long, 5-(7)-14 mm. broad, obtuse or truncate or emarginate, starch-free zone $\frac{1}{4}$ - $\frac{1}{2}$ of petal length, 3 primary veins branching at or below the nectary; nectary 0.2-0.5 mm. from base of petal; nectary-lobe oblong or tapering slightly toward apex, 0.2-1 mm. long, truncate or usually emarginate, attached to petal at base only or attached laterally for part or all of length. *Stamens* 30-70. *Carpels* 20-(35)-65; flat, ovate; style short, arching or recoiled, style and dorsal surface

TABLE 1.
Variation in R. graniticulus.

Locality.	Dissection of Lamina.	Length of Terminal Petiolule.	Number of Carpels.	Achene Beak.
Mt. Buffalo ..	Ternate to bi-ternate with segments lobed or dentate.	5-(10)-15 mm.	20-(30)-35	Stout, arching, recoiled at tip.
Mt. Buller ..	Ternate with segments ternately or biternately lobed and often dentate, or (rarely) deeply ternately lobed.	3-(5)-20 mm.	30-(40)-50	Usually slender, arching, recoiled at tip.
Mt. Kosciusko	Ternately dissected or lobed with segments lobed or dentate.	0-5 mm.	30-(45)-50	Stout, strongly recurved.
Mt. Franklin-Adaminaby.	Obovate and evenly 5-20 toothed, or ternately dissected or lobed with dentate segments.	0-2 mm.	20-(30)-45	Stout, recurved.

of achene often dark brown. *Achenes* in a globular head 6-9 mm. diam.; lenticular, obovate-cuneate to semi-orbicular, 2-3.5 mm. long, 1.7-2.5 mm. dorsiventrally, 0.7-1.0 mm. laterally, shouldered and slightly rugose near base of style, lateral faces smooth, margins narrowly ridged; style stout or rather slender, 0.7-1 mm. long, arching or strongly recurved, usually with a recoiled tip. *Fruiting receptacle* 3-5 mm. long, 0.7-3 mm. diam.; staminal zone glabrous; achene zone hirsute and elliptic to orbicular.

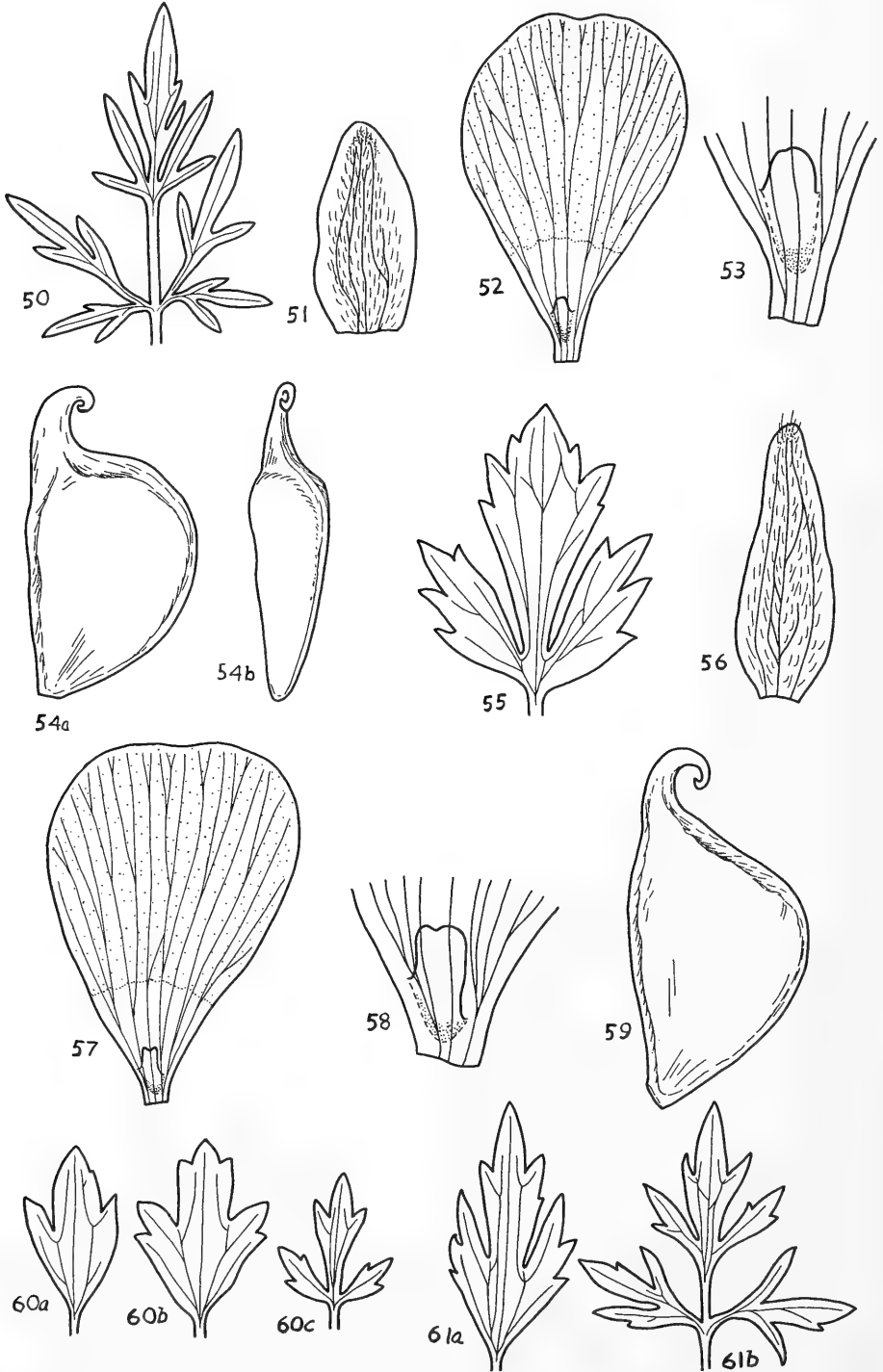
Chromosome number: $2n=16$. Voucher specimens: Guthrie's Creek, Mt. Kosciusko area, B. G. Briggs, 6.1.1959 (SYD); Kiandra, B. G. Briggs, 10.1.1959 (SYD).

Range: Mountains of southern New South Wales and eastern Victoria, from Mt. Franklin south to Mt. Buller; but absent from Mt. Hotham and the Bogong High Plains.

Ecological distribution: Sub-alpine grassland and sometimes swamps, 3,800-6,600 ft. altitude. On the Mt. Buffalo Plateau it occurs in sub-alpine grassland ranging from dry ridges to wetter sites on valley floors and is also plentiful in *Sphagnum* bogs. Elsewhere it is limited to dry grassland situations on well-drained slopes and ridges.

Holotype: Mt. Buffalo Plateau below Stonehenge, in sub-alpine pasture on granite, about 4,600 ft. altitude, R. Melville, 27.12.1952, no. 2579 (K, isotypes Mel! N.S.W.!).

In addition to the holotype a paratype was cited from the Kosciusko area, N.S.W. (N.S.W. 15884!). Mt. Buller in Victoria and the area from Mt. Franklin to Adaminaby



Text-figs. 50-54.—*R. eichleranus* B. G. Briggs. 50, Leaf; 51, Sepal $\times 4$; 52, Petal; 53, Nectary; 54a, b, Achene, lateral and dorsal views. From isotypes.
 Text-figs. 55-61.—*R. victoriensis* B. G. Briggs. 55, 60-61, Leaves; 56, Sepal $\times 4$; 57, Petal; 58, Nectary; 59, Achene. 55-59 from isotypes, 60 from Pretty Valley, Bogong High Plains, Vic., 61 from Mt. Hotham, Vic.

in N.S.W. and A.C.T. also support plants which are similar to those from the type locality. The populations in these four areas differ from one another in features of leaf dissection and in other minor characters (see Table 1). The limits of variation in these features differ between regions, but no discontinuities could be distinguished sufficient for the establishment of varieties.

The study of a larger range of material has considerably widened the variation limits beyond those recorded in the original description.

Specimens examined:

NEW SOUTH WALES: Mt. Franklin, A.C.T., C. Rathgeber, 11.3.1956 (SYD); Mt. Ginini, nr. Mt. Franklin, B. G. Briggs, 10.1957 (SYD); Mt. Gingera, B. G. Briggs, 10.1957 (SYD); Mt. Gingera, A.C.T., M. Tindale, 16.1.1954 (NSW 44666); Mt. Gingera, A.C.T., C. W. E. Moore, 4.2.1953, no. 2272 (NSW 44655), no. 2313 (NSW 44656), no. 2314 (NSW 44657), no. 2315 (NSW 44654); Rules Point, N. of Kiandra, B. G. Briggs, 10.3.1956 (SYD); 1 ml. N. of Kiandra, B. G. Briggs, 3.1956 (NSW 44664); Kiandra distr., E. Betcher, 2.1897 (NSW 44658); Kiandra, B. G. Briggs, 10.3.1956 (SYD), 5.12.1956 (SYD); Toolong Ra., 18 m. S.W. of Kiandra, J. Thompson, 20.1.1958 (NSW 44660); Happy Jack's Plain, nr. Kiandra, B. G. Briggs, 10.3.1956 (SYD), 5.12.1956 (SYD); Wilson's Valley, Kosciusko area, B. G. Briggs, 18.1.1957 (SYD); above Dainer's Gap, Plains of Heaven Track, Mt. Kosciusko area, J. Garden, 9.1.1956 (NSW 44653, 44668, 44669); Pretty Point, Mt. Kosciusko, J. H. Maiden and W. Forsyth, January, 1899 (NSW 44650); Hotel Kosciusko, B. G. Briggs, 18.2.1957 (SYD), Prussian Creek, Kosciusko area, B. G. Briggs, 16.1.1956 (SYD); nr. Smiggin Holes, Kosciusko area, B. G. Briggs, 16.1.1956 (SYD); Piper's Gap, Mt. Kosciusko, J. Garden, 9.1.1956 (NSW 44652); Guthrie's Creek, Kosciusko area, B. G. Briggs, 16.1.1956 (SYD), 6.1.1959 (SYD); Near Betts Creek south of the Paralyser, HJ. Eichler, 24.1.1957, no. 13463 (AD 95735041); Betts Creek, S. of Main Kosciusko Rd., J. Garden, 10.1.1956 (NSW 44651); Betts Camp, Mt. Kosciusko, J. H. Maiden, 16.2.1914 (NSW 44670); Betts Camp, Kosciusko area, B. G. Briggs, 14.1.1957 (SYD); Spencer's Creek, Mt. Kosciusko, HJ. Eichler, 25.1.1957, no. 13513 (AD 95742009), 4.2.1957, no. 13626 (AD 95746011); Near Spencer's Creek Camp, Kosciusko area, B. G. Briggs, 20.1.1957 (SYD); Spencer's Creek Bridge, Kosciusko area, B. G. Briggs, 3.2.1953 (SYD); Near Trapyard Creek, ca. 8 km. E.N.E. of Mt. Kosciusko, HJ. Eichler, 25.1.1957, no. 13489 (AD 95735046), no. 13490 (AD 95735045); Trapyard Creek, Kosciusko area, B. G. Briggs, 16.1.1956 (SYD); Top of Bett's Valley, nr. Thredbo Valley, Kosciusko area, B. G. Briggs, 19.1.1957 (SYD); Thredbo River Gorge, Mt. Kosciusko, L. A. S. Johnson and E. F. Constable, 19.1.1951 (NSW 15884); Snowy River, nr. Charlottes Pass, Kosciusko area, B. G. Briggs, 17.1.1956 (SYD); Seaman's Hut, Mt. Kosciusko, per J. Collins, 1952 (NSW 44649); near North Ramshead, Kosciusko area, B. G. Briggs, 18.1.1956 (SYD); Thredbo Ski Village, near Mt. Kosciusko, B. G. Briggs, 7.1.1959 (SYD); Mt. Kosciusko, 6,000' (MEL); Kosciusko, N. C. Beadle, 5.2.1952 (SYD); Kosciusko, J. McLuckie and A. H. K. Petrie, 1.1924 (SYD); Mt. Kosciusko, Miss T. Harris (NSW 44671, 44662), 10.1.1930 (NSW 44647); Mt. Kosciusko, A. T. Hotchkiss, 31.12.1953 (NSW 27085); Mt. Kosciusko, 5,500 ft. to sum., J. H. Maiden, '93 (NSW 44661); Mungyang Mountains, F.v.M. (MEL).

VICTORIA: Alps, C. French, Jr., 12.1904, pro parte (MEL); Summit Buffalo Mts., C. Walter (MEL), Jan. 1899 (NSW 44645); Mt. Buffalo, R. H. Cambage, 19.1.1913, no. 3757 (NSW 44646); Lake Catani, Mt. Buffalo, B. G. Briggs, 1.1956 (NSW 44640); Reservoir, Mt. Buffalo, B. G. Briggs, 1.1956 (SYD); Mt. Dunn, Mt. Buffalo Plateau, B. G. Briggs, 1.1956 (SYD); Eagle Point, Mt. Buffalo, B. G. Briggs, 1.1956 (SYD); near Leviathan, Mt. Buffalo, B. G. Briggs, 1.1956 (SYD); Blackfellow's Plain, Mt. Buffalo, B. G. Briggs, 1.1956 (SYD); near the Hump, Mt. Buffalo, B. G. Briggs, 1.1956 (SYD); Mt. Buller, near Ski Village, B. G. Briggs, 1.1956 (SYD); C.S.I.R.O. Ski Hut, Mt. Buller, B. G. Briggs, 1.1956 (SYD); Mt. Buller Summit, B. G. Briggs, 1.1956 (SYD).

(9) *RANUNCULUS EICHLERANUS*, sp. nov. (Text-figs. 4, 50-54.)

Herbae perennes pilis brevibus appressisque instructae. Caules floriferi simplices. Folia plerumque radicalia segmentis terno- vel biterno-lobatis ternata, lobis linearilanceolatis. Sepala patentia. Petala aureo-flava et obovato-cuneata. Lobi nectariorum oblongi. Achenia lenticularia glabraeque rostris recurvatis praedita.

Perennial herb with fibrous roots. *Flowering stems* 5-(15)-24 cm. tall, simple, densely covered with short antrorse-appressed hairs. *Leaves* mostly basal, with short appressed hairs, 0.5-1 mm. long, densely covering petioles and lower surfaces of laminae but scattered on upper surfaces of laminae: basal leaves with petioles 2-(8)-15 cm. long, membranous toward the margin at the base; laminae ovate in outline, 15-(25)-40 mm. long, 12-(22)-35 mm. broad, ternate with segments ternately or biternately-lobed or with lateral segments bifid, lobes linear-lanceolate acute and sometimes dentate,

terminal petiolules 3-(10)-18 mm. long and lateral ones to 6 mm. long: cauline leaves often present, sessile or petiolate, simple and linear or orbicular and ternately-lobed or dissected. *Flowers* 16-20 mm. diam. *Sepals* 5, green, spreading, concave, elliptic to narrow-ovate 6-7.5 mm. long, 2.5-4 mm. broad, abaxial surface covered with short appressed hairs, membranous and glabrous toward the margin. *Petals* 5, golden-yellow, obovate-cuneate, 7-12 mm. long, 5-7 mm. broad, obtuse or emarginate, starch-free zone $\frac{1}{3}$ of petal length, 3 primary veins branching at nectary; nectary 0.5-1.5 mm. above base of petal; nectary-lobe oblong, 0.7-1.5 mm. long, emarginate or obtuse, attached laterally to petal for $\frac{1}{2}$ - $\frac{2}{3}$ of its length. *Stamens* 35-65. *Carpels* 35-65; flat, ovate; style short and straight with a recurved tip. *Achenes* in a globular head 7-9 mm. diam.; sublenticular, obovate-cuneate to semi-orbicular, 2.5-3.5 mm. long, 1.8-2.5 mm. dorsiventrally, 0.8-1.0 mm. laterally, slightly rugose and shouldered below the beak, margins narrowly ridged, lateral faces smooth; beak slender or rather stout, 0.8-1.5 mm. long, arching and recoiled at the tip. *Fruiting receptacle* 3-4 mm. long, 1.0-1.5 mm. diam., staminal zone glabrous, achene zone hirsute and elliptic.

Chromosome number: $2n = 16$. No voucher kept.

Range: Mt. Hotham, Victoria.

Ecological distribution: Sub-alpine grassland and woodland, mostly on sheltered slopes; about 5,000 ft. altitude.

Holotype: Top of Dibbin's Spur, nr. Mt. Hotham, B. G. Briggs, 28.12.1955 (NSW). *Isotypes*: AD, K, SYD.

The species is named after Dr. Hj. Eichler, Director of the State Herbarium of South Australia, a noted authority on the Ranunculaceae.

Specimens examined:

Near Mt. Loch, Mt. Hotham, B. G. Briggs, 29.12.1956 (SYD); Mt. Hotham, B. G. Briggs, 31.12.1956 (NSW 44644), 1.1956 (NSW 44642); Near Chalet, Mt. Hotham, B. G. Briggs, 1.1956 (SYD); C.R.B. Hut, Mt. Hotham, B. G. Briggs, 1.1956 (SYD); 4 ml. S.W. of Mt. Hotham, B. G. Briggs, 1.1.1956 (SYD); Alps, C. French, Jr., 12.1904, pro parte (MEL).

(10) RANUNCULUS VICTORIENSIS, sp. nov. (Text-figs. 4, 55-61.)

Herbae perennes pilis brevibus plerumque appressis sed in pagina superiore saepe subpatentibus obtectae. Caules floriferi simplices. Folia plerumque radicalia aut simplicia prope apicem utrinque profunde semel incisa pluridentatae aut lobis lanceolatis ternata biternatae. Sepala patentia. Petala aureo-flava, obovato-cuneata. Lobi nectariorum oblongi. Achenia lenticularia glabraque rostris rectis vel recurvatis praedita.

Perennial herb with fibrous roots. *Flowering stems* 5-(15)-28 cm. tall, simple, densely covered with short antrorse-appressed hairs. *Leaves* mostly basal; petioles and laminae densely covered with short appressed hairs 0.5-1 mm. long, upper surface of laminae with appressed or sub-erect hairs 0.5-2 mm. long; basal leaves with petioles 2-(8)-17 cm. long, membranous toward the margin at the base; laminae ovate in outline, 12-(25)-50 mm. long, length 1-2 times breadth, ternately or biternately dissected or lobed with dentate segments or simple with 2 deep incisions near the apex or with several shallow notches, when ternate the terminal petiolule to 1 cm. long and the lateral ones to 5 mm. long, lobes lanceolate to broad-lanceolate and acute: cauline leaves occasionally present, shortly petiolate, lanceolate, entire or ternately-lobed. *Flowers* 16-30 mm. diam. *Sepals* 5, green, spreading, concave, elliptic to ovate-cuneate, 5-7 mm. long, 2-4 mm. broad, abaxial surface covered with short appressed hairs, membranous and glabrous toward the margin. *Petals* 5, golden-yellow, obovate-cuneate, 8-14 mm. long, 6-8 mm. broad, obtuse or truncate, starch-free zone $\frac{1}{4}$ - $\frac{1}{3}$ of petal length, 3 primary veins branching at nectary; nectary 0.5-1.5 mm. above base of petal; nectary-lobe oblong, 0.7-1.5 mm. long, usually emarginate, attached at base only or attached laterally to petal for up to $\frac{1}{2}$ of length. *Stamens* 35-65. *Carpels* 30-60; flat, ovate; style short and straight with a recurved tip. *Achenes* in a globular head 7-9 mm. diam.; lenticular, obovate-cuneate to semi-orbicular, 2.5-3.5 mm. long, 2-3 mm. dorsiventrally,

0.7–1.2 mm. laterally, slightly rugose and shouldered below the beak, margins narrowly ridged, lateral faces smooth; beak stout, 0.8–1.5 mm. long, arching or straight with a recurved tip. *Fruiting receptacle* 3–5 mm. long, 1–1.5 mm. diam.; staminal zone sparsely hirsute, achene zone hirsute and elliptic.

Chromosome number: $2n=16$. No voucher kept.

Range: Bogong High Plains and Mt. Hotham, Victoria.

Ecological distribution: Sub-alpine grassland, above 5,000 ft. altitude.

Holotype: Near Wallace's Hut, Rocky Valley, Bogong High Plains, B. G. Briggs, 26.12.1955 (NSW). *Isotypes*: AD, B, BM, G, K, MEL, NY, P, SYD.

Specimens examined:

Bogong High Plains, Fall's Creek, Ski Village, Hj. Eichler, 31.1.1958, no. 14633 (AD 95829015), no. 14638 (AD 95829023), 2.2.1958, no. 14668 (AD 95829020); Fall's Creek Ski Village, B. G. Briggs, 28.12.1955 (SYD); Mt. McKay, Bogong High Plains, B. Briggs, 1.1956 (NSW 44641); Rocky Valley, Bogong High Plains, Hj. Eichler, 3.2.1958, no. 14688 (AD 95829008), no. 14708 (AD 95828070); Rocky Valley, Bogong High Plains, B. G. Briggs, 1.1956 (NSW 44643); Basalt Hill, Bogong High Plains, B. G. Briggs, 2.1.1956 (SYD); surroundings of Mt. Nelse, Bogong High Plains, Hj. Eichler, 13.2.1958, no. 14850 (AD 95826105); Bogong High Plains, Pretty Valley, Hj. Eichler, 4.2.1958, no. 14724 (AD 95829014), 5.2.1958, no. 14731 (AD 95829012); Pretty Valley, Bogong High Plains, B. G. Briggs, 1.1956 (SYD); Mt. Cope, Bogong High Plains, C. I. Skewes, 15.1.1954 (MEL); Mt. Hotham, B. G. Briggs, 1.1956 (NSW 44642, SYD).

This species appears to be a stabilized hybrid derivative of *R. eichleranus* and *R. muelleri* Benth. var. *muelleri*. Evidence for this view will be presented elsewhere. The species is very variable, but few plants approach closely the limits of variation found in stands of either putative parental species remote from opportunity for hybridization. Its range, more than one hundred square miles, includes most of the ecologically suitable area of the Bogong High Plains—Mt. Hotham mountain-block. Over most of this range it has completely replaced both parental species. The evolutionary future of this population is apparently not wholly dependent on that of the parental species.

(11) *RANUNCULUS MUELLERI* Benth. *Fl. Aust.*, 1:13.1863. (Text-figs. 4, 62–67.)

Perennial herb with fibrous roots. *Flowering stems* simple, 2.0–16 cm. long, densely covered with short antrorse-appressed hairs. *Leaves* usually all basal; petioles and lower surfaces of laminae densely covered with short appressed hairs, upper surfaces of laminae with rigid appressed or spreading hairs 2–4 mm. long arising from small tubercles: basal leaves with petioles 0.5–9 cm. long, grooved adaxially, basally flattened and often tinged with purple, membranous toward the margin at the base; laminae elliptic to obovate and acute, 8–27 mm. long, breadth $\frac{1}{4}$ – $\frac{2}{3}$ of length, entire or with 1–2 shallow incisions near apex, base obtuse or cuneate; bracts occasionally present, sessile and linear, 1–1.5 mm. long. *Flowers* solitary, 15–(20)–35 mm. diam. *Sepals* 5, green, spreading, concave, elliptic to narrow ovate, 5–(8)–13 mm. long, 2–5 mm. broad, obtuse or truncate, usually hooded at apex, 3 primary veins forking from the base, abaxial surface covered with short appressed hairs, usually glabrous and membranous towards the margin. *Petals* 5, golden-yellow, obovate-cuneate, 7–(10)–22 mm. long, 5–9 mm. broad, obtuse or truncate or emarginate, starch-free zone $\frac{1}{4}$ – $\frac{1}{3}$ of petal length, with 3 primary veins forking at or below the nectary; nectary 0.5–1.5 mm. above base of petal, in a shallow pocket with no distinct lobe or usually with a triangular lobe to 0.5 (rarely 2) mm. long. *Stamens* 15–(40)–70. *Carpels* 30–(50)–120; flat, elliptic, style straight with a recurved tip. *Achenes* in a globular head 7–14 mm. diam., lenticular, semi-elliptic to semi-orbicular, 2–3 mm. long, 1–2.2 mm. dorsiventrally, 0.8–1.2 mm. laterally, margins narrowly ridged, lateral faces smooth; tapering gradually into a stout beak 1–2.2 mm. long, straight and usually terminating in a short laterally-inclined hook. *Fruiting receptacle* 3–6 mm. long, 2–3.5 mm. diam.; staminal zone glabrous; achene zone elliptic or orbicular and sparsely hirsute.

Var. MUELLERI.

Flowering stems 2–(10)–16 cm. long. *Leaves* usually all basal; petioles 1–(6)–9 cm. long; laminae elliptic, 8–(20)–28 mm. long with breadth $\frac{1}{4}$ – $\frac{1}{2}$ of length, upper surface with rigid appressed or sub-erect hairs 2–3 mm. long, margins with appressed hairs. *Achenes* semi-elliptic to semi-orbicular, beak 1–1.5 mm. long.

Chromosome number: $2n=16$. Voucher specimen: Guthrie's Creek, Mt. Kosciusko area, B. G. Briggs, 10.1.1959 (SYD). Also Smith-White, unpublished.

Range: Kosciusko Plateau, New South Wales; Bogong High Plains, Victoria.

Ecological distribution: Alpine and sub-alpine grassland. Above 6,000 ft. altitude it extends throughout all grassland and herbfield communities, including those on dry slopes. Between 5,500 and 6,000 ft. the species is limited to wetter situations on valley floors.

Typification: The type collection cited by Bentham is "Summits of the Munyang mountains. F. Mueller". Material in the Kew Herbarium determined by Bentham is labelled "Summits of the Australian Alps. F. Mueller"; however, Melville considers (personal communication) that some of the specimens are an exact match for others in Melbourne Herbarium written up by Mueller as originating from the Munyang mountains. Both the names "*R. muelleri*" and "*R. lappaceus* var. *subsericeus*" appear on the Kew sheet; however, Melville considers that "the authorship of the words '*R. lappaceus* var. *subsericeus*' . . . is open to very grave doubts. The words '*R. lappaceus* var.' may be in Bentham's hand, but '*subsericeus*' is almost certainly not." The material appears to include two collections. A lectotype is erected to include only one collection, all plants of which clearly belong to var. *muelleri*. Accordingly the four specimens in the upper left corner are excluded from the lectotype.

Lectotype: Summits of the Australian Alps, F. Mueller (K), excluding the four specimens on the upper left of the sheet (see Plate xv).

Specimens examined:

NEW SOUTH WALES: Club Lake, Mt. Kosciusko, L. A. S. Johnson, 20.1.1951 (NSW 1878); Club Lake, Kosciusko area, B. G. Briggs, 17.1.1956 (SYD); Club Lake Creek, Kosciusko area, B. G. Briggs, 17.1.1956 (SYD); Bett's Creek, J. Garden, 10.1.1956 (NSW 44817); Spencer's Creek, Kosciusko area, B. G. Briggs, 3.2.1958 (SYD); Trapyard Creek, Kosciusko area, B. G. Briggs, 12.1.1956 (SYD); near Mt. Stillwell, Kosciusko area, B. G. Briggs, 14.1.1956 (SYD); Mt. Kosciusko, Rawson's Pass, A. T. Hotchkiss (NSW 44819); Upper Snowy R. area, Mt. Kosciusko, M. Mueller, 30.12.1953, no. 1723 (NSW 44818); Merritt's Creek, Kosciusko area, B. G. Briggs, 15.1.1956 (SYD), 8.3.1956 (SYD); below Lake Cootapatamba, Mt. Kosciusko, J. Garden, 7.1.1956 (NSW 44815); near North Ramshead, Kosciusko area, B. G. Briggs, 13.1.1956 (SYD); Tree Line to 7,000 ft., Mt. Kosciusko, J. H. Maiden and W. Forsyth, Jan. 1899 (NSW 27055); Kosciusko, 6,500 ft., N. C. Beadle, 5.2.1952 (SYD); Kosciusko, J. McL. and A.P., 1924 (SYD); Kosciusko, P. Brough, 2.1927 (SYD).

VICTORIA: Bogong Range, F. v. Mueller, 1854 (MEL); Flourbag, Bright-Omeo Rd., D. J. Paton, 20.11.1918 (MEL).

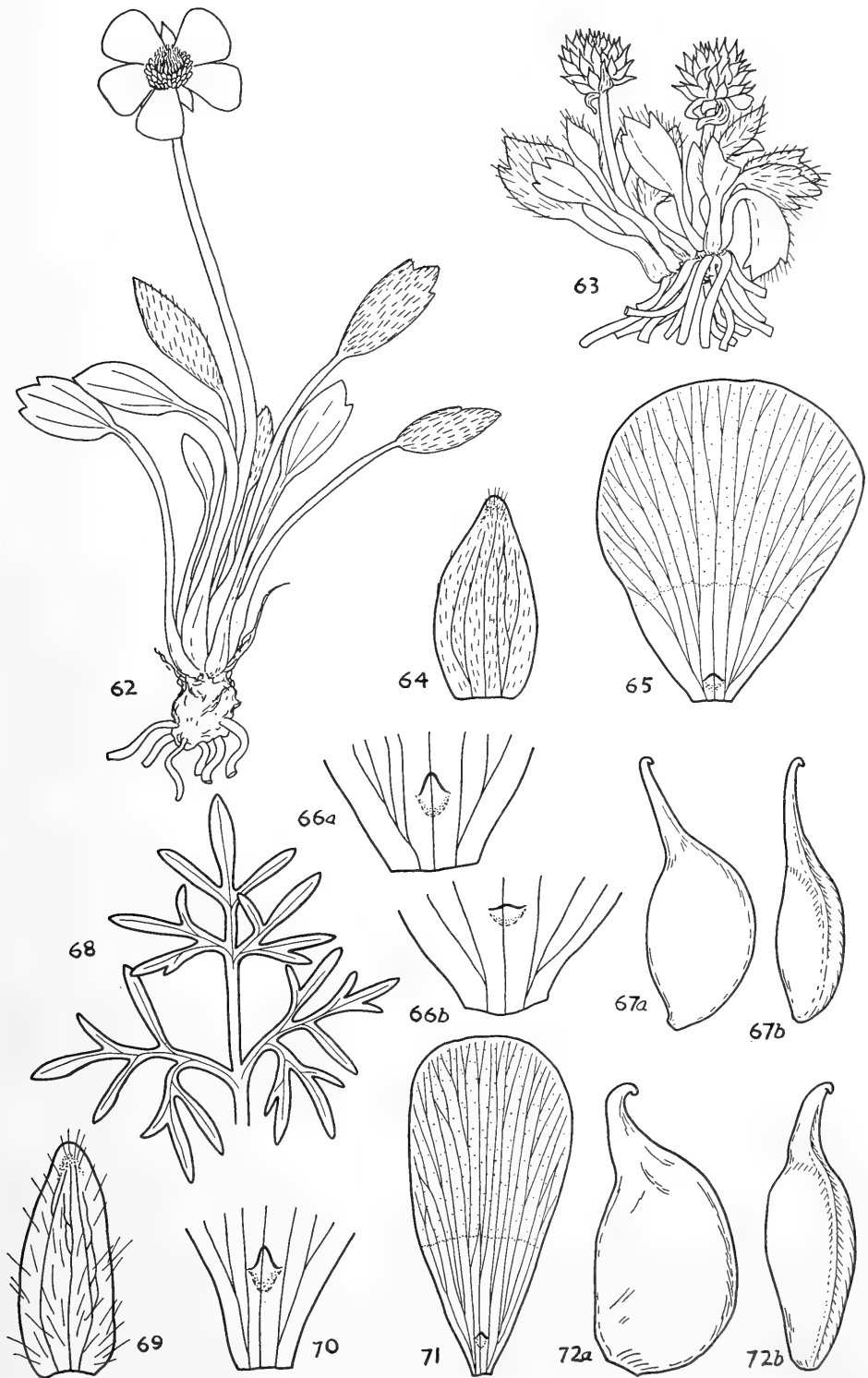
Var. BREVICAILIS, var. nov.

Caules floriferi 2–4 cm. longi quam folia vix longiores. *Petioles* 0.5–2.5 cm. longi. *Laminae* ellipticae vel obovatae plerumque quam petiolas in pagina superiore pilis longis patentibus obtectae.

Flowering stems 2–4 cm. long. *Leaves* all basal; petioles 0.5–2.5 cm. long; laminae elliptic to obovate, 9–(15)–28 mm. long with breadth $\frac{1}{3}$ – $\frac{2}{3}$ of length, margins and upper surface covered with rigid spreading hairs 3–4 mm. long. *Achenes* semi-orbicular, beak 1.2–2.2 mm. long.

Chromosome number: $2n=16$. Voucher specimen: Saddle between Mt. Lee and Carruther's Peak, Kosciusko area, B. G. Briggs, 3.1.1959 (SYD).

Range: Mt. Kosciusko Plateau, N.S.W.; main range from Mt. Twynam to Kosciusko summit.



Text-figs. 62, 64-67.—*R. muelleri* Benth. var. *muelleri*. 62, Habit; 64, Sepal $\times 4$; 65, Petal; 66a, b, Nectaries; 67a, b, Achene, lateral and dorsal views. From Merritt's Creek, Kosciusko area, N.S.W.

Text-fig. 63.—*R. muelleri* Benth. var. *brevicaulis* B. G. Briggs. Holotype $\times 1$.

Text-figs. 68-72.—*R. dissectifolius* F. v. Muell. ex Benth. 68, Leaf; 69, Sepal $\times 4$; 70, Nectary; 71, Petal; 72a, b, Achene, lateral and dorsal views. From Bett's Creek, Kosciusko area, N.S.W.

Ecological distribution: Fjeldmark communities on wind-swept ridges, above 6,700 ft. alt.

Holotype: Mt. Lee, Mt. Kosciusko area, B. G. Briggs, 3.1.1959 (NSW). *Isotypes:* AD, BM, K, SYD.

The morphological differences between the varieties are small and are largely quantitative in nature; however, they provide a discontinuity in the variation pattern within the species. Additional evidence supporting the recognition of the varieties will be presented in another paper. In brief, this evidence shows the restriction of the varieties to different habitats with intermediate forms common only in the narrow ecotone between the habitats; also the varietal differences have been shown to remain constant in transplants grown under uniform conditions and in seedlings raised in Sydney. The varieties must differ genotypically and not merely as a result of environmental modification of the phenotype.

Specimens examined:

Between Mt. Lee and Carruther's Peak, Kosciusko area, B. G. Briggs, 5.3.1956 (SYD): near L. Albina, Kosciusko, C. Skottsborg and A. B. Costin, 11.3.1949 (NSW 27057); Australian Alps, F. v. Mueller (NSW 27056).

(12) RANUNCULUS DISSECTIFOLIUS F. v. Muell. ex Benth. *Fl. Aust.*, 1:11.1863. (Text-figs. 68-72.)

Perennial herb with fibrous roots. *Flowering stems* simple, 6-(16)-25 cm. tall, hirsute with appressed or spreading hairs. *Leaves* mostly basal; hirsute; petioles and lower surfaces of laminae densely covered with long patent hairs, upper surfaces glabrous or sparsely hirsute: basal leaves with petioles 2-(8)-12 cm. long, basally flattened, membranous toward the margin at the base and often tinged with purple; laminae ovate to orbicular in outline, 10-(20)-45 mm. long and about as broad, ternate with terminal petiolules 5-(10)-22 mm. long and lateral ones 1-(5)-10 mm. long, segments ternate or once or twice ternately-lobed and sometimes dentate, lobes and teeth linear to linear-lanceolate and acute: cauline leaves occasionally present, shortly petiolate, ternate or ternately-lobed. *Flowers* solitary, 15-(24)-32 mm. diam. *Sepals* 5, green, spreading, concave, elliptic to obovate-cuneate, 5-9 mm. long, 2.5-4.5 mm. broad, hooded at apex, 3-rarely 5 primary veins forking from near base, abaxial surface densely hirsute with long spreading hairs, membranous and usually glabrous toward the margin. *Petals* 6-(10)-14, golden-yellow, narrow to broad obovate-cuneate, 7-(12)-16 mm. long, 3-7 mm. broad, truncate or emarginate, starch-free zone $\frac{3}{8}$ - $\frac{1}{2}$ of petal length, 3 primary veins forking at nectary; nectary 0.7-1.5 mm. above base of petal terminating a thickened ridge, gland in a small pocket with a triangular or oblong lobe 0.1-1 mm. long. *Stamens* 35-50. *Carpels* 40-(70)-100; flat, obovate; style straight with a recurved tip. *Achenes* in a globular head 8-10 mm. diam.; semicircular, lenticular, 2.0-2.5 mm. long, 1.3-1.8 mm. dorsiventrally, 1.0-1.2 mm. laterally, lateral faces smooth, marginal ridges obscure, tapering gradually into a stout straight or incurved beak 1.0-1.8 mm. long. *Fruiting receptacle* 4-7 mm. long; staminal zone glabrous; achene zone elliptic or conical and hirsute with long hairs.

Chromosome number: $2n = 16$. Voucher specimen: Bett's Creek, Mt. Kosciusko area, B. G. Briggs, 10.1.1959 (SYD).

Range: Mt. Kosciusko plateau, N.S.W.

Ecological distribution: *Sphagnum* bogs and wet grassland in alpine and sub-alpine areas, 5,700-6,600 ft. altitude.

Holotype: In wet alpine meadows of the Munyang Mountains, Vic., F. v. Mueller (K, photo. CANB, SYD, isotypes MEL! NSW!).

The locality of the holotype is recorded as Munyang Mountains, Vic. Munyang Mountains is an old name for the Mt. Kosciusko area, N.S.W. It appears that this record of the species in Victoria is an error and that it is limited to the Mt. Kosciusko area, N.S.W.

The holotype and the numerous isotypes at Melbourne show the characteristic form of the species. The isotypes at Sydney include a rootstock and several detached leaves representing the normal condition, and also a small plant with very narrow leaf segments which appears to be a hybrid *R. dissectifolius* F. v. Muell. ex Benth. \times *R. millanii* F. v. Muell.

Specimens examined:

Mount Kosciusko, Jan. 1855 (MEL); Kosciusko, 5,800 ft., N. C. Beadle, 5.2.1952 (SYD); Piper's Gap, Mt. Kosciusko, J. Garden, 9.1.1956 (NSW 44715); Piper's Gap, Kosciusko area, B. G. Briggs, 2.2.1958 (SYD); The Perisher, Mt. Kosciusko, A. B. Costin, 21.1.1951 (NSW 18423); Bett's Creek, S. of main Kosciusko Road, J. Garden, 10.1.1956 (NSW 44716); Bett's Creek, Kosciusko area, B. G. Briggs, 9.1.1959 (SYD); Bett's Camp, Kosciusko area, B. G. Briggs, 4.3.1956 (SYD); Spencer's Creek, Kosciusko area, B. G. Briggs, 3.2.1958 (SYD); Trappyard Creek, Kosciusko area, B. G. Briggs, 3.2.1958 (SYD); Charlotte Pass, Mt. Kosciusko, A. T. Hotchkiss, 4.1.1954 (NSW 44714, SYD); near Trappyard Creek, ca. 8 km. ENE of Mt. Kosciusko, H. J. Eichler, 25.1.1957, no. 13488 (AD 95735047); Upper Snowy River, Mt. Kosciusko, M. Mueller, 30.12.1953, no. 1731 (NSW 44712).

(13) *RANUNCULUS CLIVICOLA*, sp. nov. (Text-figs. 73-77.)

Herbae perennes pilis brevibus plerumque patentibus obtectae. Caules floriferi foliati et plerumque ramosi et 2-4 flores ferentes. Folia radicalia 3-5 segmentis vel terno-vel biterno-lobatis pinnatisecta. Sepala patentia. Petala aureo-flava, obovato-cuneata. Lobi nectariorum oblongi. Achenia sublenticularia glabraque rostris longis et saltem prope apicibus recurvatis praedita.

Perennial herb with fibrous roots. Flowering stems 12-(20)-50 cm. tall, branched with 2-4 flowers or rarely simple, sparsely covered with short hairs patent below but appressed above. Leaves mostly basal, sparsely or densely covered with short patent hairs; basal leaves with petioles 2.5-(12)-25 cm. long, basally flattened, membranous toward the margin at the base; laminae orbicular to deltoid in outline, 1-(2.5)-6.5 cm. long, and about as broad, pinnately divided into 3-5 segments with the terminal petiolule 1-(10)-30 mm. long and lateral petiolules 1-8 mm. long, segments ternately or biternately-lobed and often dentate; lower cauline leaves similar to basal leaves; upper leaves often sessile, usually ternately lobed and dentate, approaching the uppermost entire and linear or lanceolate bracts. Flowers 18-(24)-35 mm. diam. Sepals 5, green, spreading, concave, elliptic or ovate, 4-7 mm. long, 2-4 mm. broad, apex hooded, often with a subterminal thickened beak, 3 principal veins forking above, abaxial surface sparsely hirsute with spreading hairs or rarely glabrous, margins hyaline and glabrous. Petals 5-8, golden-yellow, obovate-cuneate, 8-14 mm. long, 5-9 mm. broad, obtuse or truncate, starch-free zone $\frac{1}{4}$ - $\frac{1}{3}$ of petal length, three principal veins branching at nectary; nectary 0.7-1.5 mm. above base of petal; nectary lobe oblong, 0.5-1.2 mm. long, 0.3-0.6 mm. broad, attached at base only or attached laterally to petal for part or all of its length. Stamens 30-45. Carpels; 40-70; glabrous, flat, ovate; style arching, 1-1.5 mm. long. Achenes in a globular head 7-10 mm. diam.; compressed, ovate to ovate-cuneate, 3-4.5 mm. long, 2.5-3 mm. dorsiventrally, 0.5-1.2 mm. laterally, marginal ridges prominent, lateral faces smooth or with a broad ridge over position of seed; beak 1.8-(2.5)-3 mm. long, straight or arching with a recurved tip. Fruiting receptacle 3-6 mm. long, 1.5-2 mm. diam.; staminal zone glabrous or sparsely hirsute, achene zone hirsute and globular or ovoid.

Chromosome number: $2n=16$. Voucher specimen: Spencer's Creek, downstream from road bridge, Mt. Kosciusko area, B. G. Briggs, 9.1.1959 (SYD).

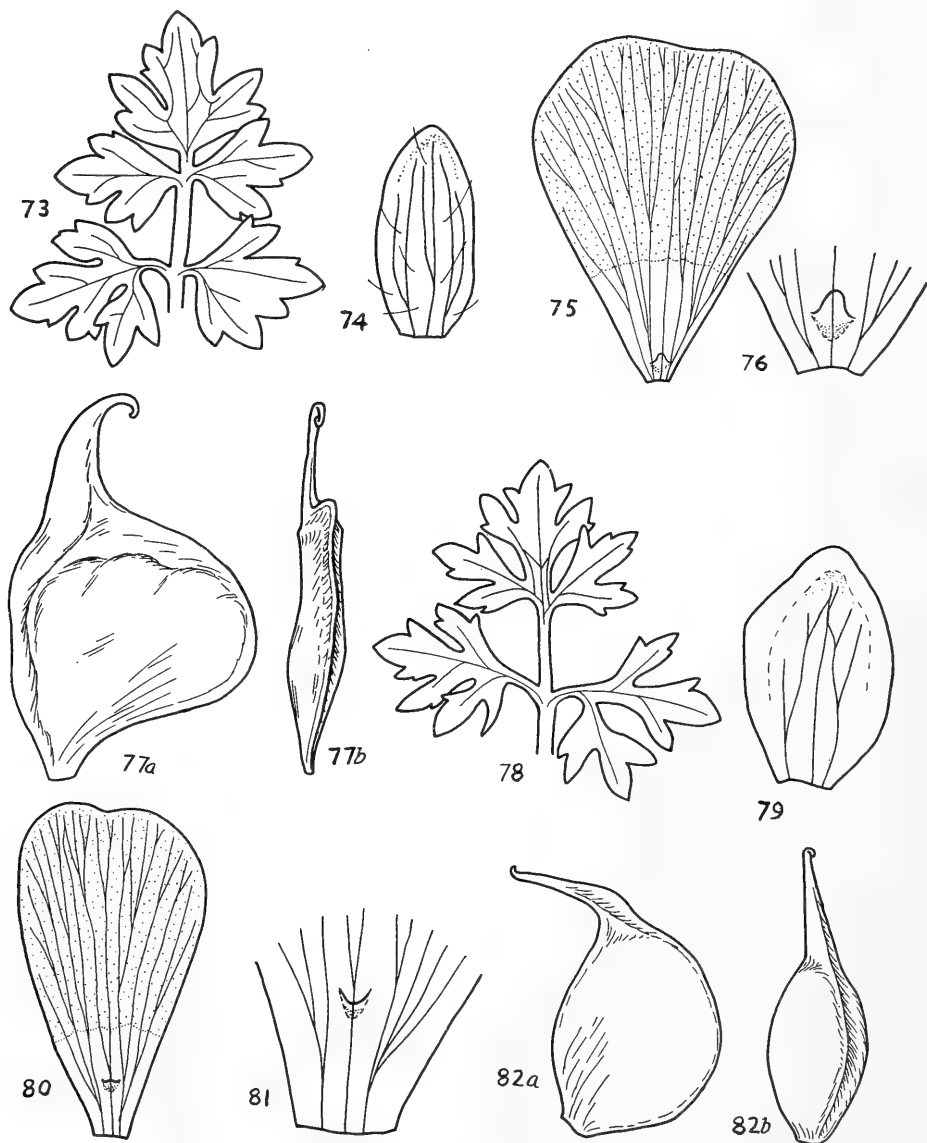
Range: Mt. Kosciusko plateau, N.S.W.

Ecological distribution: Wet situations below semi-permanent snow-patches in the sub-alpine tract, 5,500-6,200 ft. altitude.

Holotype: Spencer's Creek, downstream from road bridge, Mt. Kosciusko area, B. G. Briggs, 3.2.1958 (NSW). Isotypes: AD, B, BM, G, K, MEL, NY, P, SYD.

Specimens examined:

Mt. Kosciusko, 5,500 ft. to summit, J. H. Maiden, 1.1898 (NSW 4478); Guthega R., nr. junction with Snowy R. Mt. Kosciusko area, B. G. Briggs, 1.1956 (SYD); The Paralyser, Mt. Kosciusko, J. Garden, 10.1.1956 (NSW 44719); Spencer's Creek, Mt. Kosciusko, H. J. Eichler, 4.2.1957, no. 13621 (AD 95746003), no. 13625 (AD 95746010); Thredbo River Gorge, Mt.



Text-figs. 73-77.—*R. clivicola* B. G. Briggs. 73, Leaf; 74, Sepal $\times 4$; 75, Petal; 76, Nectary; 77a, b, Achene, lateral and dorsal views. 73-76 from isotypes, 77 from Merritt's Spur, Kosciusko area, N.S.W.

Text-figs. 78-82.—*R. niphophilus* B. G. Briggs. 78, Leaf; 79, Sepal $\times 4$; 80, Petal; 81, Nectary; 82a, b, Achene, lateral and dorsal views. From isotypes.

Kosciusko, L. A. S. Johnson and E. F. Constable, 19.1.1951 (NSW 15773); Saddle from Betts Creek to Thredbo R. Valley, B. Briggs, 6.2.1957 (AD 95748022, SYD); Merritt's Spur, Mt. Kosciusko, B. Briggs, III.1956 (NSW 44707, SYD); Thredbo Gorge near North Ramshead,

Mt. Kosciusko area, B. G. Briggs, 4.2.1956 (SYD); Ski Lift, Thredbo Village, nr. Mt. Kosciusko, B. G. Briggs, 7.1.1959 (SYD).

(14) *RANUNCULUS NIPHOPHILUS*, sp. nov. (Text-figs. 78-82.)

Herbae perennes glabrae vel pilis sparsis longis et patentibus obtectae. Caules floriferi simplices. Folia plerumque radicalia ternata vel biternata. Sepala patentia. Petala aureo-flava, obovato-cuneata. Nectaria sine lobis in fovea posita. Achenia lenticularia glabraque rostris tenuibus incurvis vel recurvatis praedita.

Perennial herb with fibrous roots. *Flowering stems* simple, 1.5-(8)-15 cm. long, glabrous or sparsely hirsute. *Leaves* mostly basal, glabrous or sparsely covered with long spreading hairs; petioles 0.8-(6)-16 cm. long, basally flattened, membranous toward the margin at the base, laminae orbicular or deltoid in outline, 6-(20)-45 mm. long and about as broad, ternate or biternate with the terminal petiolule 3-(8)-16 mm. long and the lateral ones 1-8 mm. long, segments acute and usually lobed and dentate: cauline leaves occasionally present; shortly petiolate and similar in form to the basal leaves or sessile entire and lanceolate. *Flowers* 12-(25)-30 mm. diam. *Sepals* 5 to rarely 7, green, spreading, concave, elliptic to ovate, 5-8 mm. long, 2-4 mm. broad, obtuse with 3 primary veins forking above, abaxial surface glabrous or sparsely covered with long spreading hairs. *Petals* 5 to rarely 7, golden-yellow, obovate-cuneate, 7-14 mm. long, 4.5-9 mm. broad, truncate or emarginate, starch-free zone $\frac{1}{3}$ of petal length, 3 primary veins forking from the base; nectary 1-2 mm. above base of petal, the gland in a small pit with no distinct lobe. *Stamens* 30-55. *Carpels* 30-(45)-80; flat ovate; style stout and straight. *Achenes* in a globular or conical head 8-12 mm. diam.: lenticular, ovate to elliptic, 2.4-2.8 mm. long, 1.2-1.7 mm. dorsiventrally, 0.8-1.2 mm. laterally, margins narrowly ridged, lateral faces smooth or slightly dimpled; style slender, 1-1.7 mm. long, straight or incurved or arching. *Fruiting receptacle* 3-5 mm. long, 1-3 mm. diam., hirsute with sparse short hairs; achene zone elliptic.

Chromosome number: $2n=16$. Voucher specimen: Club Lake, Mt. Kosciusko area, B. G. Briggs, 20.1.1959 (SYD).

Range: Mt. Kosciusko Plateau, N.S.W.

Ecological distribution: Wet situations below semi-permanent snow patches mainly in the alpine tract, above 5,500 ft. altitude.

Holotype: Club Lake, Mt. Kosciusko area, B. G. Briggs, 17.1.1956 (NSW). *Isotypes*: AD, B, BM, G, K, MEL, NY, P, SYD.

Specimens examined:

Blue Lake, ca. 6.5 km. north of Mt. Kosciusko, Hj. Eichler, 5.2.1957, no. 13667 (AD 95748021); Blue Lake, Kosciusko area, B. G. Briggs, 20.1.1955 (SYD); Club Lake, Mt. Kosciusko, L. A. S. Johnson and E. F. Constable, 20.1.1951 (NSW 15759); Lake Albina, Mt. Kosciusko, C. Skottsberg and A. B. Costin, 11.3.1949 (NSW 44838); Mt. Kosciusko area, Lake Albina, Hj. Eichler, 1.2.1957, no. 13581 (AD 95745018), no. 13586 (AD 95745013); Mt. Kosciusko area, top of Wilkinson's Valley, Hj. Eichler, 29.1.1957, no. 13565 (AD 95748047); Mt. Kosciusko area, Mt. Townsend, saddle north-east of summit, Hj. Eichler, 29.1.1957, no. 13563 (AD 95748048); North east of Summit, Mt. Kosciusko, N. C. Ford, 17.1.1954 (NSW 44837); Kosciusko, Dr. F. Mueller, Jan. '55 (MEL); Mt. Kosciusko, 6,000 ft., E. Gauba, 7.1.1950 (AD); Mt. Kosciusko, R. Helms, 2.1892 (NSW 44839); Kosciusko, J. McL. and A.H.K.P., 1.1924 (SYD), 1.1925 (SYD), Herb. Rodway, no. 12700 (NSW 44840); Mt. Kosciusko, J. H. Maiden and W. Forsyth, 1.1899 (NSW 44836), pro parte (NSW 44841); Kosciusko, N. C. Beadle, 5.2.1952 (NSW 44835, SYD); nr. Mt. Stillwell, Kosciusko area, B. G. Briggs, 15.1.1956 (SYD); Mt. Kosciusko area: tributary of Snowy River running from Etheridge Range near Rawson Pass to Lake Cootapatamba, Hj. Eichler, 26.1.1957, no. 13528 (AD 95745027); above Lake Cootapatamba, Mt. Kosciusko, J. Garden, 7.1.1956 (NSW 44842); Near top of Merritt's Spur, Kosciusko area, B. G. Briggs, 15.1.1956 (SYD); Thredbo Gorge, S. of North Ramshead, Kosciusko area, B. G. Briggs, 15.1.1956 (SYD).

(15) *RANUNCULUS PRODUCTUS*, sp. nov. (Text-figs. 83-86.)

Herbae perennes pilis brevibus appressisque instructae. Caules floriferi plerumque simplices post florendum producti. Folia plerumque radicalia, pinnatisecta segmentis ovatis trilobatisque. Sepala patentia. Petala pallido-flava elliptica 1.5-2.5 mm. longa.

Lobi nectariorum semi-orbiculati. Achenia lenticularia glabraque rostris brevibus tenuibus recurvatis praedita.

Perennial herb with fibrous roots. *Flowering stems* usually simple, rarely branching near the base, 1-(3)-rarely 20 cm. long at flowering, elongating to 7-(20)-45 cm. at fruiting; at first very densely covered with short antrorse-appressed hairs, after elongation the hairs dense immediately under the flower but scattered below. *Leaves* mostly basal, densely covered with short antrorse-appressed hairs: basal leaves with petioles 5-8.5 cm. long, membranous towards the margin at the base; laminae ovate in outline 7-(14)-35 mm. long, 7-(12)-20 mm. broad, pinnately divided into 3-7 ovate segments, lateral petiolules 1-(4)-13 mm. long, segments ternately lobed, with the terminal lobe entire or tridentate and the lateral lobes often bifid: cauline leaves occasionally present, shortly petiolate, laminae similar to those of basal leaves or tridentate or entire and linear-lanceolate. *Flowers* 3-4 mm. diam. *Sepals* 5, green, spreading or rarely slightly reflexed, concave, ovate or elliptic, 2-2.5 mm. long, 1-2 mm. broad, hooded at apex with a subterminal thickened beak, 1-3 principal veins forking above, abaxial surface covered with short spreading hairs, margins membranous and glabrous. *Petals* 5, pale yellow, elliptic to broad-lanceolate, 1.5-2.5 mm. long, 0.8-1 mm. broad, no starch present, 3 principal veins simple or branching above the nectary; nectary 0.2-0.5 mm. above base of petal; nectary-lobe semi-orbicular, almost as broad as the petal, obtuse or truncate, attached to petal at base only. *Stamens* 15-20. *Carpels* 25-45; flat, ovate, with short recurved styles. *Achenes* in a globular head 4-6 mm. diam.; lenticular, elliptic to semi-orbicular, 1.5-2.2 mm. long, 1.0-1.6 mm. dorsiventrally, 0.5-0.7 mm. laterally, shouldered below the beak, margin narrowly ridged, lateral faces smooth; beak slender, strongly recurved, 0.3-0.8 mm. long. *Fruiting receptacle* 1.5-3.5 mm. long, 0.6-1.2 mm. diam.; staminal zone glabrous or nearly so, achene zone hirsute and elliptic or globular.

Chromosome number: $2n = 16$. Voucher specimen: Isotype (SYD).

Range: Mt. Kosciusko plateau, N.S.W.

Ecological distribution: Wet grassland situations on sloping ground, 4,600-5,600 ft. altitude.

Holotype: Daner's Gap, Mt. Kosciusko area, B. G. Briggs, 5.1.1959 (NSW). *Isotypes:* AD, B, BM, G, K, MEL, NY, P, SYD.

Specimens examined:

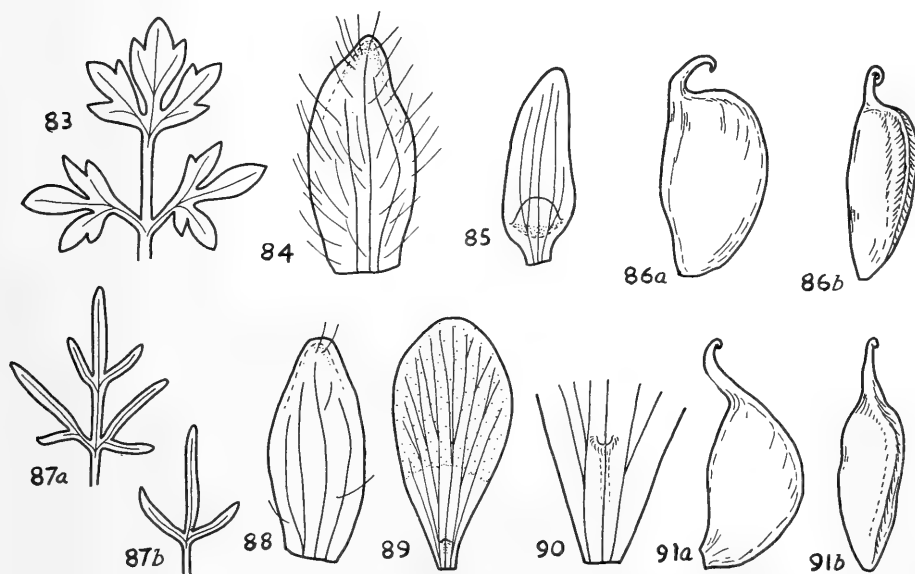
Diggers Creek, Mt. Kosciusko, L. A. S. Johnson and E. F. Constable, 23.1.1951 (NSW 44638); Diggers Creek, Mt. Kosciusko, B. G. Briggs, 3.3.1956 (SYD); Hotel Kosciusko, B. Briggs, III.1956 (NSW 44636, SYD), 5.1.1959 (SYD); Wragges Creek, Kosciusko area, B. G. Briggs, 2.3.1956 (SYD); Prussian Creek, Mt. Kosciusko, B. Briggs, III.1956 (NSW 44635, SYD); Piper's Creek, Kosciusko area, B. G. Briggs, 2.3.1956 (SYD); Smiggins Holes, Mt. Kosciusko, A. T. Hotchkiss, 1.1.1954 (NSW 44637, SYD); Perisher Gap, Kosciusko area, 3.3.1956 (SYD); Friday Flat, upper Thredbo R., near Mt. Kosciusko, B. G. Briggs, 7.1.1959 (SYD).

(16) RANUNCULUS MILLANII F. v. Muell. in Hook. *Kew Journ.*, 7:358.1855. F. v. Muell., *The Plants indigenous to the Colony of Victoria*, 1:6.1860. (Text-figs. 4, 87-91.)

Perennial herb with fibrous roots, spreading by stolons. *Stolons* 1-3 cm. long, sometimes becoming erect and terminating in a cluster of leaves and flowering stems. *Flowering stems* simple, 5-(15)-80 mm. long, sparsely covered with long spreading hairs. *Leaves* usually all basal, glabrous or sparsely covered with long spreading hairs: basal leaves with petioles 5-(12)-80 mm. long, basally flattened, membranous toward the margin at the base; laminae 4-(12)-20 mm. long and about as broad, pinnately divided into 3-5 linear segments 0.5-2 mm. broad, lateral segments often bi- or tri-fid; cauline leaves occasionally present, sessile and linear. *Flowers* 6-(12)-17 mm. diam. *Sepals* 5 to rarely 6, green, spreading, concave, elliptic or oblong, 2-4.5 mm. long, and about half as broad, sometimes hooded at apex, 2-3 primary veins usually forking from the base, abaxial surface glabrous or sparsely hirsute, hyaline toward the margin.

Petals 5, rarely to 12, white, not glossy, obovate or obovate-cuneate, 3.5–(6)–8 mm. long, 2–4 mm. broad, obtuse or emarginate, starch-free zone $\frac{1}{3}$ – $\frac{1}{2}$ of petal length, three primary veins forking from the base; nectary 0.8–2 mm. from base of petal, in a small pocket terminating a projecting ridge, the gland in a small pit with no distinct lobe or rarely with a small triangular lobe to 0.2 mm. long, sometimes with rudimentary or well-developed nectaries above several veins. *Stamens* 8–(22)–35. *Carpels* 9–(12)–25; flat, ovate; style stout and straight with a recurved tip. *Achenes* in a globular head 4–6 mm. diam., lenticular, elliptic to ovate, 2–2.4 mm. long, 1.2–1.8 mm. dorsiventrally, 0.5–0.8 mm. laterally, slightly rugose near base of style, lateral faces smooth, margins narrowly ridged; style 0.5–1 mm. long, erect or incurved and often with a recoiled tip. *Fruiting receptacle* 1–1.5 mm. long; staminal zone glabrous; achene zone elliptic and hirsute.

Chromosome number: $2n=16$. Voucher specimen: Bett's Creek, Mt. Kosciusko area, B. G. Briggs, 9.1.1959 (SYD). Also Smith-White, unpublished.



Text-figs. 83–86.—*R. productus* B. G. Briggs. 83, Leaf; 84, Sepal $\times 8$; 85, Petal $\times 8$; 86a, b, Achene, lateral and dorsal views. From isotypes.

Text-figs. 87–91.—*R. millanii*. F. v. Muell. 87, Leaves $\times 1.3$; 88, Sepal; 89, Petal; 90, Nectary; 91a, b, Achene, lateral and dorsal views. From Merritt's Creek, Kosciusko area, N.S.W.

Range: High mountain areas of southern New South Wales and eastern Victoria, from Mt. Gingera south to Mt. Wellington.

Ecological distribution: Swamp and fen situations, particularly depressions subject to flooding, above 4,500 ft. altitude.

Syntypes: Summit of Mt. Wellington, Gippsland, F. v. Mueller (MEL!). The collection is mounted on two herbarium sheets.

Specimens examined:

NEW SOUTH WALES: Mt. Gingera, C. W. E. Moore, 19.2.1954, no. 2876 (NSW 44701); 5 ml. S. of Rules Point, B. G. Briggs, 20.2.1957 (SYD); Kiandra district, W. Forsyth, 12.01 (NSW 44687); Happy Jack's Plain, ca. 15 ml. S. of Kiandra, J. Thompson, 18.1.1958 (NSW 44702); Plains of Heaven track, Mt. Kosciusko area, J. Garden, 9.1.1956 (NSW 44689, 44691); Mt. Kosciusko, Pretty Point, R. Helms, 2.93 (NSW 44686); below Club Lake, Mt. Kosciusko, L. A. S. Johnson, 20.1.1951 (NSW 15877); Bett's Creek, S. of main Kosciusko Rd., J. Garden, 10.1.1956 (NSW 44688); along Snowy River, Charlottes Pass, Mt. Kosciusko, A. T. Hotchkiss, January 4, 1954, no. 238 (SYD); Upper Snowy R. area, M. Mueller, 30.12.1953, no. 1721 (NSW 44698); Merritt's Creek, Kosciusko area, B. G. Briggs, 4.1.1959 (SYD); below Lake

Cootapatamba, Mt. Kosciusko, J. Garden, 7.1.1956 (NSW 44690); Mt. Kosciusko, Tree Line to 7,000 ft., J. H. Maiden and W. Forsyth, January 1899 (NSW 44693); Mt. Kosciusko, 5,500-6,500 ft., Baron von Mueller (NSW 44704); Mt. Kosciusko, F. v. Mueller, 1875 (MEL); Mt. Kosciusko, 7,300 ft., D. Sullivan (?), Jan. 1884 (MEL); Mt. Kosciusko, M. and F., Feb. '99 (NSW 44692); Mt. Kosciusko, Miss T. Harris, 12.1924 (NSW 44696); Kosciusko, N. C. W. Beadle, 5.2.1952 (SYD); Kosciusko district, per J. Collins, 1952 (NSW 44694); Mt. Kosciusko, A. T. Hotchkiss, 4.1.1954 (NSW 44697, SYD); Mt. Kosciusko, A. C. Taylor, 16.3.1954 (NSW 44695); Munyang Mountains, 6-7,000 ft., F. v. Mueller, Jan. 1874 (MEL); Summit of the Australian Alps, F. v. Mueller ex Herb. Sonder (MEL);

VICTORIA: Mt. Buffalo Plateau, H. C. E. Stewart, 6.1.1950 (MEL); Valley E. of the Horn, Mt. Buffalo, R. Melville, 27.12.1952, no. 2584 (NSW 44700); Bogong Ranges, Dr. F. v. Mueller, Dec. 54 (MEL); Bentley's Plain, Mt. Nugong, R. Melville, 26.1.1953, no. 3123 (MEL, NSW 44699); Highest summits of Alps, D. Sullivan, Jan. 1884 (MEL).

PUTATIVE NATURAL HYBRIDS.

Morphological intermediates are found suggesting hybridization between many of these species. Studies on hybridization within the group will be reported separately. Due to these intermediates the true limits of some species are difficult to define. Collections apparently contaminated by hybridization have, as far as possible, been excluded when determining the variation limits of the species.

The probable hybrid origin of *R. victoriensis* has already been mentioned. In all other cases the hybrids are limited to zones of contact between stands of the putative parental species and cannot be considered as independent populations. Therefore it does not appear appropriate to give them formal recognition by the application of names. For this reason *R. ligulatus* Melville has not been included in the taxonomic treatment as it is considered to be a hybrid, *R. graniticolus* Melville × *R. millanii* Benth.

Acknowledgements.

The Directors of the various State herbaria helped considerably by the prompt and protracted loan of specimens. Miss N. T. Burbidge, of C.S.I.R.O., Canberra, and taxonomists at various overseas herbaria provided photographs and assisted in tracing type specimens. Dr. R. Melville gave valuable help with problems concerning material at the Royal Botanic Gardens, Kew. Mr. L. A. S. Johnson, of the N.S.W. National Herbarium, assisted with the Latin diagnoses. My thanks are also due to Dr. Hj. Eichler, Director of the State Herbarium of South Australia, and to Mrs. M. Thompson of the N.S.W. National Herbarium who gave help on many aspects of the work. In particular I am indebted to Mr. R. C. Carolin and Dr. S. Smith-White of this Department for guidance at all stages of this study.

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EXPLANATION OF PLATE XV.

Sheet bearing lectotype of *R. muelleri* Benth. var. *muelleri*. 1. Lectotype of *R. muelleri* var. *muelleri*. 2. Specimens excluded from lectotype.

DIADOXUS ERYTHRURUS (WHITE) (COLEOPTERA-BUPRESTIDAE), ATTACK
OF FIRE-DAMAGED *CALLITRIS* SPP.

By P. HADLINGTON* and M. J. GARDNER.†

(Plate xvi.)

[Read 30th September, 1959.]

Synopsis.

The Buprestid *Diadoxus erythrus* (White), the cypress pine jewel beetle, whose larvae feed in the conductive tissues of trunks and branches of *Callitris* spp. and *Cupressus* spp., is recorded as a pest of these species under certain environmental conditions.

Attack by foliage-destroying insects and fire are factors considered to predispose the *Callitris* spp. and *Cupressus* spp. to infestation by *D. erythrus*, particularly when these predisposing factors are followed by periods of low rainfall.

The biology of *D. erythrus* and its larval parasites, and the factors contributing to the greater susceptibility of *Cupressus* spp. to attack by *D. erythrus* are considered.

INTRODUCTION.

Attack on *Callitris* spp. by *D. erythrus* (White), the cypress pine jewel beetle, was first recorded by von Lendenfeld (1885) when he noted its occurrence in western New South Wales. Since then the bionomics of this insect have been considered by French (1911), Froggatt (1923 and 1927), Pescott (1932), Hadlington (1951), Zeck (1955) and Brimblecombe (1956).

Diadoxus scalaris (L. & G.), a larger species, also occurs in association with *D. erythrus*. Its coloration and feeding habits are similar to those of *D. erythrus*, but during investigations on fire damaged cypress pine *D. scalaris* was encountered only rarely, most of the attack being due to the smaller species.

After fires have occurred in the cypress pine areas of New South Wales, timber arriving in Sydney from the burnt forests some months later has consistently shown damage by the jewel beetle. Such timber is considered suitable for normal constructional purposes and there is no danger of the insect infesting other timber, but the emergence holes are large and detract from its commercial value. There is thus a tendency to discard affected timber, or utilize it where appearance is of little concern.

Severe forest fires occurred in the Pilliga National Forest (near Baradine) in November, 1951, and in Euglo and Manna State Forests (near Forbes) in December, 1957. The fire-damaged trees were subsequently attacked by *D. erythrus* and the observations on these infestations form the basis of this paper.

DISTRIBUTION AND HOSTS.

Froggatt (1923) stated that *D. erythrus* probably occurs wherever cypress pine grows naturally. The distribution of *D. erythrus* has apparently been extended on the coast and highlands of New South Wales because of the introduction of *Cupressus* spp. to those areas.

The main hosts are *Callitris hugelii* (Carr.) and *C. endlicheri* (Parl.), and French (1911) and Pescott (1932) have recorded *Cupressus macrocarpa* var. *lambertiana* Gordon, growing near Melbourne, Victoria, as a host. French (1911) collected *D. erythrus* in an area where no *Callitris* spp. or *Cupressus* spp. occurred and concluded that *Acacia aneura* F. v. M. was a host plant. The fact that the beetles may have emerged from cypress pine brought into the area appears to have been overlooked.

BIOLOGY.

D. erythrus has been described and figured by Saunders (1868). French (1911) records that the female beetle oviposits in crevices in the bark, but more usually attack is initiated in fire scars or other injury.

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The larvae are typical of the Buprestidae, having the thoracic segments dorso-ventrally flattened and much wider than the abdominal segments. The young larvae commence to feed in the phloem and wood-cambium, and later damage the inner bark. They etch the outer surface of the sapwood while feeding and compact their faeces and chewed wood in the channels behind them. When larvae are present in large numbers, or should attack continue during successive years, the phloem and cambium around the circumference of the tree may be destroyed. When fully fed, the larvae which have been feeding in the bark bore into the sapwood to pupate. The entrance to the tunnel is closed with loosely compacted wood and faeces. The beetles emerge from the bark through oval holes measuring approximately $\frac{1}{4}$ inch across the long axis.

The time taken to complete the life cycle is variable, and is dependent on the time of the year when oviposition occurred. In summer, the period may be as short as three months, while in the case of those insects which over-winter as larvae or pupae the period may be extended to ten months or more under unfavourable conditions. From observations made in the Baradine district on the over-wintering generation, adults emerged during September and October. At least two generations are sometimes possible in one year. The beetles are present from September to April, and larvae may be found beneath the bark of attacked trees at any time during the year. Larvae have been observed in all but the very early instars during June, July and August.

TABLE 1.

Denobolie State Forest. Area burnt 15/11/51.			Euglo State Forest. Area burnt 2/12/57.		
Date.	Rainfall.	Recovery.	Date.	Rainfall.	Recovery.
1951—			1957—		
November	95 points	Nil	December	138 points	Nil
December	73 "	Nil	1958—		
1952—			January	217 "	Nil
January	39 "	Nil	February	126 "	Nil
February	312 "	Nil	March	421 "	Nil
March	434 "	Evident	April	99 "	Evident
April	146 "	Evident			

HOST SUSCEPTIBILITY.

Pescott (1932) states that in Western Australia landholders had been advised not to plant *C. macrocarpa* var. *lambertiana* where *Callitris* spp. had previously grown.

D. erythrurus does not attack living trees of the native *Callitris* spp. unless they have been weakened or injured, and thus predisposed to attack.

The following factors may render a tree liable to infestation:

A. *Injury by Fire*: Forest fires occurred on the Pilliga National Forest in 1951 and on Euglo and Manna State Forests in 1957. *D. erythrurus* adults oviposited in the damaged bark of *C. hugelii*. Where the fire was most intense the cambium and phloem regions around the circumference of the tree were often completely destroyed, producing conditions which were unfavourable to the development of the larvae. In trees which were only slightly burnt and the damage to the phloem and cambium was localized the larvae were able to develop and encroach into the healthy tissue as the damage to the phloem and cambium was localized, while in trees which had been affected on one side only, larvae were able to develop on the edges of the damage. Negligible infestation occurred in the branches and upper portions of the bole since these parts of the tree were unaffected by fire damage. In this way, fire produces favourable conditions within the tree for the development of *D. erythrurus*.

B. *Mechanical Injury*: During normal logging operations, damage to the boles of trees occasionally occurs, rendering the tree susceptible to infestation.

C. *Rainfall*: When investigating the incidence of *D. erythrurus* in the Lachlan River area, von Lendenfeld (1885) indicated a correlation between low rainfall and the abundance of the beetle. He records that in 1883 *Callitris* spp. had taken possession of areas near the Lachlan River, superseding the broad-leaved tree species which had previously constituted the forest. He states that official rainfall data were not available for inland areas for that period, and relates Sydney rainfall to that of the interior, suggesting that the lower rainfall recorded at Sydney indicated an isochrone drought for that area. For the period 1840 to 1863 (Sydney rainfall 48 inches) von Lendenfeld indicates that *D. erythrurus* was not unusually abundant. From 1862-1880 (Sydney rainfall 55 inches) he states that *Callitris* spp. were spreading, and for the period 1880-1884 (Sydney rainfall 40 inches) he observed that *Callitris* spp. were being heavily attacked by *D. erythrurus*. He concluded that periods of low rainfall are favourable to *D. erythrurus*, while periods of high rainfall favour the growth of *Callitris* spp. and reduce the incidence of *D. erythrurus*.

Pescott (1932) suggests that a wet winter followed by a hot summer caused mortalities of *Callitris* spp. in the mallee areas of Victoria. The trees weakened by excessive water were later attacked by *D. erythrurus* which caused their death.

D. *Insects*: *Callitris hugelii* growing at Pennant Hills, a suburb of Sydney, has been attacked by buprestid larvae following defoliation by *Zenarge turneri* Rohwer, the cypress pine sawfly. Trees which had been affected previously by *Z. turneri* on Corrigle State Forest, near West Wyalong, were similarly attacked by bark feeding insects. Froggatt (1923) records *Z. turneri* as a pest of cypress pine.

Neochmosis juniperi de Geer,* the cypress pine aphid, at times has occurred in large numbers, and Froggatt (1927) stated that *Callitris* spp. were so severely infested that the foliage of large trees was wilting and turning yellow. Hartigan and Taylor (unpublished report—Forestry Commission of New South Wales, 1949), while investigating a disease of *Callitris* spp. in the Baradine and Grenfell areas, recorded that severe infestation by *N. juniperi* was followed by yellowing of the foliage, general die-back, defoliation and death of the trees. They indicate that *N. juniperi* was a precursor to a sooty mould which developed on the sugary secretion produced by the aphids. The years prior to their investigation had been wet, and they considered that the sooty mould was encouraged by moist weather and aphid infestation. They suggest that the mould growing in the necrotic tissue functioned as a wound parasite. They also found that where a tree had suddenly died after it had shown promise of recovery, *D. erythrurus* was present under the bark, and it appeared that death was due to the destruction of the phloem and cambium by the larvae of this insect.

MORTALITY FACTORS.

(a) *Parasites and Predators.*

The incidence of parasitism was studied in June, 1952, following the fires of 1951 on the Pilliga National Forest. These studies were confined to observations and rearing of larvae. Most of the parasites were obtained by removing sections of the bark and collecting the larvae and pupae of the parasites. The effect of these parasites was reflected in the small number of *D. erythrurus* larvae actively feeding at the time of the observations. The determinations of the parasites which are located in the collection of the Forestry Commission of New South Wales were made by the Commonwealth Institute of Entomology. These parasites are now discussed:

(1) *Doryctes diadoxi* Nixon (Braconidae): This was the most abundant species, and occurred singly during the early instars, but pupated in cocoons which each contained six to eight larvae. The cocoons were located in the channels of *D. erythrurus* larvae. *D. diadoxi*, which was described by Nixon (1954), appeared to be ectophagous. Thompson (1953) records species of this genus as parasites of the Buprestidae.

(2) *Polymoria* sp. (Eupelmidae): The larvae of this species occurred singly in the various instars. They were probably ectophagous, and may have been either parasitic

* Determined by M. Casimir, Department of Agriculture, N.S.W.

or hyperparasitic on *D. erythrurus*. The females possessed a jumping habit which appeared to be their principal method of locomotion. The pupae were collected singly. Thompson (1954) records a species of this genus to be parasitic on the Buprestidae.

(3) *Metapelma* sp. (Eupelmidae): This larger species occurred in association with *Polymoria* sp. Thompson (1954) records species of this genus to be parasitic on the Buprestidae.

(4) *Megalyra* sp. (Megalyridae) Species A: These larvae occurred singly in the channels of *D. erythrurus*. Rodd (1951) recorded *Megalyra* sp. to be parasitic on the larvae of Coleoptera.

(5) *Megalyra* sp. (Megalyridae) Species B: Collected from the channels of *D. erythrurus*.

(6) *Thaumasura* sp. (Cleonymidae): The larvae of this species occurred singly in the channels of *D. erythrurus*. Thompson (1954) has recorded parasitism of the Curculionidae by species of this genus.

(7) *Pristaulacus* sp. (Evaniidae): This species was collected on the surface of the bark of *C. hugelii*. Thompson (1954) has recorded a species of this genus to be parasitic on the Cerambycidae.

(8) *Cleridae*: Larvae of this family were found active in the channels.

(b) *Sandarac Resin*.

Following the fires at Baradine in 1951, observations were made on tree recovery which was evident during 1952 on Pilliga National Forest (Pickaxe and Denobolie sections). During 1958 at Forbes (Euglo South and Manna State Forests) a study was made of the association of *D. erythrurus* with cypress pine damaged by fire in 1957. In all areas many trees were killed by the effect of fire on the cambium and phloem tissues, after which they produced no green foliage. Other trees less affected produced new foliage and appeared to be alive. Some trees in the latter group showed a temporary recovery before dying, while others continued to produce foliage. For some months after the fire it was not possible to determine, by superficial examination, which trees would die, except those which had no functional bark around the circumference of the tree. The recovery of trees followed appreciable rainfall, as shown in Table 1. It was observed also that resin exuded from the bark of many of the trees after such rainfall.

When the bark was removed from trees which had shown temporary recovery and then death, extensive damage by *D. erythrurus* larvae was evident, and in all cases the girdling of the tree was complete. The trees which continued to produce foliage frequently showed evidence of *D. erythrurus* attack, but the larvae were flaccid and translucent, their digestive tract being devoid of food. Dead larvae showed no evidence of parasitism and were generally confined to the area adjacent to the healthy tissue. The compacted faeces in the channels close to the living tissues and at the margins of infestation had been invaded by sandarac resin,* which prevented further encroachment on living tissues by the larvae. This material was not produced in quantity during the early stages of attack and only after appreciable rain was the resin evident along the margins of the attack.

In the Pilliga National Forest the trees commenced to produce foliage during March and April. This recovery was accompanied by the production of resin which was evident as drops on the surface of the bark. Removal of the bark showed the resin to be present in the galleries, although more particularly it had accumulated along the margins of healthy tissues.

The effect of rainfall on the production of sandarac resin by fire-injured *Callitris* spp. was again observed on Euglo State Forest. The rainfall for the period December-

* Commercial sandarac resin is also obtained from the North African species *Tetraclinis articulata* (Vahl) Masters. Mantel *et al.* (1942) give the main constituents as sandaracolic acid and callitrolic acid. Howes (1949) states that there are only minor differences between Australian and North African sandarac. The essential oil of African sandarac contains a diterpene and a pinene, whereas Australian sandarac contains only a pinene.

February was 481 points, during which time there appeared to be little recovery. In March, 421 points were recorded, and this was followed by resin and foliage production. In May, 1958, the sandarac resin was observed to affect the larvae in a similar manner to that previously described.

Sandarac resin has been recorded by Baker and Smith (1910) to exude from the bark of *Callitris* spp. in response to injury.

Bamber (1959—personal communication), during a study of the bark of *C. hugelii*, found that the resin canals were formed within one to four cells of the cambium by proliferation of the parenchyma cells. He determined that the resin of the resin canals was liquid in the phloem and solid in the rhytidome. *D. erythrus* larvae rupture the cambium, preventing future production of resin canals in the area of damage. Normally the resin canals immediately adjacent to the damaged tissue produce a liquid resin which flows into the larval channels. This flow appears to be greater after substantial rain and is sufficient to exclude the larvae.

In considering the relative susceptibility of *Callitris hugelii*, *C. endlicheri* and *Cupressus macrocarpa* var. *lambertiana* to *D. erythrus* the alcohol solubles in the bark were estimated after exhaustive extraction with boiling water.* The percentage alcohol soluble content of *C. hugelii* was 8.89, *C. endlicheri* 9.58 and *C. macrocarpa* var. *lambertiana* 5.07. These figures therefore include all the alcohol soluble resin in the barks. In the case of the *Callitris* spp. this resin is sandarac resin, but *Cupressus* sp. do not contain sandarac resin.

DISCUSSION.

D. erythrus usually requires an injury for the initiation of attack, but unless this injury is accompanied by other conditions such as damage to the crown of the tree or periods of low rainfall the infestation does not necessarily progress. Forest fires frequently damage the crowns of trees as well as injuring the bark, thus producing conditions favourable to the development of *D. erythrus*. Trees affected in this way are not only susceptible to attack, but are likely to be completely girdled by the jewel beetle larvae particularly if periods of low rainfall occur.

When substantial rains (approximately three inches or more within a month) occur after a fire the tree produces sandarac resin freely and numerous tears are formed on the surface of the outer bark. No quantitative estimations of the alcohol soluble content of the bark prior to and after rain have been made. This information would establish correlation between the activity of the tree and the production of sandarac resin, but entails a prior knowledge of the occurrence of a major forest fire.

When freshly produced, this resin is clear and sticky, and the young larvae may avoid coming into contact with it. It appears that larvae are not able to encroach on the cells actively producing resin.

The introduced species *C. macrocarpa* var. *lambertiana* does not require to be injured before *D. erythrus* can initiate its attack. Brimblecombe (1956), in referring to the introduced *Cupressus* spp., states that attack four or more years after planting is a common occurrence. Unlike the *Callitris* spp., the introduced species does not appear able to resist the ingress of *D. erythrus* by the production of resin. The bark of *Cupressus* spp. is not known to contain sandarac resin, although a resin is exuded from the bark after injury. In addition, the alcohol-soluble content of the bark of *C. macrocarpa* var. *lambertiana* is significantly less than that of *C. hugelii* or *C. endlicheri*. Bamber,† when comparing the bark structure of *C. macrocarpa* var. *lambertiana* with that of *C. hugelii* and *C. endlicheri*, found that the resin canal formation was less frequent in *C. macrocarpa* var. *lambertiana*. The fibre layers which are a bark characteristic of the family Cupressaceae are much less abundant in *Cupressus*

* Bark samples of *C. hugelii* and *C. endlicheri* from six trees of each species from Warraderry State Forest near Forbes on 28th May, 1958. *C. macrocarpa* var. *lambertiana* samples were collected at Sydney during May, 1958. Analyses by F. R. Humphreys, Forestry Commission of N.S.W.

† Personal communication.

macrocarpa var. *lambertiana* than in *Callitris* spp. The walls of the fibres of *Callitris* spp. were also thicker. He also records that the tannin content of the living phloem cells is higher in the two *Callitris* spp. The significance of these various differences is not known, but they should not be overlooked when considering the relative susceptibilities of these species to *D. erythrurus*.

Parasites and predators were abundant immediately after the high rainfall was recorded, but later examinations showed that their numbers had fallen markedly, probably because the *D. erythrurus* larvae had been affected by the resin production. Prior to the channels being invaded by the resin, these biotic factors had reduced the numbers of *D. erythrurus* considerably, and in their absence the progress of attack would have been accelerated. Therefore, parasites and predators would have their greatest effect on the population of *D. erythrurus* during prolonged dry weather and before resin flowed into the channels.

It is doubtful if drought alone causes major changes in the stand composition of the cypress pine forests by predisposing *Callitris* spp. to the attack of the jewel beetle. The changes recorded by von Lendenfeld may have occurred, but the more gradual effect of settlement on stand composition in these areas has not been investigated. There has been a tendency to produce tree-stands composed largely of cypress pine at the expense of the eucalypt species which grow naturally in association with it. This trend is more likely to accentuate attack by insects.

Von Lendenfeld's observations suggest that the trees had been weakened, predisposing them to the attack of *D. erythrurus*. If his rainfall data from Sydney were parallel to that of the interior it is likely that the periods of high rainfall favoured an increase of *N. juniperi*. Attack by this aphid would not be followed by *D. erythrurus* infestation as long as the rainfall remained high and resin was produced abundantly. When the drier periods were experienced *D. erythrurus* possibly became established in the weakened trees, producing the high mortality observed by von Lendenfeld in 1885. The trees weakened by *N. juniperi* would be unlikely to produce resin in sufficient amounts to terminate the infestation of *D. erythrurus*.

Fire damaged trees which have been attacked and subsequently recovered, and have retained an area of functional bark and cambium sufficient for the tree to continue to re-foliage, present problems in the conversion of the log to sawn timber. That section of the bole which has had the conductive tissue destroyed does not produce new wood or bark, and as a result a malformed log results. The main value in leaving such trees is for seed production, as these are often needed after a forest fire, particularly if the tree mortality is high.

After forest fires, or attack by foliage feeding insects, reference to rainfall data should lead to a better understanding of the capacity of cypress pine to recover in particular areas and so assist in the marketing problems which follow.

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EXPLANATION OF PLATE XVI.

- 1.—A stand of fire damaged cypress pine.
- 2.—An accumulation of sandarac resin at a point of injury.
- 3.—Channels of *D. erythrurus*. Since the tree from which this bark was removed had been previously ringbarked no resin is to be noticed invading the material in the channels.
- 4.—A tree which has recovered from attack by *D. erythrurus*. An accumulation of resin may be seen along the front of attack.

WOODY GALL, A SUSPECTED VIRUS DISEASE OF ROUGH LEMON AND
OTHER CITRUS VARIETIES.

By LILIAN R. FRASER, New South Wales Department of Agriculture.
(Plate xvii.)

[Read 30th September, 1959.]

Synopsis.

A disease is described which causes the development of woody galls on the trunk and branches of some citrus species. The outgrowth arises as an outward growing cone of woody tissue originating at cambial level. In older limbs it ultimately becomes a large compound structure with numerous blunt bark-covered growing points. The variety most commonly affected is the rough lemon, but infected trees of Eureka lemon and sour orange have been found. The disease is transmissible by budding and is presumed to be a virus. The name woody gall virus is proposed.

During 1953 a survey of citrus trees for infestation by the gall wasp (*Eurytoma fellis* (Gir.)) was commenced by field officers and entomologists of the New South Wales Department of Agriculture. In the course of this survey a type of gall development was found which was not caused by wasp attack (Pl. xvii, fig. 1). This disease was extremely prevalent on seedling trees of the rough lemon variety in the coastal strip north of Sydney, from Dee Why to Avalon. This district is not near any commercial citrus growing centre, but oranges, lemons, mandarins and occasionally grapefruit are grown in home gardens and the rough lemon is popular with some householders because of its hardiness and all year round cropping habit.

VARIETIES AFFECTED.

During the past three years the same disease has been found in a number of localities in addition to that in which it was first observed. In most cases the affected trees are rough lemon seedlings, but three orchards have been found in which the rough lemon stocks of a number of budded trees are galled (Pl. xvii, fig. 2). In addition, two trees of sour orange and one of Eureka lemon have been found which show symptoms of the disease. There is, however, no evidence to suggest that the disease is spreading or likely to spread in the areas where citrus is grown commercially.

The occurrences so far known are listed in the appendix.

SYMPTOMS.

Outgrowths develop on all above ground parts of the rough lemon trees, except the current season's growth. Occasional galls have been seen on crown roots. They vary in size from simple rounded swellings on the younger wood (Pl. xvii, fig. 3) to large complex knobbed growths on the larger branches and main trunk (Pl. xvii, fig. 4). The gall tissue is woody, but not so dense and hard as normal citrus wood, and small pockets and thin arcs of gum are present in the tissue. The outgrowths are covered with unbroken bark. Anatomical examination of swellings indicates that most appear to be initiated at an early stage of growth. They originate at cambial level, with the formation of a section of radially oriented xylem elements. As secondary growth continues this gall initial takes the form of a cone which gradually increases in size and grows outwards. After one or two seasons' growth this structure has developed a broad diffuse growing point and it extends outward at a much greater rate than the normal stem tissue. As the gall enlarges secondary and tertiary growing points appear, and the large compound galls seen on trunks and main limbs are condensed, profusely and irregularly branched structures with a large number of growing points.

The intensity of gall development varies considerably. Some trees show very numerous galls, others only a few. The size of galls also varies from small to large and the shape varies from rather effuse to protuberant.

There is no apparent detrimental effect on size and vigour of orange or mandarin trees growing as scions on galled rough lemon stocks. Adjacent trees of the same planting, on ungalled stocks, are not larger or in better condition. It is difficult to judge the effect of galls on the vigour of seedling rough lemon trees, but very heavily galled trees appear to be slightly reduced in vigour as compared with unaffected trees.

No trace of any pathogenic organism has been found in the tissue of galls.

TRANSMISSION OF GALL DISEASE.

1. *By Bud Insertion.*—Two sources of inoculum were used: (a) a mature heavily galled rough lemon seedling tree from Dee Why and (b) a mature heavily galled rough lemon seedling tree from the McDonald River district. Ten seedlings each of rough lemon and sweet orange were inoculated by budding from each source on the 11th December, 1955. An equal number of unbudded seedlings of the same source was retained as controls. The seedlings were in the 5-leaf stage when budded. The inoculating buds were not permitted to grow.

No gall production occurred in the first season following inoculation. By July, 1957, eighteen months after inoculation, swellings were present on the main stem of all inoculated rough lemon seedlings (Pl. xvii, fig. 5), and occasionally on the larger roots. No similar growths were produced on the uninoculated rough lemon and sweet orange seedlings, or on the inoculated sweet orange seedlings. Further work is in progress to determine the reaction of a range of citrus species and varieties to infection.

2. *Failure of Seed Transmission.*—Seed was collected from the heavily galled tree which had served as the source of budwood (a), and 100 seedlings were grown. None of these has developed any swellings during a period of 3½ years.

DISCUSSION.

As a result of its successful transfer by budding it is presumed that woody gall disease is caused by a virus, and the name Woody Gall virus is proposed. The galls produced are structurally distinct from the sphaeroblasts which are not uncommon in the bark of many citrus species and varieties. These bodies are spheroidal and originate and for the most part remain outside the vascular cylinder. Several types of out-growth have been briefly described by Fawcett and Bitancourt (1943), but none of these resembles the woody gall condition closely enough to suggest identity. The most similar, referred to by them as knobby bark, occurs on sweet orange as well as lemon, and appears to be related to the sphaeroblast type of growth rather than to woody gall.

Field observations indicate that Valencia and Washington Navel oranges and Emperor mandarins are either resistant to infection or are symptomless carriers of the disease. The presence of woody gall disease in seedling rough lemon trees, and the high percentage of infection in several localized areas, suggest that there is an active vector. If this is so, it is somewhat difficult to explain why the disease is not more common and widespread than it appears to be at present.

The distribution of the disease in a number of localities remote from commercial citrus growing districts and in several cases remote from citrus of any kind suggests the possibility that it has been introduced into rough lemon from a non-citrus source.

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APPENDIX.

KNOWN OCCURRENCES OF WOODY GALL DISEASE IN NEW SOUTH WALES.

Rough lemon seedling trees of various ages, in home gardens in the Dee Why to Avalon area, near Sydney.

A small community of seedling lemon trees up to about twenty years old, naturalized in bushland on the McDonald River, near Wiseman's Ferry. Citrus has

been grown for many years along the Hawkesbury and McDonald Rivers in discontinuous areas of suitable soil. This community was several miles from any commercial orchard.

A single rough lemon seedling tree of indefinite age growing in natural bushland at Minnemurra, isolated by at least fifty miles from the nearest commercial citrus area.

A single mature rough lemon seedling tree at Gresford (Pl. xvii, fig. 3), in open farming country well isolated from commercial citrus.

Rough lemon stocks of forty-year old Valencia orange trees in a block of about ten acres at Cornwallis, Windsor district. Many of the trees carried one to several galls of long standing on the butts below the bud union and in a few cases also on the crown roots. Some of the galls had started to decay. No galls were present on the Valencia orange scions.

Rough lemon rootstocks of ten-year old Washington Navel orange trees in a block of about two acres at Castle Hill (Pl. xvii, fig. 2). Almost all the trees were affected with large multiple galls, but no outgrowths were present on the Washington Navel orange scions. No galls could be found on trees of Eureka lemon on rough lemon stock in an adjoining block.

A mature Eureka lemon on rough lemon at Kenthurst. This tree showed a single large gall of structure identical with those on rough lemon.

Slight to moderate gall development on rough lemon stocks of Emperor mandarins about fourteen years old at Monak, Murray River.

Slight to moderate gall development on single trees of seedling rough lemon in orchards at Grose Vale, Wright's Creek, Narara, Wyong, home gardens at Coogee and Gordon and in the Sydney Botanic Gardens.

Slight gall development on two six-year old seedling sour orange trees at the Citrus Experiment Station, Narara. These trees are growing adjacent to natural bushland.

EXPLANATION OF PLATE XVII.

- 1.—Branch of mature rough lemon tree, showing typical growth of woody galls. $\times \frac{1}{2}$
- 2.—Base of trunk of ten-year old tree of Washington navel orange on rough lemon rootstock, showing multiple galls on rootstock below bud union. $\times \frac{1}{2}$.
- 3.—Early development of galls on young branch of a rough lemon tree. $\times 1$.
- 4.—Large old galls on main branch of a mature rough lemon tree. $\times \frac{1}{2}$.
- 5.—Galls developing on rough lemon seedling tree, eighteen months after inoculation by budding. $\times 1$.

LIGHT AS A CONTROL IN THE GERMINATION AND DEVELOPMENT OF
SEVERAL MISTLETOE SPECIES.

By J. F. RIGBY.

[Read 30th September, 1959.]

Synopsis.

It is shown that daylight is necessary at some stage in the germination and early development of some mistletoes.

When, in the ripe fruit, the embryo is white, no germination can occur unless sunlight falls on the seed after the removal of the pericarp. If the embryo is green, germination can occur in the dark, but continued growth will stop unless the surface of the endosperm is coloured.

When the surface of the endosperm is coloured, growth will continue in the dark, but no clamp will form unless light is permitted to fall on the seedling.

The orientation of the seed has no effect on its ability to germinate.

Introduction.

Germination tests in light and darkness were carried out on the species listed below. *Amyema miquelii* was also tested in various orientations.

Germination is defined as an enlargement in size of the embryo recognizable to the naked eye.

Species Tested.

The species tested are listed below, with the colour of both embryo and the surface of the endosperm, and the locality where collected.

Amyema pendula: Embryo white; endosperm white; collected Blackburn (Vic.), 1956-1957.

Muellerina eucalyptifolia: Embryo green; endosperm white; collected Eildon (Vic.), December, 1957.

Amyema miquelii: Embryo green; endosperm white; collected Emmaville (N.S.W.), September, 1958.

Lysiana exocarpi: Embryo green; endosperm bright green with four longitudinal straw coloured ribs passing medially between the longitudinal furrows mentioned by Brittlebank (1908) who found that fruits at Myrning possessed five furrows; collected Swanwater (Vic.), April, 1958.

Amyema linophylla: Embryo green; endosperm red with longitudinal deep red ribs, these rapidly become purple on exposure to light. The inter-rib reddish colour appears as if it were derived from diluted pigment permeating outwards from the ribs. Blakely (1923, p. 146) described the seeds as white. Collected Swanwater (Vic.), April, 1958.

Techniques Adopted.

All seed was used within 24 hours of collection.

The pericarp was removed, then the seed was stuck to a vertically placed sheet of glass unless otherwise stated. The viscin formed an ideal adhesive. The viscin was reinforced by a colourless thread, normally contained within the viscin, that arises in the region of the hilum. It is more adhesive than the viscin. The thread appears to be the one by which seeds hang from twigs after being passed by birds.

All seeds were supplied with moisture and air, but no nutritive substances.

Samples in light were so placed as to receive as much direct sunlight as possible.

Germination in the Dark.

Amyema pendula.—Seed rotted away, with no evidence of life.

Muellerina eucalyptifolia.—The embryo expanded noticeably for the first two or three days, then became dormant. Neither endosperm nor embryo rotted as in *A. pendula*.

Lysiana exocarpi.—The embryo first showed signs of growth four hours after extrusion. Growth continued rapidly—a relative term with mistletoes—until the seedlings were between $\frac{3}{4}$ and 1 inch high after $2\frac{1}{2}$ months. The stem with the adhesive cushion at its end grew vertically upwards and appeared etiolated—pale green colour, slender and much elongated stem and adhesive cushion. The adhesive cushion was thimble shaped, approximately three times as long as that of a seedling grown in daylight.

In this case seeds were grown on the ends of corks to which the seeds adhered by a lacquer formed from dried viscin. After four or five weeks in some seedlings the lacquer cracked, which allowed the endosperm and seedling to roll over in such a manner that the direction of growth was inverted. The adhesive cushion made weak movements to change the direction of growth towards horizontal. A disc formed at the base of the cotyledons at about 2 months, where abscission occurred at $2\frac{1}{2}$ to 3 months. After abscission no further growth occurred. The seedlings lived up to 3 weeks in this state. All were dead $3\frac{1}{2}$ months after extrusion from the pericarp.

Amyema linophylla.—This species was seen to be following a similar pattern to *Lysiana exocarpi*, but at a slower rate, so after 15 days the test was stopped.

Germination in Daylight.

Amyema pendula.—Growth was very slow. From 4 to 6 weeks after extrusion from the pericarp leaves appeared. The leaves always remained very small, never exceeding 2 mm. throughout life. Little further development occurred after the appearance of the leaves. After 5 months all seedlings were dead.

Muellerina eucalyptifolia and *Amyema miquelii*.—In both species the embryo expanded in the same manner as plants grown in the dark, and continued to grow at a uniform rate for a fortnight, when tests were concluded.

Lysiana exocarpi.—Growth commenced four hours after extrusion and continued unabated, but at a slower rate than in the seedlings germinated in the dark. The hypocotyl at first grew vertically, but within a week it curved away from the light until the adhesive cushion touched a solid object, a cork. Contact became permanent with the cork a fortnight after extrusion. When the convex adhesive cushion touched the cork it developed a central dimple, which expanded to make the cushion concave within two days. The clamp then became fixed. All seedlings had died after two months.

Amyema linophylla.—A similar but slower growth rate to *Lysiana exocarpi* was shown. First evidence of growth occurred after one day when the embryo elongated and the dark red ribs became purple. In four days the purple pigment had covered most of the endosperm. The change of colour was the most dramatic effect of exposure to daylight.

In *Muellerina eucalyptifolia* and *Amyema pendula* light was shone on the seed through the support; the hypocotyl grew away from the source of light, not necessarily towards the support. This is in complete agreement with Blakely (1922a) and McLuckie (1923).

Growth in Alternating Daylight and Dark.

Muellerina eucalyptifolia.—Growth had entirely ceased after four days for seeds germinated in the dark. The seedlings were then put in the sun for one day. This proved a sufficient stimulus for growth to continue for up to two days in the dark, when growth ceased. Light exposure was repeated with the same result. The shortest exposure tried was four hours, which provided an adequate stimulus.

Lysiana exocarpi.—When seedlings germinated in the dark were placed in daylight, they behaved as seedlings grown in daylight.

Growth in Various Orientations.

This was tried only for *Amyema miquelii*, the only species for which large quantities of seed were available.

Twenty seeds per test: (a) Grown in the pendulous or normal position; 95% germination. (b) Grown horizontally; 90% germination. (c) Grown inverted; 100% germination.

Discussion.

With the mistletoe species tested, light appears to be the controlling factor for successful germination and adhesion of the plant to the host. The effect of light may be predicted from the presence or absence of colour in the embryo and/or on the surface of the endosperm.

If the embryo is white, daylight is necessary before any evidence of growth can occur. If the embryo is green, growth can commence, but will continue only if the surface of the endosperm is coloured other than white. If it is white, sunlight is necessary before growth will continue. When the surface of the endosperm is coloured, sunlight is necessary before the adhesive cushion will attach to the host, but growth to the stage preceding attachment will occur.

The orientation of the seedling has no effect on successful germination.

It is of interest to note that *Muellerina celastroidea*, for which the germination was described by McLuckie (1923), appears to conform to the hypothesis stated above. This species was not examined by the author.

McLuckie states that the embryo contains chlorophyll even when enclosed in the fruit, also that the endosperm is white. He found that germination would occur only in light, but made no statement on the fate of the seed grown in the dark.

Acknowledgements.

The author would like to thank both Mrs. S. G. M. Carr of the Botany Department, University of Melbourne, for many useful suggestions during the course of this study which was conducted as a hobby, and Mr. L. A. S. Johnson of the Botanic Gardens, Sydney, for assistance with the nomenclature.

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A REVISION OF *NITELLA CRISTATA* BRAUN (CHARACEAE) AND ITS ALLIES.
PART I. EXPERIMENTAL TAXONOMY.

By T. C. CHAMBERS, University of Sydney, and MARY B. WILLIAMS.*

(Plate xviii; three Text-figures.)

[Read 28th October, 1959.]

Synopsis.

Clones of three forms of *Nitella cristata* Braun (Characeae) were grown under different light, temperature and day-length conditions. The resulting environmental variations indicate that relative length and form of fertile and sterile whorls are not reliable diagnostic characters for this species.

INTRODUCTION.

Few cryptogamic groups have been subjected to controlled environment experiments such as are now commonly used in the experimental taxonomy of higher plants. Members of the Characeae are ideal subjects for these experiments as they are easy to propagate clonally and the non-sterile aqueous conditions that they demand require only the control of temperature and light, and avoid the complex problems of humidity adjustment. Here, possibly for the first time, these methods are applied to a multi-cellular algal group, in an attempt to sort out some difficult forms which may be referred to as "the *cristata* group" of *Nitella*.

Braun (1852) described *Nitella cristata*, based on material collected by Charles Stuart from South Esk River, Tasmania, in 1848, and *N. cristata* var. *ambigua*, based on a specimen collected by Ferdinand von Mueller near Melbourne, Victoria, in 1852. The variety was distinguished by having the fertile whorls not very distinct from the sterile ones and the spores smaller and with a thinner crest. No measurements were given in either case.

Kuetzing (1857) studied duplicates of the specimens seen by Braun (from Sonder's herbarium instead of Mueller's) and published drawings which are of very little use diagnostically. In their world monograph, Braun and Nordstedt (1882) added some measurements to the descriptions, but cited specimens merely as "Tasmanian" and "Neu-Holland sö" (south-east), probably in reference to the types.

Meanwhile, Braun (1860) examined a specimen collected by Gunn from near Launceston, Tasmania, and published for it the locality data with the nomen nudum *N. diffusa*. When Braun and Nordstedt (1882) validly published the name, the specimen was cited merely as "Tasmanien", but presumably this referred to Gunn's specimen.

N. diffusa was differentiated from *N. cristata* chiefly by the fertile whorls not being congested into heads; since this was also diagnostic of *N. cristata* var. *ambigua*, and since the spore sizes of the three taxa overlap, it is difficult to see how they could have been distinguished at this time. The features of the three taxa, as then known, are set out in Table 1.

Nordstedt (1889) drew attention to the importance of spore-wall decoration in distinguishing species. From "Tasmanien originalex" he described the spore-wall of *N. diffusa* as granulate; from Charles Stuart's collection No. 753 he described the outer spore-wall of *N. cristata* as tuberculate. Williams (1959) has shown that the spore-wall of the type (Stuart 219) differs from that of Stuart 753. The spore-wall of *N. cristata* var. *ambigua* was not described and the type specimen has not been traced.

* Linnean Macleay Fellow of the Society in Botany, 1955-58.

Subsequently Nordstedt (1918) and Groves and Allen (1935) have ignored *N. cristata* var. *ambigua* while maintaining *N. cristata* and *N. diffusa*, which they distinguished primarily on the characteristics of the fertile whorls, together with spore size and spore-wall decoration. Groves and Allen commented on the difficulty of separating the two species.

TABLE 1.
Morphological Features of Nitella diffusa and Two Varieties of N. cristata, as Known in 1889.

	<i>N. cristata</i> var. <i>cristata</i> Braun, 1852.	<i>N. cristata</i> var. <i>ambigua</i> Braun, 1852.	<i>N. diffusa</i> Braun in Braun and Nordstedt, 1882.
Original specimen	Stuart 219. In Tasmania <i>ad flumen</i> South Esk River, 1848. LECTOTYPE.	F. Mueller, Sept., 1882. "In aquis stagnantibus prope Melbourne."	Tasmania, rare, Gunn, 1874, Habitat, Distillery Creek, Launceston. Rivulet near Penquite. HOLOTYPE.
Stem diameter ..	Strong, to 1 mm.	0.72-0.75	0.5-0.6
Sterile branchlets ..	6	—	6
(a) Furcation ..	Simple or 1-furcate.	—	2×, partly 3×.
(c) Secondary rays	3-5	—	Not given.
(d) Tertiary rays ..	2-3	—	Not given.
(e) Dactyls ..	Very short, often forming 3-celled "mucro".	—	3-4 cells, gradually shorter and thinner, ultimate one very short and acute.
Fertile branchlets	Short, forming elongate, interrupted heads; twice furcate, dactyls rigid, diverg- ing, 3-celled, gradually narrowing, acute.	Not sharply distinct from sterile.	Not sharply distinct from sterile. 5-6 mm. long. Forming heads (<i>vide</i> Willis).
Fertile whorls ..	Forming heads.	Not forming heads.	Not forming heads.
Spirals of oogonium	6-7	—	8
Oospore length ..	0.34-0.37	0.30-0.35	0.32-0.37
Spore width ..	0.31-0.32	0.26-0.28	0.30-0.32
Spore striae ..	Thick, prominent.	—	—
Spore wall ..	Sparsely verrucate outer, finely baculate inner.	Unknown.	Fine-grained dotted, i.e., finely baculate.
Antheridium ..	0.50-0.58 mm.	—	—

The following experiments were designed to test whether, in fact, the relative length and form of fertile whorls are modified by environment and therefore may be unreliable characters for taxonomic use. In addition it was hoped to gain some insight into the physiology of growth of *Nitella*.

EXPERIMENTAL MATERIAL.

It was not possible to examine experimentally a complete range of forms referable to *N. cristata*. The following were selected for experimental study, the choice being limited by the necessity of using the same sex in all experiments and of selecting forms representative of the morphological range. Voucher specimens have been prepared and will be lodged in the National Herbarium of New South Wales.

1. *Gledswood*.—A form with rather diffuse fertile whorls, referable to *N. cristata* var. *ambigua*.

Locality: A dam on "Gledswood" property 7 miles N.E. of Camden on the Hume Highway, N.S.W. *Voucher specimens:* 13.vii.1955, Mary B. Williams. 271.1, 271.2 (male and female).

TABLE 2.
Morphological Features of Three Forms Assigned to Nitella cristata and Used in Controlled Environment Experiments.

	Gledswood.	Kiefer's Dam.	Long Plains Creek.
Height (cm.)	10-15	5-10	15
Stem diameter (mm.) ..	0.5	0.5-0.575	0.75-1.0
Sterile branchlet number	6	6	6
Stem branchlet length (mm.)	Lower, 3-4 Upper, 1	Lower, 10 Upper, 6-8	Lower, 17 Upper, 10
Furcation	1-2 ×	1-2 ×	1 ×, occasionally partly 2 ×
Relative length primary ray.	$\frac{1}{2}$ - $\frac{1}{3}$ total length.	$\frac{1}{2}$ - $\frac{2}{3}$ total length, 3-4 mm.	Almost whole length exceeds $\frac{2}{3}$.
Secondary rays:			
Number	(2)-3-(5)	(3)-4(5)	(1-2)-3
Length (mm.) ..	10-15	1-2.5	Less than 1.
Tertiary rays:			
Number	2-3	2-3	—
Length (mm.) ..	1-1.8	1	If present, less than 1.
Dactyl morphology ..	2-3 celled, lower cells gradually narrowing distally. Ultimate cell short, conical, acute.	2-3 celled, lower cells narrowing distally. Ultimate cell short, conical, acute.	2-3 celled, lower cells narrowing distally. Ultimate cell small, conical, acute.
Fertile branchlet length	Up to 5 mm.	2.5-5	Less than 2*
Fertile whorls	Lower fertile whorls similar to sterile, upper forming loose heads.	Lower fertile whorls like sterile, upper forming loose heads.	Sharply distinct from sterile.*
Oogonial position ..	Solitary or aggregate, generally at all free nodes.	Solitary or aggregate, generally at all free nodes.	Solitary at 1st or 2nd nodes.*
Oogonium length (mm.)	0.44-0.48	0.42-0.48	0.65
Spirals	7	—	—
Oospore length (mm.) ..	0.32-0.33	Unripe.	0.36-0.44*
Striae	5-6	—	5-6*
Spore wall†	Outer verrucate over inner finely baculate.	Outer verrucate over inner baculate.	Outer verrucate over inner baculate.
Antheridia length (mm.)	0.40-0.50	—	—
Chromosome number ..	9	? 9	? 9*

* Field material not fertile. Measurements taken from similar material collected Leech Creek, on Monaro Highway, 3 miles east of Nimmitabel, MBW No. 108.

† For terminology, see Williams, 1959.

2. *Kiefer's Dam.*—A form with compact fertile whorls, referable to *N. cristata* var. *ambigua*, but differing slightly from Gledswood.

Locality: A dam on the property of J. Kiefer, 3 miles N.E. of Armidale on Rockvale Road, N.S.W. *Voucher specimens:* 22.ix.1955, leg. J. A. Sutherland, Mary B. Williams 335; do., 28.x.1955, Mary B. Williams 333 (ex culture).

3. *Long Plains Creek*.—A form with restricted forking, very short dactyls and very compact fertile whorls, doubtfully referable to *N. cristata* Braun.

Locality: Long Plains Creek, on the old Adaminaby-Kiandra Road 5 miles from Adaminaby, N.S.W. *Voucher specimens*: 8.ii.1955, Mary B. Williams 106, 111; do., 24.xi.1955, Mary B. Williams 362 (ex culture). Also see a specimen from a creek on Monaro Highway, 3 miles E. of Nimmitabel, N.S.W., 7.ii.1955, Mary B. Williams 108.

Morphological features of original material of these three forms are compared in Table 2.

METHODS.

Single male plants of each of the forms described in Table 2 were grown in enamel pots 17 cm. high holding 1 in. of sieved pond-mud covered with a few millimetres of sand and 4 litres of tap water. These were covered with a semi-opaque polythene film to reduce water loss and to diffuse light. After two months' growth in a glasshouse

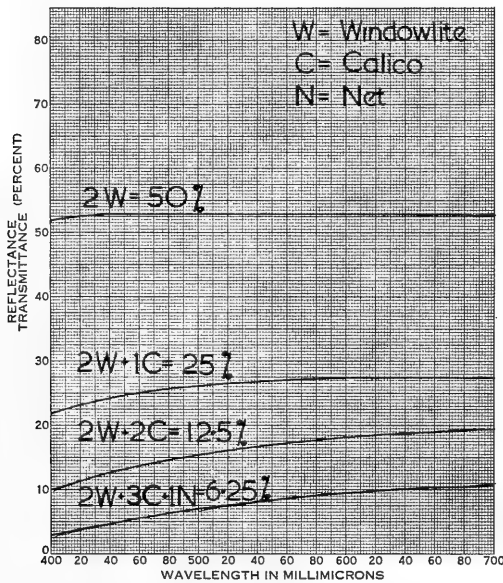


FIG. 1.—The light transmission characteristics of the "windowlite" screens.

(November-December, 1957), the resulting clones were dissected into shoot tip cuttings each three internodes long, and also into pieces of rooted bulbil. These ramets were planted singly in jars 7.5 cm. high holding 130 c.c. of mud covered with a few millimetres of sand. The mud was freshly collected from "Gledswood" pond and thoroughly mixed until homogeneous. The jars were placed in white enamel pots (15 in. high with a volume of 8 litres), 11 jars in each pot arranged so that there were 3 or 4 replicates of each of the 3 forms per pot. These pots were then filled with tapwater and placed in duplicate under each of the various temperature and light conditions described in Figures 2 and 3. The water was drained and replaced every second week.

The 6.25-100 per cent. light set were placed on open ground in full sunlight, or under screens made of one or more thicknesses of "windowlite" interleaved with calico and mosquito net, of which the transmission characteristics are described in Figure 1. These screens lacked any serious peaks of absorption and the light conditions should have been essentially those encountered by the field material. As the experiment was set up in December the plants in this set were subjected to long day conditions. The 15 degrees C. at 50 per cent light group were placed in a large water bath thermostatically controlled by refrigeration, and covered by a 50 per cent. light screen

all within a glasshouse. The short-day set were placed in a thermostatically controlled room at 15 degrees C., and given 8 hours of light in 24 under thirteen 40-watt Osram "Warm White" tubes spaced at $1\frac{3}{4}$ inches. The top of each pot was $7\frac{1}{2}$ inches below the lights and a 50 per cent. light screen was placed on top of half the set.

At one month and again at two and a half months the clones were removed, sorted, and a typical strand selected from each plant. This was mounted in water (boiled, to minimize bubble formation) between glass plates in the negative carrier of an enlarger, and a direct photographic print of known magnification made. From these and with further reference to a preserved sample a series of average mature sterile whorl diagrams was constructed.

The percentage daylight, the low temperature at 50 per cent. daylight, and the short-day sets cannot be compared directly owing to the different qualities of daylight and fluorescent light.

RESULTS AND DISCUSSION.

Daylight Intensity Experiment.

(a) *Vegetative Development.*

With increasing daylight intensity up to 25 per cent. the plants of the "Gledswood" and "Kiefer's Dam" clones showed a general increase in size. They had longer primary rays and larger whorls (Fig. 2) together with longer shoots. At 50 per cent. light the plants were more compact but with less growth, and the secondary rays were of more regular dimensions. Under 100 per cent. light the plants were distinctly stunted. However, this group was unprotected from both atmospheric contamination and the overheating effects of direct sunlight and therefore cannot be directly compared with other treatments. The "Long Plains Creek" clone showed increase in size of the rays up to 12.5 per cent. light; only under this light condition was there a noticeable development of the secondaries, which under other treatments were reduced to very small dimensions.

It is suggested that while light is limiting, growth is proportional to increase in intensity to somewhere above 25 per cent. daylight, where some other factor becomes limiting. With these experiments it is difficult to separate the effects of light and temperature because temperature was not controlled in the daylight set. The water temperature at midday varied between 25°C. and 29°C. and was usually 1°C. or 2°C. higher under 50 per cent. light than under 6.25 per cent. light. Plants in the field die down in very hot sunny weather and the death of shoots under these unfavourable "light" conditions may be related to increase in respiration dependent on the associated higher temperature. This has been shown to apply to *Chara australis* (Chambers, 1958; unpublished).

(b) *Reproductive Development.*

Sex organs were formed in the Kiefer's Dam and Gledswood clones under all conditions except 100 per cent. daylight, where the plants were not healthy. None of the Long Plains Creek plants formed sex organs under any of the conditions. The development of fertile whorls was first noted in 50 per cent. light after four weeks and occurred a little earlier in the Kiefer's Dam than in the Gledswood clone. The form of the fertile whorls was more diffuse in lower light (Pl. xviii).

Although it is possible that these plants with diffuse fruiting heads might ultimately have developed the compact habit of the higher light forms, nevertheless Plate xviii clearly illustrates that at a given age, mature plants of genetically identical clones may exhibit a range from diffuse to compact fertile whorls under the different light conditions. The shortening of whorl branchlets and internode length in high light intensity is perhaps analogous to rosette formation in higher plants.

This experiment shows that the length of fertile whorls relative to sterile is not a reliable diagnostic character for the determination of species.

Day-length Experiment.

In short-day conditions (8 hours' light) under fluorescent light the various clones under the 50 per cent. light screens were markedly larger and more diffuse than those in 100 per cent. light. The Gledswood and Kiefer's Dam plants diverged more noticeably than in the daylight experiment—the Gledswood having more forking and greater

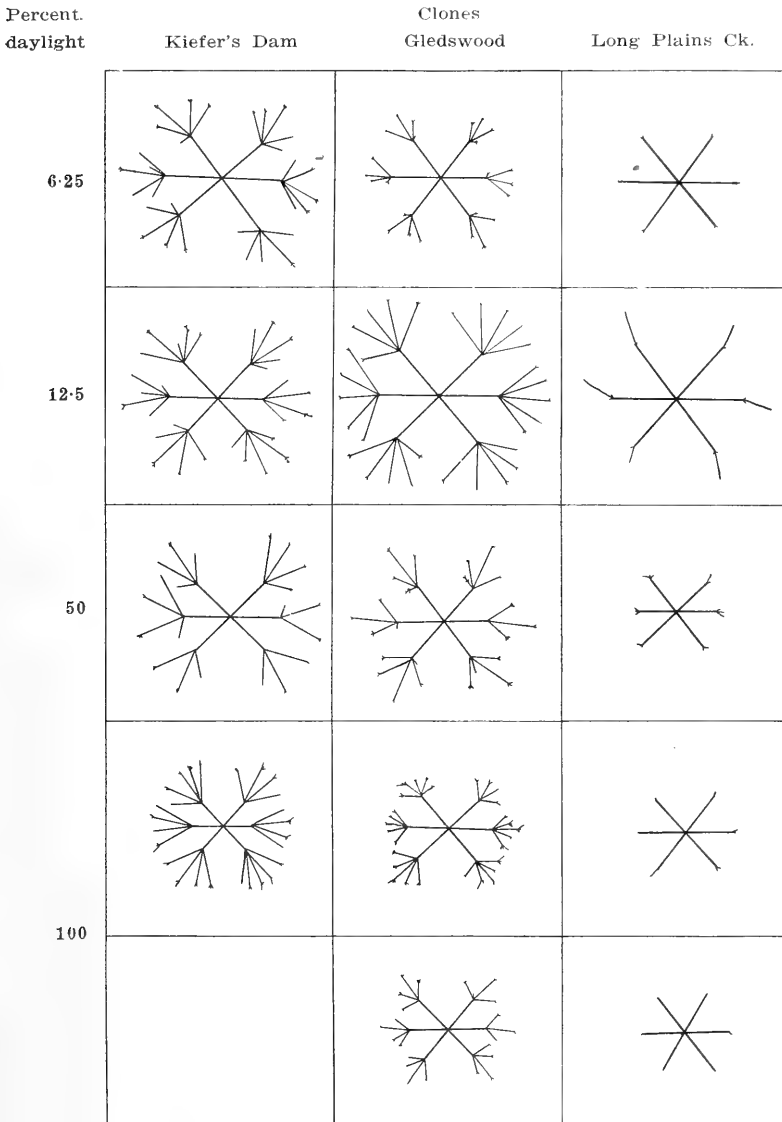


FIG. 2.—Effect of different daylight intensities on the morphology of the sterile whorls in three members of the *cristata* group after 2 months' growth.

development of tertiary and quaternary rays (Fig. 3). As this experiment was at 15°C. it is difficult to designate this as a light or temperature effect. However, plants kept at 15°C. long-day (30 per cent. daylight), although not directly comparable with other conditions, do show, in the low temperature, whorls much larger and more diffuse than in any of the other daylight conditions.

The Gledswood and Kiefer's Dam clones developed sex organs after one month's growth in both the short-day and long-day experimental conditions, the fertile whorls being longer in low light intensity as before. Formation of fertile whorls in short-day conditions could have been the result of pre-conditioning since the plants were grown from cuttings previously subjected to the long days of December. The photoperiod behaviour of *Nitella* is uncertain despite the work of Karling (1924). League and Greulach (1955) showed that with *Vaucheria* fruiting response to a long-day photo-

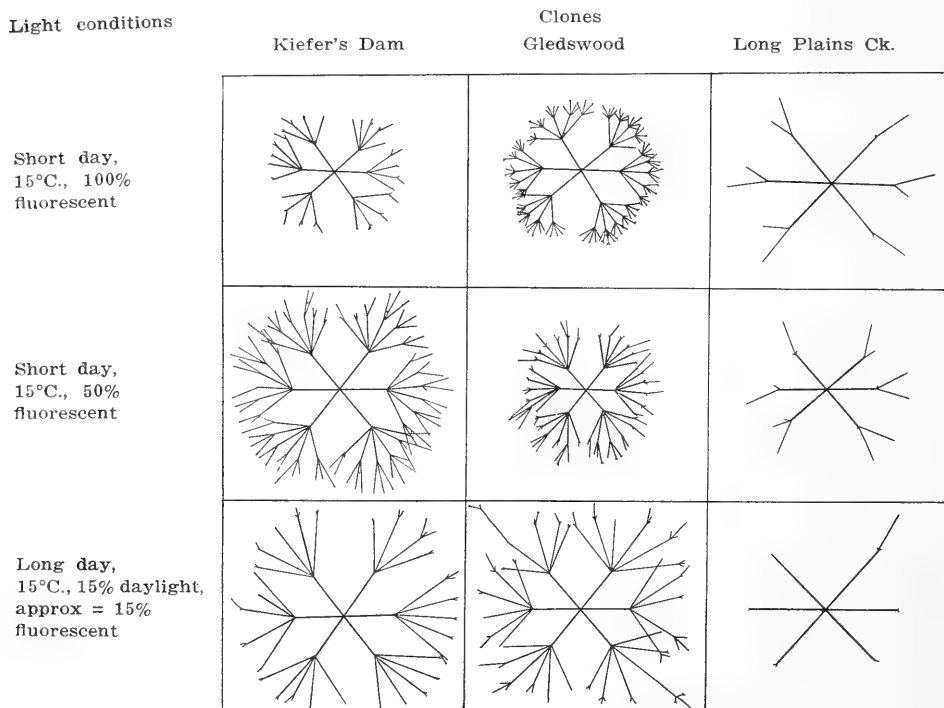


FIG. 3.—Effect of short and long day conditions on clones at uniform temperature.

period is due to an accumulation of food reserves under more favourable anabolic conditions. This response to long-day conditions is nutritional rather than a true photoperiod reaction. It is possible that *Nitella* resembles *Vaucheria* and has no true photoperiodic response. This is further suggested by the observation that the number of fertile whorls per shoot was increased in the higher light treatments (Pl. xviii).

Conclusions.

The Gledswood and Kiefer's Dam clones showed a morphologically similar response to changes of temperature, light, and day length. Small differences were observed, but these were within the limits of the description of the taxa *N. cristata* Braun. This was not the case with the Long Plains Creek clone which maintained a striking distinctness of form and fruiting behaviour which clearly suggests that it should be regarded as a separate species.

The taxonomic implications from the work described in this paper are used in a new treatment of the *Nitella cristata* group (Williams, 1959).

These findings demonstrate that techniques recognized as valuable in higher plant taxonomy are also useful when applied to lower groups, and an experimental approach to the variability of other difficult species in the Characeae would be of great benefit in clarifying their taxonomy.

Acknowledgements.

The authors wish to thank Professor R. L. Crocker for provision of facilities in the Department of Botany, University of Sydney, and Associate Professor F. V. Mercer, of the same Department, and Dr. H. S. McKee, Plant Physiology Unit, C.S.I.R.O., for reading and criticizing the manuscript. They would also like to thank the owners of "Gledswood", Narellan, for their co-operation in field studies at all times.

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EXPLANATION OF PLATE XVIII.

Effect of different daylight intensities on fertile whorl morphology in two members of the *Cristata* group after 2½ months' growth.

A REVISION OF *NITELLA CRISTATA* BRAUN (CHARACEAE) AND ITS ALLIES.

PART II. TAXONOMY.

By MARY B. WILLIAMS.*

(Six Text-figures.)

[Read 28th October, 1959.]

Synopsis.

Evidence that certain key characters may be subject to modification by the environment is used in a revision of some of the dioecious Pluricellulatae of the genus *Nitella* Ag. em. Braun (Characeae). *N. cristata* Braun and *N. diffusa* Braun and Nordstedt are redefined, two new species are described, and a key to the four species is given.

INTRODUCTION.

The three taxa *Nitella cristata* Braun, *N. cristata* var. *ambigua* Braun, and *N. diffusa* Braun were not satisfactorily distinguished in the original descriptions and have given much difficulty to subsequent workers. Their taxonomic history is outlined and a tabular comparison of their diagnostic characters is made by Chambers and Williams (1959), who also show that emphasis on length of fertile whorls as a key character has been misplaced because it is readily modified by environment. Accordingly, the *N. cristata* group is here revised.

Material borrowed from Australian herbaria (listed below) proved to be limited in quantity, collected chiefly from localities close to early settlement areas, and often insufficient for determination. It was supplemented by the writer's own collections.

More than two hundred specimens were examined from the writer's collections (designated MBW) and from the following institutions: Queensland Herbarium and Botanic Gardens, Brisbane (BRI), National Herbarium of New South Wales (NSW), and National Herbarium of Victoria, Melbourne (MEL). No other Australian herbaria had specimens of the group. Overseas material was not sought, as the only likely source was Berlin-Dahlem Museum where all the algal specimens were destroyed in the war (Alston, 1948).

All specimens except those from Brisbane and one incomplete set of the writer's duplicates were damaged or destroyed by fire at the University of New England in February, 1958. The Melbourne collection, containing types and specimens determined by Nordstedt, fortunately suffered less damage than others. Notes and drawings of specimens examined before the fire were not damaged.

Specimens were examined fresh where possible, otherwise from material preserved in formalin-acetic-alcohol or dried. Fragments of dried material were hydrated in warm 20% ammonium hydroxide, washed, mounted in 10% glycerine, and later made into permanent glycerine jelly preparations. Measurements were made with a calibrated ocular micrometer, oospore dimensions being reported exclusive of appendages (older literature may not be consistent in this respect). Most authors have given such measurements in microns, but millimetres are used here for measurements greater than 100 μ in order to avoid reporting digits that are not significant.

Oospore-wall preparations were made by crushing and dissecting ripe oospores which were then softened and cleared of debris in a drop of hot 20% chromic acid, washed, and mounted in glycerine or (after dehydration) in Euparal. Sometimes mounting was in Sirax which has a high refractive index of about 1.66.

Examination of suitable fragments was carried out using oil immersion ($\times 950$), and drawings were made with the aid of a camera lucida. In studying fine decorations,

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attention was paid to Welcker's Rule and LO analysis, i.e., with successive adjustment of focus, a protuberance or solid portion shows first as a bright island followed by a dark one (an LO-pattern, from L, *lux*, and O, *obscuritas*); a hollow shows first dark, then bright (an OL-pattern) (Erdtman, 1956).

In an attempt to give more precise descriptions of oospore-wall decorations, terms have been borrowed from the nomenclature of pollen morphology (Faegri and Iverson, 1950), as follows:

Verrucate: decorated with verrucae, more or less isodiametric sculpturing elements which in at least one dimension are greater than or equal to 1μ , and whose greatest diameter is greater than or equal to the height. The elements are neither distally pointed nor constricted at the base. The ratio of smallest to greatest diameter is less than two.

Rugulate: decorated with rugulae, more or less elongated sculpturing elements which in at least one dimension are greater than or equal to 1μ and whose longest diameter is at least twice the shortest diameter.

Baculate: decorated with baculae (i.e., little rods, "Stabchen"), small sculpturing elements neither pointed nor club-shaped, which in at least one dimension are greater than or equal to 1μ and whose greatest diameter is less than the height.

Clavate: decorated with clavae, small sculpturing elements like baculae, but distally thickened so that they are club-shaped.

The term *oospore-wall* is considered preferable to *membrane* because of the special physiological implications of the latter. Other terminology follows that of Wood (1949).

The chromosome number, determined from orcein-crush preparations of fresh antheridia, was $n=9$ in all cases examined.

The following descriptions are inclusive, i.e., based on the range of specimens seen rather than on a single representative. A great number of specimens were sterile or immature, precluding definite determination. These have not been cited. In this category are most of the specimens from Queensland Herbarium, which were annotated by Groves and cited by Groves and Allen (1935). *Specimens examined* are arranged by locality, as far as possible from north to south and west to east.

The writer's collections will be housed at the New South Wales National Herbarium, with duplicates issued where possible to the University of Sydney Botany Department, University of New England Botany Department, and other Australian herbaria.

NITELLA Agardh em. Braun.

Sect. *Homoeoclemae* J. Groves, *J. Linn. Soc. Lon., Bot.*, 46: 360 (1924).

Subsect. *Arthrodactylae* Groves and Bullock-Webster, *British Charaphyta*, 1: 86, 110 (1920). Series Pluricellulatae.

NITELLA CRISTATA Braun, *Linnaea*, 25: 706 (1852), emend.

Kuetzing, *Tab. Phycol.*, 7: 16, Tab. 41, fig. 1 (1857); Braun and Nordstedt, *Abh. preuss. Akad. Wiss. Berlin* (1882): 82, Pl. 6, fig. 165; Nordstedt, *Hedwigia*, 7-8: 185 (1888); Nordstedt, *Acta Univ. Lundens.*, 25: 5, 13, 28-29, fig. 17 (1889); Nordstedt, *Proc. Roy. Soc. Vict.*, 31: 1-6 (1918); Groves and Allen, *Proc. Roy. Soc. Qd.*, 46: 49-50 (1935).

Plant dioecious, up to 20 cm. high. *Stem* about 0.5-1 mm. in diameter. *Sterile branchlets* 6 in a whorl, simple or once, partly twice (occasionally 3 times) furcate, about 1-4 cm. long; the secondary rays 2-5, tertiary rays 2-5, dactyls 2-5, rigid, divergent and unequal, usually some longer than 1 mm., with (2)-3-(4) cells, gradually narrowing distally, the ultimate cell short, acute and conical, not longer than twice its width. *Fertile branchlets* usually somewhat shorter than sterile, the whorls often forming heads, but not sharply distinct from sterile. *Oogonia* solitary or two-three together, at any branchlet-node, with 6-9 spirals, 0.48-0.57 mm. long. *Oospore* 0.32-0.45 mm. long, striae 5-7(-8), with a prominent wing. *Oospore-wall* laminated, the outer lamina and wing, or the wing alone, sparsely or densely verrucate, the verrucae about 2-3 μ in diameter and 2 μ high, and 1-3 diameters apart; the underlying lamina closely

baculate, the baculae slightly less than 1μ in diameter and $1-1\frac{1}{2}\mu$ high, about 1 diameter apart, some of them almost clavate in outline. *Antheridium* 0.37–0.50 mm. in diameter.

Illustrations: See under varieties. Braun and Nordstedt, *Abh. k. Akad. Wiss. Berlin*, 1882, Pl. 6, fig. 165. Nordstedt, *Acta Univ. Lundens*, 25: fig. 17.

Specimens Seen: See under varieties.

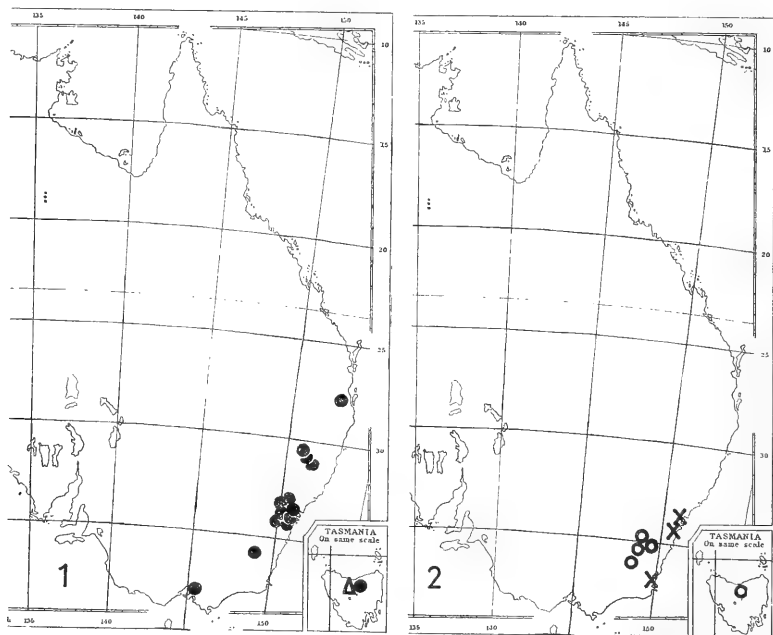
Distribution: See under varieties.

Type Locality: South Esk River, Tasmania.

NITELLA CRISTATA var. *CRISTATA*. (Figs 1, 3i, j.)

Lectotype: Charles Stuart 219, "In Tasmania ad flumen South Esk River 1848" (MEL).

Plant dioecious, large, flexible. *Stem* about 0.7 mm. in diameter. *Sterile branchlets* 6 in a whorl, simple or once to partly twice furcate; secondary rays 3–5, tertiary 2–3; dactyl 2–3, usually 2–3-celled, gradually narrowing distally, the ultimate cell conical, acute. *Fertile branchlets* short, twice furcate, forming elongated interrupted heads, the dactyls rigid and diverging, 3-celled, gradually narrowing distally, acute. *Oogonia*



Figs. 1-2.—Distribution of *N. cristata* var. *cristata* Braun Δ ; *N. cristata* var. *ambigua* Braun \bullet ; *N. microteles* Williams \circ ; and *N. reticulata* Williams \times .

solitary or 2–3 together at any node. *Oospore* 0.34–0.42 mm. long; striae 5–6, prominently winged. *Oospore-wall* with an outer layer sparsely verrucate on wings alone or on wings plus body of spore, the verrucae about 2μ in diameter and $1\frac{1}{2}-2\mu$ high, and 2–3 diameters apart; with middle layer which is finely baculate, the baculae less than 1μ in diameter, about 1μ high, and 1 diameter apart, some of them clavate in outline; with inner layer smooth. *Antheridia* unknown.

Other Illustrations: Kuetzing, 1857, *Tab. phyc.*, Pl. 41, fig. 1a.

Specimens Examined: Lectotype, as above.

Distribution: Tasmania, known only from the type locality. (Fig. 1.)

Remarks: When describing *N. cristata*, Braun cited the sterile specimens, Stuart Nos. 5, 217, and 788, as well as the fertile Stuart 219, and did not designate a type. Stuart 219 is selected as the lectotype because it is the only fertile specimen; the other syntypes are here excluded from var. *cristata* on the grounds that their size and dactyl characteristics make them referable to *N. breviteles*.

The oospore-wall decoration of *N. cristata* was originally described by Nordstedt (1889) after examining a Stuart specimen No. 753 from the type locality, but not part of the type. I examined Stuart No. 753 (later destroyed by fire) as well as the type, Stuart No. 219, and found that the spore-wall decorations did not correspond. My notes about specimen No. 753 indicate that its spore-wall decoration was similar to that shown in Figure 3*h* for var. *ambigua* and much coarser than that of 219, shown in Figure 3*j*.

The epithet *cristata* is attached to an extreme form among a range of plants bearing verrucate spore-wall decorations; the sparsely verrucate outer lamina, with some size differences, seems to warrant the maintenance of a variety distinct from the bulk of material placed under *N. cristata*, although only one specimen is known.

NITELLA CRISTATA VAR. AMBIGUA Braun, *Linnaea*, 25: 706 (1852). (Figs 1, 3*g*, *h*, 5*c*.)

Kuetzing, *Tab. Phycol.*, 7: 16-17, Pl. 41, fig. 1*b*; Braun and Nordstedt, *Abh. preuss. Akad. Wiss. Berlin* (1882): 14, 82.

Neotype: Creek on the Oxley Highway 5.4 miles east of Walcha, N.S.W., 5.iv.1958, Mary B. Williams 600.

Plant dioecious, medium to large, flexible. *Stem* about 0.5-1 mm. in diameter. *Sterile branchlets* simple or once to twice furcate, 1-6 cm. long, secondary rays 2-5, tertiary 2-3(-5); dactyls with 2-3(-4) cells, which gradually narrow distally to an acute, conical apical cell. *Fertile branchlets* usually twice furcate, the dactyls rigid and divergent; fertile whorls usually somewhat shorter than sterile, but not sharply distinct. *Oogonia* solitary or 2-3 together at any node, with (6)-7(-9) spirals. *Oospore* 0.32-0.45 mm. long; striae 5-7, prominently winged. *Oospore-wall* laminate, the outer layer strongly verrucate, the verrucae about 3-5 μ in diameter, 2-3 μ high, about 1 diameter apart, 10-12 per fossa; a middle layer finely baculate, the baculae slightly less than 1 μ in diameter, about 1-1 $\frac{1}{2}$ μ high, 1 diameter apart, some being clavate in outline; the inner layer smooth. *Antheridium* 0.37-0.50 mm. in diameter.

Specimens Examined: QUEENSLAND: Highfields, F. M. Bailey (BRI 007729). NEW SOUTH WALES: Duval Creek, 12 miles N. of Armidale on the New England Highway, 22.iii.58, Mary B. Williams 420; dam on property of J. Kiefer, 3 miles N.E. of Armidale on Rockvale Rd., leg. J. A. Sutherland, 5.viii.55, MBW 335; do., MBW 333, ex culture; creek 5.4 miles E. of Walcha on Oxley Highway, 5.iv.58, MBW 600 (neotype); Hacking River at the Causeway, National Park, ca. 20 miles S. of Sydney, —.vii.57, MBW 419; Turon River, 6 miles S. of Capertee, 25.iv.54, leg. G. Packham, MBW P442; Weeney Creek, 1 mile W. of Kurrajong, 17.xi.56, MBW 405; temporary swamp, $\frac{1}{4}$ mile N.W. of Richmond in old meander of the Hawkesbury River, 25.v.58, MBW 421, 423; Parramatta, Rev. Dr. Woolls (MEL); shallow pool in dry creek bed, $\frac{1}{4}$ mile E. of Kingswood on the Great Western Highway, 17.xi.56, MBW 406; Werriberri Creek on the Camden-Oakdale Rd., 0.8 mile S.W. of The Oaks, 8.ii.57, MBW 408; dam on Gledswood property, 7 miles N.E. of Camden on the Hume Highway, 13.vii.55, MBW 271.1, 271.2; creek just E. of Mittagong on the Hume Highway, 29.v.56, MBW 393; roadside pond about 12 miles S.W. of Cooma on the Cooma-Jindabyne Rd., alt. ca. 3000 feet, 12.x.57, leg. B. Briggs, MBW 424. VICTORIA: Growing in fresh water at Box Hill (9 miles E. of Melbourne), G. French (MEL). TASMANIA: South Esk River, Dec., Charles Stuart 753 (destroyed by fire).

Other Illustrations: Kuetzing, *Tab. Phycol.*, 7: Pl. 41, fig. 1*b*.

Distribution: Common in pools and streams in New South Wales, Victoria and Tasmania. (Fig. 1.)

Remarks: Braun established var. *ambigua* on a specimen cited as "In aquis stagnantibus prope Melbourne Sept. 1852 legit Dr. F. Mueller. Inter *N. Cristatam* et *tasmanicam* quasi media". His description indicates rather that it was intermediate between *cristata* and *diffusa* and the name *ambigua* probably implied doubt as to its status. Chambers and Williams tabulate the differences between the three taxa and point out that, at the time of the original description, var. *ambigua* was distinguished

merely by having fertile whorls more diffuse and spores slightly smaller than *N. cristata*. These characters alone would not justify the retention of var. *ambigua* since fertile whorl morphology varies with environment (Chambers and Williams, 1959).

Investigations of all specimens conforming with Braun's descriptions of var. *ambigua* have shown that the outer spore-wall decoration is always coarsely verrucate, in contrast with that of the type specimen for *N. cristata* (Figs. 3h and j).

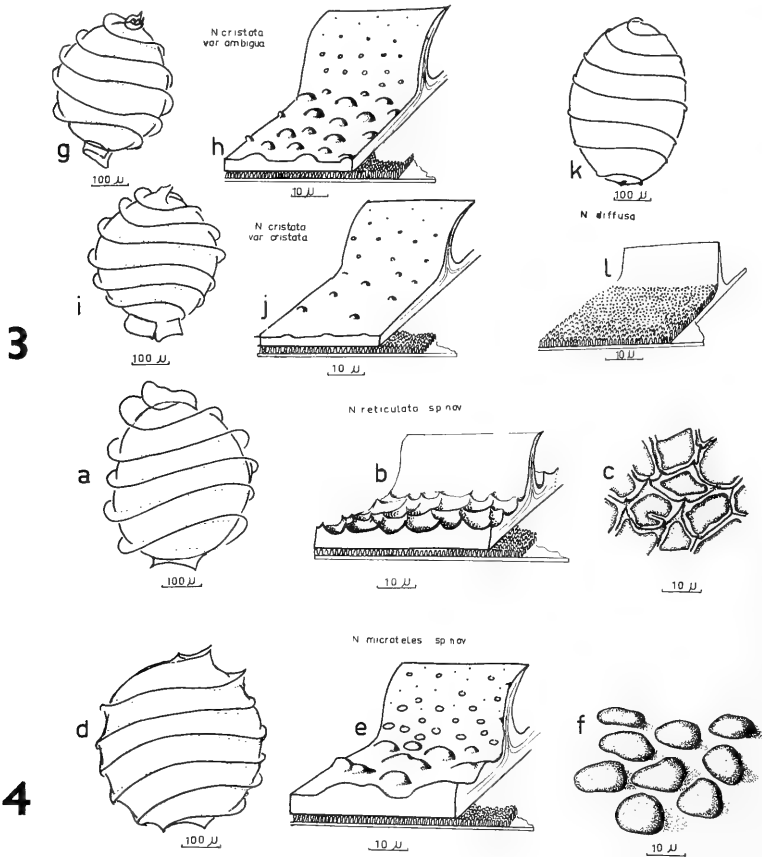


Fig. 3.—g, h, *N. cristata* var. *ambigua* Braun: g, oospore; h, three-dimensional reconstruction of spore-wall decoration, showing winged stria, outer verrucate lamina, middle baculate lamina and inner smooth lamina, from camera lucida drawings of MBW 346, holotype for var. *ambigua*. i, j, *N. cristata* var. *cristata* Braun: i, oospore; j, as in h, from Stuart 219, lectotype for *N. cristata*. k, l, *N. diffusa* Braun and Nordstedt: k, oospore; l, three-dimensional reconstruction of spore-wall decoration, showing winged stria, outer baculate lamina and inner smooth lamina, from c.l. drawings of MBW P439.

Fig. 4.—a, b, c, *N. reticulata*, sp. nov.: a, oospore; b, three-dimensional reconstruction of spore-wall decoration showing the winged stria, reticulate outer lamina, baculate middle lamina, and smooth inner lamina, from camera lucida drawings of MBW 346, holotype for *N. reticulata*; c, surface view of same. d, e, f, *N. microteles*, sp. nov.: d, oospore; e, three-dimensional reconstruction of spore-wall decoration showing winged stria, coarsely verrucate outer lamina, baculate middle lamina, and smooth inner lamina, from c.l. drawings of MBW 108, holotype for *N. microteles*; f, surface view of same.

Unfortunately the spore-wall decoration of the original specimen of var. *ambigua* has never been described; the specimen cannot be found among the collections of Melbourne or Kew and probably perished with Braun's types in Berlin.

Nevertheless it was felt that var. *ambigua* should be retained and its description amplified to include material with coarsely verrucate outer spore-wall, this being the

condition of all specimens seen. A neotype has been chosen from my own collections which fits the descriptions of var. *ambigua* given by Braun, *l.c.*, and by Braun and Nordstedt, *l.c.*; older material such as French's collection from Box Hill near Melbourne is too poorly preserved to be considered despite the desirability of its having been collected near the type locality.

NITELLA RETICULATA, sp. nov. (Figs 2, 4a, b, c, 5a.)

N. cristata sensu Nordstedt, *Acta Univ. Lundens*, 25: 29 (1889).

Holotype: Dune pond, Maroubra Beach, N.S.W., 20.vii.1955, Mary B. Williams 341.

Homoeoclema, arthroductyla, pluricellulata, gymnocephala, dioecia.

Planta magna, fruticosa, rigida, ferme 20 cm. alta. *Ramuli steriles* 6 verticillo dispositi, 2-3 cm. longi, semel, partim bis furcati, radiis secundariis 3-5, tertiariis 1-3; *dactylis* inaequalibus, aliis minus 1 mm., aliis 2-5 mm., rigidis et divergentibus; bis aut ter, nonnumquam quater-cellulatis, cellulis sensim adversus apicem usque ad apicis cellulam acutam, conicam angustioribus. *Ramuli fertiles* plerumque bis furcati, non multum contracti, sed paulo breviores et rigidiores ramulis sterilibus, quasi racemos axillares et terminales formantes. *Oogonia* 1-3 in omni furca aggregata. *Oospora* 0.37-0.40 mm. longa, striis 5-6, clarissime alatis. *Oosporae membranam* lamina exteriore valde reticulata, luminibus quasi reticuli 4 μ diam., muris ferme 2-3 μ altis, in nodo omni spissatis et elevatis, alibi tenuibus; lamina media tenuiter baculata, baculis minus 1 μ diam., et ferme 1 μ altis diametro suo separatis; lamina interiore omnino levi. *Antheridium* 0.46-0.50 mm. altum.

Planta a *N. cristata* distinguenda oospora magna et oosporae membrano reticulato; a *N. microteles*, ramulis sterilibus bis furcatis et dactylis longioribus.

Plant large, bushy, rigid; about 20 cm. high. *Sterile branchlets* 6 in whorl, 2-3 cm. long, once, partly twice furcate; secondary rays 3-5, tertiary 1-3; dactyls unequal, some less than 1 mm., some 2-5 mm., rigid and diverging, 2-3, occasionally 4-celled, the cells gradually narrowing distally to an acute conical apical cell. *Fertile branchlets* regularly twice furcate, not greatly contracted, but somewhat shorter and more rigid than the sterile, forming axillary and terminal clusters. *Oogonia* 1-3 together in any fork, with 6-7(-8) spirals. *Oospore* 0.37-0.40 mm. long; striae 5-6, prominently winged. *Oospore-wall* with an outer layer strongly reticulate, the meshes 4 μ across, the muri about 2-3 μ high, thickened and raised at the nodes, elsewhere thin; middle layer finely baculate, the baculae less than 1 μ in diameter, about 1 μ high, 1 diameter apart, some being clavate in outline; and the innermost layer completely smooth. *Antheridium* 0.46-0.50 mm. high.

Species Examined: NEW SOUTH WALES: Holotype, as above.

Distribution: On the coasts of New South Wales and Victoria in brackish waters up to half the chloride concentration of sea-water; also inland Victoria, *vide* Nordstedt, *Acta Univ. Lundens*, 25: 29. (Fig. 2.)

Remarks: Under *N. cristata* Nordstedt gives three localities for plants with reticulate spore-walls: Goulbourne River (Victoria), Lewis No. 6; Genoa (Victoria), Jan. 1887, W. Bauerlen No. 341; Hurstville, near Port Jackson (New South Wales), 1884, Whitelegge No. 2. The last two specimens were destroyed in the New England fire. They were probably referable to *N. reticulata*, since the habitats, being coastal, could have been saline. A Goulbourne River specimen collected by Lewis, but with no number (MEL), cannot be determined with certainty because it has no ripe spores.

N. reticulata is distinguished from *N. cristata*, *N. microteles* and *N. diffusa* morphologically by its reticulate spore-wall, and ecologically by its preference for saline habitats, which would effectively isolate it from the freshwater species. It is distinguished from *N. gelatinosa* Braun and *N. tasmanica* (F. Mueller) Braun by the fertile whorls which are diffuse and not enveloped in mucus.

NITELLA MICROTELES, sp. nov. (Figs 2, 4d, e, f, 5b.)

N. cristata Braun, *Linnaea*, 25: 706, pro parte.

Holotype: Creek on the Monaro Highway 3 miles E. of Nimmitabel, N.S.W., N.S.W., 7.ii.1955, Mary B. Williams 108.

Homoeoclema, arthroductyla, pluricellulata, gymnocephala, dioecia.

Planta robusta rigidaque, pallide viridis. *Internodia* ferme 1 mm. diam. *Ramuli steriles* 6 verticillo dispositi, 1–2 cm. longi, obscure semel furcati, radiis secundariis (i.e. dactylis) 2–3, brevissimis et inaequalibus, plerumque minus 1 mm. longis, 2–3 cellulatis, cellulis inferioribus sensim adversus apicem angustioribus, apicis cella late conica, acuta. *Ramuli fertiles* bis furcati, ferme 2 mm. longi, radiis rigidis et

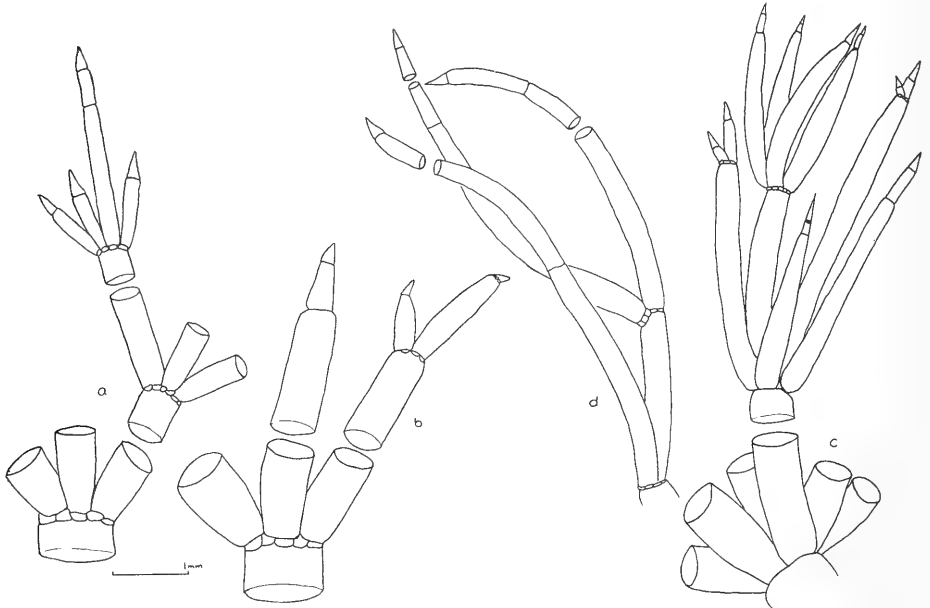


Fig. 5.—Camera lucida drawings of sterile branchlets: a, *N. reticulata*, sp. nov., from MBW 346; b, *N. microteles*, sp. nov., from MBW 108; c, *N. cristata* var. *ambigua* Braun, from MBW 600; d, *N. diffusa* Braun and Nordstedt, from MBW P439.

divergentibus; verticillis positi valdissime contractis, a sterilibus conspicue distinctis, capita aut terminalia aut axillaria formantibus. *Oogona* 0.65 mm. longa, 1–3 in furca omni aggregata. *Oospora* 0.37–0.44 mm. longa; striis 5–6, clarissime alatis. *Oosporae membranum* lamina exteriore valde verrucata, verricis ferme 3–5 μ diam., 2–3 μ altis (nonnullis quidem aliquantum ad ferme 9 μ elongatis), 1–2 diametris suis separatis, ferme 8 in fossa omni positis; lamina media tenuiter baculata, baculis minus 1 μ diam., ferme 1 μ altis, diametro suo separatis; lamina interiore omnino levi. *Antheridii* mensura ignota.

Planta a *N. cristata* distinguenda ramosis sterilibus unifurcatis, dactylis brevissimis, verticillis fertilibus valde contractis, spore magna.

Plant dioecious, stout and rigid, pale green. *Stem* about 1 mm. in diameter. *Sterile branchlets* 6 in a whorl, 1–2 cm. long, obscurely once furcate, the secondary rays (dactyls) very short but unequal, usually less than 1 mm. long, with 2–3 cells, the ultimate two narrowing distally, the apical one broadly conical and acute. *Fertile branchlets* twice furcate, about 2 mm. long, the rays being rigid and diverging; the fertile whorls extremely contracted, and sharply distinct from sterile, forming terminal or axillary heads. *Oogonia* 0.65 mm. long, 1–3 together in all forks, with 6–7 (–8) spirals.

Oospore 0.37–0.44 mm. long; striae 5–6, very prominently winged. *Oospore-wall* with outer layer strongly verrucate to rugulate, the verrucae about 3–5 μ in diameter, 2–3 μ high, 1–2 diameters apart, some elongated to 9 μ , forming rugulae with middle layer finely baculate, the baculae less than 1 μ in diameter, about 1 μ in height, with inner layer completely smooth. *Antheridium* unknown.

Specimens Examined: NEW SOUTH WALES: Holotype, as above; Long Plains Creek, on the old Adaminaby-Kiandra Road, 5 miles from Adaminaby, 8.ii.1955, MBW 106, 111, 362 ex culture; creek on the Adaminaby-Jindabyne Road at Braemar, 8.ii.1955, specimens destroyed. VICTORIA: South Esk River, Tasmania, C. Stuart, 5, 217 and 788 (MEL).

Distribution: Tasmania; New South Wales, alpine regions, in slowly running streams with soft muddy substratum. (Fig. 2.)

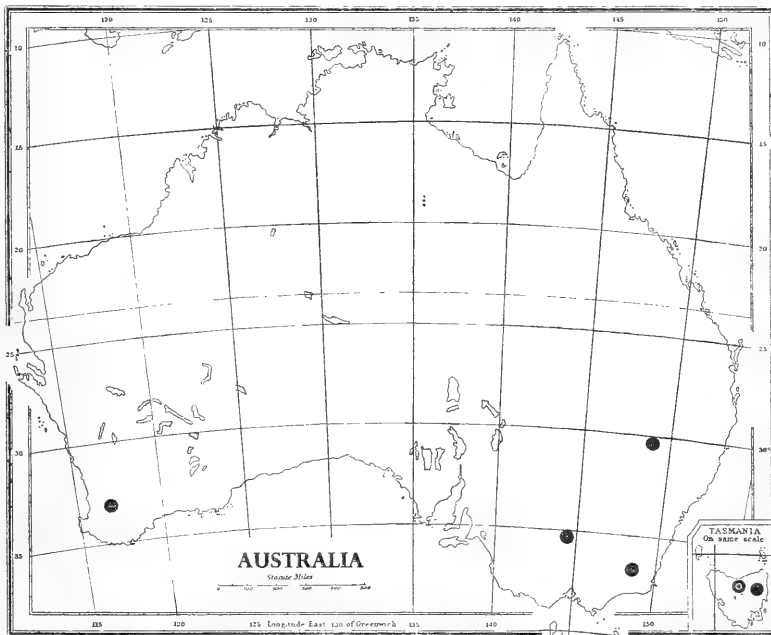


Fig. 6.—Distribution of *N. diffusa* Braun and Nordstedt ● and its type locality ○.

Remarks: The verrucate spore-wall indicates that this material has a close affinity with *N. cristata* var. *ambigua*, but the large size and restricted forking differentiate it. Its distinctive habit and fruiting behaviour in different experimental environments (Chambers and Williams, 1959) suggest that it should be treated as a separate species. It is distinguished from *N. diffusa* and *N. reticulata* by the verrucate spore-wall, and from *N. tricellularis* Nordstedt, which it resembles vegetatively, by being dioecious.

NITELLA DIFFUSA Braun and Nordstedt, *Abh. preuss. Akad. Wiss. Berlin* (1882): 14, 80. (Figs 3k, l, 5d, 6.)

Braun in J. D. Hooker, *Flora Tasm.* II: 159–160 (1860) sine descript.; Braun, *Abh. preuss. Akad. Wiss. Berlin* (1867): 797, nom. tant.; Nordstedt, *Acta Univ. Lundens.* 25: 13, 28 (1889); Groves and Allen, *Proc. Roy. Soc. Qd.*, 46: 49 (1935).

Holotype: Gunn 1574, hab. Distillery Creek, Launceston: Rivulet near Penquite (non vidi).

Plant dioecious, loose and flexible, slender. *Sterile branchlets* 6 in a whorl, to 1 cm. long, 2, partly 3 times furcate; secondary rays fairly regularly (2)–3; tertiary rays 2–3; dactyls not greatly divergent, about 5 mm. long, 2–3(4)-celled, the lower cells

not narrowing appreciably, the ultimate one short, conical acute. *Fertile branchlets* like sterile; fertile whorls not sharply distinct from sterile, 2-6 mm. in diameter, forming loose terminal clusters. *Oogonia* solitary or 2-3 together, in any fork, with 6-8(-9) spirals. *Oospore* 0.29-0.37 mm.; striae 6-8, fairly prominent. *Oospore-wall* with outer layer densely baculate, the baculae of the order of 1μ in height, less than 1μ in diameter, about 1 diameter apart; with inner layer smooth. *Antheridium* 0.30-0.48.

Other Illustrations: Braun and Nordstedt, *Abh. preuss. Akad. Wiss.* Berlin (1882): figs. 155-157; Nordstedt, *Acta Univ. Lundens.*, 25; Fig. 8.

Specimens Examined: QUEENSLAND: None of the specimens cited by Groves and Allen, *l.c.*, is complete enough for determination. I believe that many of them are referable to *N. cristata* var. *ambigua*. NEW SOUTH WALES: Piangobla, Moongulla (W. of the Barwon River), 16.viii.1955, leg. J. T. Waterhouse (specimen destroyed); Bett's Creek, Kosciusko State Park on the road to Mt. Kosciusko (specimen destroyed); small pond near Spencer's Creek, Kosciusko State Park, $\frac{1}{4}$ mile upstream from the road to the summit, 3.i.1954, leg. A. T. Hotchkiss, M.B.W. P439, P443 and dried specimens made from this preserved material; Edward River, F. Mueller, viii.1875 (MEL). TASMANIA: St. Paul's River, Stuart 751 (MEL). WESTERN AUSTRALIA: Karoling, R. Helms, 17.xi.1891 (MEL).

Distribution: Possibly Queensland; New South Wales mainly from alpine regions; Tasmania; Western Australia. (Fig. 6.)

Remarks: Chambers and Williams (1959) discuss the typification of *N. diffusa*. Mr. J. H. Willis has kindly examined the specimen at Kew bearing the same label as the type, and which he believes is an isotype. He reports that it has fertile whorls shorter than the sterile, that the spore is 290μ long and is "very minutely reticulate". This is the surface appearance of the condition which I describe as baculate (Fig. 3). On the assumption of other charologists that spore-wall decoration is a conservative character, I have maintained *N. diffusa* as a separate species. Specimens which I have interpreted as *N. diffusa* show much longer dactyls than *N. cristata*. (Fig. 5.)

Key to the dioecious non-gelatinous homoeoclemous Phricellulatae of the genus Nitella Ag. emend. Braun.

1. Sterile branchlets appearing simple in lower whorls, 1, partly 2 times furcate in upper whorls, the dactyls unequal but usually some longer than 1 mm.
2. Outer oospore-wall or wings with coarse verrucae or reticuli about 2μ - 3μ in height or diameter, visible in low power.
3. Outer spore-wall and wings, or wings alone, set with verrucae about 2μ diameter, 1-2 diameters apart *N. cristata* Braun.
4. Verrucae sparsely and irregularly distributed on wings alone or occasionally on the body of the spore: inner spore wall set with very fine baculae about 1μ in diameter and height; spore 0.34-0.37 mm. long *N. cristata* var. *cristata*.
- 4.* Verrucae densely distributed on wings and body of spore; inner spore wall set with very fine baculae about 1μ in diameter and height; spore 0.32-0.45 mm. long *N. cristata* var. *ambigua*.
- 3.* Outer spore-wall and wings strongly reticulate, the muri of the reticulum thickened and raised at the nodes, elsewhere thin, about 2μ - 3μ high; spore 0.37-0.40 mm. long *N. reticulata*.
- 2.* Outer spore-wall closely set with very fine baculae about 1μ in diameter and height, appearing granulate in surface view; spore 0.32-0.38 (-0.43) mm.; dactyls of fertile whorls longer than gametangia, not rigid and divergent *N. diffusa*.
- 1.* Sterile branchlets appearing simple throughout, really obscurely once furcate; the dactyls usually all less than 1 mm. long; fertile branchlets sharply contracted, 2 times furcate; spore 0.36-0.44 mm. long. outer wall strongly verrucate, the verrucae about 2μ - 3μ in diameter, or elongated to about 9μ , forming rugulose *N. microteles*.

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SOME SILURIAN LAMELLIBRANCHS FROM NEW SOUTH WALES.

By KATHLEEN SHERRARD.

(Plate xix.)

[Read 28th October, 1959.]

INTRODUCTION.

Lamellibranchs from the Silurian of New South Wales described in this paper are from various sources. Some were obtained from Hatton's Corner, Yass, from a bed which also contained *Monograptus nilssoni* and *M. bohemicus*. Consequently their age (Lower Ludlow) and zone (*M. nilssoni*, zone 33) are known definitely (Brown and Sherrard, 1952).

A second group was found in the Nanima-Ginninderra-Boambolo district, south of Yass. At one locality there, the common occurrence of *Cosmogoniophora*, a subgenus confined to the Silurian, determines the age (Sherrard, 1952). Elsewhere in the same district, some lamellibranchs occur in strata conformably below graptolite-bearing beds of known age, while Mr. A. J. Shearsby has collected them at Forest Creek, Boambolo.

Thirdly, there are included specimens from the Jenkins Collections of the University of Sydney Geological Department. These come from Yass beds which lie conformably below the bed with *Monograptus nilssoni* mentioned above.

A fourth group of specimens, now in the Australian Museum, was collected by John Mitchell in the Bowning district, but from localities unknown precisely. In some cases he labelled the specimens either U.T.B., M.T.B. or L.T.B (Upper, Middle or Lower Trilobite Bed). The age of these Trilobite Beds relative to that of graptolite-bearing strata has been worked out (Brown and Sherrard, 1952, p. 130). Dr. Ida Browne (1954) considers that the Upper Trilobite Bed marks the top of the Silurian.

Fifthly, there is a large collection from the Cootamundra district (Gill, 1940), while a sixth consists of lamellibranchs from other Silurian localities in New South Wales. Both these groups are housed in the Australian Museum.

Lamellibranchs of Silurian age from New South Wales which have previously been recorded (Etheridge, 1880; De Koninck, 1898; Fletcher, 1943; Stevens, 1959) are also listed.

A study of the lamellibranchs in the first six groups given above confirms the conclusions expressed by Zittel in his introduction to the Class Lamellibranchiata (p. 502, 1913 edition). He pointed out that the Silurian was characterized by the presence of palaeoconch, taxodont and older schizodont lamellibranchs. This exactly describes these collections except for the fairly large representation of the genera *Goniophora* and *Paracylas*. Genera from other sections of the Lamellibranchiata are rare.

Lamellibranchs of simple and primitive type without a denticulated hinge grouped by Neumayr among the Palaeoconchae made almost their only appearance in abundance in the late Silurian of Bohemia and of the Eastern Alps, and the Lower Upper Devonian (Portage) of the State of New York. "These peculiar genera never appeared before or since for the most part", wrote Clarke (1903). The few representatives of such Palaeoconchae as *Slava*, *Lunulicardium*, *Paracardium*, *Panenka* in the New South Wales Silurian link it with these faunas. Barrande's perhaps unnecessarily large number of species among these lamellibranchs does not seem to have been reviewed as have his taxodonts by Pfab (1934) and some of his Aviculas by Ruzicka (1949, 1950).

Among other Palaeoconchae from the Bowning district, numerous specimens, though first referred to the genus *Leptodomus*, have finally been determined as *Grammysioidea*, a subgenus of *Grammysia*, but without its characteristic fold and sulcus. Though Leriche (1912) considered the fold in *Grammysia* disappears with age and Beushausen (1895) quotes Hall as considering the transversal fold in *Grammysia* as of trifling importance, Williams and Breger (1916, p. 130) concluded, after a thorough investigation of the literature, that the name "*Grammysia*" ought to be restricted to those shells in which the fold and sulcus are developed at least in some stage of the life-history. Since these shells from Bowning under discussion in no case showed a fold, they were therefore not referred to *Grammysia*, but placed at first in *Leptodomus* because they resemble the type of *L. maccoyanus* Chapman in the National Museum, Melbourne, a specimen which Chapman tells us (1908, p. 17) was selected by McCoy, the author of the genus, as an example of *Leptodomus*. Against this allocation are the facts that McCoy established the genus for a Carboniferous fossil and that *Leptodomus* has a gaping shell, which does not seem to be the general case for these specimens. Although there are several examples in the collection from Bowning at the Australian Museum, of two valves in contact at the umbo but wide apart below, this condition may have developed after death because of the strong ligament, and cannot be taken as evidence of a gape.

Other possible ascriptions were rejected because the shells show no sign of the radial marking which characterizes *Pholadella* and *Rhytmya*. *Sphenomya* has no ligamental groove and *Sphenotus* has teeth. Opinions differ about the development of the lunule in *Cuneamyia*, Williams and Breger (1916, p. 131) saying it is weak and McLearn (1924, p. 96) the opposite. Consequently these particular shells seem best placed in *Grammysioidea*.

There are fewer representatives of true *Grammysia*. In these, the sulcus, though observable, is not pronounced. A *Grammysia* from Cootamundra is of use in dating the rocks from which it comes, since its characteristic fold runs from the beak to the post-ventral angle, not vertically downward from the beak. This condition is found only in *Grammysias* of pre-Devonian age (Williams and Breger, 1916, p. 136).

Lunulicardium is placed with the Palaeoconchae following Neumayr (Zittel, 1913, p. 437). *Palaeosolen* is also included there. Zittel, though he placed *Palaeosolen* in the family Solenidae, says "the Silurian forms heretofore referred to this family, do not seem to belong there".

Confusion has arisen in palaeontological literature over the *Ctenodonta-Palaeoneilo-Nuculites* group of Taxodont lamellibranchs, and specimens from New South Wales examined for this paper do little towards establishing clear distinctions. After the priority of Salter's genus *Ctenodonta* over Hall's *Tellinomya* was recognized (Oehlert, 1888; Beushausen, 1895), palaeontologists failed to agree as to the placing of fossils in *Ctenodonta* or in Hall's later genus *Palaeoneilo*. In synonymies listed by Mailleux (1932, 1937) the same species is seen to have passed from one genus to the other and back again more than once. Beushausen (1895) divided the genus *Ctenodonta* into several subgenera, one being *Palaeoneilo* and another *Tancrediopsis*. Clarke (1907) on the other hand made *Nuculites* a subgenus of *Palaeoneilo*. *Ctenodonta* is also confused with *Nucula* and with *Tellinites* (Williams and Breger, 1916, pp. 163, 173) as well as with *Nuculites*. Several specimens in the Sedgwick Museum at Cambridge are labelled *Ctenodonta* (? *Nuculites*). Further, *Nuculites* is generally acknowledged as synonymous with *Cleidophorus* (*Clidophorus* of some American authors) and *Cucullella*.

The main reason for these uncertainties is probably the condition of the palaeozoic fossils which are often somewhat battered casts or moulds, such as are many of those described here. The casts cannot always be entirely detached from rock matrix, so that their hinges are not completely revealed. In such cases portions of concentric growth lines near the cardinal edge can look not unlike the clavicular ridge of *Nuculites*, which is often quite short in that genus. Ulrich (1897) has referred to the difficulty in some cases of establishing the anterior end of a palaeozoic shell.

After protracted and careful study of Nuculoid shells in these collections, it has been decided that none can be separated as *Otenodonta* except those of the subgenus *Tancrediopsis*.

Species of *Nuculites*, *Nuculana* and *Nuculopsis* have been recognized. In the case of the last, since most specimens are preserved as external casts of the two valves joined and closed, the presence of the chondrophore cannot be determined. However, Girty (1911), the founder of the genus, is not absolutely certain of its presence, saying that the taxodont teeth of his type (which is not figured) are not interrupted by it, but that it is probably below them. In any case this feature cannot always have been used in identification, since of Fleming's twenty-two type specimens of *Nuculopsis gibbosa* in Edinburgh, Schenck (1934) tells us all but one have the two valves tightly closed, as are all fifty-five in the Musée at Brussels.

The correct placing of the species described here as *Actinopterella formosa* has been difficult. It is more erect and symmetrical than other species of the genus described in this paper. Its allocation to *Aviculopecten* was thought of, but Newell (1937), who has made an exhaustive study of that genus, states that it does not occur below the Lower Carboniferous. Then its placing in the Silurian genus *Palaeopecten* was considered. Williams (1913) established this genus for *Avicula? danbyi* McCoy from the Upper Ludlow of Westmoreland. He stated that the type shell was nearly symmetrical in outline. Though he subsequently (Williams and Breger, 1916) placed *Avicula? danbyi* in the synonymy of *Follmanella* (presumably because of the backward prolongation of some specimens), one specimen of *Avicula danbyi* var. in the Sedgwick Museum is similar to *Actinopterella formosa*, n. sp., in outline and ornament. Its length and height are each 20 mm., whereas all but about six of nearly one hundred measurements of Late Palaeozoic species of *Aviculopecten* given by Newell (1937) have greater height than length. In *Actinopterella formosa* the length is the greater.

Etheridge and Dun (1906) used the word *Palaeopecten* not in the generic sense but as a collective term for pectinoids of Upper Palaeozoic age.

The terms *Modiolopsis* and *Modiomorpha* have often been used interchangeably. Williams and Breger (1916, p. 216) consider Upper Palaeozoic Modiolopsoids are dentate and therefore should be placed in *Modiomorpha*, whereas Lower Palaeozoic shells of this type are edentulous and conformable with *Modiolopsis*. However, this rule is not universally followed. *Cypricardella* which might be confused with *Modiomorpha elongata*, n. sp., from Taralga is squarer, while *Colpomya* has hinge and basal margin sub-parallel and a stronger umbonal ridge than *Modiolopsis*.

Cyrtodontia is included among the Schizodonta. It is referred to by Williams and Breger (1916, p. 153) as among the "schizodontic shells".

PREVIOUS INVESTIGATIONS.

The Silurian lamellibranchs of New South Wales have been mentioned in books and papers of the geology of the State or sections of it by W. B. Clarke, De Koninck, R. Etheridge, jr., Jenkins, Shearsby, Sussmilch, David and Browne, John Mitchell, I. A. Brown, Fletcher, Gill and others, but systematic descriptions are rare.

De Koninck (1898) described *Pterinea ampliata* and *P. pumila* from the Silurian and *P. laminosa* and other lamellibranchs from the Devonian. However, it is possible some confusion between Silurian and Devonian specimens occurred during transit to De Koninck, because his description of *P. laminosa* is considered (Chapman, 1909) to refer to a lamellibranch abundant in the Silurian of Yass, though listed by De Koninck among the Devonian fossils. As is well known, the types of his descriptions were destroyed by fire.

From a specimen of shale of Silurian age from the Bombala district which was presented to the British Museum, Etheridge, jr. (1880), described *Anodontopsis australis*. Among Silurian lamellibranchs in the Australian Museum collections, are slabs of shale from Yass profusely covered with badly preserved shells and labelled in

1902, possibly by Etheridge himself, *Anodontopsis australis*. This lamellibranch is almost certainly that which is commonest in the Yass beds at Yass where it is associated with the ostracod *Leperditia*. Chapman (1909), in a paper on the ostracod, referred to the lamellibranch as that which De Koninck had described as *P. laminosa*, but which was probably the early pterinoid form, *Rhombopteria*. It is described as *Rhombopteria* in this paper. When McCoy (1851) established the genus *Anodontopsis* he included in it various species which were later considered by Chapman (1908) and Williams and Breger (1916) to belong to several different genera, none of which was *Anodontopsis*.

A provisional list of lamellibranch genera from Cootamundra was given by Mr. E. D. Gill (1940) in a paper describing a trilobite from the same locality.

Mr. H. O. Fletcher (1943) has described and figured *Conocardium davidus* Dun from the Silurian of Oakey Creek, near Molong.

Cosmogoniophora sinuosa has been described and figured (Sherrard, 1952).

Dr. N. C. Stevens (1959) has referred to a discovery of portions of a large lamellibranch at Cooleman Caves. Through the courtesy of Dr. Stevens, I have seen this specimen. Though not certainly identifiable, it looks as if it might be related to the *Panenka-Lunulicardium* group.

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OCCURRENCES OF LAMELLIBRANCHS.

I.—On the same slabs as *Monograptus nilssoni* and *M. bohemicus* at Hatton's Corner, Yass: *Actinopterella minuta*, n. sp., very rare; *Pteronitella rugosa*, n. sp., very rare; *Cardiola (Stava) fibrosa* Sow., very rare.

Age: Lower Ludlow (Zone of *M. nilssoni*, Zone 33).

II.—Yass Series at Yass: *Rhombopteria laminosa* (De Koninck), very common; *Orthonota* sp., very common; *Ctenodonta (Tancrediopsis) victoriae* (Chapman), common; *Grammysia compressa*, n. sp., common; *Actinopterella minuta*, n. sp., rare; *A. formosa*, n. sp., rare; *Paracyclas orbiculata*, n. sp., rare; *Goniophora* sp., rare.

These are in strata conformably below beds of the zone of *M. nilssoni* (Zone 33).

III.—Middle Trilobite Bed, Bowning: *Goniophora* sp., very rare.

This bed immediately overlies the zone of *M. nilssoni* (Zone 33).

IV.—Upper Trilobite Bed, Bowning: *Nuculites pseudodeltoides* Reed, common; *Ctenodonta (Tancrediopsis) victoriae* (Chapman), common; *Grammysia (Grammysioidea) declivis*, n. sp., common; *Grammysia ampla*, n. sp., very rare; *Modiolopsis elongata*, n. sp., very rare; *Paracyclas orbiculata*, n. sp., very rare.

This bed is at the top of the Silurian (Browne, 1954).

V.—Bowning (Mitchell Collection): *Nuculites pseudodeltoides* Reed, common; *N. scissa*, n. sp., common; *Ctenodonta (Tancrediopsis) victoriae* (Chapman), common; *C. (T.) elegantula*, n. sp., rare; *C. (T.) minuta*, n. sp., common; *Grammysia (Grammysioidea) declivis*, n. sp., common; *Actinopterella lamellosa*, n. sp., rare; *A. minuta*, n. sp., rare; *Nuculopsis triangula*, n. sp., common; *Rhombopteria laminosa* (De Koninck), rare; *Lunulicardium* sp., rare; *Modiolopsis elongata*, n. sp., rare; *Paracardium cf. filosum* Chapman, rare; *Cypricardinia contexta* Barr., very rare.

The strata in which these occur are probably near the zone of *M. scanicus* (Zone 34).

VI.—Silverdale.

(a) Portion 36, Par. Derringullen, near Bowning: *Nuculopsis triangula*, n. sp., rare. This occurs in the same bed as *M. scanicus*.

(b) Limestone Creek, Silverdale (Fletcher, 1943): *Conocardium* sp. This occurs in a bed immediately underlying the zone of *M. scanicus*.

VII.—Nanima-Bedulluck District (Sherrard, 1952).

(a) Nanima Trig.: *Cosmogoniophora sinuosa* Sherrard, very common; *Rhombopteria laminosa* (De Koninck), very common; *Paracyclas orbiculata*, n. sp., rare.

These are probably of Upper Ludlow age.

(b) Spring Range road, Ginninderra (Sherrard, 1952): *Cyrtodonta lissa*, n. sp., very rare; ? *Nuculopsis* sp., rare.

These occur in strata conformably underlying strata with *M. testis* var. *inornatus* (Zone 31).

VIII.—Forest Creek, Boambolo, south-west of Yass: *Cyrtodonta lissa*, n. sp., common; *Grammysia compressa*, n. sp., common; *Paracyclas orbiculata*, n. sp., rare; *Grammysioidea declivis*, n. sp., rare; *Goniophora* sp.

IX.—Bowning, opposite Advance Hall: *Nuculopsis triangula*, n. sp.

X.—Barrandella Shales, Yass District.

(a) Black Range road, east of Derringullen Creek bridge: ? *Nuculopsis* sp.

(b) Wee Jasper road, 6 miles south of Yass: cf. *Mytilarca* sp.

The Barrandella shales are of Wenlock age (Brown and Sherrard, 1952).

XI.—Bombala District.—*Lunulicardium quedongensis*, n. sp.; *Anodontopsis australis* Etheridge, jnr. (1880).

Dr. Dorothy Hill (1943), who has seen in the Australian Museum, but not described, a collection of corals from the same locality as *Lunulicardium quedongensis* at Quedong near Bombala, considers "this fauna is near to or possibly identical in age with that of Yass".

XII.—Near Cootamundra.

(a) Near Cootamundra: *Nuculites scissa*, n. sp., very common; *Nuculana striata*, n. sp., very common; *Palaeosolen planus*, n. sp., very common; *Leiopteria gregaria*, n. sp., very common; *Grammysia obliqua* (McCoy), rare; *Paracyclas orbiculata*, n. sp., rare; *Tancrediopsis delicatula*, n. sp., rare; *Actinopterella* sp., rare; *Rhombopteria obliqua*, n. sp., rare.

Since *Grammysia obliqua* (McCoy) is of pre-Devonian age (Williams and Breger, 1916), this collection's age is determined.

(b) Temora road, 2½ miles from Cootamundra: *Paracardium* cf. *filosum* Chapman, rare; *Panenka cingulata* Chapman, rare; *Rhombopteria obliqua*, n. sp., rare.

Specimens of the Upper Silurian trilobite, *Gravicalymene cootamundrensis* Gill (1940) from Oak's Creek, Cootamundra, in the National Museum, Melbourne, are preserved in fine, white siltstone which seems identical with the matrix in which collection XII (b) occurs. All specimens from Cootamundra in this Museum and in the Australian Museum, Sydney, were presented by the late Mr. W. E. Williams of Cootamundra.

XIII.—Taralga: *Modiolopsis elongata*, n. sp.

XIV.—Oakey Creek, near Molong: *Conocardium davidus* Dun (Fletcher, 1943).

XV.—Dangelong, 14 miles east of Cooma: *Pterinea ampliata* De Koninck (1898). The age is given as Llandovery by De Koninck.

The Yass and Bowning assemblages of lamellibranchs recall those recorded from Melbournian and Yeringian localities in Victoria, while there is a striking similarity between the list of genera recorded from Yass and Bowning and that from the Upper Ludlow of Woolhope, England (Reed, 1927), and to a less extent to that from Bulth

(Straw, 1937) and from Arisaig, Nova Scotia (McLearn, 1924). The Cootamundra assemblage recalls somewhat that from the Devonian locality at Buchan Caves, Victoria (Talent, 1956).

Just as Hind (1910) wrote of Silurian lamellibranchs from Girvan, Scotland, it has been asserted that Australian faunas from the Silurian have a Devonian aspect, but wider collecting will be necessary before an authoritative statement can be made on this question so far as the lamellibranchs of New South Wales are concerned, since, apart from the collections from Cootamundra and a few of the species from the Yass-Bowling district, their occurrence is sparse. There would seem to be a facies control of the preservation in abundance of individuals. It is noticeable that lamellibranchs which are found prolifically in the Silurian of New South Wales occur in mudstones or siltstones where they may be piled and even crushed on top of one another. In a sandy facies, however, they are generally found singly.

The fossils occur most commonly as external casts (steinkerns), that is, reproductions in infilled material of the external shapes of the original shell on which the external markings have often been impressed through the shell. Very rarely fragments of the external shell remain on this cast also. The external casts may be detached from rock matrix or not. Less commonly the mould is preserved, that is, the hollow in which the fossil once rested and on which the external markings are shown.

SYSTEMATIC DESCRIPTIONS.

PALAEOCONCHA.

Genus GRAMMYSIA De Verneuil.

GRAMMYSIA OBLIQUA McCoy, 1855. (Pl. xix, fig. 12.)

British Palaeozoic Fossils, p. 182 and Pl. xvii, fig. 2, Mem. Geol. Soc. G.B.

Cast and mould of exterior of right valve; inequilateral, cylindrical, rather flat. Umbo prominent in anterior third. Narrow distinct fold passes from umbo to post-ventral angle. A fold in this position instead of in the usual position for *Grammysia* which is from the umbo to the centre of the ventral margin is only found in *Grammysias* of pre-Devonian age (Williams and Breger, 1916, p. 136), and can be seen in McCoy's type from Llangibby Castle, Usk, Wales, Specimen No. 24101, Geol. Surv. Great Britain Collection. In the specimen under description there is a faint sinus in the ventral margin behind the fold. Regular concentric growth lines (2 to 1 mm.) pass across valve uninterrupted by fold. Lunule and escutcheon present. Anterior adductor scar present but not posterior. Length 12 mm., height 6 mm.

Locality: Cootamundra.

McLearn (1924) illustrates *Grammysia obliqua*, Stonehouse formation, Arisaig, Nova Scotia, with a similar fold. The plate of *G. obliqua* from near Edinburgh (Lamont, 1954) does not resemble *G. obliqua* from Cootamundra.

GRAMMYSIA AMPLA, n. sp. (Pl. xix, fig. 1.)

Holotype: Australian Museum No. F48878.

Cast of one left valve, inequilateral, ovate; dorsal margin nearly straight, anterior margin curved, ventral margin straight except for sinus at post-ventral angle where fold emerges, posterior margin rostrate. Umbonal slope low. Umbo near anterior-dorsal angle, not prominent. Rather indistinct sulcus passes from umbo to post-ventral angle. Concentric growth lines on body of valve only seen in a band about 5 mm. wide parallel to ventral margin, though better developed on post-cardinal slope. Lunule and escutcheon present. Muscle scars not seen. Length 32 mm., height 20 mm., depth 4 mm.

Locality: Upper Trilobite Beds, Chapman's Selection, Bowling.

Though this species has an oblique fold like *G. obliqua*, the two species differ greatly in size and ornament. *G. ampla* resembles *Cuneamya holmesi* Lamont (1954) from near Edinburgh.

GRAMMYSIA COMPRESSA, n. sp. (Pl. xix, fig. 3.)

Holotype: Sydney University Geological Department No. 8572.

External casts of both valves joined. Equivalve, inequilateral. Anterior end truncated but broad, posterior narrow and rostrate. Prominent well-rounded slope from umbo to post-ventral angle. Ventral margin with shallow concave sinus. Umbones almost terminal, curved over and meeting across hinge-line. Very slight indication of fold from umbo to centre of ventral edge. Ornamented by very strong concentric ribs, 6 per cm. Well-developed lunule and escutcheon. Valves appear to gape slightly at anterior and posterior ends, but this may have taken place after death. No internal features can be seen. Length 30 mm., height 18 mm., depth 7 mm.

Locality: Yass Beds, Yass.

This species can be compared with *G. arcuata* Conrad.

Subgenus GRAMMYSIOIDEA Williams and Breger.

GRAMMYSIOIDEA DECLIVIS, n. sp. (Pl. xix, figs. 2, 15.)

Holotype: Australian Museum No. F27901.

Equivalve, inequilateral, trigonal shape. Posterior wider than anterior end. Anterior-cardinal angle bent back towards umbo forming strongly marked lunule. Ventral margin slopes downward towards posterior angle with more or less well-developed sinus. Posterior margin truncated. Hinge line long and slightly arched. Umbones in anterior third, prosogyrate, very prominent, in contact over pronounced ligamental furrow along hinge line. Strongly developed rounded ridge runs from umbo to post-ventral angle with almost concave furrow between it and dorsal margin. No internal features can be described as all specimens are external casts. Hinge edentulous. Ornament: well-marked concentric ridges, uninterrupted by a sulcus. Length 20 mm., height 14 mm., depth 3 mm.

Locality: Bowning.

Genus PALAEOSOLEN Hall.

PALAEOSOLEN PLANUS, n. sp. (Pl. xix, fig. 4.)

Holotype: Australian Museum No. 32976.

Preserved as moulds and casts, single and joined. Possibly distorted by flattening. Transversely elongate, very inequilateral, equivalve. Cardinal and basal margins nearly parallel and equal. Posterior margin truncate, anterior margin with pronounced flare and re-entrant notch, causing gape about half-way between cardinal and ventral margins. Inside cardinal edge is a flattened strip widening to 1 mm. at post-cardinal angle. Concentric striae parallel to posterior and ventral margins and gathered tightly into anterior notch. More prominent striae at 1 mm. intervals with several finer in between. Low umbo at anterior tenth. Low carina from umbo to posterior-ventral angle. Length 30 mm., height 10 mm., depth about 2 mm.

Palaeosolen planus resembles the plate of *P. simplex* Clarke (Clarke, 1907) and also specimen No. 7869, National Museum, Melbourne, *Orthonota australis* Chapman.

Locality: As for *Grammysia obliqua*.

Genus ORTHONOTA Conrad.

Cf. ORTHONOTA sp.

Numerous casts of joined valves, extremely poorly preserved. Tumid. Rectangular outline, elongated, dorsal and ventral margins nearly parallel. Posterior margin truncated. Prominent post-umbonal slope. Umbo depressed, at anterior third. Suggestion of concentric growth lines. Length 20 mm., height 8 mm., depth 3 mm.

Locality: Yass Beds; Cliftonwood, Portion 100, Par. Yass.

Genus PANENKA Barrande.

PANENKA CINGULATA Chapman. (Pl. xix, fig. 5.)

One left valve preserved as a mould of the external surface. Regularly triangular in shape. Posterior edge concave, anterior covered. Ventral margin evenly rounded. Surface of shell undulatory. Convex near umbo and concave near ventral margin.

Umbo fairly prominent, gibbous. About 16 regularly rounded deeply indented radial ribs pass from umbo to central margin. These are crossed by about three indefinite, concentric undulations. Length 15 mm., height 10 mm., depth 3 mm.

Locality: Cootamundra.

Genus LUNULICARDIUM Munster.

LUNULICARDIUM QUEDONGENSIS, n. sp. (Pl. xix, fig. 6.)

Holotype: Australian Museum No. F23306.

External cast of valve of which one side is obscured by limestone matrix, apparently trigonal outline and inequilateral, very convex with triangular reflexed flange near post-dorsal angle cutting off posterior margin. Umbo somewhat broken, apparently sub-central and strongly gibbous, overhanging hinge-line. Strongly marked radial ribs, 5 in 10 mm., about 0.1 mm. deep, seen most prominently over central and ventral region, not near umbo. Intercalation of extra ribs seen near ventral margin. Faint chevron-shaped concentric markings on flange and neighbouring portions of shell. Development of granules seen in remaining fragment of external shell. No internal characters can be seen. Some authors, including Munster, the founder of the genus, consider the flange is developed to the anterior of the beak, becoming a lunule. Length 40 mm., height about 30 mm., depth 19 mm.

Locality: Quedong, near Bombala.

Genus CARDIOLA Broderip.

Subgenus SLAVA Barrande.

CARDIOLA (SLAVA) FIBROSA Sow. (Pl. xix, fig. 13.)

One valve (left) external cast, oval outline continuous except along hinge-line which is shattered. Umbo broken but apparently nearly central. Very strongly marked concentric ridges, separated by grooves, the valve thus being divided into five low steps, each of which is slightly arched and about 3 mm. wide at greatest width, but closer together near cardinal margin. Faint, discontinuous rounded radial striae, 2 mm. apart, more strongly marked over erect body. Between each radial, three series of pores. Neither muscular impressions nor pallial line detectable. Length 12 mm., height 16 mm., depth 2 mm.

This specimen closely resembles British Museum specimen No. L28844, *Slava* aff. *bohemicus* from Pl, Kosor, with which it has been directly compared, and is of much the same size. L28844 is labelled "a juvenile form". *Slava imperficiens* Barr. (283, Taf. III, Heritsch, 1929), Kokberg, Eastern Alps, is similar. *Slava fibrosa* when adult shows a fringe of fine radiating striae just inside the ventral margin. This cannot be seen on the Yass specimen, though curiously enough the lamellibranch overlies on one side a nautiloid which shows just this ornament. Barrande says young *Cardiola fibrosa* have no fringe.

Locality: Hatton's Corner, Yass. On slab with *Monograptus bohemicus*.

Genus PARACARDIUM Barrande.

PARACARDIUM cf. FILOSUM Chapman. (Pl. xix, fig. 14.)

Preserved as right valve, thin-shelled. Anterior and posterior edges slope almost equally with long regular convex ventral margin. Shell nearly flat. Umbo depressed, central. Prominent radial striae from near beak to ventral edge which is denticulate. Radial striae more strongly impressed near ventral margin than dorsally. Radii crossed by poorly defined concentric rugosities, 2 mm. apart. No internal characters visible. Length 11 mm., height 12 mm., depth 2 mm.

Locality: Bowning.

Genus TELLINOPSIS Hall.

TELLINOPSIS FLABELLIFORMIS, n. sp. (Pl. xix, fig. 18.)

Holotype: Australian Museum No. F29393.

Material: One well-preserved valve retaining a small portion of its smooth, external surface. Undistorted, almost isosceles triangle with dorsal margin very slightly arched

at umbo making greatest length of valve. Pronounced folds from umbo to both antero-dorsal and post-dorsal angles leave depressions between the folds and the dorsal margin which slopes from the umbo to the antero- and post-dorsal angles. Almost unbroken curve around anterior, ventral and posterior margins interrupted only by slight emarginations. Umbo nearly central and prominent above hinge, over which it protrudes very slightly. It is difficult to determine in which direction the umbo points. Williams and Breger (1916), in describing *Tellinites* (equivalent to *Tellinopsis*), say the umbo is directed vertically, which seems to be the case here. Discontinuous concentric striae, about 1.5 mm. apart, are noticeable near the ventral margin, but not on the body of the shell. Faint suggestion of radial markings. Muscle scars and pallial line cannot be seen. Hinge without teeth and with distinct external groove presumably for ligament. Length 27 mm., height 14 mm., depth 4 mm.

Locality: Bowning.

TAXODONTA.

Genus CTENODONTA Salter.

Subgenus TANCREDIOPSIS Beushausen.

TANCREDIOPSIS VICTORIAE (Chapman). (Pl. xix, fig. 7.)

Palaeoneilo victoriae Chapman, 1908, 33; Pl. III, figs. 47-49.

Material preserved in various ways: as casts of both valves in contact or of both valves joined only at umbo and splayed out by pressure; as single valves remaining in rock matrix, also as a mould. Most of these are distorted by pressure from above or from both sides until some valves in contact are flattened to wafers. Undistorted shells are equivalve, inequilateral, of cylindrical shape with posterior section about $1\frac{1}{2}$ times length of anterior section; while anterior is nearly twice as wide as posterior, so that ventral margin slopes posteriorly upward with sometimes a concave flange bounding its edge. Posterior margin rostrate, anterior rounded. From the umbo an almost angular ridge runs to the postero-ventral angle bounding a large escutcheon above it. Umbones nearly central, depressed, not full, prosogyrate, curving inward over hinge-line. Ornamented by very strongly marked concentric ridges (12 in 5 mm.), rounded. These are less prominent towards the ventral edge. Ligamental groove. Muscular impressions and pallial line cannot be seen. Prominent taxodont teeth, 2 per mm., evenly spaced and equal in size on posterior and anterior sides of umbo, none beneath it, half-moon shaped with open end towards umbo. Length 23-19 mm., height 10-8 mm., depth 2-3 mm.

Locality: Yass and Bowning, common in both Yass and Hume Beds.

By comparison with the holotype of *Tancrediopsis victoriae* (Chapman) No. 7915 National Museum, Melbourne, specimens from Yass and Bowning can be identified as conspecific.

Reed (1931) figures *Tancrediopsis ludensis*, sp. n., from the Lower Ludlow of the Ludlow district of England, drawing attention to its alliance to *T. victoriae* (Chapman). McLearn (1924) compares his *T. altistriata* from Ross Brook formation, Arisaig, Canada, with *T. victoriae* (Chapman) also. Mailleux's (1937) plates of *Palaeoneilo maureri dunensis* Beushausen from Lower Devonian of Belgium are also comparable with *T. victoriae* from Yass.

TANCREDIOPSIS DELICATULA, n. sp. (Pl. xix, fig. 20.)

Holotype: Australian Museum No. F27931.

Similar oval outline to *T. victoriae* with anterior margin rounded and posterior margin rostrate. Umbo at anterior third. Post-umbonal ridge prominent, rounded. A flange swings round outer margin from cardinal-anterior angle and is doubled back into a furrow round ventral margin. Ornament: very fine delicately etched concentric striae about 10 to millimetre. Length 11 mm., height 5 mm., depth 1 mm.

Locality: Bowning.

TANCREDIOPSIS MINUTA, n. sp. (Pl. xix, fig. 16.)

Holotype: Australian Museum No. F29429.

There are a number of these small shells which scarcely differ from *T. victoriae* except in size and proportion of height to length. Length of type 10 mm., height 6 mm. *T. lauta* McLearn is similar, though narrower.

Locality: Bowning.

Genus NUCULITES Conrad.

NUCULITES PSEUDODELTOIDES Reed. (Pl. xix, fig. 17.)

Material preserved in casts and moulds of single valves, some crushed others undistorted. Equivalve, slightly inequilateral, nearly circular margin, but cardinal margin somewhat flattened towards posterior angle because umbonal slope falls to a furrow before reaching cardinal margin. Anterior and ventral margins rounded, posterior margin slightly rostrate. Umbones central, slightly raised above cardinal margin, would just meet if two valves preserved in contact. Slope from umbo to all margins smoothly convex. Faint concentric striae near ventral margin, six per millimetre. Anterior adductor scar distinct, large, anterior to clavicular ridge, close to ventral margin, rather deep; posterior adductor scar indistinct. Pallial line simple. Very short clavicular ridge, about one-fifth height of shell. Many taxodont teeth which can be seen to continue beneath the beak in some specimens and which increase in size away from umbo. Teeth in form of acute angles with the apices directed anteriorly as is characteristic of *Nucula applanans* Barrande according to Pfab (1934), now *Ctenodonta applanans*, an Ordovician species. Length 17 mm., height 13 mm., depth 3 mm.

Locality: Bowning.

Undoubtedly the distinction between these shells and *Ctenodonta* is very slight, since the clavicular ridge is so short and shallow. Clarke refers (1907, p. 232) to a species of *Nuculites* with only the "barest indication of an anterior clavicle", while Reed (1927), in comparing his *Nuculites pseudodeltoides* with the holotype of *Nucula deltoidea* Phillips, adds "there seems no clavicular ridge". Nevertheless, the plate of *N. deltoidea* Phillips (Mem. Geol. Surv. G. Brit., II, 1848, Pl. XXII, 5) is very like the Bowning specimens of *N. pseudodeltoides*.

NUCULITES SCISSA, n. sp. (Pl. xix, fig. 19.)

Holotype: Australian Museum No. F27897.

Preserved in sandstone and siltstone as casts and moulds of left and right valves. Holotype, cast of a right valve. Inequilateral, equivalve, cylindrical. Cardinal margin arched; anterior rounded, ventral slightly indented by wide shallow sinus; posterior, rostrate. Posterior and anterior ends of about equal width. Post-umbonal slope very prominent, making shell almost cylindrical. Low umbones at anterior third, protrude slightly above hinge. Faint concentric striae near ventral margin, scarcely visible on umbonal slope. Small distinct adductor impressions seen on some moulds. Pallial line faint. Prominent vertical clavicular slit at anterior end of cast (ridge on moulds), strong ligamental furrow seen on some casts. Series of taxodont teeth, V-shaped with acute angle directed anteriorly. Holotype length 12 mm., height 7 mm., depth 4 mm. of one valve.

Locality: Upper Beds, Bowning.

Specimens of *Nuculites* from Cootamundra are sometimes considerably larger than those from Bowning, being more than 20 mm. long in some cases, but many of them are shattered and enlarged by squashing and being packed on top of each other. Since some relatively undamaged moulds from this locality agree closely with the holotype, all are included in this species.

Genus *NUCULOPSIS* Girty.*NUCULOPSIS TRIANGULA*, n. sp. (Pl. xix, fig. 21.)

Holotype: Australian Museum No. F29410.

Trigonal outline, slightly inequilateral, equivalve; dorsal margin slightly arched, passing by sharp angle at either end to convex posterior and anterior margins. Ventral margin also convex. Shell tumid. Both ends of equal height. Umbones very prominent, prosogyrate, pointed, central to one-third distance from anterior; nearly in contact over narrow area, swollen. Trace of external ligamental groove. Faint concentric striae seen near ventral margin. Pallial line simple, small raised adductor muscles, taxodont teeth sometimes seen, as in mould from Portion 36, Par. Derringullen. Length 10 mm., height 8 mm., depth 3 mm.

Locality: Bowning.

Ctenodonta chapmani Opik (Opik, 1953, Pl. VI, fig. 37), Heathcote, Victoria, seems similar to *Nuculopsis triangula*, n. sp., in shape, but is smaller.

Genus *NUCULANA* Link.*NUCULANA STRIATA*, n. sp. (Pl. xix, fig. 22.)

Holotype: Australian Museum F32995.

Preservation in large numbers as casts and moulds of single valves. All are small, with the largest about 15 mm. long and 6 mm. high, and ranging down to 6 mm. long and 4 mm. high. Valves often shattered by flattening, but apparently originally equivalve, inequilateral. Undamaged external casts show somewhat swollen valves. Elongated posteriorly to rostrate projection. Ventral and anterior margins rounded. Cardinal margin in low arch. Posterior end narrower than anterior. Rounded umbonal-posterior ridge sloping in one direction to cardinal margin and in other to slight hollow which makes sinus on ventral margin. Umbones not prominent, internal moulds suggest opisthogyrate character; nearly central, but slightly anterior. Small, squarish posterior adductor scar rather deeply excavated. Small pallial sinus. Small, regular, taxodont teeth which are interrupted at the centre as can be seen in some specimens. Strongly marked concentric striae, about 0.6 mm. apart, with more finely marked striae between them.

N. striata is extraordinarily like plates of *Leda acuta* in Gardner (*U.S.G.S.*, Prof. Pap. 142, 1926, Pl. II, figs 13-16) which is Tertiary.

Locality: As for *Grammysia obliqua*.

SCHIZODONTA.

Genus *RHOMBOPTERIA* Jackson.*RHOMBOPTERIA LAMINOSA* (De Koninck). (Pl. xix, fig. 25.)*Pterinea laminosa* De Koninck, 1898.

Neotype: Sydney University Geological Department No. 8570.

Preserved in sandy matrix as external and internal casts and moulds of single valves. Shells are often crowded together so that they have become cracked and distorted by flattening. Inequilateral, inequivalve, left valve has a low, oblique and convex umbonal slope from cardinal to ventral margin. Right valve flat to resupinate, though this may be partly due to pressure. Body oblique, about 15 degrees to vertical. Large, triangular posterior ear, very small anterior ear. Hinge-line horizontal posteriorly, then slightly arched, less than greatest length of shell. Very shallow sinuses sometimes seen below antero-cardinal angle and more rarely below post-cardinal angle, beneath which anterior, posterior and ventral margins form an unbroken convex curve. Surface of posterior ear concave as seen in internal mould, separated from body of shell by pronounced ridge. Umbo in anterior quarter, scarcely projects above hinge. Low and blunt. Ornament: Angular, concentric lamellar folds (2-3 per mm.) seen in fragment of external shell. Moulds and casts also show irregular, concentric laminations and a few, faint broken radial striae. The rough

surface produced by these folds makes the detection of adductor scars almost impossible. Ligamental area narrow groove, strongly striated at right angles to its length by growth lines. Small raised grooves slightly behind the umbo may represent posterior lateral teeth. Length 18 mm., height 18 mm., depth about 2 mm.

Locality: Yass Beds, Yass.

Rhombopteria laminosa is undoubtedly difficult to distinguish from *Leiopteria gregaria* except for the resupinate right valve of *Rhombopteria*.

RHOMBOPTERIA OBLIQUA, n. sp. (Pl. xix, fig. 26.)

Holotype: Australian Museum F32985, F32986 (counterparts).

Well-preserved, undistorted cast and mould of left valve. Inequilateral, oblique body 20 to 40 degrees from vertical. Slightly developed anterior and posterior ears separated by very shallow sinuses from otherwise uninterrupted convex curve round anterior, ventral and posterior margins. Umbones gibbous, projecting strongly over hinge-line at anterior third. Pronounced ridge from umbo to ventro-posterior angle. Hinge-line interrupted by prominent umbo. No ligamental groove. Large shallow anterior adductor scar connected by faint pallial line to rectangular posterior scar on wing. Strongly marked concentric lamellar growth lines 1 mm. apart on body of shell, but bunched closely together on dorsal margin near anterior and posterior angles. A few interrupted radial ridges near ventral margin. Length 10 mm., height 10 mm., depth 4 mm.

These shells have not the large posterior wing, completely separated anterior wing and ligamental groove of *Leiopteria*, nor the continuous radial striae of *Actinoptereella*. They have not the circular outline of *Megambonia*. They resemble Clarke's (1903) plate 12, figs. 1-8, of *Posidonia mesacostalis*. Weigelt (1922; in Kegel, 1925) asserts that *Posidonia* is a synonym of *Rhombopteria* and results from a special facies.

Locality: As for *Grammysia obliqua*.

Genus ACTINOPTERELLA Williams.

ACTINOPTERELLA MINUTA, n. sp. (Pl. xix, fig. 23.)

Holotype: Australian Museum No. F48880; right valve No. F29403.

Several well-preserved left and one right valves. External moulds and casts. Both valves convex, straight hinge-line which is greatest length of shell. Relatively large, slightly convex upward, posterior ear marked off from body of shell by furrow. Anterior ear is small, more convex than posterior, and is separated from anterior margin by sinus and from body of shell by furrow. Posterior margin is concave with comparatively large sinus marking off ear. Ventral margin rounded. Slope continuous from umbo to post-ventral angle. Body oblique, between 30 and 50 degrees to vertical. Prominent umbo rising slightly above hinge-line at anterior third. About 30 to 35 strongly marked rounded radial ribs on body and sometimes on posterior ear of left valve but not on anterior ear. On right valve very faint radial ribs at ventral margin of body and on posterior ear. About 20 concentric lamellae occur distinctly on anterior ear and the anterior section of body, especially of left valve, but very faintly on posterior ear. These are less well developed than the radial striae. Well-marked byssal sinus. Narrow ligamental area. Neither muscular impressions nor pallial sinus can be distinguished. Posterior lateral tooth parallel to and just below ligamental area. Two small cardinal teeth in front of umbo. *Actinoptereella minuta* resembles closely in appearance and size Barrande's plate of *Avicula ? Pterinea migrans* (Vol. VI, Pl. 229, fig. XII, 1-12) which Ruzicka (1950) names *Leiopteria (Actinopteria) migrans migrans* from Zone e gamma (Zone of *Monograptus hercynicus* and *M. uniformis*). Ruzicka refigures it on Tab. I, Pl. I (18), fig. 5. Also comparable with *Actinoptereella minuta*, n. sp., are *Actinopteria communis* (Maryland Geol. Surv. Dev., Pl. LXXVI, fig. 4) and *Actinoptereella peninsularis* from the Devonian (La Rocque, 1950). Length 9 mm., height 6 mm.

Locality of Holotype: Hatton's Corner, Yass (Zone of *Monograptus nilssoni*).

ACTINOPTERELLA LAMELLOSA, n. sp. (Pl. xix, fig. 9.)

Holotype: Australian Museum No. F2750.

Left valves poorly preserved. Anterior ear cannot be seen. Hinge-line not greatest length of shell. Body very convex, posterior ear less convex than body. Body oblique, about sixty degrees to vertical. Umbo raised 5 mm. above cardinal line, directed anteriorly. Concentric lamellar wrinkles, radiating striae, rounded in groups of two, with furrow between. Ornamentation strongest on body, very faint on posterior ear. Body too oblique for *Limoptera*, for which it might otherwise be taken. Length 25 mm., height 25 mm., depth 8 mm.

Locality: Bowning.

ACTINOPTERELLA FORMOSA, n. sp. (Pl. xix, fig. 28.)

Holotype: Sydney University Geological Department No. 8571.

One left valve, external cast, well preserved, undistorted. Straight hinge-line, well-developed anterior and posterior ears, the latter twice the size of the former. Anterior ear very slightly convex upward, separated from the body of shell by radial furrow. Posterior ear flat. Outline nearly semi-circular except for shallow relatively large sinus on anterior margin beneath ear. Body nearly erect and almost flat. Umbo depressed, below hinge-line at anterior third. Rounded radial costae on body (except on umbo) and posterior ear, not on anterior ear except along margin. Around margin 48 costae on body, 24 on posterior ear having increased by bifurcation on both and apparently by implantation also on body. Less prominent concentric rugosities (fila of Newell) 3 per mm., which are continued on to both ears. Small deep posterior muscle scar(?) can be detected. Narrow ligamental area with discontinuous longitudinal ridges. Length 18 mm., height 14 mm., depth 1 mm.

Locality: Yass Beds, Yass.

Actinoptereella minuta occurs on the same slab. *A. formosa* resembles *Actinoptereella boydi* (*Actinoptereella* according to Williams and Breger, 1916) from the Yeringian of Victoria (Chapman, 1908, Pl. V, fig. 70), but is not so deep.

Genus PTERONITELLA Billings.

PTERONITELLA RUGOSA, n. sp. (Pl. xix, fig. 8.)

Holotype: Australian Museum No. F48881.

One right valve, external cast, slightly convex over body, well preserved, undistorted, inequilateral. Posterior wing flat, anterior with very low arch, separated from body by furrow. Almost perfect semi-circular outline of shell made by almost continuous curve round posterior, ventral and anterior margins with very slight sinuses below both postero-cardinal and antero-cardinal angles. Hinge-line greatest length. Anterior wing small and posterior wing large. Umbo at anterior third, very low and depressed, rises 0.25 mm. above hinge. Body nearly erect, about 10 degrees from vertical, falls in low slope to ventral margin, not resupinate.

Ornament: Concentric, rough, raised lamellae, irregular, not continuous, faint radial striae stronger over body section, where they are about 0.5 mm. apart, hardly visible on posterior and anterior sections, about 2 mm. apart on ventral margin. This radial striation is known on *Pteronitella*, though rarely (Williams and Breger, 1916, p. 193). External ligamental area, narrow, 0.1 mm. wide, well developed posteriorly. One posterior lateral tooth nearly parallel to (5 degrees to horizontal) and close to hinge, between two grooves, extending half distance between umbo and postero-cardinal angle. Neither cardinal teeth nor muscle scars visible. Length 11 mm., height 7 mm., 1 mm. deep.

Locality: Hatton's Corner, Yass, associated with *Monograptus nilssoni* and *M. bohemicus*.

Remarks: *P. rugosa* can be compared closely with the figure of *Pterinea condor* Salter from the Lower Ludlow of Dudley, England, though *P. rugosa* is much smaller, *P. condor* is now taken as a *Pteronitella* (Reed, 1902, 1927).

Genus *LEIOPTERIA* Hall.*LEIOPTERIA GREGARIA*, n. sp. (Pl. xix, figs. 24, 31.)

Holotype: Australian Museum No. F33019.

All specimens are casts and moulds in sandy shale and often crowded on top of one another so that only part of each is visible. In the collection from Cootamundra, moulds and casts of left valves immeasurably outnumber those of right valves, which may be due to the animal resting on its left valve when alive. The shells are equivalve and inequilateral, bi-convex. The dorsal margin straight, making greatest length of shell, and extending in the holotype to a spur at post-cardinal angle, but the preservation of this angle is unusual. There is an acute sinus beneath this spur, after which posterior margin forms convex curve which continues round ventral margin to a very shallow sinus beneath small anterior ear. Body oblique, umbonal slope (about 35 degrees to vertical) continuing to posterior-ventral angle. Umbonal slope falls abruptly to anterior-dorsal angle and more gently to a sulcus which forms the border of the large triangular posterior wing which is itself very slightly arched. Anterior ear small, triangular and raised by a steep slope from the main body to a different plane. This ear, according to Spriestersbach (1909), is the most important feature of the genus. However, in the Cootamundra material it is seldom seen, and lying as it does on a different level from the rest of the shell, it must have broken easily. Umbo at anterior third, prosogyrate, blunt and broad, projecting above and over hinge-line. Ornament: Concentric, lamellar very irregular growth lines which are carried strongly on to anterior wing and a few broken radials causing crenulations such as Spriestersbach (1909) describes in his diagnosis. Ligamental area extends nearly three-quarters length of shell making an elongated triangle less than 1 mm. wide at its base on posterior margin. Longitudinal striae form a groove on a mould and ridge on a cast. Growth lines continue across it. Muscular impressions are extremely difficult to detect on the broken rough surface produced by the coarse growth lines. Teeth cannot be detected. Spriestersbach mentions the difficulty of seeing these in single valves.

Leiopteria gregaria closely resembles plates of *Avicula impotens* Barrande (Pl. 229, fig. I, 1) now named *Leiopteria (L.) occulta* by Ruzicka (1950) from Zone e beta of the Silurian. It is also similar to *Pterinea twenhofeli* McLearn and *P. kerfornei* Oehlert. *Tentaculites* occurs with *L. gregaria* at Cootamundra. On one specimen there are 22 casts or moulds of *L. gregaria* crowded on to a block of shale measuring 12 cm. by 4 cm. Only one of these is a right valve. Length 20 mm., height 22 mm., depth 2 mm.

Locality: As for *Grammysia obliqua*.

There are specimens of *Leiopteria* from Cootamundra which are considerably larger than the holotype of *L. gregaria*, being more than 30 mm. long and 35 mm. wide and 5 mm. deep, but none are sufficiently well preserved for determination as a separate species.

Genus *MYTILARCA* Hall.Cf. *MYTILARCA* sp. (Pl. xix, fig. 30.)

Cast of one left valve, broken at umbo, rhombic outline. Cardinal margin straight, sloping towards posterior angle. Anterior margin curved, ventral and posterior margins with shallow sinuses. Very prominent umbonal slope to post-ventral angle. Faintly marked concentric striae, more noticeable away from umbo. These make crenulations along cardinal margin, near post-cardinal angle. Length 10 mm., height 15 mm., depth 4 mm.

Locality: Barrandella shales, 6 miles south of Yass.

Genus *CYRTODONTA* Billings.*CYRTODONTA LISSA*, n. sp. (Pl. xix, fig. 29, 31, 32.)

Holotype: Australian Museum No. F48882.

Holotype is well-preserved internal cast of right valve, quadrate, inequilateral. Dorsal margin nearly straight, passing into truncate posterior margin which makes greatest height of shell. Anterior and ventral margins form smooth curve which slope.

to post-ventral angle. Very pronounced nearly angular umbonal slope with flattened cardinal furrow posterior to it. Body oblique. Tip of umbo broken in this specimen, but must have been prominent and prosogyrate; central. Surface smooth. Pear-shaped anterior adductor scar at antero-dorsal angle with vertical buttress on its posterior edge. Posterior adductor scar on cardinal slope, larger and fainter than anterior. Pallial line simple. Two curved teeth anterior to umbo on hinge plate. Posterior to umbo two teeth, thin and parallel to hinge, one of these curving around a cardinal tooth into a strong hook under umbo. Ligamental groove along dorsal margin. Length 13 mm., height 14 mm., depth 4 mm.

Locality: Spring Range Road, Ginninderra.

I have also placed in this species numerous undistorted internal casts of two joined valves collected by Mr. A. J. Shearsby from Forest Creek, Boambolo. They range in size up to a length of 35 mm., a height of 40 mm. and depth of 25 mm. The left valve is generally the more convex. The umbones are strongly gibbous and rise above the hinge-line, but are not quite in contact across it. While in some respects these shells agree with *Whitella* Ulrich, they have not the prominent umbo nor the well-developed escutcheon prescribed for that genus. They show faint concentric markings.

DYSODONTA.

Genus MODIOLOPSIS Hall.

MODIOLOPSIS ELONGATA, n. sp. (Pl. xix, fig. 11.)

Holotype: Australian Museum F27817.

Cast of left valve preserved in fine, ferruginous sandy loam. Bulbous, cylindrical, compressed anteriorly, cardinal line arched, posterior greatly expanded into convex curve. Ventral margin curves from rounded anterior-ventral angle into sinus, then steeply downward to posterior ventral angle. Broad ill-defined ridge extending to post-ventral angle. Umbo depressed, scarcely visible, nearly terminal. Faint, irregular concentric growth lines on body of shell, none on posterior ventral extension. No lunule nor escutcheon, faintly defined groove for ligament. Adductor impressions well marked, especially heart-shaped anterior; posterior larger and fainter. Pallial line simple. Length 15 mm., height 11 mm., depth 4 mm. (one valve).

The basal margin of *M. elongata* is more inclined than in ? *M. complanata* Sowerby described by Chapman (1908) or than *M. melbournensis* Chapman (1908).

Locality: Balheary, near Taralga.

Genus GONIOPHORA Phillips.

Subgenus COSMOGONIOPHORA McLearn.

COSMOGONIOPHORA SINUOSA Sherrard, *J. & Proc. Roy. Soc. N.S.W.*, 1952, 85, 78, Pl. VI, 7.

Holotype: Australian Museum Collection No. F44214.

Type specimen preserved in fine reddish-yellow shale. Casts and moulds in profusion at type locality. Some specimens distorted and fractured as is common in *Goniophora* (Leriche *et al.*, 1912, p. 51).

Shells equivalve, inequilateral, sub-trapezoidal. Cardinal margin straight, anterior and ventral margins form smooth curve until point where umbonal ridge projects as canal, as seen in mould. Posterior margin convex. Posterior end usually rather wider than anterior. Umbonal ridge strongly carinated, makes angle of 30 degrees with ventral margin. Umbones low, depressed and blunt, prosogyrate, situated about two-thirds distance from posterior to anterior. Post-umbonal slope depressed. Distinct circular anterior scar rather excavated, posterior scar oval, larger but fainter. Simple pallial line distinct on some casts. One cardinal tooth with spoon-shaped upper surface seen in some specimens. Well-marked concentric growth lines, 4 per millimetre, less strongly marked to the posterior of umbonal ridge. Radial striae on either side of and close to umbonal ridge. Radial striae *above* the umbonal ridge are characteristic of the subgenus and only seen in the Silurian (McLearn, 1924). Specimens of *C. sinuosa* are closely comparable with *Goniophora* aff. *cymbaeformis*, No. 21987, Geological Survey

of Gt. Britain, presented by Sir R. I. Murchison, with which they have been directly compared. Maximum length 21 mm., maximum height 10.5 mm., depth of each valve 0.4 mm. Greatest length about mid-width.

Locality: Portion 84, Par. Nanima, near Nanima Trig.; Vallance's Hill, Portion 177, Par. Nanima.

Goniophora sp. has been collected from the Middle Tribolite Bed, Bowning, and from the Yass Beds.

Genus CYPRICARDINIA Hall.

CYPRICARDINIA CONTEXTA Barrande. (Pl. xix, fig. 27.)

Cast of one small right valve, inequilateral, trapezoidal. Cardinal margin rises towards posterior, making shell wider at posterior end than at anterior. Anterior margin rounded, posterior margin rounded, rather flared. Ventral margin with very slight sinuation. Umbonal slope steep and rather angular towards both antero-ventral and post-ventral angles. Umbo very prominent at anterior third, prosogyrate, curves over nearly to cardinal edge. Lunule developed. Ornament: about 10 very prominent deeply impressed concentric ridges. Short radials connect these giving an imbricated appearance. Internal features cannot be seen. Length 9 mm., height 7 mm., depth 3 mm.

A larger, less well-preserved shell may also belong here.

Locality: Bowning.

Genus PARACYCLAS Hall.

PARACYCLAS ORBICULATA, n. sp. (Pl. xix, fig. 10.)

Holotype: Australian Museum No. F48883.

Internal cast of left valve poorly preserved in porous sandstone. Nearly circular, slightly convex, umbo central, fairly prominent, rising slightly above hinge-line. Adductor impressions large but faint. Pallial line apparently in shallow furrow. Flattened area runs along slightly arched cardinal margin. Pronounced oblique furrow along post-cardinal margin. Surface smooth. Length 14 mm., height 15 mm., depth about 3 mm.

Locality: Portion 177, Par. Nanima, near Morumbateman, Yass district.

De Koninek (1898) described but did not figure *Paracyclas elliptica* collected by W. B. Clarke and said to be from the Devonian of the Yass district. Dimensions are similar to *P. orbiculata*. Chapman (1909) recorded (cf.) *Paracyclas* sp. from the Silurian of Yass. Australian Museum specimen No. F27913 collected by Mitchell and labelled presumably by him, *Paracyclas*, U.T.B., Bowning, is apparently the same species. It is an external mould, 14 mm. long, 12 mm. high. It shows regular concentric ridges 1 mm. apart, for 6 mm. within the ventral margin. *P. orbiculata* is similar in size and description to *P. fletcheri* from Gaspé, Canada (Northrop, 1939).

SUMMARY.

Thirty-one Silurian lamellibranchs are described, including twenty new species. The relation of beds in which the lamellibranchs occur to beds known to contain graptolites is given where possible. By this means an exact age can be stated for the lamellibranch-bearing strata in some cases. A summary of previous references to Silurian lamellibranchs in New South Wales is included. Correlations with Silurian lamellibranchs from other countries are suggested.

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EXPLANATION OF PLATE.

Nos. 1-13, 31, 32 approximately natural size; Nos. 14-30 approximately $\times 2$.

1. *Grammysia ampla*, n. sp., Bowning, A.M. No. F48878. 2. *Grammysioidea declivis*, n. sp., Upper Trilobite Bed, Bowning, A.M. No. F27876. 3. *Grammysia compressa*, n. sp., Yass Beds, Sydney University Geological Department Collection No. 8572. 4. *Palaeosolen planus*, n. sp., Cootamundra, A.M. No. F32976. 5. *Panenka cingulata* Chapman, Cootamundra, A.M. No. F31882. 6. *Lunulicardium qudongensis*, n. sp. (posterior view), Quedong, near Bombala, A.M. No. F23306. 7. *Tancrediopsis victoricae* (Chapman), Yass Beds, Syd. Univ. Geol. Dep., No. 8573. 8. *Pteronitella rugosa*, n. sp., Hatton's Corner, Yass, A.M. No. F48881. 9. *Actinopterella lamellosa*, n. sp., Bowning, A.M. No. F2750. 10. *Paracyclas orbiculata*, n. sp., Morumbatman, near Yass, A.M. No. F48883. 11. *Modiolopsis elongata*, n. sp., Balheary, near Taralga, A.M. No. 27817. 12. *Grammysia obliqua*, n. sp., Cootamundra, A.M. No. 32975. 13. *Cardiola (Slava) fibrosa* Sow., Hatton's Corner, Yass, A.M. No. F48879. 14. *Paracardium cf. filosum* Chapman, Bowning, A.M. No. F49131. 15. *Grammysioidea declivis*, n. sp., Bowning, A.M. No. F27901. 16. *Tancrediopsis minuta*, n. sp., Bowning, A.M. No. F29429. 17. *Nuculites pseudodeltoides* Reed, Bowning, A.M. No. F29431. 18. *Tellimopsis flabelliformis*, n. sp., Bowning, A.M. No. F29393. 19. *Nuculites scissa*, n. sp., Upper Beds, Bowning, A.M. No. F27897. 20. *Tancrediopsis delicatula*, n. sp., Bowning, A.M. No. F27931. 21. *Nuculopsis triangula*, n. sp., Bowning, A.M. No. F29410. 22. *Nuculana striata*, n. sp., Cootamundra, A.M. No. F32995. 23. *Actinopterella minuta*, n. sp., Hatton's Corner, Yass, A.M. No. F48880. 24. *Leiopteria gregaria*, n. sp., Cootamundra, A.M. No. F33019. 25. *Rhombopteria laminosa* (De Koninck), Yass Beds, Yass, Syd. Univ. Geol. Dep. No. 8570. 26. *Rhombopteria obliqua*, n. sp., Cootamundra, A.M. No. F32985. 27. *Cypricardinia contexta* Barrande, Bowning, A.M. No. F29435. 28. *Actinopterella formosa*, n. sp., Yass Beds, Yass, Syd. Univ. Geol. Dep. No. 8571. 29. *Cyrtodonta lissa*, n. sp., Ginniderra, A.M. No. F48882. 30. Cf. *Mytilarca* sp., Barrandella Shales, 6 miles south of Yass. 31. *Cyrtodonta lissa*, n. sp., Forest Creek, Boambolo, A.M. No. F49138 (posterior view). 32. *Cyrtodonta lissa*, n. sp., Forest Creek, Boambolo, A.M. No. F49138. Left valve.

A NEW SPECIES OF HILARA (DIPTERA, EMPIDIDAE) FROM
NEW SOUTH WALES.

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Oxford, England.

(Communicated by C. E. Chadwick.)

(Four Text-figures.)

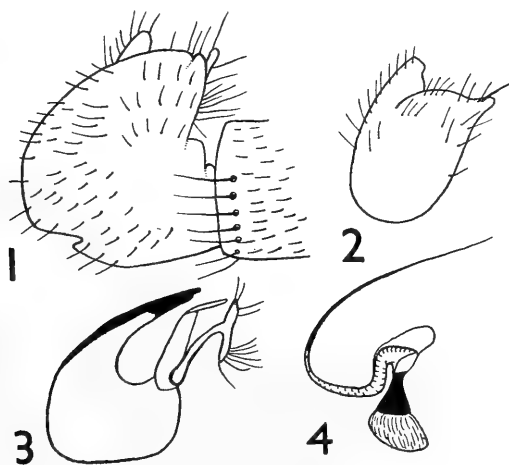
[Read 25th November, 1959.]

Among some *Empididae* collected by Mr. C. E. Chadwick at mercury vapour light in New South Wales was the following new species of *Hilara* which he has very kindly asked me to describe.

HILARA MINNAMURRA, sp. nov.

An entirely yellow-brown species.

♂. Occiput and frons yellow-brown, short black haired with pair of longer diverging ocellar bristles, some longer curved hairs above eyes. Two basal segments of antennae reddish-brown, third segment reddish-brown, darker towards tip. Arista darker, slightly longer than third antennal segment. Thorax yellow-brown with three dark brown



Figs 1-4.—Hypopygium of *Hilara minnamurra*, n. sp. 1, Hypopygium; 2, Lateral Lamella; 3, Ventral Lamella; 4, Penis.

stripes upon which are situated the short black, biserial acrostichal and bi-triserial dorsocentral bristles. The latter commence uniserial, becoming biserial post humerally and irregularly triserial posteriorly in some specimens. The last dorsocentral, before the scutellum, is longer, about as long as lateral scutellar bristle. The longest of the preceding dorsocentrals does not exceed half the length of the long bristle. Scutellum with 6 black bristles, apical pair strongest. Few black hairs on prosternum between front coxae, pleurae bare. Abdomen yellow-brown, short black haired with slender black bristles on hind margin of each segment. Hypopygium (Figs 1-4). Legs yellow-brown, anterior and median pairs of legs short haired, posterior tibiae and tarsi with long bristle-like hairs. Anterior metatarsi swollen evenly along whole length. Wings yellowish with brown veins. Squamae and halteres concolorous with rest of body.

♀. Resembles male, but all legs short haired and front tarsi simple.
Length 6.5 mm.

Holotype ♂ and allotype ♀, also paratypes 7♂♂, 5♀♀, in the Department of Agriculture, Sydney. In addition paratypes 1♂, 1♀, each in the Hope Department of Entomology, Oxford, England, and the author's collection. All collected at Minnamurra Falls, N.S.W., at mercury vapour light by C. E. Chadwick on 15th February, 1958.

This species resembles the New Zealand species *H. rectecta* Collin, in general colour, but is much larger; it does not resemble any of the Tasmanian species described by White (1916). In Collin's (1933) key to South American species it runs to *H. luteolimbata* Collin, but does not resemble that species in colour, size or genitalia characters.

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THE ANATOMY OF THE BARKS OF FIVE SPECIES OF CALLITRIS VENT.

By R. K. BAMBER.

(Plates xx-xxi.)

[Read 25th November, 1959.]

Synopsis.

In this paper, detailed anatomical descriptions of the bark of five species of *Callitris* Vent. are given. A key for the identification of these five species based on the bark anatomy has been devised.

The resin canals are considered to be schizogenous rather than lysigenous in origin as recorded elsewhere. The presence of bordered pits and unusual thickening of phloem fibre walls is noted. Crystal sand of unknown constitution has been found in the middle lamella of the radial walls of the cells. The stringy and compact types of bark found in *Callitris* have been related to the anatomy.

INTRODUCTION.

The Australian genus *Callitris* and the ornamental species *Cupressus macrocarpa* Hartweg differ markedly in their resistance to the cypress pine jewel beetle. While *Callitris* spp. are able to survive attacks by this beetle on the phloem, cambium and outer sapwood, *Cupressus macrocarpa* readily succumbs. To assist in the study of the cypress pine jewel beetle by Hadlington and Gardner (1959), this study of the anatomy of five species of *Callitris* and comparison with the anatomy of *Cupressus macrocarpa* and *C. lusitanica* has been made.

A broad study of the bark anatomy of the genus *Callitris* Vent. was included by Baker and Smith (1910) in their research on the pines of Australia, but details of the cell dimensions, the nature of the expansion of the phloem parenchyma and the differences in structure between various species were not given. Their account of resin canal formation and the terms used for the description of the bark anatomy are also in need of revision in the light of descriptions by the more recent authors on bark anatomy (Eames and McDaniels, 1947; Esau, 1950 and 1953; Chang, 1952; and Chattaway, 1954).

MATERIALS.

The following species were selected for study: *Callitris hugelii* (Carr) Franco (Syn. *C. glauca* R.Br.), 4 trees; *Callitris endlicheri* (Parl) Syn. *C. calcarata* (A. Cunn. ex Mirb) F. Muell., 4 trees; *Callitris macleayana* F. Muell., 3 trees; *Callitris rhomboidea* R.Br. ex A. et L. C. Rich., 4 trees; *Callitris intratropica* Baker and Smith, 3 trees; *Cupressus macrocarpa* Hartweg, 3 trees (planted); *Cupressus lusitanica* Miller, 2 trees (planted).

The nomenclature for the *Callitris* is taken from the revision of the genus by Garden (1957).

METHODS.

The material was prepared for examination by means of standard techniques using Johansen (1940) as a guide. It was found more satisfactory to use isopropyl alcohol for dehydration prior to embedding.

For the observation of crystal sand it was found necessary to remove tanniferous materials by treatment with acetic acid and hydrogen peroxide. This solution also served for maceration. Softening of bark with chemical treatment prior to sectioning was not necessary.

In the calculation of volumes of fibres, the linear method of Chalk (1956) was used. For the calculation of volume of resin canals the method described by Brown,

Panshin and Forsaith (1949) was followed, in which photomicrographs are weighed before and after the various tissues are cut out. This method was found to be more rapid and accurate than a planimeter.

DESCRIPTION OF BARK ANATOMY.

General.

While the barks of all species of *Callitris* examined are made up of phloem, narrow periderm and a persistent rhytidome built of successive layers of dead phloem separated by fine periderm layers, the general appearance of the barks and the thickness of barks vary considerably. Both *C. hugelii* and *C. endlicheri* develop, in mature trees, a thick outer bark (up to $1\frac{1}{2}$ in.) with large vertical furrows, the texture of the bark being hard and compact. On the other hand *C. rhomboidea* develops a hard compact outer bark which is much thinner, up to $\frac{1}{4}$ in., and has small vertical furrows. Both *C. intratropica* and *C. macleayana* develop a loose fibrous outer bark. In the former this outer bark is somewhat thinner (up to $\frac{1}{2}$ in.) and more compact than in the latter (up to $1\frac{1}{2}$ in.) which is well known as the stringybark cypress, having a very loose fibrous bark.

The inner bark (phloem) of all species is thin, approximately $\frac{1}{8}$ in., and very hard. When the bark is freshly cut the inner phloem appears cream to yellow, turning reddish towards the periderm and darkening to brown-black in the outer bark.

The resin canals are clearly seen with the eye, the resin exuding freely from the canals of the phloem. In the rhytidome the resin is solid, the canals appearing as white dots.

Arrangement of Phloem Tissues.

The phloem of all species of *Callitris* examined is made up of regular concentric layers of sieve cells, phloem fibres and phloem parenchyma together with phloem rays. The layers are repeated in the following sequence: sieve cell, fibre, sieve cell, parenchyma. This sequence is consistently maintained in all species examined and does not appear to be seasonal.

Phloem Fibres.

The phloem fibres of all species of *Callitris* examined appeared thick-walled with small lumen, thickening of the wall occurring rapidly after division from the cambium and being completed three or four cells from the cambium.

The walls of the fibres are profusely pitted (Pl. xx, fig. 1), the pits being bordered, the chamber very small and the aperture narrowed axially (Pl. xx, fig. 2). Due to the profuse pitting and large degree of thickening of the walls, the lumen surface of the fibre shows a characteristic corrugated appearance in the longitudinal direction (Pl. xx, fig. 1). Also unusual is the tendency for the pit aperture to be oriented diagonally. While many pits are oriented towards the radial walls forming pit pairs, some are oriented towards the tangential wall or else diagonally without forming a pit pair and are thus blind.

Phloem fibres of *Callitris* are characteristically rectangular in section, being considerably wider, tangentially (15 to 45μ), than radially (9 to 27μ).

Some differences between species is apparent in the average fibre length. In *C. endlicheri*, *C. hugelii* and *C. rhomboidea* it is approximately the same, being 2.6 mm., 2.7 mm. and 2.6 mm., respectively; in *C. intratropica* it is 3.2 mm. and in *C. macleayana* 3.6 mm. These differences are paralleled somewhat by the differences in the average fibre length of the xylem, for example, *C. hugelii* 2.4 mm., *C. endlicheri* 3.1 mm., *C. rhomboidea* 2.6 mm., *C. macleayana* 4.2 mm. and *C. intratropica* 4.2 mm.

The volume of phloem occupied by fibres ranges from 18% in *C. endlicheri* to 26% in *C. macleayana*. In the outer bark (rhytidome) these percentages do not hold, due to expansion of the parenchyma.

Sieve Cells.

Sieve cells are the principal cells of *Callitris* phloem and comprise 50% of the phloem cells, apart from the rays. They appear generally similar in size to the phloem fibres, measuring from 15 to 27 μ tangentially and from 9 to 27 μ radially. The length of the sieve cells has not been measured, but they appear to be a little shorter than the fibres.

The rectangular appearance of the fibres in transverse section is not always shared by the sieve cells. In the inner phloem they are inclined to be swollen, compressing the adjacent parenchyma cells, whereas in the outer phloem the sieve cells become in turn compressed by the expanding parenchyma cells. In *Callitris macleayana* the sieve cells retain their rounded form in the outer phloem and rhytidome and it is the adjacent parenchyma which is collapsed (Pl. xx, fig. 3). Sieve areas are clearly defined, being more or less circular and about 15 μ in diameter. The sieve areas are profuse and are spaced at from 3 to 10 μ apart. The sieve pits are clearly defined in the older sieve cells (Pl. xxi, fig. 10).

The ends of the sieve cells are rounded. The wall of the sieve cell is thin, not lignified in the inner phloem, and with no secondary thickening.

Phloem Parenchyma.

The parenchyma cells of the inner phloem are much shorter than the adjacent sieve cells and fibres, being from 0.06 to 0.12 mm. long; but they are of similar tangential and radial dimensions, being 15–27 μ by 9–27 μ .

Towards the outside of the phloem and in the inner rhytidome, significant changes occur in the phloem parenchyma, due to the expansion of these cells and change in the nature and amount of the tanniniferous deposits. In *Callitris hugelii* the phloem parenchyma in the outer phloem measured up to 60 μ tangentially by 115 μ radially, with *C. endlicheri*, 27 μ by 60 μ (Pl. xx, fig. 4), and *C. rhomboidea*, 75 μ by 115 μ . In *C. macleayana*, no significant change in the size of the phloem parenchyma cells is observed. However, after the outer phloem cells are cut off from the inner phloem by the formation of a deeper seated periderm, expansion of occasional concentric layers of phloem parenchyma occurs (Pl. xx, fig. 3), the parenchyma cells in other layers collapsing. Only a small amount of expansion occurs in the phloem parenchyma in the phloem and rhytidome of *C. intratropica* (Pl. xxi, fig. 5).

In *C. endlicheri*, *C. hugelii* and *C. rhomboidea*, the expansion of the phloem parenchyma partially destroys the regular concentric formation of phloem cells (Pl. xx, fig. 4, and Pl. xxi, fig. 6). In *C. macleayana* and *C. intratropica* the regular concentric pattern is maintained in the fibrous layers of the rhytidome (Pl. xx, fig. 3).

The tannin-like deposits of the phloem parenchyma cells appeared granular and pale brown in the phloem. After separation from the living phloem by the periderm, the tannin-like material becomes dark red-brown in colour and separates as a solid material from the cell walls. These deposits are very prolific in *C. endlicheri*, *hugelii*, *intratropica* (Pl. xxi, fig. 5) and *rhomboidea*, but scarce in *C. macleayana*.

Phloem Rays.

Phloem rays are uniseriate and mostly four or five cells high. In the inner phloem, the deposits of tanniniferous materials are pale in colour, but towards the outer phloem they become much darker and more abundant. Some small enlargement of phloem ray cells occurs, particularly in the region of division of phloem parenchyma or formation of resin canal. The tannin-like materials of the ray parenchyma change in colour and appearance between the phloem and rhytidome as with the phloem parenchyma.

Resin Canals.

The resin canals are formed by division and subsequent separation of parenchyma cells, the epithelial cells of the canal being thin-walled (Pl. xxi, fig. 9). This division commences very close to the cambium. After formation, the resin canals increase in size until they become part of the rhytidome. The division of parenchyma to form

canals occurs in *C. endlicheri* in about every 4th to 6th row of parenchyma and follows a concentric pattern. The canals continue vertically for a considerable distance and in *C. macleayana* were measured to 4 in. Resin canal formation appears to be of natural occurrence in the bark of *Callitris* spp., their frequency being a function of species rather than injury. There is considerable variation, in both size and frequency of resin canals of the phloem, in the five species examined, as shown in the following table:

<i>Species.</i>	<i>Number of Resin Canals per sq. mm.</i>	<i>Size of Resin Canals.</i>
<i>Callitris endlicheri</i>	14 to 20	0.08 to 0.16 mm.
<i>C. hugelii</i>	6 to 13	0.13 to 0.19 mm.
<i>C. intratropica</i>	1.3 to 3.8	0.21 mm.
<i>C. rhomboidea</i>	1.3	0.09 to 0.4 mm.
<i>C. macleayana</i>	0.5 to 0.75	0.21 mm.

Periderm.

Periderm formation occurs by division of phloem parenchyma; it is concentric in pattern and is similar in all the species of *Callitris* examined. The phellogen is from two to three cells wide, while the phellogen consists of a single or double layer of thin-walled cells. The phellem produced varies from 3 to 6 cells in width. The phellem cells are thin-walled and free of deposits, whereas the phellogen frequently shows intense tanniferous deposits. The phellem cells measure approximately 0.03 to 0.054 mm. in height.

In the rhytidome of a tree approximately 20 years old, 10 corky layers were counted. The corky layers (phellem) appear as fine pale-brown bands more or less concentric.

Rhytidome.

The rhytidome of *Callitris* consists mainly of old phloem tissue which has been cut off by successive periderms and fine cork layers. As was shown in the observations of phloem parenchyma, the various forms of the rhytidome are due to the characteristics of these parenchyma cells.

Nature of Cell Walls.

When stained with safranin and fast green the secondary wall of the phloem fibres shows lignification close to the region of differentiation. The primary wall of the phloem fibres does not show lignification until the outer phloem or rhytidome does, the thin primary wall readily separating from the secondary wall on sectioning. The primary walls of the other cells of the phloem behave similarly to this staining reaction, lignification not being found until the outer phloem or rhytidome is lignified.

The primary walls of all the phloem cells give a positive reaction for cellulose with iodine and sulphuric acid.

Crystal Sand.

Abundant deposits of a fine crystalline material were found in *C. hugelii*, *C. endlicheri*, *C. rhomboidea*, *C. intratropica*, *Cupressus macrocarpa* and *Cupressus lusitanica*. The crystal sand is deposited in the middle lamella of the radial walls of all cells, and is laid down at the time of fibre differentiation. It appears to extend through the phloem in radial rows within the middle lamella. These deposits were not found in *C. macleayana*. This material appears similar to the crystal sand reported by Chang (1952) as occurring in the sieve cells of *Chamaecyparis thyoides* (L.) B.S.P. The crystal sand is difficult to distinguish in a normal preparation, due to the large amounts of tanniferous material present, and treatment with acetic acid and hydrogen peroxide is required to remove the deposits before observation can be made. It can be observed, however, in thin sections particularly if polarized light is used. The crystals are insoluble in a mixture of 30 per cent. hydrogen peroxide and glacial acetic acid, strong sulphuric acid, hydrofluoric acid, sodium hydroxide and ammonium hydroxide. The chemical nature is unknown.

DISCUSSION.

The characteristic form of *Callitris* bark in which uniseriate bands or layers of sieve cells alternate with uniseriate layers of phloem fibres and phloem parenchyma was first shown by Baker and Smith (1910). Mention of this alternating concentric phloem structure has been made for the members of the family Cupressaceae by De Bary (1877, reported by Takamatsu, 1928), and Takamatsu (1928), and for *Sequoia sempervirens* Endl. and *Libocedrus decurrens* Torrey by Abbe and Crafts (1939). Chang (1952) makes use of the alternating structure as a diagnostic feature in the identification of the families Cupressaceae and Taxodiaceae.

Baker and Smith (1910) also commented on the structure of barks of the main Australian Coniferae and it is surprising that the modern bark authors referred to in this paper have not made reference to their work.

The structure of the phloem fibres is interesting in several ways. Firstly, the pits are numerous and definitely bordered, even though the pit chamber is quite small and sometimes indistinct. This is at variance with Chang's (1952) observation of some of the American Cupressaceae in which simple pits are reported. The combination of numerous pits and bordered pits in these phloem fibres is similar to the combination of numerous pits and bordered pits in fibre tracheids of xylem (I.A.W.A. Glossary, 1957). The pits which are aligned diagonally or radially are naturally blind, as the cells with which they make contact (sieve cells) have only primary walls through which conduction can occur. These blind pits of the fibres may coincide with sieve areas of the sieve cells. Pit pairs, naturally, are only found on the radial walls of the fibres.

No reference has been found in the literature as to whether the corrugated inner surface of the fibre wall occurs in other fibres of either phloem or xylem. Uneven inner cell walls resulting from thickening of pitted walls is, of course, well known in end walls of ray parenchyma cells in the xylem of the family Pinaceae.

The non-collapse of sieve cells of *C. macleayana* is also worthy of note, as collapse of sieve tubes is thought to be a characteristic of the older phloem (Holdheide, 1953). In other respects the sieve cells are the same as those described by Chang (1952).

While all the five species of *Callitris* examined have similar structures in their phloem (except in regard to the size and frequency of resin canals and length of fibres), the gross characteristics differ. These differences are due to the expansion of the parenchyma in the outer phloem and rhytidome. The large amount of expansion of phloem parenchyma in *C. hugelii*, *C. endlicheri* and *C. rhomboidea* disrupts the concentric fibre layers and the deposition of large amounts of "tannins" renders the mass of expanded cells compact. In *C. macleayana* the expansion of parenchyma is limited to occasional concentric layers allowing the fibrous nature of the phloem to be retained in the outer bark and permitting loosening of the fibrous layers. This loosening is assisted by the relatively small amount of tannin-like material deposited. *C. intratropica* retains the characteristics of the phloem in the rhytidome as only moderate expansion of parenchyma occurs. Chattaway (1954) has indicated the presence of expanded phloem parenchyma cells in certain species of *Eucalyptus* classified as "stringybarks". It is also suggested by Chattaway (1954) that this expansion of phloem parenchyma is associated with the death of these cells.

The occurrence of crystal sand in the middle lamella of the radial cell walls in certain species of *Callitris* and *Cupressus* appears of some interest, firstly, as crystalline deposits have rarely been recorded in the phloem cell wall (Chang records crystalline material in walls of *Taxus brevifolia* Nutt.), and secondly, as the material is laid down in continuous radial rows.

Baker and Smith (1910) concluded that the resin canals of *Callitris* were of lysigenous origin and that the resin (sandarac) was contained in cells or cavities. They attribute to this the difficulty of tapping *Callitris* trees so as to obtain a flow of resin as is done with turpentine. This, however, is not correct; the resin canals are

of schizogenous formation and the resin is secreted by the epithelial cells of the canal. The difficulty of obtaining a flow of resin is no doubt due to some physical characteristic of the resin as the canals appear to run vertically up the tree.

COMPARISON OF CALLITRIS AND CUPRESSUS BARK.

Bark of *Cupressus macrocarpa* grown in Sydney gardens (Pl. xxi, fig. 7) differs from *Callitris* in the following respects: (1) The concentric fibre layers are laid down irregularly, sometimes only four fibre layers being present in the entire phloem, and the bark is therefore softer than *Callitris*. (2) Resin canals are scarce in young trees sampled from Sydney. Although one sample from a large tree in Melbourne had a moderate number, the frequency of resin canals does not approach their high frequency in *Callitris*. (3) Tannin-like deposits of the phloem parenchyma are not dense.

It is suggested by Hadlington and Gardner (1959) that these marked differences in the structure of *Callitris* and *Cupressus* bark may account in some part for the differences in their susceptibility to attack by the cypress pine jewel beetle.

Examination of *Cupressus lusitanica* showed a moderate number of resin canals which agreed with Chang's (1952) comments for *C. lusitanica*. As in *C. macrocarpa*, the concentric fibre layers of *C. lusitanica* are irregular and the tannin-like deposits light.

IDENTIFICATION OF CALLITRIS SPECIES ON THE BASIS OF BARK ANATOMY.

The anatomy of the bark on the genus *Callitris* fits the key outlined by Chang (1952) for the classification of the North American Cupressaceae. Separation from the other genera of this family described by Chang (1952) can be made by use of the following features: (1) greater frequency of resin canals; (2) deposition of sandarac resin (Baker & Smith, 1910); (3) expansion of parenchyma cells in outer phloem and/or rhytidome.

A key for the identification of the five species examined here is suggested as follows:

1. No expansion of parenchyma in phloem. Expansion of occasional parenchyma layers in rhytidome *C. macleayana*.
- 1.* Parenchyma expanded in outer phloem 2.
2. Expansion of parenchyma moderate in outer phloem and rhytidome. Fibre layers regular in rhytidome *C. intratropica*.
- 2.* Expansion of parenchyma extreme in outer phloem and rhytidome. Fibre layers of rhytidome broken by parenchyma expansion 3.
3. Resin canals few, approximately 1-3 per sq. mm. *C. rhomboidea*.
Resin canals from 6 to 13 per sq. mm. *C. hugelii* (Pl. xxi, fig. 3).
Resin canals from 14 to 20 per sq. mm. *C. endlicheri* (Pl. xxi, fig. 9).

ACKNOWLEDGEMENT.

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The writer wishes to thank Dr. M. M. Chattaway of C.S.I.R.O., Melbourne, for helpful comments and Mr. Rex Johnstone of the Division of Wood Technology for silica analyses. The assistance of the Photography Section of this Division in the preparation of the photomicrographs is also appreciated. Three of the *C. intratropica* samples examined in this paper were kindly loaned by the Australian Forestry School, Canberra.

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EXPLANATION OF PLATES XX-XXI.

Plate xx.

1: Macerated phloem fibre of *Callitris endlicheri*. Corrugated inner surface of fibre and high frequency of pits are shown. Magnification $\times 600$. 2: Transverse section of *Callitris macleayana* phloem. A bordered pit is shown in a phloem fibre. $\times 540$. 3: Transverse section of *Callitris macleayana* bark. Periderm pe., phloem ph., rhytidome rh., expanded parenchyma ep. $\times 60$. 4: Transverse section of *Callitris endlicheri* bark. Expansion of phloem parenchyma in the outer phloem is shown. $\times 150$.

Plate xxi.

5: Transverse section of *Callitris intratropica* rhytidome. The slightly expanded parenchyma cells show abundant deposits of tanniferous material. $\times 60$. 6: Transverse section of *Callitris rhomboidea* phloem. Expansion of phloem parenchyma and subsequent loss of concentric pattern is shown. The cambium side is at the bottom of figure. $\times 60$. 7: Transverse section of inner phloem of *Cupressus macrocarpa*. Three fibre layers can be seen crossing the section. $\times 48$. 8: Transverse section of *Callitris hugelii* phloem. Compare frequency of resin canals with Figure 9. $\times 60$. 9: Transverse section of *Callitris endlicheri* phloem. $\times 60$. 10: Radial longitudinal section of *C. endlicheri* phloem. Short swollen parenchyma cells (p.c.) occur between the long, thin phloem fibres (p.f.) and sieve cells (s.c.). The circular sieve areas (s.a.) of the sieve cells can just be seen. $\times 190$.

SOME SPECIES OF *CULEX* (*LOPHOCERAOMYIA*) FROM NEW GUINEA AND ADJACENT ISLANDS, WITH DESCRIPTIONS OF FOUR NEW SPECIES AND NOTES ON THE MALE OF *CULEX FRAUDATRIX* THEOBALD. (DIPTERA: CULICIDAE.)

By DONALD H. COLLESS, Department of Parasitology, University of Malaya.

(Three Text-figures.)

[Read 25th November, 1959.]

During studies of the Malayan members of the genus *Culex*, subgenus *Lophoceraomyia*, it has become obvious that certain species, in particular *C. fraudatrix*, have been consistently misidentified from many countries; apart from references to the type specimens, practically every published record of this latter species is now of doubtful validity. However, studies of type material held in the British Museum (Natural History) and several collections of material from New Guinea, the type-area of *C. fraudatrix*, now make it possible to define more accurately the taxonomic characters of the latter species, while a number of new species and locality records have also come to light, as described below.

In this subgenus, male specimens are readily identified, principally by features of the antennal scale tufts and the terminalia. In particular, the scale tuft on antennal segment 6 (counting the torus as segment 1) and the dorsal submarginal setae on the coxite serve to identify most species; additional useful characters are found in the setae and basal processes of the palps, the dorsal setae of the proboscis, and, on the coxite, the shape of the dorsal margin and the processes of the subapical lobe. The presence of abdominal banding and pleural scales may also be diagnostic in both sexes. The females, however, are often difficult, and sometimes impossible, to identify with existing criteria. For accurate definition of their taxonomy, one must work back from the male, either through the larva, or directly from siblings reared from single egg rafts. The larvae of many species are not well defined as yet, and some are probably difficult to identify, but, in Malaya at least, most species can be identified in this stage, using the usual characters. The branching of the larval prothoracic hairs is a very useful character in this subgenus, and it is to be regretted that many extant descriptions neglect to mention these hairs.

In describing the male terminalia, I have omitted any mention of the paraprocts, since these present a variety of appearances with only slight alterations in viewing position. Characters of the male antennae are described mainly from slide preparations, which are essential for observing the finer details, and segment numbers follow the usual convention in which the torus is counted as segment 1. In numbering palp segments, the long central segment is No. 3, while the junction of segments 1 and 2 is visible usually just beyond the apices of the basal processes (Fig. 1a).*

CULEX (L.) *FRAUDATRIX* Theobald, 1905.

Theobald, F. V., 1905: *Ann. Mus. Nat. Hung.*, 3: 94.

Types: Holotype male and presumed paratype male from the National Museum of Hungary, at present on loan in the British Museum (Natural History).

Type Locality: Friedrich-Wilhelmshafen, New Guinea.

* Since writing the above, I have found that this numbering is incorrect; also that very useful characters occur on the paraprocts. These points will be discussed in a future publication.

MALE: The following description is based on the type series, and a number of additional specimens, almost certainly of this species, from New Guinea, New Britain, and New Ireland.

Head. Vertex with dark upright scales, the recumbent scales fine and pale-brown on a triangular central area, broad and pale laterally, with a border of broad, rather grey scales around the eye margins. Proboscis (Fig. 1a) dark, with a double row of hairs dorsally on the apical half, many of these with rather sigmoid curvature and about twice as long as the proboscis is wide; also, a number of forward-slanting hairs ventrally on the apical third, and a transverse row of short, stiff bristles near the extreme base. Palps (Fig. 1a) longer than proboscis by rather more than the length of the terminal segment, each with a pair of basal processes of which only the outer members are visible from above. Seg. 3 with short fine ventral hairs, massed near the base and absent from near the apex, and a tuft of much longer hairs ventro-laterally on the basal half. Segs. 4 and 5 profusely clad with long hairs.

Antenna. Seg. 6 (Fig. 1b) with prominent tuft of 15–20 scales, most of them about the same length and about as long as the next 4–5 antennal segments; the most dorsal (internal) 5–8 scales dark with blunt apices, the more ventral ones with fine pointed apices and with an increasing length of apical pale coloration; these more ventral scales rather variable in shape, from near-lanceolate to very elongate with long fine parallel-sided tip. Seg. 7 with large external tuft of strong twisted setae, and internal tuft of similar straight setae. Seg. 8 with small, rather comb-like external tuft of twisted setae, and internal tuft of very broad setae, twisted at their apices. Seg. 9 with several short setae externally, and an internal tuft of long sigmoid setae, apparently fused basally. Seg. 10 with external tuft of about 4 long, blade-like leaflets, with fine, abruptly tapered apices, and internal tuft of 5–10 shorter setae. Seg. 11 with internal tuft of about 6 relatively short stout setae.

Thorax. Integument deep brown, with sparse fine brown recumbent scales. Pleurae without scales.

Legs uniformly brown-scaled, except on the under-surfaces of the femora, which are pale.

Wing. Branches of vein 2 with rather broad clavate scales. Fork of vein 2 a little distal to that of vein 4.

Abdomen. Uniformly brown-scaled, unornamented.

Terminalia: Coxite (Fig. 2e) with dorsal margin slightly convex on the basal half, with marginal row of 5–6 setae, and, a little inside these on the external surface, 3 long prominent setae with curved apices, their bases forming a triangle and *not a straight line*; occasionally there may be 2 or 4 setae, on one side only. Subapical lobe (Fig. 2f) with three strong, rod-like processes with expanded and/or hooked tips, 5–6 short, blade-like processes, and two clavate leaflets, the external one with longitudinal striations. Lateral plate of phallosome with long pointed process, curved at approximately 90 degrees, the posterior angle usually with several very small teeth. Ninth tergite with 2–4 very short setae.

FEMALE and LARVA: Not yet known.

Specimens Seen: New Guinea: Friedrich-Wilhelmshafen, 2♂♂ (type series); Wewak, 1♂; Sauri, 1♂; Vanimo, 1♂. New Britain: Pondo, 3♂♂. New Ireland: Kavieng, 2♂♂. I have also briefly examined specimens from North Queensland, Australia, which almost certainly belong to this species.

Identification: The unornamented thorax and abdomen, together with the large tuft of 15–20 long scales on antennal segment 6, distinguishes *C. fraudatrix* from all other members of the subgenus found in New Guinea, while finer details of shape and relative length of the more ventral scales in the tuft distinguish it from closely related species found in the Oriental region; these latter are to be described in a future publication. The non-linear arrangement of the dorsal, submarginal setae on the coxite also distinguishes *C. fraudatrix* from all but *C. atracus*, n. sp.

Notes: The type specimens of *C. fraudatrix* are rather badly damaged. In particular, the holotype lacks palps and antennae, but there is a topotypical paratype

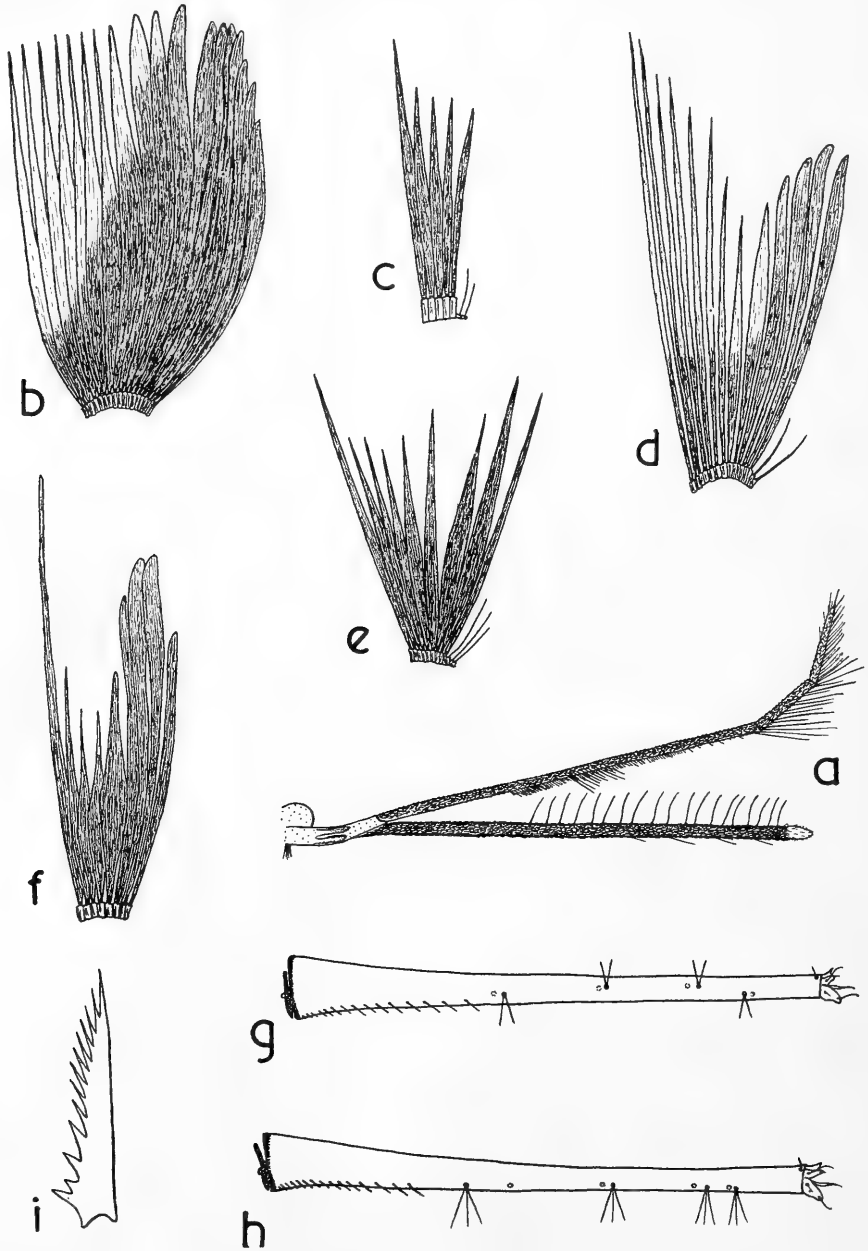


Fig. 1.—(a) *C. fraudatrix*, male palp and proboscis. (b) to (f) Scale tufts from seg. 6 of male antennae, dorsal scales to right: (b) *C. fraudatrix*; (c) *C. pseudornatus*, n. sp.; (d) *C. petersi*, n. sp.; (e) *C. atracus*, n. sp.; (f) *C. christiani*, n. sp. (g), (h) Larval siphons: (g) *C. petersi*, n. sp.; (h) *C. christiani*, n. sp. (i) Larval pecten tooth, *C. petersi*, n. sp.

which possesses antennae and most of one palp; its terminalia are identical with those of the holotype and there seems no doubt that the two are conspecific. However, this paratype does not show the ventro-lateral tuft of long hairs near the base of palp segment 3, seen in other undamaged specimens, but I feel that this is almost certainly

due to loss of the hairs by rubbing. In all other important characters, the specimens described above appear to be conspecific with the type, the variation seen being probably of geographic origin. As regards the latter point, it is worth noting that the specimens from New Britain and New Ireland do seem to differ from the type in one small detail; the setae near the centre of the external surface of the coxite tend to be a little longer than in specimens from New Guinea. Also, in one specimen from Kavieng and one from Pondo, the submarginal setae were placed almost in line.

It is hoped that the above description will serve to clarify the position as to the range of this species, which has been erroneously identified from many areas away from New Guinea. Examination of collections from the Oriental Region provides no evidence of its occurrence here, and it quite certainly does not occur in Malaya. Its range in other parts of the Australasian Region and Eastern Indonesia remains to be worked out. Likewise, the characters of the female and immature stages remain to be described, by correlation with known males.

With the exception of the types, all specimens described are to be returned to the School of Public Health and Tropical Medicine, Sydney.

CULEX (L.) ATRACUS, n. sp.

Types: Holotype and one paratype, both males, to be placed in the British Museum (Natural History); 7 paratype males to be returned to the School of Public Health and Tropical Medicine, Sydney; 2 paratype males to be placed in the United States National Museum.

Type Locality: Kavieng, New Ireland.

MALE: Very similar to *C. fraudatrix*, with apparently identical terminalia (Fig. 3c), but differing as follows: *Palp*: Seg. 3 with the tuft of ventro-lateral hairs usually not so well developed, often not apparent. *Antenna*: Seg. 6 (Fig. 1e) with tuft of 7-10 dark, fine-pointed scales, the longest about as long as the next 4 segments; relative lengths rather variable, but the first or second most dorsal and/or the most ventral usually longer and often narrower than the others; also, dorsal to the scales, 2-4 small setae.

FEMALE and LARVA: Not yet known.

Specimens Seen: New Britain: Keravat, 3♂♂. New Ireland: Kavieng, 8♂♂.

Identification: The form of the tuft on antennal segment 6, together with the *fraudatrix*-like terminalia, clearly differentiates this species from all other members of the subgenus.

Notes: The form of the terminalia suggests that *C. atracus* is closely related to *C. fraudatrix*, although this is not borne out by characters of the antenna. In the latter feature, there are distinct resemblances to several Malayan species, though present records suggest that *C. atracus* is confined in its distribution to the islands east of New Guinea.

CULEX (L.) SP. A-2 near *fraudatrix* Theo.

A single male specimen appears to belong to a rather rare Malayan species, closely related to *C. fraudatrix*. The code name used above is that in current use in studies of the Malayan fauna, and will be referred to when the latter are published. It is rather surprising to find this species amongst New Guinea material, but the identification seems to be correct, due to certain very distinctive features of the terminalia and antenna. These are described below.

MALE: Very similar to *C. fraudatrix*, but differing as follows: *Palp*: Seg. 3 with the short ventral hairs scanty, more or less confined to the basal half, not forming a ventro-lateral tuft; basal processes shorter and finer than in *fraudatrix*. *Antenna*: Tuft on seg. 6 with several lanceolate scales at about the centre, these about half as long as the more dorsal scales. *Terminalia*: Coxite (Fig. 2c) with more pronounced convexity on the basal half of the dorsal margin, and the three submarginal setae with their bases placed in a straight line. Subapical lobe (Fig. 2d): the most external of the

three rod-like processes with a pronounced "elbowed" curvature, the most internal one also rather "elbowed", and more expanded apically.

Specimens Seen: New Guinea: Vanimo, 1♂.

CULEX (L.) ORNATUS (Theobald), 1905.

Theobald, F. V., 1905: *Ann. Mus. Nat. Hung.*, 3: 100 (*Melanoconion ornatus*).

I have seen two specimens which agree well with the description of this species given by King and Hoogstraal (1955). The ornamentation of thorax and abdomen, the scaling of the pleurae, and the male terminalia are all particularly distinctive. The following characters may be noted as additional to, or differing slightly from, those described by King and Hoogstraal:

MALE:

Palp: Seg. 3 as in *C. fraudatrix*, the ventro-lateral tuft very conspicuous, its hairs about $\frac{1}{4}$ the length of the segment; basal processes well developed. *Proboscis* with double row of rather short hairs dorsally on the apical half, the longest (towards the apex) being scarcely longer than the width of the proboscis. *Propleural hairs* profuse, more than 20 in number (similar in the female). *Terminalia*: Style with apical crest of fine chitinous ridges, not setae, continuing back a little past the true seta. Subapical lobe with one of the stout processes of the basal lobule much more expanded than the other two, almost leaflet-like, with truncate apex drawn out into two sharp points.

Specimens Seen: New Guinea: Aitape, 1♂. New Britain: Keravat, 1♀.

CULEX (L.) PSEUDORNATUS, n. sp.

Types: Holotype male and allotype female to be placed in the British Museum (Natural History); paratype male and female to be returned to the School of Public Health and Tropical Medicine, Sydney.

Type Locality: Edie Creek, New Guinea.

MALE:

Vertex with upright scales mainly pale golden-brown, some of the more lateral ones dark; recumbent scales fine and pale on the central third, broad and dark external to these, and broad and pale at the extreme lateral corners; the latter scales extend inwards to form a pale margin around the eyes.

Proboscis and palps resembling those of *C. fraudatrix*, but the dorsal hairs of the proboscis extend well onto the basal half; also, palp without any ventro-lateral hair tuft on seg. 3, and with rather shorter basal processes.

Antennal seg. 6 (Fig. 1c) with rather inconspicuous tuft of about 5 dark pointed scales, preceded dorsally by 2-3 short setae. The length of the scales increases ventrally, the most ventral one about as long as the next 3 segments. Other segments as in *C. fraudatrix*.

Thoracic integument brown, largely clothed with fine pale scales, which form a pattern rather similar to that seen in *C. ornatus*; as follows: one broad pale central longitudinal band, extending back over about the anterior half, and two lateral pale bands, which curve around, and to some extent across, the fossae and extend back, around the prescutellar bare space, to the scutellum; on the anterior two-thirds, the pale bands are separated by two longitudinal dark lines of unscathed integument. All lobes of the scutellum with narrow pale scales. Pleura with a small patch of pale scales at the dorsal angle of the sternopleuron.

Wing with rather broad scales on the branches of vein 2; bases of the fork cells level.

Abdomen with broad basal pale bands on tergites II-VII. Venter pale-scaled.

Legs uniformly dark, except for the femora which are pale on their under-surfaces, the hind-femora being largely pale on the basal half.

Terminalia: Coxite (Fig. 2a) with dorsal margin only slightly sigmoid, with numerous short setae placed in 3-4 rows, and, internal to these, a submarginal row of 5-7 long, sharply-curved setae. Subapical lobe with the usual 3 rod-like processes on

the basal lobule, their apices not markedly expanded; the distal lobule with 2 clear, clavate leaflets, and 2 setae, one strong and one fine. Lateral process of phallosome (Fig. 2*b*) resembling that of *C. fraudatrix*, but posterior angle of the median process more produced, with more numerous teeth. Ninth tergite with 7-10 rather prominent setae, about $\frac{1}{3}$ - $\frac{1}{2}$ the length of the paraproct.

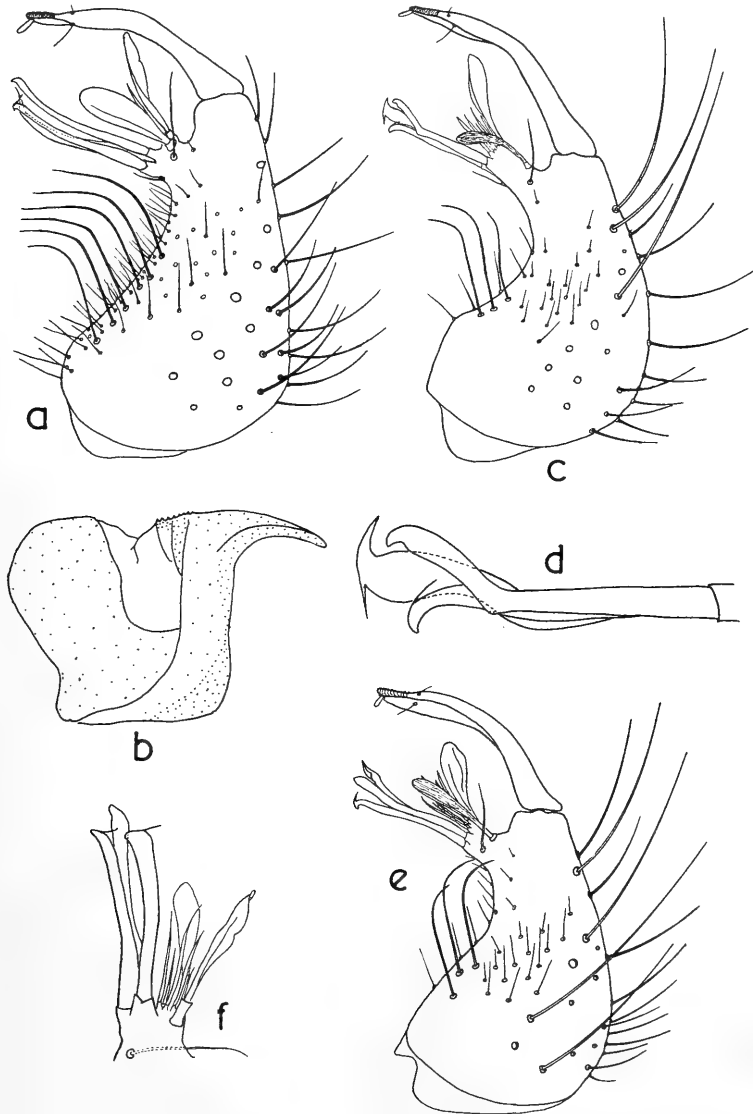


Fig. 2.—(a), (b) *C. pseudornatus*, n. sp.: (a) coxite; (b) right half of phallosome, lateral external view. (c), (d) *C. sp. A.2* near *fraudatrix*: (c) coxite; (d) rod-like processes of subapical lobe. (e), (f) *C. fraudatrix*: (e) coxite; (f) subapical lobe.

FEMALE:

Ornamentation as described for the male; one specimen with rather more brown scaling in the fossae, the other with the scutum mainly pale-scaled on the anterior half.

LARVA: Not seen.

Identification: The thoracic ornamentation separates this species from all but *C. ornatus*, and *C. christiani*, n. sp., from which it is distinguished by the complete

abdominal bands, the small scale-tuft on antennal segment 6, and various features of the male terminalia, palps, and proboscis.

Specimens Seen: Type series only.

Notes: The ornamentation and, to some extent, the characters of the terminalia, suggest a relationship between this species and *C. ornatus*, but there are marked differences in antennal characters. A similar situation is seen in other pairs of apparently related species (e.g., see under *C. atracus*), which suggests that the structures of segment 6 of the male antenna may alter relatively rapidly under evolutionary pressure, in its broadest sense. In this case, known distributions suggest that *C. ornatus* is coastal and *C. pseudornatus* a highland form.

CULEX (L.) PETERSI, n. sp.

Types: Holotype male and allotype female, both with correlated larval and pupal skins, and 1 morphotype larva to be placed in the British Museum (Natural History); paratype male and female, both with correlated larval and pupal skins, and 1 morphotype larva to be placed in the School of Public Health and Tropical Medicine Sydney; paratype male and female, both with correlated larval and pupal skins, to be placed in the United States National Museum.

Type Locality: Minj, Western Highlands, New Guinea.

MALE: Generally similar to *C. fraudatrix*, differing as follows: *Palp*: Seg. 3 with sparser ventral hairs and no ventro-lateral tuft; basal processes longer, their apices almost level with apex of palp segment 1. *Antenna*: Scale tuft on seg. 6 (Fig. 1*d*) with 3-4 dark, blunt-tipped scales dorsally, these about as long as the next 4 segments, then several shorter lanceolate scales and a series of 8-10 very narrow pointed scales of increasing length; the latter, and sometimes the lanceolate scales, pale on the apical half or more; also, dorsal to the scales, several short setae. *Terminalia*: Coxite (Fig. 3*d*) rather resembling that of *C. fraudatrix*, but the 3 submarginal setae with their bases in line, and the most basal one rather weak and straight. Subapical lobe (Fig. 3*e*) with 3 rod-like processes as figured, apical lobule with 2 leaflets, the external one truncate apically; also 6 shorter processes, 3 curved, 1 straight, 1 curved with serrate margin, and 1 with apex expanded and then narrowing abruptly to a fine tip. Lateral plate of phallosome rather similar to that of *C. pseudornatus*. Ninth tergite with 3-6 short setae.

FEMALE: Resembles the male in ornamentation, but the more posterior abdominal tergites with small, indistinct, lateral pale spots. Scutum uniformly brown-scaled.

LARVA: Antenna dark at the extreme base and on the portion distal to the tuft. Shaft spiculate dorsally, externally, and ventrally near the base; a few spicules laterally, distal to the tuft. Apical bristle with apex almost level with those of the subapical bristles. Clypeal spines fairly stout, dark. Mentum with 7-9 teeth each side of the large central tooth, the most lateral ones very small. Head hairs: No. 7, 8-11-branched; Nos. 5 and 6 bifid; No. 4, 2-3-branched, about as long as the distance between its base and that of hair No. 5; No. 8, 3-5-branched; No. 9, 6-8-branched.

Thorax lightly spiculate on dorsal and ventral surfaces. Prothoracic hairs 1, 2, 4, 5, and 6 all single; hair 3 single or bifid, short; hair 7, 3-branched; hair 8, 2-3-branched.

Upper lateral hairs 3-branched on abdominal segs. I-III, 3-5-branched on the other segments. Pentad hairs: No. 1, 5-branched; No. 2, usually bifid, rarely single; No. 3, 8-branched; No. 4, single; No. 5, 4-5-branched. Lateral comb of about 50 elongate scales, with rounded apices and complete fringe.

Siphon (Fig. 1*g*) with prominent acus; index 6.6-8.1 (in 3 whole larvae); siphon/saddle ratio 4.1-4.5, mean 4.3. Tufts 1-3-branched, usually bifid, and about as long as the width of the siphon; 8-9 in number and rather regularly paired, the two central pairs placed laterally, contrasting markedly with the near-ventral apical pair. Pecten of 13-15 spines (Fig. 1*i*), with even fringe grading to fairly strong basal denticles.

Saddle completely encircling anal segment, with lightly spiculate posterior border; ventral brush with 12 tufts; saddle hair 2-3-branched; *isc.* 3-4-branched; papillae more than twice as long as saddle, strongly tapered to fine rounded apices.

Specimens Seen: Type series only.

Identification: *C. petersi* is distinguished mainly by the form of the scale-tuft on antennal segment 6 of the male; also by characters of the terminalia, in particular, the truncate leaflet on the subapical lobe of the coxite. The larva cannot be distinguished with any certainty from those of *C. leei*, *C. ornatus*, or *C. marksae*, on the basis of published descriptions, while differences from *C. christiani*, n. sp., are described below.

Notes: The type series was bred from larvae taken in shallow pools with emergent vegetation, at an altitude of 5,140 feet (coll. S. H. Christian). The species is dedicated to Dr W. Peters of the New Guinea Department of Public Health.

CULEX (L.) CHRISTIANI, n. sp.

Types: Holotype male and allotype female, both with correlated larval and pupal skins, and a series of morphotype larvae to be placed in the British Museum (Natural History); male paratype with correlated larval and pupal skins, and a series of morphotype larvae to be placed in the School of Public Health and Tropical Medicine, Sydney; a similar series to be placed in the United States National Museum.

Type Locality: Minj, Western Highlands, New Guinea.

MALE: Resembles *C. petersi*, differing as follows: *Antenna:* Seg. 6 (Fig. 1f) with scales all dark, the more dorsal 4-5 broad and blunt-tipped, followed by 3-4 shorter pointed scales, and then several very narrow scales with long fine tips of increasing length; the latter grade into the long ventral setae. *Thorax* with indistinct pattern of the type described below for the female; pale scaling only clearly apparent at the anterior margin of the scutum and on the scutellum, but the pair of submedian bare lines is obvious. *Abdominal tergites* with basal pale bands of moderate width (see notes below). *Terminalia:* Coxite (Fig. 3a) rather resembling that of *C. pseudornatus*, with numerous short setae on the dorsal margin, but with a submarginal row of only 3-5 long curved setae, the basal one rather weak. Subapical lobe (Fig. 3b) with the usual 3 rod-like processes, and, on the distal lobule, 2 clear clavate leaflets and 6 shorter processes, one of them expanded apically and one curved with a serrate margin (the serrations may not always be apparent).

FEMALE: Ornamentation of head and thorax similar to that described for *C. pseudornatus*, but rather reduced, and with darker integument; in particular, the pale scaling is virtually absent over and around the fossae. Sternopleuron with only 1-2 small pale scales along posterior border.

LARVA: Very similar to that of *C. petersi*, but differing as follows: *Antenna* more deeply pigmented on the central region of the shaft. *Prothoracic hair* 4 with 2 branches. *Pentad hair* 2 unbranched. *Siphon* (Fig. 1h) a little longer—index 9.0-9.4 (in 7 whole larvae); siphon/saddle ratio 4.1-5.3, mean 4.8. *Siphon tufts* (Fig. 1h) 3-5-branched, usually 3- or 4-branched; usually less regularly paired, and all similarly ventro-lateral in position.

Specimens Seen: Type series only.

Identification: In both sexes, the ornamentation of the thorax distinguishes *C. christiani* from all but *pseudornatus* and *ornatus*, from which it is separated by the absence of any definite scale patch on the pleurae. The male antenna and terminalia are also characteristic. Existing descriptions of larvae allow comparison only with *C. kuhnsi*, which has a highly spiculate integument, while differences from *C. petersi* are given above.

Notes: The abdomen is described above as possessing basal pale bands. However, this was observed in only a single male specimen. In the remainder, such bands were not seen, but I am reasonably certain that this was due to shrivelling of the abdomens of the specimens concerned. The specimen showing definite bands has been selected as holotype.

On adult characters, *C. christiani* seems most closely related to *C. pseudornatus*, and, like it, seems to be a highland form. The type series was bred from larvae taken in the same pools as the series of *C. petersi*.

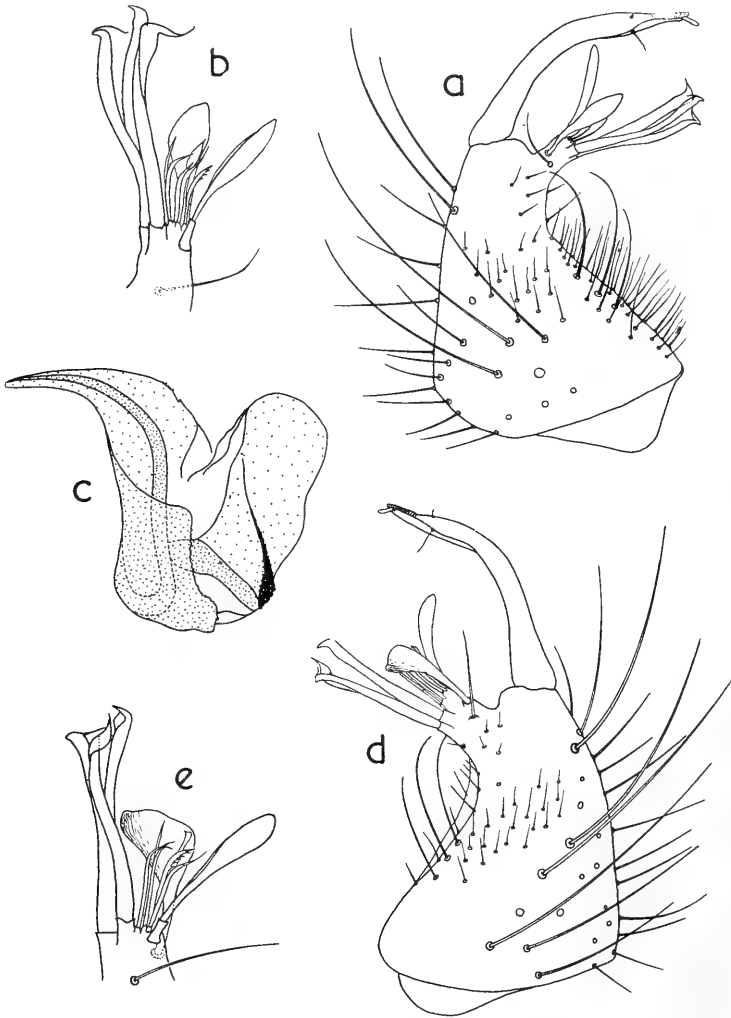


Fig. 3.—(a), (b) *C. christiani*, n. sp.: (a) coxite; (b) subapical lobe. (c) *C. atracus*, n. sp., right half of phallosome, lateral internal view. (d), (e) *C. petersi*, n. sp.: (d) coxite; (e) subapical lobe.

The species is dedicated to the collector, Mr S. H. Christian, of the New Guinea Department of Public Health.

Acknowledgements.

I am deeply indebted to Dr W. Peters and Mr S. H. Christian, of the Department of Public Health, Territory of Papua and New Guinea, and to Mr D. J. Lee, of the School of Public Health and Tropical Medicine, Sydney, for the gift or loan of specimens from New Guinea; also to Mr P. F. Mattingly, of the British Museum (Natural History), for information concerning the type specimens of *C. fraudatrix*.

Reference.

KING, W. V., and HOOGSTRAAL, H., 1955.—Three new species of New Guinea *Culex*, subgenus *Lophoceromyia*, with notes on other species. *Proc. ent. Soc. Wash.*, 57: 1.

NOTES ON AUSTRALIAN THYNNINAE.

IV. THE MORPHOLOGY OF THYNNOIDES RUFITHORAX TURNER WITH NOTES ON THE PREPUPAL LARVA AND THE COCOON.

By B. B. GIVEN, Entomology Division, D.S.I.R., Nelson, New Zealand.

*(Communicated by Dr. A. J. Nicholson.)***(Twenty-three Text-figures.)**

[Read 25th November, 1959.]

Synopsis.

The species is taken as a typical example of the tribe Thynnini as represented in Australia. The structure of the larva and adult is described in relation to homology and taxonomic usage. Cocoon structure and function are discussed.

INTRODUCTION.

In a recent paper (Salter, 1957) there is an excellent comprehensive account of the history of taxonomic usage of morphological terms and structures in the Thynninae of Australia. This superbly illustrated account is rightly confined to characters which have been taxonomically used, but refers only to the male. The present account covers all external areas of both sexes, the tentorial structures of adult and larva, and details of cocoon structure and function. In this it will be useful in supplementing Salter's account. It also presents new material, particularly in relation to the cocoon, and tentorial homology.

The writer is indebted to Dr A. J. Nicholson, Chief of the Division of Entomology, C.S.I.R.O., Canberra, for communicating this paper for publication, and to Mr E. F. Riek and Dr P. B. Carne, also of the Division of Entomology, for careful and constructive criticism of the typescript.

MORPHOLOGY.

A. The Prepupal Larva (Figs 1-3).

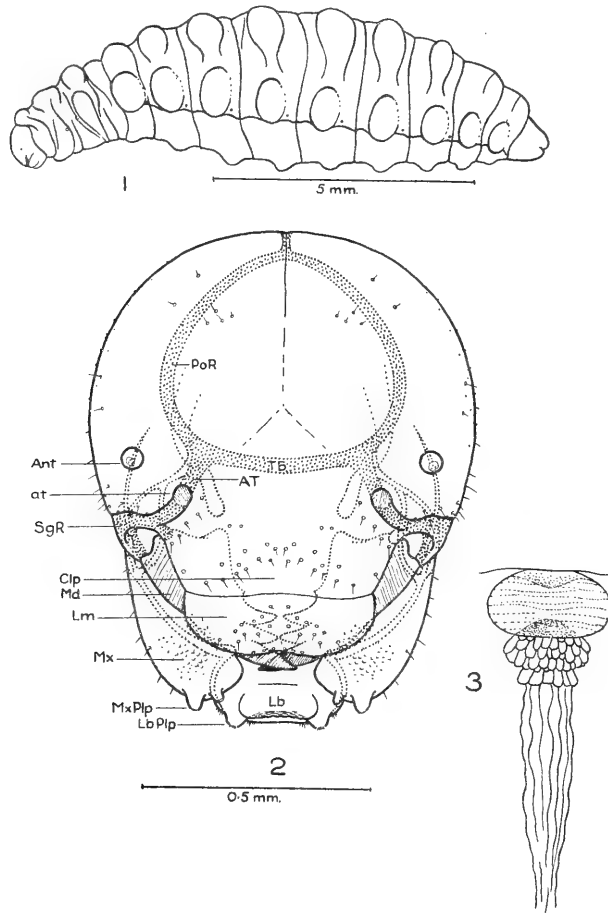
Creamy white in colour, broadly spindle-shaped, head small, dorsal and ventral welts prominent, pleural fold with rather bulbous segmental protrusions on abdominal segments. Integument devoid of hairs or denticles except on the head.

The head (Fig. 2) is not entirely comparable with the normal aculeate larval type. The mandibles (Md) are very large and well developed, tridentate, each with a small pointed tubercle below the basal tooth. The clypeus (Clp) is clearly divided from the labrum (Lm). Maxillae (Mx) are well developed and, apart from the palps (Mx Plp), have smaller papillate structures which appear to arise above glandular organs. The labium (Lb) has a pair of palps (Lb plp), and the opening of the salivary glands is terminal beneath an upper lobe. Vestiture is confined to denticles on the upper surface of the maxillae and lateral margins of the labrum, with small hairs and placoid sensillae on the clypeus, maxillae, labrum, labium and capsule as illustrated. The antennae (Ant) are only slightly raised.

The most interesting features of the head are the tentorium and related structures. The usual larval structures are greatly reduced or missing, the strongest development being in structures homologous with those of the adult. No epistoma or clypeal arch is present, and the hypostoma, labial ring, etc., are reduced. These structures are illustrated in dotted outline but not stippled. The stippled structures are those which are considered to be homologous with the tentorium of the adult or immature stages of more primitive insects. The pleurostoma or subgenal ridge (SgR) is well developed.

leading to the mandibular articulations from well-developed anterior tentorial pits. Anterior tentorial arms (AT), tentorial bridge (TB) and postoccipital ring (Por) are well developed.

The examination of final larval exuvia indicated ecdysis to follow a posterior longitudinal splitting along the longitudinal line of the epicranial suture (which is faintly visible only prior to ecdysis), which does not progress to the level of the tentorial pits.



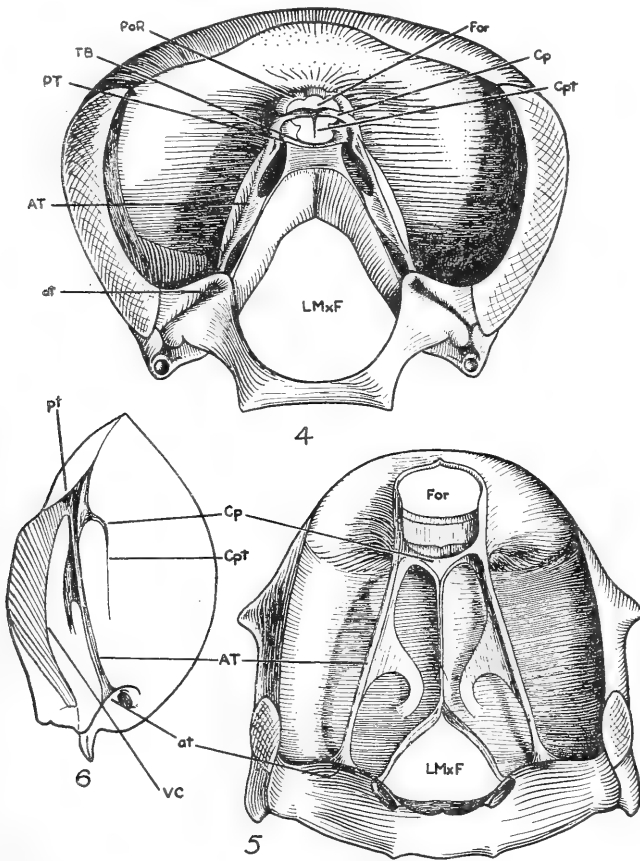
Figs 1-3.—1, Prepupal larva. 2, Larval head, anterior. 3, Larval spiracle.

The spiracles (Fig. 3) are all similar. The atrium is oblate spheroidal, indented both externally and internally and with rather fine and irregular annulations. Below the atrium is a rather diffuse, apparently cellular mass probably having some valvular function. The trachea leading from this is flaccid, very thin walled and lacking in annular thickening. The diameter of the atrium is 0.06 mm.

B. The Adult (Figs 4-17).

The remarkable aspect of adult morphology is in the extreme dimorphism displayed. In this account, only certain aspects related to homology of larval and adult structures, homology of male and female structures, and systematic usage are discussed. For the most part, the figures will be left to tell their own story.

Figures 4, 5 and 6 illustrate the tentorial development of the male and female, and homology of parts with those of the larva (Fig. 1) is indicated by lettering. The great degree of elongation of the head and reduction in size of the labiomaxillary fossa in relation to assisted feeding of the female (Given, 1954) is indicated by the difference in space between the labiomaxillary fossa (LMxF) and the occipital foramen (For) in the two sexes. This extension is accompanied by the formation of a ventral carina (VC) and elongation and modification of other elements as illustrated. The great degree of reduction of compound eyes and complete lack of ocelli in the female is also a result of male-dependence.



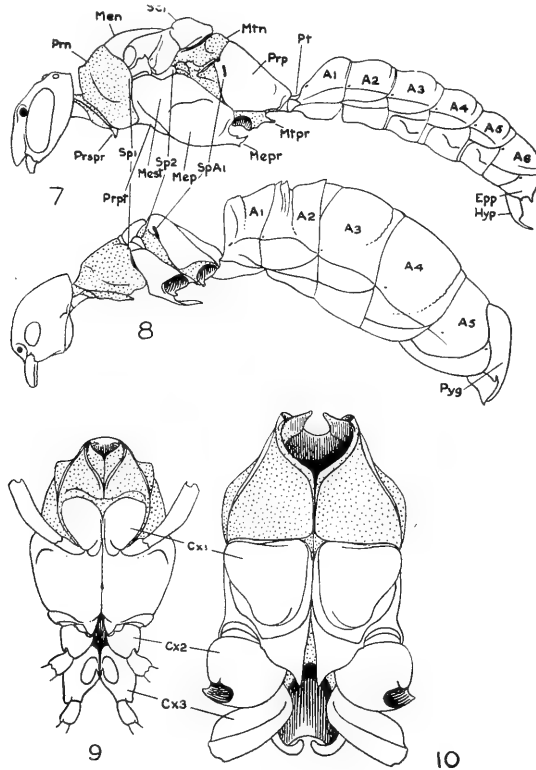
Figs 4-6.—4, Male head, anterior, to show tentorium, etc. 5, Female head, anterior, to show tentorium, etc. 6, Female head, lateral, to show tentorium, etc.

Modification of thoracic elements in the female in accordance with the digging habit as against the flight requirements of the male is striking. This is particularly clearly seen in Figures 9 and 10 which display the relative size of the coxae of the two sexes. It should be noted that these figures are not to scale, the female thorax being drawn more highly magnified than the male. For ease of comparison and interpretation, visible portions of the pro- and metathorax are stippled. In the male, both thoracic spiracles are covered by overlapping plates, whereas in the female only the first spiracle is so covered.

The ultimate abdominal spiracle on the female is illustrated on the fifth segment. Actually it is beneath this plate on the sixth tergite (pygidium). The numbering of abdominal segments is in accordance with systematic rather than comparative morpho-

logical usage, the propodeum or median segment (Prp) being regarded as part of the thoracic structure. The sixth dorsal plate of the female abdomen is termed the pygidium (Pyg) as Turner used this term, and likewise the seventh dorsal plate of the male is termed the epipygium, although these structures are analogous, being the ultimate abdominal coverings for the modified genital segments.

The genital segments proper are illustrated in Figures 11-13 (male) and 16 (female). The male organs vary so greatly in different genera and species that homology is sometimes difficult to interpret. The structures of the female are more



Figs 7-10.—7, Male, lateral. 8, Female, lateral. 9, Male thorax, ventral. 10, Female thorax, ventral.

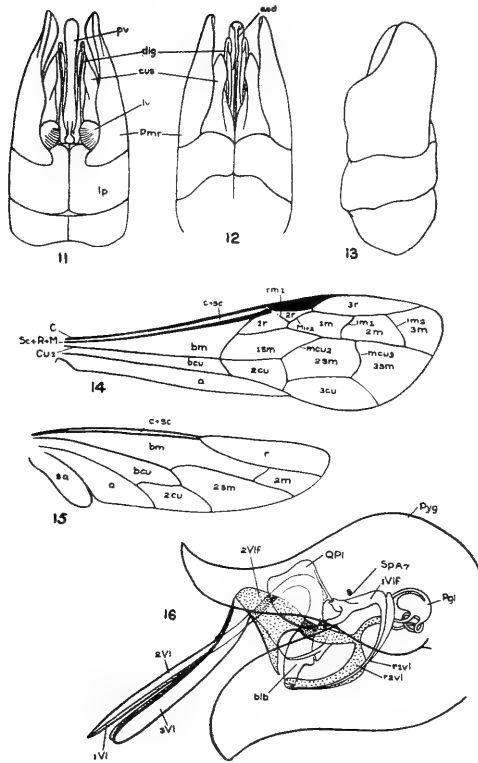
typical of aculeate hymenoptera as a whole, showing less degree of specialization. The male organs in *T. rufithorax* are not modified to the degree noted in species of some other genera, and the structure may be readily identified in accordance with the terminology of Snodgrass (1941). The function and manner of coupling for female transportation and copulation has been previously illustrated (Given, 1954).

The wing venation illustrated in Figures 14 and 15 is interpreted according to Tillyard's "New System" (1926) and the "Jurinian" naming of veins and cells as used by Turner is given in the key to lettering of wings at the end of this paper. To date these are the only systems used in the systematics of the Thynninae.

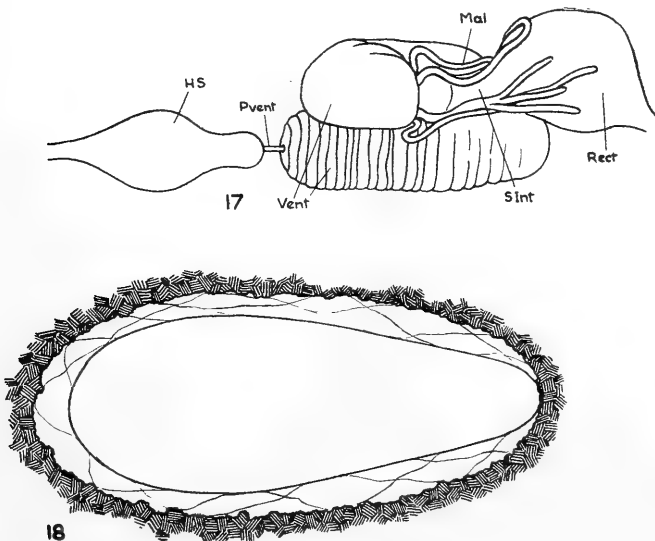
It is of interest that the alimentary tract of the male (Fig. 17) is remarkably similar to that of the worker honey-bee (Snodgrass, 1925, p. 154). This is to be expected as both are nectar gatherers which regurgitate from a "honey-stomach" (HS).

The Cocoon (Figs 18-23).

As has been previously recorded (Given, 1957), there is reason to believe that the relationship between soil-water and adult emergence is a close one. This infers



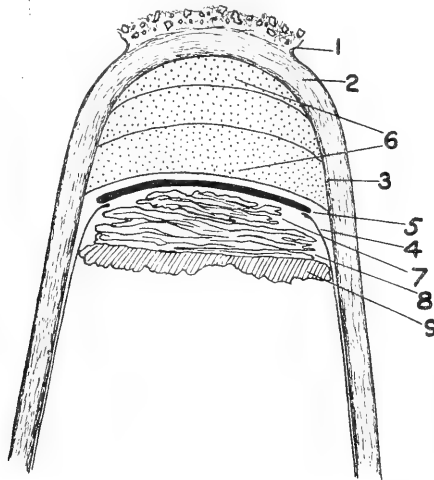
Figs 11-16.—11, Male genitalia, dorsal. 12, Male genitalia, ventral. 13, Male genitalia, lateral. 14, Fore-wing. 15, Hind-wing. 16, Female genitalia, lateral.



Figs 17-18.—17, Male, alimentary tract. 18, Cocoon in earth cell, longitudinal section.

a sensitivity of the prepupa within the cocoon to water outside the cocoon, which in turn infers nice physical properties of water conduction in the cocoon structure.

Figure 18 illustrates in diagrammatic section, the cocoon within its earth cell. It will be noted that loose silken fibres suspend the cocoon so that it is out of contact with the soil except at its small end, which will be referred to as the posterior end.



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Fig. 19.—Posterior end of cocoon, longitudinal section.

This suspension within the earth cell indicates that the interior moisture conditioning of the cocoon is through the posterior end. Examination discloses that at this end the outer layer of the cocoon turns outward, exposing inner layers to soil contact. The inner layers have loose fibres at this point, which incorporate soil particles in the cocoon structure (Fig. 19).

TABLE 1.
Layers Separated from Hemithynnus Cocoon. (Layers numbered from inside to outside.)

Layer.	Fibre Type.	Layer Thickness.	Mesh Sealed or Unsealed.
1	Fig. 23.	Medium.	Partly sealed.
2	Finer than 23.	Thin.	Completely sealed.
3	Fig. 21.	Very thin.	Completely sealed.
4	Finer than 23.	Thin.	Completely sealed.
5	Finer than 23.	Thick.	Completely sealed.
6	Fig. 21.	Medium.	Partly sealed.
7	Fig. 21.	Thin.	Unsealed.
8	Fig. 20.	Medium.	Unsealed.
9	Fig. 20.	Very thin.	Unsealed.
10	Fig. 20.	Very thin.	Unsealed.
11	Fig. 20.	Thin.	Unsealed.
12	Fig. 20.	Thin.	Unsealed.
13	Fig. 23.	Medium.	Completely sealed.

Careful examination of a sectioned cocoon wall shows the presence of a number of layers, and to facilitate examination of these layers, a cocoon of a larger species (*Hemithynnus* sp.) was carefully dissected after first examining the two different ones in order to ensure that there were no obvious differences in structure. The layers determined may be classified as in Table 1.

Condensing Table 1 to simpler terms, the general characteristics of the cocoon wall can be readily seen (Table 2).

Layer 1 (Fig. 19, 4) is incomplete and loosely attached to the more compact and complete cocoon structure. It plays no obvious part in moisture conduction, but may serve to separate the pupa or prepupa from layer 2 when this is wet, or it may be laid down as part of the excretory process in the final elimination of unwanted body products. This layer is usually a dark brown in colour, as also is the pad (Fig. 19, 5) separating the larval excrement (6) from the exuvia (7, 8) and the meconial excrement (9). This pad, like layer 1, is rapidly permeable to water.

TABLE 2.
Grouped Characteristics of Cocoon Layers of Hemithynnus sp.

Layer.	Fibre Type.	Sealed or Unsealed.	Water Resistance.
1 } 2 }	Fine. }	Partly sealed.	Rapidly permeable.
3 } 4 } 5 }	Medium. } Fine. }	Sealed.	Permeable.
6 } 7 }	Medium. }	Partly sealed.	Porous.
8 } 9 } 10 }	Coarse. }	Unsealed.	Porous.
11 } 12 }			
13	Medium.	Sealed.	Almost impermeable.

The outermost layer is a light amber colour and very tough. Intermediate coarse layers (7, 12) are red-brown in colour and form a very porous layer highly reminiscent of rubberized horsehair mattress filling. Layer 6 is intermediate, and layers 2 to 5 are reddish-gold and have the consistency of tough paper glazed on the inner surface.

The outermost layer (layer 13) is difficult to moisten, and does not become completely saturated in less than 24 hours' contact with water. Through the posterior end of the cocoon which has direct soil contact, water is almost immediately conducted on contact, and penetration of all internal layers to number 2, is complete within 10 minutes. However, although layer 2 becomes saturated, no free water collects within the cocoon after 48 hours of partial immersion.

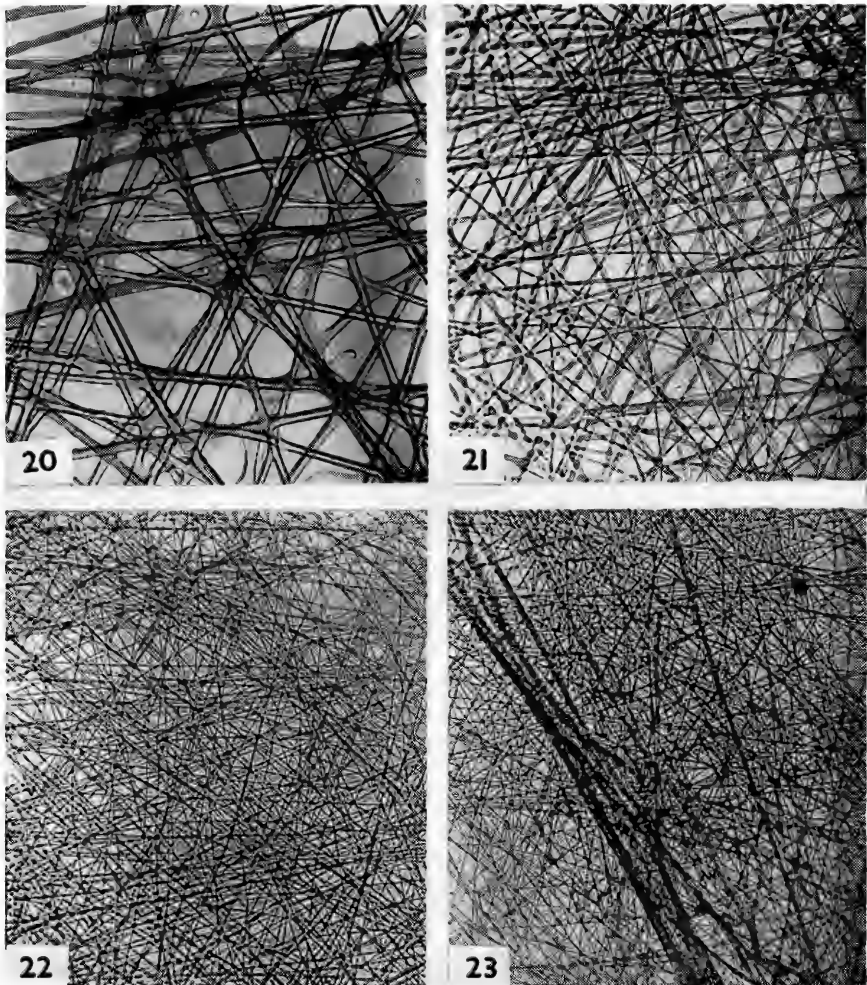
The faecal layers (Fig. 19, 6) rapidly absorb moisture, and to a less extent the pad (Fig. 19, 5) is also absorptive. This may assist in prolonging and regulating the high humidity within the cocoon, and this entire hydrostatic structure may even serve a gas exchange function in relation to carbon dioxide/oxygen balance within the cocoon.

An examination of the faecal material (Fig. 19, 6) discloses the presence of chitin fragments, bristles, soil particles and coarse silk fibres in a dark brown amorphous matrix. This indicates that in the final stages of feeding on the host, the gut, its contents, and the host integument are ingested. The final meconial excrement (Fig. 19, 9) is a pure white, amorphous mass.

TECHNIQUE.

The larva was described from a single specimen removed from a cocoon, fixed in Kahle's fluid and preserved in 70% ethyl alcohol. The head was first treated with hot 5% caustic potash solution, washed in water and temporarily mounted in Berlese's

fluid. Detail was drawn during progressive clearing in this medium, after which the head was removed from the mountant, washed, overstained in acid fuchsin, destained in acid alcohol, completely dehydrated in absolute alcohol and permanently mounted in euparal. From this permanent mount, final details were drawn. The spiracle was drawn from the unstained larval skin mounted in euparal after caustic treatment.



Figs 20-23.—20, Cocoon fibres, coarse, porous layer. 21, Cocoon fibres, intermediate layer. 22, Cocoon fibres, fine, fixed inner layer. 23, Cocoon fibres, fine, free inner layer. $\times 70$.

Examination of adult heads was based mainly on material cleaned by boiling in 10% caustic potash, washed, acidulated with dilute hydrochloric acid, bleached in chlorine water and mounted in euparal. Prior to treatment, one male head from a dried specimen was mounted on a wooden match-stick and the vertex ground away on a very fine scalpel hone. The final mount after cleaning and bleaching proved to be highly satisfactory for examination of internal structures. Adult thorax and abdomen examinations were from dried specimens and from slide mounts of material treated in caustic potash and chlorine water.

Cocoon layer examinations were from permanent mounts in euparal of separated layer samples.

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Key to lettering of figures (except wings).

A1-A6, Abdominal segments; aed, Aedeagus; Ant, Antenna; AT, Anterior tentorial arm; at, Anterior tentorial pit; bbb, Bulbous swelling of ovipositor shaft; Clp, Clypeus; Cp, Corporo-tentorium; Cpt, Corpotendon; cus, Cuspis or distivolsella; Cx1-Cx3, Coxae; dig, Digitus; Epp, Epipygium; For, Foramen magnum or occipital foramen; HS, Honey stomach or crop; Hyp, Hypopygium; Lb, Labium; LbPlp, Labial palp; Lm, Labrum; LMxF, Labimaxillary fossa; Ip, Parameral plate or basiparamere; Iv, Volsellar plate or basivolsella; Mal, Malpighian tubules; Md, Mandible; Men, Mesonotum or mesoscutum; Mep, Mesepimeron; Mepr, Mesosternal intercoxal process; Mest, Mesepisternum; Mtn, Metanotum; Mtr, Metasternal intercoxal process; Mx, Maxilla; MxPlp, Maxillary palp; Pgl, Poison gland; Pmr, Paramere; PoR, Postoccipital ring; Prn, Pronotum; Prp, Propodeum or median segment; Prspr, Prosternal intercoxal process; PT, Posterior tentorial arm; Pt, Petiole or pedicel; pt, Posterior tentorial pit; Pv, Penis valve or lamina aedeagal; Pvent, Proventriculus; Pyg, Pygidium; QPl, Quadrate plate; Rect, Rectum; r1vl, r2vl, Rami of valvulae; Scl, Mesoscutellum or scutellum; SInt, Small intestine; SgR, Subgenal ridge or pleurostoma; Spl, Sp2, Thoracic spiracles; SpA1, Propodeal spiracle; TB, Tentorial bridge; VC, Ventral carina; Vent, Ventriculus; 1VL, 2VL, 3VL, Valvulae; 1VLF, 2VLF, Valvifers.

Lettering of Wings.

Notation. "New System" (Tillyard, 1926). "Jurinian" System.

Cells.

a	Anal	Anal
bcu	Basicubital	Median
bm	Basimedial	Subcostal
c + sc	Costal plus first subcostal	Costal
2cu	Second cubital	
3cu	Third cubital	Second posterior
1m	First median	Second cubital
2m	Second median	Third cubital
3m	Third median	Fourth cubital
r	Radial	Cubital
1r	First radial	First cubital
2r	Second radial	First radial
3r	Third radial	Second radial
sa	Subanal	
1sm	First submedian	First discoidal
2sm	Second submedian	Second discoidal
3sm	Third submedian	First posterior

Veins and cross-veins.

C	Costa	Costa
Cu1	Cubitus, first branch	Median
im1	First inter-median	Second transverse cubital
im2	Second inter-median	Third transverse cubital
M1 + 2	Media, basal piece	First transverse cubital
mcu2	Second medio-cubital	First recurrent
mcu3	Third medio-cubital	Second recurrent
Sc + R + M	Principal vein	Subcostal

Numbering of Figure 19.

1. Termination of outer layer.
2. Porous layer.
3. Sealed inner layer.
4. Loose inner layer.
5. Silk pad.
6. Larval faeces.
7. Larval exuvium.
8. Pupal exuvium.
9. Meconial excrement.

NOTES ON AUSTRALIAN THYNNINAE.

V. AEOLOTHYNNUS MULTIGUTTATUS ASHMEAD AND ISWAROIDES KOEBELEI ASHMEAD.

By B. B. GIVEN, Entomology Division, D.S.I.R., Nelson, New Zealand.

*(Communicated by Dr. A. J. Nicholson.)**(Eight Text-figures.)*

[Read 25th November, 1959.]

Synopsis.

A paratype male of *A. multiguttatus* is figured and the status of the genus is briefly discussed. Notes made on *I. koebelei* by Dr Karl V. Krombein are quoted. Both these species have been previously known to Australian workers only from original descriptions which are inadequate.

Acknowledgement.

This paper, which records essential information on the group, has been produced entirely from information given and a specimen sent by Dr Karl V. Krombein of the Entomology Research Branch, Agricultural Research Service, U.S. Department of Agriculture. To Dr Krombein and to the United States National Museum authorities who allowed the paratype specimen of *Aeolothynnus multiguttatus* Ashmead to be sent to New Zealand for examination, I express my thanks.

The writer is indebted to Dr A. J. Nicholson, Chief of the Division of Entomology, C.S.I.R.O., Canberra, for communicating this paper for publication, and to Mr E. F. Riek and Dr P. B. Carne, also of the Division of Entomology, for careful and constructive criticism of the typescript.

AEOLOTHYNNUS MULTIGUTTATUS Ashmead.

The genus *Aeolothynnus* was erected by Ashmead in 1903 with the genotype *A. multiguttatus*. The genus was then very poorly defined and has been frequently misinterpreted by subsequent workers. It is unfortunate that R. E. Turner did not see Ashmead's type material when he was working on the group. The "Genera Insectorum" is usually considered to be authoritative, and this fact has led to Turner's work of 1910 being accepted much more widely than is merited. His interpretation of this genus in both 1908 and 1910 was quite incorrect.

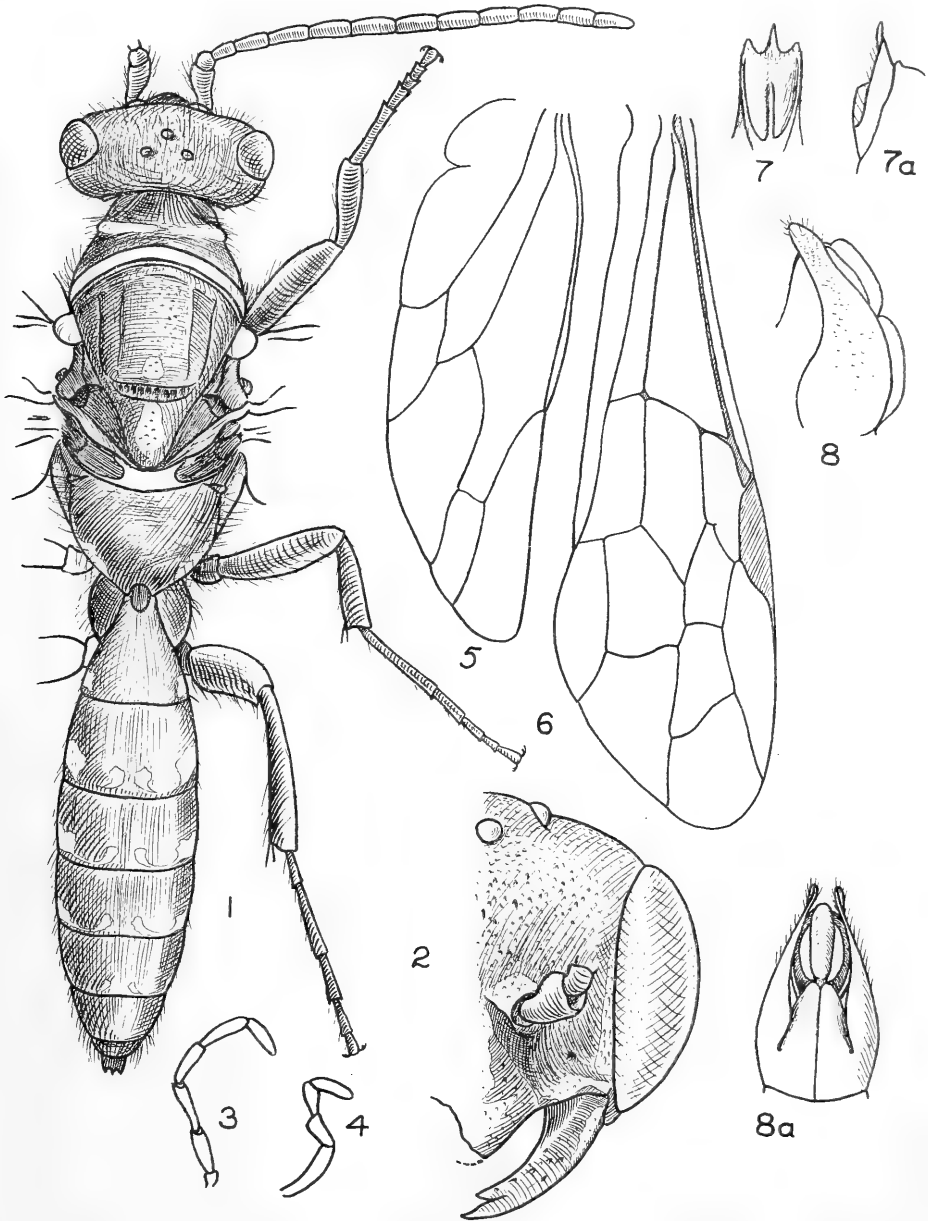
Rohwer (1910) published the first description of the genotype, Ashmead (1903) having given mere key distinctions. (Turner had considered the genotype undescribed, ignoring the description based on Ashmead's key and used the generic name, substituting a genotype of his own selection, *Thynnus cerceroides* Smith). Rohwer (1910) stated that *T. cerceroides* and *A. multiguttatus* were not congeneric and therefore the genus *Aeolothynnus* Turner was left without a name as that name was valid for the genotype *multiguttatus* of Ashmead. Rohwer (1910) proposed the name *Turnerella* for Turner's genus. However, this generic title was preoccupied, and both Turner (1911) and Rohwer (1910a) appreciated this at about the same time. Turner (1911) then proposed the name *Eurohweria* for his genus, but he was forestalled by Rohwer (1910a) who proposed the name *Thynnoturneria*.

The position then was that Turner's genus was *Thynnoturneria* while *Aeolothynnus* of Ashmead with the genotype *A. multiguttatus* stood.

In order to clarify Ashmead's genus, a paratype male was borrowed from the United States National Museum by the writer and is here illustrated. This specimen does not appear to be congeneric with any material collected by the writer, but doubt-

less will prove to be so with specimens in Australian collections. It is considered that the figures in this paper will prove sufficient for accurate generic determination.

The length of the paratype male is 7.5 mm.



Text-figs. 1-8.—*Acolothynnus multiguttatus* Ashmead, male. 1, entire insect, dorsal; 2, head, anterior; 3, maxillary palp; 4, labial palp; 5, hind wing; 6, fore wing; 7, hypopygium, ventral; 7A, hypopygium, lateral; 8, genitalia, lateral; 8A, genitalia, dorsal.

ISWAROIDES KOEBELEI Ashmead.

In reply to a request that Ashmead's type should be examined, the following information was received from Dr Karl. V. Krombein:

"The male type of *Iswaroides koebelei* Ashm. runs to *Thynnoturneria* (= *Aeolothynnus* Turner not Ashmead) without question in Turner's key. The maxillary palpi are 6-segmented as you surmised. The basal joint is small and was not apparent until I had relaxed the specimen and moved the labial palpus which covered the basal part of the maxillary. The shape of the hypopygium and pygidium are consistent with *Thynnoturneria* males, and *koebelei* also has the curious sternal protuberances laterally on the third and fifth.

"The female allotype of *koebelei* lacks the transverse ridges on second tergum, but is nothing like a female *Ariphron* or *Tachynomyia*. Disregarding the characters of the second tergum in couplets 10-14 in Turner's key, this female runs to *Thynnoturneria*. The mouthparts are missing as Rohwer noted. The pygidium does not seem out of character for *Thynnoturneria*. Some additions and modifications of Rohwer's description of the female are as follows: width of head at apex a little more than half the greatest width; in addition to the humeral protuberances the pronotal disc has a low median protuberance at anterior margin; sixth sternum entirely smooth and with lateral hair tuft; fifth sternum smooth in middle, rugosely punctate laterally; pygidium obovate, widest about two-thirds the distance from base, smooth surface rather strongly convex."

In making the above statement, Dr Krombein was not working without reliable material of the genus *Thynnoturneria* as the writer had sent him specimens of this genus after seeing Turner's material. The position of *Iswaroides* must then be considered to be as follows:

Genus ISWAROIDES Ashmead, 1899. *J.N.Y. ent. soc.*, 7: 50.

Thynnus (*Aeolothynnus*) (part) Turner, 1908, *Proc. Linn. Soc. N.S.W.*, 33: 113.—*Aeolothynnus* Turner, 1910, *Gen. Ins.*, 105: 39.—*Turnerella* Rohwer, 1910, *Ent. News*, 21: 249.—*Thynnoturneria* Rohwer, 1910, *Ent. News*, 21: 474.—*Eurohweria* Turner, 1911, *Ann. Mag. nat. Hist.*, (8), 8: 608.

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WILLIAM NOEL BENSON, 1885-1957.

*(Memorial Series, No. 16.)**(With Portrait, Plate xxii.)*

The death of Professor William Noel Benson on August 20, 1957, removed a most versatile and distinguished geologist, who had for more than half a century made outstanding contributions to geological research in Australia and New Zealand which won him international recognition.

Born near London on 26th December, 1885, he was the son of William Benson, a shipping manager and member of an English Quaker family. Shortly after his birth the family came to Tasmania, where the young Benson received his schooling at the Friends' High School, Hobart. At the age of 18 he entered the University of Tasmania and completed a 1st year Science course. On the removal of the family to Sydney he transferred *ad eundem statum* to the University of Sydney and graduated in 1907 in Geology and Chemistry. After a year as Junior Demonstrator in Geology he went to the University of Adelaide as Acting Lecturer in Mineralogy and Petrology during Mr. (later Sir Douglas) Mawson's absence in Antarctica with the Shackleton expedition. Returning to Sydney, he resumed his teaching post in the University, and began the study of the serpentines, spilites and allied rocks of the Great Serpentine Belt of western New England, N.S.W. The award of an 1851 Exhibition Scholarship in 1911 enabled him to spend two years in petrological study and research at the University of Cambridge under Harker, Bonney and Marr, leading to the degree of B.A. (research), the Ph.D. degree having not then been established. The researches of Dewey and Flett, Bailey and others had brought the spilitic suite into prominence in Britain, and Benson's arrival, fresh from his discovery of some of the finest occurrences in the world and with ample material for study, was most opportune. A third year was spent abroad in a tour, in the company of his family, of European countries, visiting places of scenic and geological interest and studying petrological collections in Swiss, German and French universities. Appointed to a Linnean Macleay Fellowship of this Society in 1913, he continued his field investigations in the Great Serpentine Belt and in the next four years published the results of his work in a series of papers in the PROCEEDINGS. He received the degree of D.Sc. of Sydney in 1916, and in the following year left Australia on his appointment to the Chair of Geology in the University of Otago, New Zealand, previously held by Dr. P. Marshall. This position he occupied for 33 years, till his resignation for health reasons a year before he was normally due to retire. From then till the time of his death he was engaged chiefly in research in Dunedin.

Benson was a very successful and inspiring teacher, and trained many students who later filled important geological posts both at home and abroad. It was a matter of gratification to him that within a few years of his arrival in Dunedin the New Zealand Geological Survey had taken four of his graduates. In the tradition of his old chief and lifelong hero, David of Sydney, he not merely taught his students, but also set them an example of enthusiasm for and vigorous activity in original research. He laid much stress on fieldwork and, in the words of his successor, D. S. Coombs, "all his former students will remember his well-loved figure forging ahead in front of panting field-parties".

It was anything but an impressive department to which he succeeded in Dunedin. New Zealand was not yet properly awake to the national importance of university education, and anyhow all its energies were being engaged by the World War then

raging. Benson found that he had not merely to lecture and demonstrate on several branches of Geology and Mineralogy (including Vertebrate Palaeontology, which he had never studied) and supervise the work of graduate students, but also to clean his own blackboard and set out and put away specimens and diagrams used in lectures. Microscope slides had to be made on "a treadle grinding-machine of very irregular habits" at which his predecessor, himself a noted petrologist, had been wont to spend his week-ends and evenings finishing off slides previously rough-ground by students for a trifling fee. There was no technical help at all, and Benson was the sole member of the teaching staff for the first 10 years of his incumbency; then he acquired the services of a lecturer, F. J. Turner, a New Zealand graduate, who relieved him of much lecturing and other work, and was a welcome collaborator in research for 20 years until his appointment as Professor of Petrology in Berkeley University, California. The enforced isolation within the four walls of his department, with no geological company but his own, Benson found very monotonous and not a little irksome, and small wonder that he took every opportunity to get away into the field.

In those days there was one University of New Zealand with constituent colleges in Auckland, Christchurch and Wellington and the University of Otago in Dunedin; all colleges taught the same curriculum and their students sat for the same papers, many of which were set by external examiners. Benson used to relate with much enjoyment how shortly after his accession to the Dunedin chair an examination paper in petrology contained a question on serpentines set by Harker of Cambridge, doubtless in recollection of the subject of Benson's special studies. Unfortunately, through lack of time, or perhaps by a supreme effort of self-restraint, Benson had touched but briefly on the ultrabasic rocks, and his students passed the question by!

His marriage in 1923 to Miss Gertrude Helen Rawson, Professor of Home Science in the University of Otago, who survives him, was a most happy event; thereafter, with a devoted wife who shared many of his interests, a house of his own and a circle of congenial friends, life in Dunedin became for him a very pleasant thing, albeit busier than ever.

Teaching, the administration of his department and participation in university affairs engaged much of his time and energy, but nearest and dearest to his heart to the end of his days was geological research, and it is chiefly for this that his name will endure. The impressive record is contained in more than 70 papers written by him, alone or in collaboration with colleagues.

Already in his student days in Tasmania geology had been his hobby, and in addition to attending the prescribed excursions he had made a point of examining geologically any district in which he happened to be, thus acquiring personal knowledge of much of the island. His early interest received further stimulus on his coming to Sydney, and he quickly became familiar with the geology of many parts of this State. While still a student he wrote a paper on the geology of the Newbridge area near Bathurst, published in our PROCEEDINGS in 1907, and three years later the results of his investigation, begun in 1905, of the Hornsby and Dundas volcanic breccia-necks near Sydney, were published by the Royal Society of New South Wales. A note on Tertiary theralitic and essexitic dolerites in 1911 drew attention to what has since been recognized as an important and widespread intrusive accompaniment of early Tertiary volcanic activity in eastern Australia.

While in Adelaide Benson studied the petrology of some of the pre-Cambrian rocks of the Mt. Lofty Range and extended his observations to the Broken Hill area of New South Wales. He recognized the existence of the long meridional Mundi Mundi fault forming the western boundary of the Barrier Ranges, and was the first to show that the Mt. Lofty plateau is really a great horst bounded by step-faults on both west and east.

Probably as the result of his South Australian experience he contemplated a comprehensive study of metamorphism in New South Wales, in the Barrier Ranges and the Cooma and Bathurst areas, but eventually his attention became focussed on the

ultrabasic rocks, and in 1909 he began work on those in the Great Serpentine Belt. The examination and mapping of this area inevitably led to a study of its other geological features, and thus was initiated that fine series of researches with which the name of Benson will always be associated. A preliminary examination of the Nundle area in the south-east before his departure for England was followed by a rapid reconnaissance survey of the whole belt—over 1,000 square miles—in 10 weeks; this included not only the igneous rocks, but also the Devonian and Carboniferous stratigraphy, the folding and thrusting, the tectonic environment of the serpentines, the palaeontology and the geomorphology of the region. All this, be it noted, in the days when Land Rovers were unknown and air photographs undreamt of, when the field geologist had to be self-propelled, and "*solvitur ambulando*" was perforce a guiding principle. Inevitably some of his interpretations were at fault, but subsequent workers have testified to the amazing accuracy of his insight and observations. His intention of studying parts of the Belt in detail was partly carried out, but eventually frustrated by his departure from Australia, and the writing up of the later parts of the Serpentine Belt series was completed during his first few years in Dunedin. The last part, embodying a reconnaissance survey of the Currabubula area, reported an extension of the Carboniferous glacial beds described the previous year from the Seaham-Paterson district by Sussmilch and David.

In New Zealand Benson threw himself with characteristic enthusiasm into local geological research. A much-needed summary of New Zealand stratigraphy, derived from published papers, verbal discussions with colleagues and personal observations, was presented as his Presidential Address to Section C of the Australasian Association for the Advancement of Science in 1921 and later published in abridged form, and for some years served as a standard text for New Zealand students.

Almost from the first he was attracted to the Cainozoic basic rocks of eastern Otago, previously examined by Marshall. The study of this extraordinarily intricate and fascinating volcanic assemblage and its tectonic environment occupied him at intervals during the rest of his life. A detailed geological map of an area of 400 square miles on a scale of 4 inches to the mile was prepared, and five major and a few minor papers on it were published between 1939 and 1946, partly with the collaboration of F. J. Turner and others, but the great work was still unfinished at the time of his death.

A most complete and exhaustive study of the geology of the area about Preservation and Chalky Inlets in the Fiordland region, made in conjunction with various colleagues including R. A. Keble of Melbourne, demonstrated *inter alia* the striking similarity of the graptolite-bearing Lower Ordovician succession to that of Victoria. Previously with Keble he had investigated the little known Ordovician graptolitic rocks in the north of the South Island.

Benson always had a keen interest in palaeontology, and described in conjunction with F. Chapman (Vic.) and W. S. Dun (N.S.W.) several elements of the Devonian and Carboniferous faunas of the Great Serpentine Belt. One of his most interesting discoveries was that of the new Lower Carboniferous coral genus *Amygdalophyllum* (originally intended to be called *Oophyllum*), which has since been found in many places beyond the confines of this State and has considerable stratigraphical value. He was ever on the lookout for Palaeozoic radiolarian rocks in New Zealand, and in 1937, to his great delight, discovered a very small lens of radiolarian limestone in an extensive and widespread sequence of argillites, greywackes and phyllites near Dunedin, which had up till then yielded no trace of fossils. The discovery was made during a holiday picnic, when, somewhat bored by feminine society, he had wandered off in search of geological diversion.

But his greatest palaeontological thrill was got from the almost accidental discovery in 1948 of late Middle Cambrian trilobites in limestone in the Cobb River country in the north of the South Island ("after teaching for 31 years that no such

things existed!"). The occurrence was further investigated in succeeding years and a rich and very varied fauna was revealed. A short account of it was given at the International Geological Congress (Mexico) in 1956.

Benson's early love for geomorphology found ample scope in New Zealand. He was particularly interested in the complex landform patterns of the southern part of the South Island, which he described in a series of interesting papers lavishly illustrated with block diagrams and panoramic sketches, in the drawing of which he had much skill. He demonstrated convincingly the existence in Fiordland of a Cretaceous peneplain much deformed, and truncated by a late Tertiary peneplain, itself subjected to Quarternary uplift and warping. Strangely enough, he does not seem to have been deeply interested in glaciology, nor in the evidences of expiring vulcanism so well exhibited in the North Island.

Through his wide acquaintance with the geology of Australia and New Zealand he was peculiarly fitted to discuss the past history of these lands in relation to each other and to the island groups of the south-west Pacific. His first paper on this topic, on Palaeozoic and Mesozoic Seas in Australasia, was one of the earliest essays in Australasian palaeogeography; another, on the Structural Features of the Margin of Australasia, was a synthesis involving an extensive survey of pertinent literature in several languages on the geology of New Guinea, Indonesia and a number of Pacific island groups.

Benson was an avid reader, a fact to which every one of his papers bears witness in the length of its appended bibliography. His wide and intimate acquaintance with geological literature is seen in his scholarly review papers on the Origin of Serpentine and Conditions accompanying the Intrusions of Basic and Ultrabasic Rocks, both inspired by his researches in New South Wales. Two compilations that involved considerable delving into literature were his Census and Index of the Burindi Fauna and Materials for the Study of the Devonian of Australia, both indispensable to students of the Upper Palaeozoic stratigraphy of Australia. With R. A. Keble he was responsible for a monumental bibliography of the Graptolites of Australia, the revision of which was one of the tasks planned for his retirement but never completed.

Many of his regional papers are prefaced with historical summaries of geological work already done, dating back to the times of the early explorers. These interesting and valuable records throw light on one of Benson's characteristics; like E. C. Andrews he was sensitively responsive to the romance of history. A scrutiny of David's Geological Map of the Commonwealth of Australia thrilled him with the visions it conjured up of venturesome journeys by the pioneers who laid the foundations of our knowledge, and the study of stratigraphy attracted him as affording entrancing glimpses through "magic casements opening on the foam" of the uncharted seas of the dim and distant past.

That the applied aspects of geology also had their appeal to him is shown by papers on landslides in relation to engineering and contributions to the study of endemic goitre in New Zealand through an examination of its incidence in relation to the regional geology and of the geological role of iodine.

During the whole period of his residence in New Zealand he retained a lively interest in Australian geology and geologists, and through his continued membership of the Royal Society of New South Wales and of this Society he was able to keep in close touch with developments in this State. In particular he followed closely the records of further work in the Great Serpentine Belt, and in letters made frequent and nostalgic reference to his travels, adventures and discoveries in it, of which he retained most vivid memories. To the work of fellow geologists he invariably accorded a tribute of unstinted praise and admiration.

Constant preoccupation with a multitude of absorbing interests was reflected in a frequent air of abstraction and occasional absent-mindedness, characteristics which were in evidence even before he left Australia. Some of his earlier papers are notable for their long *erratum* lists, and for their paucity of subheadings and paragraphs.

These were the marks of a mind eager and overflowing with ideas clamouring for expression, and were clearly related to the impossibility of making his pen keep pace with his thoughts; they were not infrequent also in his letters, typed by himself, to his intimate friends. He was a prolific correspondent, whose letters were usually long and packed with interesting information, comment and reminiscence, largely geological but often personal, manifesting a generous nature, a sly but gentle humour, and keen enjoyment of the strenuous life. Sometimes he deplored the superficiality engendered by having to lecture on so many aspects of geology, and the difficulty of keeping abreast of current petrological thought and technique.

Apart from occasional short visits to Australia and attendance at Pacific Science Congress meetings there and in Japan, his first real respite from 17 years of continuous teaching came late in 1933, when, having gained a Carnegie Fellowship, he embarked for England accompanied by his wife and by 800 rock specimens and more than 1,000 micro-slides which he took in the hope (vain, as it turned out) of completing his study of the Otago volcanic rocks away from interruptions. This was typical of the man, for, overworked and mentally and physically fatigued as he often was, his usual method of finding relief was by a change of occupation. Once, when at the end of a strenuous academic year, he entered hospital for an operation, he had what he called "about the most restful spell I had enjoyed [!] during several exceedingly busy years".

Continuous work at high pressure eventually and inevitably told on an overtaxed heart, and Benson was forced to give up active teaching at the end of 1949. For a year he rated as Research Professor, and after his formal retirement continued to occupy a room in the Geology Department. He accepted the situation philosophically, and was even able to write: "I am immensely grateful that my time is no longer interrupted by teaching and administrative work nor by examining, the most distasteful of all duties." He planned to finish the work on the Middle Cambrian beds and above all the Memoir on the Dunedin rocks (which through its sheer magnitude had become a regular Old Man of the Sea), and to this end made another trip overseas with his wife. On the way back in 1955 he was able to spend a few days in Sydney in happy reunion with some of his oldest and dearest friends. Back in New Zealand he settled down to work again, but to his disappointment found himself physically unable to revisit several critical exposures of volcanic rocks in the hilly country in and about Dunedin, while geological reading was handicapped by the fact that the University Library was up two flights' of stairs. When health permitted he busied himself with a final review of his Dunedin typescript, and, as a diversion, with the revision of the bibliography of Australian graptolites and the writing of a short paper on examples of tide-controlled underwater topography in New South Wales and New Zealand.

With great eagerness he looked forward to giving a 'short account of his Middle Cambrian discovery at the Dunedin Australian and New Zealand Association for the Advancement of Science meeting in January, 1957, and to showing the 'visitors some features of his Dunedin lavas in the field with the aid of a series of "dissected block-diagrams that almost talk". This, as he foresaw, was his geological swan-song, and a few months later he died after a short illness.

Benson's eminent services to geology were recognized during his lifetime. He was chosen President of Section C of the Australasian Association for the Advancement of Science in 1921, and President of the Royal Society of New Zealand, 1945-7. He received in 1933 the Hector Medal and in 1944 the Hutton Medal of the Royal Society of New Zealand, in 1945 the Clarke Memorial Medal of the Royal Society of New South Wales, the Lyell Fund of the Geological Society of London in 1923, and its Lyell Medal in 1939, and the Mueller Medal of the Australian and New Zealand Association for the Advancement of Science in 1951. He was elected a Fellow of the Royal Society in 1941, a correspondent of the Geological Society of America in 1949 and an honorary member of the Mineralogical Society in 1954. On his retirement he received the honorary degree of Doctor of Science from the University of New Zealand.

I have to thank Prof. D. A. Brown, University College, Canberra, for kindly procuring the photograph and checking the manuscript.

W.R.B.

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SIR DOUGLAS MAWSON. 1882-1958.

*(Memorial Series, No. 17.)**(With Portrait, Plate xxiii.)*

Douglas Mawson was a personality and indeed a very inspiring one. A naval colleague of his in conversation many years ago said that no one in polar exploration, arctic or antarctic, had ever before gone into such detail and taken so much care in fitting out his expeditions as Mawson had done. Moreover, as was written of one who lost his life in the antarctic, he was indeed a very gallant gentleman. He was elected a member of our Society in 1905, became an Honorary Life Member in 1951, and at the time of his death on October 14, 1958, was its second oldest member.

Mawson was born at Bradford in Yorkshire on May 5, 1882, of sturdy yeoman stock on his father's side. His mother came from the Isle of Man, and so he was called Douglas. He was very proud of his Manx ancestry, and thus, when his inherited farming interests led him to pasture sheep on his property, Harewood near Kuitpo, he chose the Manx three-legged emblem as his brand. He came to Sydney as a child with his parents whose venture in farming was not successful. As a small child a two-mile walk to school probably helped to build up his stamina, to be shown in later years.

He was educated at the Fort Street School, Sydney. At the University of Sydney he took his B.E., Mining, in 1901. He became a demonstrator in chemistry in 1902, carried out geological investigations in the New Hebrides in 1903, obtained his B.Sc. in 1904, and was appointed lecturer in mineralogy and petrology at the University of Adelaide in 1905. In 1909 he took his D.Sc. in Adelaide. In 1907 he was invited to join the Shackleton Antarctic Expedition as physicist, and was one of those who made the first ascent of Mt. Erebus. With Professor T. W. Edgeworth David and Dr. A. F. Mackay, he located the South Magnetic Pole, his physique and common sense contributing materially to the safety of his companions. The Australasian Association for the Advancement of Science supported his suggestion for an expedition to explore the unknown portions of the Antarctic continent, and early in 1911 he went to England to make arrangements for the voyage under Captain John King Davis. *Aurora* was fitted out and she sailed from Hobart on December 2.

Anyone reading "The Home of the Blizzard" will see in its modestly written pages, with poetic description here and there, the type of man that Mawson was. No wonder that he had attracted to his expedition the finest set of young men available as colleagues in a great adventure. Captain Davis in command of *Aurora* was a tower of strength. In perils at sea, icebergs, the closing in of icefields and hurricanes, in perils on land, crevasses innumerable, avalanches, blizzards and blinding snow; in constant danger from losing their way, from exhaustion, starvation, frost-bite and snow-blindness; endless hours of meditation in tents waiting for the merciless winds to abate—such were the experiences of these devoted men. Every item of food had been assessed in real value and weight, every article of equipment tested in every way. The objects of the Expedition were entirely scientific—meteorological, geographical, physical and biological—and there was throughout no attempt at spectacular glamour. While the other parties, though in constant jeopardy, eventually returned safely to the Base, Mawson was the sole survivor of his, Ninnis with his sledge and dogs having lost his life in a crevasse, and Mertz in spite of his stamina and cheerfulness dying beside Mawson in the tent from exhaustion and starvation. A supreme effort and his magnificent physique and, one may add with all reverence, the intervention of Providence, enabled Mawson to stumble over the remaining hundred miles alone—to reach the Base seven hours after *Aurora* had sailed! There is no evidence in his writing of the grievous disappointment this must have been. One is reminded of the

tragedy of the survivors of the Burke and Wills Expedition on the Cooper, a Central Australian type of country with which in after years Mawson was very familiar, where a few hours again meant so much. Mawson, with the relief party left behind, returned to Australia in the summer of 1914 and received the well-deserved honour of knighthood.

The outbreak of the First World War in 1914 held up the publication of the results, but eventually these were completed and, under the heading "Australasian Antarctic Expedition, 1911-1914", comprised 22 volumes in 3 series.

During the war Mawson was commissioned as a staff officer, his main duty being concerned with the supply of munitions to the various fronts. Mawson received the O.B.E. for work done in 1915-18 in connection with the International Commission supplying allied countries with munitions. He was at first attached to the Russian section of the Commission. After the Russian debacle he was appointed, with rank of major, to the International Commission of Armament in London in charge of explosive and chemical supplies to allied countries. He had to visit many of the factories supplying these materials.

In 1920 Mawson was elevated to the Chair of Geology and Mineralogy in the University of Adelaide. This entailed the rearrangement of courses and necessarily considerable teaching. However, he found time for much field work, on foot, by camel, in buggies and finally by motor truck. Whenever possible students accompanied him, for them a most rewarding time. Its wealth of minerals attracted him to Broken Hill where he recognized two divisions of the Precambrian Rocks of the region. His Antarctic experience made him very interested in glaciation and he found that the Proterozoic glacial beds which Professor Howchin had found in the bed of the Sturt River near Adelaide had a wide distribution and so were of great importance. The discovery of uranium ores at Radium Hill and at Mt. Painter in the north-east extremity of the Flinders Range attracted him at once to these localities and here he again found Proterozoic sediments and glacial beds. Over many years he made field trips to the uranium deposits and the Flinders Range in general. He published a series of papers on his results which form a valuable contribution to the stratigraphy of Australia and also indicate the wide extent and the long duration of the Proterozoic glaciation. Mawson was also interested in the activities of algae from the geological point of view and in the origin of carbonaceous sediments.

Fifteen years after Mawson's return from the Expedition of 1911-14 the Antarctic was still calling him. He organized the British Australian New Zealand Antarctic Research (BANZARE) Expeditions of 1929-30 and 1930-31, visits to the Antarctic Continent during the summer period. With specialists aboard in various fields, a wealth of scientific information was obtained. It is perhaps hardly realized what an abundance of lowly forms of life exist in the cold waters of the Antarctic, a riot of life perhaps greater than that of tropical seas, and sustaining indirectly the bulky forms of whales, sea-elephants, sea-leopards and seals, the vast colonies of courtly penguins, the elegant forms of snow and Antarctic and other petrels such as the dappled cape pigeons, and on the islands near by stately albatrosses. The results of these expeditions have not yet been fully completed.

Douglas Mawson's tall and commanding presence suggesting a Viking ancestry made him noteworthy in any gathering. He and Lady Mawson were indeed a remarkable couple. As a geologist alone he made a name for himself, reflected in the full Bibliography of his papers published by the Royal Society of South Australia. His scientific work in the Antarctic and his leadership there brought him well-deserved fame. But he had many other avenues of activity. Thus he was appointed Honorary Curator of Mineralogy at the South Australian Museum in 1908, in 1934 he represented the Royal Society of South Australia on the Board of Governors of the Public Library, Museum and Art Gallery, in 1940 when the Museum became a Government Department he was appointed a member of the Museum Board, and in 1951 he became the very efficient Chairman of that Board. His interest in forestry helped the South Australian

Conservators of Forests in the earlier days when difficulties innumerable were encountered before the forests began to pay their way. He bought about 1,200 acres of land near the State Forest of Kuitpo and cleared the land, a sawmill making use of the native red-gum timber. Part was laid down to pasture and part to pines and ornamental trees. (Thomas Mawson was a well-known landscape gardener in England.) Here he worked hard, his staunch yeoman ancestry asserting itself in his love for the soil. His planning and attention to detail here, as in the Antarctic, brought their own rewards. He also was the leading figure in several commercial interests in trees.

Mawson was married in 1914, after his return from the Antarctic, to Paquita, the pet name of Francisca Adriana, youngest daughter of Guillaume Delprat, General Manager of the Broken Hill Proprietary Limited. The elder of their two daughters, Patricia, married Ifor Thomas, now Lecturer in Zoology in the University of Adelaide; the younger, Jessica, Peter McEwin of Glen Lindsay, Hindmarsh Valley. Both have offspring to carry on the traditions of capacity and leadership manifested by their forebears.

Mawson was knighted in 1914, receiving the accolade from His Majesty King George V during his honeymoon in London. He was awarded the O.B.E. in 1920. He was elected a Fellow of the Royal Society in 1923 and of the Geological Society of London in 1918, receiving its Bigsby Medal in 1919. He was President of the Australasian Association for the Advancement of Science in 1935-37 and of the Royal Society of South Australia in 1924-25 and in 1944-45, receiving the Verco Medal in 1931. He was a Foundation Member of the Australian Academy of Science, of which he was for a time a Vice-President. Other honours conferred on him included Royal Geographical Society's Antarctic Medal, 1909, and Founder's Medal, 1915; King's Polar Medal (3 bars); Gold Medals of the American, Chicago and Paris Geographical Societies; Nachtigal Gold Medal of Gesellschaft für Erdkunde, Berlin, 1928; Mueller Memorial Medal of Australasian Association for the Advancement of Science, 1930; Founder's Medal of the Royal Geographical Society of Australia (Queensland), 1931; Order of SS. Maurice and Lazarus of Italy, 1920; Commander of Order of Crown of Italy, 1923.

The Mawson's home at Brighton, a seaside suburb of Adelaide, though close to the sea, was so protected from the breezes that a delightful garden was established. Here were entertained from time to time such polar notabilities, geographers and geologists of note and lesser scientific lights as happened to pass through Adelaide on their several occasions. Amongst them may be mentioned Stefansson, Wilkins, W. H. Hobbs, Paul Siple, Lord Novar, Caldenius, Baas Becking, Lester King, E. C. Abendanon, G. Gaylord Simpson, H. L. Movius. On Lady Mawson's side, distinguished Dutch guests were similarly welcomed. Sir Edgeworth David, under whose spell Mawson had come as a student, and who in the Shackleton Expedition owed his survival to Mawson, was a frequent visitor.

Mawson was primarily responsible for getting Great Britain to annex and to hand to Australia the Australian Sector of Antarctica which comprises about 2,472,000 out of the 5,000,000 square miles of that Continent.

He named King George V Land and Queen Mary Land (1911-14) and Kemp Land and MacRobertson Land and confirmed Enderby Land (1929-30). Princess Elizabeth Land, Sabrina Coast, Banzare Coast and Wilkes Coast were named in 1930-31.

Mawson, the important meteorological station on the Antarctic Continent, was so named by the Commonwealth of Australia in 1954. In May, 1919, the Mount Field National Park Board in Tasmania named a mountain within its territory after Sir Douglas. Mt. Mawson is 4,300 feet high, more than 100 feet higher than Mt. Wellington near Hobart. In 1958 a shelter hut was built on it and named "Mawson Hut".

A full Bibliography of the writings by Sir Douglas, comprising 123 items, has been published in the *Transactions of the Royal Society of South Australia* in April, 1959 (Vol. 82, pp. 2-6), to which Transactions he contributed no less than 50 papers, the first

in 1906 and the last in 1958, and two more to its Memoirs. He made two contributions to this Society, one in 1905 on "The Geology of the New Hebrides", and the second in 1906 on "The Minerals and Genesis of the Veins and Schlieren Traversing the Aegirine-Syenite in the Bowral Quarries". Besides the Royal Society of South Australia, the sister Royal Societies of Tasmania (the oldest), New South Wales and Victoria published papers by him. In 1935 he contributed the Obituary Notice of Sir Edgeworth David to the Royal Society of London. Similarly, to the Proceedings of the Geological Society of London, he wrote the Obituary Notices in 1938 of Charles Chewings of the MacDonnell Ranges fame, and of Professor Walter Howchin, his predecessor in the Chair at Adelaide. His second paper, published in 1904, was a note on the Geology of the New Hebrides, and in 1957, in the third from last of his writings, he returned again to notes made when he visited these islands at the commencement of his career in a paper appearing in the "Records of the South Australian Museum" entitled "Knee Moulded Pots from the New Hebrides". His interest in radioactivity, shown so strikingly in later years, began early in his career, for in 1904 with Professor Laby he published in the Proceedings of the Royal Society of New South Wales "Preliminary Observations on Radioactivity and the Occurrence of Radium in Australian Minerals". His Commemoration Address to the University of Adelaide in 1925 was on "Some Aspects of Forestry in South Australia". The "Home of the Blizzard" was published in two volumes in 1915 and an abridged and revised edition in one volume in 1931.

Mawson retired from his Chair at the end of 1952, but not from his many activities. Lady Mawson, engaged in writing the life of her father which found expression in "A Vision of Steel", had difficulty in curbing and controlling a mind still finding much of moment to accomplish but set in a body with commencing infirmities. The latter were indignantly minimized, but occasionally Lady Mawson got the upper hand and kept him at home from a meeting. As Chairman of the South Australian Museum Board he attended his last meeting on September 9, 1958. In August he took part in the deliberations of the Council of the Australian and New Zealand Association for the Advancement of Science in Adelaide. In October he lapsed gradually into unconsciousness and died peacefully on October 14, 1958.

The Federal Government asked permission to accord him a Commonwealth State Funeral. At this the Governor-General was represented as well as the Federal and State Governments. The Lieutenant-Governor and Chancellor of the University, Sir Mellis Napier, the Premier, Sir Thomas Playford, the Deputy Chancellor and the Vice-Chancellor of the University and many other distinguished citizens were present. The service included Mawson's favourite and singularly appropriate hymn "Rock of Ages". At the impressive ceremony held later in the Cathedral, under the auspices of the University of Adelaide, a fine address was delivered by the Bishop. Thus a great explorer and leader and man of science was laid to rest in a corner of the old Church of England Cemetery at Brighton.

"Is not short paine well borne, that bringes long ease
 And layes the soul to sleepe in quiet grave?
 Sleepe after toyle, port after stormie seas,
 Ease after warre, death after life, does greatly please."

J.B.C.

APPENDIX.

A complete list of the books and papers written by Sir Douglas Mawson has been published in the *Transactions of the Royal Society of South Australia*, Volume 82, 1959, pages 2-6.

In biological literature his name is honoured by the generic names *Mawsonella* and *Mawsonia*, and the specific name *mawsoni* has been given, by various workers, to more than sixty species representative of most of the major groups of invertebrates as well as a few fishes, lichens and algae.

The following are the details of the publication of the scientific results of his two Antarctic expeditions:

Australasian Antarctic Expedition, 1911-1914. Scientific Reports.

Series A. Geology. Volumes 1-5.

Series B. Meteorology and terrestrial magnetism, etc. Volumes 1-7.

Series C. Biology. Volumes 1-10.

This completes the Scientific Reports.

British, Australian and New Zealand Antarctic Research Expedition, 1929-1931. Reports.

Series A. Vol. I (in preparation). Vol. II, Parts 1-8. Vol. III, Parts 1-2. Vol. IV, Part 1 (Part 2 in preparation). (Other Reports, including Glaciology, are also in preparation.)

Series B. Vols I (Parts 1-4), II, III, IV (Parts 1-10), V (Parts 1-6), VI (Parts 1-14), VII, VIII (Part 1; Parts 2-4 in press). About 15-20 more parts will be published.

ABSTRACT OF PROCEEDINGS

ORDINARY MONTHLY MEETING.

25th MARCH, 1959.

Dr. T. G. Vallance, President, in the chair.

The Chairman offered congratulations to Mr. Mervyn E. Griffiths on obtaining the degree of Doctor of Science, and to Mr. J. W. McGarity, M.Sc.Agr., Mr. A. K. O'Gower, M.Sc., Mr. G. H. Packham, M.Sc., and Mrs. Dorothy A. Thorp, B.Sc., on the award of the degree of Doctor of Philosophy.

The Chairman announced that library accessions amounting to 69 volumes, 561 parts or numbers, 83 bulletins, 15 reports and 56 pamphlets, total 784, had been received since last meeting.

PAPERS READ (by title only).

1. Physiological Specialization of *Melampsora Uni* (Pers.) Lév. in Australia. By H. B. Kerr.
2. The Families of Cycads and the Zamiaceae of Australia. By L. A. S. Johnson.

ORDINARY MONTHLY MEETING.

29th APRIL, 1959.

Dr. T. G. Vallance, President, in the chair.

The following were elected Ordinary Members of the Society: Dr. D. T. Anderson, Sydney University; The Rev. Colin E. B. H. Burgess, Haberfield, N.S.W.; and Dr. J. R. Simons, Turramurra, N.S.W.

The Chairman announced that the Council had elected the following office-bearers for the 1959-60 session: Vice-Presidents: Dr. S. Smith-White, Dr. Lilian Fraser, Mr. S. J. Copland and Professor F. V. Mercer; Hon. Treasurer: Dr. A. B. Walkom, Hon. Secretaries: Dr. W. R. Browne and Dr. A. B. Walkom; also Dr. I. V. Newman as a member of Council in place of Mr. A. J. Bearup.

The Chairman announced that library accessions amounting to 11 volumes, 161 parts or numbers, 30 bulletins, 4 reports and 10 pamphlets, total 216, had been received since the last meeting.

The Chairman reminded members that under the joint auspices of the Royal Society of New South Wales and this Society a meeting will be held in the Main Hall, Science House, 157 Gloucester Street, Sydney, on Wednesday, 3rd June, 1959, to celebrate the centenary of the publication of Darwin's "Origin of Species". The commemorative address will be delivered by Professor P. D. F. Murray.

The Chairman drew the attention of members to the Darwin exhibit now installed in the front hall of the Australian Museum, College Street, Sydney.

PAPERS READ.

1. Notes on Australian Mosquitoes (Diptera, Culicidae). IV. *Aedes alboannulatus* Complex in Victoria. By N. V. Dobrotworsky.
2. Descriptions of two New Species of *Curis* and one New Species of *Stigmodera* (Buprestidae). By C. M. Deuquet.

LECTURETTE.

A lecturette, illustrated by films, entitled "Wild Life of Macquarie Island" was given by Mr. Durno Murray, Senior Research Officer, C.S.I.R.O., McMaster Laboratory, Sydney.

ORDINARY MONTHLY MEETING.

27th MAY, 1959.

Dr. T. G. Vallance, President, in the chair.

The Chairman offered congratulations to Dr. K. A. W. Crook on obtaining the degree of Ph.D. of the University of New England and obtaining a post-doctoral fellowship of the University of Alberta (Canada).

The Chairman announced that Professor Bernard J. F. Ralph had been elected a member of Council in place of Dr. Dorothy Thorp.

The Chairman announced that library accessions amounting to 20 volumes, 215 parts or numbers, 6 bulletins, 7 reports and 8 pamphlets, total 256, had been received since last meeting.

The Chairman reminded members that under the joint auspices of the Royal Society of New South Wales and this Society a meeting will be held on Wednesday, 3rd June, 1959, in the Main Hall, Science House, 157 Gloucester Street, Sydney, at 7.45 p.m., to celebrate the centenary of the publication of Darwin's "Origin of Species". The commemorative address entitled "Charles Darwin" will be given by Professor P. D. F. Murray.

PAPERS READ.

1. An Annotated Catalogue of Described Australian Tabaninae (Diptera, Tabanidae). By I. M. Mackerras.

2. Observations on the Ecology of the Phasmatid, *Otenomorphodes tessulata* (Gray). By P. Hadlington and F. Hoschke.

3. Observations on some Australian Forest Insects. 4. *Xyleborus truncatus* Erichson, 1842 (Coleoptera: Scolytidae), associated with dying *Eucalyptus saligna* Smith (Sydney Blue-Gum). By K. M. Moore.

NOTES AND EXHIBITS.

Dr. I. V. Newman exhibited sporophores of the gasteromycetous fungus *Pisolithus tinctorius*, which at present grows in profusion in the 1-2-foot strip of screenings edging the tarred surface of bituminous roads. It is not obvious in the adjacent bush near the road. The roads on which it was seen were from Wilberforce through Colo and Colo Heights to the end of the bitumen beyond Grassy Hill, and between Wiseman's Ferry and Dural. Along the dirt roads from above (south of) Colo, through Portland Ferry to Wiseman's Ferry it was not to be seen. Where the fungus appeared along the roads it was a very prominent feature of the roadside, even where the road is banked above the general ground level, as on the outside of curves. The largest specimens noted would be 20 cm. or more across; some of the sporophores were roughly hemispherical, others somewhat acorn-shaped.

Dr. W. R. Browne contributed a note stressing the importance, in the Cainozoic geological history of eastern Australia, of at least two major epochs of uplift, in early and middle Tertiary time, in addition to the Kosciusko (late Pliocene?) epoch.

ORDINARY MONTHLY MEETING.

24th JUNE, 1959.

Dr. T. G. Vallance, President, in the chair.

The President referred to the death on 4th June, 1959, of Mr. Anthony Musgrave, Entomologist of the Australian Museum, Sydney, who had been a member of the Society since 1920

The Chairman announced that library accessions amounting to 10 volumes, 132 parts or numbers, 12 bulletins, 1 report and 3 pamphlets, total 153, had been received since last meeting.

The Chairman brought to the notice of members the proposal of the Wild Life Preservation Society to hold a photographic exhibition from 9th to 20th November, 1959.

PAPERS READ.

1. The Effects of Inorganic Salts on Dividing Cells. By Mary M. Hindmarsh.
2. The Genus *Conostylis* R.Br. I. Leaf Anatomy. By J. W. Green.
3. Some East Australian Sea-grass Communities. By E. J. Ferguson Wood.
4. Diptera of Katoomba. Part 3. Stratiomyiidae and Tachinidae. By G. H. Hardy.
5. Somatic Hybridization between *Puccinia graminis* var. *tritici* and *Puccinia graminis* var. *secalis*. By I. A. Watson and N. H. Luig.

LECTURETTE.

A lecturette entitled "Fossil Spores and Pollen Grains" was delivered by Mr. J. P. F. Hennelly.

ORDINARY MONTHLY MEETING.

29th JULY, 1959.

Dr. T. G. Vallance, President, in the chair.

Mr. R. K. Bamber, A.S.T.C. (Science), Wahroonga, N.S.W., and Mr. K. G. Campbell, D.F.C., B.Sc.(For.), Dip.For., Epping, N.S.W., were elected Ordinary Members of the Society.

The Chairman announced that library accessions amounting to 9 volumes, 101 parts or numbers, 6 bulletins, 5 reports and 5 pamphlets, total 126, had been received since last meeting.

The Chairman drew the attention of members to Subscribers' Day and Camp Fire Evening at the "Muogamarra" Sanctuary on Saturday, 12th September, 1959, and the appeal for emergency and general voluntary assistance for the Volunteer Bush Fire Brigade of the Sanctuary.

PAPERS READ.

1. Iron Deficiency in *Eucalyptus dives* Schauer. By W. D. Andrew and D. J. David. (*Communicated by Professor L. D. Pryor.*)
2. The Reproduction and Early Life History of the Gastropod *Cymatilesta spengleri* (Perry) (Fam. Cymatidae). By D. T. Anderson. (*Communicated by Miss I. Bennett.*)
3. Floral Structure and Anatomy in the Family Goodeniaceae Dumort. By R. C. Carolin.
4. A New Mite Parasite (*Harpyrhynchus*) from the Roselle Parakeet (Trombidiformes, Acari). By R. F. Lawrence. (*Communicated by Dr. A. R. Woodhill.*)

EXHIBIT.

A selection of the Stuart Drawings was on exhibit. The Chairman explained that the collection would shortly be transferred to the Mitchell Library on permanent loan.

SYMPOSIUM.

A symposium on "Laterite" was held, the principal speakers being Dr. W. R. Browne, Mr. P. H. Walker (C.S.I.R.O. Division of Soils) and Professor F. V. Mercer (deputizing for Professor R. L. Crocker, who was unable to attend).

ORDINARY MONTHLY MEETING.

26th AUGUST, 1959.

Dr. S. Smith-White, Vice-President, in the chair.

Mr. G. McC. Chippendale, B.Sc., Alice Springs, Northern Territory, was elected an Ordinary Member of the Society.

The Chairman offered the congratulations of members to Dr. R. N. Robertson on his appointment as a full-time member of the Executive of the C.S.I.R.O., and to Dr. W. R. Browne on the award by A.N.Z.A.A.S. of the Mueller Medal.

The Chairman announced that library accessions amounting to 11 volumes, 73 parts or numbers, 13 bulletins, 4 reports and 9 pamphlets, total 100, had been received since last meeting.

The Chairman brought to the attention of members the Crosbie Morrison Memorial Appeal organized by the Trustees of the National Museum of Victoria, Russell Street, Melbourne, C.I, Victoria, to which address donations in response to the Appeal may be sent.

PAPERS READ.

1. Pollen Tetrad Segregation in *Astroloma pinifolium* and *Acrotriche fasciculiflora*. By S. Smith-White.
2. Pollen Tetrad Patterns in *Leschenaultia*. By P. G. Martin and W. J. Peacock.
3. Seed Coat Anatomy and Taxonomy in *Eucalyptus*. II. By E. Gauba and L. D. Pryor.
4. Experimental Crossing of *Aedes (Stegomyia) aegypti* Linnaeus and *Aedes (Stegomyia) albopictus* Skuse (Diptera, Culicidae). By A. R. Woodhill.

EXHIBITS.

1. Mr. J. F. Rigby: *Glossopteris* species from the Illawarra Coal Measures. Typical specimens of *Glossopteris browniana* and *G. indica*, the commonest species distributed throughout the Permian Gondwanaland continent, were exhibited along with *G. ampla* and *G. mitchellii*. A probable *G. angustifolia* which is symmetrical about the mid-rib compared with specimens from Newcastle illustrated by Walkom and Feistmantel which are asymmetrical, also a small leaf with venation comparable with Feistmantel's *G. elegans* of the Greta Coal Measures but size and shape (even if considered as a young leaf) definitely atypical, were also exhibited.
2. Dr. A. R. Woodhill: Lantern slide showing mosaic between green and brown forms of a Scarab Beetle, *Anoplostethus opalinus* from Western Australia.
3. Dr. S. Smith-White: Lantern slides of the chromosomes of *Sowerbaea laxiflora* and of *S. juncea*. The former is confined to the west and south-west of Western Australia, and the latter occurs on the east coast, from southern Queensland to Victoria. *S. laxiflora* has $n = 4$, with one pair of short chromosomes and 3 pairs of long chromosomes. *S. juncea* has $n = 8$, with 2 pairs of short chromosomes and 6 pairs of long chromosomes. *S. juncea* is tetraploid, and in respect to chromosome morphology, autotetraploid. Its meiotic behaviour, however, is also tetraploid. The two species are very similar except in ways which may be direct consequences of ploidy *per se*. They must be vicarious. They are separated by 2,000 miles in space, and perhaps by 20 million years in time, and in that time they have maintained their close similarity.

ORDINARY MONTHLY MEETING

30th SEPTEMBER, 1959.

Dr. T. G. Vallance, President, in the chair.

Mr. M. J. Gardner, B.Sc. (For.), Dip.For. (A.F.S.), Baradine, N.S.W., 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, 1960, 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 up to £800, according to qualifications. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 4th November, 1959.

The Chairman announced that library accessions amounting to 13 volumes, 160 parts or numbers, 12 bulletins, 1 report and 12 pamphlets, total 198, had been received since last meeting.

PAPERS READ.

1. *Ranunculus lappaceus* and Allied Species of the Australian Mainland. By Barbara G. Briggs.
2. *Diadoxus erythrurus* (White) (Coleoptera-Buprestidae) Attack of Fire-damaged *Callitris* spp. By P. Hadlington and M. J. Gardner.
3. Woody Gall, a Suspected Virus Disease of Rough Lemon and other Citrus Varieties. By Lilian R. Fraser.
4. Light as a Control in the Germination and Development of Several Mistletoe Species. By J. F. Rigby.

EXHIBIT.

Mrs. Messmer exhibited specimens of *Ranunculus* from the Kosciusko plateau.

LECTURETTE.

A lecturette was given by Mr. Roger C. Carolin, entitled "Vegetation of South-East England", illustrated by Kodachrome slides by Mr. R. F. Cosser.

ORDINARY MONTHLY MEETING.

28th OCTOBER, 1959.

Dr. T. G. Vallance, President, in the chair.

Mr. I. A. Staff, B.Sc., Dip.Ed., Unanderra, N.S.W., 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, 1960, 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 up to £800, according to qualifications. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 4th November, 1959.

The Chairman announced that library accessions amounting to 16 volumes, 114 parts or numbers, 12 bulletins, 8 reports and 3 pamphlets, total 153, had been received since last meeting.

PAPERS READ.

1. A Revision of *Nitella cristata* Braun (Characeae) and its Allies. Part I. Experimental Taxonomy. By T. C. Chambers and Mary B. Williams.
2. A Revision of *Nitella cristata* Braun (Characeae) and its Allies. Part II. Taxonomy. By Mary B. Williams.
3. Some Silurian Lamellibranchs from New South Wales. By Kathleen Sherrard.

LECTURETTE.

An illustrated lecturette entitled "Some Problems of New Guinea Zoogeography" was delivered by Dr. D. F. McMichael.

ORDINARY MONTHLY MEETING.

25th NOVEMBER, 1959.

Dr T. G. Vallance, President, in the chair.

Mr S. H. James, M.Sc., Bankstown, N.S.W., was elected an Ordinary Member of the Society.

The Chairman referred to the death on 3rd November, 1959, of Mrs Nance (Anne) Zeck, wife of Mr E. H. Zeck, who had been a member of the Society since 1949.

The Chairman announced that Library Accessions amounting to 11 volumes, 63 parts or numbers, 5 bulletins and 6 pamphlets, total 85, had been received since last meeting.

PAPERS READ.

1. The Anatomy of the Barks of Five Species of *Callitris* Vent. By R. K. Bamber.
2. Some species of *Culex* (*Lophoceraomyia*) from New Guinea and Adjacent Islands, with Descriptions of Four New Species and Notes on the Male of *Culex fraudatrix* Theobald (Diptera, Culicidae). By Donald H. Colless.
3. Notes on Australian Thynninae. IV. The Morphology of *Thynnoides rufithorax* Turner with Notes on the Prepupal Larva and the Cocoon. By B. B. Given. (*Communicated by Dr A. J. Nicholson.*)
4. Notes on Australian Thynninae. V. *Aeolothynnus multiguttatus* Ashmead and *Iswaroides koebelei* Ashmead. By B. B. Given. (*Communicated by Dr A. J. Nicholson.*)
5. A New Species of *Hilara* (Diptera, Empididae) from New South Wales. By Kenneth G. V. Smith. (*Communicated by Mr C. E. Chadwick.*)

NOTES AND EXHIBITS.

Note by Dr J. W. Evans—"Endemic Family of Insects". Groups of insects, and doubtless also of other organisms which have the status of a family, are usually represented in more than one geographical province. This is because the characteristics which separate them from other families will, in most instances, have become differentiated in Pre-Tertiary times. Apart from two relict families of Leafhoppers which occur in the neotropical region, the only family of these insects which is restricted to a single geographical area is the Eurymelidae. This family, apart from sparse representation in New Guinea and New Caledonia, is confined to Australia. Some particulars of the biology of Eurymelids were given, illustrated by colour transparencies taken by Mr Justice Myers.

Mrs Pearl R. Messmer exhibited *Helmholtzia glaberrima* (Phylidraceae) from Binnaburra, McPherson Range, collected on 18th May, 1951, as a very small specimen. The rapid increase in size of the clump to 2 feet 6 inches in diameter, under cultivation, under widely differing conditions over a period of three years, was mentioned. The specimen differs in many features from descriptions of *H. glaberrima*.

Dr S. Smith-White exhibited (a) plants of *Cephalotus follicularis* Labill., the Western Australian pitcher plant, grown from small cuttings forwarded by airmail. The cuttings were planted in a mixture of equal parts of peat and peat-moss, and kept under artificial swamp conditions. (b) Seedling progeny of a tree of *Eucalyptus ptilularis* Sm., collected by Mr Ross Florence in the Kendall district. The seedlings exhibited segregation for albinism, approximately in a 1:3 ratio. The parent tree was apparently heterozygous for the albino gene. Other seedling lots from the same locality did not show the segregation. Segregations of this sort could be used in the investigation of inbreeding-outbreeding balance in Eucalypt species.

Mr S. H. James submitted the following note: Permanent interchange hybridity in *Laurentia petraea* (F. Muell.) E. Wimm. was reported. Slides illustrating the ring of 14 chromosomes characteristic of a population of this species from Merridin, Western Australia, were shown. These were compared with the normal association of seven bivalents as seen in a plant from Mt. Olga Chasm. The change from the normal cross-pollinating mechanism to the selfing mechanism concomitant with this hybridity was illustrated by slides and with living material.

Dr I. V. Newman had, a year ago, exhibited shoots of a prostrate form of *Acacia spectabilis*, growing on the south side of a clay cutting on the railway, several hundred yards on the Hornsby side of Pymble railway station. He now showed lantern slides of the plant with the neighbouring erect plants of the species. The slides showed the "aggressiveness" of the prostrate habit—a very strong down-growing of any stems which may have begun to grow upwards. This is not a habit of stem weakness. He also exhibited a photograph of an apparently similar habit of *A. mollissima*. This photograph was sent by Dr A. A. Moffett, of the Wattle Research Institute of the University of Natal, at Pietermaritzburg in South Africa. There, one tree of *A. mollissima*, on selfing, segregates into normal, procumbent, and upright dwarf

forms. The photograph shows a plant, rather lax, straggling, and sparsely leafy, in comparison with the compact and densely leafy prostrate *A. spectabilis*. This "spectabilis" density seems to appear in back-crosses of an *A. decurrens* × *A. mollissima* F₁ to the original, segregating parent (*A. mollissima*). This information is given in a letter from Dr Moffett, dated 2nd April, 1959, in which he speaks of genetical study of the *A. mollissima* problem being done at the Wattle Research Institute. It is hoped to begin such a study of the *A. spectabilis* prostrate form here in the near future.

Dr W. R. Browne exhibited transparencies of New Zealand glaciers and outwash terraces.

LIST OF MEMBERS.
(15th December, 1959.)

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.
- 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 Arousseau, Marcel, B.Sc., 229 Woodland Street, Balgowlah, N.S.W.
- 1952 Baas-Becking, L. G. M., Ph.D., D.Sc., Bureau of Mineral Resources, Geology and Geophysics, Childers Street, Turner, Canberra, A.C.T.
- 1952 Baehni, Professor Charles, Dr.sc., Conservatoire botanique, Université de Genève, 192, rue de Lausanne, Genève, Switzerland.
- 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.
- 1955 Barlow, Bryan Alwyn, B.Sc., Department of Botany, University of Queensland, George Street, Brisbane, Queensland.
- 1956 Barnard, Robert Alexander Stephen, 34 Weldon Street, Burwood, N.S.W.
- 1954 Baur, George Norton, B.Sc., B.Sc.For., Dip.For., Research Section, The Forestry Office, Coff's Harbour Jetty, N.S.W.
- 1935 *Beadle, Professor Noel Charles William, D.Sc., University of New England, Armidale, 5N, N.S.W.
- 1946 Bearup, Arthur Joseph, B.Sc., 66 Pacific Avenue, Penshurst, N.S.W.
- 1940 Beattie, Joan Marion, D.Sc. (née Crockford), c.o. Mr. G. A. Beattie, Golden Plateau Mine, Cracow, Queensland.
- 1952 Bennett, Miss Isobel Ida, Department of Zoology, Sydney University.
- 1948 Besly, Miss Mary Ann Catherine, B.A., Department of Zoology, Sydney University.
- 1958 Blake, Clifford Douglas, B.Sc.Agr., Division of Science Services, N.S.W. Department of Agriculture, P.O. Box 823, Murwillumbah, N.S.W.
- 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.
- 1946 Brett, Robert Gordon Lindsay, B.Sc., 7 Petty Street, West Hobart, Tasmania.
- 1955 Briggs, Miss Barbara Gillian, 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.
- 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, Department of Agriculture, Farrer Place, Sydney.
- 1956 Chambers, Thomas Carrick, M.Sc. (N.Z.), Department of Botany, Sydney University.
- 1959 Chippendale, George McCartney, B.Sc., Lindsay Avenue, Alice Springs, Northern Territory, Australia.
- 1947 Christian, Stanley Hinton, Malaria Control, Department of Public Health, Banz, Western Highlands, via Lae, 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.
- 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, 4 Blane Street, Granville, N.S.W.
- 1931 Colefax, Allen Neville, B.Sc., Department of Zoology, Sydney University.
- 1946 Colless, Donald Henry, Ph.D. (Univ. of Malaya), Department of Parasitology, Faculty of Medicine, University of Malaya, Sepoy Lines, Singapore 3, Malaya.
- 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, Warrabee, 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, University of Alberta, Edmonton, Alberta, Canada.
- 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.
- 1953 de Bavay, Mrs. Jill Armson, B.Sc. (*née* Whitehouse), 35 Hargrave Street, Armidale 5N, N.S.W.
- 1937 Dequet, 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.
- 1958 Donnelly, Robert Bede, 32 Victoria Street, Waverley, N.S.W.
- 1954 Douglas, Geoffrey William, B.Agr.Sci., 226 Clarendon Street, East Melbourne, C.2, Victoria.
- 1948 Drover, Donald P., Ph.D. (W.A.), c.o. Institute of Agriculture, University of Western Australia, Nedlands, Western Australia.
- 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 Edean, Robert, M.Sc., Department of Zoology, University of Queensland, Brisbane, Queensland.
- 1930 English, Miss Kathleen Mary Isabel, B.Sc., 2 Shirley Road, Roseville, N.S.W.
- 1957 Evans, Miss Gretchen Pamela, c.o. Department of Botany, Sydney University.
- 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.
- 1948 Fraser, Ian McLennan, Ph.D. (Cambridge), School of Medicine, College of Medical Evangelists, Loma Linda, California, U.S.A.
- 1930 Fraser, Miss Lilian Ross, D.Sc., "Hopetoun", 25 Bellamy Street, Pennant Hills, N.S.W.
- 1956 Freeland, John Percy, 19 Central Avenue, Como, N.S.W.

- 1959 Gardner, Mervyn John, B.Sc.For., Syd., Dip.For. (A.F.S.), 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., c.o. Department of Agriculture, Mahalapye, Bechuanaland Protectorate, Via Union of South Africa.
- 1917 Hardy, George Huddleston Hurlstone, "Karambi", Letitia Street, Katoomba, N.S.W.
- 1958 Hennelly, John Patten Forde, B.Sc., Highs Road, West Pennant Hills, N.S.W.
- 1951 Hewitt, Bernard Robert, B.Sc., M.Sc. (N.S.W. Univ. Tech.), Department of Agriculture and Stock, Toowoomba, Queensland.
- 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. (*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.
- 1938 Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., Australian Forestry School, Canberra, A.C.T.
- 1952 Jessup, Rupert William, M.Sc., 38 Cox Street, Ainslie, Canberra, A.C.T.
- 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.
- 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.
- 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. F.A.O. of United Nations, Viale delle Terme di Caracalla, Rome, Italy.
- 1938 Kesteven, Hereward Leighton, D.Sc., M.D., Ch.M., 326 Beaconsfield Terrace, Brighton, Brisbane, Queensland.
- 1957 Kindred, Miss Berenice May, B.Sc., 58 Caroline Street, Kingsgrove, N.S.W.
- 1956 Langdon, Raymond Forbes Newton, M.Agr.Sc., Ph.D., Department of Botany, University of Queensland, George Street, Brisbane, Queensland.
- 1939 Langford-Smith, Trevor, M.Sc., Ph.D. (Aust. Nat. Univ.), Department of Geography, Sydney University.
- 1946 *Lawrence, James Joscelyn, B.Sc., School of Public Health and Tropical Medicine, Sydney University.
- 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, 184 Falcon Street, North Sydney, N.S.W.
- 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, 378 Wilson Street, Albury East, N.S.W.
- 1948 Macintosh, Professor Neil William George, M.B., B.S., Department of Anatomy, Sydney University.
- 1922 Mackerras, Ian Murray, M.B., Ch.M., B.Sc., Queensland Institute of Medical Research, Herston Road, Herston N9, Brisbane, Queensland.
- 1931 *Mair, Herbert Knowles Charles, B.Sc., Royal Botanic Gardens, Sydney.
- 1948 Marks, Miss Elizabeth Nesta, M.Sc., Ph.D., Department of Entomology, University of Queensland, Brisbane, Queensland.
- 1959 Marlow, Basil Joseph Guy, B.Sc., Australian Museum, College Street, Sydney.
- 1957 Martin, Anthony Richard Henry, M.A., Ph.D., Department of Botany, Sydney University.
- 1953 Martin, Mrs. Hilda Ruth Brownell, B.Sc. (*née* Simons), Lot 1, cnr. Villiers and Chamberlain Roads, Padstow, N.S.W.
- 1933 Maze, Wilson Harold, M.Sc., University of Sydney.
- 1951 McAlpine, David Kendray, B.Sc., 12 St. Thomas Street, Bronte, N.S.W.
- 1932 McCulloch, Robert Nicholson, M.B.E., D.Sc.Agr., B.Sc., Roseworthy Agricultural College, Roseworthy, South Australia.
- 1957 McCusker, Miss Alison, M.Sc., Department of Botany, Sydney University.
- 1954 McDonald, Miss Patricia M., B.Sc., Dip.Ed., 29 Dee Why Parade, Dee Why, N.S.W.
- 1956 McGarity, John William, M.Sc.Agr., Ph.D., c.o. Faculty of Agriculture, University of Adelaide, Adelaide, South Australia.
- 1948 McKee, Hugh Shaw, B.A., D.Phil. (Oxon.), c/- Department of Botany, Sydney University.
- 1957 McKenna, Nigel Reece, 45 Bear Street, Chermiside, Brisbane, Queensland.
- 1952 McMichael, Donald Fred, B.Sc., Ph.D. (Harvard), Australian Museum, College Street, Sydney.
- 1947 McMillan, Bruce, M.B., B.S., D.T.M. & H. (Eng.), D.A.P. & E., F.R.E.S., School of Public Health and Tropical Medicine, Sydney University.
- 1957 Menzies, Miss Barbara Patricia, M.Sc. (N.Z.), Ph.D. (Cantab.), 16 Lucerne Road, Remuera, Auckland, S.E.2, New Zealand.
- 1944 Mercer, Professor Frank Verdun, B.Sc., Ph.D. (Camb.), Department of Botany, Sydney University.
- 1948 Mercer, Mrs. Greta, B.A., B.Sc. (*née* Baddams), 13 Hampton Road, Keswick, South Australia.
- 1947 Messmer, Mrs. Pearl Ray, c.o. Bank of New South Wales, 47 Berkeley Square, Mayfair, London, W.1, England.
- 1952 *Meyer, George Rex, B.Sc., Dip.Ed., B.A., M.Ed., 91 Bowden Street, Ryde, N.S.W.
- 1949 *Miller, Allen Horace, B.Sc., Dip.Ed., 6 College Avenue, Armidale 5N, N.S.W.
- 1938 Miller, David, C.B.E., Ph.D., M.Sc., F.R.S.N.Z., F.R.E.S., 112 Rutherford Street, Nelson, New Zealand.
- 1948 Millerd, Miss Alison Adèle, M.Sc., Ph.D., Waite Agricultural Research Institute, Private Mail Bag No. 1, Adelaide, South Australia.
- 1947 Millett, Mervyn Richard Oke, B.A., 18 Albion Road, Box Hill, E11, Victoria.
- 1958 Moore, Kenneth Milton, Cutrock Road, Lisarow, N.S.W.
- 1955 Morgan, Mrs. Eva, M.Sc., 4 Haberfield Road, Haberfield, N.S.W.
- 1958 Moss, Francis John, 70 Victoria Road, West Pennant Hills, N.S.W.
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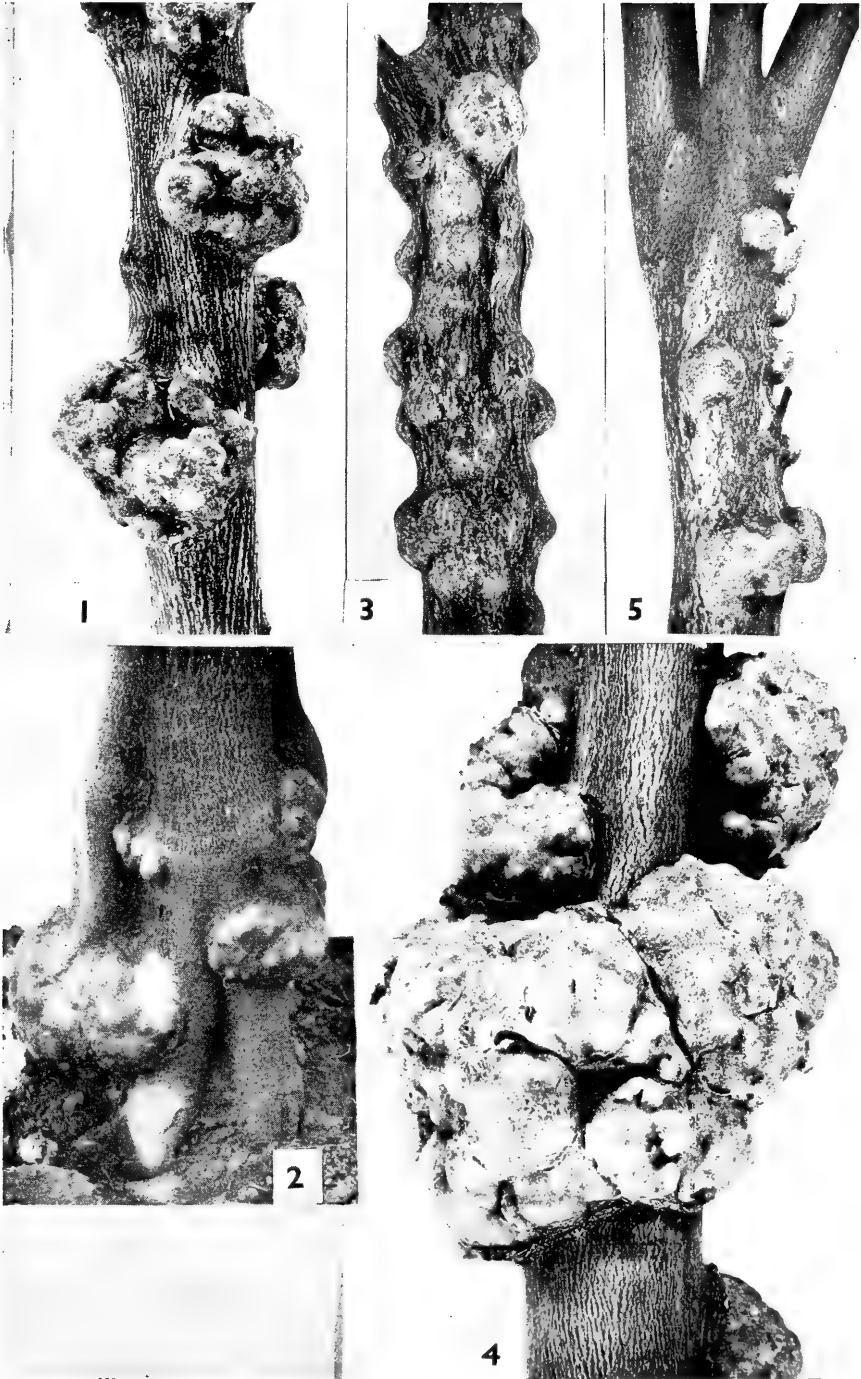


1. Lectotype of *Ranunculus muelleri*. 2. Specimens excluded from the lectotype.



Diadozus erythrusus attack on fire-damaged *Callitris*.





Woody galls on citrus trees.

Clones

6.25

12.5

25

50

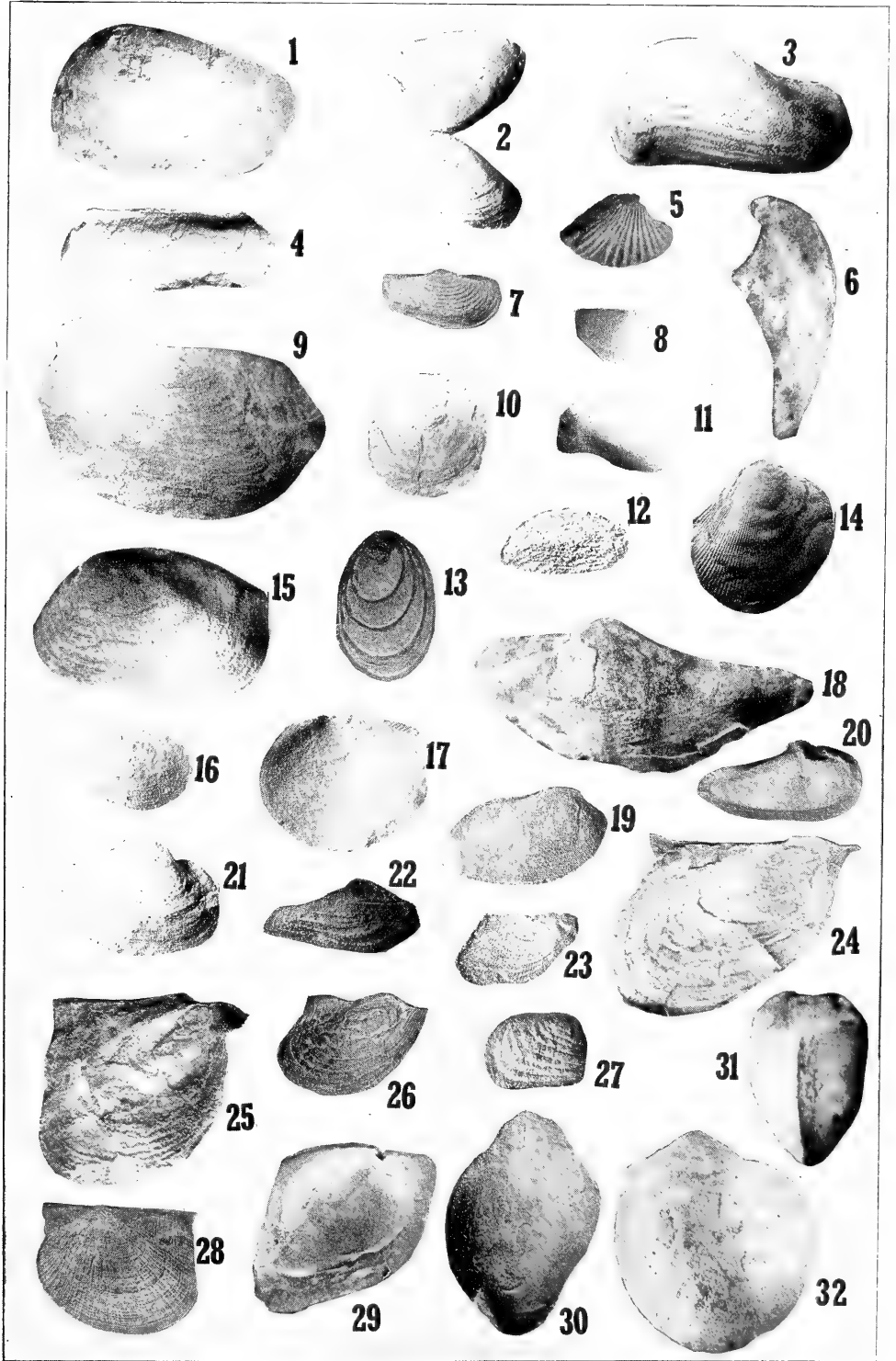
Percent. Daylight

Kiefer's Dam

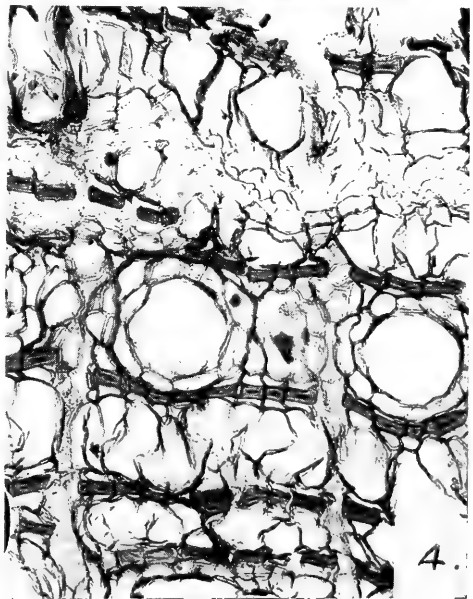
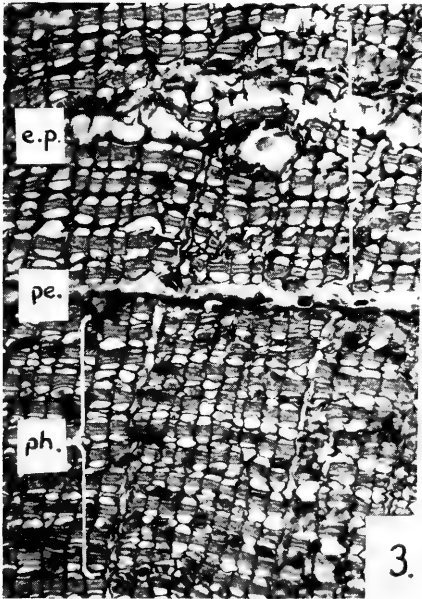
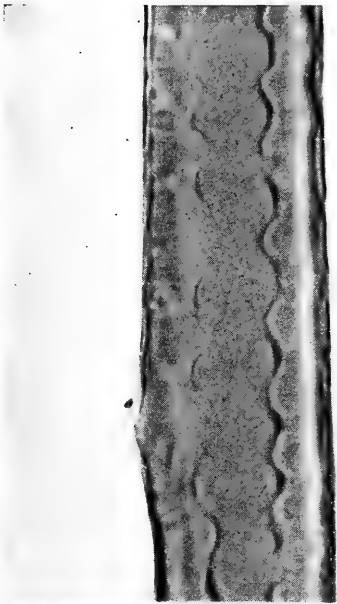


Giletswood



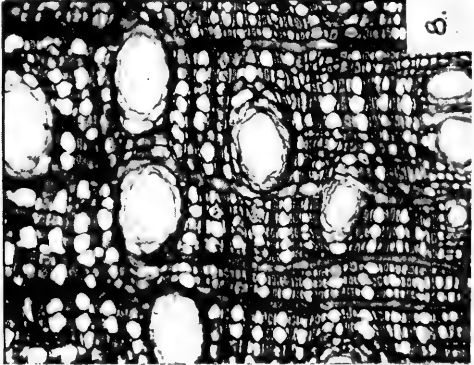
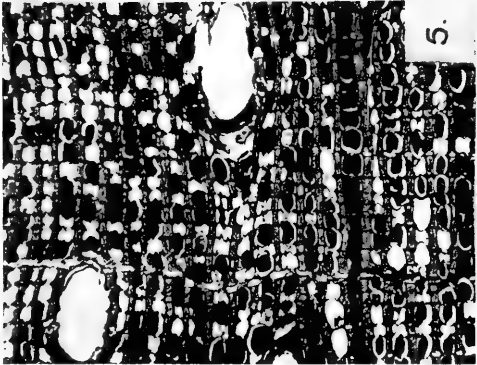
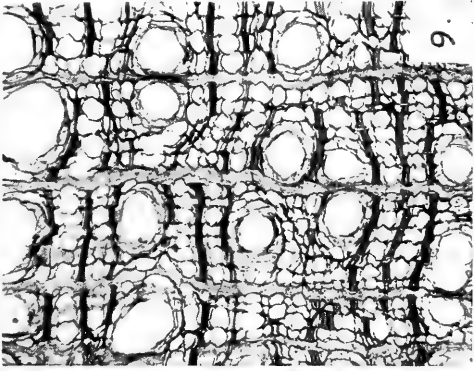
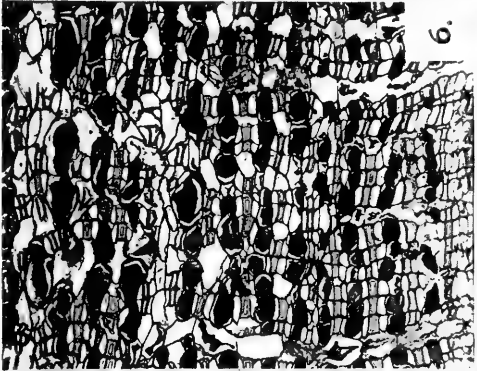
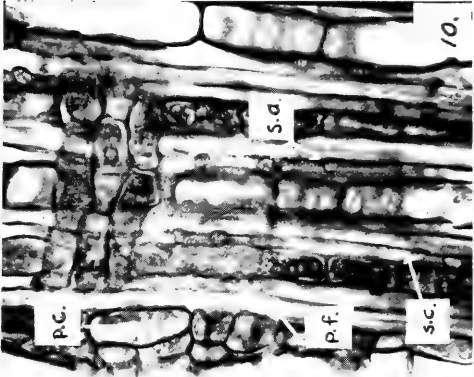
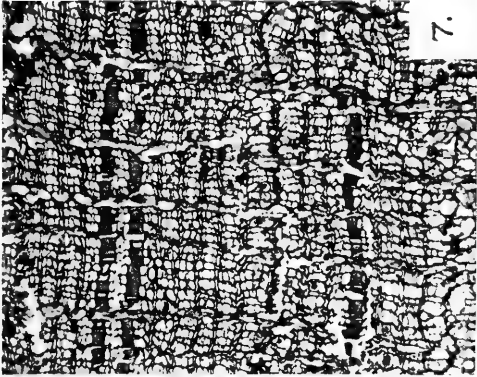


Silurian Lamellibranchs from New South Wales.

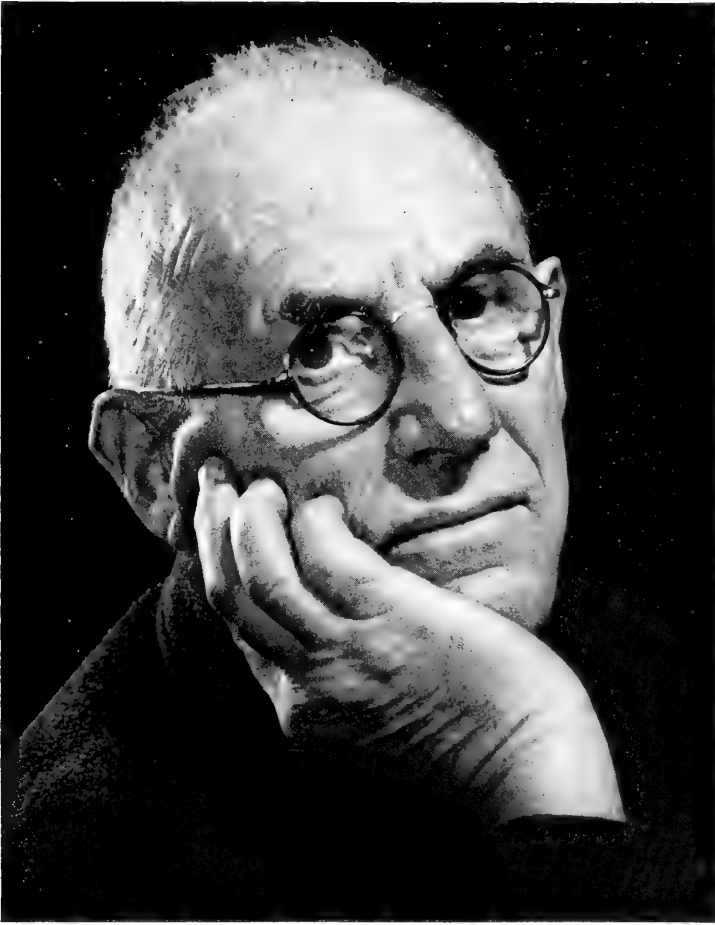


Barks of *Callitris*.

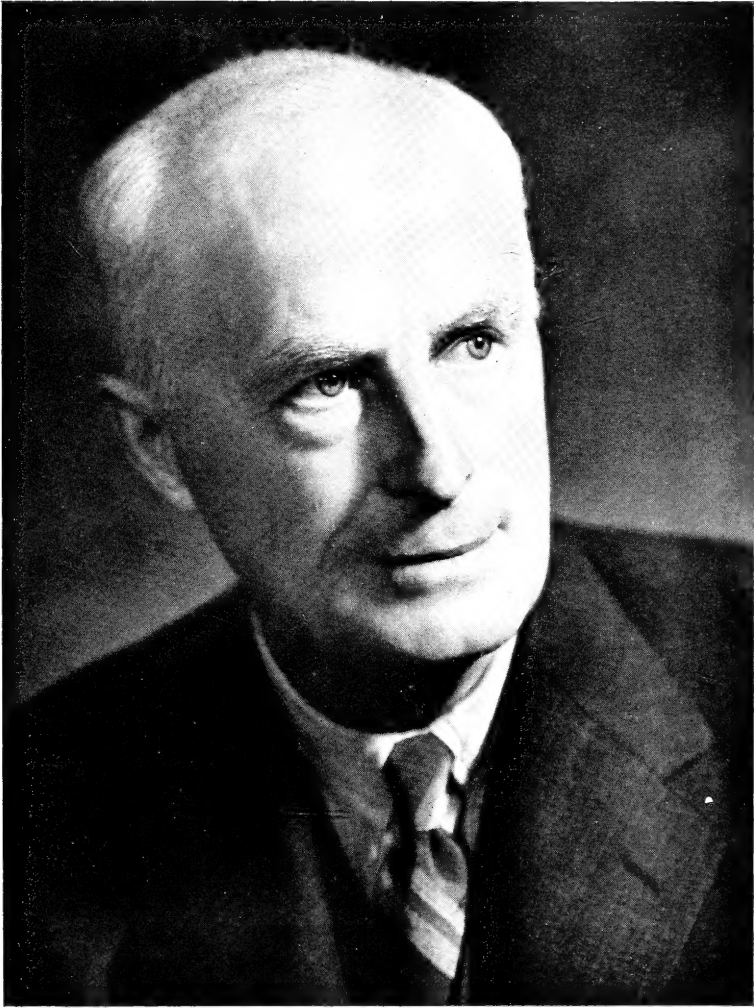




Barks of *Callitris* and *Cupressus*.



W.N. Benson



Douglas Manson

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