THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1962

VOL. LXXXVII.

WITH SIXTEEN PLATES.

306 Text-figures.

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(Issued 30th July, 1962.)

CONTENTS.

PART 2 (No. 399).

(Issued 10th January, 1963.)

CONTENTS.

PART 3 (No. 400).

(Issued 8th April, 1963.)

ANNUAL GENERAL MEETING.

28th March, 1962.

The Eighty-Seventh Annual General Meeting was held in the Society's Rooms, Science House, Sydney, on Wednesday, 28th March, 1962.

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

The minutes of the Eighty-Sixth Annual General Meeting, 29th March, 1961, were read and confirmed.

The Honorary Treasurer (Dr. A. B. Walkom) presented the balance sheets for the year ending 28th February, 1962, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A., and his motion that they be received and adopted was carried unanimously.

In the absence overseas of the President (Professor J. M. Vincent) the Honorary Secretary (Dr. W. R. Browne) read the first portion of the Presidential Address as follows:

I wish to thank the Society for the privilege of having filled the position of President during the past year, and the Council for its support in conducting the Society's affairs. Particularly once again, there must be recorded our deep gratitude to Dr. W. R. Browne and Dr. A. B. Walkom for their continued services as Honorary Secretary and Honorary Treasurer-Editor. I should also like to express appreciation to Miss G. L. Allpress, our Assistant Secretary. Together with all members of Council, I am conscious of how much we owe to the efficient management of the regular affairs of the Society and the maintenance of its library.

Report on the Affairs of the Society for the Year.

The Society's Proceedings for 1961, Vol. 86, Parts 1 and 2, were published in 1961 and Part 3 in February, 1962. Volume 86 consists of 322 pages, 11 plates and 215 text-figures. An increase in the charges for printing the Proceedings commencing with Vol. 87 (1962), Part 1, was made in November, 1961. Revised Library Regulations were adopted by the Council on 22nd March, 1961.

During the year twelve new members were added to the list, two members died, five members resigned and two were removed from the list of members. The numerical strength of the Society at 1st March, 1962, was: Ordinary members, 241; Life Members, 31; Corresponding Member, 1; total, 273.

Lecturettes were given at the following meetings: April, Collecting Insects in Tasmania, by Mr. D. K. McAlpine; June, Pollen and its Chronological Significance, by Dr. A. R. H. Martin; July, The New Zealand Glow-worm, by Dr. Aola Richards; September, Geographical Patterns of Chromosome Change in the Australian Flora, by Dr. S. Smith-White; October, The Argentine Ant Eradication Campaign in Sydney, by Mr. Gordon Pasfield; November, The Impact of New Techniques on Taxonomy, by Mr. R. C. Carolin. The discussions which followed the lecturettes gave an added interest to the proceedings of the meetings. Our thanks and appreciation are expressed to the lecturers. Owing to the holding of the A.N.Z.A.A.S. meeting in Brisbane from 29th May to 2nd June, 1961, no Ordinary Monthly Meeting of the Society was held in May.

Library accessions from scientific institutions and societies on the exchange list amounted to 1,962, compared with 1,912 in the previous year. Members and institutions continued to borrow books and periodicals from the library as previously, and many requests for microfilm and photo-printing copies of old and rare articles were granted by sending the required publication on loan to the Fisher Library, University of Sydney, for that purpose. The following new exchange relations were entered into by the Society: Academie des Sciences de Bulgarie, Sofia, Bulgaria; Botanical Institute, University of Zagreb, Zagreb, Yugoslavia; Instituto de Zoologia (Museu Bocage), Lisbon, Portugal. Council decided, for various reasons, to discontinue exchange of publications

with the following: University of Pennsylvania, Philadelphia, U.S.A.; Indian Agricultural Research Institute, New Delhi, India; U.S. Department of Agriculture, Washington, U.S.A.; Institut Pasteur, Tunis, Tunisia, and New Zealand Oceanographic Institute, Wellington, New Zealand. A number of members took advantage of the Council's offer of the Macleay Memorial Volume and Jubilee Brochure.

Mr. G. P. Whitley, F.R.Z.S., and Miss Elizabeth C. Pope, M.Sc., C.M.Z.S., were elected members of Council in December, 1961, in place of Dr. J. W. Evans, who had resigned, and the late Mr. A. N. Colefax.

Mr. S. J. Copland and Dr. I. V. Newman, who were appointed the Society's delegates to the Conservation Conference held on 18th November, 1961, presented a report to the Council.

Dr. I. V. Newman represented the Society at an Extraordinary General Meeting of the National Parks Association of N.S.W. (Central Region) on 28th November, 1961, to consider a merger between the Association and the Caloola Club.

The total net return from the Society's one-third ownership of Science House for the year ended 31st August, 1961, was £1,274/18/10.

Linnean Macleay Fellowships.

Mr. W. J. Peacock, B.Sc., was reappointed to a Linnean Macleay Fellowship in Botany tenable for one year from 1st January, 1962. A summary of Mr. Peacock's research during the past year is as follows:

During the year research was carried out in two main fields, one being cyto-evolutionary studies in the Goodeniaceae, the other concerning problems of chromosome structure. A polyploid series has been found in *Goodenia bellidifolia*, diploid, tetraploid, hexaploid and octoploid forms occurring. The fact that the chromosome races have sharply defined, non-overlapping, but adjoining areas of distribution, indicates that the different forms have strict eco-physiological tolerances. When this is considered with the actual distribution pattern, a reasonable inference can be made that polyploidy has been of prime importance in migration of the species into the new habitats provided by the elevation of the Great Dividing Range in the late Pliocene. Another example of comparatively recent evolutionary change is found in *Dampiera stricta* which also contains intraspecific polyploids, ranging from diploids to decaploids. Of particular interest is the relationship between the diploid and tetraploid forms in the central and southern coastal regions of New South Wales. In contrast to the geographically separated occurrences of chromosome races in *G. bellidifolia*, the diploid and tetraploid of *D. stricta* occur in the one area in a complex mosaic. The tetraploid appears to be replacing the diploid which has a disjunct relic distribution. *Brunonia australis* presents two pan-Australian patterns of change, one in level of polyploidy, the other in the frequency of structural hybrids. That migration has been from west to east is indicated both by the occurrence of tetraploid and octoploid forms in the south-east of the continent and by the high frequency of interchanges in eastern populations. An interesting point is that there is strong evidence that *Brunonia* has entered Tasmania in two separate migrations, one probably being as recent as the Pleistocene. A number of other species in the Goodeniaceae show geographical patterns and are being investigated. Research has also been carried out on certain problems of chromosome structure. An analysis using X-ray breakage techniques has demonstrated that *Brunonia australis* and *Vicia faba* have subchromatids which have both structural and functional significance. The analysis has been carried another stage further in *Brunonia* in which a quadripartite structure of the chromatid has been shown. *Vicia* was chosen in the above experiments because recent studies on chromosome duplication using autoradiographic techniques indicated that the chromatid of *Vicia faba* was of a unineme structure. Since the results of the X-ray and autoradiographic analyses were not in agreement, the autoradiographic experiments (Taylor, Wood and Hughes) were repeated. The results obtained did not parallel those obtained by Taylor *et al.* (other workers have also failed to repeat these experiments); however, the new results were compatible with the X-ray experiments. Further experiments are in progress.

Linnean Macleay Lectureship in Microbiology.

Dr. Y. T. Tchan, Linnean Macleay Lecturer in Microbiology, University of Sydney, submitted the following report on his work for the year ended 31st December, 1961: "Since my return from study leave my activity has been mainly concerned with teaching. However, some research has been carried out during this period. The presence of *Azotobacter* in the Rhizospheres of wheat has been studied. Attempts to establish *Azotobacter* in the vicinity of the root system of Australian varieties of wheat have been unsuccessful, but some suggestions of stimulation could be noticed. This requires further study. Further work has been done to correlate the algal and field trial methods of stimulating the mineral requirement of soil. This work will probably be completed during 1962. Study of the Gram stain by Electron-Microscopy has been handicapped by the difficulty of marking ultra-thin sections. New embedding methods are under investigation, to overcome the difficulties."

Obituaries.

It is with regret that the following deaths during the year are recorded:

Michel Francois (Michael Frank) Albert died at his home, "Boomerang", Elizabeth Bay, Sydney, on 19th January, 1962, at the age of 87. Mr. Albert was educated at Fort Street High School and the University of Sydney. He entered the music publishing company of J. Albert & Son, Pty., Ltd., established by his father. In association with two other partners he formed the Australian Broadcasting Company, which established the Australian National Broadcasting Service, later taken over by the Australian Broadcasting Commission. At the time of his death Mr. Albert was chairman of the Commonwealth Broadcasting Corporation with stations in Sydney (2UW), Brisbane (4BC) and a country district of Queensland. He was a founder-director of the Australian Performing Rights Association. During his lifetime Mr. Albert made substantial gifts to many institutions, including the University of Sydney, where he helped to form the Chair of Music, St. Paul's College and the Red Cross. He was a fellow of the Royal Geographical Society and a founder-director of the Royal Motor Yacht Club of N.S.W. He was also a founder-member of the Royal Automobile Club and a member of the University Club and the Royal Sydney Yacht Squadron. Mr. Albert joined this Society in 1927, taking up Life Membership on his election.

Allen Neville Colefax, B.Sc., died in Sydney on 7th December, 1961, at the age of 53. He was Senior Lecturer in Zoology at the University of Sydney, for fourteen years, regularly broadcast popular science talks in the A.B.C. Children's Hour, and was known to thousands of radio listeners as "Tom the Naturalist". At the Council meeting of the Society on 13th December, 1961, the following motion was carried, members standing in silence: "That this Council desires to place on record its great sorrow and sense of loss in the death of Allen Neville Colefax. Mr. Colefax was elected a member of the Society in 1931, was President in 1951 and was a member of Council from 1943 till the time of his death. He served the Society wisely and well, and endeared himself to his colleagues on the Council by his modesty, sincerity and unaffected kindliness. The members of Council wish to express their deep sympathy with his wife and family." Mr. Colefax contributed four papers to the Proceedings, also two with Professor W. J. Dakin and one with Mr. G. P. Whitley.

PRESIDENTIAL ADDRESS.

Australian Studies of the Root-nodule Bacteria. A Review. (For full text see pages 8-38.)

This review deals with Australian work with the root-nodule bacteria since the pioneering efforts of the Society's first Bacteriologist, Dr. R. Greig-Smith. A short historical account tracing the establishment of research groups interested in the subject between then and the present day is followed by a more detailed treatment under the headings: *the bacterium, interaction between bacterium and host,* and *application of*

knowledge. Studies of the bacterium itself deal with cytology and composition (which have been relatively neglected in the past), antigenic composition of the rhizobia, factors affecting their growth, antagonistic and mutually beneficial effects involving rhizobia themselves and in relation to other organisms, bacteriophage, variation (developed particularly in connection with a relatively well studied set of substrains), and taxonomy (in which fresh interest is developing). The interaction between bacterium and its host is treated first in relation to general considerations of the symbiosis; then in more detail in respect of the morphology and metabolism of the nodule, specificity in relation to invasion and fixation and the influence exercised by the environment. So far as it is possible to treat it separately, this knowledge is applied to a consideration of the need for seed inoculation in Australia, the supply of seed inoculants and requirements for their successful use.

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

President: Professor B. J. F. Ralph, B.Sc., Ph.D., A.A.C.I.

Members of Council: R. H. Anderson, B.Sc.Agr.; Elizabeth C. Pope, M.Sc., C.M.Z.S.; E. Le G. Troughton, C.M.Z.S., F.R.Z.S.; T. G. Vallance, B.Sc., Ph.D.; J. M. Vincent, D.Sc.Agr., Dip.Bact.; and G. P. Whitley, F.R.Z.S.

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

Following the declaration the Chairman installed Professor Ralph as President.

GENERAL ACCOUNT. Balance Sheet at 28th February, 1962.

LIABILITIES.

	£ s. d.	£ s. d.
Accumulated Funds—		
Amount received from Sir William Macleay during his lifetime	14,000 0 0	
Further sum bequeathed by his will	6,000 0 0	
		20,000 0 0
Contingencies Reserve		15,899 1 4
		35,899 1 4
Current Liabilities—		
Bookbinding Account	1,089 7 7	
Income Account	2,864 14 5	
Suspense	7 17 10	
		3,961 19 10
		£39,861 1 2

ASSETS.

	£ s. d.	£ s. d.
Fixed Assets—		
Commonwealth Loans, at cost	15,048 10 0	
Debentures:		
Metropolitan Water, Sewerage and Drainage Board, at cost	7,344 7 6	
Science House (one-third share), at cost	14,835 4 4	
		37,228 1 10
Current Assets—		
Cash in hand	10 0 0	
Commercial Banking Company of Sydney, Ltd.	2,622 19 4	
		2,632 19 4
		£39,861 1 2

INCOME ACCOUNT. Year Ended 28th February, 1962.

	£ s. d.	£ s. d.
To Salary		780 0 0
„ Printing Proceedings	1,494 0 0	
„ Printing Reprints	406 18 0	
„ Blocks	248 19 0	
		2,149 17 0
„ Insurance		13 9 10
„ Postage	127 9 9	
„ Petty Cash	32 14 2	
		160 3 11
„ Audit	16 16 0	
„ Printing and Stationery	109 8 2	
„ Expenses	137 18 10	
„ Cleaning	58 10 0	
„ Library	23 9 11	
		346 2 11
„ Balance to 1962-63		2,864 14 5
		£6,314 8 1

	£ s. d.	£ s. d.
By Balance from 1960-61		1,116 14 0
„ Subscriptions:		
1961-62	426 6 0	
Arrears	31 10 0	
In Advance	6 6 0	
		464 2 0
„ Entrance Fees		9 9 0
„ Interest		1,169 2 3
„ Science House		1,274 18 10
„ Rent		51 7 6
„ Sales		553 18 11
„ N.S.W. Government Grant		200 0 0
„ Fellowships Account (surplus income at 28th February, 1962, transferred)		1,033 17 6
„ Bank Expenses		1 17 1
„ Sale of Reprints		281 9 0
„ Postcard Sales		2 12 0
„ Donation		5 0 0
„ Printing Grant (in advance)		150 0 0
		£6,314 8 1

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, 1962, 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, 1962, as shown by the books. Certificates of the investments have been inspected.

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

Sydney, 9th March, 1962.

A. B. Walkom,
Hon. Treasurer.

2nd March, 1962.

LINNEAN SOCIETY OF NEW SOUTH WALES.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

Balance Sheet at 28th February, 1962.

LIABILITIES.	£	s.	d.	ASSETS	£	s.	d.	£	s.	d.
Accumulated Funds—				Fixed Assets—						
Amount bequeathed by Sir William Macleay	35,000	0	0	Commonwealth Loans, at cost	30,447	15	0			
Surplus Income Capitalized	22,834	3	4	Debentures:						
				Metropolitan Water, Sewerage and Drainage Board, at cost	16,648	9	9			
				Rural Bank of N.S.W., at cost	2,172	15	0			
				Loan on Mortgage	6,035	0	0			
								55,303	19	9
				Current Assets—						
				Commercial Banking Company of Sydney, Ltd.				2,530	3	7
	£57,834	3	4					£57,834	3	4

INCOME ACCOUNT. Year Ended 28th February, 1962.

	£	s.	d.		£	s.	d.
To Salary of Linnean Macleay Fellow	1,416	13	4	By Interest	2,644	4	6
„ Research Expenses	160	7	3				
„ Capital Account	22	19	5				
„ Bank Charge and Loss on Redemption	10	7	0				
„ Balance, being Surplus Income transferred to General Account	1,033	17	6				
	£2,644	4	6		£2,644	4	6

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1962, 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, 1962, as shown by the books. Certificates of the investments have been inspected.

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

Sydney, 9th March, 1962.

A. B. WALKOM,
Hon. Treasurer

2nd March, 1962.

LINNEAN SOCIETY OF NEW SOUTH WALES.

BACTERIOLOGY ACCOUNT

Balance Sheet at 28th February, 1962.

LIABILITIES.	£ s. d.	£ s. d.
Accumulated Funds—		
Amount bequeathed by Sir William Macleay	12,000 0 0	
Accumulated Income Capitalized	6,310 0 0	
Research Fund	10 0 0	
		18,320 0 0
Current Liability—		
Income Account at 28th February, 1962		224 4 2
		£18,544 4 2

ASSETS.	£ s. d.	£ s. d.
Fixed Assets—		
Commonwealth Loans, at cost	15,318 2 6	
Debentures:		
Metropolitan Water, Sewerage and Drainage Board, at cost	800 0 0	
Loan on Mortgage	2,200 0 0	
		18,318 2 6
Current Assets—		
Commercial Banking Company of Sydney, Ltd.		226 1 8
		£18,544 4 2

INCOME ACCOUNT. Year Ended 28th February, 1962.

	£ s. d.		£ s. d.
To University of Sydney (towards salary of Lecturer)	975 0 0	By Balance from 1960-61	279 17 6
„ Balance to 1962-63	224 4 2	„ Interest	919 6 8
	£1,199 4 2		£1,199 4 2

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, 1962, 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, 1962, as shown by the books. Certificates of the investments have been inspected.

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

Sydney, 9th March, 1962.

A. B. WALKOM,
Hon. Treasurer.

2nd March, 1962.

PRESIDENTIAL ADDRESS.
AUSTRALIAN STUDIES OF THE ROOT–NODULE BACTERIA. A REVIEW.

By J. M. Vincent.

[28th March, 1962.]

Synopsis.

This review deals with Australian work with the root-nodule bacteria since the pioneering efforts of the Society's first Bacteriologist, Dr. R. Greig-Smith. A short historical account tracing the establishment of research groups interested in the subject between then and the present day is followed by a more detailed treatment under the headings: *the bacterium*, *interaction between bacterium and host,* and *application of knowledge.*

Studies of the bacterium itself deal with cytology and composition (which have been relatively neglected in the past), antigenic composition of the rhizobia, factors affecting their growth, antagonistic and mutually beneficial effects involving rhizobia themselves and in relation to other organisms, bacteriophage, variation (developed particularly in connection with a relatively well studied set of substrains), and taxonomy (in which fresh interest is developing).

The interaction between bacterium and its host is treated first in relation to general considerations of the symbiosis; then in more detail in respect of the morphology and metabolism of the nodule, specificity in relation to invasion and fixation and the influence exercised by the environment.

So far as it is possible to treat it separately, this knowledge is applied to a consideration of the need for seed inoculation in Australia, the supply of seed inoculants and requirements for their successful use.

Introduction.

It is now more than 60 years since this Society's first Macleay Bacteriologist, Dr. R. Greig-Smith, published on the root-nodule bacteria (Greig-Smith, 1899, 1901, 1906*a-c*, 1907 and 1911). Whilst it is true that, in the absence of plant tests, some of Greig-Smith's cultures could be of doubtful validity, and that most of his generalizations (Greig-Smith, 1906*c* and 1907) as to a relationship between gum production and nitrogen fixation can hardly be sustained today, the fact remains that he pioneered this field in Australia when knowledge of the organisms anywhere was in its beginnings.

Otherwise Australian work during the first 30 years of the century rested largely with State Departments of Agriculture and led to the issuing of cultures to farmers (New South Wales, 1914; Western Australia, 1926; and most other States by 1938).

Strong, while attached to the Council for Scientific and Industrial Research Division of Soils in Adelaide, which was at that time responsible for the issue of cultures in South Australia, published his important paper on specificity between *Rhizobium* and clover host (Strong, 1937). Since then the root-nodule bacteria have remained one of the interests of the C.S.I.R.O. Division of Soils.

Work at Sydney University was commenced independently by Jensen and myself at about the same time (1939). Jensen, again as the Society's Bacteriologist, published a valuable series of papers on the root-nodule bacteria between 1941 and 1948. My own work is continuing and has had the cooperation of many students and post-graduate colleagues. Pate, during the time he was on the staff at the Botany School, continued in Sydney the work he had commenced in Northern Ireland and to which he has since returned.

The active interest of the C.S.I.R.O. Division of Plant Industry in Canberra goes back, on the one hand, to 1942 with the nutritional work initiated by Anderson, and, on the other, to the establishment by Nutman in 1953 of the group now headed by Bergersen.

State Departments of Agriculture, notably New South Wales, Western Australia, Tasmania and Queensland, have continued their earlier interest. In Queensland the particular problems of the tropical legume were tackled first by McKnight (1949) in the Department and with great vigour and initiative by Norris (1956) of the C.S.I.R.O.

Most recently the Department of Agriculture in Papua–New Guinea has become actively interested in rhizobial problems.

The growth of interest and increase in the amount of Australian work is indicated by the dates of the papers on which this review is based. More than four times as many papers were published between the years 1941 and 1950 as in the previous ten years, and between 1951 and 1960 the number had again more than doubled.

It has been my pleasure to attempt this collation and presentation of what has become a considerable body of significant work.

I. The Bacterium.

1. *Cytology and Composition.*

A start has recently been made in applying newer techniques of electron microscopy to the study of the fine structure of *Rhizobium trifolii* (Vincent, Humphrey and North, in preparation). In this way a classical double-layer cell wall and a double-layer cytoplasmic membrane of similar dimensions have been demonstrated. A large part of the area inside the cytoplasmic membrane is occupied by granules about 50–80 mμ in diameter. These have been demonstrated in thin sections and are liberated by rupturing the cell mechanically.

The well-known unevenness of staining of *Rhizobium* appears to be due to one to several large spherical aggregations of polymeric β-hydroxybutyrate that can amount to 40–50% of the cell dry weight. These bodies can be readily demonstrated with Sudan black and do not take up ordinary basic dyes. Extraction with chloroform removes the highly refractile polymer, and hence the strikingly granular appearance under the phase microscope, and leaves the corresponding parts of the cell weakly stainable with basophilic dyes. This suggests that the polymer is impregnated on a basophilic (? protein-containing) material rather than simply displacing the cytoplasm. To some extent the abundance of polymer reflects the age of the cells; even more the abundance of carbon-containing nutrient.

The composition of the water-soluble extra-cellular gums has been studied for 17 strains, representing 4 species. The most striking result (Humphrey and Vincent, 1959) was that all of the 7 strains of *Rh. meliloti* produced polysaccharides that contained glucose but lacked glucuronic acid, whereas the latter was to be found in all of the remaining 10 strains that represented *Rh. trifolii*, *Rh. leguminosarum* and *Rh. phaseoli*. These ten could be grouped according to the proportion of glucuronic acid, but these groupings bore no relationship to species, as defined by invasive ability. Nor was there any apparent relationship between the nature of the gum and the somatic agglutinogens of the bacterial strains. In the course of this work, Humphrey (1959) also found that six out of seven of the strains of *Rh. trifolii* contained 4-O-methyl glucuronic acid. The seven strains of *Rh. meliloti* and the one of *Rh. phaseoli* lacked this component which was, however, found in one of the two strains of *Rh. leguminosarum*. This appears to be the first report of this compound being found associated with a bacterium, although it is common enough in plant hemicelluloses.

From a systematics point of view it is relevant to note that gums of *Azotobacter* and *Beijerinckia*, though not studied in the same detail (Humphrey, unpublished), were certainly different from those of *Rhizobium*. Information as to the nature of the gum produced by *Agrobacterium* and rhizobia of the cowpea miscellany (if they can be induced to produce sufficient gum for study) would be of interest in relation to the taxonomy of the root-nodule bacteria generally.

Cell wall preparations of *Rh. trifolii* contained the rigid ("R") layer components: glucosamine, muramic acid, glutamic acid alanine, and diaminopimelic acid, and the wide range of amino-acids generally found in the walls of Gram-negative bacteria (Humphrey and Vincent, in preparation). In this case such amino-acids comprised: lysine, aspartic acid, glycine, serine, valine, methionine, leucine and tryptophane. Glucose (or galactose) and rhamnose were also present. Humphrey and Vincent, seeking an explanation of the peculiar swollen shape of calcium-deficient cells (Vincent and Colburn, 1961), the walls of which still contain the "R" layer components, suggested

that this element might provide rigidity by stabilizing areas of excess negative charge in the "R" layer components. It has recently been shown by the author that strontium (not barium) can replace calcium, though less efficiently, in providing normal rod-shaped cells.

2. *Antigenic Constitution.*

Earlier work from the author's laboratory was largely concerned with the more detailed analysis of the antigenic composition of *Rh. meliloti* and *Rh. trifolii*, by separating the flagellar and somatic reactions, and using cross absorption tests (Vincent, 1941 and 1942; Hughes and Vincent, 1942; Purchase and Vincent, 1949; Purchase, Vincent and Ward, 1951*a*; Vincent, 1953). This work has been dealt with in a consolidated account on a previous occasion (Vincent, 1954*a*), which also discusses the several applications the method has been put to in the author's laboratory.

Practically all the work done with *Rhizobium* has involved the agglutination reaction which remains the easiest technique to apply. Neither complement fixation nor precipitation has been used at all widely. Unpublished results recently obtained in this laboratory by Mrs. J. Dorman have shown that, with the exception of some non-reciprocal reactions to low titre, complement-fixation tests amongst rhizobia of clover, pea, lucerne, bean, cowpea, peanut, soybean, lupin and lotus have followed closely the situation as revealed by agglutination. Reciprocal cross reactions in both agglutination and complement fixation were found between clover and pea, cowpea and peanut, lupin and lotus. Otherwise no cross reaction was found.

Bloomfield (1959) has extended the author's preliminary serological study of variants of *Rh. trifolii*, SU297 and SU298. His findings will be discussed under Variation.

3. *Growth.*

(*a*) *Hydrogen-ion Concentration.*

Jensen (1942*a*) has provided valuable information about the influence of pH on the growth of *Rh. trifolii* and *Rh. meliloti* and noted the greater acid tolerance of the former. He also found that *Rh. trifolii* had difficulty in initiating growth at a faintly alkaline reaction when the medium was well buffered. The critical acid reaction for the growth of *Rh. trifolii* was in the vicinity of pH 5·2, although one out of 24 strains was able to grow at pH 4·9 in buffered soil extract. The corresponding critical pH for *Rh. meliloti* was 5·4. These observations have fitted in very well with field experience, both so far as the natural occurrence of these two species of *Rhizobium* is concerned, and in relation to the degree of difficulty in establishing the *Rh. trifolii* in acid soil (Vincent and Waters, 1954). This species failed to grow at pH 4·8–5·0 and grew optimally in the vicinity of pH 7, there being some degree of inhibition under more alkaline conditions (comp. Jensen, above).

(*b*) *Requirement of Divalent Cations.*

The use of $CaCO_3$ or $Ca(OH)_2$, especially in experiments with soil, has caused some confusion as to whether the benefit was due to its effect on pH, or due to calcium as such. Norris has indeed been led to conclude that *Rhizobium* does not need calcium (Norris, 1958*a* and 1959*a*). This is, however, contrary to our experience with *Rh. trifolii* and *Rh. meliloti* (Mullens and Vincent, unpublished) and that of Bergersen (1961*c*), the last with two strains of "cowpea" rhizobia as well. It is apparent that Norris's failure to detect a calcium effect was due to restrictions imposed in his study by the desire to check a large collection of strains, necessarily in less detail. There is good reason to believe that the conditions Norris provided for growth were sub-optimal and that this, combined with the generally semi-quantitative nature of his assessments, prevented a more positive result. The author's detailed study of the response of total growth to concentration of calcium (Vincent, 1962) shows clearly why the undoubted stimulatory effects of low concentrations of this element are difficult to define. For example, the 0·016 mM calcium in Loneragan and Dowling's basal medium (Loneragan and Dowling, 1958) is close to the amount this writer found sufficient for

the maximum growth of *Rh. trifolii*. Moreover, the gross morphological changes in calcium-deficient cells (Vincent and Colburn, 1961) leave no doubt as to the importance of this element. There is also appreciable loss of viability in cells that are deprived of calcium (Vincent, 1962).

A peculiar effect of calcium has been seen in a further variant of the culture of *Rh. trifolii* (SU298/531), with which most of my growth studies have been done. The growth of the variant in the presence of calcium is at first more rapid than in its absence, but after about 48 hours the tube containing calcium shows no further increase in turbidity whilst the tube without calcium continues to grow. *Rh. trifolii*, SU 298, is lysogenic (Marshall, 1956), and the cessation of growth of the "calcium-sensitive" variant might be associated with the maturation and liberation of bacteriophage in the presence of this element. The calcium sensitivity phenomenon is prevented by raising the pH from 6 to 6·5, or 7, and by the addition of glutamate to the medium.

Strontium, but neither magnesium nor barium, has been found to substitute for calcium, for the maintenance of normal growth and morphology, but at about four times the molarity. Strontium and barium, but again not magnesium, cause the "calcium-sensitive" effect.

A growth response to magnesium is readily demonstrated (Norris, 1958*a* and 1959*a*) and again the author's quantitative data show clearly why this is so. An equal increment of total growth was found to require about eight times the increase of molar concentration of magnesium as of calcium. The morphological effects of magnesium deficiency were quite different from those due to a shortage of calcium (Vincent and Colburn, 1961), but viability was again and even more affected.

The detailed studies of the author have also shown that in addition to the quite low and specific requirements for calcium (0·025 mM) and magnesium (0·1 mM) there is a much greater and non-specific need for divalent cations (0·4–0·6 mM).

(*c*) *Temperature Requirements.*

Bowen and Kennedy (1959) have reported the maximal temperature tolerance in the growth of 87 strains of rhizobia of temperate and tropical legumes. Amongst the temperate strains those of the medic group (*Rh. meliloti*) were the most tolerant of heat (36·5°–42·5° C.), being 8° higher on the average than those of pea and clover (31°–38° C.). The large collection of isolates from tropical legumes growing in Queensland ranged from the lowest to amongst the highest (30°–42° C.). It is interesting that the tropical rhizobia include some strains that are every bit as sensitive to heat as the pea and clover isolates. In the case of the Queensland isolates, Bowen and Kennedy could find no correlation between heat tolerance and the geographic latitude of their place of origin, nor any relationship to species of host. Soils under cover of tropical growth could, of course, be sufficiently shaded to explain the presence of heat intolerant strains in such situations.

(*d*) *Form of Nitrogen.*

Bergersen (1961*c*) found that glutamate was much superior to nitrate or the ammonium ion as nitrogen source in a defined medium, and gave as good growth as that obtained with yeast extract. The relatively poor growth that Bergersen obtained with *Rh. trifolii* growing on nitrate is contrary to my own experience with this species, but our results are in agreement so far as the extremely poor growth obtained with NH_4^+. This ion not only fails to support satisfactory growth of *Rh. trifolii* and *Rh. meliloti*, but exercises an inhibitory effect on the good growth ordinarily obtained with nitrate. This inhibitory action operates where the ammonium is supplied as NH_4NO_3 or $(NH_4)_2SO_4$.

4. *Death of Rhizobia.*

Like other Gram-negative bacteria, the rhizobia are likely to die rapidly under drying conditions. The important question of their survival has been recently reviewed

(Vincent, 1959) in an article that consolidates the experience of a good many Australian workers, especially those who have been working on this subject at the Sydney School of Agriculture. The temperature at which a culture is stored is of very great importance, the death rate being doubled for a rise of approximately 12° C.

(a) Storage at Low Temperature.

Bloomfield (1959) has obtained data on the survival of clover cultures during long storage in the refrigerator and in the deep-frozen state. Whereas the recovery of viable cells after 18 months in the refrigerator (approximately 2° C.) was sporadic, there was no difficulty when cells were kept deep frozen (1–5% survival).

(b) Effect of Elevated Temperature.

Bowen and Kennedy (1959) have provided a valuable study of the effect of elevated temperatures on the survival of a range of rhizobial strains in sterile sand. Abstracting the data of their Table 2, and expressing death rate at 40° C. as the average logarithmic hourly decline during the first 10 hours, or for a shorter period when no survivors could be recovered at that time, one obtains the material of Table 1.

TABLE 1.

Heat Tolerance of Rhizobia.
(Data from Bowen and Kennedy, 1959.)

Maximum Temperature for Growth °C.	Hourly Death Rate at 40° C.	Strain.	Host.
40	0·13	Rothamsted A H	*Medicago sativa.*
38·5	0·17	QA 549	*Centrosema pubescens.*
36·5	0·19	QA 679	*M. sativa.*
36	0·12	QA 323	*Pultenaea villosa.*
32–35	0·25	QA 837	*C. pubescens.*
33	0·48	Roth. Clover F.	*Trifolium pratense.*
33	0·35	QA 851	*C. pubescens.*
32	0·37	TA 1	*Trifolium.*
32	0·38	SU 302	*Vicia sativa.*

There is a very good inverse relationship between maximum temperature for growth, and death rate at 40° C. The two lucerne strains were amongst the most tolerant of high temperature; the clover and pea strains, the least. The tropical isolates are scattered throughout the table and show no evidence of particular adaptation to high temperature. Strains Roth. AH, QA549, QA851 and TA1 were tested at two levels of inoculum size and agreed well with the results tabulated above. There was no regular relationship between survival and inoculum size.

(c) Death on Drying.

Lyophilized cultures, dried from 10% sucrose, and stored at 2° C. over the same period gave recoveries of from 1% to 13% according to substrain. Old (3½ years) freeze-dried cultures of *Rh. trifolii* showed no further decline in viability after the early rapid death that had occurred in those preliminary experiments.

The survival of rhizobia on glass beads and on seed has been studied in the author's laboratory for several years. Early results due to McLeod (quoted Vincent, 1959) showed very great improvement due to the incorporation of sucrose into the drying medium. Even better results could be obtained using maltose which was markedly superior to any of a range of defined substances, including its β-isomer (cellobiose), though it in turn was slightly inferior to gum arabic (Vincent, Thompson and Donovan, 1962). Death rate during drying from a plain water suspension was inversely related to the concentration of cells applied to the surface, but maltose seemed to remove any dependence on inoculum size.

Higher R.H. (60%) appeared to be inferior for survival of rhizobia compared with drier conditions (0%–20%).

(*d*) *Toxic Factor in Seed Coat.*

Thompson (1960) and Bowen (1961) have independently shown a toxic effect in a water-soluble extract of some legume seeds. This factor is heat stable and appears to be associated with the seed coat, not the embryo. Legumes differed in the toxicity of their seed (e.g., seed of subterranean clover > white clover > lucerne). Survival experiments (Vincent, Thompson and Donovan, 1962) that compared the death of rhizobia on seeds and glass beads, and on the latter impregnated with an equivalent amount of water-soluble extract, showed that this fraction indeed caused rapid death of the bacteria in the early stages of drying. Gum arabic provided some protection against the toxic factor. Bowen (1961), besides, like Thompson, obtaining marked toxicity with diffusates of subterranean clover, compared with the low toxicity of lucerne, found a toxic diffusate from the seed of a tropical legume (*Centrosema pubescens*). He also found that the seed diffusate restricted rhizobial multiplication near the sown seed and that there were interesting differences amongst *Rhizobium* and other rhizosphere organisms in their susceptibility to this factor. *Agrobacterium radiobacter* was only slightly inhibited, but another organism of the *Xanthomonas-Flavobacterium* group was even more affected than *Rh. trifolii*. Thompson (1960, 1961) has results to indicate that the physical separation of seed coat and inoculum, by coating the seed with inert material, is one way of overcoming this effect. Some of the benefit of seed pelleting could be attributed to this.

5. *Antagonistic and Associative Effects.*

(*a*) *Between Rhizobia and other Microorganisms.*

Jensen (1942*b*) obtained no benefit from the presence of *Azotobacter* added to nodulated legumes. Harris (1953) showed that some bacteria were able to improve nodulation by a weakly nodulating strain in a laboratory test. The data do not, however, permit one to determine whether the benefit arose from better rhizobial proliferation or whether it operated in respect of the more intimate act of invasion.

Others have attributed cases of nodulation failure to antagonism by other rhizosphere inhabitants. Hely, Bergersen and Brockwell (1957) were of the opinion that repeated difficulties they had experienced in obtaining satisfactory nodulation in a soil of reasonably high pH could have been due to failure of the inoculum to colonize the rhizosphere. This they attributed to antagonism by other rhizosphere organisms, although the detailed nature of the antagonism eluded their detailed investigation. The difficulty could be overcome by the use of a heavy inoculum, or modification of the environment, either by means of charcoal or by the incorporation of bentonite and an organic nutrient in a pellet to favour rhizobial multiplication, presumably selectively (Bergersen, Brockwell and Thompson, 1958). Experiments with non-nutritive as well as nutritive seed pellets have led Thompson (1961) to doubt this explanation. This worker believes that the important modification introduced by pelleting is separation of *Rhizobium* from direct contact with the toxic seed coat. The responses that Thompson obtained on soils pH 6 and higher were not related to the chemical properties of the pelleting material, but any form of pelleted seed was superior to having lime banded in the seed's vicinity. This differed from the situation in more acid soils (pH 5·1), in which the ability of the pelleting or banded material to neutralize acidity in the vicinity of the inoculated seed was much more important than physical separation. Thompson's explanation includes the reasonable idea that soils could differ in their ability to remove or destroy the toxic factor. Thompson also found that although inoculated seed sown in two of the "problem" soils responded to pelleting, fumigation was without effect. An old observation (Bockman and Vincent, unpublished) that two problem soils from similar localities, brought back to the laboratory in the form of undisturbed cores, permitted abundant nodulation, could be explained as the result of modifying the rhizosphere environment by this handling and abundant watering. On

the other hand, it could also fit in with Thompson's proposal, in that the concentration of a water-soluble toxic diffusate from the seed could have been reduced by the passage of freely draining water.

Antagonistic effects have also been invoked to account for difficulties in the establishment of subterranean clover in certain Western Australian soils (Cass Smith and Holland, 1958). Improvement following on the use of soil fumigants has been taken to indicate antagonism by indigenous microorganisms. Holland (personal communication) is continuing a detailed investigation that has so far given results that are compatible with the hypothesis.

(*b*) *Competition amongst Rhizobia.*

Competition between strains of rhizobia in the vicinity of plant roots is of interest when we are concerned with establishing a new strain. Vincent and Waters (1953) studied the relative growth of several strains of *Rh. trifolii* in association with clover plants grown in tubes of seedling agar. Some strains were able to outgrow others, their relative success in this regard being quite independent of the species of *Trifolium* on which they were growing. Though unable to affect the relative proportion of strains growing in association with the host's roots, the host species definitely determined the relative success of strains in forming the nodules.

Harris (1954) introduced the term "incursiveness" to describe the relative ability of a *Rhizobium* to progress away from the place of its introduction. It is, in fact, not easy to define the extent to which a strain's success in soil might be due to such a characteristic and those that have adopted the term seem to use it to describe relative success in forming nodules in competition with other strains. It is doubtful whether there is any merit in using the term in this loose fashion.

6. *Bacteriophage.*

There has not as yet been much work done on the rhizobiophage in Australia. Marshall and Vincent (1954) found that in the case of three phages isolated from near the roots of a clover plant there was a relationship between somatic antigens of the bacterium and susceptibility to bacteriophage: a situation similar to that reported with several other kinds of bacteriophage. All of the 13 out of 64 cultures of *Rh. trifolii* that were lysed by one or more of the three phages had a somatic antigen in common with SU297. However, 18 non-susceptible strains also shared an antigen with SU297. The latter result could indicate either that adsorption at an antigenic receptor site was not sufficient to guarantee phage proliferation, or that other antigens besides receptor sites were involved. A relationship has been postulated below (p. 16) between the possession of type antigen and susceptibility amongst substrains of *Rh. trifolii*, SU298.

Marshall (1956*a*), the first to demonstrate the lysogenic condition in *Rhizobium*, showed that *Rh. trifolii*, SU298, was the lysogenic; SU297, the indicator strain. Marshall found this for only three of the four colony types that had been recorded for SU298 (Vincent, 1954*a*). Bloomfield (1959) successfully repeated the work with the same three substrains (A–C) and was able to extend the demonstration to the D-type substrain. The explanation of the difference between Bloomfield's and Marshall's results seems to lie in a very low ratio of liberated phage particles in type D cultures, and Bloomfield's use of a more satisfactory medium.

Bloomfield also obtained good results with a defined medium based on Norris (1958*a*), provided it contained some added calcium (approximately 1 mM being sufficient).

7. *Variation.*

Variation is frequently encountered in the rhizobia, in respect of cultural characteristics, invasibility, effectiveness or symbiosis, sensitivity to bacteriophage and serology (Jensen, 1942; Vincent, 1944 and 1954*a*). The relative stability of at least part of the cell's antigenic constitution has provided a convenient means of establishing the fact that one is in fact dealing with a variant. This is particularly useful when the lost character in question is virulence.

The author has encountered loss of invasiveness in several cultures in the course of working with a large collection of rhizobia over a period of some 20 years. Loss of effectiveness has been encountered rather more often and together they constitute a hazard in the maintenance of stock cultures, especially for commercial inoculants.

TABLE 2.

Comparison of Variants of Rh. trifolii, *SU297 and SU298.*

Strain	SU297.		SU298.			
Type	A	B	C	A	B	D
Colonies	2–3 mm. High convex, differentiated translucent edge.	0·5 mm. High convex, uniform, opaque white.	2–3 mm. High convex, differentiated translucent edge ; ring or halo.	2–3 mm. High convex, differentiated translucent edge.	0·5 mm. High convex, uniform, opaque white.	2–3 mm. Low raised, uniform, translucent.
Gum	++	±	++	+++	±	++
Metabolism[1] ..	++	±	++	++	±	++
Serology[1]						
Reaction with antisera to :						
297A ..	+a	+	+	+	+	+
297B ..	+a	+a	+	+	+	±
298C ..	+	+	+a	+	+	±
298A ..	+	+	+a	+a	+	±
298B ..	+	+	+a	+	+a	±
298D ..	?	?	–	–	–	+a
94 ..	+	+	–	–	–	+
306 ..	+	+	–	–	–	±
Antigenic constitution* : ..	g t_1 p	g t_1	g t_2 p	g p	g t_2	(t_1) p′
Bacteriophage sensitivity						
PU5[2]	–	–	+	–	+	–
298[1]	+	+	–	–	–	–
Lysogeny[1] [2]	–	–	+	+	+	±
Symbiosis						
Nodulation ..	Early.	Late.	Early.	Early.	Late.	Early.
Effectivity (Subterranean clover)	Effective.	Ineffective, beaded.	Effective.	Effective.	Ineffective, beaded.	Ineffective. small white.
Bacteroids[3] ..	Persistent.	Less marked, non-persistent.	Persistent.	Persistent.	Less marked, non-persistent.	Less marked, non-persistent.
Glycogen[3] ..	–	+ Non-persistent.	–	–	–	+ Non-persistent.

[1] Bloomfield (1959) ; [2] Marshall and Vincent, 1954 ; [3] Bergersen, 1955.

* g = group antigen. p = polysaccharide antigen.
t_1 = 297 type. p′ = " mucoid " antigen.
t_2 = 298 type. a = fully absorbed.

Cultural variation is very common, and one can expect many old lines to show two or more colony types. It is fortunate that this frequent cultural variation is not necessarily accompanied by loss of virulence or effectiveness, although in the cases of *Rh. trifolii*, SU297, and SU298, the latter has indeed occurred.

This collection of substrains (Vincent, 1954*a*) has become perhaps the best-studied group of rhizobial variants at our disposal. Bloomfield (1959) undertook a detailed

comparison and his results, together with those of others who have worked with all, or some of the substrains, can be expanded in tabular form to provide interesting reference material (see Table 2).

The most striking characteristic that led to recognition of the variants was the colonial form which largely reflected the production of abundant gum (particularly in types A and C) or its virtual absence (type B). When the writer came to tabulate the data it became apparent that they fitted into a much better pattern if one took the "C" type of SU298 to be the parent form comparable with SU297, type A. It was therefore gratifying to find, on referring back to the original records, that the types A, B and D of SU298 did in fact derive from a "C" type culture. Morphologically, apart from gum production already noted, there appeared to be no differences between substrains. The two B type variants appeared to be less vigorous in their fermentation. Serologically all strains had common completely cross-absorbable flagellar antigen(s) (Bloomfield, 1959). The situation with somatic agglutinogens was more complex, but can be reasonably interpreted.

Cross agglutination between strains SU297 and SU298 can be explained in terms of a group ("*g*") antigen. The peculiar behaviour of the type D substrain of SU298 is interpreted as partly due to its lacking this antigen. If one postulates "*p*" as the antigen associated with the production of polysaccharide gum, and "*t*" as a strain specific (type) antigen, mutation to small colony type can be interpreted as associated with loss of "*p*"; in the case of SU297 (A $\rightarrow$ B), $g\,t_1\,p \rightarrow g\,t_1$; with SU298 (C $\rightarrow$ B), $g\,t_2\,p \rightarrow g\,t_2$. If t_1 is necessary for attack by phage 298, and t_2 for attack by phage PU5, then the variation C $\rightarrow$ A can be interpreted as loss of t_2. The more drastic changes in type D can be indicated as $g\,t_2\,p \rightarrow (t_1)\,p_1$ to explain loss of group reactivity, an incomplete t_1 antigen (that may be intermediate between t_2 and t_1) and modified production of gum as indicated by colony appearance. Further, if the liberation of active phage, and hence demonstration of lysogeny, is associated with the absence of t_1, then it is not unreasonable to expect that cells with the incomplete (t_1) will produce some phage, though only sparsely, as has been demonstrated (Marshall, 1956*a*; Bloomfield, 1959). Table 2 also tabulates data on the symbiotic behaviour of the substrains, both macroscopic and microscopic. According to the analysis I have suggested the "*p*" antigen would correlate with earliness of invasion, effective nodulation of subterranean clover and the morphological conditions associated with the effective nature of the nodule. A good deal of the above analysis is speculative, but it opens up promising avenues for further investigation of this interesting collection of variants.

Further variation has been encountered with the small colony (B) type of SU298. The colony of this variant was about the same size as the small colony type, but translucent, not opaque, and, unlike the parent small colony type, was sensitive to calcium, strontium or barium when grown in a defined medium, pH6, having nitrate as the source of N (see p. 11).

8. *Taxonomy and Phylogeny.*

Norris (1956) has provided a stimulating reappraisal of the possible evolutionary position of the rhizobia *vis-a-vis* their hosts. He cautions against the practice of generalizing from the few well-studied temperate legumes, which he regards for the most part as an evolutionary *cul-de-sac*. Rather he looks to the "cowpea miscellany" as the ancestral type with properties and host associations that reflect conditions of low soil fertility and generally a primitive situation of open pollination. The rhizobia of calcium-demanding hosts, characteristic of more fertile temperate regions (such as species in the tribes Vicieae and Trifolieae), are thought to have evolved to take advantage of "huge tracts of calcareous land left by the retreat of the shallow Cretaceous seas", where they thrived and developed calcicole habits. To some extent later findings have tended to blur the sharp outlines in this early presentation of Norris's views, but he has done the study of the root-nodule bacteria a great service by jolting us out of a complacent acceptance of temperate legumes and their rhizobia, as the norm.

Western Australian workers (Lange, 1961; and Graham and Parker) have of recent years combined a study of the rhizobia associated with indigenous legumes with problems of their taxonomy and of rhizobia in general. Graham (personal communication) has provided a critical re-assessment of past efforts and has used his own evidence with a large collection of strains to determine what worthwhile relationships and distinctions might be arrived at. In line with current thinking generally these workers recognize that infective characteristics, on which "species" have so far been constructed, although still of some value, can no longer be used as the primary basis of speciation. Morphological characteristics are of limited use, but some cultural features (rapidity of growth, fermentative powers), combined with plant invasibility, serology and bacteriophage susceptibility, appear to provide three groups whose boundaries are rarely transgressed. These are: (1) *Rh. trifolii*, *Rh. leguminosarum*, *Rh. phaseoli*. (2) *Rh. meliloti*. (3) *Rh. japonicum*, *Rh. lupini* and the cowpea miscellany. However, the subdivision remains unsatisfactory because the first two groups contain isolates from only 12 genera, leaving the third to accommodate all the others. Graham expects that this last heterogeneous group will have to be further subdivided and (like Lange) looks to Sneath's application of Adansonian analysis to achieve this.

This method of analysis can be used to determine what relationships there might be between the three groups of rhizobia and other soil forms. According to Graham "the vast schism which lies between the three groups of the rhizobia is more than can be explained in terms of evolution pressure" (comp. Norris, 1956). They may have evolved separately and differences between them might eventually justify their separation into three genera. *Rh. meliloti* appears to be well separated from the others, but, according to Graham, might be related to *Agrobacterium radiobacter*. (It would be of interest to determine whether the latter shares the distinctive composition of its extracellular polysaccharide with that of *Rh. meliloti* (Humphrey and Vincent, 1959). An Adansonian analysis might also throw light on whether *Agrobacterium radiobacter* can be regarded as an ancestral rhizobial condition or whether other organisms have equal or better claim. An evolutionary sequence of this nature, going through *Rh. meliloti*, would not directly conform with Norris's ideas as to ancestral forms, though no doubt the two ideas could be accommodated by regarding the lucerne organism as an offshoot of a main path via a common lucerne-like form. Some of the conflict would also be removed by postulating several parallel evolutionary pathways.

The isolation of a red strain of *Rhizobium*, with marked specificity towards *Lotononis* (Norris, 1958*b*), illustrates again how difficult it is to generalize about organisms that form symbioses with members of the family Leguminosae.

II. Interaction between Bacterium and Host.

A very large part of the work with *Rhizobium* has been concerned with the interaction between it and the host. In this account, I propose first to deal with general symbiotic relationships, to follow this with a review of significant Australian work on the morphology and metabolism of the functioning nodule, to examine specificities in the relationship, and finally to look at the effects of environmental factors.

1. *The Symbiotic Relationship.*

Pate (1958*a*, 1958*b*) has recorded studies he made before coming to Australia, which illustrate an approach of the "whole-plant" physiologist to the study of the legume-bacterium symbiosis. Pate related stages in the development of the symbiosis quantitatively, with the development of the host, and studied the influence of environmental factors on both. Later work (Dart and Pate, 1959) was particularly concerned with the effects of delayed introduction of the bacteria into the seedling environment. Total nodule production was increased by such delays and the distribution of nodules on the root reflected the areas behind the root tip that still carried invasible root hairs. It seemed that "infection centres" were distributed in regular fashion along the root, but very little of the plant's infection potential was exploited under any inoculation regime.

As others had found, existing nodules restricted subsequent root growth and nodulation. The same authors found that with the single pair of strains they worked with, the ineffective partner occupied more positions on the primary root than would be expected from the nodulating capacities of each strain in single culture.

Bowen (1959*a*) has studied the growth and nodulation of *Centrosema pubescens* under field conditions in Queensland. Nodulation continued throughout growth, but the disposition of the nodules, by new infections and senescence of old nodules, changed according to the vegetative growth of the host. Nodules formed progressively on new stoloniferous roots and older nodules were eliminated from the tap-root system. Cutting, to simulate heavy grazing, caused a loss of about two-thirds of the roots and inactivation and sloughing off of a major part of the nodules.

Nutman (1959) has found that for a particular variety of subterranean clover, the total nodule volume (the product of size and number) was constant with 12 strains of *Rhizobium* even though size and number varied. Two host lines each had its own particular nodule volume and progeny were intermediate.

Lange and Parker (1960) have shown that nodule-distribution patterns of four species of lupins differed and that in such studies it would be unwise to generalize from a limited sampling of legumes. *Lupinus angustifolius* showed no preferential siting of nodules at the crown, tap root or lateral roots. *L. luteus* sited them preferentially on crown and tap root, *L. digitatus* on tap root below the crown, and *L. mutabilis* on crown and laterals.

Pate (1958*c*) and Kefford, Brockwell and Zwar (1960) have been concerned with growth substance production. Pate records five substances, three of which (predominantly indole acetic acid) were classed as promoters and two as inhibitors. Kefford *et al.* regard indole acetic acid as probably the most important auxin produced by the combined action of plant roots that excrete tryptophane, and of the bacteria that convert it to the auxin. They suggest that a colony of bacteria on a root hair could produce indole acetic acid which would make the cell wall plastic and produce osmotic conditions that would cause the root hair cytoplasm to retreat before the colony, and so advance the infection thread. The same process at pit areas between cells could result in progress of the thread from cell to cell. Initiation of a nodule in the invaded cortex could result from the combined action of indole acetic acid and a sufficiently high level of kinin produced by a disomatic cell.

At the time when the question as to whether legumes excreted nitrogenous compounds was a lively one, Swaby (1945) found no evidence of such a process being at all considerable under Australian conditions. Of a different order quantitatively, but likely to have marked effects on associated bacterial populations, are the water-soluble vitamins that appear to be excreted relatively freely by representative legumes (Rovira and Harris, 1961), and, of course, tryptophane noted above. Old nodule tissue has its nitrogen readily mineralized and so made available to associated non-leguminous plants (Jensen and Frith, 1944). The quantitative extent of this will, however, be variable and generally small.

It is very easy at times to mistake nematode galls for root-nodules, and it seems, in the author's not very precise observations, that a nematode infection exercises an antagonistic effect on nodulation. This might be due to relatively dry conditions favouring the nematode at the same time as they militate against *Rhizobium*. Robinson (1961) has noted cases of marked infestation of the nodule itself by the nematode and gives figures that indicate considerable reduction of infestation by fumigation.

2. *Morphology and Metabolism of the Nodule.*

Bergersen (1955) carried out a detailed study of the morphology of the bacteroids in the nodules of subterranean clover. He found that the mature bacteroids of the effective nodule had the nucleus separated by a perinuclear region from the cytoplasm, which contained several mitochondria-like granules. The ineffective variants of *Rh. trifolii* listed by Vincent (1954*a*) differed from the effective substrains of the parent

strains, in that, whereas bacteroids persisted in the latter and no glycogen was found, the bacteroids were less conspicuous in the early stages of the ineffective nodules and were absent after 30–40 days. These ineffective forms were similar to two other Australian ineffective isolates obtained from white clover, though all differed from the one English culture (clover F, Rothamsted) in which bacteroids persisted and glycogen was built up. Bergersen (1957*b*) was also able to demonstrate an interesting morphological cause of ineffectiveness in a variant of *Rh. trifolii*, SU220. In this case the nodule bacteria were not released from the infection threads; instead, they continued to multiply within the threads at the expense of the host tissue. Bergersen suggested that the basic cause of this could be due to failure of the variant to stimulate division of tetraploid cells, and the diploid tissue, in turn, not causing the release of bacteria from the infection thread.

Bergersen and Nutman (1957) have related recessive genes which cause an ineffective symbiosis in red clover to nodule structure and cytology. One type of ineffectiveness (i_1) was due to failure of the particular bacterial strain to produce bacteroids with that host, but in the other type (i_e), abnormal divisions of host tissue near the bacteria released from infection threads, give disorganized tumour-like growth and no bacteroids. With more vigorously effective rhizobia a mixed condition having varying degrees of effectiveness occurs and this correlates with and underlines the importance of bacteroid formation.

Bergersen (1957*a*) also noted the occurrence of a thick layer of polysaccharide-like material between the host cells. This occurred transitorily where the nodule was effective, but persisted in the case of ineffective nodules. This material was regarded as a reserve of carbohydrate produced by the host, which, in the case of an effective association, becomes used up with products of fixation. The cytology of soybean root nodules was studied by means of the electron microscope. Cells of *Rhizobium* isolated from these nodules appeared to lack walls, and Bergersen and Briggs (1958) interpret the "walls" they see around groups of bacteroids as due to encasement by outgrowths from the infection threads. Bacterial growth which takes place subsequent to cessation of host cell division is then thought to occur within the membranes. Growth of the latter keeps pace with bacterial multiplication so that a large number of bacteria become surrounded by interconnected membranes.

Bergersen and his colleagues have been responsible for a series of important papers (Bergersen, 1958; Appleby and Bergersen, 1958; Bergersen and Briggs, 1958; Bergersen, 1960*a*, 1960*b*) that have led to the formulation of a hypothesis concerned with symbiotic nitrogen fixation in the following terms:

1. Primary reactions of the activation of nitrogen and its reduction to ammonia occur in the membrane envelope.

2. This activated nitrogen is the ultimate acceptor in an electron transport train which begins in the bacteroids.

3. Hæmoglobin, lying in solution within the membrane envelope, is one of the links providing for electron transport (Bergersen and Wilson, 1959).

4. The host supplies carbon compounds which are partially oxidized by the bacteroids and serve as the source of electrons for the reduction of activated nitrogen.

5. Products of incomplete oxidation of the substrates then serve as acceptors of NH_3 in the production of amino-acids by the bacteroids. These amino-acids become available to the host.

Bergersen (1961*a*) has also shown that the hæmatin content per unit of the effective central tissue volume of the nodule was remarkably constant. From this it follows that hæmatin content might correlate with nitrogen fixation because it is an index of the volume of active tissue, not necessarily because of a causal relationship between nodule hæmoglobin concentration and the rate of nitrogen fixation. However, Bergersen is of the opinion that this relatively constant tissue value for each of the two host

species (red and subterranean clovers) supports the view that there is a relationship between hæmoglobin and fixation, such as postulated in the hypothesis. The same worker (Bergersen, 1961*b*) has investigated the amount of nitrate reductase in nodule homogenates as a function of nodule age. The results show that the highest value for whole cells was obtained when the nodules were 10 days old, about a week before nitrogen fixation commenced and when the nodules were still without hæmoglobin or mature nodule cells. The suggestion that the nitrate reductase activity of soybean-nodule bacteroids is induced by products of nitrogen fixation must therefore be discounted. Bergersen concludes that the nature of the induction of this enzyme in the nodule is not known nor is the significance of the enzyme in the functioning nodule understood.

3. *Specificity in Relation to Invasion and Efficiency of Fixation.*

(*a*) *Clover–Pea Groups.*

Strong (1937), in his pioneer work with host specificity amongst the clover rhizobia, was able to divide the eight strains he worked with into two contrasting groups according to whether they were effective with subterranean clover on the one hand or with red and white clover on the other. When, however, a larger collection was examined (Jensen and Vincent, 1941; Jensen, 1942*a*; Vincent, 1945), it became apparent that the rule was far from absolute. A large amount of work, overseas and in Australia, has helped to clarify the matter, at least for the relatively tidy group of clovers of chief agronomic interest in temperate regions. Vincent (1954*a*), in summarizing his own results and those of colleagues, was able to nominate effectiveness subgroups that expressed a likelihood of agreement or disagreement amongst clover hosts in their symbiosis with strains of rhizobia. Nutman (1959) added *Trifolium dubium* to subgroup A and five other species of *Trifolium* to subgroup B. *T. ambiguum* remains the sole representative of subgroup C. Our knowledge of the latter has been considerably expanded by Hely (1957), whilst Norris (1959*d*) has reported on the particular affinities of African species of *Trifolium*.

Hely, accepting the fact that most of the strains isolated from regular clover hosts will invade *T. ambiguum* with difficulty, if at all, exposed his diverse genetic host material to samples of Australian soil, and worked with nodules so formed. In spite of this initial selective act, he found three-quarters of the isolates failed to nodulate any of the hexaploid hosts and 23% failed to nodulate diploid hosts. A smaller collection of strains isolated in New Zealand also yielded a large proportion of non-nodulated plants. These isolates were all able to nodulate *T. repens* and *T. subterraneum* and were obviously poorly adapted to *T. ambiguum*. Strains that had originally come from Turkey, within the natural range of *T. ambiguum*, nodulated this host much more freely and it was only with the diploid testing host that a significant proportion of the plants (7–24%) were without nodules. All of the Turkish strains nodulated all plants of four other species of *Trifolium*, including white and subterranean clovers. The Australian and New Zealand cultures were almost all wholly ineffective on *T. ambiguum*. The majority were effective on *T. repens*, but ineffective on *T. subterraneum*. The Turkish isolates gave a proportion of isolates effective with *T. ambiguum* that varied, according to interaction between host material and strain, from 4% to 75%. Most were completely ineffective on *T. repens* and the other clovers.

The situation in the clover group has become even more complicated now that information is becoming available concerning African species of *Trifolium* (Norris, 1959*d*). Nodulation of these by rhizobia isolated from, and regularly nodulating, European species, was frequent but irregular and the association was always ineffective. The two "African rhizobia" nodulated most of the African species regularly, but one of these was always ineffective and this one failed to nodulate *T. cheranganiense*. Norris included a reciprocal comparison involving members of tribe Vicieae and isolates therefrom, with species of European and African *Trifolium*. Three out of the four clover rhizobia formed nodules on some plants of *Pisum* (the negative *Rhizobium*

was the effective South African isolate from *T. rueppellianum*) and all of the isolates ex. Vicieae were able to form nodules on some plants of European and African species of *Trifolium*. All of these associations appeared to be ineffective.

As pointed out by Norris (1959*d*), his findings, and those of others, are steadily pointing to a closer relationship between the Trifolieae, the Vicieae and the rhizobia that nodulate within and between them. One feels obliged to agree that the apparent cross-inoculation homogeneity recorded amongst clovers in the past has been the result of studying relatively few species all of European and Mediterranean origin. Norris has suggested that a detailed study of *Rhizobium* relationships between Vicieae and Trifolieae might throw considerable light on taxonomic relationships amongst the hosts. Harris (personal communication) has indicated that the pea-vetch group is, from the point of view of effectiveness patterns, a very complicated one. Rating rhizobia on the number of effective associations they formed with the seven testing hosts, Harris found the following distribution:

Effectiveness Rating.	No. of Strains.
7	1
4	3
3	2
2	5
1	7
0	6

Hosts varied, too, in the frequency with which they were effectively nodulated with the rhizobia. *Lathyrus ochrus* most readily formed an effective association (with 12 strains), *Lens esculenta* least (with 2).

(*b*) *Medicago-Melilotus Group.*

Strong (1940) made brief reference to specificity controlling effectiveness in the *Medicago-Melilotus* group. A later investigation of a larger collection of Australian isolates (Purchase, Vincent and Ward, 1951*b*) showed how complex the relationship was, both in invasion and in connection with the effectiveness of the association.

(i) *Nodulation Subgroups.*—Three nodulation subgroups, based on the work just mentioned and further information obtained in the author's laboratory, were put forward in an earlier review (Vincent, 1954*a*). All of the isolates that nodulated *Medicago denticulata* also nodulated the eight other species of *Medicago* and *Melilotus alba*. The reaction of the same collection of hosts to the isolates from *M. laciniata* varied from those that were fully compatible (*M. sativa* and *Mel. alba*) to others that were fully resistant (*M. denticulata* and *M. murex.*). Most of the remaining species were seldom nodulated by the *M. laciniata* strains, but *M. rigidula* occupied an intermediate position. 31/33 strains listed by Vincent as subgroup A were isolated from *M. laciniata*. Almost all of the isolates from *M. denticulata* (75/77) were in subgroup B and 31/54 isolations from a large collection on other host species belonged in this group also. However, this latter collection also provided 23 strains which, because they failed to nodulate either of the specialized hosts (*M. laciniata* or *M. denticulata*), though still nodulating lucerne, qualified for subgroup C. There was a tendency for *M. sativa* isolations and stock cultures to be in this group. A smaller part of the collection was anomalous in giving sporadic nodulation with one or more of the hosts. Nodulation of the species from which the isolate was made was generally reliable. Detailed results (Purchase, Vincent and Ward, 1951*b*) recorded 10 anomalous isolates from *M. laciniata* able sporadically to nodulate *M. denticulata*.

Brockwell and Hely (1961) have recently added to this a study of 33 isolates from soils of four localities, including 13 sub-localities, tested on 14 host species (*Medicago*, 11, *Melilotus*, 3). There is a considerable measure of agreement between these results

and our earlier findings, although differences in presentation necessitate a good deal of rearrangement to facilitate any comparison.

One immediate difference between our results and those of Brockwell and Hely is the uniformly positive nodulation these workers obtained with *M. denticulata*. This means that none of their isolates fell into subgroup C.

The behaviour of strains which were classified as falling into subgroups A and B in respect of eleven testing hosts was summarized in Table 2 of Vincent (1954*a*). Hosts could be considered as (i) those that consistently distinguished between the subgroups (*M. laciniata*, *M. denticulata* (in our results) and *M. murex*); (ii) those that were freely nodulated by both groups ("bridging" hosts), *M. sativa* and *Mel. alba*; and (iii) a large group of species that were fully compatible with subgroup B but variably so with subgroup A. In turn, *Rh. meliloti* of invasiveness subgroup A would be distinguished by its ability to nodulate *M. laciniata* and the difficulty it would experience in nodulating one or more other *Medicago* species. Organisms of subgroup B would have compatibility difficulties with *M. laciniata*, but would freely nodulate the remainder.

If now one applies these criteria to a retabulation of Brockwell and Hely's data and takes account at the same time of the earlier results, one finds: (i) that the four isolates from *M. laciniata* fall into subgroup A as re-defined, even though in these cases they freely nodulate *M. denticulata* and *M. tribuloides*; (ii) that the remainder fall into subgroup B in that they generally fail to nodulate *M. laciniata*, or in a few cases, nodulate it sporadically. Most other hosts are freely nodulated, but *M. rigidula* is generally difficult to nodulate.

It would seem desirable to retain the first recommended invasiveness subgroupings (Vincent, 1954*a*) as a framework for future development and modification rather than assign new meanings to these symbols in groupings that do not take account of, and are in fact incompatible with earlier findings with another collection of rhizobia.

(ii) *Host Effectiveness Subgroups.*—Effectiveness subgroups can be postulated, though somewhat tentatively. One should, however, be clear on the difference between these and nodulation subgroups. The latter classifies a rhizobial strain in terms of its ability or inability to nodulate particular hosts, the former groups hosts according to their tendency to behave similarly to each other in association with particular strains.

Our results of nitrogen-fixation with four hosts (*M. laciniata*, *M. denticulata*, *M. sativa* and *Mel. alba*; Vincent, Purchase and Ward, 1951*b*; Vincent, 1954*a*) showed that none of the isolates from *M. laciniata* growing at Curlewis was effective on that host, although a few of them were moderately effective on *M. sativa* or *Mel. alba*. A few effective isolates for *M. laciniata* were obtained later near Trangie; in agreement with Hely's observations of effective-looking plants in that region (Hely, personal communication).

A comparison of *quantitative* results for associations formed by *M. sativa* and *Mel. alba* with 78 strains of rhizobia led to significant agreement ($r = +0{\cdot}39$; $P < 0{\cdot}01$). None was found between *M. sativa* and *M. denticulata* ($r = -0{\cdot}20$; P, 0·2–0·1). In the light of these results the failure of some of our lucerne isolates to invade *M. denticulata* (our invasive subgroup C) might be considered a further manifestation of incompatibility between lucerne strains and the burr medic. Jensen (1942*a*) had some indications, too, that a burr medic subgroup differs from that of lucerne, and that *M. tribuloides* belongs to the former.

In Table 3 I have endeavoured to expand earlier groupings to conform with Brockwell and Hely's results and, by the use of Roman numerals, avoid one cause of confusion between invasiveness and effectiveness subgroups. Brockwell and Hely's graphic representation of their assessment of nitrogen fixation by the many host-*Rhizobium* associations they studied, agrees reasonably well with the earlier effectiveness groupings. *M. sativa* and *Mel. alba* show very close agreement with each other, the previous tentative inclusion of *Mel. officinalis* receives some support, and *M. minima* can be added to make up the newly defined Group I. *M. rigidula* and *M. falcata* show

considerable similarity to each other, but are sufficiently different from other hosts to be given a grouping of their own (Group II). *M. laciniata* stands alone and is now Group VI. The species I had previously put together as B should be broken up into two groups (III and V) with two additional species (*M. lupulina* and *M. orbicularis*) inserted as IV.

The new listing provides a rough order of increasing specialization between host and bacterium in fixation as one goes from I to V and VI. Although Brockwell and Hely could find no relationship between nodulation and fixation patterns, retention of our earlier invasiveness groupings gives a reasonable measure of correlation, though not absolutely. This is indicated by the "Nature of Hosts" column in the table.

TABLE 3.

Fixation (Effectiveness) Sub-groups in Hosts of the "Lucerne" Inoculation Group.

Old Fixation Group.	Vincent (1954*a*) Hosts.	Brockwell and Hely (1961). Hosts.	Nature of Hosts.	New Fixation Groups.
A	*M. sativa.*	*M. sativa.*	Bridging.	I
	Mel. alba.	*Mel. alba.*	,,	
	(*Mel. officinalis*)	(*Mel. officinalis*)	,,	
		M. minima.	,,	
		M. rigidula.	(Bridging)	II
		M. falcata.	Bridging	
B	(*M. tribuloides*)	*M. tribuloides*	B	III
		M. praecox.	,,	
		M. lupulina.	,,	IV
		M. orbicularis.	,,	
	M. denticulata.	*M. denticulata.*	B	V
	M. arabica.	*M. arabica.*	,,	
	(*Mel. indica*).	*Mel. indica.*	Bridging	
C	*M. laciniata.*	*M. laciniata.*	A	VI

All of the hosts in Fixation Group I, characterized by ability to fix nitrogen with all strains (except those isolated from *M. laciniata*), could be classified as bridging hosts in that they were generally nodulated by all isolates. If the ability to act as a bridging host is indicative of a certain genetic flexibility, this could also explain how such strains can fix nitrogen with so many strains of rhizobia. Fixation Group II showed moderately wide fixation range, though generally of much lower order. Of these hosts *M. falcata* was a bridging host and so to some extent was *M. rigidula*, when one takes both investigations into account.

The remaining hosts, except *Mel. indica*, were relatively specialized both in respect of invasion and fixation. *Mel. indica* stands out as a striking exception to the general trend of the table being as specialized as the other two members of Group V in its fixation, but definitely a bridging host so far as invasion is concerned. Agreement in other cases seems too good to be fortuitous and perhaps studies with further isolates will explain the anomaly.

Hely and Brockwell (1960) have remarked that the indigenous *Trigonella suavissima* is abundantly and effectively nodulated in certain Australian inland soils and that its nodule bacteria belong to the lucerne group as they are able to nodulate various species of *Medicago* and fix nitrogen with some of them. Some unpublished results obtained in this laboratory (Vincent and Waters) seem to show some affinity between *M. laciniata* and *T. suavissima*. Whereas 14/27 strains isolated from *M. denticulata* and several other species failed to nodulate *Trigonella suavissima*, all of 18 isolates from *M. laciniata* formed nodules with the indigenous host. Many of these same

strains also fixed some nitrogen with the *Trigonella* so that the average yield of 71 mg. (green-weight/plant) was significantly better than the non-nodulated (44 mg.) or those that were nodulated with isolates from *M. denticulata* and related species (48 mg.). Perhaps it is not unreasonable to attribute the sporadic, and generally ineffective nodulation of *M. laciniata*, to rhizobia normally associated with indigenous *Trigonella suavissima*.

Twenty-six lines of *M. tribuloides*, each of known and different origin, showed the following range of symbiotic behaviour (Vincent and Gibson, unpublished): early and late nodulation (12–21 days); ineffective to highly effective associations; low to high nodule numbers (8—greater than 25 per plant).

(*c*) *The Cowpea Group.*

McKnight (1949) pioneered a study of the nodulating and nitrogen-fixing properties of isolates from native legumes (chiefly from Queensland) and the cowpea, and found them generally able to nodulate the latter whilst ranging from fully effective to completely ineffective.

(i) *Invasiveness.*—Bowen (1956) has put together all recorded data for Queensland indigenous legumes and cross-inoculation data when these are available. With very few exceptions these isolates are recorded as nodulating in the cowpea group. Bowen himself adds records of 29 new species as being nodulated and 11 further species able to nodulate cowpea. Two species of *Sesbania* were not in the cowpea miscellany. Norris (1956) writes of the "unruly mob" of the cowpea group as containing all members of Mimosoideae and all members of Caesalpinioideae that have been typed. Although within Papilionatae there are many temperate species, the group as a whole is principally made up of tropical legumes.

Norris (1958*b*) has reported what appears to be an extreme example of specialization. *Lotononis bainesii* was resistant to nodulation by isolations from 31 species of 18 genera. Isolation from some nodules of widely separated plants of *Lotononis* itself yielded red colonies which were then uniformly recoverable from nodules of inoculated plants of *Lotononis* in the field. At the same time such cultures, which were able to nodulate *Lotononis*, formed nodules on only three other host species (in a collection of 31 species, 21 genera). These associations were all ineffective.

Bowen (1959*b*) has shown that *Centrosema pubescens* is resistant to almost all other strains isolated from members of the cowpea group. This point, and the intermediate condition with *Centrosema plumieri*, are illustrated in the following abridged indications of Bowen's infection data.

	Number of non-homologous strains nodulating specified test host.
Vigna sinensis	27/27
Phaseolus lathyroides	26/26
Centrosema plumieri	11/27
Centrosema pubescens	2/25

All cases positive with *C. pubescens* nodulated *C. plumieri* as well. One of the two *C. pubescens* heterologous positive associations was ineffective on this host and on *C. plumieri*.

Isolates from the South American species, *C. pubescens* and *C. plumieri*, were reciprocally able to nodulate, but that from the North American *C. virginianum* nodulated the first two hosts very sparsely. Bowen notes a report that *C. pubescens* is closely self-pollinated, but Norris (1956) has commented on the fact that the closely self-fertile *Phaseolus lathyroides* nodulates promiscuously also. In spite of this specificity Bowen records that in some parts of Queensland *C. pubescens* occurs well nodulated without any history of seed inoculation.

Bowen and Kennedy (1961) have subsequently demonstrated that there are sparsely and profusely nodulating lines of *C. pubescens*, although it was observed that some *Rhizobium* strains could nodulate the "sparsely" nodulating lines satisfactorily and cause good plant growth. The authors were able to show convincing evidence of line differences in the number of nodules produced in vegetatively propagated plants of sparsely and abundantly nodulating selections. These selections showed significant differences in numbers of nodules, but not in total nodule weight or in plant yield. Some bacterial lines appeared to be able to nodulate "sparse" lines practically as well as "profuse".

(ii) *Effectiveness.*—Twenty of the 21 strains isolated were able to nodulate *C. pubescens* effectively. Eleven of them, though fixing appreciable nitrogen, could be classed (P, 1%) as inferior to the nitrogen control. Only four were inferior to the best symbiosis. In an intrageneric study Bowen found that the isolate from *C. virginianum* was ineffective on the other two hosts; those from *C. plumieri* and *C. pubescens* were satisfactory and indistinguishable on *C. plumieri*, though none was very good on *C pubescens*. Such agreement between *C. plumieri* and *C. pubescens* leads Bowen to comment on this as an example of the possibility of establishing effectiveness subgroupings in the "tropical legume miscellany".

4. *Influence of Environment on Nodule Formation.*

Although there has been a relatively large amount of work done on this problem, much of it applied to particular field situations, it has generally been difficult to disentagle those factors that operate in respect of the survival or multiplication of the bacteria, and those that affect invasion and subsequent stages of nodule maturation. Of necessity, therefore, the effects that have been observed have often to be interpreted to the best of our knowledge of what factors determine the matter in more defined situations.

(*a*) *Hydrogen-ion Concentration.*

The deleterious effect of normal superphosphate, and the benefits which Cass Smith and Pittman (1939) obtained from its neutralization, are generally taken to operate by affecting survival of the bacteria added with the seed. Similarly, Jensen's observations (Jensen, 1943) of the effect of pH on nodulation of clover (limiting pH for reliable nodulation, 4·7 to 4·8) and *Medicago* (limiting pH about 5·8 to 5·9) agree closely with his earlier findings as to respective pH ranges permitting growth of the bacteria concerned (Jensen, 1942*a*). Spencer (1950) found that nodulation of subterranean clover was increased in an initially acid soil (pH 4·9–5·1), provided pH was raised and calcium was supplied, and that the effect of low pH could be offset, to some extent, by increasing the number of rhizobia added on the seed. These observations are compatible with those of Jensen (1941) who found that nodulation could occur under conditions too acid for rhizobial growth, and with the survival and growth data in an acid soil obtained by Vincent and Waters (1954). In both cases the value passed through an optimum (Spencer, 5·7–7·1; Vincent and Waters, 6·4–6·6 to 7·1–7·4).

(*b*) *Calcium, Magnesium, Phosphate and Nitrate.*

The specific role of calcium in nodulation has been greatly clarified by Loneragan and Dowling (1958) who showed the importance of this element itself and its interaction with pH. 0·01 mM calcium and pH 4·0 represented the lower limits, when the other was in excess. The authors noted that this amount of calcium was greater than that required for maximum growth of the bacterium, and also in excess of the plant's own requirement (nitrate supplied). On the other hand, they were of the opinion that the effects of H^+ and Ca^{++} on nodulation could be related to their influence on the level of calcium in the plant, this possibly then determining the success or failure of the early steps leading to nodule maturation (note also Andrew and Norris, 1961). The actual stage at which the deficiency exercised its effect was not, however, defined, and it is possible that the invasive step is the one directly affected. Loneragan

and Dowling's findings are perhaps complicated by the presence of 5 mM KNO_3 in view of the antagonistic effect the NO_3^- exercises on nodulation (Gibson and Nutman, 1960).

Whilst considering these effects of calcium on legumes like clovers and *Medicago*, we need to heed the warning of Norris (1956) against dealing with the much larger and diverse group of tropical (? ancestral) legumes by simple analogy. A current view (Norris, 1959*b* and *c*; Andrew and Norris, 1961) is that the tropical legume needs calcium, but, being an efficient extractor of this element from calcium-deficient soils, it can obtain its requirements more readily. The hypothesis is an attractive one, but close examination of the data (Andrew and Norris, 1961), and the authors' own assessment of it, indicates that the situation is not so straightforward. Not only does one temperate species (*T. repens*) nodulate very well at the low calcium saturation level of unamended soil (in fact, on the basis of weight of nodules/g. root tissue, exceeding three of the five tropical species), but all of the four temperate species reach their virtual maximum weight of nodule tissue at the next calcium level when the same three tropical legumes are still submaximal. None the less, one would certainly agree that species differ in their calcium requirements and "that the use of lime on tropical soils should be on a rational, not a traditional basis".

Loneragan (1960) discounts the suggestion of Norris (1959*a*) that magnesium would affect nodulation by limiting the growth of rhizobia in the soil, on the grounds that the plant would experience deficiency at concentrations still in excess of those at which rhizobial growth would be checked.

Methods have been devised whereby the placement of a relatively small amount of lime or dolomite in the vicinity of the inoculated seed provides an environment having its pH more suitable for the survival and multiplication of rhizobia, as well as providing the calcium that would assist invasion and/or the formation of functioning nodules. Lime pelleting (Loneragan *et al.*, 1955; Cass Smith and Goss, 1958) is a practical measure for achieving this result with a minimum of lime.

Phosphate-deficient soils showed reduced nodulation in the absence of phosphate, even when lime was adequate (Vincent and Crofts, 1958).

Gibson and Nutman (1960) have found, in tube tests on agar, that the initiation of nodules was delayed by traces of nitrite and nitrate (as low as 6·5 p.p.m.), but not at these low concentrations by such other forms of combined nitrogen as ammonia, asparagine or urea. On the other hand, a small initial concentration of any of these forms of combined nitrogen (20 p.p.m. N) increased the number of nodules formed. These results, and the fact that media used in early experiments were made up with water containing this amount of nitrate N, led the authors to conclude that the effects of preplanting red clover and lucerne could be explained in terms of removal of this nitrate by the preplant.

(*c*) *Temperature.*

Elevated temperatures are likely to interfere with nodulation: an effect which has been observed from time to time in the author's laboratory in connection with the determination of rhizobial numbers by a plant dilution method (Date and Vincent, 1962) and in unpublished investigations with lines of *Medicago tribuloides* (Gibson, Roughley, and the author). In these cases delay or prevention of nodulation was associated with more rapid growth of the host, and it was apparent that the optimum temperature for nodule formation was appreciably less than that for most rapid growth of the host plant. Pate (1961) has studied the influence of temperature on the nodulation of vetch and barrel medic and in each case finds optima towards the extremes permitting growth of the host. Bacterial strains differed in their reaction to temperature. Our results had also given indications of differences in the way host lines reacted to such a factor in the environment.

(*d*) *Host Plant.*

There has not been a great deal of work done as yet on the effect the host plant exercises on the growth of rhizobia near its roots. Rovira (1961) has, however, shown

stimulation of clover rhizobia both by *Paspalum* and clover roots, particularly when the addition of lime permitted better growth of the plant. Clover was rather more stimulating than *Paspalum*. The degree of differential stimulation can be seen most clearly by expressing Rovira's data as the proportion of rhizobia to total bacterial count:

Fertilizer.	Host.	Ratio of Rhizobia/Total Bacteria.	
		Rhizosphere.	Non-Rhizosphere.
Nil	Paspalum	0·07	0·05
	Clover	0·14	0·15
Lime	Paspalum	0·31	0·02
	Clover	0·88	0·02
Lime and minerals ..	Paspalum	0·09	0·07
	Clover	0·74	0·03

In another investigation, however, Sperber and Rovira (1959) had found only one culture of *Rh. trifolii* in 318 isolates from the rhizospheres of subterranean clover and rye-grass. The difference between this result and that of Rovira (1961) could be attributed to selection against *Rhizobium* in the plating procedure used in the earlier paper.

Vincent and Waters (1953) found that, although the nature of the clover host seemed to exercise no effect on the relative growth of several strains of rhizobia in the vicinity of the roots, each host exercised a selection so far as the proportion of nodules due to different strains was concerned.

Purchase and Nutman (1957) have used the ability of a large population of avirulent clover rhizobia to suppress (or considerably reduce) the multiplication of an introduced virulent clover strain, to study the relationship between the number of virulent bacteria in the rhizosphere and the number of nodules formed. Their results show that the large number of nodule bacteria found in the rhizosphere of clover grown in a test-tube is much greater than that which is needed to ensure maximum nodulation. The fact that each additional infection required a disproportionate increase in the number of virulent bacteria was taken to be incompatible with a hypothesis of a uniformly susceptible root, but to conform with the concept of there being a limited number of discrete foci availabe for infection. The fact that a lucerne strain did not suppress the growth of an associated clover strain in the same way as the avirulent clover strain was an interesting side issue.

5. *Effect of Environment on Nitrogen Fixation.*

(*a*) *Nutritive Factors and H-ion Concentration.*

Since Anderson (1942) observed stimulation of clovers by wood ash and found this to be due to molybdenum, a very large volume of work has been done in Australia on the importance of this element in permitting efficient nitrogen-fixation in the potentially effective nodule. Jensen and Betty (1943) attempted to demonstrate the specific effect of molybdenum in fixation by the legume nodule. Their paper shows very clearly difficulties that can be encountered in the glasshouse when dealing with an element which is capable of giving a maximum response at a very low concentration. Sand cultures had to be exhausted by continued cropping with lucerne before a molybdenum response could be demonstrated. However, Jensen and Betty were able to demonstrate stimulation of fixation by Mo, and the fact that the root-nodules were particularly rich in this element (five times to fifteen times the roots, which in turn contained more than the tops). Lucerne plants also took up more Mo when fixing nitrogen than when using the combined form. A continuation of this study (Jensen, 1946), using pots of sand having a very low molybdenum content, showed marked decrease in yield by Mo-deficient plants which, however, developed a larger mass of nodule sub-

stance than did plants with an adequate supply of Mo. The gain of nitrogen per unit weight of nodule substance was about 2½ times as great in normal as in Mo-deficient nodules. Nitrate improved the growth of Mo-deficient plants and plants supplied with combined nitrogen generally contained less Mo. Jensen concluded that Mo was essential for the process of N fixation and that, for efficient functioning, nodules needed to contain 3 p.p.m.–20 p.p.m. of this element. Later Jensen (1948) calculated that for lucerne, 10–25 p.p.m. Mo, based on dry nodule substance, appeared necessary for maximum N-fixing ability. Comparable figures for subterranean clover were 4–8 p.p.m.

Anderson and Thomas (1946) followed up Anderson's earlier observations and obtained molybdenum deficiencies in pot culture experiments with soil that had shown marked Mo responses in the field. Their detailed work with inoculated legumes showed that the need for Mo could be much more readily demonstrated when the plant was dependent on atmospheric nitrogen. Like Jensen (1946), they found more nodules when Mo was deficient, but these were obviously much less efficient. Anderson and Oertel (1946) showed that the use of phosphate improved the host's ability to respond to molybdenum. One of the effects of heavy lime dressings was to make more Mo available. Both Jensen and Betty (1943) and Anderson and Oertel (1946) found that vanadium could not replace Mo in this effect.

Later Anderson and Spencer (1949, 1950*a*, 1950*b*) were able to show the different roles of molybdenum and sulphur: the former most strikingly involved in a part of the fixation sequence, the latter concerned with the synthesis by which combined inorganic sources of nitrogen were converted to organic form. In its absence there was increase in non-protein N in the clover, and a decrease in nodule number (compare with molybdenum). Sulphur appears to affect symbiotic nitrogen fixation chiefly through its effect on nitrogen metabolism within the plant.

Field experiments confirming the relationship between the functioning nodule and Mo, and the effect of heavy dosages of lime, substantiated the earlier indications (Anderson and Moye, 1952). Anderson (1956*a*, *b* and *c*) has provided several comprehensive reviews.

Jensen (1944) found a marked difference between *Trifolium* and *Medicago* in their efficiency of fixation relative to pH. When adequate calcium and phosphorus were provided, the net gain of N by subterranean clover in soil as acid as pH 5 was not improved by liming to give pH 7–7·5. On the other hand, although nodulated lucerne continued to fix nitrogen at pH 5, the gain was greatly increased by liming. These results were likely to have been complicated by a shortage of Mo, and in 1948 Jensen, in a very thorough reinvestigation of the matter, found that, with Mo not limiting, efficiency of fixation by lucerne (average of 5 experiments), subterranean clover (4 experiments) and white clover (1 experiment) was unaffected down to pH. 4·5–4·8 for clovers, to below 5 for lucerne. The one experiment done with barrel medic gave approximately a quarter of the fixation at pH 5 comp. pH 7·4. Jensen concluded, from calculations based on his data, that the rate of nitrogen turnover in the nodule would at least be the equivalent of bacteroid N daily for lucerne and each two days for clover: figures which seemed to favour the idea of continuous N transfer without any need to postulate appreciable cell autolysis.

Combined nitrogen supplied as NH_4^+ or NO_3^-, in quantities comparable with the amount of N fixed in the same time, had relatively little effect on the number of nodules but reduced their efficiency. Both hosts grew equally well at pH 4·5–5·0 as at 7·0–7·5, when given combined N (Jensen, 1948).

Loneragan (1959) showed a specific calcium effect on nitrogen fixation under conditions of moderate calcium deficiency, whereas, when the calcium deficiency was extreme, its effect operated directly on plant growth. The effect of moderate calcium deficiency on the nitrogen metabolism of plant tops was very much like the Mo effect. The analytical and experimental evidence cannot be explained by any effect of the calcium deficiency on nitrogen uptake and suggests a specific function in N fixation.

Nitrogen deficiency induced by low Ca (like low Mo) was associated with an increase of nodule numbers—a secondary effect of the deficiency.

Nodules of plants grown in low Ca also showed premature degeneration. This is not a secondary effect of N deficiency in that it does not occur with Mo deficiency alone. However, like Jensen (1947), Loneragan found that the nodules of subterranean clover had a lower calcium content than the tops. It seems likely, either that the functioning calcium is associated with restricted regions of the nodule, or that the calcium could affect the process of nitrogen fixation through the supply of metabolites from the plant. Perhaps translocation of carbohydrate is involved.

Other deficiencies, and other unfavourable conditions in the environment, can affect fixation by affecting plant growth (Loneragan, 1960). Sulphur deficiency affects the amount of nitrogen fixed by disturbing post-fixation metabolism of the plant. Such indirect effects as these are characterized by the inability of the affected legume to respond to the addition of combined N. Non-legumes, too, might show the same effects, but note that a legume might have a special requirement even though this is not operating *via* N-fixation. This is illustrated in the case of Ca at some levels and P. Subterranean clover is less able to obtain its P than grasses.

(*b*) *Temperature.*

Meyer and Anderson (1959) have recently reported a virtual cessation of fixation by nodulated subterranean clover plants at 30° C. Pate (1961) has also shown optimal temperatures for fixation (expressed as mg. N fixed/plant) with some effect associated with a particular strain of *Rhizobium*. In both of these investigations the data do not enable one to determine the extent to which there is a difference in efficiency per unit of nodule tissue or whether it is an over-all non-specific matter operating on fixation through the plant. Short-term fixation by equal nodule masses could help to define the matter.

Gibson (1961) has also reported on the influence of root temperature and the interaction between temperatures, host and bacterial strain. Experimentally, Gibson's procedures are interesting in that he did, in fact, commence with a uniform population of well-nodulated plants which he then exposed to the temperatures concerned. Controls were established as non-nodulated plants receiving NH_4NO_3. As index of efficiency of fixation, Gibson took the nitrogen fixed as a percentage of the combined N assimilated by the control plants at each temperature. All of the four host × bacterial strain combinations increased to a maximum at about 22° C. With Tallarook variety of subclover, *Rh. trifolii* strain TA1 was superior to NA30 at all temperatures (5°–30° C.), but with Dwalganup as host, NA30 appeared to be the better at lower temperatures (up to 18° C.), though TA1 was again the better at 26° and beyond.

(*c*) *Development of Host.*

Pate (1958*b*), following the relationship between nodule growth, haemoglobin content and nitrogen accumulation on the one hand, and stages of host development on the other, found that the average nodule size and efficiency increase as nodule populations age, possibly due to elimination of the smaller members of effective nodule populations. There are marked decreases in nodule numbers and total weight at flowering and early fruiting (vetch and pea). Removal of flower buds delays these effects.

III. Application of Knowledge.

A great deal of the interest in the root-nodule bacteria in Australia, as in other countries, has centred on means of making the best use of the ability of the effectively nodulated legume to fix nitrogen. This can involve encouraging the rhizobia that occur in the soil or on uncleaned seed (Strong, 1938), taking steps to ensure successful seed inoculation, as well, perhaps, adjusting the environment so as to permit efficient functioning of the nodule (e.g., by supplying molybdenum when needed).

1. *The Need for Seed Inoculation.*

Early experiments were often confused by the presence of rhizobia already in the soil, and no doubt by such complications as the use of faulty cultures, the incorrect application of cultures that could have given satisfactory results, and limitations imposed by nutritional deficiencies in the host plant. There is probably a good deal of material hidden in departmental files so that the account that follows will undoubtedly be incomplete.

In New South Wales beneficial results from inoculation had been demonstrated by 1931 and instances of favourable response mounted in subsequent years (Roughley, personal communication).

The author's experience with subterranean and crimson clovers, barrel medic, field pea and vetch in the red soils of the Lismore Region (Vincent, 1954*b*) was one of the most striking examples of sparseness of rhizobia in acid soils and, in the case of the two clovers, the general ineffectiveness of most of those rhizobia that did occur. A more extensive survey was also reported by the author (Vincent, 1954*a*) and detailed studies have been undertaken in the New England Region of the State (Baird, 1955) and in the north-west (Vincent and Crofts, 1958).

A generalization that has emerged (Vincent, 1954*a*) is that where higher rainfall areas favour white clover as the common naturally occurring clover, they are likely to harbour a large proportion of strains that are parasitic, or only weakly effective, with subterranean, crimson and ball clovers.

Purchase, Vincent and Ward (1951*b*) found that the smaller part of the naturally occurring strains of medic rhizobia in a representative north-western locality was even moderately effective on both lucerne and *M. denticulata*. *M. laciniata* was often without nodules and, when nodulated, yielded cultures that were commonly ineffective on that host. Hely and Brockwell (1960) and Brockwell and Hely (1961) found fully effective associations with species of *Medicago* and *Melilotus* the exception rather than the rule in a collection of isolates from Queensland and New South Wales. Pittman (1938) and Cass Smith (1938), Cass Smith and Pittman (1939), showed responses that could result from inoculation of legumes sown into certain Western Australian soils and Strong (1938), in South Australia, found that there were advantages in inoculating even the unpolished seed of subterranean clover, that could be expected to carry some rhizobia on its coat. Differences with lucerne and field pea were most striking. Strong (1940) also paid some attention to the possibility of disadvantageous competition by naturally occurring ineffective strains.

Results recently reported by Harris (1961) with relatively non-acid soils (pH $>$ 6) illustrate the situation where, although inoculation gave a worthwhile improvement in the first year, it was not vital to the successful establishment of clover. In such soils the clover rhizobia seem able to establish themselves with relative ease, and it is no doubt because of this, as well as climatic factors, that subterranean clover has been able to achieve its early successes in the more southerly parts of Australia. It is, however, likely that many areas which have failed to permit its natural spread can be brought under this clover by a combination of seed inoculation and soil improvement.

McKnight (1949) had shown in Queensland that truly native strains of rhizobia, though freely causing effective-looking nodules with indigenous hosts, could not be depended on to form effective nodules with cowpea itself, even though they were able to invade it. Apart from the particular problems associated with specificities in the cowpea miscellany, early failures of pasture establishment in the coastal lowlands of southern Queensland were largely due to the need for successful seed inoculation and the unsatisfactory inoculants that were first used (Bryan and Andrew, 1955).

2. *Supply of Legume Inoculants in Australia.*

Records supplied by Roughley (personal communication) show that as early as 1914 the Biology Branch of the New South Wales Department of Agriculture despatched a few cultures to farmers. This was followed by the Western Australian Department

of Agriculture in 1926 (Pittman, 1938) and then by South Australia (Soil Microbiology Section of the then Council for Scientific and Industrial Research, 1938), Queensland Department of Agriculture, 1937-1938, and the Tasmanian Department, 1938. With a rapidly increasing demand for cultures in the succeeding years the New South Wales Department developed the manufacture of peat inoculants in 1946 and these were successfully used for some years, although other States persisted with agar cultures.

Prior to 1954 almost all legume inoculants, sold or distributed free in Australia, were provided by government or semi-government bodies. In that year the New South Wales Department vacated the field in favour of private enterprise at a time when the culture business was growing rapidly and was obviously becoming too large to be handled by a government laboratory.

The change-over period was, however, marked by many difficulties that became apparent both as a result of scientific appraisal of the quality of representative inoculants (Brockwell, 1954; Waters, 1954) and from numerous complaints by farmers and field officers. The fact that the beginning of commercial production coincided with a more general awareness of the need for effective nodulation and ability to recognize the signs of failure, and that many new and relatively difficult areas were being established, highlighted the difficulties. The author (Vincent, 1954*c*) emphasized the need for the proper production and control of inoculants, analysed reasons for failures and suggested safeguards and standards.

Out of this dissatisfaction, and with the co-operation of the laboratory investigator and the manufacturer alike, there evolved a voluntary control organization provided jointly by the University of Sydney and the New South Wales Department of Agriculture (U–DALS; Vincent, 1958). This has resulted in a steady improvement in the quality of legume inoculants produced in Australia (McLeod, Roughley and Vincent, 1961) so that their standard has now become acceptable to all State authorities who have virtually ceased production except for special purposes.

3. *Requirements for the Successful Use of Seed Inoculants.*

(*a*) *Selection and Maintenance of Correct Strain.*

The strain, or strains, used for the inoculation of a particular legume need to be able: (i) to nodulate the host; (ii) to fix nitrogen efficiently in association with it; (iii) to do these things under field conditions. These needs have been recognized for a long time (Cass Smith, 1938; Strong, 1940), but inoculants have not uncommonly failed on one or all three counts and caused trouble in consequence (Vincent and Waters, 1954; Jenkins, Vincent and Waters, 1954; Bryan and Andrew, 1955; and other cases quoted by Vincent, 1954*a*).

The chances of selecting a good strain for a particular host are increased if the original selection is made from effectively nodulated plants of the same species growing in a field situation that permits ready differentiation between efficient and poor nitrogen-fixing associations (e.g., Vincent, 1954*b*). Such a procedure does not, however, tell us much about the performance of the same isolates on other species or varieties in the same inoculation group. Some trends can be established (e.g., positive correlation of strain behaviour on white and red clover, and the negative trends with respect to white compared with subterranean clover (Vincent, 1954*a*)), but the successful agronomic use of any particular rhizobial strain requires it to be tested with the host concerned. No statistical statement of probability substitutes for this, useful as it might be for the leads it provides.

Whatever the basis of the original selection, newly isolated strains will need to be tested against older strains. These comparisons are mostly conveniently made in the laboratory and the glasshouse to provide a "short list" based on a certain minimum performance. The investigator must, however, move into the field and there determine what ability the strain has to achieve its effective nodulation under more severe conditions.

Tube tests on agar media are very convenient for the first sorting of small-seeded legumes (e.g., Vincent, 1954*b*) and there is no reason for believing that potentially useful strains will be overlooked by such screening. Early indications of success or failure to fix nitrogen can be obtained by observing the stage at which the cotyledons lose their colour (Vincent, 1945), or by using anthocyanin-rich varieties of subterranean clover (Brockwell, 1956) or barrel medic (Brockwell, 1958). Dry weights or, more simply, green weights generally provide good and relatively speedy differentiation, which is considerably improved by using top weights in preference to total plant. Because of limitations imposed by tube size (6″ × 1¼″), the larger-seeded subterranean clover is likely to give about a twofold improvement over the uninoculated control, whereas with small-seeded white clover the figure is increased to six times. It is fair to note, however, that the relatively narrow range for subterranean clover is largely offset by greater uniformity between replicates (Vincent, 1956).

Large-seeded legumes need to be allowed to develop much further to obtain a similar degree of differentiation. This means open culture of some sort, but the hazards of the open pot of sand can be overcome by one of several modifications of the Leonard jar, which has the principal virtue of being watered from below.

Tests in soil are preferably done in the field, though glasshouse trials—especially if using soil cores, as in the writer's laboratory, can remove some of the seasonal hazards. Unprotected pots in the glasshouse provide considerable opportunities for contamination by air-borne rhizobia, and offer an artificially favourable environment.

There are good reasons, both in production and use, to select strains that perform effectively with as many host species and varieties as possible. There is obviously a limit to the extent this can be provided, particularly when one takes account of the need for field tests. Wide geographic range of usefulness is also desirable. With the clovers we have been fortunate in having several strains at our disposal, which nodulate all the common species quite efficiently, and which seem to have had no particular climatic or other environmental barriers. Any attempt to "synthesize" a wide spectrum culture by mixing strains, some of which are ineffective, with some of the recommended hosts, would be dangerous in the absence of much more information about their mutually competitive effect.

Marshall (1956*b*), in one of the few studies in which the proportion of different strains competing for growth has been determined, found that one strain could be almost completely overgrown by another. Marshall's results can be summarized:

	Percent. of Each Strain Recovered from a Mixture of				
	NA30 and Clover F, as :		NA30, SU297 and SU298 as :		
	NA30.	Clover F.	NA30.	SU297.	SU298.
(*a*) Four days growth in broth ..	5	95	4	12	84
(*b*) Broth (*a*) mixed with peat* ..	5	95	5	15	80
(*c*) Grown singly and introduced to peat in approx. equal numbers..	10	90	0	5	95

* At a concentration that allowed 9× to 53× multiplication in the peat.

It is apparent that to maintain a more equal representation of strains they should be propagated separately in the broth and added to the peat in sufficient number to minimize the amount of subsequent proliferation and hence the opportunity one would have to outgrow the others.

Strains should be maintained with a minimum need for subculturing and opportunity for growth, in order to minimize loss of symbiotic properties such as invasiveness or effectiveness (Vincent, 1954*a*). Lyophilization probably provides the best means of strain storage. In any case the retention of desired properties should be periodically checked in glasshouse and in the field.

(*b*) *Form of Inoculum.*

Although a good deal of trouble has been encountered with peat cultures, there is every reason to believe that, provided there are adequate controls to ensure its quality, this form of culture can be as good as agar. There are in fact indications that peat exercises a protective effect on the survival of rhizobia added to the seed.

Lyophilized cultures, provided methods are good enough to avoid excessive death of rhizobia during the drying stage, can yield large numbers of viable rhizobia. Moreover, this form of culture seems rather less dependent on post-manufacture storage time and conditions. On the other hand, if used as a simple suspension in water, they will lack any protection afforded by peat at that stage.

(*c*) *Survival of Rhizobia in Culture and after Use.*

Survival of rhizobia in relation to commercial inoculants is likely to be important: (i) between production and use; (ii) on the surface of the inoculated seed; (iii) in the soil.

The temperature of storage is very important in its effects on survival in culture. Date, working in this laboratory, has found that the rate of death in culture (whether agar or non-sterilized peat) doubled for a rise of approximately 12°–13° C. There were indications of better survival in sterilized peat and the temperature dependence was largely removed. Old freeze-dried cultures of *Rh. trifolii* have remained remarkably stable for 3½ years at room temperature, and we have had very little trouble in recovering viable cells in our rhizobial collection which was routinely lyophilized more than three years ago. Roughley and McLeod (1961) have recorded the survival of commercial freeze-dried cultures over the six-month period. Survival at 5° C. was very good (70% of the post-drying count), but this was reduced to 4% at 25° C., 2% at 30° C. and 1% at 37° C. This was better than commercial peats (0·1% at 25° C.), but not much different from a laboratory-prepared non-sterile peat (1–2%), and inferior to a culture made up in sterilized peat (at least 50% after six months at 25° C.).

Survival and Multiplication of the Rhizobia on the Seed and near the Seedling.

Certain field conditions are unfavourable, such as acid soils (Vincent and Waters, 1954; Vincent and Crofts, 1958), unneutralized superphosphate (Strong, 1938; Cass Smith and Pittman, 1939), contact with trace element mixture (Jenkins, Vincent and Waters, 1954), too much or too little water (Swaby and Noonan, 1946) and elevated temperatures.

The use of "neutralized" superphosphate, to avoid toxic effects due to acidity in the fertilizer itself, and as a means of providing a more favourable environment in the vicinity of inoculated seed sown in acid soils, has been advocated for some years (Pittman and Anderson, 1944) and is nowadays common practice. The benefits derived from this are most likely due to better survival and multiplication in the improved environment.

Temperature tolerance data obtained by Bowen and Kennedy (1959) have already been discussed. In addition, a glasshouse trial of ability to nodulate the host sown after holding the inoculated seed in sand for up to nine hours at 40° C. showed better persistence by the more heat tolerant QA549 than the heat susceptible QA837. However, as the authors point out, the difference is one of degree, and even the higher inoculum level of the more heat resistant strain would have been seriously reduced in numbers of survivors had the elevated temperature been extended several hours. The authors complete their work with a useful summary of the temperatures they and others have recorded for unshaded soil under Australian conditions. Temperatures in excess of 40° C. are common and this can readily continue for six hours in the one day. Shading, particularly by grass or trash cover, could well make the difference between survival or death of the root-nodule bacteria: one of the reasons for the adoption of the sod seeding technique by the Sydney group (Breakwell and Jenkins, 1951) in their pasture improvement programme on the far north coast of New South Wales.

The improvement reported by Millington (1955) as a result of deep placement of inoculum could be attributed to better survival of the bacteria due to reduced desiccation. Temperature would not seem to have been an important factor at the time of the year these trials were established (autumn).

Milthorpe (1945) compared the toxicity of a range of anti-fungal seed dusts; Braithwaite, Jane and Swain (1958) have likewise provided some information as to the effect of certain insecticides on nodulation, presumably affecting the survival of added rhizobia.

Our own quantitative results in the laboratory (Vincent, Thompson and Donovan, 1962) and with field trials (Date and Vincent, unpublished) emphasize hazards associated with pre-inoculation, viz., the inoculation of seeds well in advance of inoculation. Certain protective measures, such as the use of maltose and gum arabic, can reduce the rate of death, and the use of a very heavy suspension of cells initially may result in there being sufficient survivors to secure nodulation, especially when tested under relatively favourable conditions (Loneragan, Moye and Anderson, 1961). A great deal more evidence is yet required before this practice can be recommended for routine use.

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SELECTING FOR VIRULENCE ON WHEAT WHILE INBREEDING *PUCCINIA GRAMINIS* VAR. *SECALIS*.

By I. A. Watson and N. H. Luig, Faculty of Agriculture, The University of Sydney.

(Plate i.)

[Read 29th March, 1962.]

Synopsis.

Field inoculum of *Puccinia graminis* var. *secalis* was collected and used to infect the alternate host. From cereal varieties mass inoculated with aeciospores nine dissimilar strains of rust were isolated, all of which attacked rye. Two were studied in some detail. H-20-a represents a strain selected on the wheat variety Yalta and the latter proved much more susceptible to this strain than to *P. graminis* var. *secalis*. A second strain H-34 was studied and it was characterized by its virulence on Little Club wheat. The reaction of wheat varieties to both strains was markedly affected by temperature.

Under Australian conditions stem rust on rye has not been of any agricultural importance. The first record of the presence of *Puccinia graminis* Pers. var. *secalis* in Australia was made by Waterhouse (1957). Since then it has been found to be widespread throughout the eastern part of the country and is by far the most prevalent cereal rust in Tasmania where it thrives on the ubiquitous *Agropyron repens* and is the main contributor to the widespread and regular infection of barberry in Tasmania.

In view of the common occurrence of rye stem rust both on barley and on rye on the mainland, the present studies with it have been made to determine the potential of this variety of *P. graminis* as a source of genes for virulence on wheat varieties. Four approaches are being made. Firstly, a large number of wheat varieties are being tested directly with *P. graminis secalis*. Secondly, sexual lines derived by selfing *P. graminis secalis* are being selected for their virulence on wheat varieties. Thirdly, somatic and sexual hybrids between wheat stem rust and rye stem rust are being examined for their ability to attack wheat varieties. Finally, F_2 populations of crosses between wheat varieties are being observed for segregates susceptible to rye stem rust.

Review of Literature.

It has been known for many years that the two varieties of *P. graminis*, viz. *tritici* and *secalis*, can be readily hybridized on the alternate host and that little if any inter sterility exists between them. Almost all the work dealing with intervarietal hybridization of the cereal rusts has been done by workers on the North American continent. Two centres were involved and the results have been characteristic of the institution where the work was done. At St. Paul, Minnesota, U.S.A., for example, Stakman *et al.* (1930) found that on crossing *P. graminis* var. *tritici* race 36 with *P. graminis* var. *secalis* race 11, a large range of pathogenic types were recovered in the F_1 generation and these included virulent and well-known races of wheat stem rust as well as certain avirulent types. Johnson (1949) at Winnipeg, Canada, found only a very limited pathogenicity towards wheat and rye in these same intervarietal crosses and, regardless of whether race 1 or race 30 of *P. graminis* var. *tritici* was used in crosses with *P. graminis* var. *secalis*, no common races of wheat stem rust were recovered in either the F_1 or F_2 generations. The races that were identified were virulent on only one or two of the standard differential varieties for *P. graminis* var. *tritici*. Typical of the races recovered was 111 which attacks only Little Club of the standard differential set.

Race 111, although having a hybrid origin, undergoes somatic recombination readily with other wheat stem rust races (Watson, 1957; Watson and Luig, 1958*b*; Ellingboe, 1961) and in this way releases much of its hidden variability.

It would appear that a combination of certain genes from the rye rust with others from the wheat rust changes the phenotypic expression of the latter. Whereas avirulence on the varieties Arnautka, Mindum and Spelmars is normally inherited as a recessive character (Johnson and Newton, 1940; Johnson, 1954), the gene concerned in the avirulence behaves as a dominant in race 111 since, from somatic and sexual material involving this latter race, types having virulence on Arnautka, Mindum and Spelmars were recovered (Watson, 1957; Wilcoxson and Paharia, 1959). Moreover, the observation that somatic recombinants may occur between *Puccinia graminis* var. *tritici* and *P. graminis* var. *secalis* (Watson and Luig, 1959; Bridgmon and Wilcoxson, 1959) suggests that a reservoir of genes for pathogenicity on wheat varieties may be harboured in the rye stem rust. Watson and Luig (1959) suggested that this latter rust may be an avirulent strain of wheat stem rust.

Materials and Methods.

A severely rusted self-sown crop of rye was observed in the Parkes, New South Wales, district in April, 1959. An examination of the uredial stage revealed that it was caused by stem rust. The paddock remained unstocked during the winter, and late in August of that year a small sheaf of straw was harvested in which the stems had developed extensive quantities of teleutospores. Without further treatment, the infected straw was used to inoculate barberries during the second week of September. Abundant infection resulted indicating that natural conditions at Parkes during the winter of 1959 had been adequate to induce germination.

The pycnial fluids were mixed and aecidiospores developed in great abundance. Mass inoculations were made onto both Black Winter Rye and to Barley B125*. In addition, individual aecidial horns were taken singly and the spores within were placed onto seedlings of these same two hosts. The uredospores that developed from either of these procedures were placed onto sets of seedlings in which the following varieties of wheat, rye and barley were represented:

1. Wheat: Little Club, Marquis, Kota, Emmer, Einkorn, Eureka, Koala, Federation, Morocco and Yalta.

2. Rye: Black Winter.

3. Barley: Barley B125 and Purple Nudum B28.

In selecting the wheat varieties the aim was to restrict attention to those very susceptible to wheat stem rust. However, from previous work (Watson and Luig, 1959) it appeared that *P. graminis* var. *secalis* may be heterozygous for the genes for virulence on the varieties Kota, Emmer, Einkorn and Yalta. Consequently these latter were included to facilitate the isolation of strains virulent on them. During the course of the experiments the day temperatures varied from 65° F to 80° F.

Experimental Results.

Among the uredial material from which the teleutospores were produced, no wheat stem rust was isolated and no strains characteristic of this latter variety of *P. graminis* were obtained from the barberry infections. All could attack rye vigorously, and from this it was concluded that the material comprised only *P. graminis* var. *secalis*.

A total of nine dissimilar strains were obtained from the aecidial material. All were virulent on rye, but their virulence for wheat depended on the variety from which the selection had been made; for example, those selected on Yalta were virulent on Yalta. The reactions of seven of the test varieties to these strains are given in Table 1.

* A Sydney University accession very susceptible to *P. graminis* from both wheat and rye.

Slight differences between the strains were shown on all varieties except B125 and Black Winter Rye, but there were clear differences on Eureka, Yalta and Little Club. The nine strains obtained from the barberry and listed in Table 1 were tested on the Stakman series of differential varieties for *P. graminis* var. *tritici*. With the exception of Little Club all reacted the same as they did to the parental strain of *P. graminis* var. *secalis*. The strain H–34 which had been selected on Little Club was the most virulent on that variety, and at temperatures above 75° F it gave a "3+" reaction, whereas on

TABLE 1.

Reaction Produced by Four Varieties of Wheat, Two of Barley and One of Rye at Day Temperatures of 65–80° F to Nine Strains obtained from Selfing P. graminis *var.* secalis.

Variety.	Parent Culture.	H-2.	H-4.	H-20.	H-20-a.	H-32.	H-34.	H-63.	H-67.	H-73.	21-Anz-2
Little Club ..	2=	2=	2−	2	2−	2=	3+	2=	2−	2=	4
Yalta	;	;++, 3=c	x+	;	3c	;1=	;	x+	x+	;	3+
Eureka ..	;1	;1	;1	;1	3c	;1	2+	;1	;1	;1	3c
Federation ..	;2−	;2−	;2−	;1+	2cn	2	;1	;2−	2	;2−	3+
Black Winter Rye ..	2, 3+	2, 3+	2, 3+	2, 3+	2, 3+	2, 3+	2, 3+	2, 3+	2, 3+	2, 3+	1+, 2
Barley B125	2+, 3c	2+, 3c	2+, 3c	2+, 3c	2+, 3c	2+, 3c	2+, 3c	2+, 3c	2+, 3c	2+, 3c	2+, 3c
Purple Nudum B28 ..	;	;	2	;	;	3cn	;	;	;	3−c	;

21-Anz-2 is *P. graminis* var. *tritici*.

this same variety the parental rye rust culture gave a "2=" reaction. Variation in reaction on Little Club has been found among isolates of *P. graminis* var. *secalis* previously (Watson and Luig, 1958*a*), but none had given a susceptible reaction at comparable temperatures.

The strain H–34 has been compared with the parental culture of rye rust and with the avirulent race 111 of wheat rust on many different varieties of wheat and the reactions of some are given in Table 2.

TABLE 2.

Reactions of a Group of Wheat Varieties to Three Cultures of P. graminis.

Variety.	Syd. Univ. No.	*P. graminis secalis.*	H-34.	*P. graminis tritici* Race 111.
Dart's × Federation ..	533	3−	3−	3+c
Sussex-Yandilla-Zaff	555	;	2	;
Chinese White Hybrid	564	;,1, 2≡	;,1, 2≡	3+c
Soft Baart	628	3−c	3−c	3+c
Dundee	737	;	3−c	2≡
Garra	738	;	3−c	;
Canberra Selection ..	739	;	3−c	;

In general the reactions of the wheat varieties to H–34 and to *P. graminis secalis* were the same, but there were many exceptions and it did not appear that the same genetic factors were giving high resistance to both rusts. The reactions of the varieties to the avirulent race 111 of *P. graminis tritici* did not appear to be correlated with those to either rye rust or H–34. Race 111 usually was more virulent than the other two on the several hundred wheat varieties tested, and it was apparent that, although the selection had created in H–34 a genotype different from that of the parent rye rust, it was by no means identical with that of race 111. These results also showed clearly that inbreeding had altered the genotype of *P. graminis secalis* for those genes concerned in virulence on varieties other than Little Club.

The second of the two strains that were studied in detail was H-20-a, the latter having been selected on Yalta. It was tested on 194 wheat varieties, but none proved susceptible, the highest reactions were "2" and 3^{-c}. This culture showed some similarity to a previous one (M-9-a) which had its origin as a somatic recombinant between *P. graminis tritici* NR–2 and *P. graminis secalis* (57241) (Watson and Luig, 1959). The culture M-9-a resembled its rye rust parent on the twelve standard differential hosts, except that it was more virulent on Little Club ("3^{c}" reaction) and on Einkorn ("3^{-c}" reaction). However, like H-20-a, its outstanding feature was the ability to attack Yalta, a variety with the gene Sr11 for stem rust resistance. This character may have been inherited from the NR–2 parent which was also virulent on Yalta.

In view of the virulence of H-20-a on Yalta, a comparison was made between the latter culture and M-9-a. When 587 wheat varieties were tested with M-9-a, 61 showed an intermediate reaction ("2" to "3^{c}" type) and 23 were susceptible ("3^{+c}" to 3+ type). The remainder were resistant. The virulence of M-9-a for these varieties, however, showed no relationship with that of H-20-a, since all 23 varieties susceptible to M-9-a were either resistant or semi-resistant to H-20-a. This suggests that in H-20-a the genes for virulence on these latter varieties have been distributed independently of those concerned in virulence on Yalta.

TABLE 3.

Reaction of Little Club, Yalta and Black Winter Rye at Three Different Temperature Ranges when Inoculated with Five Different Cultures of P. graminis.

Culture.	70–85° F.			60–70° F.			45–60° F.		
	Little Club	Yalta.	Black Winter.	Little Club.	Yalta.	Black Winter.	Little Club.	Yalta.	Black Winter.
P. graminis tritici 21–2	4	4	1^{++}, 2^{-}	4	4	1^{+}, 2^{-}	4	3^{+}	;1
M-9-a	3^{c}	3	1, 2, 3^{+}	2	x^{+}	1, 2	2^{-}	x^{-}	;1
H-20-a	2	3^{+}	4	2^{-}	x^{+}	4	;1	;	3^{+}
H-34	3^{+}	;1	4	3^{+c}	;1	4	2	;	3^{+}
P. graminis secalis ..	$;1^{+}$	;1	4	;1	;1	4	;1	;	3^{+}

There was some evidence that the physiological system derived from *P. graminis secalis*, and concerned in the virulence shown on Yalta by strain H-20-a, was different from the system derived from *P. graminis tritici* and concerned in the virulence on Yalta shown by strain 21-Anz-2. The reaction of Yalta to strains of *P. graminis tritici* is not sensitive to temperature, and to avirulent strains the variety is resistant through a wide range of temperature from 60° F at least to 80° F. To virulent strains a susceptible reaction is shown throughout the same range. In contrast with this, however, the reaction of Yalta to H-20-a was greatly affected by temperature, as shown in Table 3. During the summer months Yalta was completely susceptible to H-20-a and, of course, to 21-Anz-2 (Plate i). At the lower temperatures of winter, however, when susceptibility to 21-Anz-2 was again evident on this variety, only hypersensitivity was shown to H-20-a. This would suggest that the basis of the virulence on Yalta in these two cultures of diverse origin is dissimilar, and that possibly a gene in Yalta ineffective at high temperatures interacts at the lower temperature to produce the hypersensitivity. The reaction of Little Club to H–34 was also affected by temperature, but even at the lower range considerable sporulation resulted.

The results of Table 3 suggest that the two strains isolated from among the selfed progeny of *P. graminis secalis* were not as virulent on the two wheat varieties as was the well-adapted strain 21–2. Whereas the latter developed and sporulated normally when night temperatures fell as low as 45° F, the derivatives were greatly retarded and in the case of H-20-a only a hypersensitive ";" reaction was produced on Little Club and Yalta.

Discussion.

Since the activities of wheat breeders in Australia began there have been drastic changes in the rust flora throughout the country. Selection has taken place in the fungus, so that hitherto unknown genes for pathogenicity have increased greatly in frequency in a relatively short time. Such changes could have occurred without the intervention of man, but it is impossible to estimate the time required for the genes to reach their present frequency.

Hybridization, inbreeding and selection experiments of the type described here show how these events may be hastened. They show processes which are doubtless occurring in nature, but the products of which have a remote chance of survival. Inbreds of *P. graminis secalis*, similar to those obtained in the current study and having the ability to attack both wheat and rye, must be the usual products of the selfing process which occurs with such regularity in Tasmania. Obviously, those that were obtained here could only survive on wheat if the appropriate host variety is present and the temperatures remain high. However, during the summer months they could reproduce on *Agropyron repens* and, from somatic recombinants with the parental strains of *P. graminis secalis*, strains could be unleashed having virulence on specific wheat varieties combined with an ability to survive and reproduce at low temperatures. Such a combination of characters may also result from further inbreeding of the cultures H–34 and H-20-a and experiments are in hand to test this possibility.

The first cycle of selection has clearly increased the virulence of rye stem rust for certain wheat varieties and further experiments will demonstrate whether continued inbreeding and selection will result in further progress towards complete virulence of this fungus on them.

The contrast in the reaction of Yalta to a standard strain of *P. graminis tritici* (21–2) and to the *P. graminis secalis* inbred progenies suggests the possibility of two dissimilar specific interactions being concerned in the virulence on Yalta of these two types of rust. While it is usual for the interaction between the fungus and wheat varieties with the gene Sr6 to be influenced by temperature, this has not been the case when varieties with the gene Sr11 are involved. It seems likely that the resistance of Yalta to H-20-a at low temperatures is not due to Sr11 but to a gene resembling Sr6 in being sensitive to temperature. It is already known (Luig, 1961) that the resistance of Sr11 is ineffective against M-9-a, and varieties such as Gabo and Charter owe their resistance to this strain to other genes not present in Yalta. Such genes can only become evident when the appropriate tests are made using avirulent fungal strains derived from intervarietal crosses and from inbreeding on the alternate host.

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EXPLANATION OF PLATE I.

Black Winter Rye, Little Club and Yalta wheat inoculated with four cultures of *P. graminis* at approximately 75° F. with two leaves of each. Left to right, Black Winter Rye, Little Club, Yalta. Cultures, reading from top of plate, are *P. graminis* var. *secalis*, H-34, H-20-a and 21-Anz-2.

A STUDY OF SOME SMUTS OF *SORGHUM* SPP.

By R. F. N. Langdon, Department of Botany, University of Queensland.

(One Text-figure.)

[Read 29th March, 1962.]

Synopsis.

From a study of some smuts of *Sorghum* spp. it is concluded that *Cintractia columellifera* McAlp. should be referred to *Sphacelotheca sorghi* (Link) Clint. *Ustilago porosa*, sp. nov., has been described from *Sorghum australiense*. The host ranges of *Sphacelotheca sorghi* and *Sphacelotheca reiliana* have been shown to include plants native to Australia, and evidence is presented that these smuts are indigenous to that continent.

The genus *Sorghum* is represented in Australia by a number of species which are part of the indigenous flora, and some introductions which include both crop plants and weeds. Smuts of the cultivated sorghums were first recorded in Australia in the latter years of the nineteenth century, and they are now well known and widespread. Records of smuts on native sorghums are few, an important reason for this being the limited mycological collecting that has been done in the warmer parts of Australia where the native sorghums grow. McAlpine (1910) described *Cintractia columellifera* from what is now known to be *Sorghum leiocladum*, but he used the name *Andropogon australis* for the host. Later workers have tried to identify various smuts on grasses of the tribe Andropogoneae with McAlpine's species and considerable confusion has resulted. Collections of smuts of native sorghums have been sent to me in recent years and these, together with material collected last century and still preserved in herbaria, have made it possible to determine the identity of *Cintractia columellifera* McAlp. Elimination of the confusion over that species and a study of certain other smuts have enabled me to present a new viewpoint on the geographic distribution of some of the smuts of sorghum.

These studies would not have been possible without the collections made in northern Australia by Dr. S. T. Blake and Mr. G. Keefer. Of great use to me have been the specimens made available from the National Herbarium, Victoria, the Waite Institute, Adelaide, and the Herbarium of the Royal Botanic Gardens, Kew. To the Directors of those institutions the author is grateful.

The following abbreviations have been used to denote the herbaria where specimens referred to are located: UQ = Herbarium, Dept. of Botany, University of Queensland; M = National Herbarium, Melbourne; W = Herbarium, Dept. of Plant Pathology, Waite Agricultural Research Institute, Adelaide; HK = Herbarium, Royal Botanic Gardens, Kew.

Sphacelotheca reiliana (Kuhn) Clint., *J. Myc.*, 8, 141. 1902.

Ustilago erythraeensis Syd., *Ann. mycol.*, Berlin, 9, 144. 1911; *Sphacelotheca erythraeensis* (Syd.) Clint. in Zundel, N. Amer. Flora, 7, 996. 1939.

Specimens examined: On *Sorghum vulgare* Pers., Brookstead, R. Morwood, 13.iii.1951 (UQ 743), Cecil Plains, R. Harrison, iv.1955 (UQ 1734); on *Zea mays* L., Lawes, N. Fox, iv.1960 (UQ 747); on *Hackelochloa granularis* (L.) Kuntze, Townsville, S. T. Blake, 20.iii.1938 (UQ 63).

Herbert and Langdon (1941) recorded *Ustilago erythraeensis* on *Hackelochloa granularis* from Queensland and noted that the size of the spores in their material was a little greater than the dimensions given by Sydow. Clinton (1939) found that the size of the spores in Sydow's specimen was greater than the spore dimensions given

in his description of the species. Queensland material is thus typical of the species and not a larger-spored strain as was once suggested.

Fischer and Shaw (1953) have indicated that *Sphacelotheca erythraeensis*, the smut of *Hackelochloa*, is not distinguishable on morphological grounds from the smut of sorghum and maize, *Sphacelotheca reiliana*, and have merged the two under the latter name. *Hackelochloa granularis* is widespread in the tropics, being indigenous in the Old World, but an introduction in the Americas. In Australia it does not extend south of the Tropic of Capricorn. The smut of *Hackelochloa*, *Sphacelotheca reiliana*, is co-extensive with its host and must be regarded as indigenous in Australia. Cobb (1891) reported a smut of maize from New South Wales, this being the first record of *Sphacelotheca reiliana* in Australia. This smut was regarded by McAlpine (1910) as an introduction to Australia. This may possibly be the case in respect of the strains of *S. reiliana* which affect the introduced crop plants, maize and sorghum.

SPHACELOTHECA SORGHI (Link) Clinton, *J. Myc.*, 8, 140. 1902.

Cintractia columellifera (Tul.) McAlp., Smuts of Australia, 1910, p. 136; *Sphacelotheca columellifera* (Tul.) Cif., *Ann. mycol.*, Berlin, 26, 1. 1928.

Specimens examined: On *Sorghum vulgare* Pers., Virginia, U.S.A., C. R. Ball, 15.v.1902 (W 1672), Texas, U.S.A., A. A. Potter, 1908 (W 1669), Colorado, U.S.A., A. A. Potter, 1910 (W 1669), Roseworthy, Sth. Aust., C. F. Stephens, 29.iii.1915 (W 1673), Gatton, Qld., P. J. Skerman, 6.iv.1939 (UQ 127); on *Sorghum leiocladum* (Hack.), C. E. Hubbard, Rockhampton (HK); Rockhampton (M); Hirstglen, Sth. Qld., R. F. Langdon & D. A. Herbert, 7.iii.1941 (UQ 341); on *Sorghum plumosum* (R.Br.) Beauv. Chillagoe, Qld., S. T. Blake, 4.iv.1938 (UQ 1942).

After each of the specimens of smut on *Sorghum* spp. had been examined, it was apparent that there were many features which they had in common, but in certain characteristics the smuts of the grass sorghums differed from those of the cultivated sorghums. There was no doubt that the latter belonged to *Sphacelotheca sorghi*. It was necessary, therefore, to consider the limits of morphological variation in that species and then to determine whether the smuts of *Sorghum leiocladum* and *S. plumosum* should be grouped with the well-known covered kernel smut of cultivated sorghum, *Sphacelotheca sorghi*. Variation in *Sphacelotheca sorghi* has been studied by Tyler (1938), who concluded that the species is highly variable, consisting of an indefinite number of physiological and morphological entities. He found lines which differed in morphological features, including diameter of chlamydospores, size of smut sori and colour of peridia, characters which other workers have also found to be variable. Tyler found that morphologically distinct races of *S. sorghi* could be recognized on the basis of chlamydospore size. Spores ranged from 3·2μ to 7·2μ in diameter. Melchers, Ficke and Johnston (1932) had observed a range of 5·0–9·0μ for chlamydospores, but could find no significant differences in size of chlamydospores of five physiologic races of *S. sorghi*. Clinton (1906) gave 5·5–8·5μ as the range in size of chlamydospores, and in other papers the range is quoted as 5·5–7μ (McAlpine, 1910), 5–8·5μ (Fischer, 1953) and 3–8μ (Zundel, 1930). Two colour groups have been noted for the peridium of the sorus in *S. sorghi*. Tyler (1938) referred to them as reddish-brown and silver-grey, and Melchers *et al.* (1932) called them brown and white. The latter authors found evidence that the peridial colour was dependent on the host reaction, the colour of peridium of a given physiologic race of the smut being brown on some varieties of sorghum, white on others. The walls of the chlamydospores of *S. sorghi* were described as smooth by early authors, but Fischer and Hirschhorn (1945) have pointed out that the apparently smooth spores, when viewed with an oil immersion objective, appear punctate to finely echinulate, the echinulations often being quite noticeable on the lighter coloured parts of the spore walls.

The characteristics of the smuts of *Sorghum* spp. that have recently been examined are given in Table 1. The spores which are globose to subglobose, vary in size and, with the exception of a smut on *Sorghum leiocladum*, fall within the usual limits for

Sphacelotheca sorghi. The spores of the smut on *Sorghum leiocladum* are rather larger than those on other *Sorghum* spp. and in one of the specimens (UQ 341) the echinulations are more prominent than on the other specimens. It is only when spores are viewed with the aid of an oil immersion objective that the echinulations can be seen in these specimens, and no special significance is attached to the variations in wall ornamentation. A few spores reach 10·5μ, a figure of this order representing the greatest dimension of a markedly subglobose spore. It is considered that the smuts of the native species, *Sorghum plumosum* and *S. leiocladum*, can be referred to *Sphacelotheca sorghi.* In spore size some specimens resemble *S. cruenta.* But the peridium of *S. cruenta* is very delicate, in contrast to the stout and persistent peridium of *S. sorghi.* All specimens examined here have peridia typical of *S. sorghi*, and there is no other character in which these specimens differ from *S. sorghi.* The name *Cintractia columellifera* which McAlpine (1910) used for a smut of *Sorghum leiocladum* (called *Andropogon australis* by McAlpine) is now put in synonymy with *Sphacelotheca*

TABLE 1.

Characteristics of Smuts on Sorghum *spp.*

Host.	Specimen Reference.	Spore Size (in Microns) (Greatest Dimensions).	Nature of Spore Wall.	Colour of Peridium.
Sorghum vulgare	UQ 127	5– 9	Punctate or finely echinulate.	Grey.
	W 1669	5– 8·5	Punctate or finely echinulate.	Brown.
	W 1672	5– 9	Punctate or finely echinulate.	Brown.
	W 1673	5– 8	Punctate.	Grey to tawny.
Sorghum plumosum ..	UQ 1942	6– 8·5	Punctate or finely echinulate.	Grey.
Sorghum leiocladum ..	HK	6– 9·5	Punctate or finely echinulate.	Brown.
	M	6– 9	Smooth, punctate or finely echinulate.	——
	UQ 341	6–10·5	A few smooth or punctate, mostly echinulate.	Brown.

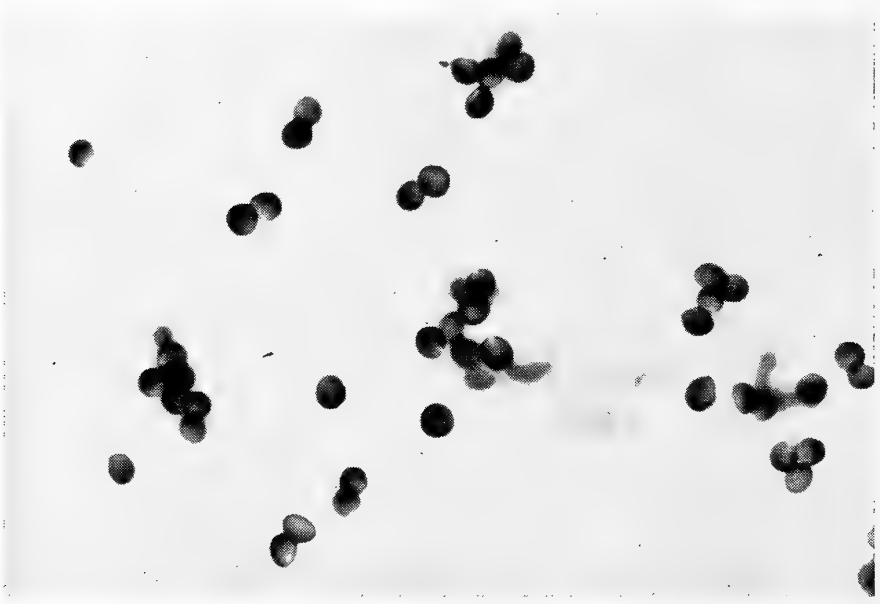
sorghi. The following notes will make clear the reasons for this and will indicate where confusion has arisen by misapplication of the name "*columellifera*".

Tulasne (1847) used the name *Ustilago carbo* var. *columellifera* for some smuts on several different grasses. Two groups, transfissa and tricophora, were defined. Berkeley (1873) recorded *U. carbo* var. *columellifera* from Rockhampton, Queensland, without stating what the host was. In the Herbarium, Royal Botanic Gardens, Kew, there is a specimen from Rockhampton labelled *Ustilago carbo* var. *columellifera.* The host was originally given as *Andropogon australis*, but there is a note on the herbarium sheet that the host is *Sorghum leiocladum* (Hack.) C. E. Hubbard, a determination made by Mr. C. E. Hubbard. McAlpine (1910) described *Cintractia columellifera* on *Andropogon australis* from Rockhampton, and listed *Ustilago carbo* var. *columellifera* as a synonym. The material studied by McAlpine was located at the National Herbarium, Melbourne, and there can be little doubt that it was part of a collection from Rockhampton that was received at Melbourne and then divided for submission to Kew. McAlpine states that the specimen he saw was labelled *Ustilago carbo* var. *columellifera*, an indication that it was but part of a collection, some of which Berkeley also had seen. The close similarity of the spores in the Kew and Melbourne collections, both of which I have examined, supports this view. McAlpine, in his description in 1910, described the spores as smooth and 7–8μ diameter. Recent examination of the material has shown that the spores are finely marked on their surfaces and exceed the limits of size suggested by McAlpine.

When reporting on a study of some species of *Cintractia*, Ciferri (1928) made some new combinations including *Sphacelotheca columellifera* (Tul.) Cif. for which *Ustilago carbo* var. *columellifera* Tul. and *Cintractia columellifera* (Tul.) McAlp. were listed as

synonyms. Ciferri saw no specimens, but it is clear that, when making the new combination, he intended it to apply to the fungus that McAlpine had worked with. Zundel (1930) published a description of a smut that he had received from New South Wales under the name of *Cintractia columellifera*, the host being given as *Andropogon intermedius*. He believed that this description would give adequate circumscription of *Sphacelotheca columellifera* (Tul.) Cif. In the following decade Zundel identified as *S. columellifera* collections on *Trachypogon* spp. from South America (Zundel, 1933) and on *Heteropogon* sp. from Africa (Zundel, 1938).

From a study of Tulasne's specimens Zundel (1939) concluded that *Ustilago carbo* var. *columellifera* was a mixture of two species, one belonging to *Sphacelotheca*, the other to *Sorosporium*. The specimen from New South Wales which he had used earlier when preparing a description of *Sphacelotheca columellifera* (Tul.) Cif., was found to be different from Tulasne's specimens, so Zundel then named it *S. McAlpineae*.



Text-fig. 1.—*Ustilago porosa*. Teleutospores (× 500).

Following this, Zundel (1943) said that the smut of *Trachypogon* from South America, which he had earlier called *Sphacelotheca columellifera*, should be recorded as *S. McAlpineae*. As indicated by Langdon (1960), the specimen on which *S. McAlpineae* was based belongs to *Sphacelotheca amphilophis*. Yen (1937) studied a smut of *Andropogon laniger* from Morocco and considered it to be the same as the smut which McAlpine (1910) had called *Cintractia columellifera*. Yen therefore transferred the species to *Sphacelotheca*. Zundel (1939) renamed *S. columellifera* (Tul.) Yen, calling it *S. yenii*, but later he recognized that the smut studied by Yen was *S. lanigeri* which had earlier been described from Persia (Magnus, 1899).

USTILAGO POROSA, sp. nov.

Sori in inflorescentia siti, longi, peridio fragili praediti. Teleutosporae subglobosae, ellipsoideae vel ovoideae, saepe irregulares, brunneae vel olivaceo-brunneae, uno latere dilutiores, 6–11 × 5·5–7·5μ; episporium laeve, poro germinationis praeditum.

Specimens examined: On *Sorghum australiense* Garber & Snyder, Anthony Lagoon, Nth. Terr., Australia, 15.v.1947, S. T. Blake (UQ 454), TYPE; on *Sorghum plumosum* (R.Br.) Beauv., Atherton, Qld., 5.iv.1960, G. Keefer (UQ 1972). (Fig. 1.)

The grey sheath surrounding the sorus is somewhat persistent. Microscopically it is thin and structureless except for a pattern of cell outlines. It stains with Sudan IV. The sheath is evidently the cuticular remnant of the tissues destroyed by the smut.

Some noteworthy features of the spores are the presence of a germ pore and the great variation in shape. The spores from *Sorghum australiense* are more deeply pigmented than the spores from *S. plumosum*. The former also tend to be a little larger than the latter, but there is a wide overlap in the range of size of spores from the two hosts.

USTILAGO SORGHI-STIPOIDEI Ling, *Sydowia*, 7, 154. 1953.

Specimen examined: On *Sorghum stipoideum* (Ewart & White) Hubbard & Gardner, Katherine, Nth. Terr., Australia, 24.iv.1947, S. T. Blake (UQ 235).

This smut has been collected only once. The material was shared with the Commonwealth Mycological Institute, Kew, and from their part of the collection (CMI 43753) Ling described and named the smut.

General Discussion.

The geographic distribution of *Sphacelotheca sorghi* is now extensive (Zundel, 1953). It is prevalent on cultivated sorghums wherever they are grown, and there can be little doubt that introductions of this smut have been made to many countries. Herbert and Langdon (1941) recorded the occurrence of *Sphacelotheca sorghi* on *Sorghum plumosum* from Queensland, noting that this was the first record of the fungus on a species of *Sorghum* that was native to Australia. Earlier in this paper it has been shown that there is a much earlier record of *Sphacelotheca sorghi* on *Sorghum leiocladum*. This was the collection from Rockhampton on which Berkeley (1873) based his record of *Ustilago carbo* var. *columellifera*. There is the possibility that the specimens were collected some years before 1873, for, during the preceding decade, there had been in that area expeditions which sent some at least of their specimens to the National Herbarium in Melbourne (Blake, 1955). It seems reasonable to take the view that collectors in Queensland 100 years ago would have collected smut fungi only by chance as they took their specimens of the grasses, for the smut sori on *Sorghum leiocladum* are somewhat concealed, being developed in the ovaries. There is no reason to suppose that the smut collection on this native sorghum is other than naturally occurring. *Sphacelotheca sorghi* is therefore to be regarded as a species indigenous to Australia. No claim is made that the sorghums introduced to Australia as crop plants have received their smut from the native sorghums, and there can be little doubt that strains of smut adapted to the crop varieties have come into Australia from time to time with imported seed.

Sphacelotheca reiliana was regarded by McAlpine (1910) as an introduction to Australia, and it is almost certain that strains of the smut have entered the country from time to time with seed of crop sorghums. But this smut is known to be on the indigenous grass, *Hackelochloa granularis*, in tropical Australia. Since the smut of this grass is coextensive with its host, it must be presumed indigenous to Australia. Because *Ustilago porosa* and *U. sorghi-stipoidei* are known only from Australia on endemic hosts, there is no doubt that they too are native to this continent.

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STUDIES IN AUSTRALIAN LORANTHACEAE. I.

Nomenclature and New Additions.

By B. A. Barlow, Department of Botany, University of Queensland.

(One Text-figure.)

[Read 29th March, 1962.]

Synopsis.

Fourteen genera and 62 species are recognized in the Australian members of the family Loranthaceae. The system of Danser is generally accepted, but the genera *Benthamina* Tiegh., *Muellerina* Tiegh., *Pilostigma* Tiegh. and *Xylochlamys* Domin are recognized. New species described are *Amylotheca petiolata, Diplatia furcata* and *Viscum pedunculatum. Dendrophthoe discolor* (*Loranthus odontocalyx* F. Muell. ex Benth. var. *propria* Blakely) and *Dendrophthoe glabrescens* (*Loranthus vitellinus* F. Muell. var. *glabrescens* Blakely) are raised from varietal rank. Other new combinations or names are *Muellerina bidwillii* (*Phrygilanthus bidwillii* (Benth.) Eichl.), *Muellerina eucalyptoides* (*Phrygilanthus eucalyptoides* (DC.) Dans.), *Muellerina myrtifolia* (*Phrygilanthus myrtifolius* (Benth.) Eichl.), *Pilostigma whitei* (*Amyema Whitei* (Blakely) Dans.); *Amyema maidenii* (*Diplatia Maideni* (Blakely) Dans.) and *Amyema thalassium* (*Loranthus maritimus* C. A. Gardn. non Merr.).

Introduction.

Investigations in the family Loranthaceae had been planned as an account of chromosome numbers of the Australian species, and observations on chromosome evolution. In the course of collecting material, however, new forms were recognized, and it became apparent that the taxonomic positions of other forms are doubtful. The situation is further confused by the common use of two different taxonomic treatments of the family, viz., those of Danser (1929, 1933) and Engler and Krause (1935). Studies in the family have therefore been extended to include a taxonomic revision and in this preliminary account the proposed nomenclature of the Australian taxa is set out together with the additions which have so far been found necessary. The synonymy is restricted to the names used in the major accounts of the Australian forms, namely, those of Bentham (1866), Van Tieghem (1895), Blakely (1922–28) and Danser (1929, 1933), and names published subsequently. Names of infraspecific taxa have not been included because intensive studies of intraspecific variation are necessary.

The author is indebted to the directors of the following herbaria for kindly making their material available: Queensland Herbarium, Brisbane; National Herbarium of New South Wales, Sydney; National Herbarium of Victoria, Melbourne; State Herbarium of South Australia, Adelaide; Herbarium of the Waite Institute, Adelaide; State Herbarium of Western Australia, Perth; Herbarium of the Northern Territory, Alice Springs. Mr. L. A. S. Johnson, National Herbarium of New South Wales, has independently reached generally similar taxonomic conclusions to those set out below, especially in regard to the delimitation of *Diplatia* and *Benthamina*, and specific limits in *Dendrophthoe*, and is thanked for his ready co-operation and helpful advice. Sincere thanks are also due to Dr. S. T. Blake, Queensland Herbarium, for his advice on taxonomic procedure and presentation.

Key Showing the Classification of the Australian Genera.

1. Flowers usually above 1 cm. long, with a distinct calyx, hermaphrodite.

Subfam. Loranthoideae.

2. Fruit dry, winged. Terrestrial, root-parasitic tree. Pollen trilobate.

Tribe Nuytsieae ..... 1. *Nuytsia.*

2.* Fruit fleshy.

Tribe Loranthinae.

3. Terrestrial, root-parasitic shrub. Pollen spherical.

Subtr. GAIADENDRINAE ..... 2. *Atkinsonia.*

3.* Shrubs parasitic on the aerial part of the host. Pollen trilobate.

4. Ovary with a well-developed, lobed mamelon, often fused to the ovary wall between the lobes, so that the ovary is 2- or more celled.

Subtr. ELYTRANTHINAE.

5. Inflorescence a raceme of triads ..... 3. *Amylotheca.*

5.* Flowers single, or in simple, usually 2-flowered umbels ..... 4. *Lysiana.*

4.* Mamelon simple or absent, never fused to the ovary wall, so that the ovary is always 1-celled.

Subtr. LORANTHINAE.

6. Anthers dorsifixed, versatile ..... 5. *Muellerina.*

6.* Anthers basifixed.

7. Petals united.

8. Inflorescence a simple raceme, sometimes only 2-flowered. Corolla nearly regular .... 6. *Dendrophthoe.*

8.* Inflorescence a simple umbel. Corolla deeply split on one side.

9. Corolla thin, lobes and anthers reflexed to one side. Peduncle without a bract .... 7. *Benthamina.*

9.* Corolla thick, almost woody. Peduncle with a bract at the top .... 8. *Xylochlamys.*

7.* Petals free.

10. Inflorescence not subtended by large foliaceous bracts enclosing the flowers.

11. Inflorescence a simple umbel ..... 9. *Pilostigma.*

11.* Inflorescence an umbel of dyads, triads or tetrads, or by reduction a head or a single dyad ..... 10. *Amyema.*

10.* Inflorescence capitate on the radially flattened end of the peduncle, subtended by two enlarged foliaceous bracts enclosing the flowers and fused at the margins over them during development ..... 11. *Diplatia.*

1.* Flowers minute, unisexual. Calyx absent or obscure. Pollen spherical.

Subfam. VISCOIDEAE.

12. Placenta central. Anthers 2-celled.

Tribe PHORADENDREAE ..... 12. *Korthalsella.*

12.* Placenta basal. Anthers 4- or more celled.

Tribe VISCEAE.

13. Anthers not fused to the perianth ..... 13. *Notothixos.*

13.* Anthers fused to the perianth ..... 14. *Viscum.*

NOMENCLATURE OF THE AUSTRALIAN SPECIES.

1. NUYTSIA R.Br., *J. Geog. Soc.*, 1 (1831) 17; Benth., *Fl. Austral.*, 3 (1866) 387; Blakely, PROC. LINN. SOC. N.S.W., 47 (1922) 200; Dans., *Verh. Akad. Wet. Amst. afd. Natuurk.*, 29 (1933) 96.

Type: *N. floribunda* (Labill.) R.Br.

N. FLORIBUNDA (Labill.) R.Br., *l.c.*; Benth., *l.c.*; Blakely, *l.c.*; *Loranthus floribundus* Labill., *Nov. Holl. Pl.*, 1 (1805) 87.

2. ATKINSONIA F. Muell., *Fragm.*, 5 (1865) 34; Benth., *Fl. Austral.*, 3 (1866) 388; Dans., *Verh. Akad. Wet. Amst. afd. Natuurk.*, 29 (1933) 40. Included in *Gaiadendron* by Blakely, PROC. LINN. SOC. N.S.W., 47 (1922) 202.

Type: *A. ligustrina* (A. Cunn. ex Lindl.) F. Muell.

A. LIGUSTRINA (A. Cunn. ex Lindl.) F. Muell., *l.c.*; Benth., *l.c.*; Dans., *l.c.*; *Nuytsia ligustrina* A. Cunn. ex Lindl., *Bot. Reg.*, 25 (1839) Swan R. App. 39; *Gaiadendron ligustrinum* (A. Cunn. ex Lindl.) Engl., Blakely, *l.c.*

3. AMYLOTHECA Tiegh., *Bull. Soc. Bot. Fr.*, 41 (1894) 261; Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 300; *Treubella* Tiegh., *l.c.*, 265, 269; *Aciella* Tiegh., *l.c.*, 435; *Decaisnina* Tiegh., *l.c.*, 42 (1895) 434, 435. Included in *Loranthus* by Blakely, PROC. LINN. SOC. N.S.W., 47 (1922) 393; 50 (1925) 1.

Type: The genus is based on *A. dictyophleba* (F. Muell.) Tiegh. and a few Malaysian species.

A. BIANGULATA (W. V. Fitzger.) Dans., *l.c.*; *Loranthus biangulatus* W. V. Fitzger., *J. Roy. Soc. W.A.*, 3 (1918) 136; Blakely, *l.c.*, 49 (1924) 95.

A. BRITTENII (Blakely) Dans., *l.c.*; *Loranthus Britteni* Blakely, *l.c.*, 49 (1924) 92.

A. DICTYOPHLEBA (F. Muell.) Tiegh., *l.c.*, 41 (1894) 262; Dans., *l.c.*; *Loranthus dictyophlebus* F. Muell., *Rept Burdek. Exp.* (1860) 14; Benth., *Fl. Austral.*, 3 (1866) 391; Blakely, *l.c.*, 50 (1925) 11; *Aciella dictyophleba* Tiegh., *l.c.*, 42 (1895) 87; *Loranthus tenuifolius* F. M. Bail., *Bot. Bull. Dep. Ag. Qd*, 16 (1903) 1, non Tiegh.; *Loranthus Beauverdiana* F. M. Bail., *Qd Ag. J.*, 21 (1908) 294.

AMYLOTHECA PETIOLATA B. A. Barlow, sp. nov.—Frutex glaber. Folia opposita elliptica, penninervia, apice rotundata basi in petiolum teretem 0·5–1·5 cm. longum attenuata, 4–10 cm. longa 2–4 cm. lata. Inflorescentia axillares e racemo 4–6 parium triadum oppositorum decussatorum secundorum; axis tenuis apicem versus parum attenuatus, basi 1·5–2 mm. crassus, 0·5–4·5 cm. longus; pedunculi triadum tenuiores 2–4 mm. longi; flores omnes sessiles. Bracteae acutae vel obtusae 1–1·5 mm. longae. Calyx cylindricus 2–3 mm. longus; limbus 0·5–1 mm. longus truncatus. Corolla 6-mera 18–24 mm. longa petalis in tubum 1–3 mm. longum cohaerentibus. Anther parte libera filameti circa dupo longior. Fig. 1, *a-b*.

Typus: R. L. Specht 537 (BRI); Bickerton Island, Gulf of Carpentaria; 11 VI 1948.

A. SIGNATA (F. Muell. ex Benth.) Dans., *l.c.*, 11 (1931) 244; *Loranthus signatus* F. Muell. ex Benth., *Fl. Austral.*, 3 (1866) 392; Blakely, *l.c.*, 49 (1924) 93; *Loranthus amplexans* Tiegh., *l.c.*, 42 (1895) 83; Blakely, *l.c.*, 49 (1924) 94; *Treubella signata* and *T. amplexans* Tiegh., *l.c.*, 42 (1895) 87; *Decaisnina signata* and *D. amplexans* Tiegh., *l.c.*, 42 (1895) 436; *Amylotheca amplexans* Dans., *l.c.* Included in *Amylotheca triflora* by Dans., *l.c.*, 302.

A. VERSTEEGII (Lauterb.) Dans., *l.c.*, 303; *Loranthus Versteegii* Lauterb., *Nov. Guin.*, 8, 1 (1910) 289.

4. LYSIANA Tiegh., *Bull. Soc. Bot. Fr.*, 41 (1894) 599; Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 342. Included in *Loranthus* by Blakely, PROC. LINN. SOC. N.S.W., 50 (1925) 1.

Type: The genus is based on the four Australian species.

L. CASUARINAE (Miq.) Tiegh., *l.c.*, 601; Dans., *l.c.*; *Loranthus Casuarinae* Miq. in Lehm., *Pl. Preiss.*, 1 (1844) 279; Blakely, *l.c.*, 5. Included in *Loranthus linophyllus* by Benth., *Fl. Austral.*, 3 (1866) 393.

L. EXOCARPI (Behr) Tiegh., *l.c.*, 603; Dans., *l.c.*; *Loranthus Exocarpi* Behr, *Linnaea*, 20 (1847) 624; Benth., *Fl. Austral.*, 3 (1866) 392; Blakely, *l.c.*, 6; *Loranthus angustifolius* R.Br. ex Benth., *Fl. Austral.*, 3 (1866) 390; *Dendrophthoe angustifolia* Tiegh., *l.c.*, 42 (1895) 85; *Loranthus vittatus* Tiegh., *l.c.*, 42 (1895) 83; *Lysiana vittata* Tiegh., *l.c.*, 42 (1895) 83; Dans., *l.c.*; *Loranthus diamantinensis* J. M. Black, *Trans. Roy. Soc. S. Aust.*, 69 (1945) 309.

L. LINEARIFOLIA Tiegh., *l.c.*, 603; Dans., *l.c.*; *Loranthus linearifolius* Hook. in Mitch., *J. Exp. Trop. Austral.*, (1848) 102, non Bert.; Benth., *Fl. Austral.*, 3 (1866) 391; *Loranthus Mitchellianus* Blakely, *l.c.*, 4.

L. MURRAYI (Tate) Tiegh., *l.c.*, 603; Dans., *l.c.*; *Loranthus Murrayi* Tate, *Trans. Roy. Soc. S. Aust.*, 6 (1883) 109; Blakely, *l.c.*, 2.

5. MUELLERINA Tiegh., *Bull. Soc. Bot. Fr.*, 42 (1895) 25; *Furcilla* Tiegh., *l.c.*, 85. Included in *Phrygilanthus* by Blakely, PROC. LINN. SOC. N.S.W., 47 (1922) 206; Dans., *Bull. Jard Bot. Buit.*, 10 (1929) 348.

Type: *Muellerina raoulii* Tiegh. (New Zealand).

MUELLERINA BIDWILLII (Benth.) B. A. Barlow, comb. nov.—*Loranthus Bidwillii* Benth., *Fl. Austral.*, 3 (1866) 390; *Furcilla Bidwillii* Tiegh., *l.c.*, 85; *Phrygilanthus Bidwillii* (Benth.) Eichl., Blakely, *l.c.*, 220; Dans., *l.c*

Text-fig. 1.—*a*, *b*, *Amylotheca petiolata*—*a*, portion of plant, × ¾; *b*, inflorescence, × 1¾. *c-e*, *Diplatia furcata*—*c*, portion of plant, × ¾; *d*, tangential sectional view of old inflorescence, nat. size; *e*, radial sectional view of inflorescence, nat. size. *f-h*, *Viscum pedunculatum*—*f*, portion of plant, × ¾; *g*, group of inflorescences, × 3; *h*, a single inflorescence, × 6.

M. CELASTROIDES (Sieb. ex Roem. & Schult.) Tiegh., *l.c.*, 85; *Loranthus celastroides* Sieb. ex Roem. & Schult., *Syst. Veg.*, 7 (1829) 163; Benth., *Fl. Austral.*, 3 (1866) 389; *Phrygilanthus celastroides* (Sieb. ex Roem. & Schult.) Eichl., Blakely, *l.c.*, 215; Dans., *l.c.*

MUELLERINA EUCALYPTOIDES (DC.) B. A. Barlow, comb. nov.—*Loranthus eucalyptifolius* Sieb. ex Roem. & Schult., *Syst. Veg.*, 7 (1829) 163, non H.B.K.; *Loranthus eucalyptoides* DC., *Prod.*, 4 (1830) 318; *Muellerina eucalyptifolia* Tiegh., *l.c.*, 85; *Phrygilanthus eucalyptifolius* (Sieb. ex Roem. & Schult.) Eichl., Blakely, *l.c.*, 208; *Phrygilanthus eucalyptoides* Dans., *l.c.* Included in *Loranthus celastroides* by Benth., *Fl. Austral.*, 3 (1866) 389.

MUELLERINA MYRTIFOLIA (Benth.) B. A. Barlow, comb. nov.—*Loranthus myrtifolius* Benth., *Fl. Austral.*, 3 (1866) 390; *Furcilla myrtifolia* Tiegh., *l.c.*, 87; *Phrygilanthus myrtifolius* (Benth.) Eichl., Blakely, *l.c.*, 219; Dans., *l.c.*

6. DENDROPHTHOE Mart., *Flora*, 1 (1830) 109; Tiegh., *Bull. Soc. Bot. Fr.*, 42 (1895) 87; Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 307. Included in *Loranthus* by Benth., *Fl. Austral.*, 3 (1866) 388; Blakely, PROC. LINN. SOC. N.S.W., 50 (1925) 1.

Type: Not indicated.

D. ACACIOIDES (Benth.) Tiegh., *l.c.*; *Loranthus acacioides* Benth., *l.c.*, 392; Blakely, *l.c.*, 13; *Amyema acacioides* Dans., *l.c.*, 293.

DENDROPHTHOE DISCOLOR B. A. Barlow, stat. et nom. nov.—*Loranthus odontocalyx* F. Muell. ex Benth. var. *propria* Blakely, *Proc. Roy. Soc. Qd*, 34 (1922) 28; *l.c.*, 21. Caules laeves, juventute lenticellis rotundis conspicuis praediti. Folia glabra, alterna vel dissita, tenuia, dorsiventralia facie superiore intensius viridia nitida, late lanceolata vel ovata, acuta, 5–12 cm. longa, 2–6 cm. lata, petiolo distincto 1–2 cm. longo praedita, penninervia nervis lateralibus patentibus cum costa angulum 45° facientes. Inflorescentia axillaris racemiformis 5–8 flora; pedicelli 1–4 mm. longi. Bractea acuta vel obtusa, circiter 1·5 mm. longa. Calyx albotomentosa limbo truncata vel aeque 5-loba 5-dentatave, 1–1·5 mm. longa. Corolla 30–50 mm. longa, extus pro more parum tomentosa intus glabra, in lobos 5 angustos subaequales fissa, tubo curvulo mediam corollam superante. Anthera filamenti parte libera admodum brevior. Fructus lageniformis, 10–15 mm. longus.

DENDROPHTHOE GLABRESCENS (Blakely) B. A. Barlow, stat. et comb. nov.—*Loranthus vitellinus* F. Muell. var. *glabrescens* Blakely, PROC. LINN. SOC. N.S.W., 50 (1925) 19. Frutex glabra. Folia alterna vel dissita, crassa, concolora, saepe glauca, lanceolata usque elliptica, 3–20 cm. longa, 1–5 cm. lata, petiolum 0·3–1·5 cm. longum attenuata, penninervia nervis lateralibus a costa acute divergentibus. Inflorescentia axillaris racemiformis 5–20 flora; pedicelli 3–5 mm. longi. Bractea pro more in pedicellum decurrens, acuta, 2 mm. longa. Calycis limbus truncatus vel obscure 5-dentatus, 1–3 mm. longus. Corolla 20–50 mm. longa in lobos 5 angustos parum inaequales fissa; tubus curvulus mediam corollam superans. Anthera filamenti parte libera paullo brevior. Fructus lageniformis, 10–15 mm. longus.

D. HOMOPLASTICA (Blakely) Dans., *l.c.*, 309; *Loranthus homoplasticus* Blakely, *l.c.*, 13.

D. ODONTOCALYX (F. Muell. ex Benth.) Tiegh., *l.c.*; *Loranthus odontocalyx* F. Muell. ex Benth., *l.c.*, 391; Blakely, *l.c.*, 19. Included in *Dendrophthoe curvata* by Dans., *l.c.*, 308. Included in *Dendrophthoe falcata* by Dans., *l.c.*, 11 (1931) 403.

D. VITELLINA (F. Muell.) Tiegh., *l.c.*; *Loranthus vitellinus* F. Muell., *Rep. Burdek. Exp.* (1860) 12; Blakely, *l.c.*, 15. Included in *Loranthus longiflorus* by Benth., *l.c.*, 391. Included in *Dendrophthoe curvata* by Dans., *l.c.*, 308. Included in *Dendrophthoe falcata* by Dans., *l.c.*, 11 (1931) 403.

7. BENTHAMINA Tiegh., *Bull. Soc. Bot. Fr.*, 42 (1895) 85. Included in *Loranthus* by Blakely, PROC. LINN. SOC. N.S.W., 50 (1925) 2. Included in *Amyema* by Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 304.

Type: *B. alyxifolia* (F. Muell. ex Benth.) Tiegh.

B. ALYXIFOLIA (F. Muell. ex Benth.) Tiegh., *l.c.*; *Loranthus alyxifolius* F. Muell. ex Benth., *Fl. Austral.*, 3 (1866) 391; Blakely, *l.c.*, 21; *Amyema alyxifolia* Dans., *l.c.*

8. XYLOCHLAMYS Domin, *Bibl. Bot.*, 89 (1921) 56. Included in *Amyema* by Dans., *Verh. Akad. Wet. Amst. afd. Natuurk.*, 29 (1933) 35.

Type: *X. queenslandica* Domin.

X. QUEENSLANDICA Domin, *l.c.*; *Amyema Xylochlamys* Dans., *l.c.*

9. PILOSTIGMA Tiegh., *Bull. Soc. Bot. Fr.*, 41 (1894) 483, non Constantin in Lecomte, *Fl. Gen. Indo-Chine*, 4 (1912) 73. Included in *Loranthus* by Blakely, PROC. LINN. SOC. N.S.W., 47 (1922) 391. Included in *Amyema* by Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 291.

Type: *P. sanguineum* (F. Muell.) Tiegh.

P. SANGUINEUM (F. Muell.) Tiegh., *l.c.*, 489; *Loranthus sanguineus* F. Muell., *Fragm.*, 1 (1859) 177; Benth., *Fl. Austral.*, 3 (1866) 393; Blakely, *l.c.*, 398; *Loranthus Mulleri* and *L. brevipes* Tiegh., *l.c.*, 42 (1895) 83; *Pilostigma Mulleri* and *P. brevipes* Tiegh., *l.c.*, 42 (1895) 84; *Loranthus spathulatus* Schwarz, *Fedde Repert.*, 24 (1928) 80; *Amyema sanguinea*, *A. Muelleri* and *A. brevipes* Dans., *l.c.*, 294, 297, 298; *Amyema spathulata* Dans., *Verh. Akad. Wet. Amst. afd. Natuurk.*, 29 (1933) 34.

PILOSTIGMA WHITEI (Blakely) B. A. Barlow, comb. nov.—*Loranthus Whitei* Blakely, PROC. LINN. SOC. N.S.W., 47 (1922) 400; *Amyema Whitei* Dans., *l.c.*, 299.

10. AMYEMA Tiegh., *Bull. Soc. Bot. Fr.*, 41 (1894) 499; Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 293. Included in *Loranthus* by Blakely, PROC. LINN. SOC. N.S.W., 47 (1922) 391.

Type: The genus is based on a number of Australian species and two from Malaysia.

A. BENTHAMII (Blakely) Dans., *l.c.*, 294; *Loranthus Benthami* Blakely, *l.c.*, 49 (1924) 86; *Loranthus haematodes* Schwarz, *Fedde Repert.*, 24 (1928) 80; *Amyema haematodes* Dans., *Verh. Akad. Wet. Amst. afd. Natuurk.*, 29 (1933) 29.

A. BIFURCATUM (Benth.) Tiegh., *l.c.*, 507; Dans., *l.c.*, 294; *Loranthus bifurcatus* Benth., *Fl. Austral.*, 3 (1866) 393; Blakely, *l.c.*, 395.

A. CAMBAGEI (Blakely) Dans., *l.c.*, 294; *Loranthus Cambagei* Blakely, *l.c.*, 48 (1923) 143.

A. CONGENER (Sieb. ex Schult & f.) Tiegh., *l.c.*, 507; Dans., *l.c.*, 294; *Loranthus congener* Sieb. ex Schult & f., *Syst.*, 7, 1 (1829) 114; Blakely, *l.c.*, 409. Included in *Loranthus pendulus* by Benth., *Fl. Austral.*, 3 (1866) 394.

A. CONSPICUUM (F. M. Bail.) Dans., *l.c.*, 294; *Loranthus conspicuus* F. M. Bail., *Qd Agr. J.*, 26 (1911) 198; Blakely, *l.c.*, 48 (1923) 147; *Loranthus glaber* and *L. Quandang* var. *villiflorus* Domin, *Bibl. Bot.*, 89 (1921) 55; *Loranthus Betchei* Blakely, *l.c.*, 48 (1923) 148; *Amyema Betchei* and *A. glabra* Dans., *l.c.*, 294, 295.

A. FERRUGINIFLORUM (W. V. Fitzger.) Dans., *l.c.*, 295; *Loranthus ferruginiflorus* W. V. Fitzger., *J. Roy. Soc. W.A.*, 3 (1918) 136; Blakely, *l.c.*, 397.

A. FITZGERALDII (Blakely) Dans., *l.c.*, 295; *Loranthus Fitzgeraldii* Blakely, *l.c.*, 49 (1924) 86.

A. GAUDICHAUDII (DC.) Tiegh., *l.c.*, 42 (1895) 84; Dans., *l.c.*, 295; *Loranthus Gaudichaudii* DC., *Prod.*, 4 (1830) 295; Blakely, *l.c.*, 48 (1923) 138.

A. GIBBERULUM (Tate) Dans., *l.c.*, 295; *Loranthus gibberulus* Tate, *Trans. Roy. Soc. S. Aust.*, 8 (1886) 71; Blakely, *l.c.*, 394; *Loranthus gibberulosus* Tiegh., *l.c.*, 42 (1895) 82; *Amyema gibberulosa* Tiegh., *l.c.*, 42 (1895) 84.

A. HILLIANUM (Blakely) Dans., *l.c.*, 296; *Loranthus Hilliana* Blakely, *l.c.*, 49 (1924) 80.

A. LINOPHYLLUM (Fenzl) Tiegh., *l.c.*, 507; Dans., *l.c.*, 296; *Loranthus linophyllus* Fenzl, *Enum. Pl. Hueg.* (1837) 65; Benth., *Fl. Austral.*, 3 (1866) 393; Blakely, *l.c.*, 48 (1923) 145.

A. LUCASII (Blakely) Dans., *l.c.*, 296; *Loranthus lucasi* Blakely, *l.c.*, 49 (1924) 80.

A. MACKAYENSE (Blakely) Dans., *l.c.*, 297; *Loranthus Mackayensis* and *L. Cycneus-Sinus* Blakely, *l.c.*, 48 (1923) 131; *Amyema Cycnei-Sinus* Dans., *l.c.*, 295.

AMYEMA MAIDENII (Blakely) B. A. Barlow, comb. nov.—*Loranthus Maideni* Blakely, PROC. LINN. SOC. N.S.W., 49 (1924) 86; *Diplatia Maideni* Dans., *l.c.*, 312.

A. MELALEUCAE (Miq.) Tiegh., *l.c.*, 42 (1895) 84; *Loranthus Melaleucae* Miq. in Lehm., *Pl. Preiss.*, 1 (1844) 281; *Loranthus Leschenaulti* Tiegh., *l.c.*, 42 (1895) 83; *Amyema Leschenaulti* Tiegh., *l.c.*, 42 (1895) 84. Included in *Loranthus miraculosus* by Blakely, *l.c.*, 48 (1923) 132.

A. MIQUELII (Lehm. ex Miq.) Tiegh., *l.c.*, 507; Dans., *l.c.*, 297; *Loranthus Miquelii* Lehm. ex Miq. in Lehm., *Pl. Preiss.*, 1 (1844) 280; Blakely, *l.c.*, 401; *Amyema aurantiaca* Tiegh., *l.c.*, 507. Included in *Loranthus pendulus* by Benth., *Fl. Austral.*, 3 (1866) 394.

A. MIRACULOSUM (Miq.) Tiegh., *l.c.*, 42 (1895) 84; Dans., *l.c.*, 297; *Loranthus miraculosus* Miq. in Lehm., *Pl. Preiss.*, 1 (1844) 281; Blakely, *l.c.*, 48 (1923) 132; *Loranthus bifurcatus* var. *Queenslandicus* Domin, *Bibl. Bot.*, 89 (1921) 55; *Amyema apiculata* Dans., *Candollea*, 7 (1937) 242. Included in *Loranthus pendulus* by Benth., *Fl. Austral.*, 3 (1866) 394.

A. NESTOR (S. Moore) Dans., *l.c.*, 297; *Loranthus Nestor* S. Moore, *J. Bot.*, 35 (1897) 170; Blakely, *l.c.*, 49 (1924) 79.

A. OBLIQUUM (Blakely) Dans., *l.c.*, 297; *Loranthus obliqua* Blakely, *l.c.*, 48 (1923) 150.

A. PENDULUM (Sieb. ex Spreng.) Tiegh., *l.c.*, 507; Dans., *l.c.*, 298; *Loranthus pendulus* Sieb. ex Spreng., *Cur. Post.* (1827) 139; Benth., *Fl. Austral.*, 3 (1866) 394; Blakely, *l.c.*, 407; *Amyema longifolia* Tiegh., *l.c.*, 42 (1895) 84.

A. PREISSII (Miq.) Tiegh., *l.c.*, 42 (1895) 84; Dans., *l.c.*, 298; *Loranthus Preissii* Miq. in Lehm., *Pl. Preiss.*, 1 (1844) 280; Blakely, *l.c.*, 48 (1923) 140. Included in *Loranthus linophyllus* by Benth., *Fl. Austral.*, 3 (1866) 393.

A. QUANDANG (Lindl.) Tiegh., *l.c.*, 507; Dans., *l.c.*, 298; *Loranthus Quandang* Lindl. in Mitch., *Three Exp.*, 2 (1838) 69; Benth., *Fl. Austral.*, 3 (1866) 395; Blakely, *l.c.*, 49 (1924) 82; *Loranthus pruinosus* Tiegh., *l.c.*, 42 (1895) 83; *Amyema cana*, *A. nutans* and *A. pruinosa* Tiegh., *l.c.*, 42 (1895) 84.

A. QUEENSLANDICUM (Blakely) Dans., *l.c.*, 298; *Loranthus Queenslandicus* Blakely, *l.c.*, 48 (1923) 130.

AMYEMA THALASSIUM B. A. Barlow, nom. nov.—*Loranthus maritimus* C. A. Gardn., *For. Dep. Bull.* (*W.A.*), 32 (1923) 46, non Merrill (1914) qui est *Amyema maritima* Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 297. (The epithet *thalassium* is from the Greek word meaning "maritime".)

11. DIPLATIA Tiegh., *Bull. Soc. Bot. Fr.*, 41 (1894) 501; Dans., *Bull. Jard. Bot. Buit.*, 10 (1929) 312. Includued in *Loranthus* by Blakely, PROC. LINN. SOC. N.S.W., 49 (1924) 90.

Type: *D. grandibractea* (F. Muell.) Tiegh.

DIPLATIA FURCATA B. A. Barlow, sp. nov.—Glabra. Folia opposita; petiolus brevis vel obscurus, teres; lamina oblanceolata, crassiuscula, in petiolum attenuata, 4–7 cm. longa, 0·4–1·2 cm. lata. Inflorescentia axillaris; pedunculus 10–25 mm. longus, apice 2–4 mm. latus; radii 2, 1·5–2 mm. longi, ad bracteas coalita; flores sessiles, in triadibus dispositi, flos medianus paulo plus elevatus. Bracteae medianae oblongo-ovatae, 14–19 mm. longae, 8–12 mm. latae, secundum radium et pedunculum decurrentes; bracteae laterales angustato-lanceolatae, acutae, deciduae, circa tertiam ovarii adaequantes. Corolla in alabastro 18–22 mm. longa, postea in petala 5 dehiscens. Fig. 1, *c-e*. Typus: L. S. Smith 624 (BRI); Dallarnil, Burnett Dist., Queensland; 28 XII 1939.

D. GRANDIBRACTEA (F. Muell.) Tiegh., *l.c.*; Dans., *l.c.*; *Loranthus grandibracteus* F. Muell., *Rep. Burdek. Exp.* (1860) 14; Benth., *Fl. Austral.*, 3 (1866) 395; Blakely, *l.c.*;

Loranthus tenuifolius Tiegh., *l.c.*, 42 (1895) 83, non F. M. Bail. (1903); *Diplatia tenuifolia* Tiegh., *l.c.*, 502.

12. KORTHALSELLA Tiegh., *Bull. Soc. Bot. Fr.*, 43 (1896) 83, 163; Blakely, PROC. LINN. SOC. N.S.W., 53 (1928) 31; Dans., *Bull. Jard. Bot. Buit.*, 14 (1937) 119; 16 (1940) 329; *Bifaria* Tiegh., *l.c.*, 163.

Type: *K. remyana* Tiegh. (Hawaii).

K. BREVIARTICULATA (Tiegh.) Dans., *l.c.*, 16 (1940) 339; *Bifaria breviarticulata* Tiegh., *l.c.*, 173; *Korthalsella australis* Blakely, *l.c.*, 32; Dans., *l.c.*, 14 (1937) 153. Included in *Viscum articulatum* by Benth., *Fl. Austral.*, 3 (1866) 396.

K. OPUNTIA (Thunb.) Merr., *Bot. Mag. Tokyo*, 30 (1916) 68; Dans., *l.c.*, 14 (1937) 133; *Viscum opuntia* Thunb., *Fl. jap.* (1784) 64; *Bifaria howensis* Tiegh., *l.c.*, 171; *Korthalsella articulata* and *K. howensis* Blakely, *l.c.*, 33, 35. Included in *Viscum articulatum* by Benth., *Fl. Austral.*, 3 (1866) 396.

13. NOTOTHIXOS Oliv., *J. Linn. Soc.*, 7 (1864) 103; Benth., *Fl. Austral.*, 3 (1866) 396; Blakely, PROC. LINN. SOC. N.S.W., 53 (1928) 38; Dans., *Bull. Jard. Bot. Buit.*, 11 (1931) 456.

Type: The genus is based on three Australian species and *N. floccosus* Oliv. (Ceylon).

N. CORNIFOLIUS Oliv., *l.c.*; Benth., *l.c.*, 397; Blakely, *l.c.*, 40.

N. INCANUS Oliv., *l.c.*; Benth., *l.c.*, 397; Blakely, *l.c.*, 42.

N. LEIOPHYLLUS K. Schum. in Schum. & Lauterb., *Nachtr.* (1905) 260; Blakely, *l.c.*, 41; Dans., *l.c.*

N. SUBAUREUS Oliv., *l.c.*; Benth., *l.c.*, 397; Blakely, *l.c.*, 41.

14. VISCUM L. *Sp. pl.* (1753) 1023; Benth., *Fl. Austral.*, 3 (1866) 395; Blakely, PROC. LINN. SOC. N.S.W., 53 (1928) 44; Dans., *Bull. Jard. Bot. Buit.*, 11 (1931) 459; *Aspidixia* Tiegh., *Bull. Soc. Bot. Fr.*, 43 (1896) 191.

Type: *V. album* L. (Europe and Asia).

V. ARTICULATUM Burm. f., *Fl. ind.* (1768) 211; Dans., *l.c.*, 460; *Viscum angulatum* Heyne ex DC. *Prod.*, 4 (1830) 283; Benth., *l.c.*, 396; Blakely, *l.c.*, 47; *Aspidixia articulata* and *A. angulata* Teigh., *l.c.*, 193.

V. BANCROFTII Blakely, *l.c.*, 46.

VISCUM PEDUNCULATUM B. A. Barlow, sp. nov.—Frutex erectus ramosissimus glaber. Folia oblonga usque elliptica, acuta, in petiolum 4–8 mm. longum attenuata, 3–nervia, 3–7 cm. longa, 1–2 cm. lata. Inflorescentiae 1–3 in axillis foliorum vivorum vel delapsorum ortae, mediana primo oriens; pedunculus 5–8 mm. longus apice par cymbiforme bractearum 2–3 mm. longum gerens. Flores 3; laterales masculae sessiles, compressi, 1·5 mm. longi, tepalis 4 triangularibus praeditae; medianus femineus, 3–4 mm. longus, tepalis 3–4 triangularibus, in pedicello 1 mm. longo sub anthesi sub fructu 2–3 mm. longo insidens; stylus parvus papilliformis. Fructus ellipsoideus usque fere globosus, truncatus, verrucosus, 6–7 mm. longus. Fig. 1, *f-h*. Typus: B. A. Barlow 128 (BRI); Ellis Beach, near Cairns, Cook District, Queensland; 12 VIII 1960.

V. WHITEI Blakely, *l.c.*, 45. Included in *Viscum orientale* by Benth., *l.c.*, 396.

DISCUSSION.

(*a*) *Systems of classification.*

Of the two subfamilies, Loranthoideae and Viscoideae, the latter has had a fairly stable taxonomic history, but the systems of classification have differed in the treatments of the former. Prior to the work of Van Tieghem (1894, 1895) most of the Old World Loranthoideae were placed in *Loranthus*, with a few distinct groups segregated as other genera (cf. Engler, 1889). Van Tieghem recognized a large number of small genera, of which several were Australian, mainly on the basis of

differences in the structure of the inflorescence. His critical observations obviously influenced Engler, who adopted Van Tieghem's system in a revised treatment of the family (Engler, 1897), but treated most of his genera as sections or subsections, so that a very large genus *Loranthus*, and other broad groups such as *Elytranthe* and *Phrygilanthus*, were retained. In his valuable revision of Australian Loranthaceae, Blakely (1922, 1923, 1924, 1925, 1928) followed Engler, and even went so far as to refer Australian species of *Elytranthe* back to *Loranthus*, so that he only accepted four Australian genera of Loranthoideae, viz., *Nuytsia*, *Gaiadendron*, *Phrygilanthus* and *Loranthus*.

Danser (1929, 1933), in a critical revision of Old World Loranthoideae, recognized a number of Van Tieghem's genera. However, his concept of generic limits was much broader than Van Tieghem's extremely narrow one, and his system has been accepted by many workers in Asia, Malaysia and Australia. Nevertheless, in Australia and New Zealand, there is still wide use of Engler's system, probably due to the influence of the works of Blakely (1922–28), Cheeseman (1925) and Engler and Krause (1935). Danser's treatment is considered the most satisfactory since it distinguishes a number of clearly natural groups, which are sharply delimited in inflorescence and flower structure, and are therefore properly given generic rank. It is to some extent supported by cytological studies (unpublished data).

In adopting Danser's treatment of the Australian species, however, some modifications are considered necessary. A number of species have been removed from the genera in which Danser placed them, some being transferred to other genera, and others placed in separate small or monotypic genera. These changes are necessary partly because Danser worked largely from Blakely's descriptions and drawings, which were sometimes not adequate for a proper interpretation of inflorescence and floral characters, and he apparently misunderstood the structure of some forms. In addition, where forms were incompletely known, Danser accepted fairly broad genera, and stated that with further investigation these may be more properly treated by the recognition of several genera. The reasons for the acceptance of small or monotypic genera for some of the distinct Australian forms are presented below.

(*b*) *Notes on the genera accepted.*

(i) *Muellerina.* The genus *Muellerina* as understood here includes the seven Old World species formerly placed in *Phrygilanthus*, which was originally circumscribed to include all of the large-flowered, hermaphrodite species of subtribe Loranthinae with versatile anthers. *Phrygilanthus* as such was one of only two genera in the family occurring in both the Old and New Worlds, thus constituting a problem in the geography of the family. Both Eichler (1868) and Danser (1931) have expressed the view that the Old World species are quite distinct from the American ones. The only reason why they hesitated to recognize separate genera is that they "could not find differences of sufficient taxonomic value". It is suggested that the difficulty in distinguishing the Old and New World groups may be due in part to the New World species of *Phrygilanthus* themselves being an artificial group (cf. Rizzini, 1952). The hexamerous, small-flowered forms with compound inflorescences, such as *P. acutifolius*, are probably close to *Struthanthus* (cf. Abbiatti, 1946), which differs primarily in being dioecious by abortion, the male and female flowers still bearing sterile organs of the other type. The tetra- or pentamerous, large-flowered forms, mostly with simple inflorescences, such as *P. verticillatus*, appear to have affinities with *Psittacanthus* (cf. MacBride, 1935), which is distinguished by its non-endospermic seed. In this respect it is likely that this latter character has received too much emphasis in the system of classification.

When these New World groups of species are compared separately with the Old World species, generic differences of the type more usual for the family may be recognized. *Muellerina* is distinct from the *Phrygilanthus acutifolius* group in its larger, pentamerous flowers, and in its well spaced raceme of opposite triads or single

flowers, which, although racemose and often terminal, is determinate in nature. From the *P. verticillatus* group it differs in the elliptical anthers and the unequal filaments, and again in the well-spaced, determinate raceme. In addition, the two groups differ in cytological characters of a fairly large order for the subfamily (unpublished data).

Too much emphasis has been placed on the condition of versatile anthers in the former delimitation of *Phrygilanthus* (cf. Danser, 1931). The occurrence of versatile anthers in *Nuytsia* and the genera of subtribe Gaiadendrinae, which has South American and Australian representatives, suggests that this condition is a primitive and formerly widespread one in the family, and that basifixed anthers is a derived condition. *Muellerina* and *Phrygilanthus* are both fairly primitive groups, probably without particularly close relationship, which have been wrongly placed together primarily because of a primitive condition which they share.

Van Tieghem (1895) recognized nine genera in the *Phyrgilanthus* group, and included the Australian species in *Muellerina* and *Furcilla*. However, the inflorescence in the latter is a simple reduction of that of the former, and each commonly produces atypical inflorescences that are identical in structure. The name *Muellerina* has priority over *Furcilla* by a few weeks. The Old World species which are to be included in *Muellerina* are: *Muellerina novoguinensis* (Krause) B.A. Barlow, comb. nov. (*Phrygilanthus novoguinensis* Krause in Engl., *Bot. Jahrb.*, 57 (1922) 491); *Muellerina obtusifolia* (Merr.) B. A. Barlow, comb. nov. (*Phrygilanthus obtusifolius* Merr., *Phil. J. Sc.*, 1, suppl. (1906) 189); and *Muellerina raoulii* Tiegh., *Bull. Soc. Bot. Fr.*, 42 (1895) 25.

(ii) *Benthamina*. This genus is accepted for the species originally described as *Loranthus alyxifolius* F. Muell. ex Benth., and placed in *Amyema* by Danser. It is distinct from Australian species of *Amyema* in a number of characters. The corolla is sympetalous and zygomorphic. A long mamelon is developed in the ovarian chamber similar to that in *Helicanthes* (cf. Johri, Agrawal and Garg, 1957). The inflorescence is a simple, two-flowered umbel, while the basic pattern in *Amyema* is an umbel of triads. The plant spreads on the host branches by means of long runners, which are absent in the Australian species of *Amyema*, and the leaves have pennate venation, which in *Amyema* only occurs in *A. nestor*. These characters place *Benthamina* near the Asian and Malaysian genera *Taxillus* and *Helicanthes*.

(iii) *Xylochlamys*. The monotypic genus *Xylochlamys* Domin was at first left as a doubtful form by Danser (1929), but later assigned to *Amyema* (Danser, 1933). It is known only from the type collection, but it is clearly distinct from the Australian species of *Amyema* in its strongly sympetalous, hexamerous corolla, split to the base on one side. The inflorescence is a single dyad, and is only approached by that of *A. gibberula*. While *Xylochlamys* is apparently fairly close to *Amyema*, it is placed in subtribe Loranthinae tentatively, since its ovary structure is unknown.

(iv) *Pilostigma*. This genus was recognized by Van Tieghem for *Loranthus sanguineus* F. Muell., primarily on the character of the hat-shaped stigma. Danser (1929) pointed out that this character has little taxonomic significance, and placed the species in *Amyema*. However, it differs from this group in the simple inflorescence, the hexamerous flowers, the very thick petals, the well-developed, cone-shaped mamelon in the ovarian chamber and the attachment to the host by long runners. *Loranthus whitei* Blakely (1922) has similar characteristics, and is likewise placed in *Pilostigma*.

(v) *Diplatia*. The genus *Diplatia* was originally established by Van Tieghem (1894) for *Loranthus grandibracteus*, and later extended by Danser (1929) to include a second species, *L. maideni*, described subsequently. *L. grandibracteus* and *L. maideni* differ in the direction of flattening of the peduncle, and hence in the arrangement of the triads on the apex of the peduncle. They also differ considerably in the degree of enlargement of the central bracts of the triads. The two species thus show a parallel development in the reduction of the inflorescence from the *Amyema* type, and represent one of the extreme types of reduction which occur in the *Amyema* group (cf. Danser, 1929). However, their different inflorescence structures show that they have no direct

relationship, and if they are placed together in *Diplatia*, then the genus is clearly artificial. *L. maideni* must be placed in *Amyema*, where it has clear affinities with some species, particularly *A. hillianum*, and the genus *Diplatia* retained for the rather distinct type represented by *L. grandibracteus*. The diagnostic feature which distinguishes *Diplatia* from *Amyema* should thus be not the contraction of the inflorescence into a capitulum, but the enlargement of the central bracts into foliaceous structures, which exceed the developing flower buds, and are initially connate at the margins over them, and this is probably the sense in which Van Tieghem originally distinguished the genus.

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THE REPRODUCTION AND EARLY LIFE HISTORIES OF THE GASTROPODS *BEMBICIUM AURATUM* (QUOY AND GAIMARD) (FAM. LITTORINIDAE), *CELLANA TRAMOSERICA* (SOWER.) (FAM. PATELLIDAE) AND *MELANERITA MELANOTRAGUS* (SMITH) (FAM. NERITIDAE).

By D. T. Anderson, University of Sydney.

(Twenty-two Text-figures.)

[Read 29th March, 1962.]

Synopsis.

1. The description of the spawn of *B. auratum* given by H. Anderson (1958) is confirmed. Development within the jelly mass takes about 10 days, the larvae then hatching as pelagic planktotrophic veligers. It is suggested that in this species, correlation of invasion of the supra-littoral with retention of spawning in rock-pools explains the absence of modification of the early life history.

2. *C. tramoserica* contains ripe gametes in both sexes from August to November. Fertilization is external and development proceeds rapidly through pelagic lecithotrophic trochophore and veliger stages, with settling occurring after three days. This mode of development contrasts with those previously described for patellids, which record an extended period of planktotrophic veliger life.

3. Spawning in *M. melanotragus* begins in the late winter and continues until the late summer. Eggs are laid in hard dome-shaped capsules attached to rock surfaces or to molluscan shells and hatch after about 14 days as pelagic lecithotrophic veligers. Pelagic life is probably short. The early life history in *M. melanotragus* is similar to that of several species of *Nerita*.

Introduction.

Little attention has been paid to prosobranch reproduction and development along the New South Wales coast (Anderson, 1960). The present investigation of the reproduction and early life histories of *Bembicium auratum*, *Cellana tramoserica* and *Melanerita melanotragus* is part of a programme designed to meet this deficiency.

B. auratum is one of the commonest New South Wales estuarine and mangrove prosobranchs and its spawn is described by H. Anderson (1958). Further details of the development of the species are recorded in the present paper.

C. tramoserica, the common patellid limpet of the New South Wales coast, has not previously been investigated from the present point of view.

M. melanotragus, an equally conspicuous component of New South Wales rock platform associations, was accorded brief attention by Hedley (1916, 1923), who identified its egg capsule, but interpreted the structure of the capsule incorrectly and did not describe development. The present work corrects and extends Hedley's observations.

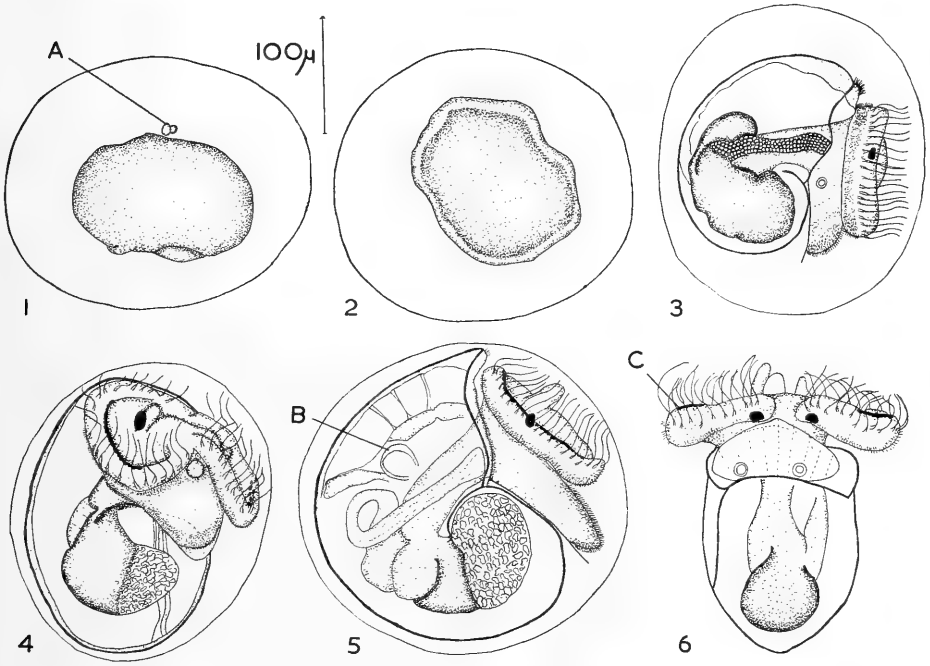
Spawning.

B. auratum.

At Folly Point, Middle Harbour, Sydney, egg masses of *B. auratum* were found during August to December, 1961, attached to the underside of stones in intertidal rock pools. They agreed with those described by H. Anderson (1958) in comprising closely packed series of small, transparent, bean-shaped jelly masses, each 2–2·5 mm. long, 1–1·5 mm. broad, containing 60–100 creamy white eggs about 120μ in diameter, surrounded by ovoid transparent envelopes averaging 265μ in length and 230μ in width. Similar masses spawned by females maintained in tanks of aerated sea water during August, 1961, confirmed Anderson's identification. Egg masses were cultured in aerated sea water and observed at frequent intervals, drawings of living embryos being made with the aid of a camera lucida.

C. tramoserica.

Natural spawning in *C. tramoserica* has not been observed. The mode of larval development indicates that eggs and sperm are shed freely into the water in the manner typical of patellids (Lebour, 1937). The early life history of the species was studied following artificial fertilization by the method of Smith (1935). Animals collected from the rock platform at Bradley's Head, on the north shore of Sydney Harbour, during July to November, 1961, were found to contain ripe gametes throughout this time. Eggs released into sea water are opaque, pale brown by reflected light and, after immersion for 30 minutes, spherical, 160μ in diameter and covered by a thin egg membrane and an irregular layer of whitish jelly (Text-fig. 7). Drawings of living embryos were made with the aid of a camera lucida.



Text-figs 1-6.—*Bembicium auratum*: 1. Gastrula, 28 hours, lateral view. 2. Early trochophore, 2 days, dorsal view. 3. Veliger, 5 days, lateral view. 4. Veliger, 6 days, ventro-lateral view. 5. Veliger, 9 days, lateral view. 6. Hatched veliger, 10½ days, ventral view. A, polar bodies; B, larval heart; C, velar pigment.

M. melanotragus.

Animals collected from Bradley's Head in the early part of June, 1961, showed ripe gametes in the males, but only small, unripe oocytes in the females. Further specimens collected on July 31, 1961, and kept in a laboratory tank deposited egg capsules on stones in the tank on August 11, 1961. At the same date, capsules began to appear in large numbers in the natural habitat, attached directly to the rock surface, especially to the under surfaces of stones in rock pools inhabited by the adults, and to the shells of other molluscs. Thereafter the capsules were common in this locality throughout the spring and early summer. Preliminary observations made in 1960 suggest that spawning continues until the autumn. The capsule (Text-figs 21, 22) is a brittle, white, flattened, elliptical dome about 2 mm. long and 1·4 mm. across, composed of several hundred spheres of varying diameter embedded as a single layer in an underlying matrix of the same material and attached by its rim to a transparent horny base plate fixed to

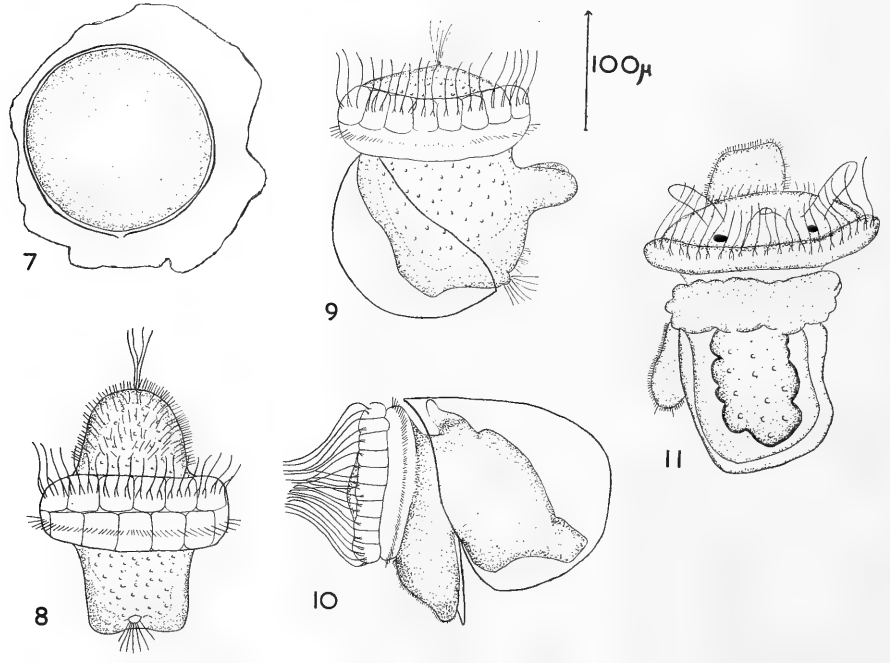
the substratum. It is filled with a soft colourless jelly in which float between 20 and 40 yellowish, yolky, translucent eggs 140μ in diameter (Text-fig. 12).

Both laboratory spawned and naturally spawned capsules were maintained in tanks of aerated sea water, successive capsules being opened at intervals to establish the developmental cycle of the contained eggs. Drawings of living embryos were made with the aid of a camera lucida.

Development.

B. auratum.

The egg develops into a flattened gastrula (placula) by the end of the first day (Text-fig. 1), a yolky trochophore with an inconspicuous prototroch of very short cilia by the end of the third (Text-fig. 2). On the fourth day, outgrowth of the foot and enlargement of the prototroch as a bilobed velum begin, a simple globular shell is secreted over the visceral mass and the young veliger begins to rotate slowly within



Text-figs 7-11.—*Cellana tramoserica*: 7. Fertilized egg. 8. Trochophore, 22 hr, dorsal view. 9. Early veliger, 48 hr, lateral view. 10. Veliger, 3 days, lateral view. 11. Settled larva, 6 days, dorsal view.

its envelope. As torsion is completed and development continues, a pair of black eyespots appears on the head, paired tentacles arise ventrolateral to the eyespots, the lateral margins of the enlarging velum become pigmented reddish-brown, the main ring of velar cilia becomes large and active and a band of fine cilia develops on the velar margin immediately behind them. At the same time, the foot becomes ciliated and develops a colourless operculum and paired otocysts, the shell enlarges, becomes brown-pigmented and slightly coiled, the yolky visceral mass develops as a coiled gut and the pulsations of a larval heart can be seen dorsal to the mauve-pigmented stomodaeum. Differentiation and enlargement of the veliger in this way (Text-figs 3–5) occupies the fifth to tenth days of development. The veliger then escapes from the jelly mass (Text-fig. 6) and swims to the water surface, its velar cilia beating rapidly in clockwise metachronal rhythm. Pelagic veligers have been maintained in laboratory tanks for four days with little apparent change, but not yet cultured beyond this stage.

C. tramoserica.

Once fertilized, the egg develops rapidly and in 22 hours a top-shaped yolky trochophore (Text-fig. 8), 210μ long and 160μ in equatorial diameter, emerges from the egg membrane and jelly. Its prototroch comprises a ring of large cells bearing long active cilia beating diagonally backwards in clockwise metachronal rhythm and a second ring of cells bearing a single band of short fine cilia. The episphere is covered by fine motionless cilia and carries a long apical tuft, held rigid during swimming but showing exploratory waving movements when the trochophore is at rest. The hyposphere is unciliated save for a fan of motionless cilia borne on a small postero-dorsal protuberance. The trochophore swims immediately to the water surface on hatching and maintains this position by alternating periods of prototrochal action (when it rises) and rest (when it sinks). It also makes occasional darting movements along a curved track.

As pelagic lecithotrophic life continues during the second day, the trochophore transforms rapidly into a veliger (Text-fig. 9). The episphere decreases in size, losing its general covering of cilia, while the hyposphere enlarges and secretes a simple cap-like shell. Mid-ventrally behind the mouth, a bilobed foot rudiment grows out.

During the third day (Text-fig. 10) the apical and postero-ventral tufts disappear. A small pair of dark eyespots forms on the now flattened episphere, the foot rudiment enlarges, loses its bilobed form, becomes finely ciliated and secretes a colourless operculum on its posterior face, the shell enlarges to a deep cup shape and becomes pearly and translucent in appearance and the visceral hump undergoes torsion. By the end of the third day torsion is complete and the veliger alternates periods of swimming with periods of settlement and exploratory muscular movements of the foot. Partial withdrawal of the head and velum into the small dorsal mantle cavity occasionally occurs and the operculum is lost from the foot.

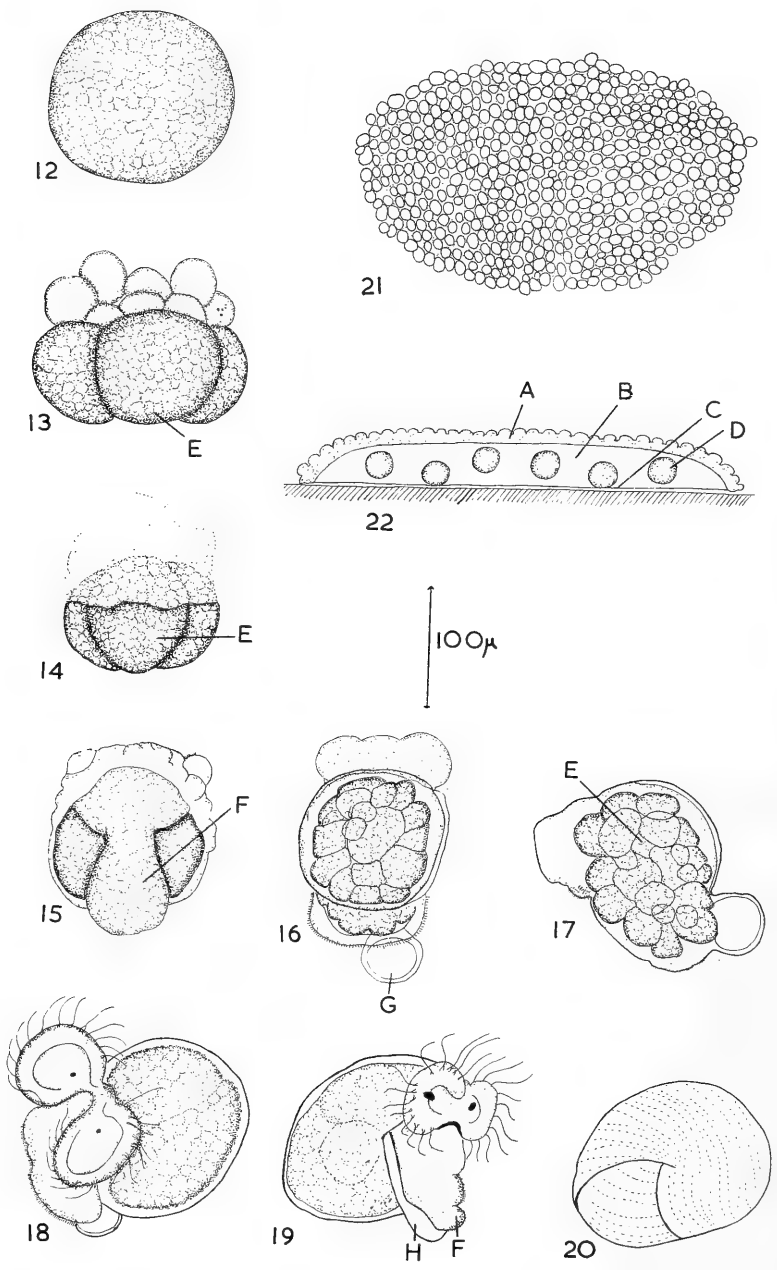
From the fourth day onwards, settlement appears to be permanent and metamorphosis gradually ensues. The lecithotrophic pelagic life of the species is thus very short, occupying only about 48 hours.

By the sixth day (Text-fig. 11) metamorphosis is well advanced. On the head, the eyespots enlarge, a pair of tentacles grows out ventro-lateral to them and a short, thick median protuberance with a small terminal papilla develops between the eyes. Although the velum itself shows a slight enlargement of two lateral lobes, the large cilia of its ventral half lose their motility and begin to regress. Those of the dorsal half remain spasmodically active, apparently playing a part, by driving a water current backwards over the animal, in maintaining stability and orientation of the large head and visceral mass on the narrow ciliated foot. The latter elongates antero-posteriorly, develops a flattened sole and a pair of long immotile cilia posteriorly and shows the typical muscular crawling action of a gastropod foot. The visceral mass continues to enlarge and shows two important changes from its condition in the pelagic veliger. The larval shell is shed soon after settling and a new shell with a slight spiral twist to the right secreted. At the antero-dorsal margin of this shell, a thickened mantle margin is formed, preparatory to secretion of the symmetrical adult shell.

M. melanotragus.

Early in spiral cleavage the yolk is confined to four large macromeres surmounted by a cap of colourless micromeres (Text-fig. 13). The macromeres later fill the interior of the highly modified trochophore (Text-fig. 14), which is completed about two days after oviposition. Little further subdivision of the macromeres takes place as the bilobed velum and the foot of the early veliger develop (Text-fig. 15) and the visceral mass is still very yolky when it becomes covered by the cap-like transparent shell (Text-figs 16, 17). The early veliger stage is attained in about five days.

The velar lobes remain small, but develop a ring of large active cilia, and the veliger, now with a globular shell (Text-fig. 18), begins to move slowly through the



Text-figs 12-22.—*Melanerita melanotragus*: 12. Egg. 13. Early stage in spiral cleavage. 14. Trochophore, 2 days. 15. Early veliger, 3 days, ventral view. 16. Veliger, 5 days, dorsal view. 17. Veliger, 5 days, lateral view. 18. Advanced veliger, 10 days, antero-lateral view. 19. Veliger about to hatch, 14 days, lateral view. 20. Shell of veliger about to hatch. 21. Egg capsule viewed from above, × 25. 22. Sectional view of capsule. A, dome of capsule; B, jelly; C, base plate; D, eggs; E, yolky macromeres; F, foot; G, refractile vesicle; H, operculum.

jelly of the capsule. A pair of small eyespots appears on the head and the foot elongates, secretes an operculum and becomes finely ciliated. A large, spherical, refractile vesicle which develops at the tip of the foot in the early veliger (Text-figs 16, 17) is still conspicuous at this stage but disappears before the veliger escapes from the capsule. Its function is unknown.

Further development of the veliger in the capsule (Text-fig. 19) proceeds by differentiation of the organs of the visceral mass, resorption of much of the yolk and increase in size of the colourless shell which becomes slightly coiled and marked by fine transverse striations (Text-fig. 20). A band of black pigment appears on the anterior face of the foot and the velar lobes gradually decrease in size. The velar cilia are still active, however, when about 14 days after oviposition the now greyish dome of the capsule is dislodged and the veligers escape into the water, becoming pelagic. How long they remain in the plankton before settling is unknown, but in view of the condition of the veliger at hatching (unused yolk reserves, regressing velum) an extended period of planktotrophic larval life seems unlikely.

Discussion.

B. auratum.

In a previous paper (Anderson, 1961), it was shown that the littorinids of the New South Wales ocean coast display a relationship between habitat and breeding similar to that of littorinid species in other parts of the world. In particular, several species combine upper littoral distribution with retention of a pelagic planktotrophic larva. The present work confirms H. Anderson's (1958) suggestion, on the basis of the form of the egg mass, that *B. auratum* similarly retains a pelagic planktotrophic veliger, in spite of an adult range extending into the supralittoral. This condition recalls that of the Atlantic mangrove species, *Littorina angulifera* (Lebour, 1945; Lenderking, 1954). The larva is similar to those of *B. nanum* (Anderson, 1961) and *Littorina littorea* (Thorson, 1946) and probably spends several weeks in the plankton before settling and metamorphosing. Absence of adaptation to resistance of desiccation in the early stages of *B. auratum* is clearly correlated with retention by the adults of the primitive habit of spawning in rock pools.

C. tramoserica.

The dimensions and form of the egg and trochophore in *C. tramoserica* are similar to those in *Patella vulgata* (Smith, 1935; Lebour, 1937; Crofts, 1955), *P. cerulea* (Patten, 1886) and *Helcion pellucidum* (= *Patina pellucida*, Lebour, 1937; Crofts, 1955). Completion of the free-swimming lecithotrophic trochophore within 24 hours of oviposition also appears to be characteristic for the family. It is notable, however, that in spite of these early similarities, the course of later development differs in *C. tramoserica* from that in other species. In *P. vulgata* the veliger becomes planktotrophic and spends several days in the plankton, developing eyes and tentacles, before settling occurs and the operculum, larval shell and velum are cast off (Smith, 1935; Crofts, 1955). The veliger of *Helcion pellucidum* also apparently becomes planktotrophic before settling (Lebour, 1937; Thorson, 1946). In *C. tramoserica*, planktonic life is much shorter (48 hours) and wholly lecithotrophic, the majority of differentiation taking place after settling.

M. melanotragus.

The little that is known of spawning in neritids indicates that the capsules of *M. melanotragus* are typical of marine species within the family. Similar capsules are produced by *Nerita albicilla*, *N. reticulata*, *N. versicolor*, *N. peloronta* and *N. tesselata* (Risbec, 1932; Andrews, 1935; Lebour, 1945). Andrews (1935) has shown that the origin of the material of the dome lies in the digestive gland and that the spheres incorporated in it are stored in a special sac at the lower end of the oviduct.

With the exception of the brackish and freshwater *Neritina fluviatilis*, whose early life history is well known (Bondensen, 1940; Thorson, 1946), earlier workers have found great difficulty in following the development of neritid eggs, which seem to be especially sensitive to culture conditions. The same difficulty was experienced in the present work, and although the hatching time of 14 days was established for capsules in the natural habitat, no instances were observed of hatching of veligers in laboratory tanks. It appears that wave action is necessary to dislodge the capsule dome and release the veligers into the water. Some marine neritids complete their development within the capsule and hatch at a fully metamorphosed crawling stage (*Nerita reticulata*, *Theodoxus meleagris* (Risbec, 1932; Andrews, 1935)), but *Nerita albicilla* and *N. tesselata* (Risbec, 1932; Lebour, 1945) appear to hatch as pelagic lecithotrophic veligers in the same manner as *M. melanotragus*.

The large size of the foot in the veliger of *M. melanotragus* and the development of a refractile vesicle at its tip are also recorded by Risbec (1932) for *Nerita albicilla* and *N. reticulata*, but the significance of both of these features is obscure.

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THE HOST PLANT RELATIONSHIP OF AN AUSTRALIAN SWALLOWTAIL, *PAPILIO AEGEUS*, AND ITS SIGNIFICANCE IN THE EVOLUTION OF HOST PLANT SELECTION.

By George O. Stride and R. Straatman, Division of Entomology, C.S.I.R.O. Tropical Pasture Research Station, Samford, Brisbane, Queensland.

(Communicated by Dr. D. F. Waterhouse.)

(Four Text-figures.)

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Synopsis.

The larvae of *Papilio aegeus*, an Australian papilionid butterfly naturally associated with the Rutaceae, can be reared in the laboratory on certain plants not belonging to this family. The larvae become conditioned in favour of the food plant on which they are reared even though this might be an abnormal one. Laboratory studies showed that female butterflies have a variable tendency to lay on abnormal host plants. It is suggested that evolution of new host plant relationships within the Papilionidae may have occurred through species, such as *P. aegeus*, which possess facultatively polyphagous larvae. Such species are capable of surviving and exploiting changes in female ovipositor habit and this ability may well lead to the development of new biological races.

Introduction.

On the basis of their larval food plants the Papilionidae may be divided into the following groups: (i) species associated with the family Aristolochiaceae; (ii) species associated with the Rutaceae; (iii) species associated with the Umbelliferae; (iv) species associated with a variety of other plants.

Using the results of his studies on the feeding behaviour of *Papilio ajax* as a basis, Dethier (1941, 1954) has advanced a theory to account for the occurrence of *Papilio* species on both Umbelliferae and Rutaceae. In nature *P. ajax* larvae normally feed on certain umbelliferous plants. In the laboratory they attack filter papers impregnated with certain of the characteristic chemical constituents of these plants, and also eat certain non-umbelliferous plants containing similar chemical constituents. In nature the larvae are also occasionally found on *Ruta* (Rutaceae), the attractive principle of this plant being methyl-nonyl-ketone, a substance chemically unrelated to the attractive substances of the Umbelliferae (Dethier, 1941).

Dethier suggests that the ancestors of the modern Umbelliferae-feeding *Papilio* were originally associated with *Citrus*-type plants, and that the larvae were stimulated to feed by the citral they contained, citral being a feeding stimulant for modern *Citrus*-feeding *Papilio*. *Citrus* belongs to the Rutaceae, and certain other members of this family, e.g., *Xanthoxylum*, contain both citral and methyl-nonyl-ketone (the attractive principle in *Ruta*). Dethier believes that certain *Papilio* species, originally associated with the *Xanthoxylum* type of plants by virtue of their contained citral, slowly became "conditioned" to the presence of methyl-nonyl-ketone. This resulted in the evolutionary development of a preferential association with those members of the Rutaceae in which methyl-nonyl-ketone was predominant, e.g., *Ruta*.

He envisages the evolution of the Umbelliferae-feeding habit as having occurred through intermediate plants such as *Dictamnus fraxinella*, a member of the Rutaceae which contains feeding stimulants for Papilionidae of the type found in the Rutaceae and of the type found in the Umbelliferae. By feeding on such plants the species became conditioned to the presence of Umbelliferae oils and later adopted the Umbelliferae as their primary host plants.

Dethier's use of the term "conditioning", as applied to a species, is vague. However, any change in host plant relationships must be associated with a change in the host plant selection of the ovipositing female, and there are two ways in which such changes might arise from conditioned behaviour. Firstly, it is possible that the selection of the ovipositing female could be influenced in favour of the plant it fed on as a larva As a general principle this idea was first suggested by Walsh (Craighead, 1923), and evidence suggests that it may be of significance in some insects (e.g., Craighead, 1921) but not in others (e.g., Larson, 1926). Secondly, it is possible that during adult life a female butterfly ovipositing on a plant containing substance A, which has an innate attraction for the butterfly, and substance B, which has no such attraction, might develop a conditioned ovipositional response towards B and eventually oviposit on plants containing this substance only.

The present work was part of an investigation into the general principles governing the evolution of host plant preferences in insects. At first it was intended to investigate experimentally the development of conditioned responses by larval and adult Papilionidae to new food plants, and thus obtain further information relevant to Dethier's theory. However, when it became evident that the evolution of host plant preferences within the Papilionidae may have arisen by a simple method of natural selection not involving the development of conditioned behaviour the investigation was closed. Although many of the results reported here are of only a preliminary nature, it is felt that they are important in that they suggest the possibility of a new approach to the problem of the evolution of the host plant relationships of the Papilionidae.

The investigation was primarily concerned with *Papilio aegeus* Don., a relatively large dark-coloured butterfly that occurs throughout eastern Australia and in New Guinea. The larvae have been recorded from a number of plant genera belonging to the Rutaceae and including *Citrus*, *Microcitrus*, *Evodia*, *Xanthoxylum*, *Flindersia*, *Choisya* and *Geijera*. The number of larval instars varies between five and six.

Methods.

(*a*) *Conditioning of Larvae to Foodplants.*

The extent to which the feeding preferences of a larva could be modified by prior feeding on other plants was investigated, larvae being reared for a period on one species of plant and then transferred to another. Their rate of feeding on the second plant was compared with that of larvae of the same instar which had been reared from hatching on the second plant. These rates were assessed by daily counts of the excreta produced. Ecdyses were indicated by the presence of the moulted head capsules among the excreta. The various days in an instar were identified as follows:

HC day count—that made on the day which included the moulted head capsule from previous instar.

1st day count—that made on day following HC day.

Mortality rates were variable and sometimes seemed to be correlated with parentage, some females producing more vigorous offspring than others. The laboratory culture of *P. aegeus* was maintained in an active breeding condition throughout the Queensland autumn to spring, but a certain loss of vigour was seen towards the end of this period.

(*b*) *Oviposition Behaviour.*

It was found that, under appropriate circumstances, *P. aegeus* females would oviposit readily when allowed to flutter at the end of a stiffened thread some 4–6 inches long, and that these conditions gave the investigator considerable control over the presentation of stimuli to the insect. The application of this simple technique will be described in some detail as it would facilitate an analytical study of chemosensory and other factors involved in the oviposition of *P. aegeus*. No such study of the oviposition behaviour of a butterfly has yet been made.

In order to harness the insect, it was strapped to a setting board in the normal "set" position, and two lengths of thread, each about 12″ long, were passed transversely under the body between the head and thorax, and thorax and abdomen respectively. The threads were drawn up around the body and all were fastened together with a small drop of quick drying cellulose adhesive applied to the back of the thorax. When the adhesive drop had dried the four free ends of the threads were twisted together and held in place by applying a dilute solution of cellulose adhesive in amyl acetate. The compound thread thus formed was held vertically above the insect until it had dried to form a light flexible rod by which the insect might be suspended. The stiffness of the rod was governed by the amount of adhesive applied along its length. If insufficient were applied the threads remained soft and flexible and invariably became entangled by the insect's movements. Too much adhesive produced a stiff rod which yielded insufficiently to the fluttering movements of the insect and discouraged the insect from attempting to fly.

Experimental insects harnessed in this way were kept on retort stands and clamps on a dimly lit area of bench, screened on three sides only. The area was artificially lighted from above when experiments were in progress. On the day of harnessing, the butterflies were held in clamps by their folded wings and fed with sugar and water. On the following day they were allowed to flutter for an hour or two on the supporting threads: oviposition responses were generally weak and erratic. Flight activity was encouraged by a gentle draught from a fan and the insects became habituated to the restrictions imposed by the harness. On the second day after harnessing, the insects usually showed oviposition responses that were reasonably consistent over short periods of time. When the insects were not being used in oviposition tests they were provided with supports on which to cling. During longer periods of inactivity (e.g., overnight) they were clamped by their wings, supports again being provided. Harnessed butterflies soon ceased to be disturbed by the presence of the investigator.

Oviposition stimuli (leaves, impregnated filter papers, etc.) were presented in a standard manner. When a leaf was to be presented to a harnessed female butterfly, the insect was first stimulated to fly by blowing gently, and the leaf then presented so that the butterfly could settle on it. A responsive female would grasp the leaf with its legs and start the rapid fluttering wing movements characteristic of oviposition. The abdomen would be flexed almost immediately and oviposition would proceed. With inadequate stimuli, or a less-responsive female, the oviposition sequence might fade out before completion, the wings ceasing to flutter and the abdomen gently returning to the normal position from that of flexion. When this occurred the leaf was quickly taken away (the loss of support stimulating further flight), and at once presented again. This was repeated until oviposition occurred or until a certain arbitrary period of time had passed from the first presentation of the stimulus. This time was the "test period" and was usually fixed at two or three minutes. If no oviposition occurred before the end of the test period a "nil" response was recorded. Otherwise, in the earlier experiments, the time elapsing between the first presentation of the stimulus and the laying of the egg was recorded. A period of several minutes was allowed to elapse between successive tests with any female.

Acceptability of Abnormal Food Plants to Larvae of P. aegeus.

In the laboratory *P. aegeus* larvae would feed on a number of plants not belonging to the Rutaceae. Particular attention was paid to the development of the larvae on the plants listed below, these either being the food plants of other Papilionidae or related thereto.

(*a*) *Petroselinum sativum*—Parsley (Umbelliferae). This plant was eaten readily by the larvae, which often developed more rapidly on parsley than did control larvae feeding on *Citrus*. *Apium graveolens* (Celery), another member of the Umbelliferae, was also accepted by the larvae.

(*b*) *Cinnamomum camphora*—Camphor Laurel (Lauraceae). This plant is a host plant of the Australian *Graphium sarpedon* Felder and *Graphium macleayanus* Leach. (Papilionidae). Young leaves appeared to be somewhat distasteful to the larvae of *P. aegeus*. On mature leaves development was either equal or inferior to that obtained on *Citrus*.

(*c*) *Anona squamosa*—Custard Apple (Anonaceae). *A. squamosa* is a host plant of the Australian *Graphium eurypylus* Westwood and *Graphium agamemnon* Rothschild (Papilionidae). *P. aegeus* larvae did not eat it.

(*d*) *Aristolochia* sp. Young larvae of *P. aegeus* ate the leaves but died within two or three days.

Certain plants, such as *Daucus carota* (carrot), were sometimes eaten readily and sometimes refused.

The acceptability of such plants varied and may have been affected by the physiological state of the plant when offered. For example, many larvae thrived on mature camphor laurel leaves, but on young leaves there was a high mortality.

To sum up, although the larvae of *P. aegeus* are only found on Rutaceae in nature, they will feed and develop on a number of other plants, some of which may be nutritionally superior to the natural host plants. In their ability to feed on plants other than their natural host plant, the larvae resemble those of *P. ajax*. Dethier suggests the acceptability of *Ruta* to larvae of *P. ajax* to be a heritage from Rutaceae-feeding ancestors, but such a hypothesis cannot explain the acceptability of parsley to the larvae of *P. aegeus*. We prefer to believe that there are, within the Papilionidae, certain species which have facultatively polyphagous larvae, and that the range of plants covered by this polyphagy is not necessarily related to the evolutionary history of the species. The apparent host for plant specificity of such species in nature is more the result of the selection of specific host plants by the ovipositing female than of innate larval food preferences.

This facultative polyphagy is not shared by the larvae of all *Citrus* Papilionidae; those of *Papilio anactus* and *Papilio fuscus*, two other Australian *Citrus* feeding species, would not feed on camphor laurel or parsley.

The Conditioning of P. aegeus Larvae to their Food Plant.

The feeding activity of a culture of larvae reared on *Citrus* is shown in Figure 1. In the 2nd-5th instars the rate of feeding increased steadily throughout the instar until it ceased prior to the moult. The figure suggests that rate of feeding increased more slowly in those larvae that took a longer time to complete the instar. However, larvae completing an instar in an apparently shorter period may have commenced feeding earlier in the day preceding the HC count than other larvae apparently taking longer to complete the instar. This would tend to bias the apparent feeding rate of the "short instar" larvae towards the high side since they would be somewhat older when excreta counts were made.

Larvae were frequently found in nature on *Flindersia collina* Bail. (Rutaceae), and the effect of changing larvae from this plant to *Citrus* and *vice versa* was investigated. In Figure 2 the feeding behaviour of larvae reared on *Flindersia* is compared with that of larvae reared on *Citrus*. In each case the larvae have been divided into categories according to the time spent in each instar and only the results from the categories containing the greatest number of larvae have been incorporated in the figure. Larvae developed more slowly on *Flindersia* than on *Citrus*. The effect on the rate of feeding of changing the food plant of the larvae is shown in Figure 3. Separate groups of larvae, containing between 10 and 20 individuals, were used for each experiment. The change from *Citrus* to *Flindersia* in (e.g.) the 4th instar was made on a group of larvae that had been reared on *Citrus* only. When the excreta were

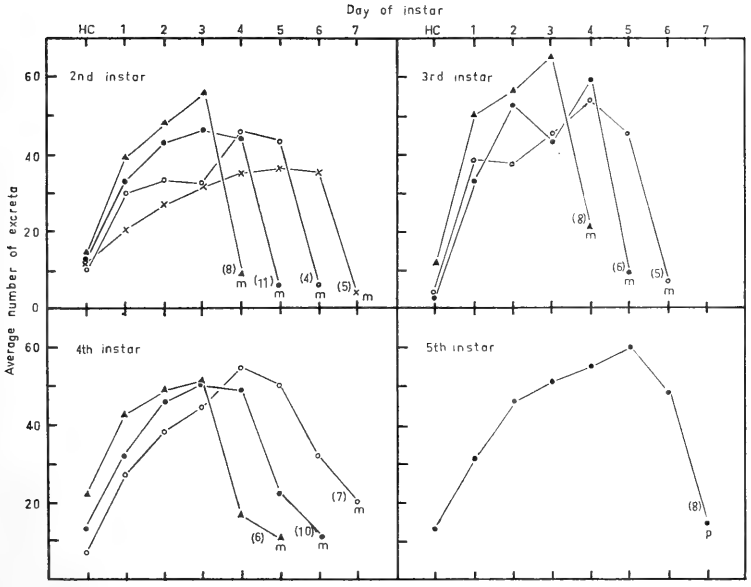

Fig. 1.—Feeding activity of *P. aegeus* larvae on *Citrus*. The figures in brackets indicate the number of larvae in the groups from which the average numbers of excreta were obtained. The different symbols indicate groups of larvae in which the instars occupied different periods of time.

m—day on which moult occurred; p—day on which pupation occurred.

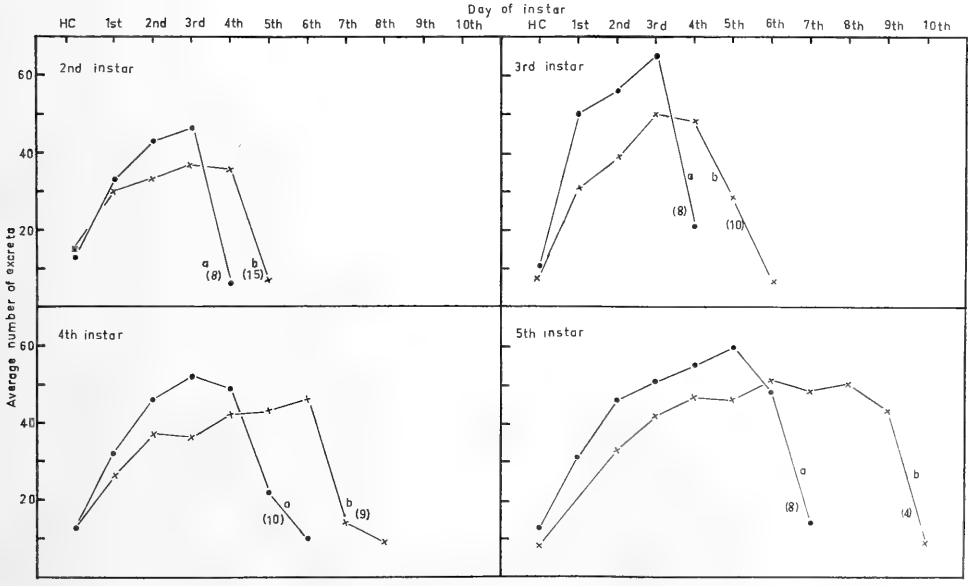

Fig. 2.—Feeding activity of *P. aegeus* larvae on *Citrus* compared with their activity on *Flindersia collina*.

a—larvae feeding on *Citrus*; b—larvae feeding on *Flindersia*.

counted on the 1st day of the 4th instar the *Citrus* food plant was replaced by *Flindersia*. This procedure ensured that the larvae had at least 24 hours in which to recover from the effect of the moult before experiencing the change of food plant. Food changes were carried out on the 1st day of the 2nd-4th instars, and on the 2nd day of the 5th instar. In Figure 3 comparisons are made between the rate of excrement production of control larvae, reared from hatching on either *Citrus* or *Flindersia*, and of experimental larvae, transferred to the plant only during the instar under consideration. The results indicate that, whatever the innate preference of the larvae with regard to these two natural food plants, conditioning occurred in favour of the plant on which they were feeding.

More surprising, perhaps, was the ready development of conditioned responses in favour of abnormal host plants. Figure 4, for example, demonstrates the considerably reduced rate of feeding on *Citrus* that resulted from prior feeding on camphor laurel

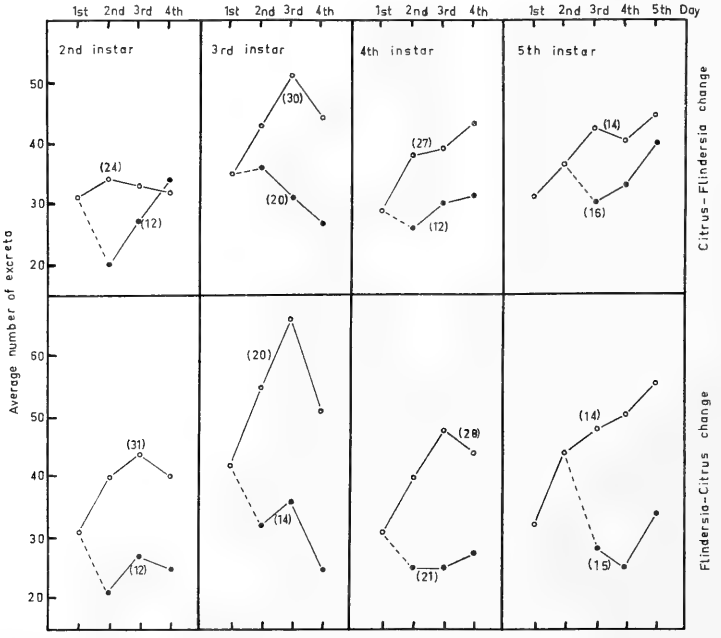

Fig. 3.—Reduction in feeding activity of *P. aegeus* larvae when transferred from *Citrus* to *Flindersia* and *vice versa*. In each frame the upper graph (open circles) shows the excreta production of larvae not undergoing a change of food plant, thus:

Citrus/Flindersia change: upper graph—larvae reared entirely on *Flindersia*; lower graph—larvae reared on *Citrus* and changed to *Flindersia* in appropriate instar.

Flindersia/Citrus change: upper graph—larvae reared entirely on *Citrus*; lower graph—larvae reared on *Flindersia* and changed to *Citrus* in appropriate instar.

A marked reduction in feeding also occurred as the result of the following food changes: camphor laurel to parsley, and *vice versa* in the 5th instar, parsley to *Citrus*, and *vice versa* in the 2nd instar. It was less certain that a reduction occurred as a result of the following changes: camphor laurel to parsley, and *vice versa* in the 2nd instar, parsley to *Citrus* in the 5th instar.

These experiments indicate that the host plant preferences of older larvae of *P. aegeus* may often be the result of conditioned behaviour rather than of innate responses.

Papilio fuscus is an Australian *Citrus-Papilio* which is somewhat similar to *P. aegeus* in general appearance, but the newly hatched larvae of which are not facultatively

polyphagous. The two species may sometimes be successfully mated by hand, and the newly hatched larvae of one such hybrid mating were examined for polyphagy. They showed the facultative polyphagy of the *P. aegeus* parent.

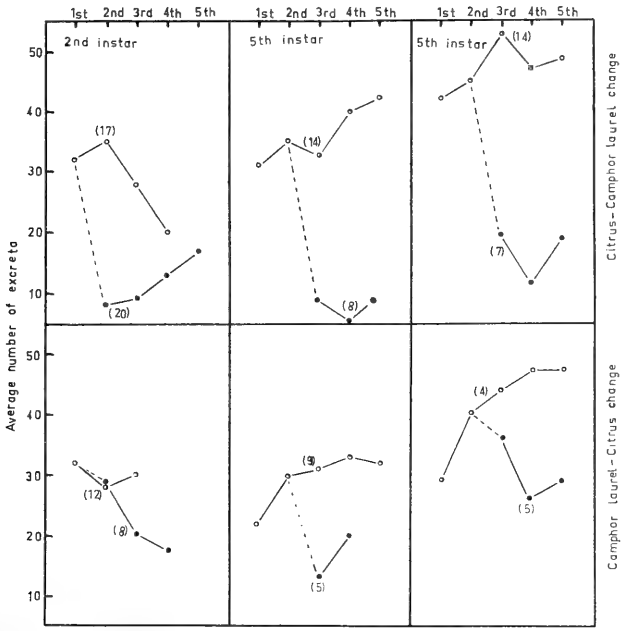

Fig. 4.—Reduction in feeding activity of *P. aegeus* larvae when transferred from *Citrus* to Camphor Laurel or *vice versa*. In each frame upper graphs (open circles) refer to larvae not undergoing a change of food plant, thus:

Citrus/Camphor Laurel change: upper graph—larvae reared entirely on Camphor Laurel; lower graph—larvae reared on *Citrus* and then transferred to Camphor Laurel.

Camphor Laurel/*Citrus* change: upper graph—larvae reared entirely on *Citrus*; lower graph—larvae reared on Camphor Laurel and then transferred to *Citrus*.

The Oviposition Behaviour of P. aegeus.

Since the larvae of *P. aegeus* are primarily somewhat polyphagous it follows that their restriction to the Rutaceae under field conditions reflects a restricted choice of host plants by the ovipositing female. The oviposition behaviour of the female was therefore broadly investigated.

Oviposition may be conveniently divided into five phases, thus: (i) the female stands on a selected leaf fluttering her wings rapidly; (ii) the abdomen is flexed forward between the legs; (iii) the ovipositor is extruded; (iv) searching movements are made with the ovipositor; (v) a suitable site having been located, the ovipositor becomes motionless and the egg is laid.

Females confined in wire cages, about 20″ cube, oviposited readily on *Citrus* sprays. In the absence of *Citrus* a minority of females would oviposit on camphor laurel or parsley, indicating that some individuals were ethologically capable of laying on non-rutaceous plants. Such observations did not permit of a very critical assessment of the oviposition tendencies of a particular female at a particular time, and in subsequent investigations harnessed butterflies were used. The results obtained on 24 trials, each with four females, were, even for the same individual, very variable. One female eight days old responded with oviposition only in the afternoon and, in those instances when a positive result was obtained, the time taken for egg laying to occur varied from 3·8 to 177 sec. A second female 11 days old responded at all trials except for three which all occurred in one test period at midday and the time for response varied from 4·3

to 177 sec. A third individual 12 days old failed to respond in three of twenty trials and the variation was from 6·5 to 91 sec. A fourth 21 days old responded relatively rapidly and on every occasion, the times ranging from 2·5 to 14·4 sec. Of these only the eight-day-old female had been allowed to lay many eggs previously.

Further observation showed that the variations in the times required to obtain a positive oviposition response arose largely from variations in Phase IV of the behavioural sequence. Since it was suspected that the searching movements of Phase IV were associated with satisfying the physical rather than the biochemical requirements of a site for the egg, and since the extrusion of the ovipositor in Phase III represented a high degree of responsiveness, the method of timing the response was changed in later experiments. The time then recorded was that elapsing between the first presentation of the stimulus and the extrusion of the ovipositor (Phase III response). The results obtained were much less variable than those obtained when Stage IV was used as the criterion for a positive response. Three of the females used in the previous test were again employed four days later. For each the times required for Stage III to be

TABLE 1.

Time in seconds elapsing between presentation of stimulus and appearance of Phase III oviposition response in three females of *P. aegeus*.

Female	A		B		E		Temp.
Age	17 days		16 days		26 days		
Time	Stimulus	Time to response	Stimulus	Time to response	Stimulus	Time to response	
10.40–10.50	C	4.7 sec	L	*	C	3.2	72°F
10.50–11.00	L	*	C	*	L	6.7	72 F
11.00–11.10	L	*	C	*	L	6.0	73°F
11.10–11.20	C	10.7	L	*	C	2.5	73°F
11.20–11.30	L	*	C	*	L	1.5	73°F
11.30–11.40	C	21.6	L	*	C	4.0	73°F
11.40–11.50	C	9.4	L	*	L	2.0	73°F
11.50–12.00	L	*	C	*	C	1.0	73°F
12.00–12.10	C	8.7	L	*	L	4.5	73°F
12.10–12.20	L	19.5	C	*	C	2.0	73°F
13.40–13.50	L	3.0	C	9.6	C	3.0	75°F
13.50–14.00	C	1.2	L	78.2	L	0.6	75°F
14.00–14.10	L	*	L	11.0	C	2.8	75°F
14.10–14.20	C	8.9	C	7.0	L	3.7	75°F
14.20–14.30	C	3.8	C	1.8	C	1.6	75°F
14.30–14.40	L	*	L	10.2	L	10.6	75°F
14.40–14.50	L	*	C	7.0	C	2.8	75°F
14.50–15.00	C	2.2	L	54.5	L	3.0	75°F

Asterisks = No response obtained. L = Camphor Laurel Leaf. C = Citrus Leaf.

reached were only long or variable on the first one or two exposures to the citrus leaf. The fifteen-day-old female failed to respond at the first attempt and took 93 seconds at the second attempt. Thereafter it responded rapidly 18 times; the mean time taken being 3·2 sec. and the range being from less than one second to a maximum of 7·8 sec. Similarly the 16-day-old female took 9·3 sec. at the first exposure and the 19 subsequent tests gave a mean of 1·9 sec.; the range was very small, being from 0·8 to 2·3 sec. The 25-day-old female took 13·6 sec. initially and the mean for the remaining 19 tests was 2·5 sec. The range was from less than one second to 5·3 sec.

The same butterflies were used a day later in an experiment in which their responses to *Citrus* leaves were compared with those to camphor laurel leaves (Table 1). The oldest butterfly, E (26 days), responded readily to both *Citrus* and camphor laurel, although its responses to the latter plant were, in general, somewhat weaker than to *Citrus*. Female B responded to neither plant during the morning, and to both plants in the afternoon, responses to camphor laurel being weaker than those to *Citrus*. Female A showed a much stronger response to *Citrus* than camphor laurel, positive responses to the latter plant being obtained in only two out of eight tests.

Five out of seven females, tested daily for their oviposition responses to *Citrus* and to parsley or camphor laurel, showed a positive response to the non-*Citrus* plant on

certain days. It should be stressed that in these experiments information was obtained only on the oviposition responses which occurred after the females were brought in contact with or very close to test leaves. No account was taken of the long distance attraction of the females to the host plant. Despite this it is thought that the responses obtained were probably a true reflection of the oviposition tendency of the insects in nature since they tended to occur either freely or not at all. During these tests the insects were allowed to lay eggs freely at the end of each day, so that no accumulation of unlaid mature eggs occurred.

Discussion.

Certain points of possible significance to the evolution of feeding habits within the Papilionidae have emerged from the present studies.

Firstly, the polyphagy of the newly hatched larva confers a certain preadaptation to new food plants. Even if the parent butterfly selects an abnormal plant for oviposition, this plant may lie within the range of plants suitable as food for the newly hatched larva.

Secondly, the conditioning of the larva towards its food plant, whether it be natural food plant or otherwise, suggests that if the newly hatched larva finds itself on a plant which supports development it will tend to stay on that plant.

Thirdly, the host plant selection of the ovipositing adult varies in specificity. Although this has been demonstrated only under very unnatural conditions in the laboratory, it is reasonable to suppose that similar changes occur in the oviposition tendencies of free living insects. If so, abnormal food plants might be selected in the field when the normal food plants were absent.

It thus seems that a species such as *P. aegeus* may be well suited to develop races with different host plant relationships through relatively simple selection processes under appropriate conditions. These could arise at the limits of the geographical range of the normal host plants, when adults migrating into areas from which the host plant was absent might tend to lay on abnormal plants, some of which would prove suitable for the development of the larvae. Selection would occur of the progeny of individuals which did not restrict oviposition to the normal host plants, and this could lead to the development of new races with altered oviposition preferences. The establishment of new biological races would be facilitated if certain abnormal host plants were generally favoured over others. Further work along the lines adopted in this investigation would provide information relevant to this suggestion.

During the present work it was evident that an insect changing a food plant association might derive a great biological advantage by the avoidance of parasites. *P. aegeus* larvae, reared on *Citrus* in a quarantine insectary, were heavily parasitized by tachinid larvae introduced as eggs that had been laid on leaves of the food plant. Those reared on parsley were never parasitized. Parasitism of *P. aegeus* larvae by tachinids in the field was often very heavy, rising above the 80% level, and would be an important factor encouraging a change of host plant should the opportunity occur. New races might thus arise from rigorous parasitic selection in favour of mutations of oviposition preferences which permitted the females to oviposit on abnormal host plants.

Summary.

1. The larva of *P. aegeus*, an Australian papilionid butterfly naturally associated with the Rutaceae, could be reared in the laboratory on certain plants not belonging to this family.

2. The larvae became conditioned in favour of the food on which they were reared even though this might be an abnormal food plant.

3. A technique for investigating the oviposition responses of *P. aegeus* was devised, and the female butterflies were found to have a variable tendency to lay on abnormal host plants.

4. It is suggested that evolution of new host plant relationships within the Papilionidae may have occurred through species, such as *P. aegeus*, which possess a facultatively polyphagous larvae. Such species could have survived and exploited changes in female oviposition habits, leading to the development of new biological races.

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A REVISED CLASSIFICATION OF THE AUSTRALIAN AMPHIURIDAE (OPHIUROIDEA).

By H. Barraclough Fell, Victoria University of Wellington, New Zealand.
(*Communicated by Elizabeth C. Pope.*)

[Read 18th April, 1962.]

Synopsis.
The Australian Amphiuridae are regrouped in 16 genera, which are keyed.

Introduction.

Since the appearance of H. L. Clark's valuable work *The Echinoderm Fauna of Australia* (1946) a considerable revision of the genera of Amphiuridae has become necessary. Details of the changes proposed are given elsewhere (Fell, 1962), and the present contribution is intended to explain the implications for the nomenclature of the Australian species. The following checklist of species shows the names under which the species appear in Clark's work cited above, together with the genera to which the species are referred in the classification here adopted.

Revised Checklist of Australian Amphiuridae.

H. L. Clark (1946).	Genera here adopted.
Amphiura trisacantha H.L.C., 1928	*Monamphiura*
catephes H.L.C., 1938	,,
phrixa H.L.C., 1938.	,,
microsoma H.L.C., 1915	*Amphinephthys.*
stictacantha H.L.C., 1938.	*Amphiura*
brachyactis H.L.C., 1938	*Pandelia*
septemspinosa H.L.C., 1915	*Monamphiura*
constricta Lym., 1879	,,
leucaspis H.L.C., 1938	,,
magnisquama H.L.C., 1938	,,
micra H.L.C., 1938	,,
ptena H.L.C., 1938	,,
velox Koehler, 1910	,,
diacritica H.L.C., 1938	*Amphinephthys*
ambigua Klr., 1905	*Amphiura*
multiremula H.L.C., 1938	,,
bidentata H.L.C., 1938	,,
dolia H.L.C., 1938	,,
nannodes H.L.C., 1938	,,
acrisia H.L.C., 1938	,,
poecila H.L.C., 1915	,,
Ctenamphiura maxima (Lym., 1879)	*Ctenamphiura*
Ophiocentrus verticillatus (Dod., 1896)	*Ophiocentrus*
fragilis H.L.C., 1938	,,
dilatatus (Klr., 1905)	,,
pilosus (Lyman, 1879)	,,
asper (Klr., 1905)	,,
Ophionephthys octacantha H.L.C., 1915	*Ophiopeltis*
decacantha H.L.C., 1938	,,
perplexa (Stimpson, 1855)	*Icalia*
tenuis H.L.C., 1938	*Ophionema*

Amphipholis squamata (D. Chiaje, 1828)	*Amphipholis*
Amphistigma minuta H.L.C., 1938	*Ophiostigma*
Amphiodia ochroleuca (Brock, 1888)	*Diamphiodia*
Ophiocnida echinata (Ljg., 1867)	*Ophiocnida*
Amphioplus lucidus Klr., 1922	*Ophionephthys*
depressus (Ljg., 1867)	*Amphioplus*
parviclypeus H.L.C., 1915	„
lobatus (Ljg., 1867)	„
didymus H.L.C., 1938	„
stenaspis H.L.C., 1938	„
Amphiacantha sexradia (Duncan, 1887)	*Amphiacantha*

Key to the Australian Genera of Amphiuridae.

1 (18) A conspicuous diastema separates the first (i.e., infradental) oral papilla from the second oral papilla. Usually only these two oral papillae on each side, but a third one may occur on or near the adoral plate.
2 (3) Numerous spines carried on the disc ..... OPHIOCENTRUS.
3 (2) No spines on disc.
4 (9) Disc naked above and below, save for the radial shields and an adjoining narrow zone of scales bordering the radial shields.
5 (6) Infradental papilla large, second oral papilla more or less vestigial. No tentacle-scales ..... OPHIONEMA.
6 (5) Infradental and second oral papillae both well-developed.
7 (8) No tentacle-scales ..... OPHIOPELTIS.
8 (7) One or two tentacle-scales ..... AMPHINEPHTHYS.
9 (4) Disc not entirely naked, having at least a continuous clothing of scales on the upper surface.
10 (15) Disc scaled above, but partly or wholly naked below.
11 (12) Disc-scales coarse, chunky, arranged in an irregular mosaic. Infradental and second oral papillae both large, flat, broad; a third spiniform oral papilla at the distal end of the jaw. Tentacle-scales present ..... CTENAMPHIURA.
12 (11) Disc-scales fine, flattened, imbricating, not chunky nor arranged in a mosaic.
13 (14) No tentacle-scales on most pores. ..... ICALIA.
14 (13) One tentacle-scale on all or most pores ..... PANDELIA.
15 (10) Disc scaled completely above and below.
16 (17) One tentacle-scale ..... MONAMPHIURA.
17 (16) Two tentacle-scales ..... AMPHIURA.
18 (1) Three or more oral papillae on each side of the jaw, with no diastema.
19 (26) Three oral papillae on each side of jaw.
20 (23) Outermost (i.e., third) oral papilla conspicuously larger than the other two.
21 (22) No spines on disc. Two tentacle-scales ..... AMPHIPHOLIS.
22 (21) Spines carried on some disc-scales ..... OPHIOSTIGMA.
23 (20) Three subequal oral papillae, the outermost not conspicuously larger than the others. Disc scaled above and below.
24 (25) Numerous scattered spines on disc ..... OPHIOCNIDA.
25 (24) No spines on disc. Two tentacle-scales ..... DIAMPHIODIA.
26 (19) Four or five oral papillae on each side of jaw, often rather irregularly arranged, or overlapping, the outermost usually placed on or near the adoral plate. Tentacle-scales present.
27 (28) Disc bearing spines or spiniform processes. Tentacle-scales leaf-like, not spiniform .. .. AMPHIACANTHA.
28 (27) No spines on disc.
29 (30) Disc naked above and below, save for the radial shields and an adjoining zone of scales bordering the radial shields. One or two tentacle-scales ..... OPHIONEPHTHYS
30 (29) Disc scaled completely above and below. Two tentacle-scales ..... AMPHIOPLUS.

MONAMPHIURA Fell, 1962.

Type species: *Amphiura alba* Mortensen, 1924.

Monamphiura is a large cosmopolitan genus to which more than 60 species may be referred. It is represented in Australian seas by ten nominal species.

Key to the Australian species of Monamphiura.

1 (2) Arms 6 (rarely 5). Arm-spines 4 or 5, short, flat, blunt ..... *velox* (Koehler).
2 (1) Arms normally 5.
3 (4) Tentacle-scale as long as ventral arm-plate, and attached to it for its full length .... *ptena* (H. L. Clark).

4 (3) Tentacle-scale attached only at its proximal end.
5 (6) Radial shields elongate, not contiguous, separated by intervening elongate scales. Arm-spines normally 3, but 4 or 5 on basal arm-joints .. *trisacantha* (H. L. Clark).
6 (5) Not so.
7 (10) Ventral arm-plates broader than long.
8 (9) Arm-spines erect, 8-10 at base of arm ..... *catephes* (H. L. Clark).
9 (8) Arm-spines more or less adpressed, 6-7 at base of arm ..... *phrixa* (H. L. Clark).
10 (7) Ventral arm-plates longer than broad.
11 (14) Radial shields elongate, disc-clothing of very numerous fine minute scales.
12 (13) Upper arm-spines acuminate ..... *septemspinosa* (H. L. Clark).
13 (12) Upper arm-spines wide, blunt ..... *constricta* (Lyman).
14 (11) Radial shields short and broad, disc-clothing of coarse scales.
15 (18) Basal arm-spines 5-6. Outer oral papilla subcircular, flat.
16 (17) Tentacle-scale elongate, almost as long as the ventral arm-plate .... *leucaspis* (H. L. Clark).
17 (16) Tentacle-scale small, about one-third of the length of the ventral arm-plate .... *magnisquama* (H. L. Clark).
18 (15) Basal arm-spines 3-4. Outer oral papilla longer than broad .. *micra* (H. L. Clark).

Amphinephthys Fell, 1962.

Type species: *Amphiura crossota* Murakami, 1943.

Amphinephthys includes at least three Pacific littoral species, and it is possible that two other species should be included, one from South Africa and one from the Caribbean. Two of the included species are Australian, the third being the type, from the Caroline Islands.

Key to the Australian species of Amphinephthys.

1 (2) Single tentacle-scale ..... *microsoma* (H. L. Clark).
2 (1) Two tentacle-scales ..... *diacritica* (H. L. Clark).

Amphiura Forbes, 1842. (Restricted.)

Type species: *Amphiura chiajei* Forbes, 1842.

Amphiura, as now restricted on the basis of the type species, comprises some forty species, both shallow- and deep-water forms being represented. The genus is cosmopolitan and is represented in Australian seas by eight species.

In his work on the Echinoderm fauna of Australia, H. L. Clark (1946, pp. 191–192) includes a number of statements which appear to be in error. The species *Amphiura stictacantha* is stated to have one tentacle-scale, whereas the type material was recorded as having two scales (H. L. Clark, 1938).

Two species, *A. ambigua* and *A. multiremula*, are keyed by Clark (1946) as having the disc naked below; the former species has been taken on a number of occasions, and all material (like the type) was fully scaled; the latter species was originally recorded as fully scaled, and its subsequent inclusion in the group with a naked underside seems to have been accidental. In the following key the records of the type material have been used as the basis of the classification.

Key to the Australian species of Amphiura.

1 (2) Arm-spines 3. A third (distal) oral papilla ..... *bidentata* H. L. Clark.
2 (1) Arm-spines 5 or more.
3 (6) Arm-spines 8-9.
4 (5) Radial shields elongate, narrow ..... *stictacantha* H. L. Clark.
5 (4) Radial shields short, divergent, barely one-sixth diameter of disc .... *multiremula* H. L. Clark.
6 (3) Arm-spines 5-7.
7 (8) Disc-scales coarse. Outer oral papilla flat, thick, opercular ..... *dolia* H. L. Clark.
8 (7) Disc-scales fine. Outer oral papilla erect.
9 (12) Primary plates not differentiated.
10 (11) Arm-spines with a glassy recurved distal hooklet, directed towards the extremity of the arm ..... *ambigua* Koehler.
11 (10) Arm-spines with no distal glassy hooklet ..... *nannodes* H. L. Clark.
12 (9) Primary plates more or less evident.
13 (14) Radial shields long, narrow, 3 or 4 times longer than broad .... *poecila* H. L. Clark.
14 (13) Radial shields small, inconspicuous, about twice as long as broad .... *acrisia* H. L. Clark.

PANDELIA Fell, 1962.

Type species: *Amphiura hinemoae* Mortensen, 1924.

Pandelia comprises about a dozen species, mostly Pacific forms. The single known Australian species, *Pandelia brachyactis* (H. L. Clark), has 5–7 arm-spines, the arms relatively short, about four times the disc-diameter.

OPHIOPELTIS Düben & Koren, 1846.

Type species: *Ophiopeltis securigera* Düben & Koren, 1846.

Ophiopeltis is a small cosmopolitan genus of some nine species, mostly from shallow water. Two species are recorded from Australia.

Key to the Australian species of Ophiopeltis.

1 (2) Arm-spines 10, the series from either side of the arm meeting on the dorsal surface of the arm, where the uppermost spines are slender, not conspicuously short .... *decacantha* (H. L. Clark).

2 (1) Arm-spines 8 (occasionally 9), the lateral series not meeting on the dorsal side of the arm, the uppermost spines short and thick, not slender .... *octacantha* (H. L. Clark).

ICALIA Fell, 1962.

Type species: *Amphiura denticulata* Koehler, 1896.

Icalia comprises about eighteen species, mostly from the Atlantic. The single species in Australian waters, *I. perplexa* (Stimpson), has extremely elongate arms and up to six arm-spines.

OPHIONEMA Lütken, 1869.

Type species: *Ophionephthys limicola* Lütken, 1869.

Ophionema comprises five known species, all from tropical littoral waters. Only one species is known from Australia, *Ophionema tenuis* (H. L. Clark), from north-west Australia. The arms are stated by Clark to be about 25 times the disc-diameter, and there are about six arm-spines.

AMPHIPHOLIS Ljungman, 1866.

Type species: *Ophiolepsis gracillima* Stimpson, 1852.

The genus is represented in Australia by the cosmopolitan and well-known species, *Amphipholis squamata* (D. Chiaje).

OPHIOSTIGMA Lütken, 1856.

Type species: *Ophiostigma tenue* Lütken, 1856.

Amphistigma H. L. Clark, 1938 was founded on a single juvenile specimen of the only known species, *A. minuta* H. L. Clark, from Lord Howe Island. It is probably to be referred to *Ophiostigma*.

DIAMPHIODIA Fell, 1962.

Type species: *Amphiura violacea* Lütken, 1856.

Diamphiodia is a cosmopolitan genus of more than thirty species, of which only one is recorded from Australia. This is *D. ochroleuca* (Brock, 1888), also occurring in Indonesia.

OPHIONEPHTHYS Lütken, 1868.

Type species: *Ophionephthys limicola* Lütken, 1869.

Although H. L. Clark (1946) recorded four species of this genus from Australia, none of the species he included can be regarded as congeneric with the type species, and they are here assigned to other genera. However, *Ophionephthys* is represented in Australia by the species *O. lucida* (Koehler), which has hitherto been included under *Amphioplus*. The species can be sufficiently identified by the key to the genera Apart from the Australian representative, five (possibly six) other species are known mainly Indo-Pacific littoral forms.

Ophiocnida Lyman, 1865.

Type species: *Ophiolepsis hispida* Le Conte, 1851.

H. L. Clark (1946) believes that the genus is represented in Australian waters by *O. echinata* (Ljungman).

Amphioplus Verrill, 1899.

Type species: *Amphiura tumida* Lyman, 1878.

As now restricted, *Amphioplus* comprises about 56 nominal species, of which five occur in Australian waters.

Key to the Australian species of Amphioplus.

1 (2) Radial shields contiguous along the radial mid-line ..... *depressus* (Ljg.).
2 (1) Radial not contiguous along the mid-line, usually elongate and separated by intervening scales.
3 (8) Radial shields reaching one-third to one-half of the distance to the centre of the disc.
4 (5) Arm-spines 6 ..... *lobatus* (Ljg.)
5 (4) Arm-spines fewer than 6; 4-5 at the arm-base, fewer beyond.
6 (7) Adoral plates contiguous proximally to the oral shield ..... *didymus* H. L. Clark.
7 (6) Adoral shields not contiguous proximally to the oral shield ..... *stenaspis* H. L. Clark.
8 (3) Radial shields small, reaching only about one-fifth of the distance from the ambitus to the centre of the disc ..... *parviclypeus* H. L. Clark.

Amphiacantha Matsumoto, 1917.

Type species: *Amphioplus acanthinus* H. L. Clark, 1911.

Amphiacantha comprises about five (possibly seven) described species, mainly Pacific in distribution. The species listed by H. L. Clark (1946), *A. sexradia* (Duncan, 1887), is dubiously reported from Western Australia.

Ctenamphiura Verrill, 1899.

Type species: *Amphiura maxima* Lyman, 1879.

Ctenamphiura probably comprises two known species, one from New Zealand, and the type species from Australia. A third nominal species (*A. sinensis* A. H. Clark) would appear rather to fall in *Diamphiodia*. The single Australian species can be recognized by the generic characters in the foregoing key.

Ophiocentrus Ljungman, 1867.

Type species: *Ophiocentrus aculeatus* Ljg., 1867.

Eleven species are at present included in the genus, which is exclusively Pacific, mainly littoral and sublittoral. There has been no change in the status of the five Australian species since H. L. Clark's key to them was published (1946), and reference may be made to that source.

Ophiactis and Ophiodaphne.

These genera, included in the Amphiuridae by H. L. Clark, are now usually regarded as forming a distinct family (Ophiactidae), together with *Ophiopholis* and *Ophiopus*.

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Clark, H. L., 1946.—The Echinoderm Fauna of Australia. Carnegie Inst. Washington Pub. 566.
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GALLS OF AGROMYZIDAE (DIPT.) ON *PITTOSPORUM UNDULATUM* ANDR.

By Erich M. Hering, Berlin.*

(*Communicated by C. E. Chadwick.*)

(Plate ii; four Text-figures.)

[Read 18th April, 1962.]

Synopsis.

Two new species of *Phytobia* (Agromyzidae) are described, one causing mine galls on the leaves, and the other galls on the stems of *Pittosporum undulatum*. Information is given on the bionomics and life-history of each.

Mr. C. E. Chadwick (Entomological Branch, New South Wales Department of Agriculture, Sydney) has for some years observed larvae in the leaves of *Pittosporum undulatum* Andr. He has collected the adults belonging to the larvae from the gall-like mines in the leaves and bred out flies from the twig galls which he found on the same plant. I acquired from him for study the material of flies, larvae and galls thus obtained. This showed that the flies belonged to a genus previously represented in Australia by only a single species. I am much obliged to Mr. Chadwick for sending this material, and also for his exceedingly careful observations on the life cycle and habits of these pests on *Pittosporum*.

To my great surprise this material from *Pittosporum* proved to consist of two different but quite closely related species which may be easily distinguished in the adult, and still more easily in the larvae and the galls produced by them. Both are new to science and are to be described below; the species of which the larva lives in mine-like galls on the leaves will be named *Phytobia* (*Praspedomyza*) *pittosporophylli*; the one living in the twig galls will be named *Phytobia* (*Praspedomyza*) *pittosporocaulis*.

Phytobia (Praspedomyza) pittosporocaulis, spec. nov.

In this and the following species the orbits are not distinguished from the interfrontalia as a ledge, as should be characteristic of this subgenus according to Hendel, but even Hendel groups in this subgenus, species which do not show this character (or only when the frons is shrunken). I consider the possession of more than three bulbs on the posterior spiracles distinctive for this subgenus.

Head.—Frons longer than width above, narrowed anteriorly; distance between inner verticals as great as distance from inner vertical to base of antenna and one and a half times as great as distance between middle lower orbitals. Ocelli forming an equilateral triangle. Orbits not abruptly elevated next to the interfrontalia. Face at mouth margin one and a half times as wide as its height to bases of antennae. Parafacials, near bases of antennae, as wide as the first antennal segment, rapidly contracting below to a very narrow strip. Lunule narrow, arched somewhat higher than a semicircle. Facial carina narrow above, broadened and flattened below.

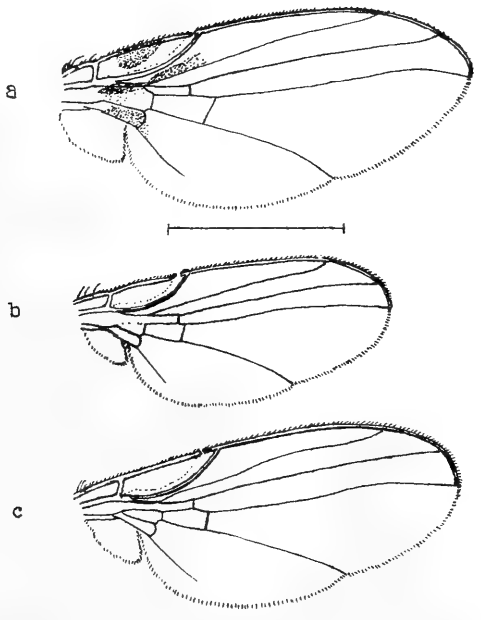
In profile frons and face visible in front of the eyes as a uniformly narrow ring. Face concave, mouth margin projecting. Ratio of vertical to horizontal diameter of eye 5:3. Width of cheek below the deepest part of the eye one-sixth, posteriorly one-fifth the vertical diameter of eye.

Bases of antennae closely approximated. Third antennal segment rounded, but distinctly widening and hatchet-shaped in front. Arista somewhat more than three times as long as the third antennal segment, quite shortly pubescent. Palpi cylindrical, proboscis widening and flattened at end.

* Present address: (West)-Berlin-Dahlem, Reichensteiner Weg 21, Germany.

Chaetotaxy.—One or two superior orbitals, reclinate and often also slightly incurved. Three or four inferior orbitals, the foremost often weaker, sometimes absent on one side. Ocellars, if depressed, reaching to the first superior orbital. Orbital hairs dense, short, reclinate, in one row anteriorly, forming several rows in places posteriorly. One to three incurved vibrissae on the vibrissal angle, three or four upwardly and outwardly directed bristles on cheek margin.

Thorax.—3 + 1 dorsocentrals, the foremost on or very slightly in front of transverse line connecting the presuturals, third dorsocentral distinctly behind suture. Second dorsocentral more than twice as far from the first as from the third. Acrostichals very irregularly arranged in four to five rows, reaching anteriorly in front of the fourth dorsocentral and extending behind the first dorsocentral in still more rows. Intra-alar lines with eight to fifteen hairs in front of the suture and three to five hairs behind; intra-alar bristle absent. Humeral callus with three to five hairs. Inner post-alar one-third to one-half as long as outer post-alar. Posterior margin of mesopleuron with one mesopleural bristle and three to five hairs, without outwardly directed hairs below the upper margin. Sternopleuron with a small hair in front of posterior upper sternopleural. Scutellum with four subequal scutellars, dorsal surface with up to five small hairs.



Text-fig. 1. Wing of (*a*) *Phytobia pittosporocaulis* Hg. ♂; (*b*) ♂ and (*c*) ♀ of *Phytobia pittosporophylli* Hg. (⊢—⊣ = 1 mm.).

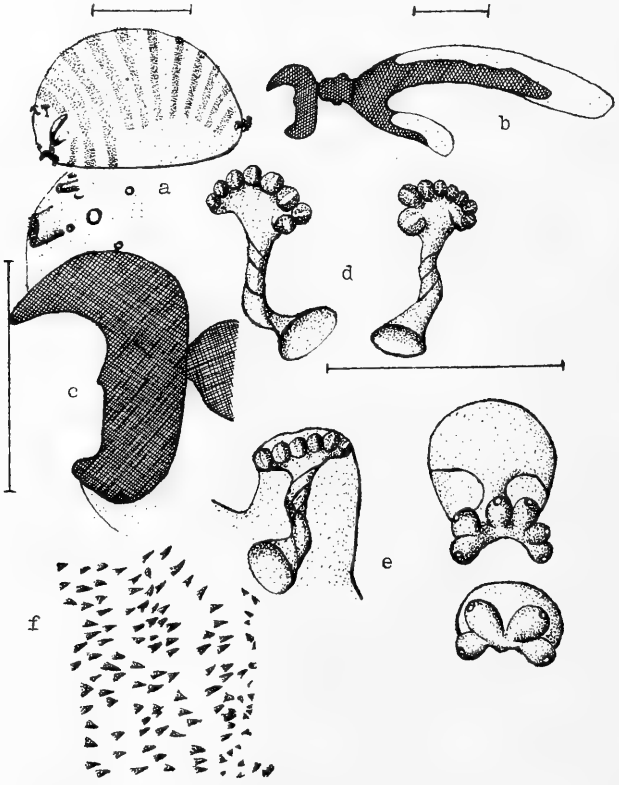
Abdomen.—Tergites with long bristles on their posterior margins. Last tergite of female more than twice as long as the penultimate. Ovipositor elongate-conical, as long as the last tergite. In the male the last tergite somewhat longer than the previous one. Hypopygium large.

Legs normal, mid-tibia without postero-dorsal bristles.

Wing (Text-fig. 1, *a*).—Costa reaching to the end of *m*. Proportions of costal sections 2:3:4 = 7:3:2 (= 45:17:12). R_{4+5} convex anteriorly, bending forwards at distal end; *m* bending posteriorly at end. *Cd* very short, last section of *cu* about $3\frac{1}{3}$ times as long as penultimate section, *ta* rarely in centre of *Cd*, usuallyl near *tp*, and below the end of r_1; form of *Cd* and position of *ta* very variable, *ta* and *tp* often extremely strongly

approximated, sometimes even one above the other. *an* not reaching hind margin of wing. Wing length $1\frac{3}{4}$ (♂) – $2\frac{1}{2}$ (♀) mm.

Coloration.—Interfrontalia light wax-yellow to dirty grey. Face deep black, only the mouth-margin narrowly edged with light yellow. Prelabrum and palpi black, proboscis light yellow. First antennal segment black, the second paler, the third predominantly yellow to reddish-yellow, the short hairs on anterior margin white. Arista black. Thorax black, mesonotum and scutellum entirely matt, with bluish-grey dusting; the lateral region not lighter, at most the sutural triangle somewhat paler. Humeral callus indistinctly yellowish posteriorly. Mesopleuron with narrow, light yellow margin above (and indistinctly so below). Sternopleuron completely black. Abdomen somewhat more shining, tergites very narrowly margined with yellow behind. Legs black, knee of fore-leg quite narrowly yellow. Wing glassy but Cc_2 shaded with grey. Squamae dirty white, with dark margins and fringe. Halteres yellow.



Text-fig. 2. *Phytobia pittosporocaulis* Hg., Larva: (*a*) Habitus, (*b*) Cephalopharyngeal skeleton, (*c*) Head region, (*d*) anterior and (*e*) posterior Spiracles, (*f*) lateral section of an abdominal band of cuticular processes (⊢—⊣ in *a* = 1 mm., in *b-e* = 0·1 mm.).

Holotype ♂ and allotype ♀ from Normanhurst (New South Wales), bred from galls on *Pittosporum undulatum* Andr. on 28.ix.1956, in Department of Agriculture, Entomological Branch, Sydney (N.S.W.); paratypes: 4 ♂, 18 ♀ from the same locality, 19–28.ix.1956; 1 ♂, 2 ♀ from Sydney, 11.ix.1956, 1 ♂ from Seaforth, 31.vii.1957, all bred from twig galls. Paratypes also in British Museum (Natural History), London, and in the Zoologisches Museum der Humboldt-Universität, Berlin, and in the Australian Museum, Sydney.

Description of Larva (Text-fig. 2).

The larva is very different from that of the following species in a number of characters. Even in its external shape it is distinguishable from the second species described below in its more compact form (Text-fig. 2, *a*); and thus has the appearance of many true gall-makers among the dipterous larvae, in contrast with related species which do not live in galls. Cuticular processes absent in the head region above and also below the mandibles, but abundantly developed on the thorax and abdomen in annular bands of small teeth. The processes (Text-fig. 2, *f*) differ quite substantially from those of the following species. Whilst in *Ph. pittosporophylli* Hg. they are almost hemispherical and show a slight point, they are here long and sharp with slightly thickened basal part. The bands of the first two thoracic segments are not differentiated from those of the abdomen in the structure and size of the spines. Prothoracic band with a maximum number (dorsally) of 12 transverse rows of teeth, the foremost rows smaller; the band is broadest dorsally, interrupted laterally. Mesothoracic band complete, spines in 12–14 transverse rows. That of metathorax similarly formed but strongly narrowed ventrally. First abdominal segment with a similar band which is, however, broadly interrupted centrally. Band of second segment with only about eight transverse rows of spines and likewise interrupted ventrally. The following bands become progressively narrower and more widely open ventrally; the third to seventh segments still have bands which are continuous dorsally, and are only interrupted ventrally. The band of the eighth segment is only developed laterally, where it is strongly formed from six rows of spines. Anal field without spines.

Antenna slender, maxillary palp short but about three times as thick as the antenna. No frontal sclerite visible. In the cephalopharyngeal skeleton (Text-fig. 2, *b*) the labial sclerite is unusually short and thick. The dorsal process of the paraclypeal phragma is about three times as long as the ventral; its strongly sclerotized deep black coloured lower part is strikingly stouter than in the following species. Both processes are thicker than in *Ph. pittosporophylli* Hg. The mandibles (Text-fig. 2, *c*) have each only one tooth, below it a small prominence as the only vestige of the second tooth; on the lower margin they are produced into an orally directed projection. Both mandibles are equally long, their teeth not therefore alternating in position.

The anterior spiracles (Text-fig. 2, *d*) have six bulbs, which stand in an ellipse, which is open on the inner side. The atrium is narrow, winding, strongly thickened where it joins the trachea. The posterior spiracles (Text-fig. 2, *e*) have four to six bulbs, their atrium is relatively shorter, also winding, considerably thickened where joining the trachea.

Apart from the general shape of the body one can also immediately distinguish this species from the other by its pointed cuticular processes, the single-toothed mandibles and the small number of bulbs on the posterior spiracles.

The Gall (Pl. ii, fig. 1, 2; Text-fig. 3*a*).

The larva lives in twig galls (shoot-axil galls) of semi-ovoid or hemispherical shape on *Pittosporum undulatum* Andr., which may attain a diameter of 5·7 mm. and which gradually extend to the cortex (Text-fig. 3*a*). The gall always lies above a point where a leaf develops with a bud actually on it. A single larva inhabits each swelling. The gall may be up to three times as thick as the twig at the point of its development but is usually smaller. Often a number of galls develop in the same twig in close proximity and occasionally their edges overlap. At oviposition the egg is inserted beneath the epidermis; this point of oviposition appears later as a pale point on the gall. The adult larva later feeds up to the edge of the epidermis; at this point the epidermis is later burst open, and the gall-former emerges into the open.

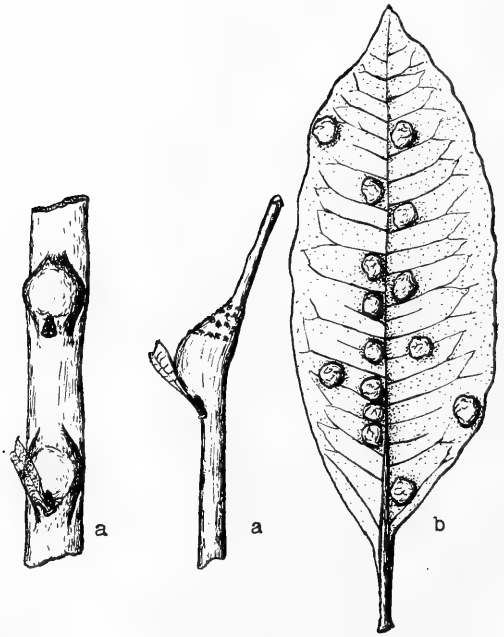
The gall formed in this way may be termed *histioid* (without organic formation) and *prosoplasmatic* (of definite size and shape). It can be classified as a hyperplasia, since it develops from increased growth and a frequent division of the cells. The larva

eats out channels in this gall-tissue of hyperplastic origin, which are concentrated in particular below the bud and finally form there a large cavity.

In the first feeding-stage the larva feeds exclusively on the parenchyma of the cortex. The cells of the cortical parenchyma rapidly increase in number and size under the influence of the gall-causing factors; they are the first food of the young larva. As a result of pressure the cells appear more cylindrical. Newly formed callus tissue penetrates into areas eaten out by the larva, the cells of which are more spherical, and they later entirely fill the feeding channel.

In the second phase the larva penetrates into the pericycle and feeds on its tissue. It feeds at the point where the fibro-vascular tissue of the leaf stalk joins the central fibro-vascular bundle, eating the outer tissues, especially parenchyma and phloem.

Plate ii, Figure 1 shows this point of junction, the "leaf-gap" of the central area, where the more strongly developed xylem is interrupted. After the larva has largely eaten this tissue, callus with large cells and delicate walls develops there; these cells are first arranged radially, but they are smaller and more regular than those formed by the phloem which is also eaten. The grains of frass are everywhere covered, enclosed and compressed in callus. Large, black grains of frass lie in the remaining area of the feeding channel.



Text-fig. 3. (*a*) Twig galls of *Phytobia pittosporocaulis* Hg., (*b*) Leaf with mine galls of *Ph. pittosporophylli* Hg. on *Pittosporum undulatum* Andr.

Although the larva first feeds only in the cortical parenchyma and in the following phase specializes in the pericycle, in the last phase of its feeding it no longer discriminates between the various tissues. The feeding channel now extends from the inner area of the fibro-vascular bundle-ring almost up to the epidermis, and substantial sections of the xylem are also eaten (constituent parts of this are still recognizable in the frass). In this way a large cavity is formed (Pl. ii, fig. 2), no longer filled with callus, probably because here the humidity of the air is too reduced, and also because the vegetation period of the plant is too far advanced and in consequence its capacity to react is too diminished. It is noteworthy that at no point is the central tissue

within the fibro-vascular bundle injured, and also the tissues immediately beneath the bud are left untouched.

From the position of the main feeding area at the junction of the central tissues of the mid-rib of the leaf with the central cylinder of the shoot, the larva obtains the maximum possible amount of nutritive elements.

PHYTOBIA (PRASPEDOMYZA) PITTOSPOROPHYLLI, spec. nov.

As this species is very similar to the one just described, it is necessary to mention here only the characteristics by which it differs from it.

Head.—Lunule broader, lower, approximately in the form of a semicircle. Frons pale yellow to leathery yellow. Only the first two antennal segments are bright yellow to yellowish-brown (rarely black); the third segment always deep black (except in specimens which are not fully pigmented). The rear two ocelli are further apart, the three ocelli form a triangle in front, with the apex of the triangle forming a right angle. Orbital hairs very sparse, in single row throughout.

Thorax.—The acrostichals arranged in only two rows, very regular, extending in front slightly beyond the fourth dorso-central, but ending behind at or slightly beyond the second dorso-central; they are somewhat longer than in the previous species. There are one to two intra-alar hairs before and behind the suture. The scutellum above always without hairs, apart from the scutellars.

Abdomen.—The last tergite of the ♀ is only 1½ times as long as the penultimate. Oviscape broad and short, equal in length to last tergite. In ♂ last tergite 1¼ times as long as the penultimate, the genital capsule smaller than in previous species.

Wing (Text-fig. 1, *b*, *c*).—The costal segments 2:3:4 are in the ratio of 3:1:⅔, the second segment is thus relatively shorter. The last segment of *cu* is about three times as long as the penultimate, the *Cd* is thus relatively shorter than in the previous species. The *ta* is usually closer to the *tp* in the ♂ than in the ♀. The blackish shading on the basal area of the wing which characterizes the previous species is here lacking. Wing length 1·7 (♂) – 2·2 (♀) mm.

♂-Holotype and ♀-allotype from Roseville (New South Wales), caught on 25.viii.1956 on young leaves of *Pittosporum undulatum* Andr.; 17 ♂, 12 ♀ paratypes from the same locality from 25.viii–2.ix.1956; 2 ♂, 4 ♀ from Hornsby, 2.ix.1956; all in Department of Agriculture, Entomological Branch, Sydney. Further paratypes: 15 ♂, 9 ♀ from Roseville, presented to the Commonwealth Institute of Entomology, London, and 15 ♂, 9 ♀ from the same locality presented to the Zoologisches Museum der Humboldt-Universität, Berlin, and 8 ♂, 4 ♀ from Roseville, presented to the Australian Museum, Sydney. The entire material was collected by Mr. C. E. Chadwick. 1 ♀ caught by Mr. F. Bagshaw on 6.ix.1956 at Normanhurst.

Description of the Larva (Text-fig. 4).

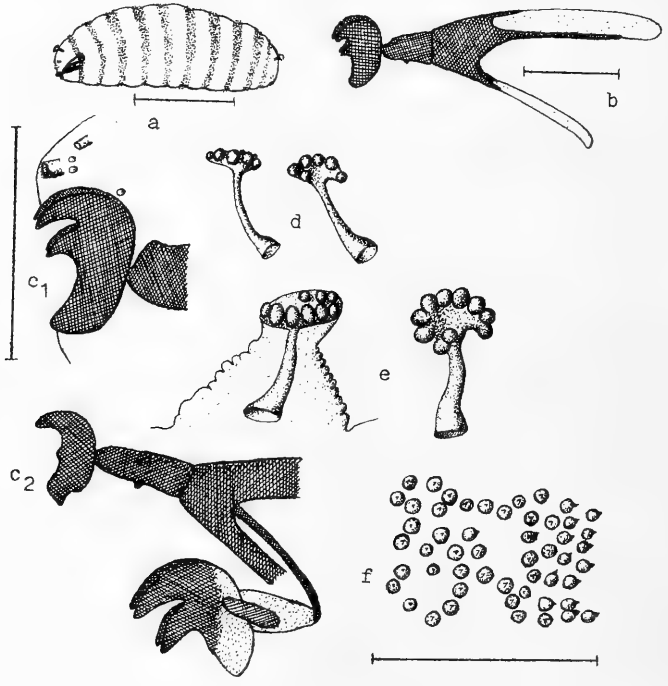
The larva (Text-fig. 4, *a*) is the normal shape of the majority of Agromyzid larvae. It is thus neither conspicuouly thin and elongated, nor is it noticeably short and thick. The cuticular processes used for movement (Wärzchen) are entirely absent in the region of the head, and also above and below the mandibles. On the prothorax there is an uninterrupted band of such processes which are arranged in 3–5 (ventrally only in 1–2) transverse rows. The band of the mesothorax is similar. On the metathorax there is a similar band with the processes in about six rows. On the first abdominal segment the band is somewhat broader, and the processes are irregularly in 8–10 rows; the bands on the second and sixth abdominal segments are similar. That of the seventh segment is narrower, and the processes are in only 6–7 irregular rows and are lacking on the dorsum, so that the band is interrupted above, while on all the previous segments it is entirely continuous. The last segment only has a small area with a few processes in the vicinity of the anal opening. All the processes are of similar shape and size (Text-fig. 4, *f*); they are roughly hemispherical and bear only the trace of a small

point, this being particularly clear in the hindmost transverse rows where the processes may also appear slightly smaller. It is noteworthy that the processes of the pro- and mesothorax are not smaller, as is usually the case in Agromyzid larvae.

Antennae slender, maxillary palps twice their thickness, the two varying little in length. A more strongly sclerotized frontal sclerite not apparent. On the cephalopharyngeal skeleton the shortness of the labial sclerite and the moderate development of the oral section of the paraclypeal phragma are very striking (Text-fig. 4, *b*). The dorsal process is about 1½ times as long as the ventral, and has entirely dark pigmentation only in the ventral areas; only the basal part of the ventral process is also entirely black. The lower arm of the dorsal process is vestigial. The mandibles have two teeth, the left one is only slightly shorter than the right and therefore the two pairs of teeth scarcely alternate (Text-fig. 4, c_1).

The anterior spiracles (Text-fig. 4, *d*) bear 6–8 bulbs, which are arranged in an ellipse open on the inner side. The atrium is long and thin, somewhat thickening at the point of transition with the trachea. The posterior spiracles (Text-fig. 4, *e*) are entirely similar; their atrium appears relatively shorter, they bear 8–10 bulbs.

In the second instar larva only the anterior tooth of the mandiles is fully developed; the rear one appears only as a small protuberance (Text-fig. 4, c_2).



Text-fig. 4. *Phytobia pittosporophylli* Hg., Larva as in Fig. 2 (c_1 = mandibles on third instar, c_2 = mandibles on second instar).

The Mine Gall (Pl. ii, fig. 3, 4; Text-fig. 3*b*).

When this paper was being prepared, there were so many flies of this species available, which had been caught on the young leaves of *Pittosporum*, that there can be little doubt that the larvae of *Phyt. pittosporophylli* represent the producer of the mine galls which are described below, although no bred specimens were obtained. Among the flies sent to me this species was far more numerous than the previous species, and similarly the mine galls which are about to be described, and which are considered to belong to this species, occurred in considerable numbers on almost every leaf.

Oviposition takes place in spring on the young leaves. The holes through which the eggs are inserted below the epidermis are made mainly on the upper surface of the leaf, near and to either side of the midrib; occasionally oviposition punctures and mine galls may be found singly near the margin of the leaf. Oviposition punctures were already found in large numbers in the young leaves on the 27th August, 1957 (Normanhurst, leg. F. Bagshaw). The hole where each egg has been laid is surrounded by a narrow violet-brown area (apparently caused by increased deposits of anthocyan). On the 16th September (Roseville, leg. C. E. Chadwick) there were already very young larvae in the young leaves which had eaten out small channels or blotches around the point of oviposition, and these appeared somewhat lighter in transmitted light. The pustules formed in the leaf in this way increase little in size during the course of the summer. In the material from the 4th May (Roseville, leg. C. E. Chadwick) they have a diameter of 3–5 mm. which does not become larger. When the first mine galls appear in the young leaves, the pustules of the previous generation can still be found in the old leaves (Text-fig. 3, *b*); in the mine galls where the larva has developed normally and produced an imago, one finds on the lower side the large, round emergence hole. The mine galls are only slightly transparent, with a brownish discoloration, raised, and in galls which have collapsed, wrinkled. Their immediate vicinity appears darker than the remainder of the leaf surface (presumably as a result of increased anthocyan deposits), particularly on the inside of the leaf.

In sections through the mine galls in young leaves (16th September) one finds cavities which are not differentiated from those of normal mine channels. The position of these feeding channels in the leaf is extremely variable. They normally lie in the palisade parenchyma, which in *Pittosporum* consists of three layers of cells. All three layers of cells may be consumed, but often the uppermost palisade layer, or a part of it, may remain. If the mine is deeper, it may also extend into the spongy parenchyma. Calius cells are not found in these mines. These formations are nevertheless not true mines, since, wherever a feeding channel occurs, the leaf is 2–3 times thicker than normal; this immediately shows the gall-like character of these mines. In autumn the mines are already substantially larger; a section across them now shows that fairly large, tender callus cells have grown into the cavity from the spongy parenchyma which are apparently eaten by the larva. Large lumps of frass fill a large area of the cavity. If the larva has not completed its development in the early spring mines (i.e., has died) the cavity becomes filled with sparse callus cells. Plate ii, figure 3 shows, to the left of the autumn mine, a lenticular cavity which is completely filled with a few large callus cells; in Plate ii, figure 4 a similar structure can be seen to the right of the large autumn mine in which the cavity is partially empty, partially filled with callus which has pushed forward dorsally a large mass of frass.

The greatest callus proliferation occurs in the area of the mine gall adjoining the midrib, a phenomenon which can be observed in normal mines on other plants, when they form callus. This occurs as a result of the increased flow of nutritive sap in the vicinity of the fibro-vascular bundles. Oviposition in the vicinity of the midrib, as normally occurs in this *Phytobia*, is thus particularly favourable for the subsequent development of the larva.

The feeding pattern of the larva of *Phytobia pittosporophylli* Hg. thus represents a further interesting case of transition from mine to gall, already recorded for a number of species of the family Agromyzidae, and it is therefore felt justifiable to use here the term "mine gall".

EXPLANATION OF PLATE II.

Fig. 1, 2. Cross-section of shoot axis of *Pittosporum undulatum* Andr. with twig gall of *Phytobia pittosporocaulis* Hg. 1: Feeding cavity in pericycle. 2: Expanded feeding cavity of last larval instar (stain: Safranin pale green F.S.).

Fig. 3, 4. Cross-section of midrib area of leaf of *Pittosporum undulatum* Andr. with mine galls of last larval instar of *Phytobia pittosporophylli* Hg. (Stain as in 1, 2.)

A NEW SPECIES OF TRIGONALID WASP PARASITIC ON THE SAWFLY *PERGA AFFINIS* KIRBY (HYMENOPTERA).

By E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra, A.C.T., Australia.

(Five Text-figures.)

[Read 18th April, 1962.]

Synopsis.

A new species of *Taeniogonalos* is described from inland New South Wales and Victoria. Re-examination of the Australian material placed in the genus *Taeniogonalos* has enabled a more satisfactory key for the separation of the species to be presented.

The trigonalid wasps of the genus *Taeniogonalos* are common parasites of Australian sawflies of the family Pergidae. This trigonalid genus has been revised by Riek (1954). Most of the material studied at that time had been collected from coastal regions. A new species is described from inland New South Wales and Victoria. The biology of the parasite is being studied by Dr. P. B. Carne.

Re-examination of the Australian material placed in the genus *Taeniogonalos* has enabled a more satisfactory key for the separation of the species to be presented.

TAENIOGONALOS VENATORIA, sp. nov.

Female.—Black, body marked with whitish-yellow and some reddish-brown; antenna usually all black, rarely pale at funicle segments 2 to 6 and then these segments pale more especially below; face black, widely marked with whitish (i.e., pale), mandibles pale except for teeth and narrowly at base, clypeus pale except at meson narrowly, pale areas very rarely joined at meson above, mesal and posterior margins of eye widely pale except at upper third, malar space pale, a pale area above antennal insertions, usually with two small pale spots below median ocellus, vertex with two pale transverse zones, separated at meson, with two small areas just anterior to their mesal ends, sometimes indistinct, occasionally joined to the transverse pale area and then normally large; colouring of head rather constant except for pale spots below median ocellus and smaller spots at vertex; colouring of thorax rather constant, thorax black, with distinct pale areas, pronotum with pale area on shoulders and anteriorly below, and usually a small spot below tegula, scutum pale anterolaterally, axilla pale distally, similar pale area on scutellum laterally, smaller transverse pale area on postscutellum, propodeum with larger pale area posterolaterally; thorax very rarely with an extra very small pale area on parapside at posteromesal corner; gaster with pale transverse bands on all but the third segment, segment 3 rarely with a very small pale spot laterally, pale bands of apical segments sometimes broken at meson; legs mostly reddish-brown, the femora more darkened, especially at base, with fore femur nearly all dark, coxae all dark, trochanters dark in part but fore trochanter pale anteriorly and hind trochanter usually all pale, trochanellus all pale; tibiae pale at base above and at least fore tibia with the pale area clearly white; wings in part almost clear but deeply infuscated over anterior third.

Antenna with scape, pedicel, and 24 funicle segments, with the apical segment somewhat longer than the penultimate. When the apical segment is shorter than the penultimate there are 25 funicle segments, due to subdivision of the normal apical segment, and when the normal penultimate segment and the preceding one are not

separated so that there are two enlarged apical segments, then there are only 23 funicle segments. Upper surface of body appearing glabrous between the ornamentation, more distinctly so on the head; gaster with the enlarged, backwardly directed ventral projection from segment 2 rounded at apex, sometimes with the process reduced and then narrower and pointed, rarely with the process completely absent; segment 3 ventrally with only a low transverse carina, in most cases just discernible (also present on those specimens with the process from the second segment reduced or absent). Tergite 2 of gaster with a rather glabrous basal triangle with irregular transverse rugae.

Male.—Not known.

Type.—Holotype ♀ and paratype ♀♀ in the C.S.I.R.O. Division of Entomology Collection, Canberra. Paratypes in the British Museum (Natural History).

Type Locality.—Benalla, Victoria (12 March, 1958, P. B. Carne), adults emerged January, 1959, reared from puparia of *Perga affinis* Kirby.

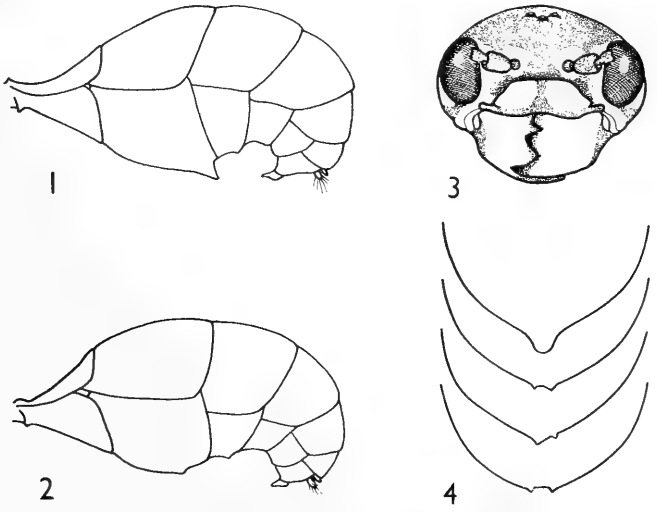


Fig. 1.—Side view of gaster of normal female. × 7.
Fig. 2.—Side view of gaster of female without process from second sternite. × 7.
Fig. 3.—Front view of head to show colour pattern. × 7.
Fig. 4.—Variation in the shape of the process from the second sternite of the gaster.

Specimens Examined.—A series of 42 female specimens from the type locality; 4 ♀♀, 5 miles S.W. Chiltern, Victoria (cocoons collected on 12th March, 1958, P. B. Carne, parasites emerged 31st March to 20th April, 1958); 15 ♀♀, 2 miles W. Rutherglen, Victoria (cocoons collected on 11 December, 1957, P. B. Carne, parasites emerged 5 April to 22 April, 1958); 19 ♀♀ W.S.W. Tumblong, New South Wales (cocoons collected on 10th December, 1957, P. B. Carne, parasites emerged 31st March to 24 April, 1958); 1 ♀ Ballarat, Victoria (28 May, 1957, M. F. Leask).

This species is very similar in most respects to *maculata*, but the whole body is more glabrous between the ornamentation. In *maculata* only the head appears glabrous to any extent. Although this difference is very obvious when the two species are compared, it is difficult to express in words. In the secondary sexual characters of the abdomen and in the structure of the antenna the two species are similar. There are some constant differences in colour, more particularly of the scutellum and the basal segments of the antenna. The species shows particular constancy of coloration except for one or two small areas on the head and one on the parapside as mentioned in the specific description.

It is most surprising that in this series of nearly one hundred specimens there is not a single male. In the series of 42 specimens from the type locality there are twelve abnormal specimens in which the ventral process from the second abdominal segment is either reduced or quite absent. In other respects these specimens have normal female genitalia and the antennae are typical female. Specimens from this locality show every gradation in this structure from full development to complete absence. In the well-developed condition this process forms a transverse lamella with a sharp distal margin. In the first stage of reduction the process is laterally compressed into a rather triangular spine. In other specimens this spine is reduced in strength

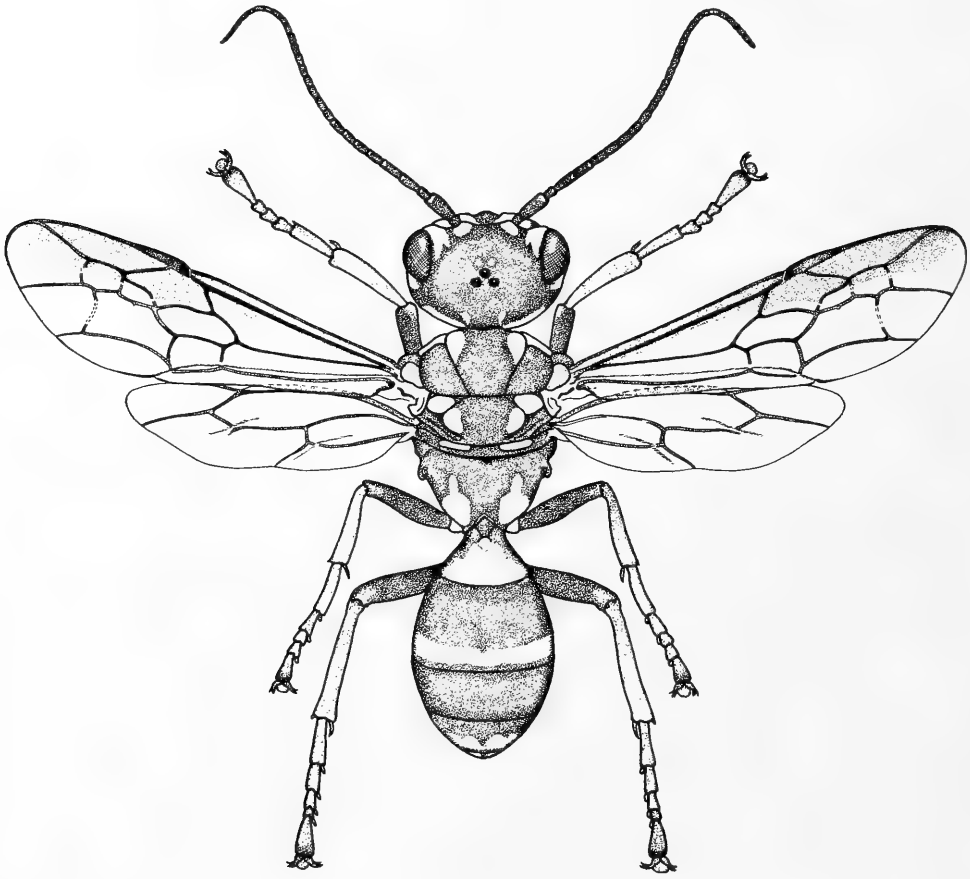


Fig. 5.—*Taeniogonalos venatoria*, sp. nov. Dorsal view. × 6.

and in a few specimens is completely absent. In those five specimens in which the spine is completely absent there is a small, round, median, sunken zone in tne corresponding position on the sternite. This sunken zone is considerably smaller and of quite a different shape from the sunken zone appearing in a similar position in males of other species and is isolated from the caudal margin of the sternite. Apart from this one character these specimens are all typical females. Reduction in the development of this process from the second sternite is most unusual in specimens from the other localities. Only one of the remaining fifty or so specimens shows a slight reduction in the process.

Key to the Australian species of Taeniogonalos.

1 (2, 7) Head and thorax all black, abdomen all reddish-brown; wing only lightly infuscated but darker at costal space and at apex anteriorly ..... *semibrunnea* (Bischoff).

2 (7, 1) Species mostly black, marked with yellow and reddish-brown; wing deeply infuscated anteriorly.

3 (4) Scutellum all dark (sometimes with a pale lateral mark in the male); scape and pedicel not as dark as head; tibiae without a clear white mark above towards base; tergite 2 of gaster entirely punctate almost to base (process from sternite 3 of gaster (♀) only a low transverse carina; process from sternite 2 entire at apex, rather blade-like; female antenna usually with 24 funicle segments, male with 23) .... *maculata* (Smith).

4 (3) Scutellum with pale lateral mark; scape and pedicel black; at least fore tibia with a clear white mark above towards base; tergite 2 of gaster with a basal subglabrous triangle crossed by irregular transverse rugae.

5 (6) Process from sternite 3 of gaster (♀) strongly produced, transverse, clearly emarginate at apex; process from sternite 2 bluntly bifid at apex; female antenna with 22 funicle segments ..... *tenebrosa* (Riek).

6 (5) Process from sternite 3 of gaster (♀) only a low transverse carina; process from sternite 2 entire, rounded at apex, rather blade-like, sometimes quite reduced; female antenna usually with 24 funicle segments (less often 23 or 25) .... *venatoria*, sp. nov.

7 (1, 2) Species strongly marked with yellow or yellow and red; wing deeply infuscated anteriorly.

8 (9, 10) Ventral process of segment 2 of gaster (♀) slightly bifid at apex; segment 3 with a lamellate process; antenna (♀) with 23 funicle segments ..... *tricolor* (Rayment).

9 (10, 8) Ventral process of segment 2 of gaster (♀) entire at apex; segment 3 without process; antenna (♀) normally with 23 funicle segments ..... *tricolor similis* (Riek).

10 (8, 9) Ventral process of segment 2 of gaster (♀) slightly bifid at apex; segment 3 with a triangular-sided process; antenna (♀) with 20 funicle segments .. *chadwicki* (Riek).

Reference.

RIEK, E. F., 1954.—Australian Trigonalidae (Hymenoptera, Ichneumonoidea). *Austr. Journ. Zool.*, 2: 296-307.

A NEW GENUS OF AUSTRALIAN STONEFLIES (PLECOPTERA, GRIPOPTERYGIDAE).

By E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

(Text-figures 1–6.)

[Read 18th April, 1962.]

Synopsis.

An early emerging species of stonefly from the subalpine streams of south-eastern Australia is placed in a new genus. The species shows affinity in the adult to the common genus *Trinotoperla* and in the nymph to the rare genus *Eunotoperla*. The nymph has an anal gill tuft quite unlike that of other genera of the family.

During the first week of September a large hatching of stoneflies was observed on the Eucumbene River, one of the subalpine streams of south-eastern Australia. There appeared to be three species in the hatch, a small, dark nemourid, a small thin species of *Leptoperla* with its characteristic long cerci, and a larger species of *Trinotoperla* or *Dinotoperla*. The latter two genera are difficult to distinguish by eye, but on size it appeared more likely to be a species of *Trinotoperla*. Closer examination of a sample revealed the presence of eight species of nemourids, three species of *Leptoperla*, one species of *Dinotoperla* and another species, the largest, which could without much difficulty be placed in *Trinotoperla*.

Cast nymphal exuviae corresponding in size with this species, as well as some smaller ones of *Leptoperla*, were collected. A few large fully developed nymphs were taken under debris (tree trunks) in the stream. Other smaller nymphs of several species of *Dinotoperla* and *Leptoperla* were abundant. The burrowing nymphs of the nemourids were not collected. There was no difficulty in associating the larger exuviae with the larger nymphs because of the most distinctive anal gills. A freshly emerged adult, still callow, and its associated exuvium leave no doubt about the association of nymph with adult. The hatch of this species was very heavy and the grassy banks bordering the lower ends of the runs of the stream were covered with adults. This may account for the relatively small number of observed nymphs of this species, though their preferred habitat may have been overlooked.

Whereas the adult is not unlike the species of *Trinotoperla*, the nymph is more like the nymph of *Eunotoperla*. A few nymphs collected on an earlier occasion were tentatively placed, as a second species, in *Eunotoperla*, while the adults were referred to a new species of *Trinotoperla*.

Adults of the species have been collected in very small numbers as late as the first week of December, but these may have been survivors from a much earlier hatch.

Family GRIPOPTERYGIDAE.

Genus Aldia, gen. nov.

Genotype, *Aldia montana*, sp. nov.

Adult.—Similar to *Trinotoperla*, but differing in head shape and slightly in wing venation. Ocelli forming an almost equilateral triangle, the median ocellus distinctly smaller than the lateral ocelli; frons not clearly produced over the clypeus; Rs forked in both wings; CuA of forewing 2-branched, both branches long; in hindwing Rs and M fused for only a short distance at base.

Nymph.—Very similar to nymph of *Eunotoperla*, but with the anal gills distinctive. Anal gills reduced to less than 20, spaced, borne at the apex of a longer than wide stalk. Frons not produced over the clypeus; facial suture between eye and lateral ocellus straight or almost so; vertex of head with a few long hairs; lacinia rather truncate at apex, without distinct teeth; posterolateral margin of head rounded; prosternum not produced posterolaterally behind the fore coxa to form a rounded knob, trochanters without apical spine; femora and tibiae all with a marginal row of dense long hairs; cerci with a row of dense long hairs on upper surface, cerci about as long as antennae but not quite as thick; caudal margin of mesonotum convex; pronotum with rounded angles.

The hair-tufts on legs, head and cerci are not quite as well developed as in *Eunotoperla* and the mature nymph is considerably smaller.

ALDIA MONTANA, sp. nov. (Figures 1–6.)

Adult.—Length of body 11 to 14 mm., cerci about 2 mm., antenna 13 to 15 mm.; forewing and costal border of hindwing with a distinct fine mottling; hindwing slightly more infuscated than forewing; head and thorax dorsally mostly dark; antenna dark; legs mostly dark, middle and hind femora dorsally with a pale spot in the middle; abdomen mostly pale, apical three segments dark, but male genitalia pale; thoracic sternites mostly dark; male and female genitalia figured.

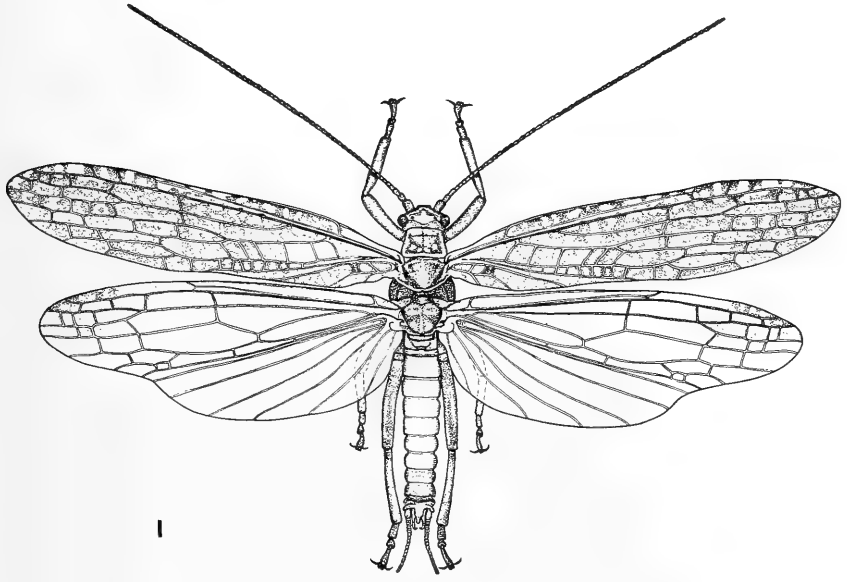
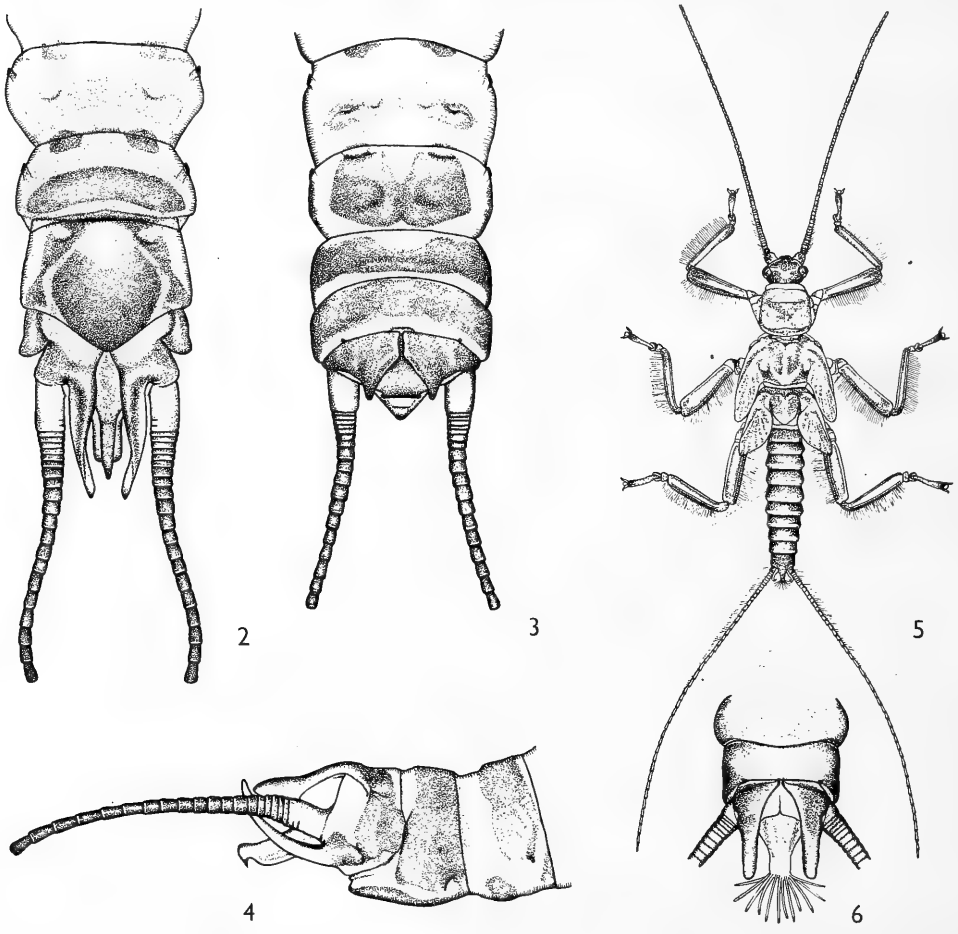


Figure 1. *Aldia montana*, gen. et. sp. nov. Adult male, × 4.

Nymph.—Length of body of mature nymph 10·0 to 11·0 mm., antennae 10 mm., cerci 10 mm. Body above, rather dark, abdomen all dark except at joints; thorax patterned, pronotum mostly pale at meson and anterior margin, meso- and metanota pale at wing bases and caudal meson; head mostly dark, but pale at vertex at meson; cerci mostly pale, narrowly dark at apex of segments; legs with a pale spot on upper surface of middle and hind femora, tarsi dark at apex, but tarsal claws pale.

Eyes somewhat bulging, postocular region short, narrowing rapidly; ocelli of almost equal size; pronotum slightly narrower anteriorly than posteriorly; hair-fringes on femora about as wide as two-thirds width of femora; first segment of the tarsus from below clearly longer than wide, distinctly larger than second segment, apical segment from below only slightly longer than basal two segments combined.

Types.—Holotype male, allotype female, typical nymph, a long series of paratype males, 6 paratype females and a long series of nymphs and cast nymphal exuviae in spirit in the C.S.I.R.O., Division of Entomology Museum, Canberra.

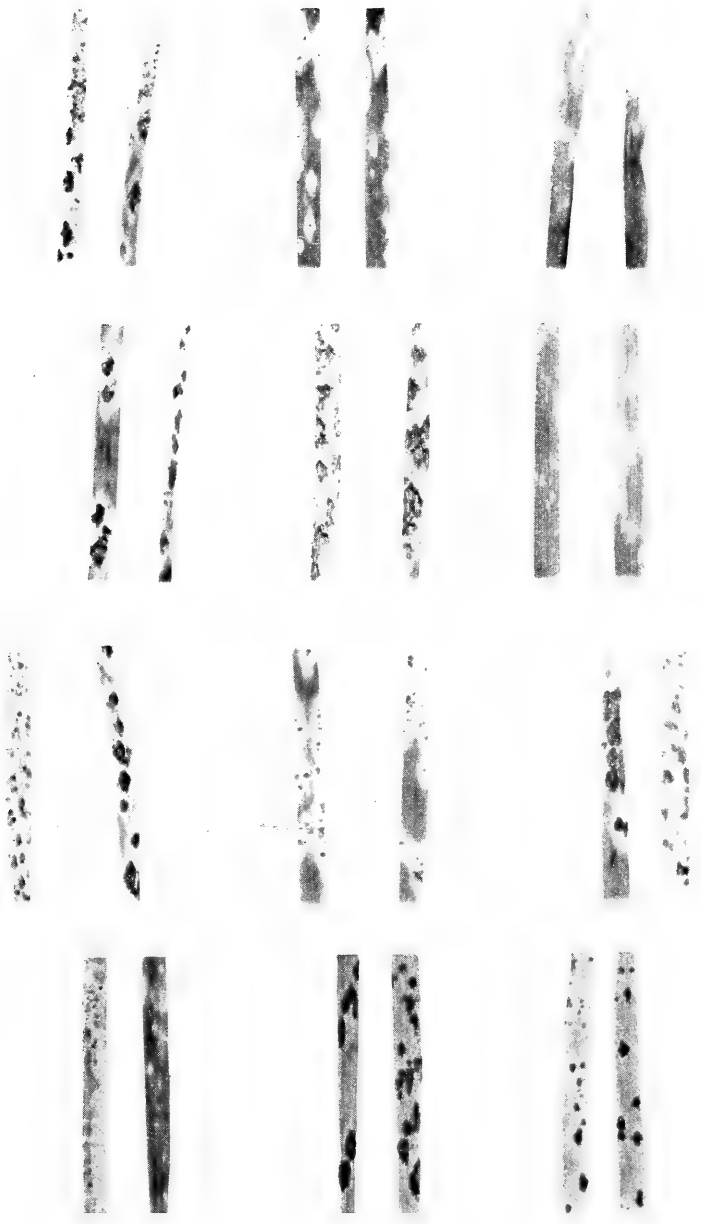


Figures 2-6. *Aldia montana,* gen. et. sp. nov. 2, Male genitalia, ventral view, × 20. 3, Female genitalia, ventral view, × 20. 4, Male genitalia, side view, × 20. 5, Mature male nymph, × *c.* 4. 6, Apex of abdomen of mature female nymph, ventral view, × 20.

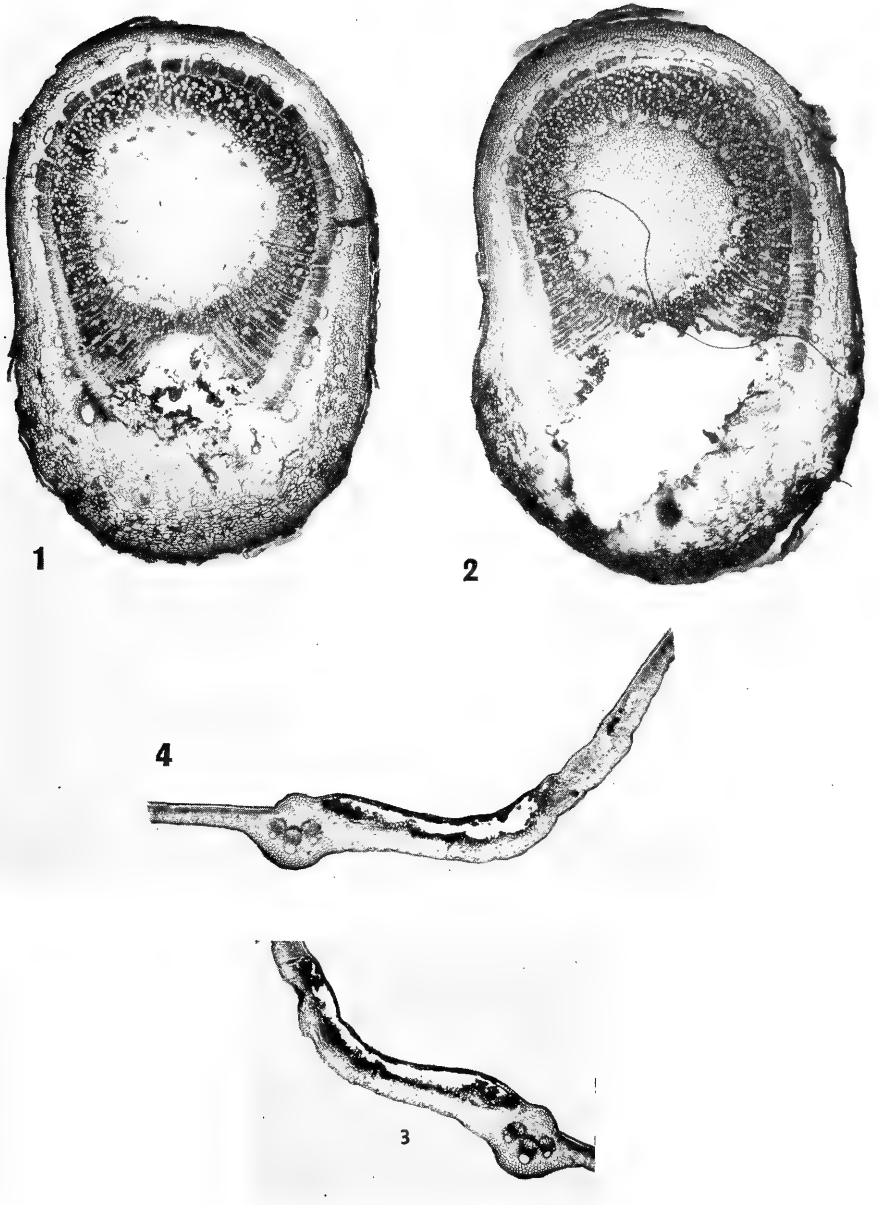
Type Locality.—Eucumbene River, Kiandra, New South Wales (6th September, 1961, E. F. Riek and A. L. Dyce).

Adults have also been collected from the type locality during October, November and December, 1960.

In dried specimens the mottling of the wings is faint.



Wheats inoculated with cultures of *P. graminis*.
Galls of *Phytobia pittosporocaulis*.



Phytobia pittosporophylli on *Pittosporum undulatum*.

ASEXUAL INTERCROSSES BETWEEN SOMATIC RECOMBINANTS OF *PUCCINIA GRAMINIS*.

By I. A. Watson and N. H. Luig, Faculty of Agriculture, The University of Sydney.

[Read 30th May, 1962.]

Synopsis.

Somatic recombinants obtained from mixing uredospores of *P. graminis* var. *tritici* and *P. graminis* var. *secalis*, as well as those obtained by mixing uredospores of different strains of the former rust, were intercrossed as dicaryons on Little Club. Three recombinants were mixed as uredospores, allowed to grow on Little Club and the resulting spores were used to infect sets of wheat varieties resistant to the components of the mixtures. Eight red and two orange variants were obtained in this way. Mutation could explain the origin of certain of these, but nuclear exchange or nuclear exchange combined with mutation at single loci appear unlikely as processes to explain the variation.

Although several workers have reported that when uredial cultures of either *P. graminis* Pers. or *P. recondita* Rob. ex Desm. are mixed, recombinant strains will arise (Nelson *et al.*, 1955; Nelson, 1956; Watson, 1957; Watson and Luig, 1958, 1959; Bridgmon, 1959; Vakili, 1959; Bridgmon and Wilcoxson, 1959; Ellingboe, 1961) no completely satisfactory explanation has been given to account for the results. The present studies were undertaken to gain a better understanding of the process by which somatic recombinants arise and also to determine whether the factors for virulence are transmitted in Mendelian fashion.

Review of Literature.

Nelson *et al.* (1955) and Nelson (1956) postulated that when different races of *P. graminis* var. *tritici* were mixed, hybrids arose by an exchange of nuclei and that instability of virulence on particular varieties resulted from the dissociation of the members of a tri-nuclear condition. Watson and Luig (1958) suggested a process similar to that of the parasexual cycle (Pontecorvo, 1956) to explain 11 somatic recombinants obtained from a cross between race 111 and orange NR–2. A mechanism involving fusion, crossing over, segregation and recombination in the dicaryophase was suggested by Vakili (1959) for *P. recondita* to explain a multiplicity of recombinants from a cross between two races having different pathogenic characters.

Garrett (1960) obtained two red and two orange recombinants from a mixture of transplanted mycelia of race 11 (orange) and race 121 (grey brown).

Bridgmon (1959) crossed two strains of *P. graminis* var. *tritici* both virulent on Einkorn, and obtained 15 recombinants, of which five were previously undescribed. Two of the five new strains proved to be avirulent on Einkorn. This result is of considerable interest since sexual crosses between parental strains virulent on Einkorn would be expected to produce progeny all virulent like the parents, since virulence on this variety is a recessive character (Johnson, 1954; Luig and Watson, 1961).

In *Melampsora lini* (Pers.) Lev. it has been suggested by Flor (1960) that nuclear exchange takes place between "+" and "–" nuclei when cultures are mixed and such a process could result in new strains. However, he obtained several recombinant races from mixing uredospores of four F_1 cultures which resulted from a sexual cross between race 1 and race 22. He explained these variants on the basis of nuclear exchange followed by single gene mutations for virulence that could be more readily detected following nuclear exchange.

Materials and Methods.

The procedure used in making somatic hybrids between dicaryons was the same as that previously described (Watson, 1957; Watson and Luig, 1958). In the initial crosses three strains were used, each of which had its origin in a single uredospore. These strains were orange NR–2 (Watson, 1957), *P. graminis* var. *secalis* 57241 (Watson and Luig, 1959) and a grey brown culture which on the standard stem rust differentials conforms in reaction type most closely to race 80. It was obtained from St. Paul, Minnesota, U.S.A., and on account of its colour is essentially a laboratory culture.

The three above strains were used in the following two crosses:

(i) Orange NR–2 × Red 57241 *P. graminis* var. *secalis*.

(ii) Orange NR–2 × Grey brown 80.

During the mixing of the uredospores and during the time when the hybrids were being produced frequent tests were made to check the purity of the parental cultures. The unusual reaction of Mentana, Spelmar and Acme which produce only ";" type reactions to these strains was clear evidence of purity. Possible contaminants would all produce on these varieties reactions unlike the ";" type.

The results from the initial cross (i) above have already been described and hybrid cultures M–9–a and M–10–a were isolated (Watson and Luig, 1959). From cross (ii) only one hybrid culture was derived, M–2. All hybrids from crosses (i) and (ii) were red in colour.

The second series of crosses on which the present work is based were made between pairs of the three hybrid cultures as follows: (iii) M–10–a × M–2; (iv) M–10–a × M–9–a; (v) M–9–a × M–2.

The mixtures of pairs of cultures were made in the usual way and grown on the variety Little Club. The resulting spore population following the inoculation was observed for variations in spore colour; the mixed population was then used to inoculate differential varieties. Six mixtures were made of cross (iii) and the resulting spores from Little Club were transferred to Reliance, Einkorn, Mindum and Yalta. Two mixtures of cross (iv) were made and the screening was done on Reliance, Kota, Kubanka, Einkorn and Mindum. The varieties Reliance, Einkorn and Mindum were used to screen the mixture of cross (v).

In those cases where variants in colour or pathogenicity were observed, they were isolated and tested on the appropriate differential varieties. One purpose of the crosses was to determine whether it is possible to reconstitute the parental cultures NR–2, red *P. graminis* var. *secalis* and grey brown 80 by mixing the progeny. Consequently, as an added precaution against contamination, the parental types were taken from the glasshouse and stored during the progress of this particular stage of the experiments.

Experimental Results.

The reaction types of ten varieties of wheat and of Black Winter Rye to the three parental strains of the initial crosses NR–2 grey brown 80 and red 57241 are given in Table 1. The reactions of these same varieties to the three hybrid strains are also presented in this table for comparison. M–2, resulting from the cross orange NR–2 × grey brown 80, was a red hybrid and presumably derived its spore colour from a combination of the factors for orange and grey brown spores present in the parents, orange NR–2 and grey brown 80 respectively. In pathogenicity the hybrid M–2 is avirulent on five wheat varieties among the ten. It has apparently inherited the dominant factors for avirulence on Reliance and Einkorn from the grey brown parent. The recessive factors for avirulence on Acme and Yalta have presumably come from the parents, orange NR–2 and grey brown 80 respectively. Avirulence on Spelmar shown by each parental culture has been transmitted to the hybrid. The two parental cultures are not equally virulent on Emmer, but the hybrid is about as virulent on this variety as the orange NR–2 parent. As the genes for virulence on Emmer are recessive (Johnson and Newton, 1940) all hybrids between these two parents would be expected to attack Emmer.

The characteristics of the cultures M–9–a and M–10–a have already been described (Watson and Luig, 1959) and their avirulence interpreted as due to genes derived from *P. graminis* var. *secalis*.

The results of making the three crosses of the second series are presented in Table 2. From cross (iii) of M–10–a × M–2 four cultures were derived and three of these were red in colour and one was orange. As shown in Table 2, the four derived

TABLE 1.

The Reactions of 10 Wheat Varieties and Black Winter Rye to Parental Strains of P. graminis *and Three Somatic Hybrids between Them.*

Variety.	Accession Number.	Parent Strains.			Progeny Strains.		
		Grey Brown 80.	Orange NR–2	Red *P. graminis* var. *secalis* 57241.	Orange NR–2 × *P. graminis* var. *secalis*.		Orange NR–2 × Grey Brown 80.
					M–9–a.	M–10–a.	M–2.
Little Club ..	1	3+	3+	;1,2–	3c	3c	3+
Marquis ..	2	2+,3	3+	;	;,2≡	X,2‡	3
Kota	4	3	3	0,;	0,;	0,;	3
Reliance ..	1047	0	3+	0	0	0	0
Spelmar ..	7	0,;	0,;	0,;	0,;	0,;	0,;
Kubanka ..	8	X	X	0,;	0,;	0,;	X+
Acme ..	9	3+	0,;	0,;	0,;	0,;	0 ;
Einkorn ..	10	;1–	3+	;1–	3–c	3–	;1–
Emmer ..	11	2+	3+	;	;1+	3	3
Yalta (Sr 11)	1373	;1	3+	;	3	;1	;1
Black Winter Rye		;1=	;1=	2,3+	1,2,3+	1,2,3+	;1=

types have been designated NR–28, NR–29, NR–30 and NR–31. NR–29 was the orange derivative and it differed from the parental culture M–2 only in colour. It is possibly a colour mutant arising from the parental type, but no work has been done to confirm this. All four cultures were very unlike the second parent M–10–a.

The culture NR–28 is clearly different from M–2 on the variety Reliance since the latter is resistant to M–2. It is unlikely that a mutation for pathogenicity is involved

TABLE 2.

Reaction of 13 Wheat Differential Varieties to Parental Strains M–10–a, M–9–a and M–2 and to 10 Hybrids from the Three Somatic Crosses between Them.

Variety.	S.U. Number.	Parents.			Progeny Strains.									
					M–10–a × M–2.				M–10–a × M–9–a.			M–9–a × M–2.		
		M–10–a.	M–9–a.	M–2.	R.	O.	R.	R.	O.	R.	R.	R.	R.	R.
Little Club ..	1	3c	3c	3+	3+	3+	3+	3c	3+	3+	3+c	3+	3+	2+
Marquis	2	X,2‡	;2≡	3	3+	3	3+	3	3+	3+	3+	3+	3+	;
Kota	4	0;	0;	3	3c	3	3	3	3	3	3	3	3	3
Reliance	1047	0	0	0	3+	0	0	0	3+	3+	3+	3+	0	0
Spelmar	7	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;
Kubanka	8	0;	0;	X+	3	X+	X+	X+	X	X	X+	X+	X+	;
Acme	9	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;
Einkorn	10	3–	3–c	;1–	;1–	;1–	;1–	;1–	3+	3+	;1–	;1–	;1–	;1–
Emmer	11	3	;1+	3	3c	3	3	3c	3+	;1=	3	3	3	;
Yalta	1373	;1	3	;1	;1	;1	X	;1	3+	;1	;1	;1	X	3
T. dicoccum ..	2698	;1	;1–	;2	;2	;2	;2	;2	;2	2+	;2	;2	;2	–
Webster	973	2–	2–	2‡	2–	2‡	2+	2	2+	3	3–c	2	2+	–
Kenya White ..	1025	;	;	;1	;1	;1	X+	3+	3c	;1	;1	2=	;2	–
Strain designation		M–10–a	M–9–a	M–2	NR–28	NR–29	NR–30	NR–31	NR–2	NR–32	NR–33	NR–34	NR–35	

The designations NR–1 to NR–26 were used in previous publications.
R = Red uredospores; O = orange uredospores.

here as Kubanka, Webster, Kota and Thew (Table 3) all show differences in their reactions to NR–28 and M–2.

The varieties Kenya White and Yalta showed reactions to NR–30 unlike those given to the parental culture M–2. The reaction type "X", produced by NR–30 on Yalta, resembled that obtained on this variety when inoculated with certain of the sexual progeny obtained by selfing *P. graminis* var. *secalis* (Watson and Luig, 1961). One of the parents of NR–30, M–10–a, arose from a somatic cross involving *P. graminis* var. *secalis*.

The fourth hybrid from this cross differed in pathogenicity from the parent M–2 on Kenya White and Webster, although on the latter the difference was not so pronounced.

From cross (iv) which involved the red parents M–10–a and M–9–a three strains were isolated. One of these was orange in colour and in a detailed comparison it was found to be identical with NR–2, the original orange culture which figured in the parentage of the red cultures M–10–a and M–9–a. During the period of time when the

TABLE 3.

Reaction of 16 Common Wheat Varieties to the Parental Strains and the Hybrids between Them.

Variety.	S.U. Number.	Parents.			Progeny Strains.									
					M-10-a × M-2.				M-10-a × M-9-a.			M-9-a × M-2.		
		M–10–a.	M–9–a.	M–2.	R.	O.	R.	R.	O.	R.	R.	R.	R.	R.
Gabo	1422	;	;1=	;1=	;1=	;1=	2=	;1=	3–[c]	;	;	;1=	;	–
Bobin	39	2≡	2≡	2–	2=	2–	2–	2	3[c]	2+	2–	2	2=	–
Eureka	1325	;	;1–	3+[c]	3+[c]	3+[c]	3+[c]	3+[c]	;1	3+[c]	3+[c]	3+[c]	3+[c]	;
Brevit	972	3+[c]	3	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	–
Loros	974	2–	2–	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	–
Mentana	1124	;	;	;	;	;	;	;	;	;	;	;	;	;
Federation ..	107	3	3=[c]	3+	3	3+	3+	3+	3+	3+	3+	3+	3+	–
Pusa	806	3–[n]	;	3+	3+	3+	3+	3+	3[c]	3+	3[c]	3+	3+	–
Chinese Spring ..	1806	3+	3[c]	3+	3	3+	3+	3+	3	3+	3	3	3+	–
Thew	203	3–[n]	;1=	3[c]	3+	3[c]	3+	3	3	3+	3+[c]	3	3	–
Morocco	1103	3+	;1	3+	3+	3+	3+	3+	3+	3+	3+	3+[c]	3+	–
Dundee	985	;	;	3	3+[c]	3	3+	3+	;1=	3+	3+	3+	3	–
Glossy Huguenot	304	2–	2+	3+[c]	3	3+[c]	3	3+	3[c]	3+	3[c]	3+	3+	–
Glenwari	1991	2=	;	3+[c]	3+[c]	3+[c]	3+	3+	;1–	3+	3[c]	3+[c]	3+	–
Mona	1168	2+	;	3+	3+	3+	3+	3+	;1	3+	3	3+	3+	–
Girral	987	2–	3=[c]	3+	3+[c]	3+	3+	3+	3+[c]	3+	3	3+	3+	–
Strain designation		M–10–a	M–9–a	M–2	NR–28	NR–29	NR–30	NR–31	NR–2	NR–32	NR–33	NR–34	NR–35	

O = Orange uredospores; R = red uredospores.

intercrosses were being made the parental cultures were stored. This removes any doubt as to the origin of the orange culture among the progeny of M–10–a and M–9–a. It has clearly been reconstituted from the mixing of red spores of these two cultures.

The other two hybrids of this cross NR–32 and NR–33 differed from both parents on several varieties. An analysis of the reactions of Emmer and Einkorn shows that NR–32 is virulent on Einkorn but avirulent on Emmer, while the reverse holds for NR–33. NR–32 was somewhat more virulent than the parents and other hybrids on Bobin W39, Webster and *T. dicoccum* as shown in Tables 2 and 3.

Cross (v), which involved the parents M–9–a and M–2, resulted in the isolation of three different strains. One of these, NR–35, showed certain similarity to NR–28 obtained from cross (iii) but was different on Kubanka. NR–35 resembled M–2 but differed slightly from it on Webster, Yalta and Kenya White. NR–36, the third strain isolated from this cross, was unusual in showing avirulence on Marquis and this character and the partial virulence on Little Club were both unusual. The culture showed certain features in common with the parent M–9–a, but the avirulence of the latter on Kota clearly differentiated it from NR–36. This culture was lost before all tests could be completed.

The experimental results obtained from this study are in general agreement with those obtained in other studies we have reported (Luig and Watson, 1961). Unusual characters which have marked the cultures under study have been maintained throughout, and consequently contamination can be discounted. The characteristic and sharp hypersensitivity shown by Acme and Mentana to the parental cultures has been inherited in all progeny cultures. The recessive gene for avirulence on Arnautka, Mindum and Spelmar was apparently present in all parental and progeny cultures. Crosses which involved a recessive gene for virulence on a particular variety, e.g., Vernal Emmer, always yielded progeny having that same virulence. M–10–a and M–2 both attack Emmer and the four strains NR–28, NR–29, NR–30 and NR–31 obtained from mating them also attack Emmer. Crosses which involved dominant or heterozygous dominant genes for avirulence on a particular variety yielded some cultures avirulent and others virulent for that variety, e.g., the cultures M–10–a, M–9–a and M–2 were avirulent on Reliance, but progeny virulent on Reliance was obtained in each cross.

The situation with regard to the variety Einkorn was somewhat different. Crosses where M–2 was mixed with M–10–a or with M–9–a did not produce a single hybrid virulent on Einkorn. On the other hand, two of the three hybrids obtained from mixing M–10–a and M–9–a were virulent on Einkorn. In fact these were more virulent on Einkorn than were the parental cultures M–10–a and M–9–a. This suggests that the 3– and 3–^{c} shown by the Einkorn when inoculated with these two cultures may not be the expression of the well recognized recessive gene for virulence on Einkorn but a modification resulting from the association with genes from *P. graminis* var. *secalis*.

Discussion.

These studies are being undertaken to determine the nature of the process involved in somatic recombination. We have suggested (Watson and Luig, 1958) the possibility that a parasexual cycle is concerned. Nelson (1956) postulated nuclear exchange as the means whereby variation took place. Flor (1960) has presented evidence in which he claims nuclear exchange combined with mutation can explain the results with flax rust, *Melampsora lini*.

It is difficult to interpret the present results on the basis of nuclear exchange, and if this process combined with mutation is suggested then simultaneous changes in pathogenicity at several loci must be presumed. From mixing the cultures M–10–a and M–9–a, both avirulent on Reliance, three hybrids were obtained and all were virulent on this variety. Virulence on Kanred and Reliance is conditioned by a single recessive gene (Johnson, 1954; Luig and Watson, 1961) and nuclear exchange could result in only one strain virulent on this variety. Reactions of certain other varieties to individual strains are equally difficult to interpret by nuclear exchange.

Among the progeny of intercrosses of red cultures two isolations were made of strains with orange-coloured spores. One of these was similar to M–2 and is presumed to be a mutation for colour from the red parent. Such mutations for colour are quite commonly detected in the glasshouse, and of all the common Australian field strains of stem rust orange spored counterparts are available as stock cultures. The isolation of an orange culture identical with the orange parent NR–2 shows clearly that parental strains may be reconstituted by mixing their progeny as somatic crosses. The fact that this parent culture was isolated lends support to the suggestion made by Flor (1960).

When two nuclei only are present in a dicaryon it could be expected that they will continue to be associated and the culture in which they occur will show a characteristic pathogenicity pattern. It is quite possible, however, that, while a certain attraction may exist between the members of this dicaryon, other nuclei may be present in other cultures which would offer a greater attraction for one or other of the nuclei in the first culture. If this is the case then somatic recombinants following nuclear exchange would be common in mixtures involving the dicaryon with the uncongenial association. From our own observations red race 111 appears to undergo somatic hybridization

readily with other strains, but for the reason of the multiplicity of strains recovered nuclear exchange alone cannot explain the results.

In the studies that have been reported to date on somatic recombinants resulting from mixing strains of *P. graminis* no consideration has been given to the importance of the cytoplasm in the expression of pathogenicity. It is conceivable that the movement of nuclei from one cytoplasm to another may itself result in a change of pathogenicity. The material has not been favourable for experiments to be made on this aspect of the problem, but the role of the cytoplasm, if any, in this phenomenon must be studied before the latter is completely understood.

Acknowledgements.

We ackrowledge financial assistance from the University of Sydney research grant and from the Wheat Industry Research Council which has made these studies possible.

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THE GENUS *WALCHIELLA* (ACARINA, TROMBICULIDAE).

By Robert Domrow, Institute for Medical Research, Kuala Lumpur.*

(Sixty-three Text-figures.)

[Read 30th May, 1962.]

Synopsis.

Material from the type series of all except one of the species ascribed to *Walchiella* has been examined to check the status of the two species described by Gunther. His *impar* is a valid species, with *asonluca* Traub and Audy as a synonym. His *bodensis* is a synonym of Walch's *oudemansi*. All other names (excluding a *nomen nudum, clauda* G'thr.) are considered valid. *Walchiella beauforti*, n. sp., is described from a porcupine, *Thecurus crassispinis* (Hystricidae) from North Borneo. A key is provided, and new illustrations for little known species.

The long-standing uncertainty about synonymy within *Walchiella*, and the opportunity of describing a new species from Borneo, have induced me to study this group, which Vercammen-Grandjean (1960) and Domrow (1960) both accord generic status among the trombiculines. Including the new species, twelve names have now been proposed for species of this genus. Two of these are synonyms (*asonluca* and *bodensis*), and one a *nomen nudum* (*clauda*), leaving nine species recognized here as valid. These may be disposed in two species groups according to the segmentation of the legs (Audy and Domrow, 1957). While preparing this paper, I have been able to examine material from the type series of all but one species, the common and characteristic *oudemansi*. Illustrations are given for all species, except two (*oudemansi* and *calunosa*) for which reliable figures have already been published. Documentation is limited to the original reference to each species and synonym, but more complete lists of references may be found in Wharton's manual (1952). Several important corrections to original descriptions have been given by Womersley and Audy (1957).

Genus Walchiella Fuller.

Walchiella Fuller, 1952, in Wharton (1952), *Mem. ent. Soc. Wash.*, 4: 95. Undated, but not earlier than March from internal evidence, see p. 150.

Walchiella Fuller, 1952, *Zool. Verh.*, 18: 220. December 12.

Type-species by monotypy *Trombicula oudemansi* Walch, 1922, *Geneesk. Tijd. Ned.-Ind.*, 62: 563.

It seems clear that the ascription of *Walchiella* to Fuller alone is correct. Wharton uses the phrase "aided by H. S. Fuller" on the title page of his manual, and on p. 95 expressly credits the genus to his associate, thus: "Genus *Walchiella* Fuller, new genus." This publication presumably antedates Fuller's study of the Oudemans collection, which is dated December 12.

Key to larvae of genus Walchiella.

1. Legs 7.7.7-segmented, with femora divided (the *lacunosa* species group) ..... 2.
   Legs 7.6.6-segmented, with femora II and III undivided (the *oudemansi* species group) .. 5.
2. AL noticeably shorter than AP ..... 3.
   AL decidedly longer than AP ..... 4.
3. Sensillae symmetrical; PL = AL ..... *beauforti.*
   Sensillae asymmetrical; PL < AL ..... *lacunosa.*
4. AL shorter than PW ..... *sarawakensis.*
   AL longer than PW ..... *nadchatrami.*
5. Chelicerae dentate ..... *oudemansi.*
   Chelicerae simple ..... 6.

* On half-time loan from the Queensland Institute of Medical Research, Brisbane, to participate in a project "Bionomics of Oriental-Australasian acarine vectors" sponsored by the George Williams Hooper Foundation (University of California Medical Center), and supported by U.S. Public Health Service Grant E-3793.

6. Dorsal setae set on distinct platelets ..... *traubi.*
   Dorsal setae set directly in cuticle ..... 7.
7. With more than 40 dorsal setae ..... *lewthwaitei.*
   With 28-30 dorsal setae ..... 8.
8. Second and fifth setae in first dorsal row longer than remainder; AW < 53, PW < 71 ..... *impar.*
   Setae in first dorsal row of uniform length; AW > 65, PW > 94 ..... *calunosa.*

THE *LACUNOSA* SPECIES GROUP, AUDY.

Diagnosis.—Legs 7.7.7-segmented, with femora divided.

WALCHIELLA BEAUFORTI, n. sp. Figs 1–12.

Diagnosis.—AL < AP; PL = AL; sensillae symmetrical.

Type Material.—Holotype larva (27461) and six paratype larvae (27454, 6, 8 and 31529, 32, 3) from a porcupine identified by J. L. Harrison as *Thecurus crassispinis* (Günther) (Hystricidae), R18638, Beaufort, British North Borneo, 18.v.1952, joint Colonial Office—U.S. Army Medical Research Units expedition. Holotype larva in British Museum (Natural History), London; paratypes in U.S. National Museum, Washington; Rocky Mountain Laboratory, Hamilton; and both my laboratories.

Larva.—Size of idiosoma (mounted) in slightly engorged specimens from 319 × 242 to 374 × 286μ; in engorged specimen 550 × 374μ.

Body Setation.—Dorsal setae cylindrical, shortly barbed, and arranged 2.6.3/3.10.8.8.6.2 in specimen illustrated. Humeral setae single, 52–54μ long; DS 44–46μ long; CS 34–40μ long. Ventral setae about 40 in number, those near anus 27–29μ long. Sternal setae 2.2.

Standard Data in Micra of Larval Scutum of W. beauforti *n.sp.*

AW.	PW.	SB.	ASB.	PSB.	SD.	AP.	AM.	AL.	PL.	Sens.
68	77	42	26	23	49	39	—	34	—	—
67	72	39	25	23	48	40	48	36	33	51 × 9
67	72	38	25	24	49	39	47	32	36	—
66	77	38	—	23	—	—	42	32	34	—
68	74	40	26	23	49	39	46	33	35	—
—	—	—	—	—	—	—	—	—	34	49 × 9

Scutum subrectangular and punctate over almost entire surface. Anterior margin with marked convexity around AM setal base. Lateral margins straight. Posterior margin shallowly biconvex. All scutal setae shortly barbed; AM > PL = AL. Sensillae quite clavate, and slightly attenuate distally. SB wide apart, slightly nearer to level of PL than that of AL. Eyes 2 + 2.

Gnathosoma.—Galeal setae nude. Chelicerae with distinct dorsal tooth just behind tricuspid cap. In addition to tarsala, the palpal formula is n.n.nnb.B + 6b.S. Tibial claw 3-pronged.

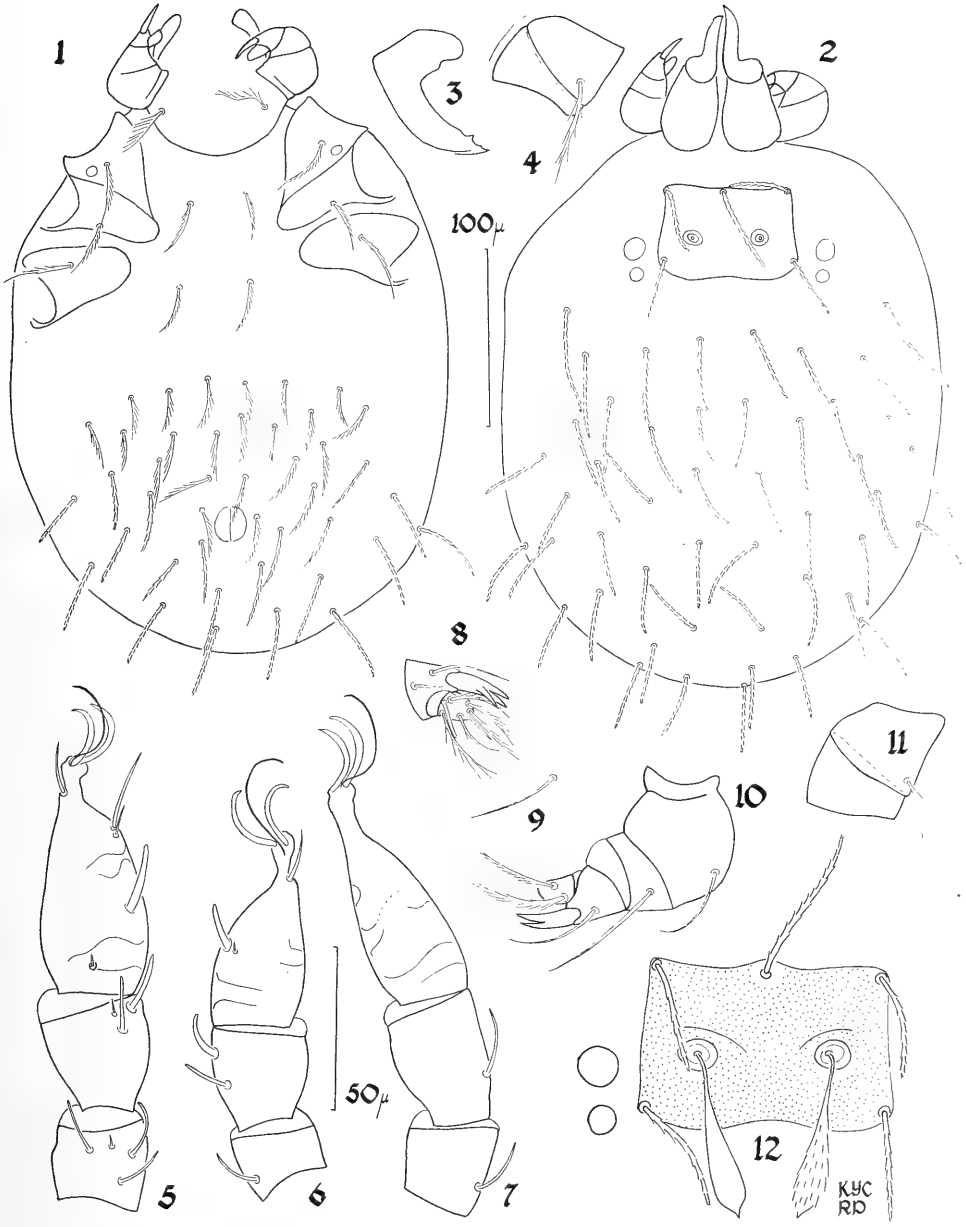
Legs all 7-segmented. Femora II and III divided, the ventral seta being branched. Specialized setation as follows—*Tarsus I* with pretarsala, subterminala, parasubterminala, tarsala and microtarsala; *tibia I* with two tibialae and microtibiala; *genu I* with three genualae and microgenuala. *Tarsus II* with pretarsala, tarsala and microtarsala; *tibia II* with two tibialae; *genu II* with genuala. *Tibia III* with tibiala; *genu III* with genuala. Tarsus I with basal and distal bars.

WALCHIELLA LACUNOSA (Gater). Figs 13–20.

Neoschöngastia lacunosa Gater, 1932, *Parasitology*, 24: 156.

Diagnosis.—AL < AP; PL < AL; sensillae asymmetrical.

Material Examined.—Eight of Gater's paratype larvae from *Rattus sabanus vociferans*, Sungei Buloh, Selangor; forty-nine larvae from Ulu Langat, Selangor, as follows—thirty-four from *R. sabanus*, 7.vii.1950, 11.i.1951, 22.iv.1952, 26.viii.1952, 18.xi.1952; five from *R. bowersi*, 7.v.1952; ten from a civet, *Prionodon linsang* (Viverridae), 13.i.1953.



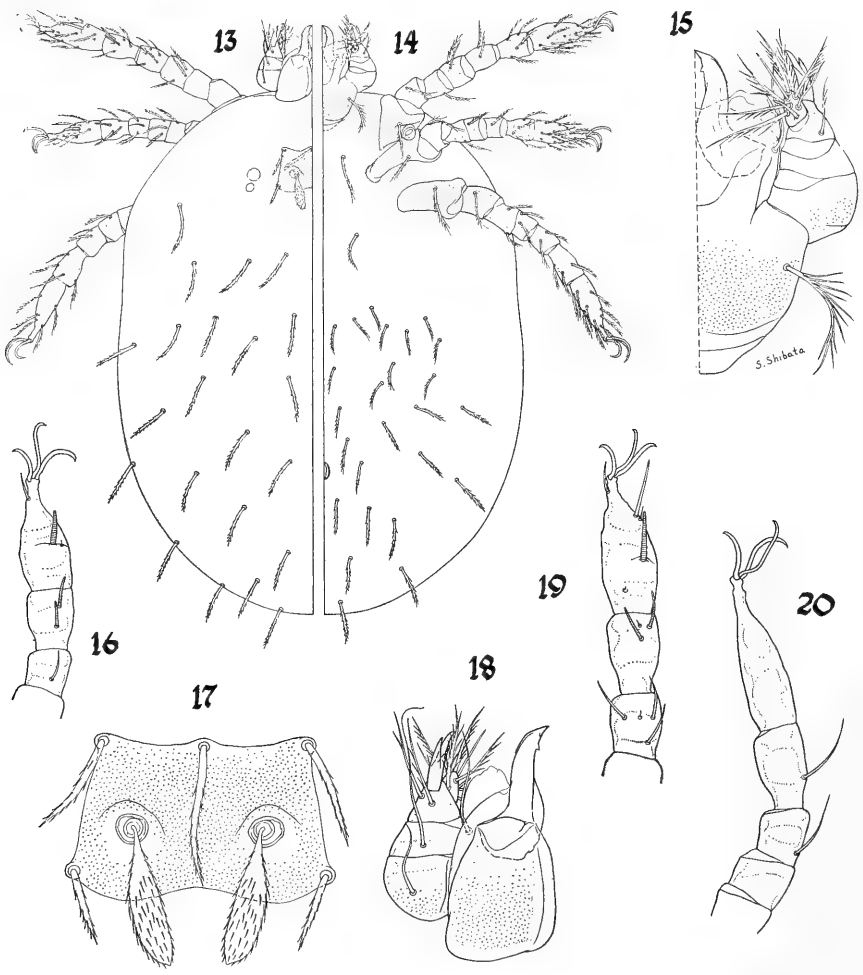
Text-figs 1-12. *Walchiella beauforti*, n. sp.—1, Venter of body; 2, Dorsum of body; 3, Chelicera in lateral view; 4, Basi- and telofemur II; 5, 6 and 7, specialized setation of legs I II and III, respectively; 8, External aspect of palpal tibiotarsus; 9, Galeal seta; 10, Internal view of palp; 11, Basi- and telofemur III; 12, Scutum and eyes.

WALCHIELLA SARAWAKENSIS (Womersley). Figs 21–28.

Schöngastia (*Ascoschöngastia*) *sarawakensis* Womersley, 1952, *Rec. S. Aust. Mus.*, 10: 201.

Diagnosis.—AL > AP; AL < PW.

Material Examined.—One larva from a moon-rat, *Echinosorex gymnurus* (Erinaceidae), Fort Leju, Tinjar, Sarawak, 15.vi.1950 (same collection data as type series); two larvae from *Rattus mülleri*, Fort Leju, 23.vi.1950; eight larvae from *Rattus* sp., Sarawak, 5.vi.1958.



Text-figs 13-20. *Walchiella lacunosa* (Gater).—13, Dorsum of body; 14, Venter of body; 15, Ventral view of gnathosoma; 16, Specialized setation of leg II; 17, Scutum; 18, Dorsal view of gnathosoma; 19 and 20, Specialized setation of legs I and III, respectively.

WALCHIELLA NADCHATRAMI (Womersley). Figs 29–36.

Schöngastia (*Ascoschöngastia*) *nadchatrami* Womersley, 1952, *Rec. S. Aust. Mus.*, 10: 200.

Diagnosis.—AL > AP; AL > PW.

Material Examined.—Two paratype larvae from *Rattus sabanus*, Bukit Lanjan, Selangor; six larvae from *R. rajah surifer* as follows—one from Kepong, Selangor,

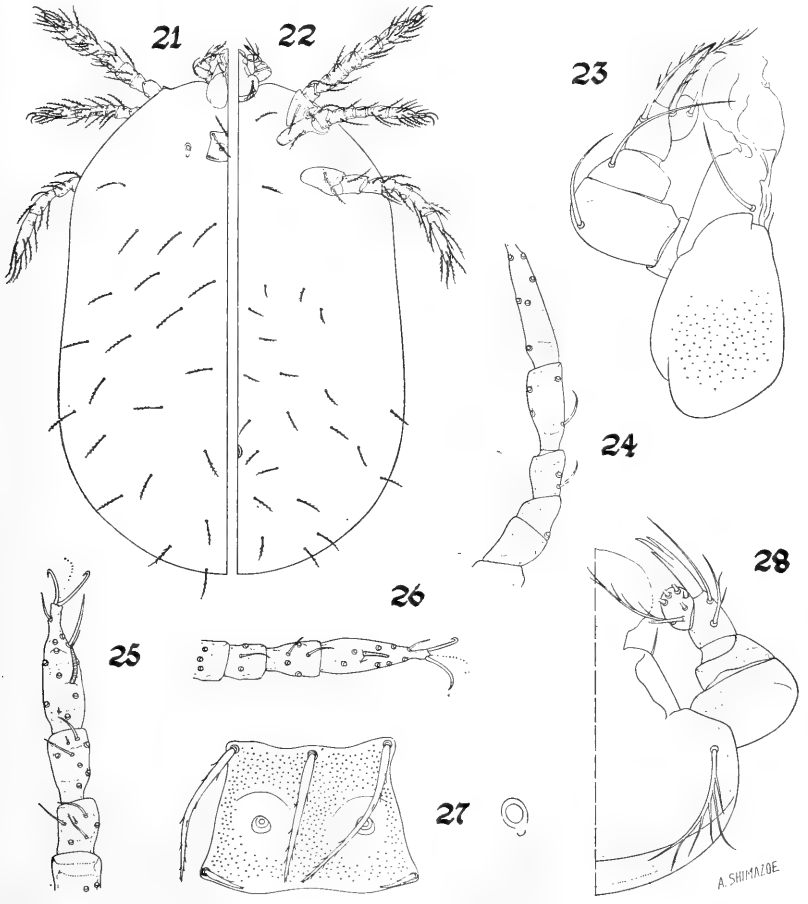
1.iii.1954; one from Bukit Lagong, Selangor, 15.iii.1954; four from Kuala Tahan, Pahang, 17.i.1955; two larvae from *R. rajah*, Sungei Buloh, Selangor, 16.v.1951; twelve larvae from *R. rattus jalorensis*, Bukit Jugra, Selangor, 15.iii., 17.iii. and 4.iv.1955.

THE *OUDEMANSI* SPECIES GROUP, AUDY AND DOMROW.

Diagnosis.—Legs 7.6.6-segmented, with femora II and III undivided.

WALCHIELLA IMPAR (Gunther). Figs 37–44.

Neoschöngastia clauda Gunther, 1938, *Med. J. Aust.*, 2: 204. *Nomen nudum. Neoschöngastia impar* Gunther, 1939, PROC. LINN. SOC. N.S.W., 64: 85. *Euschöngastia (Walchiella) asonluca* Traub and Audy, 1954, *Stud. Inst. med. Res., Malaya*, 26: 84. *New synonymy.*

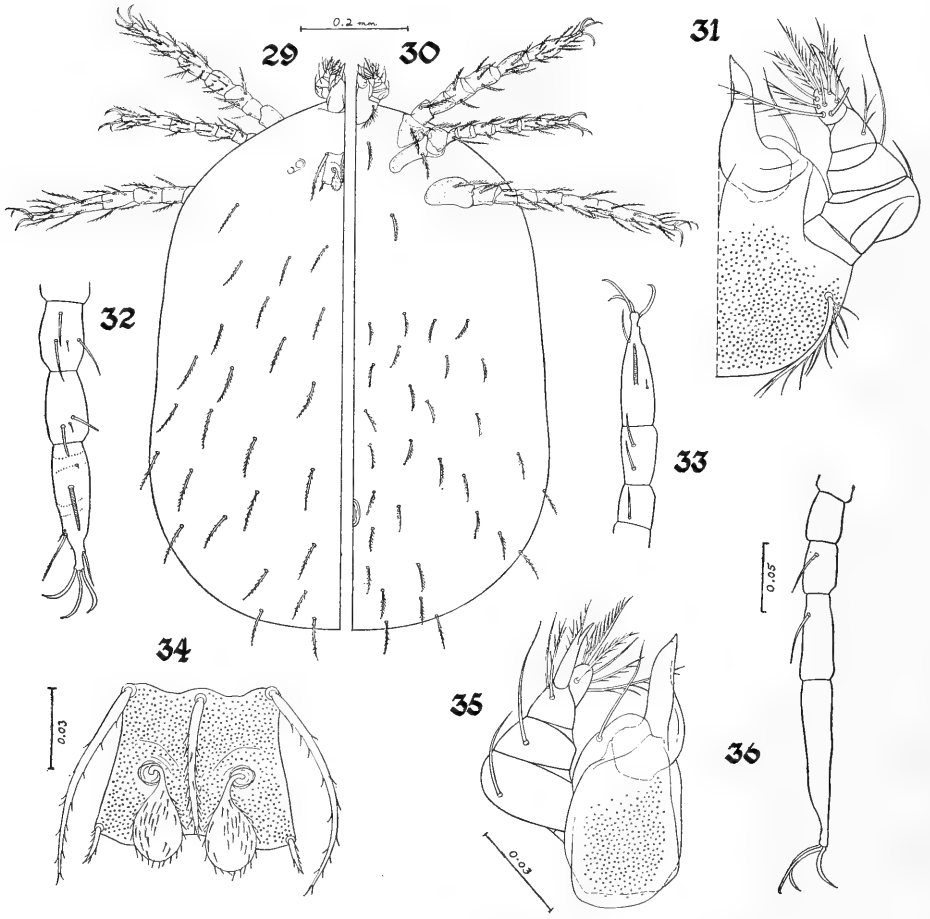


Text-figs 21-28. *Walchiella sarawakensis* (Womersley).—21, Dorsum of body; 22, Venter of body; 23, dorsal view of gnathosoma; 24, 25 and 26, Specialized setation of legs III, I and II, respectively; 27, Scutum and eyes; 28, Ventral view of gnathosoma.

Diagnosis.—Chelicerae simple; dorsal setae not set on platelets; with 28–30 dorsal setae; second and fifth setae in first dorsal row longer than remainder; scutum small.

Material Examined.—Of *impar*, the lectotype larva and four paratype larvae designated by Audy from Gunther's material, host unknown; two larval "type specimens" of Gunther, host unknown; two larval "paratypes" remounted and relabelled from Gunther's material by Womersley from a marsupial bandicoot, *Echymipera kalubu*

*kalubu** (Peramelidae); three larvae remounted by Womersley, but with Gunther's label, *E. k. kalubu*; twelve larvae mounted by Gunther, still attached to strip of ear margin of *Rattus browni*. All of this material of Gunther is from Bulolo, New Guinea. Further specimens examined from New Guinea are two larvae from *R. exulans concolor*, Sansapore, C. Mohr; four larvae from *R. ruber ringens*, Sansapore, C.M.; four larvae from juvenile rat, Sansapore, 1944, C.M.; two larvae from *E. k. kalubu*, Sansapore, W. D. Fitzwater; nineteen larvae, ear of rat, Lae, 1, 2 and 3.viii.1944, C. Davis.

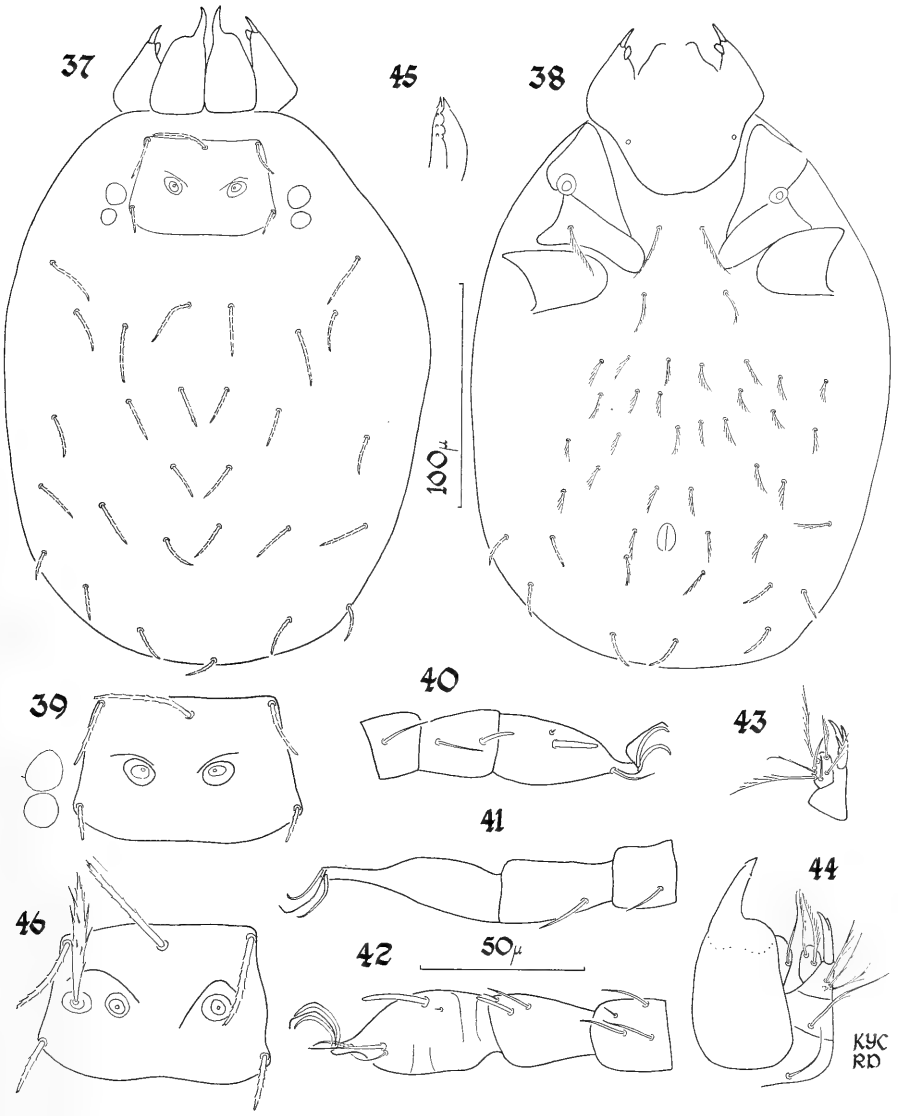


Text-figs 29-36. *Walchiella nadchatrami* (Womersley).—29, Dorsum of body; 30, Venter of body; 31, Ventral view of gnathosoma; 32 and 33, Specialized setation of legs I and II, respectively; 34, Scutum; 35, Dorsal view of gnathosoma; 36, Specialized setation of leg III.

Of *asonluca*, two paratype larvae from *Tupaia tana* (Tupaiidae), Stapok Road, Kuching, Sarawak; twenty-four larvae from *T. glis ferruginea*, Kuching, 22.xi.1950.

Notes.—In Audy and Domrow (1957), the four paragraphs under "Remarks" on *W. impar* were added by one of us at the last moment. In view of Gunther's descriptions of the chelicerae of *impar* and *bodensis*, I would have then been dubious as to their synonymy. Now, after an examination of authentic material of both species, I agree with Audy that *W. impar* is distinct from *W. oudemansi*, but find *bodensis* a synonym of the latter.

* This and certain other host names have been amended according to modern authorities, after Womersley and Audy (1957).



Text-figs 37-44. *Walchiella impar* (Gunther).—37, Dorsum of body; 38, Venter of body; 39, Scutum and eyes; 40, 41 and 42, Specialized setation of legs II, III and I, respectively; 43, Ventral view of palpal tibiotarsus; 44, Dorsal view of gnathosoma. (All figures from Gunther's paratypes.)

Text-figs 45-46. *Walchiella oudemansi* (Walch).—45, Left chelicera in dorsal view, and right chelicera in dorsolateral view, of specimen from type series of *Neoschöngastia bodensis* Gunther (this figure is to a slightly larger scale than the others, having been prepared with a × 100 lens, not a × 95); 46, Abnormal scutum of larva from *Rattus mülleri,* Ulu Langat, Selangor, Malaya, 19.xi.1959. Slide 71251.

WALCHIELLA CALUNOSA (Traub and Audy).

Euschöngastia (*Walchiella*) *calunosa* Traub and Audy, 1954, *Stud. Inst. med. Res., Malaya*, 26: 84. Figs 36–45.

Diagnosis.—Chelicerae simple; dorsal setae 28–30, uniform in length, and not set on platelets; scutum large.

Material Examined.—Four paratype larvae from *Rattus rattus baluensis*, Kamborangah, Mt. Kinabalu, 7,800′, British North Borneo.

Standard Data in Micra of Larval Scutum of W. impar (*Gunther*).*

AW.	PW.	SB.	ASB.	PSB.	SD.	AP.	AM.	AL.	PL.
47	62	25	22	21	43	31	36	19	13
48	63	26	23	22	45	31	—	21	13
49	63	27	23	—	—	31	—	19	13
50	65	27	22	22	44	31	35	21	11
60	70	32	26	23	49	32	36	21	13

* All from Gunther's paratypes, the first four exhibiting unstressed scuta. The fifth specimen has its scutum stretched and minutely cracked as figured by Traub and Evans (1957) for *Gahrliepia* (*Walchia*) *rustica* (Gater). Thus measurements involving the scutum itself are large, while the lengths of setae are normal.

WALCHIELLA LEWTHWAITEI (Womersley). Figs 47–55.

Schöngastia (*Schöngastia*) *lewthwaitei* Womersley, 1952, *Rec. S. Aust. Mus.*, 10: 154.

Diagnosis.—Chelicerae simple; dorsal setae more than 40, not set on platelets.

Material Examined.—Two paratype larvae from *Tupaia glis belangeri* Imphal, Manipur, India.

WALCHIELLA TRAUBI (Womersley). Figs 56–63.

Schöngastia (*Ascoschöngastia*) *traubi* Womersley, 1952, *Rec. S. Aust. Mus.*, 10: 222.

Diagnosis.—Chelicerae simple. Dorsal setae set on distinct platelets.

Material Examined.—One paratype larva from *Suncus* sp. (Soricidae), Shinbwiyang, Burma; four larvae from scrotum of two *Rattus niveiventer* (identified by Lim), plateau at 4,100′, NE of Khontum, South Vietnam, 9 and 10.vi.1960, R. Leech and Lim Boo Liat.

Standard Data in Micra of Larval Scutum of W. lewthwaitei (*Wom.*).

AW.	PW.	SB.	ASB.	PSB.	SD.	AP.	AM.	AL.	PL.
70	81	39	32	23	55	43	43	35	38
67	79	37	33	24	57	47	46	38	36

WALCHIELLA OUDEMANSI (Walch). Figs 45–46.

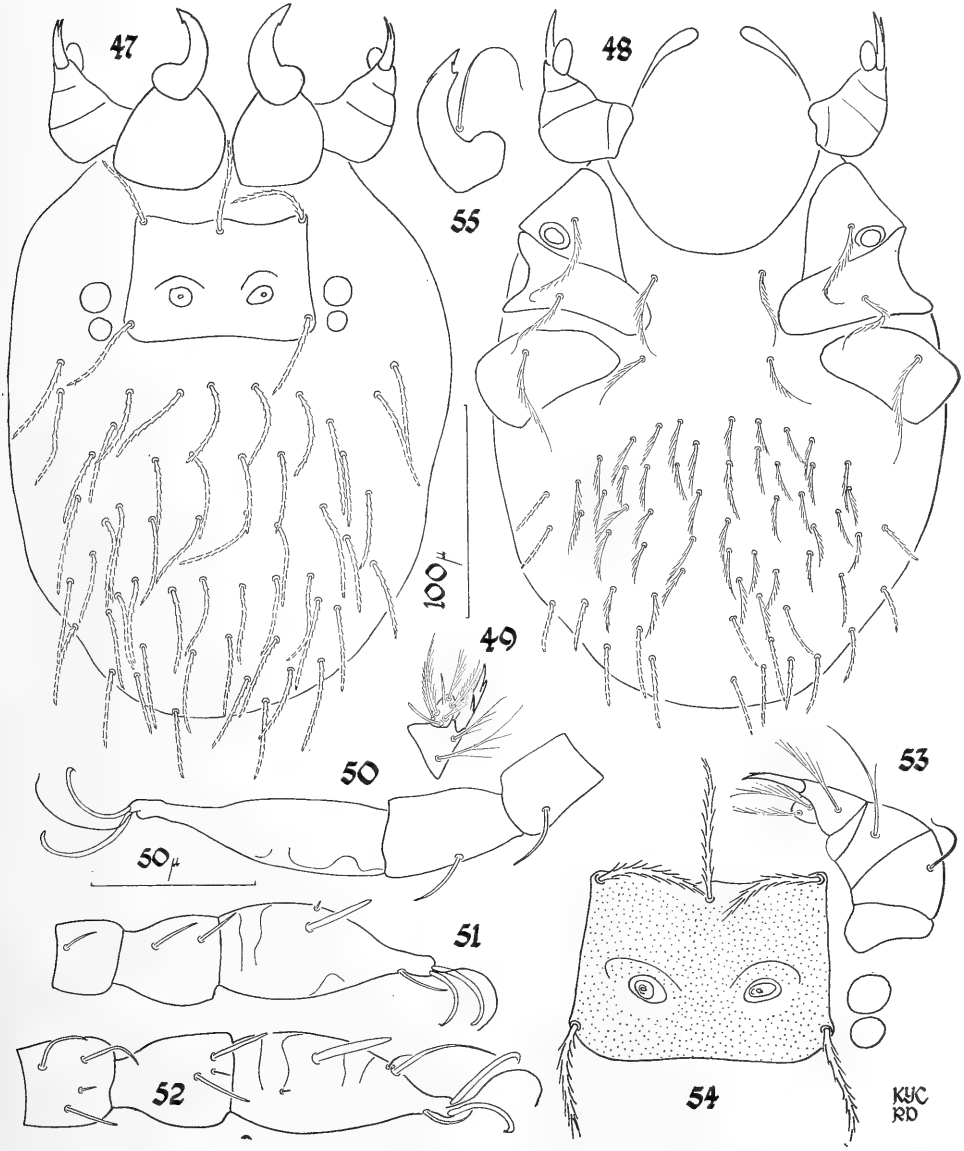
Trombicula oudemansi Walch, 1922, *Geneesk. Tijd. Ned.-Ind.*, 62: 563. Figs 18–21. *Neoschöngastia bodensis* Gunther, 1940, PROC. LINN. SOC. N.S.W., 65: 482.* *Euschöngastia* (*Walchiella*) *"FAT"* Audy, 1956, *Bull. Raffles Mus.*, 28: 96.

Diagnosis.—Chelicerae with widely set dentations, see Audy and Domrow (1957), fig. 10.

Material Examined.—Of *oudemansi*, eighty-six larvae from a flying squirrel, *Petaurista petaurista* (Sciuridae), Kepong, Selangor, 26.ix.1952; two larvae from *Echinosorex gymnurus*, Ulu Langat, Selangor, 18.xii.1951; twenty-five larvae from *Rattus*

* Audy says a third form in his care "labelled *N. bodensis* by Gunther is a distinct undescribed species". The slide in question is labelled (with a South Australian Museum label in Womersley's hand) "Paratype *Neoschöngastia bodensis* Gthr., on mouse deer, Bode Rv., B. N. Borneo, 8/39, C. Gth." (Gunther says the specimens were collected in September, 1939, by G. M. Rio). The label further bears a pencilled note by Womersley "not so", which is correct—the specimen is a *Guntherana*, apparently a mislabelled *G.* (*Derrickiella*) *smithi* (Womersley).

mülleri, Ulu Langat, 2.ix.1952; one larva from *R. mülleri*, Pahang Road, 30 miles from Kuala Lumpur, 17.v.1956; two larvae from *R. mülleri*, Ulu Gombak, Selangor, 25.vii.1956 and 29.ix.1956; one larva from *R. mülleri*, Ampang, Selangor, 5.viii.1959; five larvae from *R. mülleri*, Ulu Langat, 17.xi.1959; one larva from *R. bowersi*, Ulu Langat,

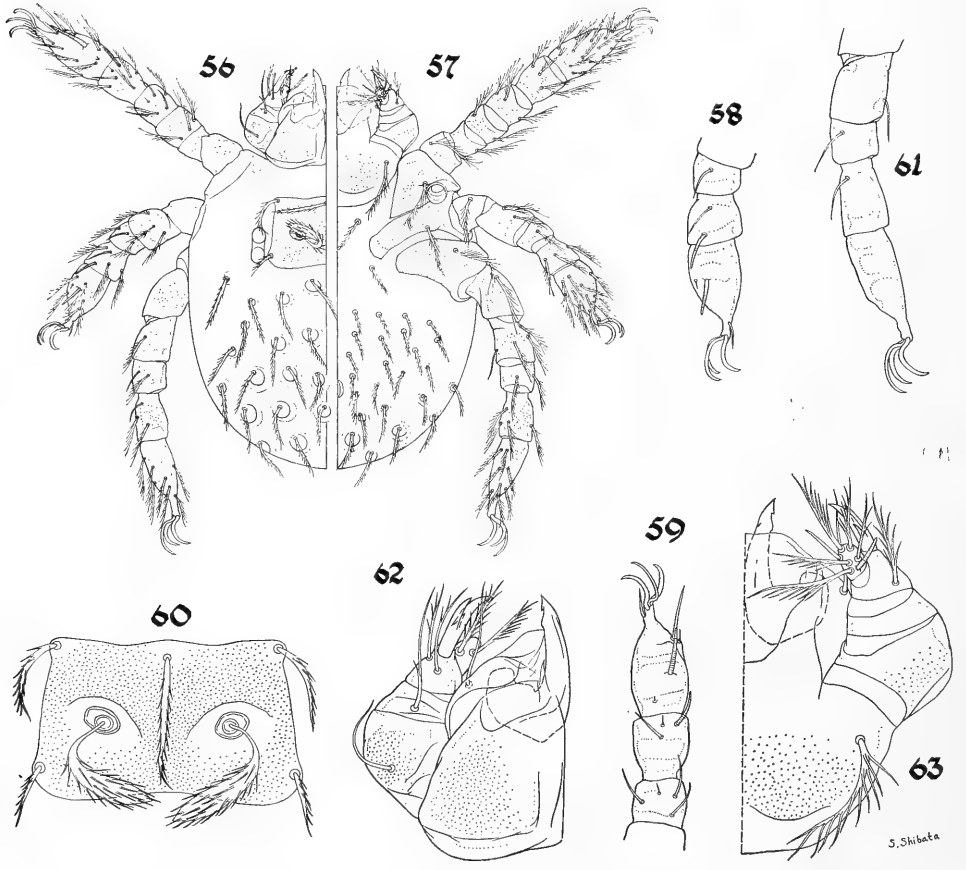


Text-figs 47-55. *Walchiella lewthwaitei* (Womersley).—47, Dorsum of body; 48, Venter of body; 49, Ventral aspect of palpal tibiotarsus; 50, 51 and 52, Specialized setation of legs III, II and I, respectively; 53, Dorsal view of gnathosoma; 54, Scutum and eyes; 55, Galeal seta, and chelicera in lateral view.

17.xi.1950; eleven larvae from *R. canus*, Bukit Lanjan, Selangor, 5.ix.1949; ten larvae from *Chiropodomys gliroides*, Kepong, 1.xii.1952; one larva from *Tupaia minor*, Mt. Kinabalu, British North Borneo, July 1951; five larvae from *T. montana*, Mt. Kinabalu, July 1951; one larva from *T. montana*, Mt. Kinabalu, no date; two larvae from *R.*

exulans, Mt. Kinabalu, July 1951; three larvae from *T. montana*, Kuching, Sarawak, 20.x.1951; three larvae from *T. glis ferruginea*, Kuching, 22.xi.1950; one larva from ear of rat, Milne Bay, New Guinea, August 1943.

Of *bodensis*, the holotype larva and two paratype larvae from a mouse deer, *Tragulus borneanus* (Tragulidae), Bode R., British North Borneo. These are all on one slide, the holotype not being specially marked, and are accompanied by one larva of *Eutrombicula wichmanni* (Oudemans). At present, the specimens are arranged in the form of a triangle ◁, with a larva in each corner, and one half-way down the vertical side. The specimen at the top is *E. wichmanni*, and I would suggest the specimen half-way down the vertical side be regarded as the holotype, since it shows the dentate chelicerae most clearly, as figured.



Text-figs 56-63.—*Walchiella traubi* (Womersley).—56, Dorsum of body; 57, Venter of body; 58 and 59, Specialized setation of legs II and I, respectively; 60, Scutum; 61, Specialized setation of leg III; 62 and 63, Dorsal and ventral views of gnathosoma, respectively.

Acknowledgements.

I am most grateful to Mr. D. J. Lee for the loan of type material of both Gunther's species, and 406 General Medical Laboratory, Yokohama, for the plates by Messrs. S. Shibata and A. Shimazoe.

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OBSERVATIONS ON SOME AUSTRALIAN FOREST INSECTS.

12. The Taxonomy of Zenarge turneri *Rohwer* (1918) (Hymenoptera: Argidae), the Cypress Pine Sawfly.

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

(Six Text-figures.)

[Read 30th May, 1962.]

Synopsis.

Attack by larvae of *Zenarge turneri* Rohwer (cypress pine sawfly) on State Forests of indigenous *Callitris hugelii* (Carr.) and on other ornamental *Callitris* and *Cupressus* spp. is widespread in New South Wales.

The taxonomy of the species was investigated and *Zenarge turneri rabus*, subsp. nov., is described. This taxonomic interpretation is supported by the results of biological investigations presented in another paper in these Proceedings.

Introduction.

From an examination of numerous specimens of this insect collected throughout its known range of distribution in New South Wales during the incidence of large populations on State Forests, it was determined that the description given by Rohwer was not applicable to specimens occurring in the western districts. There was thus some doubt concerning the taxonomy of *Zenarge turneri*, and aspects of its morphology, distribution, hosts and general biology were investigated.

Taxonomy.

Zenarge turneri Rohwer 1918.

The genus is monotypic.

The original description of the species by Rohwer (1918) was based on one male and two female specimens collected at Killara, Sydney (type locality), on 17th August, 1913, by R. E. Turner, after whom the species was named. In that paper it is stated that a type female and an allotype male were deposited in The British Museum (Natural History) and a paratype female in the United States National Museum. In a personal communication (July, 1961) Dr. R. B. Benson of the British Museum mentioned that there were 2 ♀♀ and 4 ♂♂ (including holotype and allotype) in the original type series in the British Museum collection, and all bear corresponding label data, namely, "N.S.Wales, Sydney. 400 ft., Aug. 17, 1913, R. E. Turner".

Additional observations on Australian sawflies were recorded by Morice (1919), who gave figures of the left wings and the antenna of a male, and the middle tibia, the saw and support of a female of *Z. turneri*.

Froggatt (1923) collected larvae of *Z. turneri* on *Frenella robusta* (= *Callitris* sp.) at Wagga Experiment Farm, but from an examination of label data on the only six female adult specimens known from that locality it is possible that McKeown, then the manager of the Experiment Farm, reared the larvae to the adult stage at Wagga. Froggatt's name does not appear on any of the labels, and McKeown's name is in parentheses on labels attached to five of these specimens. This is not consistent with Froggatt's method of labelling, and the data are given under "Specimens Examined".

Benson (1945) refers to the apparent primitiveness of this insect, with its unique host-association, and this is consistent with the phylogeny of the indigenous *Callitris* spp. which are considered to be a primitive group.

Specimens corresponding to the description of the type ♀ have been collected in New South Wales by the writer, at Wentworth Falls, Woodford, Armidale, Pennant Hills, Maroota, Kulnura and Broke. These specimens were relatively homogeneous as a separate group, larger than those occurring on *C. hugelii* in western districts (Table A), and the coloration of the female abdomen, except for the black areas, was consistently ferruginous as described by Rohwer (Table B).

From an examination of a large number of specimens from many areas throughout western New South Wales, the morphology, colour characteristics and host associations of these populations were found to be also relatively homogeneous even though certain differences in coloration occurred between localized populations (Tables B, C and D). Rohwer's description of the ♀ type specimen was not applicable to specimens of these populations.

A new subspecies based on the results of investigations into the biology and morphology of numerous specimens reared and collected from many areas is erected for specimens of the western populations.

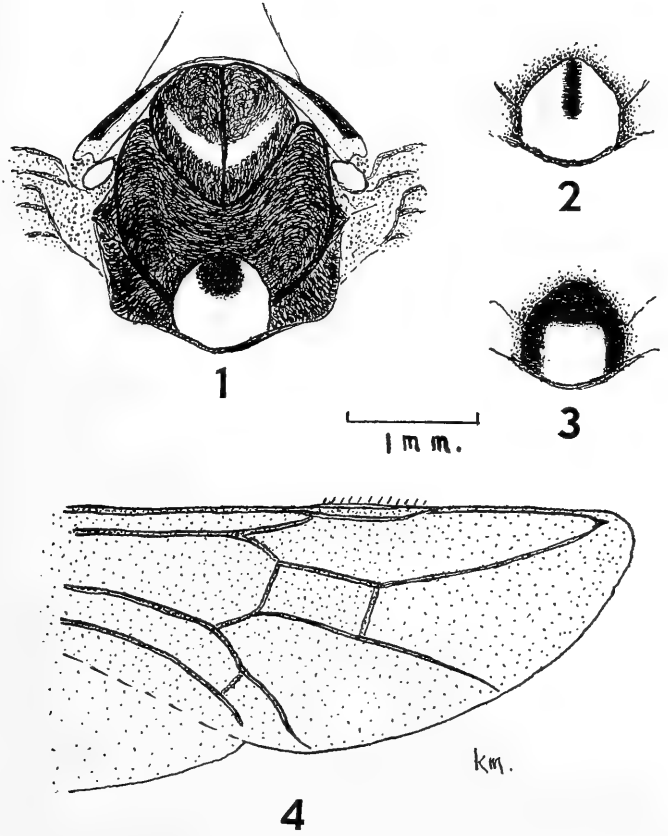

Fig. 1.—Thorax of adult of *Zenarge turneri rabus,* subsp. nov., showing white crescent on prescutum and black spot on scutellum of females.

Fig. 2.—Scutellum of female adults from Wagga, showing black bar (*Zenarge turneri rabus,* subsp. nov.).

Fig. 3.—Scutellum of female adults of *Zenarge turneri turneri* from Wentworth Falls, showing white area.

Fig. 4.—Portion of hindwing of *Zenarge turneri rabus,* subsp. nov., showing prolongation of apical vein.

ZENARGE TURNERI RABUS, subsp. nov. (here designated).

(L. *rabus* = dark coloured.)

Type Locality: Corringle State Forest, Compartment 1; 20 miles north of West Wyalong (Forbes Forestry District, West Wyalong Subdistrict).

Holotype ♀: Length (excluding antennae) 8·0 mm. Length of forewing 7·6 mm. Head with black area surrounding ocelli and extending almost to eyes and bases of antennae, and to posterior aspect of head where it extends laterally to half of eyes; a brown mottled area between eyes and posterior aspect of head; remainder creamy white;

mandibles tipped black. Prescutum black, with a white crescent convex posteriorly, near posterior border (Figure 1). Scutellum white, with a small anterior median black spot (Fig. 1). All abdominal segments are black dorsally; intersegmental areas and ventral abdomen are cream to pale yellow. Subcostal vein of hindwing produced beyond tip of cell R_1 (Fig. 4). Posterior tibiae black. Each leg with two distal tibial spurs; middle tibiae each with two preapical spurs; hind tibiae each with one preapical spur; posterior tarsi with two proximal segments black, and the three distal segments creamy white.

The type ♀ specimen has been selected to represent the extreme in the range of coloration, by which it may be separated most readily from *Zenarge turneri turneri.*

The females of *Zenarge turneri rabus* may always be separated from those of *Zenarge turneri turneri* as the posterior tibiae are all black, while in the latter species they are always white proximally for about one-quarter of their length.

Allotype ♂: Length, 7·5 mm. Length of forewing, 6·0 mm. Prescutum without white mark. Scutellum with anterior third black, remainder creamy white. Abdomen ferruginous with segment two black dorso-laterally and segment six with an indistinct dark transverse line across anterior border. Subcostal vein of hindwing produced beyond tip of cell R_1. Posterior tarsi with three proximal segments black, and two distal segments white.

No constant colour characteristic or morphological difference was found in the males of this subspecies to separate them from those of *Zenarge turneri turneri* (Tables A, C and D).

Host Plant: *Callitris hugelii* (Carr.) Franco (white cypress pine).

Types: The holotype ♀ labelled "Corringle S.F., 19 x 1957, K. M. Moore. Emerged 10 ii 1958" and allotype ♂ labelled "Corringle S.F., 19 x 1957, K. M. Moore. Emerged 2 xii 1957", together with a slide of the saw of the holotype, are lodged with The Australian Museum, Sydney, N.S.W.

Paratypes: A series of 162 ♀♀ and 130 ♂♂, designated paratypes, are distributed as follows: *To The Australian Museum*, Sydney: 11 ♀♀, 2 ♂♂, Corringle S.F., 6 x 1960, K. M. Moore; 16 ♀♀, 4 ♂♂, Corringle S.F., 19 x 1957, K. M. Moore; 8 ♀♀, 2 ♂♂, Corringle S.F., 23 ix 1959, K. M. Moore; 8 ♀♀, 2 ♂♂, Strahorn S.F., x 1960, K. M. Moore; 1 ♀, 1 ♂, Dubbo N.S.W., 17 x 1957, K. M. Moore; 1 ♀, 3 ♂♂, Red Hill S.F., 25 ii 1959, K. M. Moore; 1 ♀, Mandalong N.S.W., 6 iii 1958, K. M. Moore; 1 ♀, Mandalong N.S.W., 27 ix 1959, K. M. Moore; 2 ♂♂, Mandalong N.S.W., 23 iii 1958, K. M. Moore; 2 ♀♀, Lakeview S.F., 18 x 1957, K. M. Moore; 2 ♀♀, 2 ♂♂, Matong S.F., 6 ii 1957, K. M. Moore; 6 ♀♀, 8 ♂♂, Matong S.F., 22 x 1957, K. M. Moore; 3 ♀♀, 15 ♂♂, Buckingbong S.F., 21 x 1957, K. M. Moore; 10 ♀♀, 15 ♂♂, Buckingbong S.F., 5 ii 1957, K. M. Moore; 2 ♂♂, Buckingbong S.F., 6 ii 1957, K. M. Moore; 15 ♀♀, 35 ♂♂, Olney S.F., 31 x 1957, K. M. Moore; 13 ♀♀, Olney S.F., 14 ii 1958, K. M. Moore; 2 ♀♀, 5 ♂♂, Olney S.F., 26 ii 1958, K. M. Moore; 7 ♀♀, 12 ♂♂, Olney S.F., 3 vi 1958, K. M. Moore. *To The British Museum (Natural History)*, London: 10 ♀♀: Corringle S.F., 19 x 1957, K. M. Moore (4); 23 ix 1959 (2); 6 x 1960 (3); 11 x 1961 (1). 4 ♂♂, Corringle S.F., 19 x 1957, K. M. Moore. *To the Division of Entomology, C.S.I.R.O.*, Canberra: 10 ♀♀: Corringle S.F., 19 x 1957, K. M. Moore (5); 23 ix 1959 (1); 6 x 1960 (4). 4 ♂♂, Corringle S.F., 19 x 1957, K. M. Moore. *To the N.S.W. Department of Agriculture*: 10 ♀♀: Corringle S.F., 19 x 1957, K. M. Moore (6); 6 x 1960 (4). 4 ♂♂, Corringle S.F., 19 x 1957, K. M. Moore. *To the Forestry Commission of N.S.W.*: 10 ♀♀: K. M. Moore. *To the Queensland Museum*, Brisbane: 10 ♀♀: Corringle S.F., 19 x 1957, K. M. Moore (5); 6 x 1960 (5). 4 ♂♂, Corringle S.F., 19 x 1957, K. M. Moore.

Seven slides of ♀ and ♂ genitalia, and five slides of ♀ and ♂ genitalia of *Zenarge turneri turneri* from Armidale, Wentworth Falls and Pennant Hills, as well as one slide showing three saws of crossbred specimens, are also lodged with The Australian Museum.

Specimens Examined: In the Division of Entomology collection, C.S.I.R.O., 1 ♀ and 1 ♂, on one card and labelled "N.S.Wales, Wagga. Larvae on *Frenella robusta.*

(McKeown) 1906". In the N.S.W. Department of Agriculture collection, 4 ♀♀, two on each of two cards labelled "Wagga. Larvae on *Frenella robusta.* (McKeown) 1906". In the Macleay Museum, University of Sydney, 1 ♂, labelled "Wagga".

There is 1 ♀ specimen and 1 ♂ specimen in the U.S. National Museum labelled "Wagga. N.S.Wales. Larvae on *Frenella robusta.* Oct. ? 1906", which have not been examined by the writer.

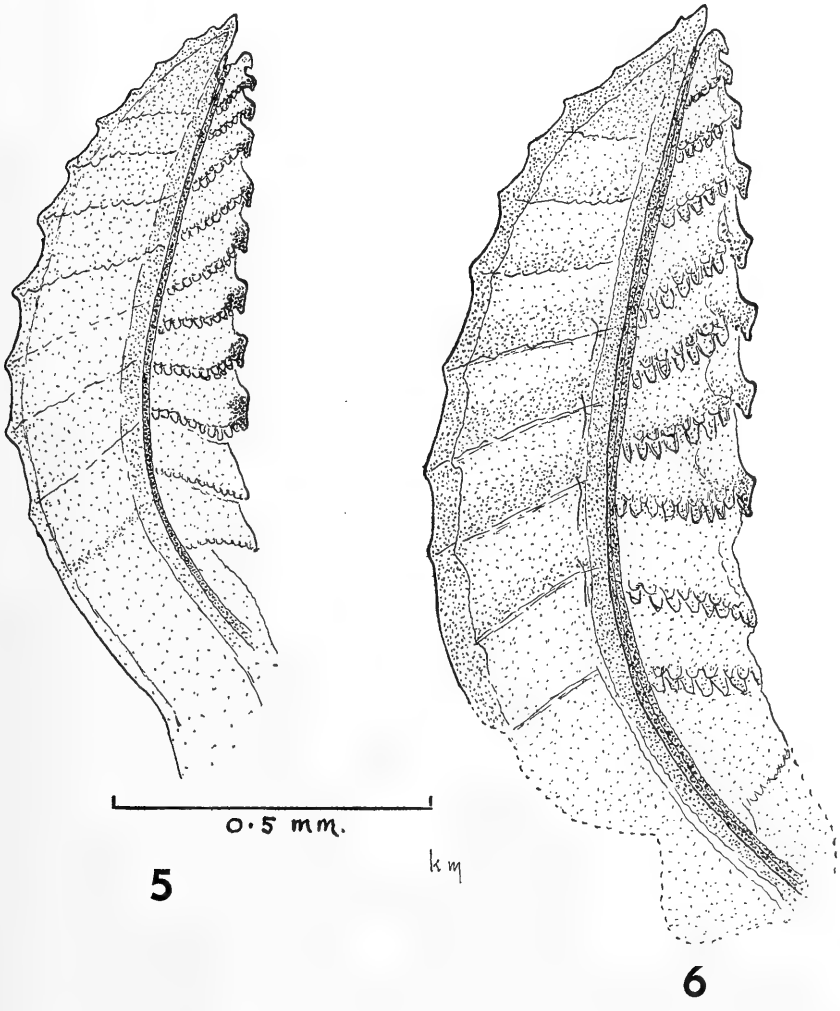

Fig. 5.—Saw and ovipositor of holotype ♀ *Zenarge turneri rabus,* subsp. nov.
Fig. 6.—Saw and ovipositor of ♀ (type series) of *Zenarge turneri turneri* in the British Museum.

Several hundred specimens from Corringle State Forest, Matong S.F. and Buckingbong S.F. (Wagga District); Strahorn S.F. and Bidden S.F. (Dubbo District); Olney S.F. and Mandalong (Newcastle District); Green Hills S.F. (Tumut District) and several other western State Forests have also been examined.

The saw and ovipositor of the type ♀ of *Zenarge turneri rabus,* and of a ♀ of the type series of *Zenarge turneri turneri* in the British Museum, are given in Figures 5 and 6 respectively, and characteristics of saws of the two subspecies are given in Table E.

Coloration of the males is not significant for taxonomic purposes, but setae on the head, thorax and abdomen of ♀♀ and ♂♂ are more sparse in *Zenarge turneri rabus* than in *Zenarge turneri turneri* and punctures are smaller and more sparse.

Most of the wing venation was found to be variable, inasmuch as cross veins were often absent, or present only in part, or portions of veins were evident where they normally did not occur; even so, a small prolongation of the subcostal vein of cell R_1 of the hindwing (Fig. 4) was relatively constant in *Zenarge turneri rabus* and usually only doubtfully occurred in a few specimens of *Zenarge turneri turneri* (Table C).

A white mark, often in the shape of a crescent on the prescutum (Fig. 1), did not occur on any male or female specimens of *Zenarge turneri turneri* from Wentworth Falls (Table C).

Certain colour characteristics were found to be variable in the various populations (Tables C and D).

The following specimens of *Zenarge turneri turneri* have also been examined: In The Australian Museum, 1 ♂ labelled "Wentworth Falls, A. Musgrave. No. K41049". In the British Museum, 1 ♀, 1 ♂, of the type series labelled "N.S.Wales, Sydney. 400 ft. Aug. 17,, 1913. R. E. Turner. 1913–438". In the C.S.I.R.O. collection, 1 ♀ labelled "Mt. Rosea, Vic., 2 x 1954. A.N.". In the N.S.W. Department of Agriculture collection, 1 ♂ labelled "Wentworth Falls, N.S.W., 19 i 1955, K. M. Moore". In the Queensland Museum. 3 ♀♀, 3 ♂♂, labelled "Sydney-Sept. 1913".

About 300 specimens from Armidale, Wentworth Falls, Pennant Hills, Maroota, Kulnura, Lisarow and Broke were also examined.

A series of ♀♀ and ♂♂ has been lodged with each of The Australian Museum, the British Museum, the C.S.I.R.O., N.S.W. Dept. of Agriculture, Forestry Commission of N.S.W. and the Queensland Museum.

A series of larvae of each of the subspecies, fixed in K.A.A.D. and preserved in 90% alcohol, has also been lodged with each of the above Institutions.

To facilitate separation of the two subspecies, their biological and morphological characteristics are summarized:

Zenarge turneri turneri.	*Zenarge turneri rabus.*
(1) *Hosts.* *Callitris muelleri.* *C. rhomboidea.* *C. endlicheri.* *Cupressus sempervirens.* *C. macrocarpa.* *C. macrocarpa lambertiana* 'Aurea' (cultivar.). *C. macrocarpa* 'Aurea' (cultivar.).	*Callitris hugelii.*
(2) *Natural Distribution.* Coast and Highlands.	Western Slopes and Plains.
(3) *Size* (see Table A). Generally larger than corresponding sex of *Z. t. rabus.*	Generally smaller than corresponding sex of *Z. t. turneri.*
(4) ♀ *Coloration* (see Table B). (*a*) Hind tibiae with proximal quarter white. (*b*) Abdominal segments 7 to 9 usually with black dorsally, sometimes with restricted additional black markings on segs. 2, 3 and 6. Remainder of abdomen ferruginous.	(*a*) Hind tibiae all black. (*b*) All abdominal segments usually with black dorsally, but occasionally restricted to segs. 2 and 6 to 9. Remainder of abdomen lemon-yellow.
(5) *Venation* (Table C and Fig. 4). Rarely with prolongation of vein at apex of cell R_1 in hindwing.	Rarely without prolongation of vein at apex of cell R_1 in hindwing.
(6) ♀ Saw (Table E and Figs 5 and 6). With 6 or 7 lateral teeth.	With 8 or 9 lateral teeth.
(7) *Life-cycle.* Not longer than 18 months.	May continue to 6 years.

TABLE A.

The original descriptions of *Z. t. turneri* adults gives the lengths as male 9 mm., female 10 mm. For comparison with the types, the following lengths of specimens of *Z. t. turneri* from Wentworth Falls, Armidale and in the Queensland Museum are given:

		Greatest.	Least.	Mean.
WF	14 ♂	10·0 mm.	8·5 mm.	9·2 mm.
	26 ♀	11·0 mm.	8·5 mm.	9·9 mm.
AR	17 ♂	9·0 mm.	7·0 mm.	8·0 mm.
	20 ♀	10·0 mm.	7·5 mm.	9·0 mm.
QM	3 ♂	9·4 mm.	8·9 mm.	9·2 mm.
	3 ♀	10·0 mm.	9·8 mm.	9·9 mm.

As contraction of specimens when drying is probably variable, the lengths in mm. of a forewing of adult specimen are given:

	Z. t. turneri.										*Z. t. rabus.*								X–	
	PH.		AR.		WF.		BM.		QM.		OL.		CR.		CR.		NA.		Lisarow.	
	♂	♀	♂	♀	♂	♀	♂§	♀§	♂	♀	♂	♀	♂	♀	♂‡	♀†	♂	♀	♂	♀
Mean (in mm.)	7·9	9·6	7·2	8·2	7·6	9·3	6·8	9·1	7·4	9·3	6·7	7·9	6·5	7·8	6·0	7·6	6·5	8·2	7·8	9·3
Number examined ..	22	10	16	24	82	71	1	1	3	3	31	19	27	49	1	1	41	23	65	15
Average of means ..					♂ 7·4 mm.									♂ 6·4 mm.					♂ 7·8 mm.	
					♀ 9·1 mm.									♀ 8·0 mm.					♀ 9·3 mm.	

Key to lettering in Tables A to E:

AM = Australian Museum.
AR = Armidale.
BM = British Museum.
CR = Corringle S.F.
CS = C.S.I.R.O.
DA = N.S.W. Dept. Agriculture.
DO = Dubbo.
MM = MacLeay Museum.
NA = Narrandera.
OL = Olney S.F.
PH = Pennant Hills.
QM = Queensland Museum.
US = United States National Museum.
WF = Wentworth Falls.
X– = Cross-bred.

* Paratype. † Holotype. ‡ Allotype. § Type series.

TABLE B.

Black Coloration on Dorsal Aspect of Female Abdominal Segments (Propodeum always Black).
(Numbers expressed as percentage.)

	Z. t. turneri.								*Z. t. rabus.*							X–
	PH.	AR.	WF.	BM.§	BM.†	QM.	CS.	US.*	OL.	CR.	CR.†	NA.	DA.	CS.	US.	Lisarow.
Black on segments:																
8 and 9	64	23	2	100		67										
7 to 9..	36	69	42		100	33		100								
6 to 9..		4	10													
2 and 7 to 9 ..			7				100									
2 and 6 to 9 ..		4	37						8	2					100	75
2, 3 and 6 to 9 ..			2						3							
2 and 5 to 9 ..													50			
2, 3 and 5 to 9 ..									8	2						
2 and 4 to 9 ..									3	2						
2 to 9..									78	94	100	100	50	100		25
Number of specimens	11	26	88	1	1	3	1	1	39	177	1	34	4	1	1	15

TABLE C.

Comparisons of Variable Features of the Two Subspecies.
(Numbers expressed as percentages.)

	Z. t. turneri.																*Z. t. rabus.*																X-.	
	WF.		AR.		PH.		BM.§		BM.		QM.		CS.		US.*		OL.		CR.		CR.		NA.		MM.		DA.		CS.		US.		Lisarow.	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂¶	♀‖
(*a*) Stub of vein at apex of cell R_1 of hindwing (Fig. 4).																																		
Present	0	6	6	28	24	0	0	0	0	0	0	0	—	100	—	0	97	96	97	92	100	100	92	97	100	—	—	100	100	100	0	100	0	33
Absent	94	84	69	28	52	55	100	100	100	100	100	100	—	0	—	100	0	0	0	0	0	0	0	0	0	—	—	0	0	0	100	0	95	13
Doubtful	6	10	25	44	24	45	0	0	0	0	0	0	—	0	—	0	3	4	3	8	0	0	8	3	0	—	—	0	0	0	0	0	5	54
Number of specimens.. ..	31	51	16	25	25	11	3	1	1	1	3	3	—	1	—	1	70	51	73	155	1	1	47	34	1	—	—	4	1	1	1	1	68	15
(*b*) Dorsal white mark on prescutum (Fig. 1).																																		
Present	0	0	23	0	40	0	100	0	100	0	100	0	—	0	—	0	16	74	2	52	0	100	25	69	100	—	—	100	100	100	100	100	0	0
Number of specimens.. ..	93	88	17	26	25	11	3	1	1	1	3	3	—	1	—	1	74	39	60	140	1	1	77	98	1	—	—	4	1	1	1	1	68	16
(*c*) White on scutellum (Figs 1 to 3).																																		
Posterior:																																		
¼ to ½	0	81	0	44	0	18	0	0	0	0	0	0	—	0	—	OBSCURED	88	15	0	0	0	0	54	7	0	—	—	0	100	0	0	0	0	0
½ to ¾	0	19	0	56	0	82	0	100	0	100	0	0	—	100	—		11	5	0	0	100	0	34	12	0	—	—	0	0	0	0	0	0	21
¾ to whole	100	0	100	0	100	0	100	0	100	0	100	100	—	0	—		0	5	93	14	0	0	0	0	0	—	—	0	0	0	0	0	100	0
Black spot anteriorly ..	0	0	0	0	0	0	0	0	0	0	0	0	—	0	—		1	75	7	86	0	100	12	81	100	—	—	50	0	0	0	0	0	79
Longitudinal black bar anteriorly	0	0	0	0	0	0	0	0	0	0	0	0	—	0	—		0	0	0	0	0	0	0	0	0	—	—	50	0	100	100	100	0	0
Number of specimens.. ..	93	72	17	23	25	11	3	1	1	1	3	3	—	1	—	1	75	39	60	138	1	1	73	98	1	—	—	4	1	1	1	1	68	14

¶ Progeny of NA ♂×WF ♀.
‖ Progeny of WF ♂×NA ♀.

TABLE D.

Coloration of Posterior Tarsal Segments.
(Numbers expressed as percentages.)

Black on Segments.	*Z. t. turneri.*									*Z. t. rabus.*								X-.
	WF.	AR.	PH.	AM.	BM.‡	BM.§	QM.	US.	CS.	OL.	CR.‡	CR.	NA.	MM.	DA.	CS.	US.	Lisarow.
♂																		
1 to 3			4					—	—	45	100	42	45					
1, 2 (seg. 3 brown) ..	1							—	—	41		35	28				100	3
1 and 2	96	94	92		100	100		—	—	14		23	27	100	100	100		97
1 (seg. 2 part black or brown)	2	6	4	100			100	—	—									
1 only	1							—	—									
Number of specimens..	157	16	24	1	1	3	3	—	—	70	1	26	40	1	3	1	1	65
♀																		
1, 2 (seg. 3 brown) ..				—	†	§				14	†	4	13	—	—			40
1 and 2		12		—						72	100	96	82	—	—	100		53
1 (2 part black or brown)	12	21	9	—		100		100		14				—	—		100	7
1 only	88	67	91	—	100		100		100				5	—	—			
Number of specimens..	86	24	11	—	1	1	3	1	1	36	1	46	22	—	—	1	1	15

TABLE E.

Characteristics of Saws of Females.

Transverse lines of serrations terminating in a single large lateral tooth (Figs 5 and 6).

NOTE: Saws of both subspecies also bear an apical hook not joined by a serrated transverse line, and 2 or 3 proximal transverse serrated lines each without a lateral tooth. The more proximal of these lines consists of vestigial serrations only.

Number of Lateral Teeth.	*Z. t. turneri.*				*Z. t. rabus.*					X–.
	AR.	WF.	PH.	BM.§	CR.	CR.†	OL.	DO.	NA.	Lisarow.
6	2									
7	1	6	3	1						
8					3	1	2	1		3
9					3		1	2	3	
Number of specimens..	3	6	3	1	6	1	3	3	3	3

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OBSERVATIONS ON SOME AUSTRALIAN FOREST INSECTS.

13. A Comparison of the Biology of the Cypress Pine Sawfly Subspecies.

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

(One Text-figure.)

[Read 30th May, 1962.]

Synopsis.

The biology of *Zenarge turneri turneri* Rohwer and *Zenarge turneri rabus* Moore (Hymenoptera: Argidae) was examined, and damage caused by large populations is described.

Distribution was investigated and rearing experiments were made to study the hosts, life cycle and diapause of the two subspecies together with their possible taxonomic implications.

Some parasites, hyperparasites and predators are recorded.

Introduction.

Numerous species of sawflies occur in New South Wales, but *Zenarge turneri rabus* Moore and *Zenarge turneri turneri* Rohwer are the only sawflies occurring on *Callitris* and *Cupressus* spp., and they are host-specific to these two genera. Large areas of the indigenous *Callitris hugelii* (Carr.) (white cypress pine), and some ornamental *Cupressus* and *Callitris* spp. have been severely attacked by sawfly larvae.

Processed timber of *C. hugelii* is utilized extensively for flooring, weatherboards, scantlings, house-foundation blocks and to a lesser degree in the manufacture of veneers and furniture. Because of its great durability it is often used in western districts for posts and telephone poles. When seasoned, it is very resistant to attack by termites and borers.

C. hugelii is widely distributed throughout the western slopes and plains of New South Wales, and as most of the cypress pine forests have been destroyed to make way for wheat and wool production, the only extensive area remaining is that in the Pilliga-Baradine region where about one million acres of white cypress occur. When conditions for growth are favourable, the average growth rate is approximately one foot to two feet in height per annum, so that it may be 80 years before trees are utilized as timber.

A number of small experimental plots were planted with *C. hugelii* in several coastal and highland areas by the Forestry Commission during the years 1936 to 1945, to determine the suitability of this species for planting in areas other than west of the Great Dividing Range where it occurs naturally.

Defoliation of this species in western districts and in some of the experimental plots by *Z. t. rabus* increased in severity during 1954, and it was observed that the coloration of female adults occurring in the experimental plots resembled that of the western specimens. The biology of the populations occurring in the various environments was then examined.

Biology.

Z. t. turneri is referred to as a needle miner of cypress pine (Riek, 1955), but observations show that neither of the subspecies are needle miners irrespective of whether the host plant is *Callitris* sp. or *Cupressus* sp.

(*a*) *Hosts.*

Attack on the following hosts has occurred in the field:

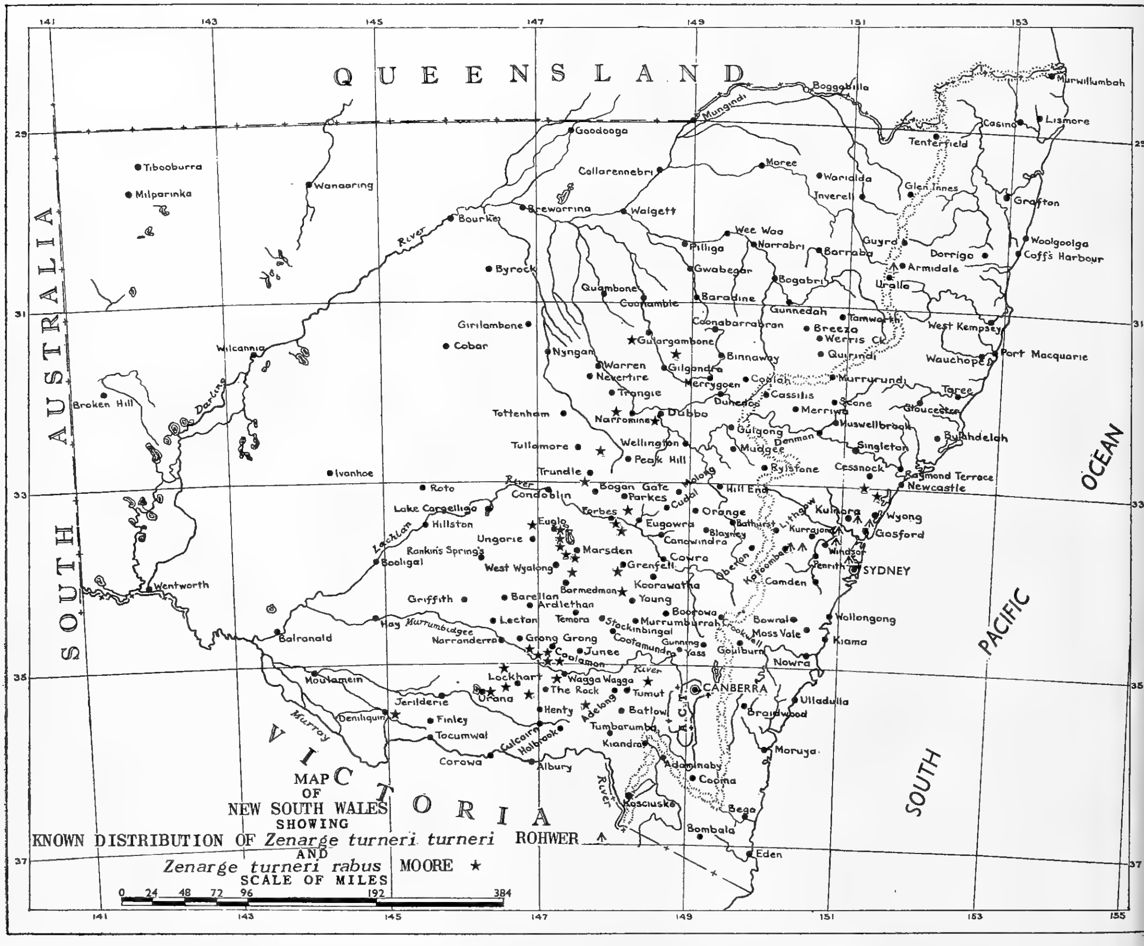
Z. t. rabus: *Callitris hugelii* (Carr.) Franco.

Z. t. turneri: *Cupressus macrocarpa* Hartw. ex Gord. (Monterey cypress pine); *C. macrocarpa* 'Aurea' cultivar. (golden cypress); *C. sempervirens* L.; *C. macrocarpa lambertiana* (Gordon) Masters 'Aurea' cultivar. (golden cypress); *Callitris rhomboidea* R.Br. ex A. et L. C. Rich. (Port Jackson cypress pine); *C. endlicheri* (Parl.) F. M. Bail. (black cypress pine); *C. muelleri* (Parl.) F. Muell.

Each of the sawfly subspecies was reared to the adult stage in cages, on *Callitris endlicheri* and *C. rhomboidea*, and details of these controlled rearings are given under "Rearing Experiments".

Froggatt (1923) mentions that *Callitris muelleri* is probably a host of *Z. t. turneri*, and this has since been confirmed.

Z. t. turneri has apparently attacked *Cupressus* spp. since their introduction to this country during the early nineteenth century, but *Z. t. rabus* is not known to attack species of this genus.



MAP OF NEW SOUTH WALES SHOWING KNOWN DISTRIBUTION OF *Zenarge turneri turneri* ROHWER ᛏ AND *Zenarge turneri rabus* MOORE ★

(*b*) *Distribution* (see map).

Z. t. turneri and *Z. t. rabus* are apparently confined to eastern Australia.

Armidale, on the Northern Tablelands, is the most northern area from which *Z. t. turneri* has been collected, and Mt. Rosea in the Grampian Mountains in Victoria, the most western and southern area. It is recorded from the following localities in N.S.W.: Coastal areas: Killara (type locality) 400 ft. altitude; Sydney (six specimens in the Queensland Museum); Pennant Hills (Forestry Commission nursery); Maroota; Galston; Broke. Highlands: Armidale (3,265 ft.); Wentworth Falls (2,844 ft.); Woodford (2,000 ft.); Kulnura (1,000 ft.).

Z. t. rabus is recorded from the following localities: Coastal areas: Mandalong (approx. 100 ft.), a Forestry experimental planting of *C. hugelii* on Olney East State

Forest. Highlands: Olney East State Forest (1,500 ft.); Red Hill State Forest (2,000 ft.). These are both Forestry experimental plantings of *C. hugelii*. Western areas: *Z. t. rabus* is widespread from near Coonamble in the north-west to beyond the N.S.W.-Victorian border, and east of a line drawn approximately through Walgett and Hay, to the western slopes of the Great Dividing Range.

About one million acres of *C. hugelii* in the Pilliga Scrub (Baradine Forestry District) are beyond the perimeter of known distribution.

No areas where populations of the two subspecies were contiguous or overlapped were found during these investigations. The areas of occurrence of *Z. t. turneri* were very limited on the coast and highlands.

(*c*) *Damage.*

Complete defoliation of large trees and areas of young regeneration of *C. hugelii* has occurred in the same area on State Forests, but young regeneration rather than the older trees appears to be preferred. In areas of thick regeneration, that occurring in low-lying areas where natural drainage is inefficient in abnormally wet seasons appears to be most heavily attacked. Heaviest attack also occurs in areas of low site-quality.

Severe damage to stands of large trees appears to be cumulative over at least two years, and dependent on the number of generations of *Z. t. rabus* appearing in the field during consecutive seasons. Most trees recover readily from a single defoliation, and there is no evidence to suggest that trees die from a single attack. Partial defoliation is relatively common in some State Forests, and during most seasons there is good recovery of attacked trees. However, large trees and regeneration growing under conditions which may be considered as unfavourable (i.e., near dams or on low-lying areas) have been heavily attacked during a series of wet years, with some mortalities resulting. This suggests a site-favourability associated with freedom from attack.

Although trees of *C. hugelii* have been reported as dying because of attack by *Z. t. rabus*, no supporting evidence could be found.

It appears that trees previously debilitated are most readily attacked. During some heavy infestations, adjacent trees or groups of trees are often free from any evidence of attack, and it is considered that death of attacked trees is usually due to factors other than attack by sawfly larvae. Infestation by *Diadoxus erythrurus* (White) (the cypress pine jewel beetle) often follows heavy attack by *Z. t. rabus* and kills many trees.

No consistent pattern of attack by either subspecies could be determined. The upper foliage of some trees is primarily attacked, from where the attack may spread to the lower foliage during the following season. On other trees the lower foliage is attacked first.

Heavy sawfly attack during spring, summer and autumn on *C. hugelii* throughout western areas was correlated with the incidence of temperatures below average, and rainfall above average, during the years 1952 and 1954 to 1956. Numerous instances of heavy attack in the West Wyalong, Narrandera, Forbes, Dubbo and Gilgandra areas were reported during those years. From December, 1956, to April, 1958, dry weather conditions persisted and no attack occurred. The heaviest and most extensive damage, cumulative over previous consecutive seasons, was during 1956.

(*d*) *Life-cycle and Habits.*

Investigations were made to examine differences in habits, hosts, diapause, etc., as a basis for a revision of the taxonomy of the species. Cages were erected over various host plants at Lisarow, on the Central Coast, and controlled rearings of both subspecies were used to procure larvae and prepupae of known ages and parentage, as this was not possible in the field. The observations given below are applicable to both subspecies unless stated otherwise.

Life-cycle.

Adults of *Z. t. rabus* do not emerge in western localities during some seasons, whereas on the coast, adults of *Z. t. turneri* usually occur each spring and autumn, or

sporadic emergences may occur from August to May, apparently depending on seasonal conditions.

The length of the life-cycle is very variable and is correlated with the length of time spent in diapause as a prepupa, in the cocoon, which may be two weeks to 18 months for *Z. t. turneri* or one month to six years for *Z. t. rabus*. At Lisarow, three consecutive generations of *Z. t. turneri* were reared during the one year; one generation during the spring, one during late summer and another during autumn.

Z. t. turneri may produce two generations in the one year at Armidale and Wentworth Falls in the highlands, as the length of time during which favourable temperatures are likely to occur in these areas would be less than in coastal areas where it would be possible for four generations to occur in the one year.

Oviposition.

Female adults commence to oviposit almost immediately after emergence from the cocoon, although some specimens groom their wings or antennae and move about on the foliage for a limited time before doing so.

When about to oviposit, usually in the current or the previous season's growth, the female alights on a shoot, climbs to the tip, turns around and commences to move down the shoot, often on the opposite side. The distal portion of the abdomen is deflexed and drawn along the surface of the shoot, so that the points of the partly protruding saw usually penetrate behind the projecting scale-like leaves. When a suitable site for oviposition is selected, the two lateral plates of the saw, each moved in opposite directions along a tongue-and-groove arrangement on their anterior concave edges, are utilized to cut a slit into the tissues of the shoot near the base of the leaf-scales, and to approximately half-way towards the next leaflet attachment, where oviposition occurs. With the claws of the metatarsi secured to the shoot posterior to the site of oviposition, the slit is cut as a rocking motion backward and forward is made by the insect. The abdomen is curved further forward as the saws penetrate to the depth required for the insertion of the egg, which is usually deposited near the centre of the shoot as a sideways rocking motion is sometimes made by the insect. The posterior of the abdomen is then raised from the shoot, when about half of the length of the saws and ovipositor sheath are exposed.

A variation in this method of oviposition was observed when caged adults oviposited in *Cupressus glabra* Sudw. As no deep cut was made into the stem, the eggs protruded for about half of their length, from the junction of the leaf-scale with the stem. Such placement of the eggs gave satisfactory emergence of larvae during the cooler months of the year, but eggs would almost certainly become desiccated during the hot dry weather typical of spring and summer during some seasons on the central coast. *C. glabra* is not known to be attacked in the field.

Eggs.

The number of eggs deposited by mated females used in rearing experiments was always greater than the number deposited by females reproducing parthenogenetically, and numerous unsuccessful attempts to oviposit were made by the latter specimens.

Eggs are laid singly, and after each is oviposited the female usually flies to another shoot where the procedure is repeated. Eggs are thus more or less randomly distributed over the tree, but with a preponderance in numbers occurring on the northern aspect during autumn.

When first oviposited, the eggs are approximately 1·3 mm. in length and 0·4 mm. in diameter. They are pale yellow, soft, translucent and arcuate, with one extremity rounded and the other tapering to a blunt point. They are often inserted less than half an inch from the tip of a growing shoot, but may also be inserted further along the shoots. About five days after oviposition during the warmer months, on the coast, the eggs become enlarged to about 1·5 mm. in length and 0·7 mm. in diameter, so that the plant tissues surrounding them are forced apart and become brownish-yellow to dark brown in colour. That portion of the chorion exposed by the separation of the

tissues of the plant stem becomes grey. The pale yellow partly-formed embryo surrounded by an almost colourless fluid is visible through the transparent chorion.

The average number of eggs dissected from five females of *Z. t. rabus* soon after emergence from the cocoons was 190. In one rearing experiment, when five females of *Z. t. turneri* were used for breeding purposes, 560 cocoons were recovered from the soil.

Larvae.

From 8 to 11 days after oviposition, on the central coast, the young larvae emerge through the expanded oviposition slit in the shoot, to commence feeding externally on the younger plant tissues at the side and below the tip of the shoot. The distal ends of attacked shoots then wither and die, and may fall to the ground. When a large population of larvae is present, the ground beneath the attacked tree may be strewn with shoot tips. The chorions are not consumed by larvae, which feed singly on the foliage, and there is no evidence of gregariousness. During the second and subsequent instars, larvae feed on the distal extremities of the shoots, with the posterior abdominal segments curled partly around the shoot below, and move backward as the shoot is consumed.

A recently emerged larva is cream to almost white, shiny and translucent prior to feeding. Female larvae soon attain a greater size than do male larvae. Four days after eclosion larvae are about 3·5 mm. to 4·5 mm. in length, and when feeding on *C. rhomboidea* are shiny and pale yellow. Eleven days after eclosion they are 5·5 mm. to 7 mm. in length, shiny and pale yellow, and at 17 days they are about 15 mm. to 18 mm. in length and pale to dark green, shiny and suffused with pale yellow. Thirty days after eclosion they are 18 mm. to 25 mm. in length, shiny and dark green.

Immediately following ecdysis, larvae are almost white in colour, and the time taken by a penultimate instar larva to shed its exuviae is about 20 minutes. It remains more or less stationary, attached to the shoot for a further one and a half hours until the head capsule darkens, when it again commences to feed.

The coloration of larvae is partly influenced by the host plant. On the golden-foliaged varieties of *Cupressus* spp., young larvae of *Z. t. turneri* are at first yellow, becoming suffused increasingly with green until the fourth instar, and are yellow-green during the last instar. On most green-foliaged varieties of host plants the young larvae are yellow or yellow-green, the yellow becoming less evident and the green more evident during the second and subsequent instars. *Z. t. rabus* larvae feeding on *C. hugelii* are yellow to yellow-green during the first instar, then become dark green, suffused blue-green on the prothoracic and eighth abdominal segments. They are usually glaucous and similar in colour to the host plant foliage.

The two posterior abdominal segments appear swollen and are usually yellow to orange, this colouring being more pronounced on specimens of *Z. t. turneri*, or specimens of *Z. t. rabus* feeding on the golden-foliaged *Cupressus* spp. On larvae feeding on *Callitris* spp. these segments are pale yellow, glaucous, or may be only a paler green than the remainder of the abdomen. These segments are always of a darker yellow on *Z. t. turneri* than those on *Z. t. rabus* on corresponding host plant species.

Fourth instar larvae of *Z. t. rabus* transferred from *C. hugelii* to *C. macrocarpa lambertiana* showed a slight colour change before pupation, the glaucous suffusion disappearing; larvae transferred in the first and second instars remained yellow until the third or fourth instars when they became suffused with pale green similar to those of *Z. t. turneri* normally occurring on this host plant.

During the feeding period, larvae pass through four instars and into the fifth, with a total larval period of 23 to 35 days. The fifth instar is completed within the cocoon as a prepupa. When fully fed, larvae crawl down the foliage, or tree trunk, at times falling to the ground. In large populations, they may collect in a mass near the base of the tree before entering the soil. Most larvae in all areas leave the foliage and enter the soil between 8 a.m. and 11 a.m.

From oviposition to the formation of the cocoon is approximately 24 days during February, or up to 40 days during April and May at Lisarow.

Larvae of either subspecies may be present during any month except July. As female larvae are larger than male larvae, there is intergradation in the sizes of larvae in each subspecies, but those of *Z. t. turneri* are about 5 mm. longer than those of *Z. t. rabus* of the same sex and age.

Last instar larvae: Length of larvae (both subspecies included) is from 15 mm. to 25 mm.; width across meso-thoracic segment, from 2 mm. to 3·5 mm. Head capsule black and shiny. General coloration is shiny green when reared on *C. macrocarpa*, *C. rhomboidea* or *C. endlicheri*, and shiny yellow-green when reared on *C. arizonica* or *C. macrocarpa lambertiana*; larvae of *Z. t. rabus* are dark green with glaucous suffusion when reared on *C. hugelii*. There is a pair of six-segmented legs on each thoracic segment, those on the prothorax being the shortest. The distal segment of each of these legs is without claws, but bears a distal pad. Pseudopods are on abdominal segments 2 to 8 and 10, although Benson (1938), referring to larvae of Argidae, mentions that pseudopods occur on segments 2 to 5, 2 to 6 or 2 to 7 and 10. The anterior aspect of the pseudopods is grey on specimens of both subspecies.

Pupae.

Pupation, occurring beneath the soil in cocoons of a white, parchment-like substance, occupies from about eight days during February to about 15 days during August or April at Lisarow. This length of time is more or less constant, irrespective of the duration, or absence, of diapause. Cocoons are usually separated in the soil unless there is a large population, and no evidence of grouping of cocoons has been found, as is the case with species of *Perga* and other genera occurring in New South Wales.

Cocoons of *Z. t. turneri* vary in size from 10 mm. to 16 mm. in length and 4 mm. to 7 mm. in diameter; those of *Z. t. rabus* are smaller than those constructed by the corresponding sex of the former subspecies. Because of adherence of soil particles, cocoons are externally of the same colour as the soil in which they occur. Larvae usually form the cocoons at depths of from one to three inches below the soil surface and beneath the spread of the foliage of the attacked tree, but in western areas some cocoons of *Z. t. rabus* were collected at a depth of seven inches in a sandy soil.

The greater number of specimens of *Z. t. rabus* reared at Lisarow entered the soil at the southern aspect of the cages, and in the field the majority were also similarly dispersed relative to the host plant. During 1957, at Corringle State Forest, 692 cocoons containing prepupae were sieved from four square feet of soil in a south-eastern direction from, and at the base of, a tree of *C. hugelii*. Large populations had occurred in the area for several seasons previously, during which time these cocoons probably accumulated, because of previous limited emergences of adults.

Adults.

The principal emergence periods are during August to November and March to May, the greater number of adults usually occurring during the latter period, although this is apparently dependent on prevailing weather conditions. Emergences of *Z. t. turneri* on the coast may occur more or less continuously from August to May. Males do not necessarily emerge prior to females.

Emergences of adults of either subspecies may be very sporadic, or may overlap to such an extent that larvae of all instars, adults, prepupae and pupae may be present at the same time during the spring or autumn months.

Adults used in experiments have not been observed to feed, and did not survive longer than three days after emergence. Dispersal is apparently restricted, for unless adults are continually disturbed they do not readily fly far from the host plant near which they emerge.

The proportions of male to female adults of the specimens reared in these investigations are expressed as percentages:

Z. t. turneri: (progeny of parents from Wentworth Falls) (551 specimens) 59:41.

Z. t. rabus: (progeny of parents from Wagga and Forbes Districts) (2,451 specimens) 21:79; (progeny of parents from Olney S.F.) (393 specimens) 65:35.

(*e*) *Parthenogenesis.*

Parthenogenetic reproduction by females of both subspecies, and by the F_1 generation hybrids from matings of *Z. t. turneri* × *Z. t. rabus* was determined, and all progeny were males.

(*f*) *Diapause.*

From controlled rearings of both subspecies it was determined that the period from the formation of the cocoon to the emergence of the adult may be as short as 20 days for both subspecies. It was no longer than 18 months for *Z. t. turneri*, but up to six years for *Z. t. rabus*. In specimens of *Z. t. rabus* collected at Olney East S.F. the length of time in diapause approximated that of populations of *Z. t. rabus* occurring in western areas and had remained more or less unmodified by the altered environment during 17 years. It is presumed that the sawfly was introduced to Olney East S.F. with the original plants of *C. hugelii*. Details of diapause in these two subspecies will be given in another paper.

(*g*) *Parasites.*

Flies of the family Tachinidae (Diptera) were reared from cocoons collected in most of the areas studied. Those from Wentworth Falls were identified as *Delta* sp.; those from western areas, Olney East S.F. and Lisarow were identified as ? *Protomeigenia* (near *Froggattimyia*) and is probably a new species. An adult specimen attacking penultimate instar larvae of *Z. t. turneri* at Lisarow deposited a single egg either on the centre of the 9th abdominal segment dorsally or on an anterior abdominal segment laterally. The dipterous larvae were entirely within the sawfly larvae after about three hours.

The tachinid species from western areas apparently has its diapause in phase with that of *Z. t. rabus*, as specimens emerged sporadically for up to five years after the collection of cocoons.

Oligochaetes were found attacking prepupae held at Lisarow in cultures, and the prepupae were usually liquefied during attack.

A minute parasitic wasp (Eulophidae: *Melittobia* sp.) destroyed numerous cultures. Only specimens in those jars which did not contain added moisture were attacked by this parasite, which had been bred previously attacking larvae and pupae of *Monerebia splendida* Guérin-Meneville (Eumenidae) (solitary or mud-nest wasp). Holes which appeared to have been made by *Melittobia* sp. were found in cocoons collected from all western areas and Lisarow, and it appears that this parasite could operate efficiently only when the soil was comparatively dry.

Six specimens only of a species of Ichneumonidae were bred from *Z. t. rabus* collected at Corringle State Forest.

(*h*) *Predators.*

At Lisarow and Olney East S.F. adults of *Polistes humilis* F. (paper nest wasp) (Vespidae) attacked sawfly larvae feeding on *C. hugelii* and *C. rhomboidea.*

An adult *Ommatius angustiventris* Macq. (Diptera: Asilidae) attacked flying male sawfly adults at Olney East S.F.

The small black ant *Iridomyrmex rufoniger* Lowne and the red and black jumping bulldog ant *Myrmecia nigrocincta* Smith both destroyed numerous larvae at Lisarow.

A number of prepupae in opened cocoons, held out-of-doors in closed Petri dishes either with or without soil for 18 months, were attacked in the dishes by lepidopterous larvae (Noctuidae: probably of the subfamily Amphipyrinae).

Larvae of hover-flies (Diptera: Syrphidae), probably *Syrphus viridiceps* Macq., attacked larvae of *Z. t. turneri* at Wentworth Falls. Flaccid sawfly larvae remained hanging on the twigs for several days after they were attacked.

Adults of *Oechalia schellenbergii* Guérin (Hemiptera: Pentatomidae) attacked larvae of *Z. t. rabus* at Strahorn S.F. (Dubbo Forestry District).

Small yellow-brown ants, *Meranoplus* sp., were suspected predators at Lisarow.

A spider, *Theridion* sp., destroyed numerous small larvae at Lisarow, and the bird *Pachycephala pectoralis* Latham (golden whistler) was also found to be a predator of larvae.

(*j*) *Hyperparasites.*

Puparia of the syrphids attacking larvae at Wentworth Falls yielded a total of 82 specimens of the Chalcidoidea, *Pachyneuron* sp. (Pteromalidae) and *Zeteticontus* sp. (Encyrtidae). From an early stage of parasitism of the syrphid larvae to the adult stage of these wasps was 15 days.

Rearing Experiments.

To compare the general biology of the two subspecies of the sawfly, a number of controlled rearing experiments were carried out on plants contained in cages in the field at Lisarow.

1. *Adaptability to Various Host Plants.*

This series of rearings was made to determine if one subspecies could complete its life cycle on the usual host plant of the other subspecies, and whether the coloration of larvae was thus modified. Results concerning the latter aspect are given under "Larvae" in the text.

Adults of *Z. t. turneri* were placed on plants of *Callitris hugelii* and *C. endlicheri*; adults of *Z. t. rabus* were placed on *Cupressus macrocarpa lambertiana* 'Aurea' cultivar., *Callitris rhomboidea* and *C. endlicheri.*

From these rearings it was found that each subspecies completed its life cycle on *C. rhomboidea* and *C. endlicheri*, although larvae of *Z. t. turneri* on the latter plant species appeared more translucent than was normal for that species, and brownish in colour, similar to larvae of *Z. t. turneri* feeding on *C. hugelii.*

C. hugelii does not occur naturally on the coast, and *Z. t. turneri* has not been found to feed naturally on that plant. The possibility of *C. hugelii* being a suitable host for *Z. t. turneri* was tested in several experiments at Lisarow. Three females, placed in a fly-gauze cage over a plant, produced 50 larvae which appeared unhealthy and more yellow in colour than was usual for that species. After attempting to feed on this plant for two weeks it was considered that they would not survive unless moved to another plant. They were transferred to a plant of *C. rhomboidea* of approximately the same height and age, on which they fed avidly and developed into apparently normal adults.

Another attempt to rear *Z. t. turneri* larvae on this plant, using 20 male and 22 female mated adults, produced 15 thin-walled cocoons, in 12 of which the prepupae deteriorated, and from the remainder two males emerged.

In other trials, numerous *Z. t. turneri* larvae of several generations were transferred during instars 2 and 3 from *C. rhomboidea* to three different plants of *C. hugelii*, to examine the possibility of their survival. After three to five days all larvae became brownish-green in colour, shrivelled and died.

From these rearings it thus appears that *Z. t. turneri* may occasionally survive, with difficulty, on *C. hugelii.*

As *C. m. lambertiana* is not extensively grown in western areas, its suitability as a host for *Z. t. rabus* was examined. Seven males and eleven females were placed in a cage with this host plant. Oviposition sites, denoted by brown scarred plant tissues, were numerous. Three small larvae were observed, but these did not survive. Again, 16 females were used, and oviposition sites were again numerous, but no larvae survived. It thus appears that *Z. t. rabus* is not able to survive from the egg stage on *C. m. lambertiana.*

Third instar larvae of *Z. t. rabus* taken from *C. hugelii* at Mandalong were placed on that host, and most of these completed their life cycle with the resultant colour-change in the larval stage as mentioned under "Larvae" in the text.

Females of *Z. t. turneri* were then placed on the same plant after an interval of three weeks, and numerous larvae successfully completed their life cycle.

Adults of *Z. t. turneri* placed in a cage containing a plant of *Cupressus glabra* Sudw. readily oviposited on that species, but larvae did not survive beyond the third instar.

2. *Parthenogenesis.*

From three unmated female adults of *Z. t. turneri* and 14 of *Z. t. rabus* approximately 100 cocoons were obtained, from which 12 males of the former subspecies and three males of the latter subspecies emerged before the remainder were destroyed by *Melittobia* sp. From an F_1 female of the mating *Z. t. turneri* ♂ × *Z. t. rabus* ♀, seven males were obtained.

3. *Cross-breeding.*

To examine any taxonomic implications, the possibility of hybridization by the two subspecies was investigated.

(i) P_1, *Z. t. turneri* ♂ × *Z. t. rabus* ♀.

Twenty-one cocoons were obtained, from which 20 adults (10% ♂♂, 90% ♀♀) emerged. The size of the larvae, cocoons and adults was slightly larger than those of *Z. t. turneri*, the larger of the two subspecies. Diapause was intermediate between that of each of the two subspecies, as was also the coloration of the posterior tibiae of the ♀♀. The first adult emerged at six months from the commencement of the prepupal stage, and the last emerged at 2½ years. A surviving prepupa deteriorated two months after the last adult had emerged. Emergences occurred over a total of 11 days within the 2½ years. One of the adult specimens emerged eight days after attaining the pupal stage. Coloration of the female abdomen varied between the extremes in coloration of the two subspecies, but predominated toward the coloration of the western populations (Table B), while coloration of the tibiae also varied similarly but predominated toward *Z. t. turneri.*

(ii) P_1, *Z. t. rabus* ♂ × *Z. t. turneri* ♀.

Eighty-four cocoons were obtained, from which 74 adults (100% males) emerged. This could be interpreted as lack of fertilization of the female, but copulation appeared to occur normally, and it is considered probable that the female was fertilized. The progeny were all very large and extremely vigorous when compared with numerous males of both subspecies previously handled, and they vigorously attempted copulation with each other. It is suggested that this is an indication that fertilization of the female occurred.

Duration of diapause was typical of that of *Z. t. turneri.* The first adult emergence occurred at six months, and the last at 18 months. Emergences during the 18 months occurred on 12 days; on one day 26 specimens emerged and on another day 22 emerged.

(iii) An attempt was made to rear specimens from the progeny of (i) × progeny of (ii).

As the days on which adults emerging from the two cultures rarely coincided, and as the progeny from (i) was limited, an opportunity to cross the progeny from these two cultures was presented once only. It cannot be stated with certainty whether a male from culture (i) or a male from culture (ii) fertilized the female from culture (i). It is likely that the male from culture (i) fertilized her, thus constituting inbreeding, although a male from culture (ii) also may have fertilized her, as both males attempted copulation.

From an examination of the resulting 22 oviposition sites the following information is recorded: Embryo partly developed, or larva, deteriorated in the egg: 13 (59%); collapsed egg-shell only, found: 4 (18%); no egg-shell found: 5 (23%).

The results of this experiment are here interpreted as an indication that a lethal genetic factor had operated against survival of progeny from this mating.

(iv) To try to maintain stock from the progeny of culture (i), two females from that culture were utilized for possible parthenogenetic reproduction. Sixteen progeny

were obtained, from which seven males emerged. The first emergence occurred at one month, and the last at nine months after commencement of the prepupal stage. The remainder of the progeny from this culture were destroyed by *Melittobia* sp. wasps.

4. *Absence of* Z. t. rabus *from Baradine Forestry District.*

Possible factors contributing to the non-occurrence of the sawfly in the Pilliga Scrub area were examined.

(*a*) It was thought that oviposition on trees in that area may have been inhibited by the size of *C. hugelii* foliage. A comparison of measurements of foliage from Merriwindi State Forest (Baradine District), Strahorn S.F. (Dubbo District) and Lisarow was made. Five shoots of foliage from each of the eastern, western, northern and southern aspects of each of five trees were measured for diameter, and length of that portion of the foliage between the joints of consecutive leaf-scales on the previous season's foliage.

Variations between the means of diameter, and length of shoot for each tree would not inhibit oviposition by the sawfly.

(*b*) Fifty tubed plants of one-year-old regeneration of *C. hugelii* and 50 open-rooted plants of three to five years of age were transplanted from Merriwindi S.F. to Strahorn S.F., and Bidden S.F. (Forbes Forestry District: Grenfell Subdistrict). As these plants did not survive, 500 plants were grown at Dubbo, from seed of Baradine origin, for transplanting in an area where previous heavy attack by *Z. t. rabus* had occurred on Strahorn S.F. This stock was transplanted during 1960 in areas marked on maps held by the Forestry Commission, and any relevant results will be given at a later date.

(*c*) A three-year-old plant was transplanted from Merriwindi S.F. to Lisarow, where successful oviposition and completion of the life-cycle by *Z. t. rabus* occurred during the first year.

(*d*) The records of winter and summer rainfall in north-western New South Wales show that Baradine is within the summer rainfall area. This factor is considered here to be the one most likely to inhibit continuing survival by *Z. t. rabus* in that area. The local soils are also very sandy, and do not retain moisture for as long a period as do the heavier soils further south.

Discussion.

From the phylogeny of *Callitris* spp., and Benson's remarks (1945) concerning *Z. t. turneri*, this sawfly and *Z. t. rabus* may be regarded as very primitive insects.

Z. t. rabus is one of the comparatively few phytophagous insects which exist in the more arid regions of the State. From the biological investigations it appears that the subspecies are at present undergoing speciation and no evidence as to which subspecies may be the more primitive could be found.

It appears that *Z. t. turneri* would be unlikely to survive readily in the hotter and drier western districts because of its host plant associations, and restricted diapause limits which would tend to inhibit survival during long, dry periods normally occurring in those areas, whereas *Z. t. rabus* populations are apparently able to survive in the cool, moist highland areas (Red Hill S.F. and Olney East S.F.) and in the warm, moist environment of the coast (Mandalong and Pennant Hills). Diapause in *Z. t. rabus* appears to be less inhibitory to its survival in these areas than would diapause in *Z. t. turneri* to its survival in western areas.

Exhaustive examinations of records and verbal statements concerning the source of origin of *C. hugelii* stock utilized in the Forestry Commission's experimental plots on the coast and highlands produced no evidence as to how *Z. t. rabus* has occurred in some of these plots. Having regard to the apparently restricted predisposition of *Z. t. rabus* to dispersal, and the isolation of some of the experimental plots where they occur, it is considered unlikely that specimens of *Z. t. rabus* have naturally arrived at, and survived in, these plots.

It is assumed that cocoons of *Z. t. rabus* were conveyed to the plots, probably via the nursery at Pennant Hills, in the soil of tubed stock used for planting during 1944

and 1945. In support of this hypothesis, it has been established that plants of *C. rhomboidea* on which attack by *Z. t. turneri* now occurs—in some instances in relatively isolated areas—were procured from the Forestry Commission's nursery at Pennant Hills where *Z. t. turneri* previously attacked tubed *Callitris* spp.

Discrete populations of *Z. t. turneri* and *Z. t. rabus* have occurred approximately 200 yards apart at Pennant Hills nursery, where the intervening area is composed of a thick stand of indigenous and introduced tree species, with an understorey of scrub and vines. No evidence of natural hybridization between these two or any other populations of the two subspecies has yet been determined.*

Although the life-cycle of *Z. t. rabus* was successfully completed at Lisarow on the *C. hugelii* three-year-old transplant from Merriwindi S.F., the metabolism and biochemistry of the transplant may have been modified by the coastal soil and environment. The degree to which such factors may have hindered any possible plant resistance to attack by *Z. t. rabus* and survival of larvae is not known, so that factors of host plant resistance to the sawfly may be operating in the Pilliga Scrub area.

From an examination of the biology of the two subspecies it appears that, apart from the coloration of the female posterior tibiae, there is not sufficient stability in other characteristics to make a specific division desirable. Differentiation of geographical populations by some minor colour characteristics is evident, and with more intensive collecting, areas may be found where populations of the two subspecies overlap or interbreed.

The evidence of the ability of the two subspecies to interbreed when brought together appears to be of considerable importance in support of the subspecific rather than the specific interpretation.

Although the one attempt to procure progeny from the second crossing of the subspecies resulted in evidence of lethal genetic factors operating in the embryonic stage, the attempt is interpreted as a pilot experiment only, for a taxonomic interpretation. As the series of experiments dealing with survival of the progeny of *Z. t. turneri* on *C. hugelii* indicated, a possibility of survival in the embryonic stage where numerous other attempts proved unsuccessful may eventually occur.

The following common names for the two subspecies are now suggested: "cypress pine sawfly" for *Zenarge turneri rabus* and "ornamental cypress sawfly" for *Zenarge turneri turneri.*

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For the identifications of parasites and predators, the writer is grateful to Mr. C. E. Chadwick of the N.S.W. Department of Agriculture; Mr. I. F. B. Common, C.S.I.R.O., Canberra; Professor V. V. Hickman of the University of Tasmania; Mr. D. K. McAlpine of The Australian Museum and Messrs. R. D. Eady and G. J. Kerrich of The British Museum (Natural History).

Considerable assistance in the field, for which the writer is grateful, was given by Senior Forester K. G. Campbell of the Entomological Research Section and District Forester J. Gardner (Baradine District Office); Foremen T. McCormick (Olney East S.F.) and H. Rodda (Strahorn S.F.) and several of the Forestry staff.

Thanks are expressed to Mr. P. C. Hely, Senior Entomologist of the N.S.W. Department of Agriculture, and to Forestry Commission staff for the map and for assistance with records on files and verbal details concerning these investigations.

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* Since this paper was submitted and accepted for publication during February, 1962, examinations of further emergences of adult female sawflies from Maroota have shown hybridization between the subspecies, the evidence being based on the coloration of the abdomen and the posterior tibiae.

The *Callitris rhomboidea* on which the specimens occurred, planted as an orchard windbreak during 1954 and now approximately 30 feet in height and consisting of about 50 to 100 trees, were all procured from the nursery of The Forestry Commission at Pennant Hills where both *Z. t. turneri* and *Z. t. rabus* are known to have occurred for many years.

This evidence thus supports the taxonomic subspecies interpretation already presented.

The writer is indebted to Dr. H. Briggs, and Messrs. A. McIndoe and K. Mair, of The National Herbarium, The Royal Botanical Gardens, Sydney, for identifications of the *Callitris* spp. and *Cupressus* spp. respectively.

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HYLA PHYLLOCHROUS GÜNTHER (AMPHIBIA) AS AN ADDITION TO THE FAUNA OF VICTORIA, WITH THE DESCRIPTION OF A NEW RACE AND A NOTE ON THE NAME OF THE GENUS.

By Stephen J. Copland.

(One Map.)

[Read 27th June, 1962.]

Synopsis.

A new race of the frog *Hyla phyllochrous* Günther is described. The known range of the species is extended about 240 miles and its first record for Victoria is established. A note is given on the nomenclature of the generic name *Hyla*.

Two rather small frogs, brilliantly green above, white to pinkish ventrally and with clear gold dorsolateral lines anteriorly, were found 10 miles north of Walhalla, Victoria, on December 29, 1961, when my daughters Janet and Christina and myself were collecting on bars of gravel and shingle in the Aberfeldy River. Both individuals were near the edge of the water where there was sparse cover from grasses and other vegetation. The two frogs proved to be *Hyla phyllochrous*, which was first described by Günther in 1863, the type locality being Sydney. They differ subspecifically, and are here described:

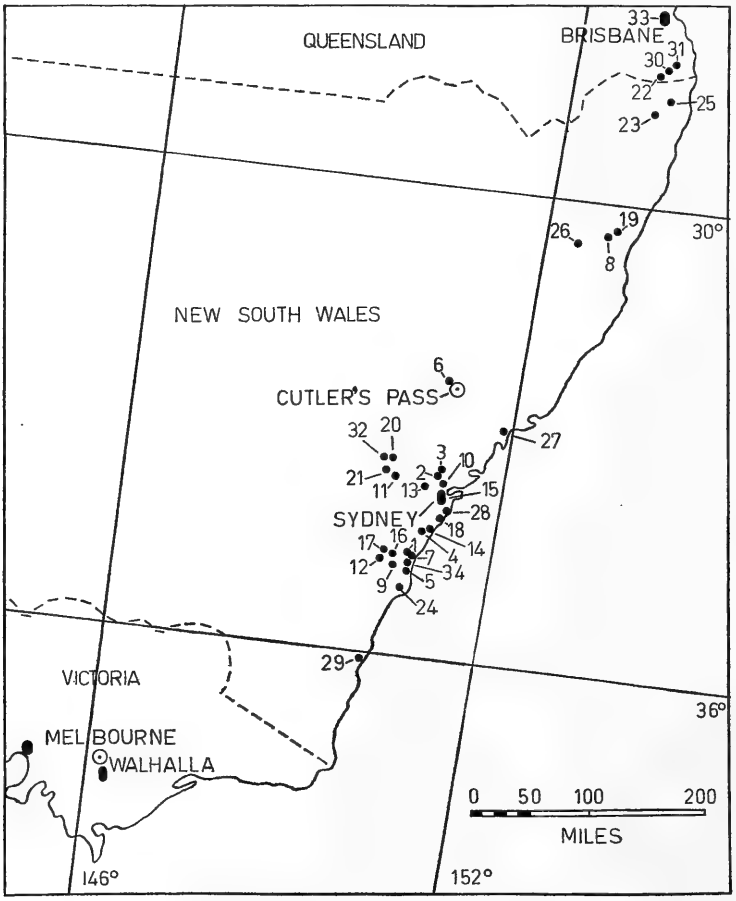
Hyla phyllochrous nudidigitus, subsp. nov.

Specimens Examined and Locality Record: 2 (A.C.7280–1), Aberfeldy River, 10 miles by road north of Walhalla, Victoria, 29.xii.1961. Holotype A.C.7280, paratype A.C.7281. Both in author's collection: holotype to be lodged in Australian Museum, Sydney.

Diagnosis: Differs from the nominate race by the absence or, at the very most a scarcely discernible rudiment of, web between the fingers (which is always quite distinct in *H. p. phyllochrous* where it is remarkably constant, averaging more than 20%), smaller finger and toe discs, and generally more indistinct tympanum.

Discussion: The head and body length of the larger specimen A.C.7280 is 25·5 mm. Both these Victorian frogs agree well in nearly every particular with a representative topotype of *H. p. phyllochrous* A.C.6146 from Warrawee, Sydney (for full description see Copland, 1957: 43). Departures from A.C.6146 are nearly always paralleled by the variation in one or more of the 66 specimens discussed in the same paper. The more important reasons for describing a new race are mentioned in the diagnosis and amplified here. Webbing between the fingers may fairly be described as absent. It is not measurable and at the most is the merest vestige. In *p. phyllochrous* the amount of webbing between the fingers is remarkably constant. That between the 2nd and 3rd fingers varies only 5% between 20 and 25% with an average of 22%. In A.C.6146 the percentages between the fingers are 28, 21 and 19. Forty specimens in the author's collection, including good series from Sydney and Megan, near Dorrigo, show variation to some extent, but the webbing is distinct in every case. Günther in his original description (1863: 251) said of the fingers "one-fourth webbed". It may be mentioned here that the extent of webbing between the toes is much as in *p. phyllochrous*, the average for the two specimens of *p. nudidigitus* being 68, 68, 77 and 62% with little difference between them. Percentages for A.C.6146 are 67, 62, 67 and 57. The finger and toe discs are smaller. (In 40 *p. phyllochrous* examined all had decidedly larger and generally much more rounded finger discs; 33 had decidedly larger toe discs while seven were slightly larger.) The tympanum is almost certainly more indistinct. In

A.C.7280 it is practically invisible, its surface being like the surrounding skin in colour and texture, but it is apparently roundish. In A.C.7281 it is more distinct, about 0·75 mm. across and contained nearly three times in the diameter of the eye. Taking a frog like



Map of south-eastern Australia showing localities from which *Hyla phyllochrous* has been recorded. The numbers all represent records for *H. p. phyllochrous*. 1 Minnamurra Falls, 2 Warrawee, Turramurra and Hornsby (all close together), 3 Bobbin Head, 4 Upper Cordeaux Dam, 5 Gerringong, 6 Barrington Tops, 7 Jamberoo, 8 Megan, 9 Kangaroo Valley, 10 Killara, Gordon and Lindfield (close together), 11 Woodford, 12 Bundanoon, 13 Seven Hills, 14 Woonona, near Bulli, 15 Sydney, 16 Burrawang, 20 miles inland from Illawarra, 17 Moss Vale, 18 Stanwell Park, 19 Lowana, 20 Mt. Irvine, 21 Blackheath (including Grose River near Blackheath), 22 National Park, Queensland, 23 Dunoon, 24 between Tomerong and Nowra, 25 Huonbrook (transcribed by me in error as Heronbrook (1957: 44)), 26 Ebor, 27 Hamilton, 28 National Park, New South Wales, 29 Lawler's Creek near Bodalla, 30 Binna Burra, 31 Beechmont, 32 Mt. Wilson, 33 Brisbane, 34 Kiama. Localities 1 to 8 are represented in the author's collection; 9 to 20 in the Australian Museum, Sydney; and 21 to 24 are literature references. For full details of specimens see Copland (1957: 44), except for the following specimens identified or collected since 1957: 2 (A.C.136-7) Upper Cordeaux Dam, 25.ix.1938; 1 (A.C.153) Gerringong, 2.x.1938; 1 (A.C.5043) Warrawee, 17.vii.1953; 1 (A.C.6143) rain forest below Barrington Tops (C. Tanner), 28.ix.1956; 1 (A.C.6150) Jamberoo (A. Keast), 14.x.1956; and 11 (A.C.6641-51) Megan, 25.xii.1957; all additional localities are in New South Wales. Specimens from localities 1 to 20 have been examined. Localities 25 to 33 are further records given by Moore (1961: 257), of which 26 to 29 are represented in the collection of the American Museum of Natural History as well as 10 and 21. Fletcher (1889: 382) notes 34. A record in the Australian Museum is for the Blue Mountains, which are west of Sydney and include 11, 20, 21 and 32. The type localities for *H. p. barringtonensis*—Cutler's Pass—and *H. p. nudidigitus*—near Walhalla—are lettered and shown by large dot-centred circles on the map.

Hyla lesueurii as a standard the tympanum can only be termed distinct in about half the specimens of *p. phyllochrous*, but if the tympanum is regarded as distinct if it can be seen plainly enough to be measured, only one out of 40 *p. phyllochrous* examined is virtually invisible, whereas in the new race it must be considered invisible in one and indistinct in the other of the only two specimens.

Collection of the new subspecies near Walhalla not only makes an addition to the small list of frogs from Victoria (see Moore, 1961: 358), but extends the known range of *phyllochrous* roughly 240 miles in a general south-westerly direction from its previously recognized southern limit at Lawler's Creek, near Bodalla, where Moore collected three specimens (1961: 257). The list of Victorian hylids now reads: *Hyla peronii, H. phyllochrous nudidigitus, H. citropus, H. maculatus, H. ewingii iuxtaewingii, H. e. verreauxii, H. e. loveridgei, H. e. calliscelis, H. aureus raniformis* and *H. lesueurii.* I have collected eight of the above 10 forms in Victoria and so can vouch for identification and localities. Specimens of *citropus* and *calliscelis*, which I have examined, have been taken by other collectors. In the case of *citropus*, as pointed out by Copland (1957: 54) and Moore (1961: 275), a locality error is possible. The only three frogs attributed to Victoria are in the Australian Museum. The circumstances under which they were entered in the register increase the possibility of a mistake but do not make it anything like a certainty. The specimens were received as part of J. J. Fletcher's extensive collection and entered in February, 1922. The frogs probably had been sorted in jars under species when received at the Museum. The three individuals catalogued as R.7560–2 are entered as from Aberfeldy, Victoria. They are preceded in the register by R.7558–9 from Waterfall, N.S.W., and followed by R.7563 from Manly, N.S.W. All are definitely *Hyla citropus.* There is no further information in the register or in the jar in which the frogs are now kept. I believe that the presence of this species in Victoria should be strongly doubted until further specimens are collected there.

Typical *H. p. phyllochrous* is a true tree frog and is usually found sitting on leaves of shrubs and trees. Banana trees are much favoured because of their broad leaves and axils. They frequent moist places, not necessarily near creeks or bodies of water. The finding of both specimens of *H. p. nudidigitus* among stones at the edge of a river probably means very little because at the time the surrounding area of Victoria was suffering a severe drought. Dryness of the normally moist hillsides would have driven many frogs to seek water. It is interesting to speculate as to what evolutionary pressure led to the extreme reduction of the southern frogs' finger webbing while it remained prominent in the presumably parental northern forms. This is the third race of *Hyla phyllochrous* to be described. To make the key in the author's 1957 paper complete the diagnosis for *H. p. nudidigitus* printed above should be inserted on page 12 immediately after *H. p. barringtonensis.*

Note on the Generic Name Hyla: It will be noted above that the customary *-a* termination of *phyllochroa* has been changed to *-us* and similarly that the masculine form of adjectives has been used when the names of other species have been mentioned. It has been customary to treat *Hyla* as a feminine noun. In spite of the error having been pointed out by Stejneger (1907: 75), Waite (1929: 258) and others, many authors have continued to use the feminine form of adjectives. I made the same mistake in a note (1961: 168). Stejneger deals with the matter concisely and may be quoted in saying that *Hyla* is "Not derived from the Greek word for wood-land, copse, as commonly stated, but from the vocative of Hylas, in Greek mythology the favorite of Hercules, who lost him in Bithynia. The crying of hyla, hyla being part of the religious ceremonies instituted in his honor. The croaking of the tree-toad suggested to Laurenti the fanciful idea of its being Hyla's priest, and thus meriting his name 'haec quasi Hylae sacerdos nomen ejusdem merita est'." The word *phyllochroa* is a coined one derived from leaf and colour. Ending in *a* it was almost certainly in the adjectival form to agree with *Hyla* as feminine. It has accordingly been changed here to give it the masculine termination *-us.* This course is supported by the fact that Günther was in the habit of

giving *-a* endings to his specific names for new Hylas. I have to thank Professor G. P. Shipp and Mr. J. Duhigg, of the Department of Greek and Department of Latin respectively in the University of Sydney, for kindly sparing the time to help me clear up this problem.

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STUDIES ON THE INHERITANCE OF RUST RESISTANCE IN OATS.

I. Inheritance of Stem Rust Resistance in Crosses Involving the Varieties Burke, Laggan, White Tartar and Anthony.

By Y. M. Upadhyaya and E. P. Baker, Faculty of Agriculture, The University of Sydney.

[Read 27th June, 1962.]

Synopsis.

The inheritance of resistance to certain oat stem rust races was studied in the varieties Burke, Laggan, White Tartar and Anthony. The former two possessed an apparently identical gene (Rd_1) for resistance to races 2 and 12, and the latter two an apparently identical gene (Rd_1^1) for resistance to races 2 and 10. With the population size studied the two genes were allelic, Rd_1 being dominant. However, with close linkage in the repulsion phase an extremely large population size would need to be tested to detect recombination and it is recognized that the genes may be alternatively closely linked and non-allelic.

Introduction.

Stem rust resistance in oats to various races is conditioned by several different genes. The genotypes which resistant varieties reveal in crosses vary with the different genotypes in the rusts to which they are tested. It is now generally conceded that similarity in race designation does not necessarily indicate entities which are identical with regard to genotype for pathogenicity. For example, Upadhyaya and Baker (1960) found that Australian oat stem rust races were genotypically different from those categorized as the same races in North America as a result of studies in crosses involving the variety Garry. The present studies were carried out to investigate the mode of inheritance of certain other oat varieties to Australian races and at the same time to compare the genotypes thereby revealed with those obtained by American workers using identical or related varieties and races of the pathogen.

Literature Review.

A summary of the situation concerning genes conferring resistance to North American races of oat stem rust is given in a paper by Welsh, Green and McKenzie (1961). Prior to the results reported in this paper, three, and possibly four, genes had been identified. One designated as gene A was possessed by Richland and related varieties; Hajira and its derivatives owed their resistance to gene B and possibly a closely linked gene C, whilst gene D was carried by White Russian and its derivatives. Green, Johnson and Welsh (1961) stated that the resistance of the variety Rodney, initially considered due to two linked genes, was probably dependent on a single gene only. They suggested that the monogenic type of segregation for resistance shown subsequently in Rodney crosses with susceptible varieties was conferred by the "BC" gene to prevent undue confusion in terminology. From studies Welsh *et al.* conducted, the variety Jostrain carried a single gene E. Canuck, a derivative of Jostrain, possessed genes B and E. The resistance of R.L.524.1 to all races with which its crosses were tested was conditioned by two major and a modifying gene. One of the major genes acted like gene B, conferring resistance to all races except 6A, 7A, 8A and 10A. The other major gene was apparently a new one designated as the F gene. This gene conferred resistance to all races excepting race 7, when the modifying gene was required in addition.

To certain Australian races Upadhyaya and Baker (1960) found that Hajira was heterogeneous and possessed in all three genes for stem rust resistance. One was apparently the A gene. The other two factors were linked with a recombination value of $26{\cdot}69 \pm 2{\cdot}29$ units. One of these factors (Hj_1) was probably identical with gene B (or C) found by North American workers; the other was a new factor designated as Hj_2.

Smith (1934) found that genes A carried by the varieties Iogold and Rainbow and D in White Russian and its derivatives were allelic. However, Koo, Moore, Myers and

Roberts (1955), from a study of inheritance involving varieties carrying combined resistances to stem and crown rusts, concluded that the A and D genes had been combined in pure breeding lines. They concluded that either combination had arisen from unequal crossing over or the genes were only "pseudoallelic" and that recombination resulted from rare crossing over. Aside from these genes and apart from the linkages previously indicated all other factors have been considered independent.

Upadhyaya and Baker (1960) reported that the varieties Burke and Laggan possessed a single gene for resistance to races 2 and 12, and that the gene was most probably identical with the Richland or A gene in each case.

TABLE 1.

Parental and F_1 Reactions in Crosses Involving the Oat Varieties Burke, Laggan, White Tartar and Anthony, to Certain Races of Stem Rust.

Parent and Cross.[1]	Seedling Reactions to Race			Adult Plant Reactions to Race		
	2	10	12	2	10	12
Burke	1,2=	3+c	1,2=	R	S	R
Laggan	1,2=	3+c	1=	R	S	R
F_1 (*a*)	1	—	1	R	—	R
Fulghum	3+c	3+c	3+c	S	S	S
F_1 (*a*)	2–	—	2–	—	—	—
(*b*)	1+	—	1	R	—	R
(*c*)	2	2	—	R	MR	—
Algerian	3+c	3+c	3+c	S	S	S
F_1 (*a*)	1	—	1	MR	—	MR
(*b*)	2	—	1,1+	R	—	MR
Bond	3+c	3+c	3+c	S	S	S
F_1 (*a*)	2	—	1	R	—	R
(*b*)	1	—	—	R–MR	—	R–MR
Palestine	3+c	—	3+c	S	—	S
F_1 (*b*)	1,2=	—	1,2=	R	—	R
White Tartar ..	2	2	3+c	R	MR	S
F_1 (*a*)	—	2	;	R	R	R
(*b*)	—	—	1,2=	R	MR	R
Anthony	2	2	3+c	R	MR	S
Gothland, Monarch and Joanette ..	3+c	3+c	3+c	S	S	S
All F_1s (*d*) ..	2	2	—	R	MR	—

[1] F_1s (*a*), (*b*), (*c*) and (*d*) involve Burke, Laggan, White Tartar and Anthony respectively.

MATERIALS AND METHODS.

The following four varieties resistant to certain races of stem rust were studied in crosses: Burke—a selection from Kherson (Callaghan, 1932); Laggan—a selection from Kelsall's from which it arose presumably due to mutation (Callaghan, 1932); White Tartar; and Anthony—produced from the cross White Russian × Victory made at the University of Minnesota, U.S.A. (Welsh *et al.*, 1953).

Three races of oat stem rust (*Puccinia graminis avenae* E. and H.) were used in these studies; these were races 2, 10 and 12 based on the key followed by Newton and Johnson (1944). The experimental procedure was as described by Upadhyaya and Baker (1960).

EXPERIMENTAL RESULTS.

Studies on the crosses of Burke and Laggan with Garry have already been reported (Upadhyaya and Baker, 1960). Those on the other crosses are reported here.

(*a*) Parental and F_1 reactions.

Parental and F_1 reactions are given in Table 1. Crosses (a), (b), (c) and (d) refer to those with Burke, Laggan, White Tartar and Anthony respectively. The reactions of the parents are shown above the reaction of the appropriate F_1.

The reactions of the F_1s, presented in Table 1, clearly showed dominance of the resistant parent involved. Only in two crosses, viz., Burke × Bond (race 2) and Algerian × Laggan (race 2), was the F_1 less resistant. In the adult stage also a slightly higher reaction type was observed in these crosses. On the other hand a more resistant reaction was observed in the cross Burke × White Tartar, when tested against race 12. That these differences were only environmental was established in the studies of later generations.

(*b*) F_2 segregation.

(i) Crosses involving Burke and Laggan.

In Table 2 are shown the segregation in different crosses of Burke and Laggan, when tested against races 2 and 12 or a mixture of races 2 and 12. The expected frequencies for the susceptible group were calculated on the assumption of the operation of a single dominant factor and are shown in brackets.

TABLE 2.

F_2 Segregation in Crosses Involving the Resistant Oat Varieties Burke and Laggan when Tested against Stem Rust Races 2 and 12.

Cross.	Race(s) Used.	F_2 Reactions. 1 to 2=	2	3+c, 4	Total.	Probability 3 : 1 Ratio (χ^2 Value).
Laggan × Burke	2 and 12	684	2	—	822	—
	12	134	2	—		
Fulghum × Burke	2 and 12	153	—	54 (51·75)[1]	207	0·8–0·7 (0·12)
	12	191	1	69 (65·25)	261	0·7–0·5 (0·29)
Algerian × Burke	2 and 12	198	—	61 (64·75)	259	0·7–0·5 (0·27)
	12	164	—	49 (53·25)	213	0·7–0·5 (0·45)
Bond × Burke	2	44	6	14 (16·00)	64	0·7–0·5 (0·33)
Burke × Victoria ..	12	261	—	100 (90·25)	361	0·2–0·1 (2·03)
Burke × Landhafer ..	2 and 12	183	—	60 (60·75)	243	0·95–0·9 (0·012)
White Tartar × Burke ..	12	166	—	51 (54·25)	217	0·7–0·5 (0·25)
Total (excluding Laggan × Burke) ..	—	1360	7	458 (456·25)	1825	0·95–0·9 (0·011)
Fulghum × Laggan ..	12	124	—	38 (40·50)	162	0·7–0·5 (0·20)
Algerian × Laggan	2 and 12	109	—	41 (37·50)	150	0·7–0·5 (0·44)
	12	156	—	46 (50·50)	202	0·5–0·3 (0·53)
Palestine × Laggan ..	2 and 12	57	1	21 (19·75)	79	0·8–0·7 (0·10)
	12[2]	192	59	94 (86·25)	345	0·5–0·3 (0·93)
Total	—	638	60	240 (234·5)	938	0·7–0·5 (0·17)

[1] Expected value for single dominant gene shown in brackets.

[2] Tested under high temperature conditions (75–85° F.).

In the cross Laggan × Burke no susceptible segregates were observed among the 822 plants tested. This indicated the presence of a common factor (or two closely linked factors) in these varieties.

In a total of 1,825 F_2 plants tested in the crosses of Burke with susceptible varieties, 458 plants were found to be susceptible, whereas 456 were expected on the basis of a single factor operation, thus showing good agreement between observed and expected results. All the individual segregations also showed a good fit. Similarly satisfactory results were obtained with the crosses of Laggan with susceptible varieties. Chi-square

values for heterogenity respectively were 3·74 (8 d.f.) and 2·03 (4 d.f.), indicating homogeneity of the data in both cases.

(ii) Crosses involving White Tartar and Anthony.

In Table 3 are given the F_2 frequencies in the various classes of reactions against races 2 and 10, in crosses involving White Tartar and Anthony. Expected ratios of the susceptible class are indicated in brackets and are based on the action of a single dominant gene for resistance.

In all cases in tests with both races a good fit to the expected values was observed, except in the cross Anthony × Gothland, where the F_2 was tested against stem rust race 2 and race 230 of crown rust simultaneously. An excessively large number of stem rust susceptible plants was evident in this case. In a similar test in the cross Bond × Laggan an excessive number of plants susceptible to stem rust were noticed.

TABLE 3.

F_2 Segregation in Crosses Involving the Resistant Oat Varieties White Tartar and Anthony when Tested against Races 2 and 10 of Stem Rust.

Cross.	Race Used.	F_2 Reactions. 2	2+	4	Total.	Probability 3 : 1 Ratio (χ^2 Value).
Fulghum × White Tartar	2	81	—	27 (27·00)[1]	108	1·0 (0·00)
	10	69	—	19 (22·00)	88	0·5–0·3 (0·55)
Total	—	150	—	46 (49·00)	196	0·7–0·5 (0·21)
Anthony × Monarch ..	2	213	—	79 (73·00)	292	0·5–0·3 (0·67)
	10[2]	453	13	164 (157·50)	630	0·7–0·5 (0·36)
Anthony × Gothland ..	2[3]	83	—	45 (32·00)	128	<0·01 (7·07)
	10	99	—	39 (34·50)	138	0·5–0·3 (0·79)
Anthony × Joanette ..	10	84	—	32 (29·00)	116	0·7–0·5 (0·41)
Total	—	862	13	314 (294·0)	1176	0·2–1·0 (1·70)

[1] Expected value for single dominant gene shown in brackets.

[2] Tested in the light and temperature controlled room.

[3] Material inoculated with race 230–Anz–1 of crown rust simultaneously, and as such the data were vitiated and not included in the total.

It is of interest that also a significantly excessive number of crown rust susceptible plants were observed in these instances on the basis of the hypothesis adopted and acceptable in other cases where segregating populations were tested only with crown rust. The reason for this interaction is not apparent. The operation of a single dominant gene conditioning the lower resistance of the varieties White Tartar and Anthony with a characteristic "2" reaction type was, however, evident from the other data.

(*c*) F_3 tests.

Tests on F_3 lines were carried out in crosses of Burke with Victoria, Bond and Trispernia and of Laggan with Palestine and Bond. Random lines were used in every case. The data are presented in Table 4. The expected frequencies are indicated, in brackets, below the observed frequencies in each case, and are based on the behaviour of a single gene pair difference in the parents giving a 1 resistant : 2 segregating : 1 susceptible F_3 ratio.

In all tests there was a good fit to the expected ratio in F_3, confirming the operation of a single factor for resistance in the varieties Laggan and Burke.

Tests in F_2 with two races in the case of the cross Laggan × White Tartar indicated that the two factors were allelomorphic (Table 5) and, therefore, F_3 lines of the crosses involving Anthony and White Tartar were not studied.

From Table 5 it will be noted that of 123 plants tested none was susceptible to race 2 and that all plants giving a '2' type reaction were resistant to race 10 indicating that they possessed the White Tartar gene in the homozygous condition. Eight plants which gave a '2–' reaction to race 2 and a '2' type reaction to race 10 were also probably

TABLE 4.

Reactions in F_3 in Crosses of Stem Rust Resistant Oat Varieties Burke and Laggan with Susceptible Varieties Tested against Races 2 and 12.

Cross.	Race(s) Used.	F_3 Reactions. Resistant.	Segregating.	Susceptible.	Total.	Probability 1 : 2 : 1 Ratio (χ^2 Value).
Burke × Victoria ..	2 and 12	27 (24·5)	41 (49·0)	30 (24·5)	98	0·3–0·2 (2·80)
Burke × Bond	2 and 12	61 (57·0)	118 (114·0)	49 (57·0)	228	0·5–0·3 (1·67)
Burke × Trispernia ..	2 and 12	35 (37·0)	74 (74·0)	39 (37·0)	148	0·9–0·8 (0·22)
Total	—	123 (118·5)	233 (237·0)	118 (118·5)	474	0·95–0·9 (0·17)
Laggan × Bond	2 and 12	51 (58·8)	125 (117·5)	58 (58·8)	235	0·5–0·3 (1·63)
Palestine × Laggan ..	2	57 (65·5)	137 (131·0)	68 (65·5)	262	0·5–0·3 (1·47)
Total	—	108 (124·3)	262 (248·5)	126 (124·3)	497	0·3–0·2 (3·00)

homozygous for the White Tartar factor. Twenty-five plants from the class resistant to race 2 and susceptible to race 10 as well as two plants semi-resistant to race 2 and susceptible to race 10 were homozygous for the Laggan factor. The heterozygous plants totalled 63 and were resistant to both races. A fit to a 1:2:1 ratio for those numbers

TABLE 5.

Relationship of F_2 Reactions on Identical Seedlings to Stem Rust Races 2 and 10 in a Cross of the Oat Varieties Laggan × White Tartar.

Reaction to Race 10.	Reaction to Race 2. 1 to 2=	2–	2	Total.
2	63	8	25	96
3+c	25	2	—	27 (30·75)[1]
	90		33 (30·75)[2]	123

[1] P value 0·5–0·3.
[2] P value 0·7–0·5.

gave a probability of more than 70 per cent for chance deviation indicating good agreement. The two genes were thus found to be allelic within the limits of the sample tested.

DISCUSSION AND CONCLUSIONS.

From these studies using Australian races of stem rust the varieties Burke and Laggan possessed one dominant factor for resistance to races 2 and 12, which was apparently identical in the two varieties; White Tartar and Anthony possessed another

gene for resistance to races 2 and 10. In spite of the fact that the Australian races possessed a different genotypic background, as evidenced from inheritance studies with crosses of the variety Garry, apparently identical factors as those operative against certain American races conditioned resistance against the same Australian races in the case of the varieties currently reported.

With the population size studied the two factors were apparently allelic, the factor common in Burke and Laggan being dominant over that in White Tartar and Anthony. However, from the number of F_2 plants tested this hypothesis could not be distinguished from linkage in the repulsion phase. As pointed out by Luig, McWhirter and Baker (1958), it becomes impossible to establish even close linkage regardless of allelism unless very large segregating populations are grown. Only 123 F_2 plants were tested in the cross Laggan × White Tartar and this gives a value of 31·11 units as the maximum distance which the two genes can be separated on the chromosome with the probability that a misleading result will not occur more often than once in twenty times. However, from previous evidence both locally and overseas on crosses involving these two genes, it is obvious that this value can be placed much lower statistically.

At the same time a paper cited previously (Koo *et al.*, 1955) indicates that crossing over may occur conventionally in a genotype heterozygous for the two genes, and that the genes may therefore be "pseudoallelic" and closely linked. The combination of resistance thereby resulting is of great merit in oat breeding as, due to close linkage, the two genes behave essentially as a single gene and confer resistance to all Australian races recorded in recent surveys. However, Waterhouse (1929) recorded race 6 capable of attacking both these genes so that the possibility of races of this type in the field must be recognized. In this connection the selection Minn. Ag. 331 received from the University of Minnesota is currently being included in the oat stem rust differential set to confirm immediately the presence of such pathogenic types, although such races can, of course, be detected by the simultaneous susceptibility of the two differential varieties Richland and White Tartar. In the case of collections comprising a mixture of appropriate races the use of this additional single variety gives an immediate confirmatory diagnosis.

From the results of rust race surveys of field collections the combined resistance is currently being used as a source of resistance in backcrossing programmes designed to incorporate stem rust resistance into the leading commercial Australian oat varieties. In these the results have followed the conventional single dominant gene behaviour pattern which is ideally suited to the backcross breeding technique.

Similarly, from studies on a relatively limited population of 822 F_2 plants, it is impossible to be certain that the genes in Burke and Laggan are identical and allelic. The maximum distance statistically that these two genes could be separated is 12·17 units. However, the fact that the genes are probably identical (and allelic) is supported by the results published by Waterhouse (1938) indicating the parallel behaviour of these varieties to the five races with which they were tested in the seedling stage. In addition, both varieties exhibit the reaction type characteristic of the Richland gene.

Following the system adopted by Upadhyaya and Baker (1960) it is proposed to designate the genes as Rd_1 in Burke (and Laggan), since it appears to be identical with the Richland gene, and Rd_1^1 in White Tartar, the superscript indicating allelism. Although, for reasons previously indicated, there is doubt as to allelism, this hypothesis is preferred until more critical work is carried out with larger segregating populations to establish the approximate linkage value for the alternative hypothesis of close linkage if such exists.

Using the system of gene symbols adopted in part by North American workers the genotypes of Laggan and White Tartar can be represented as AA bcbc dd ee ff gg and aa bcbc DD ee ff gg respectively where G is used to denote the second linked gene in Garry (and Hajira) found using certain Australian races. With the local scheme which is considered to indicate better allelism and the important varietal source in

which the genes in question were first found, the corresponding genotypes would be Rd_1Rd_1 hj_1hj_2/hj_1hj_2 jo_1jo_1 rl_1rl_1 and $Rd_1{}^1Rd_1{}^1$ hj_1hj_2/hj_1hj_2 jo_1jo_1 rl_1rl_1 respectively; in this scheme Jo_1 is the abbreviation for Joanette in which gene E was first found and Rl_1, for a similar reason, represents R.L.524·1 in which one of the major genes is F.

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A TRIGONALID WASP (HYMENOPTERA, TRIGONALIDAE) FROM AN ANTHELID COCOON (LEPIDOPTERA, ANTHELIDAE).

By E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra.

(Five Text-figures.)

[Read 27th June, 1962.]

Synopsis.

Some stages in the life-history of a trigonalid wasp, *Taeniogonalos* sp., bred as a secondary parasite of an anthelid, are outlined. An anthelid is an unusual host for Australian Trigonalidae.

On 16th February, 1961, Mr. Murray Upton collected three anthelid larvae beneath bark on trunks of *Eucalyptus viminalis* at Lee's Spring, Australian Capital Territory, at an altitude of 4,000 ft. The larvae fed readily on eucalypt leaves in an outdoor insectary at Canberra and all three pupated towards the end of February, 1961. One cocoon yielded an adult moth, *Anthela* sp. (det. I.F.B. Common), on 5th September, 1961. The second yielded a large number of *Apanteles* sp. (Braconidae). A male trigonalid, *Taeniogonalos* sp., emerged from the third cocoon on 20th November, 1961. As this was an unusual host record for an Australian trigonalid, a detailed examination of the anthelid cocoon was undertaken.

Other trigonalid wasps have been bred as hyperparasites from the nests of Vespoidea (Cooper, 1954) and as hyperparasites of sawfly larvae through an ichneumonid or tachinid primary parasite (Clausen, 1940). The Australian species, *Taeniogonalos maculatus* Smith, has been recorded as a primary parasite of sawflies of the genus *Perga* (Raff, 1934).

The eggs of Australian species of *Taeniogonalos* are deposited on eucalypt leaves close to the leaf margin. The female sits on the upper surface of the leaf, curls the apex of the gaster over the edge and passes the ovipositor up from below to deposit the eggs on the under side of the leaf. Processes from the sternites of the basad segments of the gaster, especially that from the second segment, grip the leaf surface from above, at a point almost directly above the tip of the ovipositor. If portion of this leaf tissue is eaten by a sawfly larva the very small trigonalid eggs develop and hatch. The larvae burrow through the gut wall into the body cavity of the sawfly larva. Under normal circumstances the sawfly must also be parasitized by an ichneumonid or tachinid before the trigonalid is able to complete its development. In the case under discussion it would appear that trigonalid eggs on a eucalypt leaf were eaten by an anthelid caterpillar.

The anthelid cocoon shows the exit hole of the trigonalid slightly to one side of the tip. The cocoon was found to contain a typical ichneumonid cocoon with a loosely woven outer layer of silk holding it firmly in place. The shrunken last larval skin of the anthelid was also present at the end remote from the exit hole.

The ichneumonid cocoon had a large rounded opening at one end through which the adult trigonalid had emerged. It was empty except for a dried mass at the far end. There was no partition separating any debris from the pupal space occupied by the trigonalid.

When this mass was treated with caustic it yielded several larval skins, exuviae and other debris. At the furthest point was the last larval skin of the ichneumonid which had spun the inner cocoon. Then followed the bodies of five or possibly six third instar trigonalid larvae with their very characteristic large heads. The sixth of these may have been only the moulted skin of the larva which ultimately developed into the one adult. Mixed with these larvae there was a considerable quantity of small chitinous particles which had apparently been torn from the inside lining of the ichneumonid cocoon by the fully grown trigonalid larva before it pupated. Then followed the fifth instar trigonalid larval skin with its distinctive three-toothed

mandibles. This skin contained a large quantity of meconium. Finally, there was the cast skin of the trigonalid pupa. The skin of the fourth instar larva was not recognized.

From the remains in the ichneumonid cocoon it would appear that the ichneumonid larva was able to spin its cocoon but did not have time to pupate. It had contained several trigonalid larvae which emerged after cocoon formation as third instar larvae

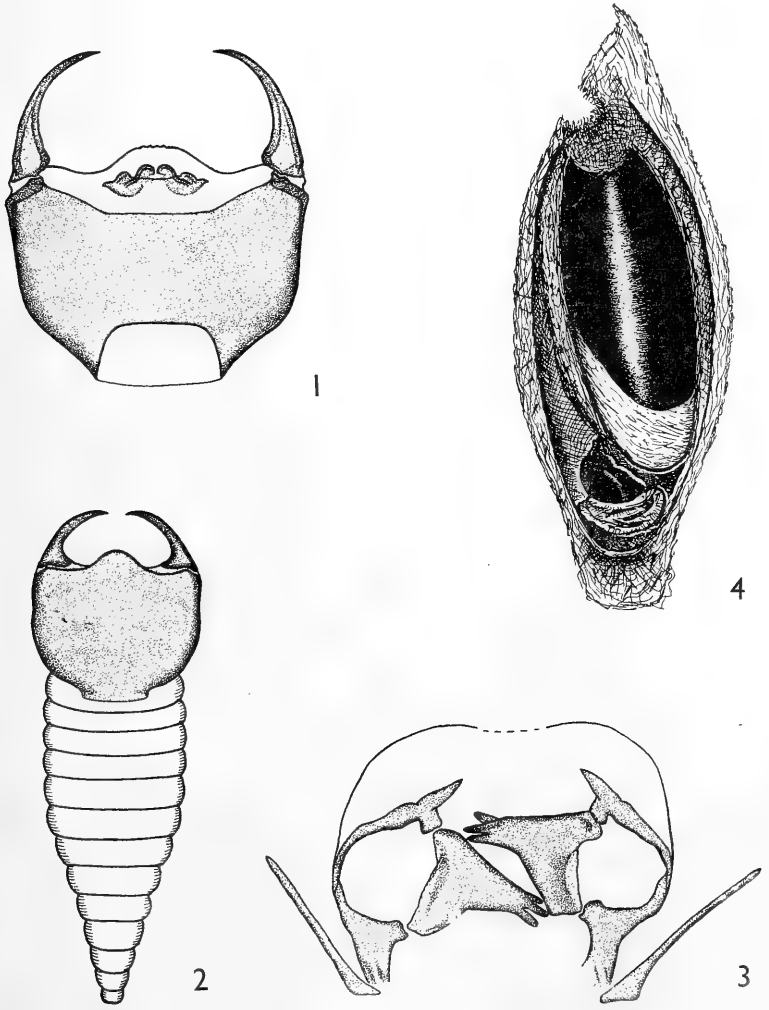

Figure 1. Head of third instar trigonalid larva, ventral view, × 45.
Figure 2. Third instar trigonalid larva, dorsal view, × 25.
Figure 3. Sclerotized portion of head of fifth instar trigonalid larva, × 45.
Figure 4. Anthelid cocoon in median longitudinal section, showing anthelid larval skin, ichneumonid cocoon and emergence hole of trigonalid, × 2.

and fed externally on it. Only one of the trigonalids completed its development, the others succumbing at the third instar.

The head capsule of the ichneumonid larva indicates that the primary parasite was a species of *Enicospilus*, but insufficient is known of the larvae of Australian species of the genus to permit specific determination.

The male trigonalid, *Taeniogonalos* sp., differs in some characters from the males of known species, but whether these differences are due to a possible abnormal host relationship or are specific cannot be determined until more adult material is collected. The emergence time of the parasite (November) is most unusual. Most adults of the genus emerge in the autumn, the earliest previous record being January.

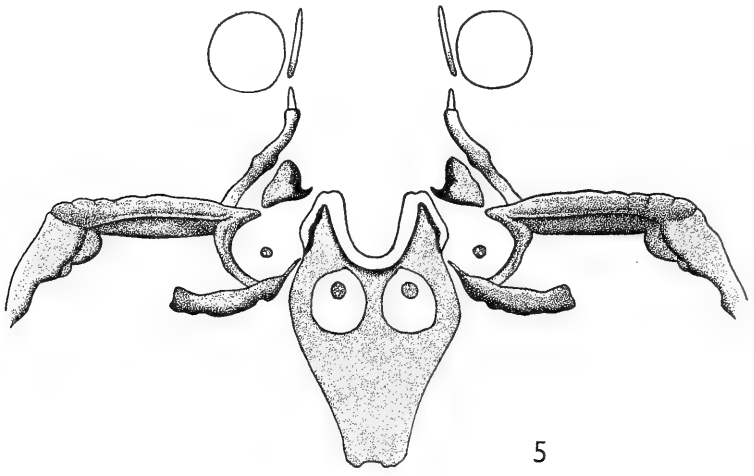

Figure 5. Sclerotized portion of head of *Enicospilus* larva, × 45.

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A NEW ENCYRTID GENUS PARASITIC ON BUG EGGS.

By E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

(Nine Text-figures.)

[Read 27th June, 1962.]

Synopsis.

A new genus of bug egg-parasites, containing species of possible economic importance, is described as *Xenoencyrtus*, with genotype *X. niger*, sp. nov.

A number of genera of the chalcidoid family Encyrtidae are known to parasitize bug eggs. A species has recently been reared from eggs of the pentatomid bug, *Nezara viridula smaragdula* (F.), an introduced pest of some economic importance. This parasite species is being cultured for possible future distribution in efforts to control the bug. A second undescribed species of the same genus, bred from the same host, is known from preserved material.

Another two species of this genus have been described from bug eggs. Girault (1915: 172) described under the genus *Ericydnus*, one species, *hemipterus*, bred from pentatomid eggs. Dodd (1917: 354) described two species, and a variety, under *Tetracnemella* and transferred *hemipterus* to that genus. At least one of Dodd's two species is congeneric with *hemipterus* which, however, differs from *Tetracnemella* quite markedly in wing venation, though it does have the broad truncate cutting edge to the mandible and the widely separated axillae that occur in the genotype species of *Tetracnemella*.

This new genus, represented by at least four species, is very similar to *Ooencyrtus* in most respects, but differs in mandible shape as well as in wing venation and structure of the axillae.

Genus Xenoencyrtus, gen. nov.

Genotype, *Xenoencyrtus niger*, sp. nov.

Very similar to *Ooencyrtus*, but mandible with a broad straight cutting edge developed from the upper two teeth; marginal vein thickened, distinctly longer than wide, slightly longer than stigmal vein, post-marginal vein only slightly developed, very much shorter than stigmal; basal funicle segments almost as long as pedicel; ocelli minute; axillae very widely separated.

In most, if not all, species of the genus there is a brachypterous as well as a fully-winged form. The brachypterous condition occurs in both sexes. In all known species the fully developed forewing has a broad infuscated band across the middle of the wing. In brachypterous specimens the apical third of the wing is infuscated. The thickened marginal vein is evident in the brachypterous as well as in the fully winged condition.

Key to species of Xenoencyrtus.

Winged forms:

1. Middle legs, except coxae, all pale; head, thorax and base of gaster dark metallic green .... *megymeni* (Dodd).
   Middle leg mostly dark but tarsus and apex of tibia pale.
   - i. Head, thorax and base of gaster dark metallic green; lateral thorax and gaster metallic purply black; middle leg pale only at tarsus and apex of tibia ..... *niger*, sp. nov.
   - ii. Head, thorax and base of gaster metallic blue; otherwise gaster metallic purply black; lateral thorax mostly dull reddish; middle leg pale at joints and with tibia mostly pale ..... *rubricatus*, sp. nov.

Brachypterous forms:

1. Head, thorax and base of gaster metallic purply blue, gaster purply black; lateral thorax with dull reddish hues; lower face more glabrous than vertex ..... *rubricatus*, sp. nov.
   Head, thorax and base of gaster metallic green, scutellum particularly green, head more blue, gaster shining black, lateral thorax shining black with some purple hues; lower face lined, more ornamented than vertex ..... *niger*, sp. nov.
   "Brilliant metallic dark green, the mesopleurum and abdomen purple" .. *hemipterus* (Grlt).

XENOENCYRTUS HEMIPTERUS (Girault).

Ericydnus hemipterus Girault, 1915: 172.—*Tetracnemella hemiptera* (Girault) Dodd, 1917: 355.

Only the brachypterous form has been described.

Types: In the Queensland Museum.

Type locality: Gordonvale, Queensland.

The species was reared from pentatomid eggs.

XENOENCYRTUS MEGYMENI (Dodd).

Tetracnemella megymeni Dodd, 1917: 354.—*Tetracnemella megymeni brachyptera* Dodd, 1917: 355.

The fully winged female and the brachypterous male and female have been described.

Types: In the South Australian Museum.

Type locality: Darwin, Northern Territory.

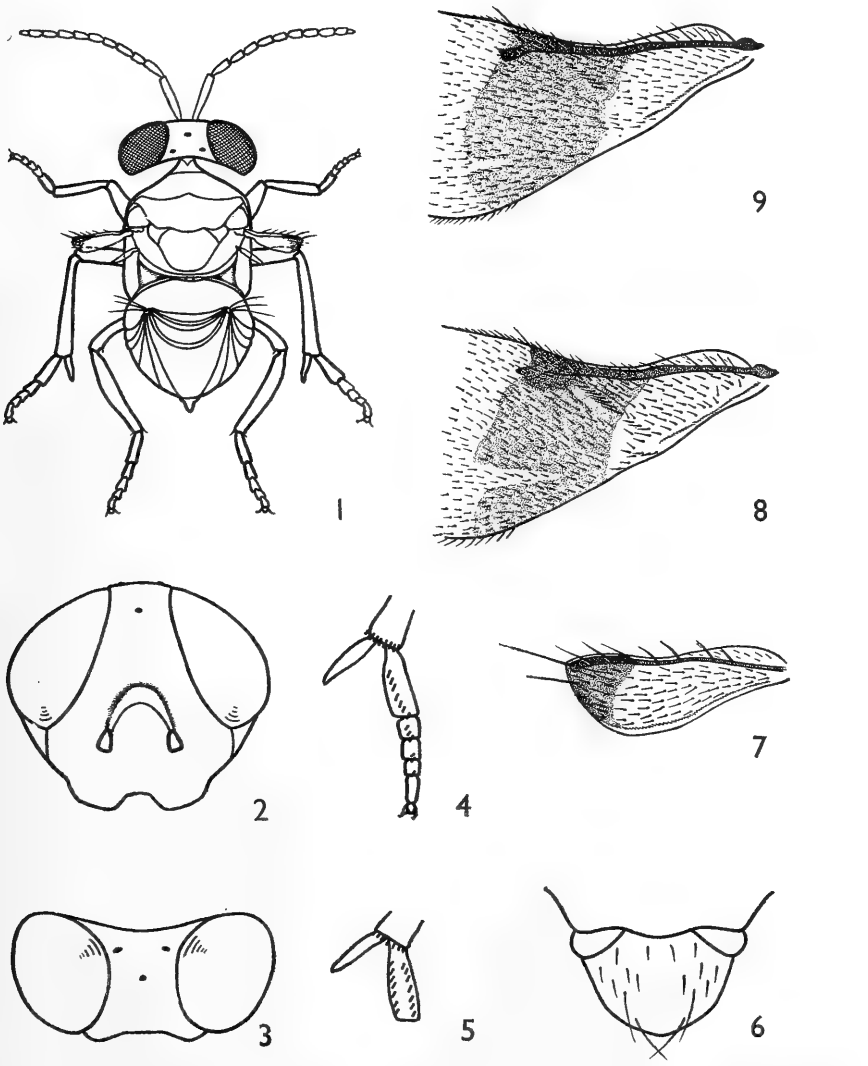
The species was bred from the eggs of the hemipteron, *Megymenum insulare* Wwd. (Pentatomidae).

XENOENCYRTUS NIGER, sp. nov. (Figs 1–8).

Female, fully winged. Head, thorax and base of gaster dark metallic green, remainder of gaster and lateral thorax metallic purply black; antenna all dark; mandibles dark; tegula dark; legs mostly metallic black, tarsi pale and apex of middle tibia narrowly pale; forewing with a transverse infuscated band towards the middle of the wing, from the bend of the submarginal vein to the apex of the stigmal vein, the band widening slightly posteriorly, the distal margin straight, oblique.

Length 1·2 to 1·3 mm.; vertex of head wide, but not quite as wide as eye width, mesal margin of eyes converging slightly to apex, vertex very finely ornamented, scaly; ocelli very small, lateral ocelli about their own diameter distant from eye, distinctly further apart than either is from median ocellus, median ocellus a little further from eye than from lateral ocellus; caudal margin of vertex concave, subcarinate; frons, in lateral view, regularly convex; scrobes clearly defined, short, deep, converging above and meeting almost in a point, very widely separated from eye margin, area between them somewhat raised but flattening to clypeal region; antennal insertions well separated, but only slightly further apart than either is from eye, distinctly closer to lower margin of clypeus than to eye; lower face and gena irregularly finely rugose, the rugae more or less vertical; gena long, twice as long as distance from antennal insertion to lower border of clypeus; lower face with only a few scattered hairs, with a single row bordering the mesal margin of the eye; scape long and thin, pedicel long, more than twice as long as wide, funicle segments thinner than pedicel, all considerably longer than wide, first funicle about two-thirds as long as pedicel, first five funicles all subequal in length, widening very slightly, sixth funicle slightly shorter than fifth; club long, only slightly expanded, clearly three-segmented, the first segment slightly the longest, apex unevenly, rather pointedly rounded; club clearly somewhat less than half as long as funicle; scutellum glabrous at apex, slightly scaly at base, hairs widely absent from meson, apical pair enlarged, erect, the others shorter and widely spaced; gaster about as long as thorax, the caudal margins of the tergites strongly convex, the apical tergite very much the largest, ovipositor valves only just visible; middle tarsus thickened, basitarsus long, about as long as the following three tarsal segments combined, apical tarsal segment clearly longer than the fourth, tarsus tapering to the apical segments which are quite narrow, basitarsal pad formed by a single row of short, spaced, rather acute tubercles on each lateral margin, the following tarsal segments with similarly placed tubercles usually three on the second segment, two on the third segment and one on the fourth segment; forewing with irregular costal margin, emarginate at the bend of the submarginal vein, costal margin convex near base producing a wide costal cell which then narrows rapidly to become linear in the region of the bend in the submarginal vein, submarginal vein somewhat thickened from the

bend to the marginal vein, marginal vein thickened but distinctly longer than wide, stigmal vein short, with an upper spur, distinctly shorter than the marginal vein, postmarginal short, only about half as long as the stigmal; area below submarginal vein with evenly spaced setae almost to base.



Figs 1-8. *Xenoencyrtus niger,* gen. et sp. nov. 1, Brachypterous female, × 40; 2, Head of winged female, front view, × 70; 3, Head of winged female, dorsal view, × 70; 4, Middle tarsus, ventro-lateral view, × 70; 5, Middle basitarsus, ventral view, × 70; 6, Scutellum and axillae, × 70; 7, Forewing, brachypterous form, × 100; 8, Basal half of forewing, fully winged form, × 70.

Fig. 9. *Xenoencyrtus rubricatus,* sp. nov. Basal half of forewing, fully winged form, × 70.

Female, brachypterous. Very similar to the fully winged female except for the wings and the colour of the middle legs. Forewings appearing white except for an apical dark triangle covering the apical quarter or so of the wing; apex of wing rather obliquely truncate, venation reaching to apex, the thickened marginal vein distinct but postmarginal and stigmal veins not distinguishable, apical bristle on marginal vein enlarged, almost twice as long as the preceding bristles; hind wing thread-like, only

about half as long as the forewing; middle tibia mostly pale, only slightly darkened towards base.

Male, fully winged. Body colouring similar to female; legs similar, but middle tibia mostly pale; forewing infuscated but less intense than in female.

Length 0·9 mm.; vertex a little wider than in female; antenna with the funicle segments clothed in long hairs, hairs distinctly longer than the width of the segments, first funicle distinctly longer than pedicel, funicle segments all subequal though decreasing slightly to the sixth segment, club only slightly expanded, a little more than twice as long as sixth funicle.

Very similar to the brachypterous male apart from the wings.

Male, brachypterous. Colouring as in brachypterous female with middle tibia mostly pale and wings darkened at apex.

Length 0·9 to 1·0 mm.; vertex slightly wider than eye width, lateral ocelli clearly more than their own diameter distant from eye, median ocellus distinctly further from eye than from lateral ocellus; scape long and thin, very slightly flattened, pedicel almost twice as long as wide, funicle segments very long, as wide as pedicel, clothed in long hairs distinctly longer than width of segments, first funicle distinctly longer than pedicel, second funicle subequal to first, succeeding funicle segments decreasing very slightly, but sixth funicle distinctly more than twice as long as wide, club large, only slightly expanded, more than twice as long as sixth funicle, apex tapering, asymmetrically rounded.

Types: Holotype ♀, allotype brachypterous ♂, typical brachypterous ♀ and typical ♂ and paratypes in the C.S.I.R.O., Division of Entomology Museum, Canberra. Paratypes in the British Museum (Nat. Hist.) and the U.S. National Museum.

Type locality: Canberra, Australia.

Host: Bred in insectary from eggs of *Nezara viridula smaragdula* (F.) (13 Oct. 1961, G. R. Wearne).

The type series has been reared from one field-collected brachypterous female.

The brachypterous form is very similar to *hemipterus*, but differs in the colour of the abdomen and of the lateral thorax. The male is normally brachypterous. Only one fully winged male has been observed. Brachypterous, as well as fully winged, females are common.

Xenoencyrtus rubricatus, sp. nov. (Fig. 9).

Female, fully winged. Head, thorax and base of gaster dark metallic blue, otherwise gaster metallic purply black; lateral thorax mostly dull reddish; antenna mostly dark, but club and apical funicle segments somewhat paler; mandibles dark; tegula dark; legs mostly metallic black, but tarsi, joints and most of middle tibia pale; forewing with a transverse infuscated band towards the middle of the wing, from the bend of the submarginal vein to the apex of the stigmal vein, the distal margin of the infuscation decidedly convex in the middle, without a narrow deep re-entrant angle towards the posterior border.

Length 1·0 to 1·1 mm.; vertex of head wide but distinctly less than eye width, mesal margin of eyes clearly converging to apex, vertex very finely ornamented, scaly; ocelli very small, lateral ocelli clearly somewhat more than their own diameter distant from eye, distinctly further apart than either is from median ocellus, median ocellus only about as far from eye as from lateral ocellus; caudal margin of vertex concave, subcarinate; frons, in lateral view, regularly convex; scrobes clearly defined, short, deep, converging above and meeting in a rounded point, very widely separated from eye margin, their margins rounded, area between them somewhat raised but flattening to clypeal region; antennal insertions well separated, but only about as far apart as each is from eye, distinctly closer to lower margin of clypeus than to eye; lower face and gena irregularly finely rugose, the rugae more or less vertical but shallow and widely spaced; gena long, twice as long as distance from antennal insertion to lower border of clypeus; lower face with only a few scattered hairs, with a single row bordering the mesal margin of the eye; scape long and thin, pedicel long, more than

twice as long as wide, funicle segments slightly thinner than pedicel, all considerably longer than wide, first funicle about two-thirds as long as pedicel, funicle segments all subequal but fifth and sixth slightly shorter, club long, only slightly expanded, clearly three-segmented, the first segment slightly the longest, club little more than a third as long as funicle, apex tapering, asymmetrically rounded; scutellum glabrous at apex, scaly over almost basal half, hairs sparse, widely absent from meson, apical pair enlarged, erect; gaster about as long as thorax; ovipositor valves only just visible; middle tarsus thickened, basitarsus long, longer than the following three tarsal segments combined, apical tarsal segment about twice as long as the fourth segment, tarsus tapering to the apical segments which are quite narrow, basitarsal pad formed by a single row of short, spaced, rather acute tubercles on each lateral margin; forewing with irregular costal margin, emarginate at the bend of the submarginal vein, as in the genotype species.

Female, brachypterous. Very similar to the fully winged female except for the wings. There is little if any difference in the colour of the legs. Wings very similar to those of *niger*, but the apex of the forewing a little more rounded.

Males. Not known.

Types: Holotype ♀, typical brachypterous ♀ and paratype females in the C.S.I.R.O. Division of Entomology Museum, Canberra. The holotype is the outermost specimen of a card mounted series of nine specimens. Paratype fully winged ♀ and paratype brachypterous ♀ in the British Museum (Nat. Hist.).

Type locality: Toowoomba, Queensland (4 Feb. 1938, H. Jarvis).

Host: Bred from eggs of *Nezara viridula.*

References.

Dodd, A. P., 1917.—Records and descriptions of Australian Chalcidoidea. *Trans. Roy. Soc. S. Austr.*, 41 : 354.

Girault, A. A., 1915.—Australian Hymenoptera, Chalcidoidea Part 7, Encyrtidae. *Mem Queensl. Mus.*, 4 : 1-184.

ZINC DEFICIENCY ON THE DARLING DOWNS, QUEENSLAND.

By B. R. Hewitt, formerly Plant Physiologist, Department of Agriculture and Stock, Queensland.

[Read 25th July, 1962.]

Synopsis.

Linseed (*Linum usitatissimum* L.) and wheat (*Triticum vulgare* L.) growing on open plain black soil of the Darling Downs showed responses to applications of zinc salts. Linseed has shown symptoms of a nutrient disorder which was not corrected by foliage sprays of zinc salts. When soil applications of zinc salts were used there was no response when the fertilizer was broadcast on the soil. Increases in yield and correction of the deficiency symptoms were obtained when the fertilizer was placed in close proximity to the seed at sowing time, for example, when the fertilizer was drilled in with the seed and when the seed was pelleted with the fertilizer. Responses to zinc salts were obtained under glasshouse conditions when these salts were applied at a high rate, broadcast on the soil.

Although wheat showed no deficiency symptoms, responses to zinc applications were obtained when the technique for applying the nutrient was similar to that for linseed.

The results from experiments made, together with field observations, indicate that the practical method to overcome the disorder is to use seed pelleted with zinc oxide.

Introduction.

Linseed crops on the Darling Downs have shown very severe symptoms of a nutrient disorder. This disorder has been marked on the alkaline black soils of the Downs grassland, but has been observed on other soil types where linseed is grown. On the alkaline black soils in particular the greatest incidence of the disorder occurs on fallowed land.

The symptoms of the disorder are similar to those described by Millikan (1946) for zinc deficiency. After emergence, sometimes within two weeks, affected plants have bronze-coloured spots on the upper leaves. Death of the apical meristem then occurs. If subsequent growth takes place this occurs by lateral branching from the base. Occasionally the upper leaves develop white necrobic areas before the death of the plant apex. This is a symptom not mentioned by Millikan. Linseed which s only moderately affected is stunted in growth and the plants have a general yellow colour.

Field observations indicate that a linseed crop which is severely zinc deficient gives yields as low as one-eighth of the normal yield. The problem then is of considerable economic importance.

Methods.

In all cases the soil used was Waco type black soil (Thompson and Beckmann, 1959). In pot trials, unless otherwise amended, 7″ earthenware pots painted inside with bituminous paint were used.

In the first phase of research on the problem indications as to the nature of the disorder were obtained from small observation trials in the field and from glasshouse trials.

Then the results from these exploratory trials were applied in full scale field trials while concomitant glasshouse trials were also made.

Results.

Experiments with Linseed.

In this section of the work the Hazeldean variety of linseed was used.

(1) It was reported by Ferres (1949) that zinc-deficiency symptoms occurred in winter sown but not in summer sown flax. In a time of planting trial in which linseed was sown each month from May to October, 1958, observations showed that the incidence of the disorder did not decrease.

(2) In a pot trial (using 4-gallon cans) linseed was grown under different treatments. These were: (*a*) Control; (*b*) Soil sterilized; (*c*) Sugar added to soil; (*d*) Ammonium nitrate added to soil.

The soil was steam sterilized for four hours at 15 lb./in.^{2}, and the experiment was divided into two parts. In one-half of the pots the cotyledons were removed from the plants immediately on emergence. The only plants which did not immediately show symptoms of the disorder were those growing in sterilized soil with the cotyledons intact.

(3) In a field observation plot it was seen that addition of sugar to the soil resulted in better growth of plants when compared with plants growing in untreated soil.

Table 1.

Effect of Zinc Sulphate as Soil Application on Growth of Linseed.

Treatment.	Average Weight Shoot in Gram.	% of Control.
Control	0·109	100
$ZnSO_4$ added at the rate of ½ cwt./ac. ..	0·119	109
,, ,, ,, 1 cwt./ac. ..	0·122	112
,, ,, ,, 2 cwt./ac. ..	0·117	107
,, ,, ,, 5 cwt./ac. ..	0·145	133
,, ,, ,, 20 cwt./ac. ..	0·132	121
,, ,, ,, 200 cwt./ac. ..	0·086	79

(4) Linseed plants, in a number of small field trials, were sprayed with solutions of the salts of zinc, manganese, iron, boron, copper, molybdenum, singly and in combination, as well as with ammonium sulphate solution. In no case was there a marked effect on the growth of linseed.

(5) There was no visible response when zinc and manganese salts and ammonium sulphate were broadcast on the soil at sowing time.

(6) Seed from different sources and with different histories was sown in order to determine whether differences in plant growth occurred. No differences were found.

Glasshouse Experiments.

In this section of the work, the usual commercial linseed variety was used (viz. Walsh).

1. In a pot trial in which there were four pots for each treatment and six plants per pot the weight of the plants dried at 105° C. was determined and the results given in Table 1.

2. In a second glasshouse trial with linseed the effect of zinc sulphate added to the soil at the rate of 5 cwt./ac. (i.e. 1·50 g. zinc sulphate) was determined. The results are given in Table 2. Table 3 shows the comparison between unfertilized and fertilized linseed.

Field Experiments.

(1) In this trial there were three treatments: (*a*) Control; (*b*) Linseed dusted with zinc oxide at the rate of 1 lb. ZnO : 15 lb. seed; (*c*) Linseed pelleted with zinc oxide at the rate of 1 lb. ZnO : 1 lb. seed.

The weight of seed obtained from each plot (18′ × 18′) in oz. is given in Table 4.

TABLE 2.

Effect of Zinc Sulphate applied to the Soil at a Rate of 5 cwt./ac. on the Growth of Linseed.

No. Plants.	Weight in Gram of Shoots Dried at 105° C.	
	Total Weight.	Weight per Plant.
	Control.	
13	1·5150	0·1157
11	1·7135	0·1558
12	1·6085	0·1174
12	1·6470	0·1374
12	1·5860	0·1321
12	1·5900	0·1325
13	1·4710	0·1131
12	1·5936	0·1328
6	0·8365	0·1394
	Fertilizer Added.	
12	2·0158	0·1680
12	1·7920	0·1500
11	1·8420	0·1675
12	2·2044	0·1837
12	2·3596	0·1883
12	1·8360	0·1530
12	2·3480	0·1874
11	1·8728	0·1703
12	2·0810	0·1734

TABLE 3.

Effect of Zinc Sulphate applied at the Rate of 5 cwt./ac. on the Growth of Linseed.

	Average Weight Plant.	% of Control.
Control plants	0·1296±0·0262 g.	100
Plants to which fertilizer added ..	0·1713±0·0213 g.	132

TABLE 4.

Yield of Linseed after Zinc Oxide Applications.

Control.	Dusted. (1 lb. ZnO : 15 lb. seed.)	Pelleted. (1 lb. ZnO : 1 lb. seed.)
80	76	104
70	72	84
72	68	84
80	106	84
70	70	76
76	88	92
68	93	88
82	64	68

	Average Weight Seed per Plot.	% of Control.
Control	75± 7 ozs.	100
Dusted seed	80±26 ozs.	107
Pelleted seed	85±19 ozs.	112

(2) In a second field trial the effect of drilling with the seed 1 cwt./ac. of zinc sulphate was determined. There were six replicates of each treatment. The weight of seed obtained from plots of size 12′ × 5 ch. is given in Table 5. The mean yields from Table 5 are given in Table 6. The result was statistically significant at the 1% level.

Experiments with Wheat.

Glasshouse Experiment.

Wheat var. Spica was used. There were four treatments: (*a*) Control; (*b*) 0·6 g. $ZnSO_4$ added per pot (= 1 cwt./ac.); (*c*) 1·2 g. $ZnSO_4$ added per pot (= 2 cwt./ac.); (*d*) 2·4 g. $ZnSO_4$ added per pot (= 4 cwt./ac.).

TABLE 5.

Field Experiment in which Zinc Sulphate was Used as a Soil Application at a Rate of 1 cwt./ac.

Plot No.	Treatment.	Yield. (lb. Linseed.)
1	Control	82
2	Fertilizer added	100·5
3	Control	79
4	Control	85
5	Fertilizer added	114
6	Control	69·5
7	Fertilizer added	100
8	Control	70·5
9	Fertilizer added	87·5
10	Fertilizer added	93·5
11	Control	74
12	Fertilizer added	95·5

TABLE 6.

Comparison of Fertilized ($ZnSO_4$ at 1 cwt./ac.) and Unfertilized Linseed.

		% of Control.
Control	843 lb./ac. linseed	100
Fertilizer added	1084 lb./ac. linseed	129

TABLE 7.

Glasshouse Experiment with Wheat (var. Spica) showing the Effect of Soil Application of Zinc Sulphate.

Treatment.	Average Weight Plant (g.).	% of Control.
1	0·94	100
2	1·11	118
3	1·06	113
4	1·17	125

Six pots were used for each treatment and six plants were grown in each pot. The shoot weights of 36 plants were determined together after drying at 105° C. and the average weight of one plant determined. The results are shown in Table 7.

Field Trial.

The effect of zinc sulphate applications on the yield of wheat was determined. Zinc sulphate at the rate of 40 lb. per acre was drilled in with the seed at sowing time. The wheat variety Seafoam was used. There were two treatments, one being the zinc

sulphate application and the other being control where no zinc sulphate was added. There were six replicates of each treatment. The yields which are given in Table 8 were poor owing to adverse weather conditions.

The mean yields from the field trial shown in Table 8 have been tabulated in Table 9.

TABLE 8.

Field Fertilizer Experiment showing Yields of Wheat, var. Seafoam, after a Soil Application of Zinc Sulphate at a Rate of 40 lb./ac.

Plot No.	Treatment.	Yield in lb. Wheat from Plot of Size 12′ × 5 Chains.
1	Fertilizer added	94
2	Fertilizer added	102
3	Fertilizer added	84
4	Control	90
5	Control	79
6	Control	75
7	Fertilizer added	89
8	Control	76
9	Control	75
10	Fertilizer added	92
11	Control	82
12	Fertilizer added	90

TABLE 9.

Mean Yields of Wheat, var. Seafoam, with Zinc Sulphate added at the Rate of 40 lb./ac.

		% of Control.
Control	875 lb./ac.	100
Fertilizer added ..	1012 lb./ac.	116

DISCUSSION.

The results from the first phase of the research indicated that a nutrient is contained in the cotyledons of linseed the absence of which caused symptoms of the disorder to appear; and that, on steam sterilization of the soil, this nutrient is released and made available to the plant.

The nutrient could be fixed by chemical or by biological tie-up. Millikan (1951) has given evidence to show that the chemical fixation, under conditions of high phosphate content of the soil, is very important. Millikan (1942) also found that steam sterilization of the soil resulted in a higher concentration of available zinc in the soil, although Davies (1949) reported a response to zinc applications after sterilization of black earths. The latter result may be due to incomplete sterilization of the soil. Certainly, Ark (1936) found that incomplete sterilization of soils on which plants exhibited zinc-deficiency symptoms induced symptoms of a toxicity. Complete sterilization of the soil used by Ark resulted in healthy plant growth.

In this present work on the Downs it was found in the field that healthy plant growth occurred when sucrose was added to the soil. Ark found that soils which produced fruit trees exhibiting little leaf disease were microbiologically predominantly bacterial. Healthy soils had a predominantly fungal population. Water, ether and alcohol extracts of diseased soils when added to corn plants growing in a complete medium produced toxicity symptoms. These symptoms were eliminated by adding additional zinc to the medium. Ark was able to isolate three bacteria from diseased

soils, two of which, when inoculated into healthy soils or complete sand culture, induced little leaf symptoms. These symptoms were overcome by adding zinc salts to the soil or medium.

Therefore it appears that the microbiological properties of the soil are extremely important for the availability of zinc to crop plants and for the appearance of zinc deficiency symptoms in those plants. This is substantiated by the present work and leads to the conclusion that when zinc salts are used as a soil application they must be in close contact with the seed. Foliage sprays of zinc salts proved to be ineffective in controlling the disorder on the Downs and this is very likely due to the fact that affected plants develop the disorder so soon after emergence that the leaf area is not sufficient to absorb an adequate amount of nutrient. Another conclusion which stems from Ark's work is that sometimes a toxin (presumably bacterial) caused toxicity symptoms in plants so that atypical zinc-deficiency symptoms may develop in crops, although these disorders may be remedied by the application of zinc salts to plant or soil.

In the second phase of the research on the disorder in linseed the first hypothesis was put into practice. The results of a number of experiments, both in the glasshouse and in the field, have been listed and in all of them there was a plant response to soil applications of zinc compounds. In the field there were two main types of treatments—zinc sulphate was drilled in with the seed and seed was pelleted with zinc oxide. In both treatments the fertilizer was in close proximity to the seed and apparently overcame the zinc fixation factor. In glasshouse trials zinc sulphate was applied at varying rates as a soil application. It was only at fairly high rates of application that substantial plant responses were obtained. This again points to the fact that the zinc-fixing capacity of the soil was quite high.

Responses to zinc compounds were also obtained with wheat in glasshouse and field trials.

All these results indicate that the use of zinc compounds on the open plains black soil of the Darling Downs would be beneficial to crops and result in increased yields. However, in some field trials very heavy applications of zinc sulphate have been used (1 cwt. acre) to achieve the results. This experimental practice could not be recommended for general use owing to the danger of eventually inducing zinc toxicity symptoms, either by the build-up of high concentrations of available zinc or to a change in soil conditions resulting in a quantitative and qualitative change in the microbiological population of the soil and a release of bound zinc. Therefore the only practical method of using zinc compounds would be to use seed pelleted with zinc oxide. In one field trial using seed pelleted with zinc oxide encouraging results were obtained.

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NOTES ON PLANT PARASITIC FUNGI. I.

By J. Walker, Biology Branch, New South Wales Department of Agriculture.

(Plate iii, figs 1–5.)

[Read 25th July, 1962.]

Synopsis.

Taxonomic notes on several plant parasitic fungi are presented. *Elsinoe hardenbergiae* n. sp. causing a leaf and stem spot of the legume *Hardenbergia violacea* is described and the following new combinations are made—*Physoderma australasica* (McAlp.) n. comb., and *Sphacelotheca valentula* (Syd.) n. comb. The description of *Phaeoseptoria eucalypti* Hansf. is emended and its method of conidium production described. *Fusarium byssinum* McAlp. is shown to be a species of *Aschersonia*; the record of the conidial stage of *Pezicula corticola* in N.S.W. is shown to be based on a *Tubercularia* sp.; several other fungi are discussed.

This paper presents notes on problems of mycological taxonomy encountered during a revision of the check list of plant diseases recorded in New South Wales. This list was published originally in 1935 (Noble, Hynes, McCleery and Birmingham, 1935) and was followed over the next six years by two supplements (Noble, Hynes, Magee, McCleery, Birmingham, Edwards, Wilson & Brown, 1937; Hynes, Magee, Edwards, Wilson, Brown, Kiely, Milthorpe & Fraser, 1941). Since that time, many plant diseases new to the State have been recorded and lists of these have been published from time to time in the *Agricultural Gazette of N.S.W.*, but, until recently, no revision of the original list and records and incorporation with them of the later records has been attempted.

This revision is now in progress and is based on a re-examination of all N.S.W. specimens filed in the Herbarium of the Biology Branch of the N.S.W. Department of Agriculture. During this work, many problems of a taxonomic nature have been encountered amongst the parasitic fungi and other information concerning new records, extensions of host range, etc., has also been obtained. In this and subsequent papers, it is intended to discuss these taxonomic problems and to give details of other findings made. After each collection, the number of the specimen in the Herbarium of the Biology Branch is quoted, and after the name of each species, references to it in the lists of N.S.W. and Australian fungi compiled by Brittlebank (1940), Cooke (1892), Costin (1954), Hynes *et al.* (1941), McAlpine (1895) and Noble *et al.* (1935, 1937) are given.

PHYCOMYCETES.

1. Synchytrium australe Speg., in *Ann. Soc. Cient. Argentina*, 11: 37, 1881.

Syn. *Synchytrium modioliensis* Cook, in *Mycologia*, 37: 288, 1945.

Although this species has not been listed previously as present in New South Wales, it has been known here for many years. The galls, at first bright yellow, then changing to red and finally almost black, are formed in profusion on leaves, petioles and young shoots of the common weed *Modiola caroliniana* (L.) Don. and make this species one of the most conspicuous chytrids present in New South Wales. Detailed descriptions of both sporangial and resting spore galls, their method of development and germination are given by Karling (1954, 1955*a*, 1955*b*).

Specimens examined: on *Modiola caroliniana*, Richmond, 5/1933, E. T. Edwards, 1755; Baulkham Hills, 3/3/1957, J. Walker, 5153; Baulkham Hills, 4/4/1959, J. Walker, 5154; Baulkham Hills, 10/11/1959, J. Walker, 5155.

2. PHYSODERMA AUSTRALASICA (McAlp.) J. Walker, n. comb.

Syn. *Protomyces australasica* McAlp., in *Agric. Gaz. N.S.W.*, 7: 155, 1896.—*Physoderma claytoniana* H. C. Greene var. *sparrowii* Savile and Parmelee, in *Mycologia*, 48: 587–8, 1956; Brittlebank, p. 92, 343, 1940.

This fungus was described by McAlpine (1896) causing small swellings on leaves and stems of *Claytonia australasica* J. Hook. from the Goulburn River flats in Victoria. It has recently been collected on the same host in New South Wales and examinations of this collection and portion of the type material have shown that the fungus is a species of *Physoderma*.

In North America, *Physoderma claytoniana* H. C. Greene was described in 1944 (Greene, 1944) and a large spored variety called *P. claytoniana* var. *sparrowii* Savile and Parmelee was described in 1956 (Savile & Parmelee, 1956). On spore size the Australian fungus appeared very similar to the var. *sparrowii* and material for comparison was sent to Professor J. Karling. He reported that the two were identical. McAlpine's specific epithet has priority and the above new combination and synonymy become necessary.

No study of *P. claytoniana* H. C. Greene has been made to see if it is in fact a different species or only a small spored variety of *P. australasica*. The fungus described by Karling (1950) under the name *P. claytoniana* H. C. Greene is in fact the large-spored *P. australasica*.

Description: Fungus causing small raised reddish spots on leaf blades and petioles. On blades, these were 1–2 mm. in diameter; on the petioles, they were somewhat elongated, roughly 2–3 mm. long and 1 mm. wide (dried material). These spots contain many golden-brown resting spores, roughly spherical to oval, usually with one side flatter than the other, (22) 25–40 (42) × (17) 21–34 (36)μ (Fig. 1) with several minute pores in the wall on the more convex side.

Specimens examined: on *Claytonia australasica*, Ardmona, Goulburn River flats, Victoria, 14/11/1895, G. H. Robinson No. 132, in Herb., Pathologists Branch, Dept. Agr., Victoria (type of *Protomyces australasica* McAlp.); Oberon, N.S.W., 4/1959, L. R. Fraser, 5758.

3. ALBUGO CENTAURII (Hansf.) Ciferri & Biga, in *Sydowia*, 9: 355, 1955.

Syn. *Cystopus centaurii* Hansf., in PROC. LINN. SOC. N.S.W., 79: 97, 1954; Brittlebank, p. 354, 1940 (as *Cystopus erythraeae* McAlp., nom. nud.); Costin, p. 68, 505, 1954 (as *Cystopus* sp.).

In Hansford's original description, the host of *A. centaurii* is given as *Centaurium spicatum* (L.) Druce. Examination of type material by L. Johnson at the National Herbarium, Sydney, has shown that the host is in fact *Centaurium erythraea* Rafn. *Centaurium erythraea* is an introduced species, the native *C. spicatum* being much less common except in some western districts of the State (Johnson, personal communication). *A. centaurii* has been recorded from several areas in eastern New South Wales and in all cases the host species has been *C. erythraea*.

This fungus was originally recorded by McAlpine and in Brittlebank's list of Australian fungi (p. 354, 1940) is listed under the name '*Cystopus erythraeae* McAlp. nom. nud.'. The earliest N.S.W. record is a specimen collected at Richmond, near Sydney, in 1910.

Specimens examined: on *Centaurium erythraea*, Richmond, 9/1910, no collector's name on packet, 2189; Kosciusko region, 4/1947, A. Costin (No. 59), 4186 (type); Oberon, 2/1954, L. R. Fraser, 4771.

ASCOMYCETES.

4. PROTOMYCES sp. on *Vittadinia australis* Rich.

Brittlebank, p. 409, 1940; Noble *et al.*, p. 41, 1935 (as '*Synchytrium* sp.').

A stem gall of *Vittadinia australis* Rich. caused by a species of *Synchytrium* has been listed by Noble *et al.* (1935). Specimens of this fungus were sent to Professor J. S. Karling, who reported that it is not a species of *Synchytrium* but that the large

spherical resting spores in the galls are probably those of a species of *Protomyces*, probably *P. macrosporus* Unger. Brittlebank (1940) lists a *Protomyces* sp. and a *Synchytrium* sp. on this host, but no details of locality, etc., are given.

Description: Galls on branches, often just above the point of branching, either completely surrounding the branch or bursting out on one side only, usually spindle-shaped, up to 25 mm. long by 8–10 mm. wide in the centre, the surface furrowed and corky, lighter in colour than the unaffected areas of the branch. Galls are firm in texture and are completely filled with a pale yellow mass, composed of spherical to subglobose to oval, a few spindle-shaped, spores, which are colourless with a very pale yellow wall 4–6 μ thick, smooth, 40–80 μ in diameter.

Specimens examined: on *Vittadinia australis*, Bathurst, 9/1923, R. J. Noble, 1528; Stockinbingal, 3/1927, R. J. Noble, 1527; Dirnaseeri, near Junee, 3/1927, R. J. Noble, 1529; Yass, 7/1935, E. T. Edwards, 1526, all as '*Synchytrium* sp.'.

5. Elsinoe hardenbergiae J. Walker, sp. nov.

Maculis in foliis amphigenis, supra atrobrunneis ad nigris, inferne brunneis, leniter elevatis, verrucosulis, rotundatis vel parvis irregularibus, 1–5 mm. diam., saepe in nervis confluentibus, margine anguste rubro-brunneo; in caulibus, maculis elongatis, 1–5 mm. longis, 1–2 mm. latis, griseis ad atrobrunneis, margine atrobrunneo. Stromatibus in maculis ex hyphis hyalinis compositis, 80–90 μ, usque ad 120 μ crassis, epidermis ex hyphis brunneis compositis, usque ad 15 μ crassis. Ascomatibus numerosis, elevatis, 50–160 μ latis, 30–120 μ altis; asci globosis, ellipsoideis vel obpyriformibus, 18–32 × 14–20 μ; ascosporis hyalinis transverse 3-septatis, ad maturitate loculo secundo longitudinaliter septato, ad septum medium constrictis, 12–16 × 4–6 μ.

Hab. in foliis et caulibus *Hardenbergiae violaceae* (Schneev.) Stearn, Werombi, prope Camden, 2/9/1959, J. Walker, 4972a (type); Goulburn, 1/1956, L. R. Fraser, 4976; Pitt Town, 7/1957, L. R. Fraser, 4977; Orangeville, prope Camden, 23/9/1959, J. Walker, 4974; Werombi, prope Camden, 23/9/1959, J. Walker, 4975, 4978, 4979.

This fungus causes a leaf and stem spot of the native leguminous shrub *Hardenbergia violacea*. On the upper surface of leaves, the spots are fawn to dark brown or almost black in colour, slightly raised with a rough, scabby surface, roughly circular in shape, individual spots being 1–5 mm. in diameter, but often running together to form larger irregular patches. The spots show a marked tendency to develop along the mid-vein of the leaf and sometimes run its full length, as well as along smaller veins. They are surrounded by a narrow reddish-brown margin of discoloured leaf tissue (Fig. 3*).

On the under surface of the leaves, spots are generally lighter in colour, but are similar in size, shape and scabby appearance to the spots on the upper surface. These spots are not the reverse of spots on the upper surface; only in a small number of cases was a spot seen to penetrate the thickness of the leaf.

On the petioles and stems, many light grey to dark brown elongated lesions, 1–5 mm. long by 1–2 mm. wide, are formed. In some cases, these are so numerous that the stems have a roughened brown appearance for much of their length. The lesions are surrounded by a dark reddish-brown margin.

The fungus forms a stromatic mass in the spots, which develops in the palisade and mesophyll tissues and eventually breaks through the epidermis and cuticle. These stromata are up to 120 μ thick, mainly 80–90 μ, with an outer rind of dark walled hyphae, up to 15 μ thick. The asci are borne in slightly raised areas of the stroma, these ascomata being 50–160 μ wide and 30–120 μ high. The asci are roughly spherical to oval or pyriform in shape, 18–32 × 14–20 μ and contain eight spores (Fig. 4). The spores are hyaline, at first 0–1 septate, later with three transverse septa and when fully mature with one longitudinal septum also in the second cell from the apex, which is usually slightly wider than the other cells. The spores measure 12–16 × 4–6 μ.

Elsinoe hardenbergiae is the third species of *Elsinoe* to be recorded on a native Australian plant and the first on a native legume. The other two species, both on Myrtaceae, are *E. tristaniae* Hansf. on *Tristania conferta* R.Br. and *E. eucalypti* Hansf.

* Figure numbers refer to Plate iii.

on an unidentified species of *Eucalyptus* (Hansford, 1954). *E. hardenbergiae* is similar to several of the other species of *Elsinoe* recorded on Leguminosae, especially to *E. calopogonii* Syd., which occurs on *Calopogonium* in Brazil, *E. canavaliae* Rac., on *Canavalia* in the Orient and *E. phaseoli* Jenkins, the cause of lima bean scab in the West Indies, Central America and the United States. In spite of its morphological similarity to these species, *E. hardenbergiae* is kept separate from them for the time being until more detailed work has established the true relationships of these and other species parasitic on legumes.

6. The genera Irene Theiss. & Syd., Asteridiella McAlp. & Appendiculella v. Höhnel.

The genus *Irene* was established by Theissen & Sydow (in Sydow, 1917) for species of Meliolaceae similar to *Meliola* but lacking true setae on either the mycelium or the perithecia. The type species was *I. inermis* (Kalchbr. & Cooke) Theiss. & Syd. Certain species included by Theissen & Sydow in this genus, however, were found to have long, thick, vermiform appendages on the perithecia and, for these species, v. Höhnel (1919) established the genus *Appendiculella* v. Höhnel. Stevens (1927, 1928) regarded v. Höhnel's genus as a synonym of *Irene* Theiss. & Sydow on the grounds that the type species *I. inermis* had perithecia with vermiform appendages and he established the genus *Irenina* Stev. for those species without either true setae or vermiform appendages. However, Doidge & Sydow (1928) in a re-examination of material of *I. inermis* have found that appendages are not present, but that the perithecial wall is very irregular and many of the surface cells are prolonged into roughly conical processes, about as high as they are wide at the base. Thus *Irene* sensu Stevens is a synonym of *Appendiculella* v. Höhnel, and *Irenina* Stevens a synonym of *Irene* Theiss. & Sydow.

As recently pointed out by Hansford (1956), the genus *Asteridiella* McAlp. described in 1897 (McAlpine, 1897*a*) is identical with *Irene* Theiss. & Sydow, based on the type *I. inermis*. Thus *Irene* Theiss. & Syd. becomes a synonym of *Asteridiella* McAlp.

It is thus necessary to transfer species formerly included in the genera *Irene* Theiss. & Syd., *Irene* sensu Stevens and *Irenina* Stevens to the genus *Appendiculella* (if the perithecia bear vermiform appendages) or to the genus *Asteridiella* (if the perithecia have no vermiform appendages or true setae). A large number of transfers to *Asteridiella* have already been proposed by Hansford (1956), but unfortunately the majority are not validly published under Art. 42 of the International Rules of Botanical Nomenclature, 1950, as they were not accompanied by reference to the place and date of publication of the basonym.

In order to clarify the position for those species occurring in Australia, the necessary new combinations are listed below, together with some that have already been made. This list includes all species listed by Hansford (1953) in the genera *Irene* or *Irenina* in his study of Australian Meliolaceae.

Asteridiella acmenae (Hansf.) Hansf., p. 136.*

Syn. *Irenina acmenae* Hansf., in Proc. Linn. Soc. N.S.W., 78 (3–4): 68–9, 1953.—As "*Asteridiella acmenae* Hansf." in *Sydowia*, 10: 46, 1956 (not validly published).

Specimens examined: on *Acmena smithii* (Poir.) Merr. & Perry, National Park, 4/1931, L. R. Fraser (No. 15), 2264a; Williams River Brush, 8/1933, L. R. Fraser (No. 103), 2290; Myrtle Gully, 8/1934, L. R. Fraser (No. 159), 2319a; on *A. smithii* var. *minor* (Maiden) Merr. & Perry, Grafton, 1/1/1935, L. R. Fraser (No. 199), 2350 (type); on *Eugenia ventenatii* Benth., Deep Creek, near Grafton, 12/1934, L. R. Fraser (No. 185), 2339.

Asteridiella australiana (Hansf.) Hansf., p. 137.*

Syn. *Irenina australiana* Hansf., in Proc. Linn. Soc. N.S.W., 78 (3–4): 69–70, 1953.—As "*Asteridiella australiana* Hansf." in *Sydowia*, 10: 47, 1956 (not validly published).

Specimen examined: on *Eucalyptus* sp., Bellbrook, 4/1/1935, L. R. Fraser (No. 182), 2337b.

Asteridiella daphnandrae (Hansf.) Hansf., p. 40.*

Syn. *Irenina daphnandrae* Hansf., in Proc. Linn. Soc. N.S.W., 78 (3–4): 64, 1953.—As "*Asteridiella daphnandrae* Hansf." in *Sydowia*, 10: 47, 1956 (not validly published).

Specimens examined: on *Daphnandra micrantha* (Tul.) Benth., Williams River brush, 8/5/1933. L. R. Fraser (No. 132), 2305 (type); Williams River Brush, 8/1935, L. R. Fraser (No. 207), 2357.

ASTERIDIELLA DODONAEAE (Hansf.) Hansf., p. 425.*

Syn. *Irenina dodonaeae* Hansf., in PROC. LINN. SOC. N.S.W., 78 (3–4): 78–9, 1953.—As "*Asteridiella dodonaeae* Hansf." in *Sydowia*, 10: 47, 1956 (not validly published).

Specimen examined: on *Dodonaea triquetra* Wendl., National Park, 11/1935, L. R. Fraser, 4238a (type).

ASTERIDIELLA DUBOISIAE (Hansf.) Hansf., p. 634.*

Syn. *Irenina duboisiae* Hansf., in PROC. LINN. SOC. N.S.W., 78 (3–4): 80, 1953.—As "*Asteridiella duboisiae* Hansf." in *Sydowia*, 10: 47, 1956 (not validly published).

Specimens examined: on *Duboisia myoporoides* R.Br., Bulga, 19/1/1934, L. R. Fraser (No. 67), 2278; Comboyne, 7/1/1935, L. R. Fraser (No. 198), 2349 (type).

ASTERIDIELLA EUCALYPTORUM (Hansf.) Hansf., p. 135.*

Syn. *Irenina eucalyptorum* Hansf., in PROC. LINN. SOC. N.S.W., 78 (3–4): 69, 1953.—As "*Asteridiella eucalyptorum* Hansf." in *Sydowia* 10: 48, 1956 (not validly published).

Specimens examined: on *Backhousia myrtifolia* (Hook.) Harv., Myrtle Gully, 8/1934, L. R. Fraser (No. 167), 2326a; Blackheath, 6/1935, L. R. Fraser (No. 217), 2367a; on *Eucalyptus* sp., Bellbrook, 4/1/1935, L. R. Fraser (No. 182), 2337a; on *E. microcorys* F. Muell., Bulga, 19/1/1934, L. R. Fraser (No. 49), 2270; on *E. saligna* Sm., Williams River brush, 8/5/1933, L. R. Fraser (No. 84), 2282a (type); Narara, 5/1941, L. R. Fraser, 4240a; on *E. triantha* Link., Williams River, 8/1933, L. R. Fraser (No. 85), 2283.

ASTERIDIELLA FRASERIANA (Syd.) Batista, apud. Batista and Maia, in *Ann. Soc. Biol. Pernambuco*, 15 (2): 449, 1957.

Syn. *Meliola fraseriana* Syd., in *Ann. Myc.*, 35: 27, 1937.—*Irenina fraseriana* (Syd.) Hansf., in PROC. LINN. SOC. N.S.W., 78 (3–4): 61, 1953.—As "*Asteridiella fraseriana* (Syd.) Hansf." in *Sydowia*, 10: 48, 1956 (not validly published).

Specimens examined: on *Cryptocarya glaucescens* R.Br., Clyde Mountain, 8/1934, L. R. Fraser (No. 153), 2315; Comboyne, 7/1/1935, L. R. Fraser (No. 200), 2351; Williams River brush, 8/1935, L. R. Fraser (No. 208), 2358; on *C. meissneri* F. Muell., Comboyne, 1/1935, L. R. Fraser (No. 24), 6341a (type of *Meliola fraseriana* Syd.).

ASTERIDIELLA HEDYCARYAE (Hansf.) Hansf., p. 40.*

Syn. *Irenina hedycaryae* Hansf., in PROC. LINN. SOC. N.S.W., 78 (3–4): 65, 1953.—As "*Asteridiella hedycaryae* Hansf." in *Sydowia*, 10: 48, 1956 (not validly published).

No specimens of this fungus, which was described from Victoria, have been seen.

ASTERIDIELLA MALLOTI (Hansf. & Thirum.) Hansf., p. 209.*

Syn. *Irenina malloti* Hansf. & Thirum., in *Farlowia*, 3: 289, 1948.—As "*Asteridiella malloti* Hansf." in *Sydowia*, 10: 49, 1956 (not validly published).

Specimens examined: on *Baloghia lucida* Endl., Williams River brush, 6/5/1933, L. R. Fraser (No. 148), 2311a; Williams River brush, 8/1935, L. R. Fraser (No. 219), 2369.

APPENDICULELLA CALOSTROMA (Desm.) v. Höhnel, in *Ann. Myc.*, 16: 213, 1918.

Syn. *Sphaeria calostroma* Desm., in *Bull. Soc. Bot. France*, 4: 1011, 1857.

A more complete synonymy for this species is given by Doidge & Sydow (1928). Hansford (1953) lists it in N.S.W. on *Rubus moluccanus* L. under the name *Irene calostroma* (Desm.) v. Höhnel.

Specimens examined: on *Rubus moluccanus* L., National Park, 11/6/1932, L. R. Fraser (No. 6), 2256; Williams River brush, 8/5/1933, L. R. Fraser (No. 112), 2297a; National Park, 11/1934, L. R. Fraser (No. 177), 2332; Megalong Valley, 6/1935, L. R. Fraser (No. 206), 2356; on *R. rosaefolius* Sm., National Park, 5/1932, L. R. Fraser (No. 11), 2261; National Park, 10/1934, L. R. Fraser (No. 163), 2322; National Park, 11/1934, L. R. Fraser (No. 175), 2330.

APPENDICULELLA KIRAIENSIS (Yamamoto) Hansf., p. 39.*

Syn. *Irene kiraiensis* Yamamoto, in *Trans. Nat. Hist. Soc. Formosa*, 31: 47, 1941.

Hansford (1953) stated that the N.S.W. fungus is different in some respects from the original description and that further collections may show that it is a different species.

Specimens examined: on *Atherosperma moschatum* Labill., Kallista, Victoria, 23/1/1935, L. R. Fraser (No. 193), 2345a; on *Cinnamomum virens* R. T. Baker, Comboyne, 6/1/1935, L. R. Fraser (No. 184), 2338b; on *Doryphora sassafras* Endl., National Park, 6/1931, L. R. Fraser (No. 26), 2266a; Clyde Mountain, 8/1934, L. R. Fraser (No. 178), 2333a.

Appendiculella megalongensis (Hansf.) Hansf., p. 232.*

Syn. *Irene megalongensis* Hansf., in Proc. Linn. Soc. N.S.W., 78 (3–4): 52, 1953.

Specimens examined: on *Ackama muelleri* Benth., Williams River brush, 8/5/1933, L. R. Fraser (No. 130), 2304; Williams River brush, 24/5/1934, L. R. Fraser (No. 157), 2317a; Williams River brush, 8/1935, L. R. Fraser (No. 214), 2364; on *Ceratopetalum apetalum* D. Don., Wahroonga, 10/1934, L. R. Fraser (No. 166), 2325b; Blackheath, 3/1935, L. R. Fraser (No. 179), 2334; Megalong Valley, 6/1935, L. R. Fraser (No. 209), 2359a (type).

7. Claviceps paspali Stev. & Hall, in *Bot. Gaz.*, 50: 462, 1910.

Brittlebank, p. 380, 1940.—Noble *et al.*, p. 28, 1935 (as '*Coniothecium* sp. assoc.').—Noble *et al.*, p. 5, 1937.

Ergot of *Paspalum dilatatum* Poir. is one of the most common plant diseases in coastal N.S.W. It was first noticed during the severe epidemic of 1935, but Noble (1936) commented that such a widespread occurrence of the disease during that season could only have originated if the disease had been present at a lower level previously.

Examination of herbarium specimens has shown that the fungus was present on the North Coast of N.S.W. as early as 1929 and it had in fact been recorded by Noble *et al.* (1935) as *Coniothecium* seed rot. The specimen concerned is three racemes of *Paspalum orbiculare* Forst. (labelled '*P. scrobiculatum*'; see Vickery (1961) for discussion of host nomenclature) showing a few spikelets with the dried drops of honeydew containing the *Sphacelia* conidia, and on one spikelet there is an abundant development of the convoluted black growth of *Epicoccum andropogonis* (Ces.) Schol-Schwarz (this probably being the basis of the original *Coniothecium* record). It is possible that a further search of herbarium material of *Paspalum* spp. may show that the ergot was present at an even earlier date.

Specimen examined: on *Paspalum orbiculare*, North Coast, 6/1929, E. T. Edwards, 3643 (as '*Coniothecium* sp. (assoc.) seed rot').

8. Pezicula corticola (Jorg.) Nannf., in *Nova Acta Reg. Soc. Sci. Uppsaliensis*, IV, 8 (2): 94, 1932.

Noble *et al.*, p. 32, 1935 (as *Myxosporium corticolum* Edgert.).

This fungus is the cause of a superficial bark canker of apples and pears in Europe and America and has been listed by Noble *et al.* (1935) under the name *Myxosporium corticolum* Edgert, on pears in New South Wales. Examination of the specimen on which this record was based has shown that this fungus is not present.

The specimen consists of several pieces of pear bark bearing many erumpent sporodochia of a *Tubercularia* sp. The sporodochia are pale pink, 700–1,000 μ in diameter, composed of an interwoven basal mass of hyphae on which is borne a dense layer of conidiophores, up to 40 μ long, 2–2·5 μ wide, branched, bearing unicellular, hyaline conidia, 6–10 (12) × 2–2·5 (3) μ, ellipsoidal to fusiform in shape. This is much smaller than measurements given in the literature for conidia of *P. corticola* (Boerema

* During the printing of this paper, my attention was drawn to the monograph on the Meliolineae published by Hansford in *Sydowia*, Beiheft 2, Dec. 1, 1961, and in which the new combinations in *Asteridiella* and *Appendiculella* listed above had already been made. As I had made the new combinations in this paper, these alterations became necessary. I am grateful to Miss Joan Dingley, D.S.I.R., New Zealand, for bringing Hansford's paper to my notice and to Dr. G. C. Ainsworth and Mr. F. C. Deighton of the Commonwealth Mycological Institute for checking the new combinations and page references.

and Gremmen, 1959). A few pycnidia of a *Cytospora* sp. are also present on this specimen.

At the present time there is no evidence that *Pezicula corticola* is present in New South Wales.

Specimen examined: on *Pyrus communis*, Orange, 9/1934, W. A. Birmingham, 1807b (as '*Myxosporium corticolum*').

BASIDIOMYCETES.

9. Aecidium cryptostemmatis W. L. Waterhouse, in Proc. Linn. Soc. N.S.W., 77: 264, 1952, without Latin diagnosis.

The name *Aecidium cryptostemmatis* was proposed by Waterhouse (1952) for an aecidial rust found on the common weed *Cryptostemma calendula* (L.) Druce (Cape weed) in the Sydney Metropolitan Area. It has not been possible to locate the specimen from which Waterhouse's description was prepared and, because of this and the fact that the species was described without a Latin diagnosis, it is suggested that the name *Aecidium cryptostemmatis* W. L. Waterhouse be considered a *nomen nudum*.

In 1956, Petrak (1956) described *Puccinia cryptostemmatis* on living leaves of *Cryptostemma niveum* (L.f.) Nichols from Jervis Bay, N.S.W. This rust consisted mainly of aecidia with a few teleutosori developing amongst them. The aecidiospore measurements given by Petrak are somewhat smaller than those for the fungus described by Waterhouse, but it appears possible that Waterhouse's fungus may be the aecidial stage of *P. cryptostemmatis* Petrak.

10. Melampsora euphorbiae-gerardianae W. Müll., in *Centr. Bak.* II, 19: 452, 548, 1907.

This rust was first recorded in Australia from Pennant Hills, N.S.W., in 1953 on *Euphorbia peplus* L. under the name *Melampsora euphorbiae* (Schub.) Cast. Since then it has become very common in coastal New South Wales. Examination of several specimens has shown that the rust is not *M. euphorbiae*, but is the closely related *M. euphorbiae-gerardianae*. This species has smaller uredospores and larger teleutospores than *M. euphorbiae* and its teleutospores have an apex distinctly thicker than the side walls in contrast to the uniformly thickened teleutospore walls of *M. euphorbiae*.

Description: Uredosori on both sides of leaves abundant, yellow to orange, raised, 1 mm. diameter and often clustered into larger masses. Uredospores pale, mostly globose, (12) 15–20 (22)μ in diameter or occasionally oblong and up to 24 × 15 μ, with a finely echinulate wall, 2–3 μ thick, germ pores not observed. In the uredosori there are abundant capitate paraphyses, up to 90 μ long, mainly 40–70 μ, with globose heads 15–27 μ in diameter, with thick walls, up to 7 μ at the apex. Teleutosori mainly on stems and leaf stalks, black, often several centimetres long, the stem slightly swollen and often twisted where they occur. Spores in side view cylindrical with rounded ends, 30–60 (70) × 9–15 (19)μ, with side walls 1–1·5 (2)μ thick, 3–5 μ thick at the apex. In end view the spores are seen to be very closely packed and have a prismatic appearance.

Specimens examined: on *Euphorbia peplus*, Pennant Hills, 9/1953, L. R. Fraser (first record in Australia), 5741: Ryde, 10/1957, K. Green, 5740; Royal Botanic Gardens, Sydney, 10/1958, W. S. Sutton, 5742.

11. Puccinia mussonii McAlp., in The Rusts of Australia, 141, 1906 (as '*mussoni*'). Brittlebank, p. 291, 394, 1940.—Noble *et al.*, p. 34, 1935.

This rust was first described by McAlpine (1906) on leaves of *Dipteracanthus australis* (R.Br.) Hassk (as *Ruellia australis* Cav.) from the Richmond River district of New South Wales. More recently, it has been collected on the same host at Toongabbie, near Sydney. A collection of a rust on *Eranthemum variabile* R.Br. has also been identified as this species and represents its first record on this host genus.

Description: Uredosori reddish-brown, on both sides of leaves and on stems, 0·75–1 mm. diameter, raised, long, covered by the epidermis of the host which is pushed up by the uredospores and later breaks open at the top, forming a 'pore' to the uredosorus. Paraphyses absent. Uredospores yellowish with a reddish-brown wall up to 3 μ thick, prominently echinulate, roughly spherical to oval, 21–34 μ diameter or 21–31 (36) × 18–

24 μ, with two equatorial germ pores. Teleutospores rare, two-celled, dark brown, with a slightly wrinkled surface, 35–46 × 26–32 μ, with a hyaline pedicel attached to the side of the basal cell or in some cases almost laterally, just below the septum. Germ pore in top cell apical, in bottom cell at the base to one side.

As noted by McAlpine (1906), this species is very similar to *P. ruelliae* (B. & Br.) Lagerh. No specimens of this rust were seen, but further studies may show that *P. mussonii* is not different from it. The specific name *mussoni* originally used by McAlpine is an orthographic error and is here corrected to *mussonii*.

Specimens examined: on *Dipteracanthus australis*, Richmond River, N.S.W., 6/1896, C. T. Musson (type, in Herb. Pathologists Branch Dept. Agric. Victoria); Toongabbie, 24/7/1954, J. Walker, 4384; on *Eranthemum variabile*, Colo River, 3/1950, L. R. Fraser, 3820.

12. Puccinia poae-nemoralis Otth, in *Mitth. Naturf. Ges. Bern*, 1870, p. 113, 1871.

Brittlebank, p. 291, 385, 1940 (as *P. poarum* Niels.).—Cooke, p. 336, 1892 (as *P. poarum* Niels.).—Costin, p. 70, 498, 1954 (as *P. poarum* Niels.).—McAlpine, p. 104, 1895 (as *P. poarum* Niels.).—Noble *et al.*, p. 30, 1935 (as *P. poarum* Niels.).

Leaf rust of *Poa annua* L. is a very common disease in eastern New South Wales during the winter and early spring. It was first recorded and figured in this State by Cobb (1890) under the name *Puccinia poarum* Nielsen and since then it has always been referred to this species. However, examination of specimens has shown that the rust present is not this species, but is in fact *P. poae-nemoralis* Otth. In the uredospore stage, which is the one most commonly seen, this species differs from *P. poarum* in having many capitate paraphyses present in the uredosori. In his original drawing, Cobb illustrated these and McAlpine (1906) mentions them in his description of this rust, under the name *P. poarum*.

Examination of specimens of leaf rust on other species of *Poa* in New South Wales has shown that in all cases the rust is *P. poae-nemoralis*.

Description: Uredosori on both sides of leaves, bright orange when fresh. Uredospores pale yellow to yellowish-orange, finely echinulate, sub-globose to ellipsoid or somewhat angular, 19–26 (30) × 16–20 μ, with 6–8 indistinct scattered germ pores in the wall, which is 2–3 μ thick. In the uredosori, there are many thick-walled, capitate paraphyses, up to 70 μ long and 6 μ wide (in the stalk) with a roughly spherical to oval head 12–17 μ in diameter and sometimes with a slight second swelling of the stalk beneath the head.

Teleutosori rare, on leaves, flower stalks and pedicels, black, shiny, elongated along the stem, up to 0·5 mm. long, covered by the epidermis. Teleutospores borne in closely packed groups separated by thin layers (4–8 μ wide) of paraphyses, which also border the sori and run up to just under the epidermis. Spores two-celled, with a reddish-brown wall 2 μ thick, often flattened and thickened up to 7 μ at the apex, with a very short hyaline to light brown stalk, the basal cell of the spore being somewhat narrower than the apical cell, 28–44 × 14–21 μ.

Specimens examined: on *Poa* sp., Snowy Mountains, 2/1953, J. Vickery, 5004b; on *Poa annua* L., Kogarah, 9/1917, no collector's name given, 231; Roseville, 10/1934, R. J. Noble, 1051; Dignam's Creek, 29/10/1953, J. Walker, 5743; Baulkham Hills, 24/9/1961, J. Walker, 6331; on "*Poa caespitosa* var. *latifolia*", Lower Snowy River, 6/11/1948, A. Costin (No. 177), 3730; on *Poa pratensis* L., Balranald, 10/1949, L. R. Fraser, 3731.

13. Puccinia stylidii McAlp., in The Rusts of Australia, p. 204, 210, 1906.

Brittlebank, p. 292, 402, 1940.—Costin, p. 70, 506, 1954.

In the original description, McAlpine (1906) states that the uredospores have only one germ pore. Examination of the type material of *Uredo stylidii* McAlp. and of Costin's N.S.W. collection of the same rust has shown that in both cases the uredospores have two germ pores.

Description: Uredosori on both leaf surfaces, raised, roughly circular, 0·75–1 mm. in diameter, or somewhat elongated, up to 1·5 mm. long, finally rupturing the epidermis which tears longitudinally revealing a pale reddish-brown spore mass. Uredospores

yellowish, mostly roughly spherical to oval, 21–26 (28) × 17–21 μ, with a pale yellow-orange wall 1·5–2 (2–5) μ thick, finely echinulate, with two germ pores arranged one on each side of the spore just above the equator or mid-way between the equator and the apex of the spore. No paraphyses present. Teleutospores not seen.

This species differs in the uredospore stage from *Uredo forsterae* G. H. Cunn. on *Forstera bidwillii* var. *densifolia* Mildb. from New Zealand (Cunningham, 1931) in having slightly smaller and less angular spores with fewer germ pores. *U. forsterae* has 3–5 scattered germ pores.

Specimens examined: on *Stylidium graminifolium* Sm., near Waterworks, Hobart, Tasmania, 11/1892, Rodway (type of *Uredo stylidii* McAlp., No. $\frac{560}{03}$ in Herb. Pathologists' Branch Dept. Agric., Victoria); Wilson's Valley, Kosciusko region, 25/4/1947, A. Costin (No. 83), 3865.

14. Uromyces proëminens (DC) Pass., in *Rab. Fungi Eur.*, 1795, 1873.

A specimen of a rust collected on *Euphorbia prostrata* Ait. at Lismore is most probably this species. Only uredosori are present on the specimen. These are quite distinct from the uredosori of the common rust found on *Euphorbia peplus* in New South Wales (*Melampsora euphorbiae-gerardianae* W. Müll.) in being darker in colour and in the absence of the large capitate paraphyses found in the *Melampsora*.

Description: Uredosori mainly on upper surface of leaves, reddish-brown, up to 2 mm. diameter, raised, surrounded by the torn epidermis. Paraphyses absent. Uredospores roughly spherical to oval, prominently echinulate, with a reddish-brown wall up to 2 μ thick, pierced by four scattered (or rarely equatorial) germ pores, 15–20 μ in diameter or up to 23 × 20 μ. No other spore stage seen.

In the one specimen seen, many of the uredosori were heavily parasitized by *Darluca filum* (Biv.-Bern. ex Fr.) Cast.

Specimen examined: on *Euphorbia prostrata*, Lismore, 3/1957, L. R. Fraser, 5700.

15. Sphacelotheca valentula (Syd.) J. Walker, n. comb.

Syn. *Ustilago valentula* Syd., in *Ann. Myc.*, 35: 24, 1937.—Hynes *et al.*, p. 4, 1941.

Examination of portion of the type collection of this smut has shown that it is a species of *Sphacelotheca*. There is a well-developed central columella of host vascular tissue and in most sori the peridium is composed almost entirely of hyaline fungal cells, sometimes with fragments of the host epidermis remaining on the outside. In a few sori, the fungal peridium is much less developed. Because of variations in the degree of development of a fungal peridium in various species assigned to the genera *Sphacelotheca* and *Ustilago*, some workers have tended to regard them as not really distinct from one another and have grouped all species in the genus *Ustilago*. In the present work, the two genera have been kept distinct and the characteristics of the species under consideration place it in *Sphacelotheca*. The spore measurements are somewhat larger than those recorded by Sydow (1937).

Description: Sori completely replacing the inflorescences, except for a central unbranched columella of host vascular tissue, up to 3 cm. long, 4–8 mm. wide, surrounded at first by a grey to pale brown peridium, which later tears, exposing the dark brown spore mass. Peridium composed of hyaline fungal cells, oblong, 7–12 × 4–6 μ, arranged in chains, sometimes bearing on its outer surface portions of the host epidermis. Spores variable in shape, from roughly spherical to angular to oval or more elongated, brown, from slightly roughened to more definitely verrucose with spines up to 0·5 μ long and scattered irregularly from 0·5–1·5 μ apart over the spore, 11–19 (23) × (7) 8–13 (15) μ, wall 1–1·5 μ thick.

Specimen examined: on *Chloris acicularis* Lindl., between Collie and Warren, 1/1936, L. R. Fraser (No. 194), 971 (isotype).

16. Tilletia cathcartae Duran & Fischer, in Duran & Fischer, The genus Tilletia, pp. 44–45, 1961.

Duran & Fischer (1961) described this smut from a specimen on *Poa* sp. (listed by them as *Poa caespitosa* Forst.) collected at Cathcart, N.S.W., in January, 1940. It

has since been found on another *Poa* sp. collected in the Snowy Mountains region and may prove to be quite a common species on this grass genus in New South Wales.

Specimens examined: on *Poa* sp., Cathcart, 14/1/1940, J. Vickery, 3733 (type); Snowy Mountains, 2/1953, J. Vickery, 5005.

17. Tolyposporium restifaciens D. Shaw, in Proc. Linn. Soc. N.S.W., 77: 142–145, 1952.

This interesting smut was described by Shaw (1952) from diseased specimens of *Stipa aristiglumis* F. Muell. collected at Breeza Plains in Northern N.S.W. in 1951. She lists an earlier collection from Piallaway made in 1950.

A much earlier collection of this smut has been found in the Biology Branch herbarium. Labelled "abnormal inflorescence of *Stipa aristiglumis* (*Stemphylium* sp. present)", it was collected at Tamworth in March, 1935, and represents the earliest record of this smut. In this collection, the spore balls of the smut were apparently mistaken for *Stemphylium* spores.

Specimens examined: on *Stipa aristiglumis* F. Muell., Tamworth, 3/1935, H. J. Hynes, 1090 (as '*Stemphylium* sp.'); Tamworth, 1951, J. King, 4304.

18. Ustilago bullata Berk. var. macrospora (Farl.) G. W. Fisch., in Manual of the North American Smut Fungi, p. 250, 1953.

Smut of brome grasses (*Bromus* spp.) caused by *Ustilago bullata* Berk. has been present in New South Wales for many years, being first recorded by Cooke (1892) on *B. arenarius* Labill. and *B. mollis* L. During an examination of specimens of this smut one was found which agreed well with the var. *macrospora* of Fischer (1953). This variety has not previously been recorded in New South Wales.

Description: Sori in flowers, destroying ovaries and bases of glumes, at first covered by a grey membrane, which later breaks, exposing the dark brown to black spore mass. Spores brown, in many cases with a darker equatorial band, finely to coarsely roughened, roughly spherical to oval, 10–15 (16) μ in diameter, or 14–20 $\times$ 10–12 μ. Wall up to 2 μ thick.

Specimen examined: on *Bromus* sp., Bathurst, 12/1918, no collector's name on packet, 200 (as '*Ustilago bromivora*').

FUNGI IMPERFECTI

19. Phaeoseptoria eucalypti Hansf., in Proc. Linn. Soc. N.S.W., 82: 225–226, 1957.

This species was described by Hansford (1957) on living leaves of *Eucalyptus grandis* (Hill) Maiden collected near Sydney. Since then it has been found on several other species of *Eucalyptus*, causing severe damage to seedlings of several species in the Forestry Commission's Nursery at West Pennant Hills, near Sydney, and has also been found on leaf spots on *E. saligna* Sm. at Canberra.

Examination of the fungus present on the above specimens showed that it differed in several respects from the original description of *P. eucalypti*, but examination of the type material showed that the same fungus was involved. In the original description, *P. eucalypti* is described as having smooth conidia, 30–40 $\times$ 4–5 μ with 1–3 transverse septa. In the type material, the conidia were seen to have oozed out of several pycnidia as curled, dark brown cirri, up to 1·5 mm. long. Spores from these cirri measured (27) 36–57 (61) $\times$ 3–5·5 (7) μ and had (1) 3–5 (7) transverse septa. In squashings of pycnidia, many smaller and presumably immature spores were seen, some being as small as 11 $\times$ 3·5 μ with 0–1 septa. In other specimens, some spores up to 70 μ long were seen.

Under high magnification, the conidial wall was seen to be covered with minute roughenings, irregular in shape and approximately 0·5 μ in diameter and less than 0·5 μ high. These were present over the whole of the outside of the spore, except the smooth base, and gave it a somewhat granular appearance in surface view and its edge a fine wavy appearance.

Just above the smooth base, the spore wall was seen to flare out slightly, forming a small ridge around the spore near the bottom of the basal cell. The smooth spore base was thus situated in the circular space formed by the spore wall (Fig. 5). This

type of conidial base has been shown by Hughes (1953), working with many species of Moniliales, to be associated with the method of conidium development and with the type of conidiophore which he termed an annellophore. In an annellophore, conidia develop successively at the tip of a conidiophore which grows on through the scar left by the former conidium to produce the new one. Examination of the present fungus has shown that typical annellophores are present inside the pycnidia.

The annellophores are 4–10 (12) × 3–4 μ and are pale brown. They are formed on the inside of the pycnidium wall and bear conidia successively as apical growths through the scar left by the former conidium. The break between the wall of the conidiophore and the conidial wall is seen on the conidiophore as a series of small ridges and on the spore as the minute flared ridge near its base. The number of annulations seen on conidiophores has been generally one to three (Fig. 5).

The presence of this method of conidium production in certain pycnidial fungi was suspected by Hughes (1953), who stated (pp. 621–622): "In a number of illustrations of cross sections of coelomycetous fructifications the sporogenous cells have been figured as more or less cylindrical with a flattened apex; furthermore, the conidia of such fungi are often shown with a flattened base and a minute marginal frill. It is not improbable that such conidia will be found to have developed from annellophores." Observations which have been made indicate that the presence of annellophores is quite common in certain pycnidial fungi and future work on conidium development in these fungi will undoubtedly provide further information on possible relationships between them. In the Melanconiales, Sutton (1961) has recently demonstrated the presence of annellophores in several species of *Pestalotiopsis*.

Because of the discrepancies between the type material and the published description of *Phaeoseptoria eucalypti*, an emended description becomes necessary. For the present, it will be left in the genus *Phaeoseptoria*. Petrak (1941) considers *Phaeoseptoria* a synonym of *Hendersonia* and *P. eucalypti* does resemble in some respects certain of the *Hendersonia*-like fungi which occur on *Eucalyptus*. A study of type material of certain species of *Phaeoseptoria* and *Hendersonia* is at present being made to resolve their true relationships.

Phaeoseptoria eucalypti Hansf. emend. J. Walker.

Pycnidia either on definite leaf spots or not, depending on the host species, hypophyllous, scattered on the affected area, partially erumpent through the torn epidermis, 130–170 μ in diameter, up to 120 μ high, black, often with a dark brown spore ooze, usually as a cirrus, up to 1·5 mm. long. Conidia brown, cylindric-fusoid, straight to slightly curved or sometimes sinuate, gradually tapering to the rounded, slightly paler, apex, with (1) 3–5 (7) transverse septa, in some cases slightly constricted at the septa, measuring (27) 36–57 (61) × 3–5·5 (7) μ; wall of conidia minutely roughened, except for the smooth slightly rounded base which is surrounded by a small ridge formed by the flaring of the spore wall (Fig. 5); conidiophores are annellophores, pale brown, borne on the inside of the pycnidial wall, 4–10 (12) × 3–4 μ, cylindrical, bearing conidia successively at their tip as apical growths through the scar left by the former conidium, and showing this as a series of minute ridges, usually 1–3, on the conidiophore (Fig. 5).

Specimens examined: on *Eucalyptus grandis*, Sydney, N. H. White, WARI 7137 (type); on *E. macarthuri*, West Pennant Hills, 30/6/1960, J. Walker, 6339; on *E. maculata*, West Pennant Hills, 30/6/1960, J. Walker, 6338; on *E. saligna*, Canberra, winter, 1959, W. Stahl, 6337; on *E. sideroxylon*, West Pennant Hills, 30/6/1960, J. Walker, 6340.

20. Colletotrichum xanthii Halst., in *Bull. Torrey Bot. Club*, 20: 250–252, 1893.

Hynes *et al.*, p. 16, 1941 (as '*Macrosporium* sp.').

A record of *Macrosporium* sp. causing a blight of Bathurst burr (*Xanthium spinosum* L.) in the Sydney Metropolitan Area is listed by Hynes *et al.* (1941). Examination of the original specimen has shown that in fact the plant is severely affected with anthracnose, caused by *Colletotrichum xanthii* Halst. (according to von Arx (1957), this name is a synonym of *C. glocosporioides* Penz.). The anthracnose-

affected areas had been heavily overgrown with an *Alternaria* of the *tenuis* type and this was the basis of the original record. A note on the herbarium packet states 'blight reported to be killing plants in fairly extensive areas'.

Anthracnose of Bathurst burr in New South Wales has been studied in detail by Butler (1951), who first recorded it in the 1947–48 season causing considerable damage to burrs in north-western New South Wales. He states that what appeared to be the same disease had occurred in Queensland in 1941. The present specimen indicates that it was also present in New South Wales at that time.

Specimen examined: on *Xanthium spinosum* L., Sydney, 19/1/1941, C. J. Magee, 4048 (as '*Macrosporium* sp.').

21. Sphaceloma populi (Sacc.) Jenkins, in *J. agric. Res.*, 44: 694, 1932.

This fungus has been found on Lombardy poplars (*Populus nigra* L. var. *italica* Dur.) at various places in coastal and tableland districts, but does not seem to be very common and has never been seen causing severe damage. It has not previously been recorded in New South Wales.

Description: Leaf spots roughly circular, up to 5 mm. diameter, or elongated along the veins, often running together to form larger irregular patches. Spots light grey, with a reddish-brown margin. Similar spots present on petioles. Acervuli present as small black dots in the centre of spots. They are seated in the palisade tissue of the leaf and eventually burst through the epidermis and cuticle. They are 110–160 μ diameter, up to 40 μ thick, and are composed of a basal layer of interwoven hyphae on which a dense palisade-like layer of brown conidiophores stands. Spores are hyaline to faintly brown, oval to slightly elongated oval, often narrowing towards one end, 4–6 × 2–3 μ.

The fungus and the leaf spot it causes are well illustrated by Jenkins (1933).

Specimens examined: on *Populus nigra* var. *italica*, Batlow, 12/1947, L. R. Fraser, 4184; Bega, 1/1953, J. Walker, 4769.

22. Alternaria crassa (Sacc.) Rands, in *Phytopathology*, 7: 337, 1917.

Syn. *Cercospora crassa* Sacc., in *Michelia*, 1: 88, 1877.—Noble *et al.*, p. 17, 1935 (as *Alternaria* sp.).

A common leaf spot of *Datura stramonium* L. in New South Wales is caused by this fungus. Neergaard (1945) compares *A. crassa* with the closely related *A. solani* (Ell. & Mart.) Sor. and considers that they can be separated on morphological, cultural and pathological characters. The main morphological character he uses to separate them is the spore beak. He states that it is much longer and thicker in *A. crassa* than in *A. solani*, that in *A. crassa* it is the same colour as the body of the spore and is never branched, whereas in *A. solani* it is lighter in colour than the body of the spore and a proportion of spores with branched beaks is seen. Comparison of N.S.W. specimens of the *Alternaria* on *Datura* with that causing early blight of potatoes and tomatoes supports Neergaard's observations.

Description: Fungus causing leaf spots, roughly circular, up to 15 mm. in diameter, sometimes fusing to form large irregular areas, light brown in colour, marked with concentric bands of darker brown, eventually tearing and giving affected leaves a tattered appearance. The fungus spores on both surfaces, but much more abundantly on the upper surface. Conidiophores occur singly or in loose groups of up to 4–5, mainly 2–3, brown, septate, generally unbranched, 20–120 × 6–8 μ, with a single depressed apical spore scar or 1–4 times geniculate. Conidia are brown, with a long beak the same colour as the body of the spore, 90–360 × (15) 16–20 (24) μ including the beak, the body of the spore being up to 120 μ long, with 5–10 (12) transverse septa and 1–5 longitudinal or oblique septa, usually in the third, fourth, fifth, eighth and ninth cells from the base.

Specimens examined: on *Datura stramonium*, Armidale, 2/1941, E. T. Edwards, 4181; Cornwallis, 18/2/1943, L. R. Fraser, 4182; Orangeville, 5/4/1946, L. R. Fraser, 4183; Lower Portland, 2/2/1960, R. J. Conroy, 6072.

23. Fusarium byssinum McAlp., in Proc. Linn. Soc. N.S.W., 22: 698, 1897.

Brittlebank, p. 37, 349, 1940.—Noble *et al.*, p. 17, 1935.

This fungus was described by McAlpine (1897*b*) from a collection made at Murwillumbah, N.S.W., on leaves of *Desmodium* sp. From the description the fungus did not appear to be a *Fusarium* and an examination of portion of the type material confirmed this.

On the leaves, the fungus forms small raised scattered pustules which are generally circular, 1–4 mm. in diameter, raised in the centre and surrounded by a margin of white mycelium. The central raised area is light fawn in colour, with several small reddish translucent areas in it. These are often elongated radially on the pustule and arranged in a circle around the margin of the central raised area (Fig. 2).

In section, the pustules were found to be composed of a mass of hyaline, septate hyphae, 3–4 μ in diameter, and the reddish translucent areas were spore-bearing cavities, roughly flask-shaped to irregular, up to 400 × 250 μ and containing a large number of hyaline, spindle-shaped, straight or slightly curved spores, measuring 11–16 × 1·5–3 μ. These were non-septate, but in many cases a prominent central vacuole was seen. Many long thin paraphyses, up to 80 μ long by approximately 1 μ wide, were present in the spore-bearing cavities. Conidiophores were not observed.

The fungus appears to be a species of *Aschersonia*, a genus of scale-insect parasites. Whilst no scale insects could be found under the pustules, examination of the type material by Mr. C. E. Chadwick, Entomologist, Department of Agriculture, showed the presence of a number of Aleurodid scale insects on the leaves and it appears most probable that the fungus is parasitic on these. In his study of the genus *Aschersonia* and the related *Hypocrella* perfect stages, Petch (1921) considers two groups of species, those with paraphyses in the pycnidia and those without. He also considered that this feature was correlated with the group of scale insects on which the fungus was parasitic, those on Aleurodidae having paraphyses and those on Leconiidae without them. The present fungus falls into the former group and, of those species listed by Petch, most resembles *Aschersonia aleyrodis* Webber and *Aschersonia placenta* Berk. & Br. (the imperfect stage of *Hypocrella raciborskii* Zimm.).

Saccardo (1899) recognized that this fungus was not a typical *Fusarium* and considered it closer to the genus *Didymopsis*. Wollenweber & Reinking (1935), in their monograph, listed *F. byssinum* McAlp. as a species of *Hymenula*, probably assuming that the pustules were sporodochia.

Specimen examined: Probably parasitic on undetermined Aleurodid scale insect on leaves of *Desmodium* sp., Murwillumbah, N.S.W., 1897, Baker, 2 (in Herb. Pathologists' Branch, Dept. of Agric., Victoria: type of *F. byssinum* McAlp.).

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EXPLANATION OF PLATE III.

1. Resting spores of *Physoderma australasica* (McAlp.) J. Walker (from the type of *Protomyces australasica* McAlp.). ×800. 2. Portion of the type of *Fusarium byssinum* McAlp. on leaf of *Desmodium* sp., showing the raised stromatic bodies with darker pycnidial cavities and marginal white hyphae of *Aschersonia* sp. ×2 (approx.). 3. *Elsinoe hardenbergiae* J. Walker on leaves of *Hardenbergia violacea* (from the type). ×1. 4. Ascus and ascospores of *Elsinoe hardenbergiae* J. Walker (from the type). ×1,000. 5. Conidiophores and conidia of *Phaeoseptoria eucalypti* Hansf. emend. J. Walker showing annellophores, method of conidium production and flared conidial wall near its base. ×760.

THE ACTUAL IDENTITY OF CAPTAIN COOK'S KANGAROO.

By Tom Iredale and Ellis Troughton.

(Two Text-figures.)

[Read 25th July, 1962.]

As shown in our Check-List (1934) of Australian mammals, as a Haplotype, the name *giganteus* as applied to the Great-Grey Kangaroo is superseded by *major*, as the type of Shaw's genus *Macropus*. In 1925 and 1937 we provided substantial evidence that the first small kangaroo shot at Cooktown and described by Cook's naturalists could not have been the great-grey kangaroo, and was actually the Cape York form of the Whiptail Wallaby.

In the first paper (1925) we acknowledged indebtedness to the past Secretary of the Linnean Society, J. J. Fletcher, M.A., B.Sc., for valuable comment and several references. We also noted that he had stated twenty years previously in the Proceedings (1905) that Solander's Journal would doubtless reveal something regarding the kangaroo; . . . that all Captain Cook's kangaroos were killed at the Endeavour River, Cooktown, and expressed the hope that attempts would be made to follow the matter up.

Our efforts to fulfil the expressed hope included: The obtaining of a copy of Solander's Latin description from the library of the British Museum (N.H.); our purchase abroad of the series of *Natursystems* of Linné, making Müller's description of "*Mus*" *canguru* available at the Australian Museum; specimens of the Cooktown whiptail wallaby and wallaroo obtained by Iredale from kangaroo-hunters, who said they had neither seen nor heard of the great-grey kangaroo in the same area, and which they would have hunted in preference!

But in reviewing our two papers, Morrison-Scott and Sawyer (1950) said it was not clear why Iredale and Troughton abandoned their original claim that Cook's kangaroo was a wallaroo in favour of the whiptail wallaby. Actually, our second paper (1937) had made it clear that it was the acquisition of skins and skulls of both the whiptail and wallaroo from Cooktown that so positively favoured the whiptail, in its more delicate proportions and wholly naked rhinarium.

"The next stage in the controversy" according to Morrison-Scott and Sawyer "was a paper by Raven (1939) who holds that the evidence is decidedly against Cook's kangaroo having been a Whiptail, or Pretty-faced Wallaby". They also stated that Raven, believing the early revisers [*sic*] to be right in identifying the Great-Grey with Cook's kangaroo, "pleads the confusion caused by the upsetting of this position", but such "pleadings" have no standing in taxonomy.

Continuing their review, Morrison-Scott and Sawyer make the prejudicial statement that "Iredale & Troughton on the one hand, and Raven on the other, perform some agile juggling with the Latin text [of Solander] in support of their respective theses" favouring the whiptail wallaby or the great-grey kangaroo. However, we now propose to demonstrate that Morrison-Scott and Sawyer have displayed a capacity for "juggling" relevant data far in excess of that attributed to Iredale and Troughton.

Our critics concurred that "in two particulars Solander's description does not encourage any leanings towards the Great-Grey theory". Indisputably, one of these

"particulars" is Solander's description of the rhinarium of the first (38 lb.) specimen as entirely naked *between* the nostrils, as characteristic of the whiptail wallaby. The rhinarium of the great-grey, on the contrary, is densely haired *between* the nostril-rims, the rostral fur continuing down to the philtrum-base. While Raven confirmed Solander's description of the rhinarium as "bare between the nostrils and the skin covered with very black fine wrinkles", he then subscribed to a remarkable evasion that "This condition is more obvious in the wallaroo *and* whiptail; but black, finely wrinkled skin does *surround each nostril* of the great gray kangaroo."

Morrison-Scott and Sawyer, also discounting the naked rhinarium in favour of the great-grey kangaroo, submit the untenable premise that: "Solander may well have had *three separate species* as well as *three separate specimens* in front of him as he wrote, and it is not possible to say which animal he had most in mind while describing the various characters." Had this been so, why single out the great-grey for positive determination? Actually, to anyone tracing the logical sequence of the dates of capture of the several macropods, with their individual weights, the interpretation by Morrison-Scott and Sawyer becomes incredible. If Solander actually had three separate specimens of three separate species for *simultaneous* description, then the great-grey was not among them because Solander did not describe any variation from the hairless rhinarium of his first specimen!

With reference to the 3rd incisor of Cook's kangaroo, and the amended view of Iredale and Troughton (1937), Raven quotes Solander's Latin phrasing "*tertium latium crassiusque, bilobum; lobis anticis minoribus*", translated as meaning plainly "third broader thicker, bilobed: with anterior lobes smaller".

This condition, Raven stated, cannot apply to the 3rd incisor of the whiptail, "but does agree with the structure of this tooth in the great gray kangaroo". But in opposition to this partial translation, we enquire how can a single *bilobed* tooth have smaller anterior *lobes*? Obviously *lobis anticis minoribus* is of plural intent, referring to both of the 3rd upper incisors. Therefore, the structure of the individual 3rd upper incisor of a great-grey kangaroo, with an anterior "double-ridge", is in absolute contrast with the plainly bilobate 3rd incisor of the whiptail wallaby.

Morrison-Scott and Sawyer agreed that Raven's view of the 3rd incisor did not favour the great-grey, but concluded that anyway "Solander's description cannot be treated as a reliable guide in the quest for Captain Cook's Kangaroo". On their preceding page, however, is the authors' contradictory dictum that "since Solander was on board Cook's ship in his capacity as a naturalist, what he has said on the subject of the kangaroos must be examined". They also point out that "Tate (1948) avoided discussion of Solander's manuscript description".

Morrison-Scott and Sawyer confirm that the only measurements given by Solander were of the first specimen shot by Mr. Gore on the 14th July, 1770; the difference in weight of 24 and 38 lb. being that between the 'clean' and 'dead weight'. They then argue Solander did give the *weights* "of all three animals taken" so that the description is "clearly composite". To the contrary, the several kangaroos could not have been the subject of *simultaneous* examination by Solander, though he appended some descriptive notes!

Factually, the specific details of Solander's description applied only to the first specimen of 38 lb. dead weight, and this weight complies with that of the southern whiptail wallaby, being within the range of 32 to 49 lb. listed respectively for females and males by Finlayson (1931). But it is not clear, argue Morrison-Scott and Sawyer, "why Troughton refers to the 38 pound animal as apparently adult when Solander says that it was possibly two or three years old. Solander's estimate . . . may not be reliable, but he was basing his view that it was not adult on the condition of the molar teeth. . . ."

This contention is quite irrelevant, since Solander could not anticipate the criteria, introduced by Oldfield Thomas (1888), for estimating the sub-adult, adult, and "aged"

sequence of macropod dentition. But the fact is that Solander's estimate of up to three years allows for "adult" growth in the whiptail wallaby; whereas 38 lb. weight in a great-grey kangaroo would allow of only an obviously immature dentition.

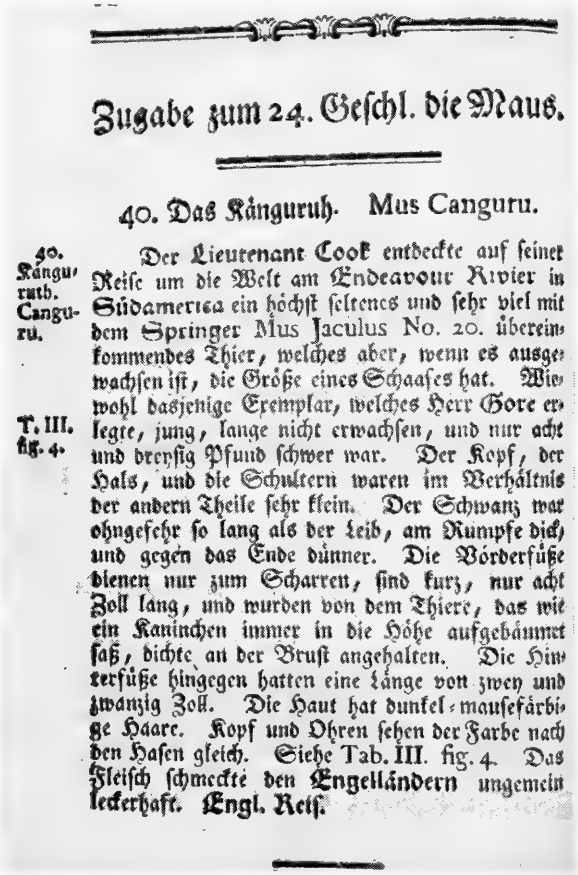
Much to Solander's credit, however, he regarded the physical characters of the rhinarium and dentition as of superior diagnostic importance to colour, but some authors have reversed this sense of values. For example, despite Solander's methodical description, his failure to include the striking cheek-marks, characterizing the *southern* race of whiptail, is argued in favour of the great-grey kangaroo. While Raven (1939), in attempting to prove the colour-identity of Cook's species with the great-grey, contrasts a photo of the latter with one of the *southern* whiptail wallaby.

Fig. 1. From a photograph of Müller's figure of his *Mus canguru* (1776). Comparison with Raven's photographic reproduction of Parkinson's original drawing (1773) shows Müller's animal, both in posture and general if somewhat stouter proportions, to be founded indubitably on the original illustration in the Hawkesworth account of *Cook's Voyages*. The left ear appears longer due to the lowering of its outer margin, but the dorsal profile of the head shows the pre-orbital depression in Hawkesworth's figure, and Raven's photo of the whiptail wallaby. Müller's artist was endeavouring to reproduce the drawing of an entirely unique form of mammal.

In stressing the great-grey's "more uniform coloration of the head and body", Raven disregards the blackish outer third of the kangaroo's much thicker tail, which contrasts strikingly with the relatively much longer "whip" tail of the wallaby, with a slight tipping of black. But the most striking difference shown in Raven's photos appears in the head of the great-grey with its strongly convex dorsal profile, and much wider angle of the jaws. Conforming with the skull, this is in striking contrast with the finely tapered head of the whiptail wallaby, as photographed by Raven, and drawn

by Parkinson; and as according with the lateral "compression" of the rostrum described by Solander.

In short, had Raven added Müller's copy of the Hawkesworth figure to his illustrative comparison, it would have served finally to confirm the identity of Müller's *canguru* with the Cape York Whiptail Wallaby. Much argument against this logical conclusion is based on the erroneous idea that Iredale and Troughton did not realize that the great-grey's range extended (inland) north of Cooktown. According to Raven, because those authors "failed to find the great gray kangaroo *at or near* Cooktown now, they assume that it did not occur there in the past". Raven then assumes that "if not



Zugabe zum 24. Geſchl. die Maus.

40. Das Känguruh. Mus Canguru.

40. Känguruh. Canguru.

Der Lieutenant Cook entdeckte auf ſeiner Reiſe um die Welt am Endeavour Rivier in Südamerica ein höchſt ſeltenes und ſehr viel mit dem Springer Mus Jaculus No. 20. übereinkommendes Thier, welches aber, wenn es ausgewachſen iſt, die Größe eines Schaafes hat. Wiewohl dasjenige Exemplar, welches Herr Gore erlegte, jung, lange nicht erwachſen, und nur acht und dreyſig Pfund ſchwer war. Der Kopf, der Hals, und die Schultern waren im Verhältnis der andern Theile ſehr klein. Der Schwanz war ohngefehr ſo lang als der Leib, am Rumpfe dick, und gegen das Ende dünner. Die Vörderfüße dienen nur zum Scharren, ſind kurz, nur acht Zoll lang, und wurden von dem Thiere, das wie ein Kaninchen immer in die Höhe aufgebäumet ſaß, dichte an der Bruſt angehalten. Die Hinterfüße hingegen hatten eine Länge von zwey und zwanzig Zoll. Die Haut hat dunkel-mauſefärbige Haare. Kopf und Ohren ſehen der Farbe nach den Haſen gleich. Siehe Tab. III. fig. 4. Das Fleiſch ſchmeckte den Engelländern ungemein leckerhaft. Engl. Reiſ.

T. III. fig. 4.

Fig. 2. From a photograph of Müller's description of *Mus canguru* in *Natursystems* (Linné), 1776. Positively based on Hawkesworth's account, the description thus establishes the identity of Müller's figure with Hawksworth's illustration. Absence of reference to the skull negatives the significance of cranial comparison with the great-grey kangaroo.

now inhabiting the *neighbourhood* of Cooktown . . . it is quite likely that the gray kangaroo . . . has only recently [*sic*] been extirpated and may well have been abundant before the country was settled by the whites".

But why *assume* that the great-grey was the only macropod species "extirpated" when in 1961 a Queensland Museum party collected both whiptail and agile wallabies, together with wallaroos, within the actual environs of Cooktown? Actually, the nearest locality for the great-grey cited by Raven (Le Souef, 1907) was about 40 miles from Cooktown, near the Bloomfield River. But it was not on Hislop's "Wyalla" property,

five miles from the coast, that in 1897 Le Souef sighted great-grey kangaroos, but actually two days' journey and 50 odd miles into the "cattle-country" of Gibson's property on the King Plains.

The closest approach to the *neighbourhood* of Cooktown is Tate's (1952) recording of great-grey specimens from Helenvale, 22 miles southward and five miles west of a branch of the Annam River. This locality adjoins the King Plains cattle-country, extending west to the discontinuous dividing ranges. However, Tate implied his own doubt that the great-grey had extended across the Annam River to Cooktown when he wrote (pp. 596–7): "It seems likely that Helenvale marks nearly the limit northward of this kangaroo on the east (lowland) side of the divide, though the species may extend a considerable way northward *behind* the sand dunes that lie between Capes Bedford and Flattery in *the Normanby River country*."

This distributional "detour" envisaged by Tate does not provide for the actual occurrence of the great-grey in the close vicinity of Cooktown, because that kangaroo has never had a coastal continuity of range, from Cairns north to across the Bloomfield River. The nearest locality from the south-west given by Tate is Mt. Carbine, on the western edge of the rain-forest zone over 80 miles from Cooktown. His nearest localities west and north of the divide from Cooktown are Ebagoola, 30 miles south of Coen and 150 miles from Cooktown. The northernmost locality, Wenlock, is in the middle of the Peninsula, west of the Sir Wm. Thompson Range, 200 miles north of Cooktown.

However, apart from the question of natural habitat, there is significant evidence to indicate that, contrary to the persistent views of some authors, the Cooktown "corridor" was never an "annexe" of the great-grey's distribution. This "Forester" Kangaroo has never been seen within the natural boundaries of the country hunted by Captain Cook's party, and the species evidently infiltrated the "cattle-country" as it opened up from the divide, towards Cooktown.

In our view, however, presence or absence of the great-grey kangaroo about Cooktown has no critical bearing on the foregoing analyses of the diagnostic characters, and taxonomic identity, of the first specimen described by Solander. We therefore now reaffirm that it was the northern form of Whiptail Wallaby, not the Great-Grey Kangaroo, to which Müller (1776) applied the name *canguru*, based on the description and figure of Hawkesworth's account of 1773.

The generic names *Jaculus* and *Jerboa* applied respectively by Erxleben and Zimmermann in 1777, with the specific names *giganteus* and *gigantea*, were obviously inspired by the "jerboa mouse" comparison by Cook's naturalists. But the name *giganteus* (= *major*) was not applied specifically to the great-grey kangaroo prior to Shaw and Nodder (1790), based on reports of its occurrence about Port Jackson by Captain Phillip and others, after settlement by the First Fleet in 1788.

Unfortunately, such coincidental factors, coupled with the "jerboa" comparison, applicable to the family in general, have resulted in an illogical "fixed idea" that the only species conceivably to have been described by Solander and named by Müller was the great-grey kangaroo! A recent example of the need for the above detailed review, and our summary of "Conclusions", in establishing the identity of the historical species is provided in the admirable production of *The Endeavour Journal of Banks* as edited by J. C. Beaglehole (1962).

In editorial references (Vol. II) to the sighting of a kangaroo (p. 84) and shooting of the first specimen (p. 94) Beaglehole identifies the animal as "possibly a young Great Grey Kangaroo, *Macropus cangaru* (Müller)" on the authority of Morrison-Scott and Sawyer. Support for this identification is indirectly implied in Beaglehole's explanatory note to the Frontispiece to Vol. II, which states that the artist, George Stubbs, "must have painted this picture for Banks in 1771 or 1772, *from a stuffed or blown-up skin* . . . of the Kongouro from New Holland".

Since Banks stated (p. 94) that the first "Beast which was killed yesterday was today Dressd for our dinner and proved excellent meat" no specimen could possibly

have served as a model for Stubbs' painting. It is further suggested by Beaglehole that the kangaroo painting "was engraved in reverse for Hawkesworth's *Voyages*, Vol. III, pl. 20". Close study of the respective illustrations, however, proves that the engraving must have preceded the painting, in which Stubbs included a number of imaginary physical "refinements".

Conclusions.

(1) The first "very slender made" kangaroo shot by Mr. Gore on July 14 (maximum weight 38 lb.) is the specific basis of Solander's description. Therefore, the largest "Animal" shot by him (Gore) on July 27, weighing 80 lb., and 54 lb. *exclusive of the entrails*, was not the subject of simultaneous description by Solander.

(2) The great-grey is excluded from the description by two main diagnostic characters of *Macropus major*: (*a*) The rhinarium, instead of being haired down to the philtrum-base, was entirely naked *between* the nostrils; (*b*) the 3rd upper incisor was simply bilobate, instead of having a "double-ridge" anteriorly.

(3) Raven confused the issue on these characters, but Morrison-Scott and Sawyer agree that they excluded the great-grey, but then assumed that Solander possibly had "three separate species . . . in front of him". This does not justify their inclusion of the great-grey, because the dates of shooting, and "dressing" of the first specimen, precluded simultaneous description. Solander *appended* some details, but did not add any variation from the naked rhinarium.

(4) The original comparison of the "slender made" kangaroo with a greyhound was indicative of the body and tail proportions of the whiptail wallaby. The maximum weight of 38 lb. was also within the range of 32–49 lb. recorded for the southern whiptail.

(5) Solander's estimate of the first specimen's age as from 2–3 years on the dentition is compatible with the "young-adult" stage in a whiptail wallaby; whereas bodily size at that stage excludes the great-grey kangaroo and a wallaroo.

(6) Raven's comparison of Hawkesworth's figure with photos of a whiptail and great-grey kangaroo (1939) disprove his claim that the kangaroo is identical with Solander's description. Conversely, comparison of Hawkesworth's illustration, with the copy accompanying Müller's description, establishes the identity of his "*Mus canguru*" with the northern form of whiptail wallaby.

(7) The great-grey's photo shows the relatively shorter and much stouter tail, with blackish terminal third; contrasting with the wallaby's "whiptail" with only a slight black tip. Traces of the whiptail's "cheek-marks" show in the Hawkesworth figure and Müller's copy.

(8) The photographic comparison emphasizes that the great-grey's head has the dorsal profile strongly convex, and wide-angled jaws; in marked contrast with the evenly tapered head of the whiptail, with the laterally compressed mandibular region as figured by Hawkesworth and Müller.

(9) Absence of any reference to the skull in Müller's description, however, invalidates subsequent claims cranially to identify his "Mus" *canguru* with the great-grey species. Certainly, such a conclusion could not be based upon the dissociated skull and mandible nominated as a "photo-lectotype" by Morrison-Scott and Sawyer.

(10) Because Erxleben's *Jaculus giganteus* and Zimmermann's *Jerboa gigantea* were founded on the "gigantic jerboa" comparison with the original "animal", presence or absence of the great-grey within the hunting-range of Cook's party has no critical bearing on the actual identity of Müller's "*Mus*" *canguru*.

(11) It is evidently established that Müller's *canguru*, as with Erxleben and Zimmermann, was based on the original small "Animal", according with the giant-jerboa comparison, as described by Solander and figured by Hawkesworth and Müller. Therefore, the original descriptions and figures of Captain Cook's Kangaroo are applicable to the Whiptail Wallaby of Cape York Peninsula, having the valid taxonomic designation of *Wallabia canguru* Müller (1776).

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Postscript added 9th August, 1962.—A paper on "The Application of the Generic Name *Macropus* Shaw 1790 and of Other Names Commonly Referred to the Grey Kangaroo" by J. H. Calaby, George Mack and W. D. L. Ride (*Memoirs of the Queensland Museum,* Vol. 14, Pt. 2), issued on 4th July, 1962, came to notice several days prior to the reading of our contribution before the Linnean Society on the 25th July.

In so far as the paper in the Queensland Museum *Memoir* purports to identify "*Mus canguru*" of Müller with the Great Grey Kangaroo, as a basis of appeal to the International Commission for Zoological Nomenclature, we now reaffirm our identification of the first (38 lb.) kangaroo described by Cook's party with the northern form of Whiptail Wallaby, as based on the description and figure in Hawkesworth's account, and as confirmed by the "on the spot" description by Solander.

Regarding Solander's Latin description, we maintain that our paper corrects, in detail and summary, the various misinterpretations placed upon Solander's description by the above authors, and Morrison-Scott and Sawyer. Especially in their improvisation that Solander's description was entirely composite, whereas the major portion refers to the first and 38 lb. animal in particular, and to which obviously were appended details of the 84 lb. animal, shot a fortnight later.

In another attempt to discredit Solander's description of the rhinarium as naked, instead of being entirely haired as in the Great Grey Kangaroo, the authors assume that "a specimen of the wallaroo in Cook's collection would account for the statement . . . that the internarial area of the kangaroo was naked". We need only reiterate that Solander's description of the rhinarium referred precisely to the 38 lb. animal. We ask, therefore, when Solander was acute enough to have later noted the naked rhinarium of a wallaroo, why should he have overlooked the closely haired rhinarium of a Great Grey specimen, at any age?

Regarding the above authors' interpretation of the cranial characters, it is notable that, as with other proponents of the Great Grey theory, their criteria are based largely on discussion of Solander's description, although Calaby, Mack and Ride *then* conclude that as the "*composite*" description was not published until 1925 (Iredale and Troughton) it "*is of no nomenclatural importance*".

However, the above authors, basing their identification of the Great Grey partly on Solander's description, and partly on a Hunterian skull of doubtful authenticity

propose the selection of a "Neotype" of similar cranial age, from beyond the Endeavour River, and almost two centuries after the visit of Captain Cook. Regarding the authors' proposed recommendation to the International Commission for the restriction of the name *Macropus* to the Great Grey (*major*) of the Sydney region, we maintain that the position of that genus is already soundly established.

In view of the foregoing, it is proposed to submit a copy of our paper, with appropriate recommendations, to the International Commission of Zoological Nomenclature for consideration along with the paper in the *Memoirs of the Queensland Museum*.

T.I. AND E.T.

THE DEVELOPMENT OF THE POLYCHAETE *GALEOLARIA CAESPITOSA* LAMARCK (FAM. SERPULIDAE).

By J. C. Andrews and D. T. Anderson, University of Sydney.

(Seven Text-figures.)

[Read 25th July, 1962.]

Synopsis.

G. caespitosa spawns throughout the year, shedding eggs and sperm freely into the water. Eggs develop rapidly into planktotrophic trochophores, which feed and grow for 13-15 days, develop three simultaneously delineated trunk segments, then settle at 19 days. Preferential settlement on adult tubes was observed. Development in *G. caespitosa* is typical of serpulids with microlecithal eggs. Settlement behaviour is presumably important in determining adult vertical distribution on the shore.

Introduction.

On the rock platforms of the New South Wales ocean coast, the serpulid *Galeolaria caespitosa* serves as a marker for a mid-littoral zone of the shore, the *Galeolaria* zone (Dakin, 1953), which on a vertical rock face may occupy a band only about 1½ feet wide. Inside the bays and harbours of the coast, in contrast, it tends to congregate thickly on rocks and wharf-piles in the lower littoral. A knowledge of its development is obviously prerequisite to the investigation of factors influencing the vertical distribution of the species and is presented here for the first time.

Material and Methods.

Adult *G. caespitosa* collected from wharf-piles in Sydney Harbour at intervals from March to November, 1961, were maintained in the laboratory in seawater tanks supplied with vigorous aeration. The species appears to breed throughout the year and no difficulty was experienced in obtaining ripe eggs and sperm during the winter months. Ripe males, with white abdomens, and ripe females, with orange abdomens, spawned freely when extracted from their tubes and placed in separate dishes of filtered seawater. The eggs were pipetted into a bowl of fresh seawater and a small quantity of sperm suspension added. Once the eggs had settled to the bottom, most of the water and excess sperm was poured off and the eggs then transferred to fresh seawater in a small tank.

For successful development it was found essential to maintain the tank at a constant temperature of 25° C., to supply gentle aeration and to change the seawater every two days. For the latter operation, the larvae were concentrated by gentle centrifugation. Food was added to the culture in the form of a suspension of the green flagellate *Nannochloris atomus* Butcher supplied by Mr. B. Wisely of the C.S.I.R.O. Division of Fisheries and Oceanography at Cronulla, N.S.W. Embryos and larvae were examined by normal and phase contrast microscopy and sketched in the living state with the aid of camera lucida.

Development.

The unfertilized eggs have a crumpled appearance when released, but, after immersion for a short period in seawater, round up to a spherical shape, with a diameter of 64μ (Text-fig. 1). They are orange-pink by reflected light, brown by transmitted light, opaque except in the region of the germinal vesicle and covered each by a membrane 2μ thick.

On insemination, the germinal vesicle breaks down and the membrane lifts from the surface of the egg. The first polar body is given off at about 45 minutes (Text-fig. 2), the second shortly after. Cleavage (Text-figs 3, 4) is spiral and equal throughout. At the temperature employed in the present study, the timing of early cleavage was as follows:

$1\frac{1}{2}$	hours	after	insemination,	1st	cleavage—	2	cells
2	„	„	„	2nd	„	— 4	„
2–$2\frac{1}{2}$	„	„	„	3rd	„	— 8	„
$2\frac{1}{2}$–3	„	„	„	4th	„	—16	„
3–$3\frac{1}{2}$	„	„	„	5th	„	—32	„

Following the formation of 32 cells, development proceeds rapidly to completion of the spherical blastula (Text-fig. 5), then to gastrulation, which takes place about 4–5 hours after insemination. The details of gastrulation cannot be discerned in external view.

The embryo now develops an equatorial ring of long, strongly beating prototrochal cilia and soon leaves the bottom of the tank to swim at random through the water, the egg membrane persisting as the larval cuticle. During the next 6–7 hours the embryo elongates antero-posteriorly, reaching a length of 80μ. The prototroch remains equatorial, separating a rounded episphere from a conical hyposphere. At the apex of the episphere an apical tuft of four long cilia develops. The first signs of a metatroch appear behind the prototroch and a broad area of feeding cilia is established between the prototroch and metatroch.

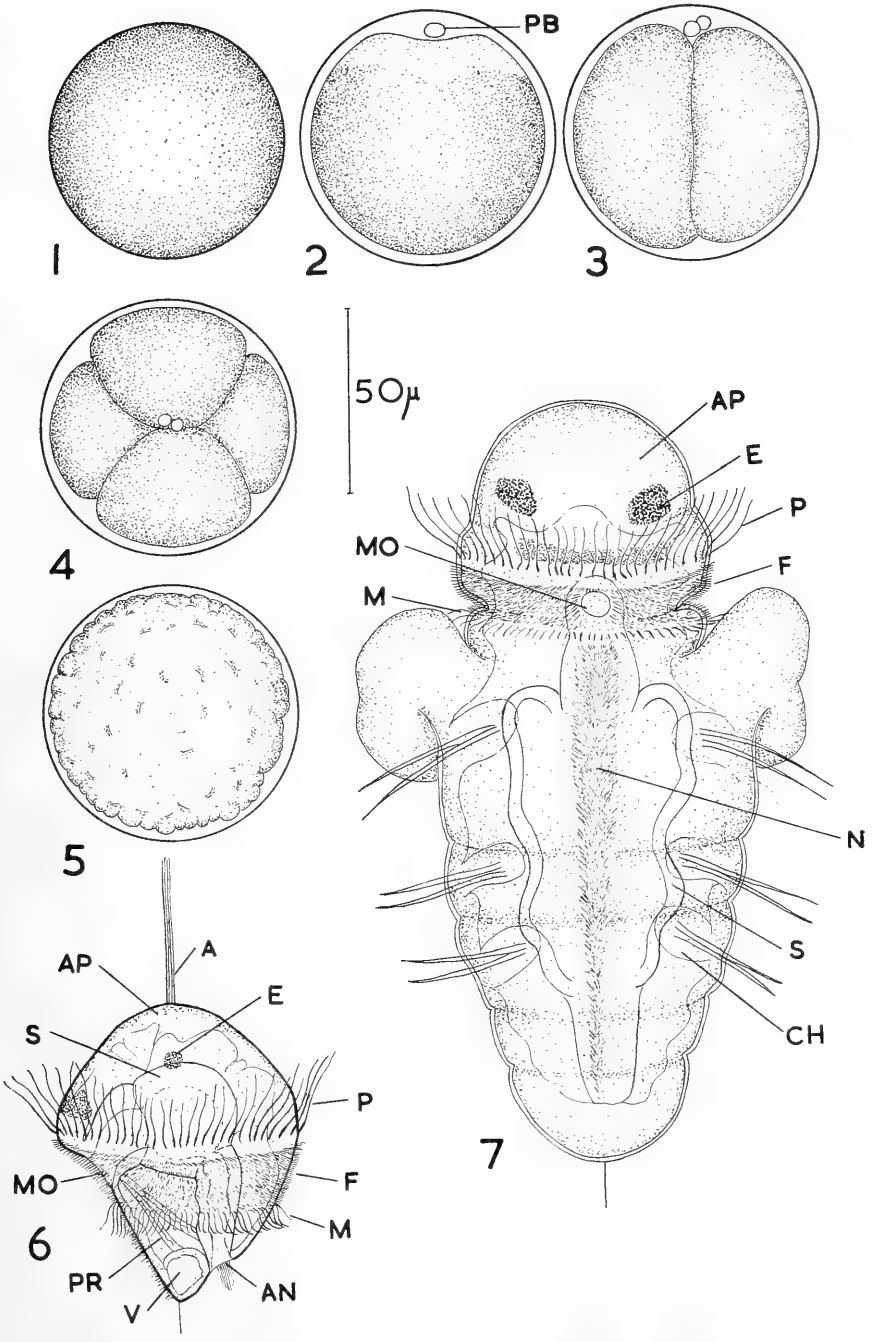
By 24 hours, the larval gut has become conspicuous, differentiation of the planktotrophic trochophore (Text-fig. 6) is more or less complete and feeding has begun. The external ciliation is augmented by a mid-ventral neurotroch on the hyposphere, a ciliary tuft projecting from the anus and a short posterior flagellum. A ring of oral cilia surrounds the mouth, situated mid-ventrally between the prototroch and metatroch. Food caught on the feeding cilia is swept by the oral cilia into the tubular ciliated stomodaeum and thence into the stomach, a large rounded organ occupying most of the episphere. The stomach is lined by short cilia which rotate the food particles as a single mass during digestion. A valve separating the stomach from the intestine opens periodically to allow passage of the stomach contents. The food mass is also rotated by cilia for a few minutes in the intestine before passing out of the anus.

At the posterior end of the hyposphere is a large anal vesicle, postero-ventral to the anus. Anal pigment is also present in the form of small red pigment granules scattered in the body wall around the anal vesicle. Elsewhere, the body wall is thin and transparent, save for thickenings produced equatorially by the swollen prototrochal cells and apically by the apical plate. On the right side of the episphere a cluster of small pigment granules forms a red eyespot.

Larval musculature is well developed in the trochophore, both in the body wall and between the body wall and the gut. Circular muscles in the wall of the episphere contract periodically to constrict the sub-apical region, while a well-developed ring of muscle underlying the metatroch contracts frequently and strongly in larvae caught by the cover slip. The most conspicuous of the muscles crossing the blastocoel runs from a projection on the apical plate to a projection on the anterior wall of the stomach at its junction with the stomodaeum, and acts in spasmodic retraction of the apical plate. Other muscle strands run from the apical plate to the stomodaeum and stomach, from the metatroch to the stomodaeum, stomach, prototroch and apical plate and from the dorsal wall of the hyposphere to the intestine.

By 48 hours a pair of protonephridia can be seen, running from the base of the stomodaeum across the blastocoel to open at the surface ventro-laterally just anterior to the anal vesicle. Flame cell activity is obvious within each protonephridium.

In the succeeding 8–9 days, as planktotrophic life continues, the trochophore grows steadily, reaching a length of about 170μ, but undergoes little other change. A broad band of reddish pigment forms ventrally in front of the prototroch early during this period, while towards 11 days a pair of ventro-lateral mesodermal bands become visible



Text-figs 1-7.—*Galeolaria caespitosa.*

1, Unfertilized egg; 2, Egg with 1st polar body; 3, 2-cell stage; 4, 4-cell stage, from animal pole; 5, Blastula; 6, Trochophore, 48 hours, lateral view; 7, 4-segment larva, 18 days, ventral view.

A, apical tuft; AN, anus; AP, apical plate; CH, chaetal sac; E, eye; F, feeding cilia; M, metatroch; MO, mouth; N, neurotroch; P, prototroch; PB, polar body; S, stomach; PR, protonephridium; V, anal vesicle.

in the hyposphere of the living larva. The left eyespot, identical with the right, appears on the 11th or 12th day.

In the period from 11 to 14 days, growth is mainly confined to the hyposphere. On the 15th day, and occasionally earlier, when the larva is about 200μ in length, the hyposphere shows signs of delineation of three simultaneously formed chaetigerous segments, each segment being initially marked by the outgrowth of two pairs of chaetae. The chaetal sacs soon become distinct, and as the segments enlarge, intersegmental annuli become visible. In the four days before settling, a small fourth trunk segment is delineated and paired ventro-lateral collar rudiments grow out immediately posterior to the metatroch. The apical tuft and anal vesicle are resorbed (Text-fig. 7). The length of the larva when it settles is about 230μ.

Settlement was observed during the present study only in cultures supplied with pieces of adult *G. caespitosa* tubes. It takes place at 19 days, when the larva, although retaining an active prototroch, adheres by its posterior end to the surface of a piece of adult tube. The anterior end continues to move actively, but the larva does not appear to creep about after becoming attached. Further development after settling has yet to be investigated.

Discussion.

In its spawning and early development, *G. caespitosa* resembles other serpulids with microlecithal eggs. As in *Eupomatus uncinatus* (Shearer, 1911; Iwanoff, 1928), *Pomatoceros triqueter* (Segrove, 1941) and *Hydroides norvegica* (Wisely, 1958), it develops rapidly into a planktotrophic trochophore, undergoes a protracted period of feeding and growth, develops three simultaneously delineated trunk segments, a fourth segment and the rudiments of the collar, loses its apical tuft and anal vesicle and then settles. The duration of planktotrophic life in *G. caespitosa*, 19 days in the conditions of the culture, compares with that of *Pomatoceros triqueter* (at least three weeks at 17° C.; Segrove, 1941), but is greater than that of *Hydroides norvegica* (8–10 days at 20° C.; Wisely, 1958).

The observations on settling in *G. caespitosa* suggest that the larvae, like many pelagic marine larvae, exhibit substratum preferences. Once attachment is achieved, however, no further exploration of the substratum appears to occur. Wisely (1958) has observed a similar absence of post-settlement exploration in *Hydroides norvegica*. It can be suggested that preferential settlement plays an important part in determining adult vertical distribution on the shore.

Acknowledgements.

The results included in this paper are drawn from a thesis presented in partial fulfilment of the requirements of the B.Sc. (Honours) degree of the University of Sydney by the junior author (J.C.A.). The work was supported by a research grant from the University of Sydney.

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A NEW SPECIES OF ECHTHROPLEXIS, AN ENCYRTID HYPERPARASITE OF LERP-FORMING PSYLLIDS ON EUCALYPTS (HYMENOPTERA, CHALCIDOIDEA).

By E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

(Seven Text-figures.)

[Read 25th July, 1962.]

Synopsis.

A new encyrtid hyperparasite of lerp-forming psyllids (*Echthroplexis psyllae*) is described.

This species has been bred as a common hyperparasite of several lerp-forming psyllids. The primary parasites of the psyllids, in these cases, are species of the similar looking encyrtid genus *Psyllaephagus*. The species is described to facilitate ecological studies on the lerp-forming psyllids of eucalypts.

Echthroplexis psyllae, sp. nov.

Female.

Body metallic black with slight purple hues; antenna all dark; legs all dark, except joints and middle and hind tarsi; tegula dark; mandibles rather dark; wings clear.

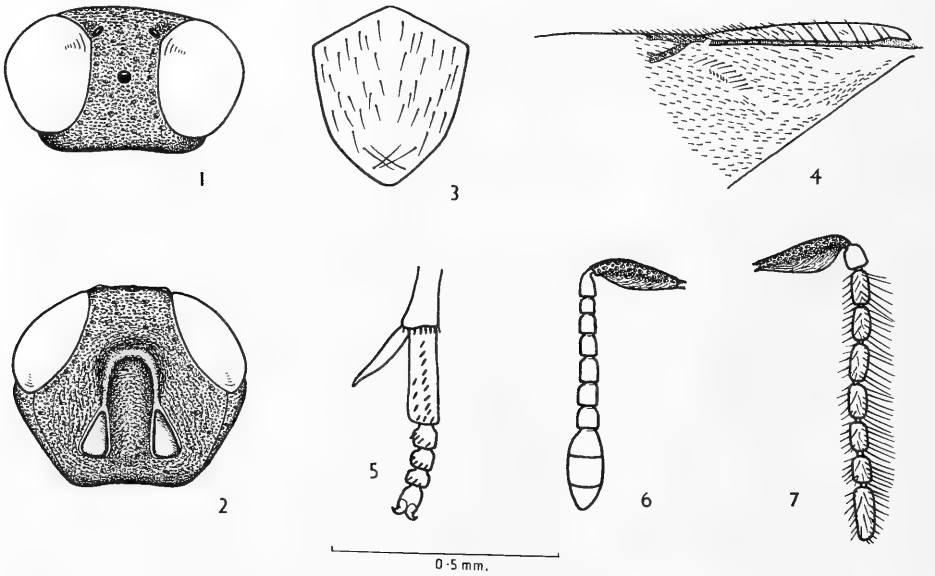
Length, excluding ovipositor, 1·3 to 1·5 mm., ovipositor about 0·4 mm.; vertex of head wide, about as wide as eye width, mesal margins of eyes converging to median ocellus, vertex very finely rugoso-punctate with a few scattered larger punctures at the bases of the short hairs; ocelli very small, lateral ocelli almost touching eye, ocelli in an almost equilateral triangle, the lateral ocelli very slightly further apart than either is from median ocellus, median ocellus much closer to eye than to lateral ocellus; scrobes clearly defined, rather deep and narrow, converging and meeting above in a rounded point, their upper limit slightly overhung by the face, scrobes very far from eye margin; areas between scrobes slightly raised, more apparently so because of the deep scrobes; lower face with only scattered, short hairs; face rather elongated, malar space as long as eye length; antennal insertions well separated but considerably closer together than either is from eye margin, almost twice as wide apart as each is from lower border of clypeus; scape long and thin, slightly expanded below, pedicel large, considerably longer than wide, flagellum relatively short, expanding distally; first funicle very small, slightly longer than wide, second distinctly larger, somewhat longer than wide, sixth funicle slightly longer than wide; club large, about as long as the distal three funicle segments, the first two club segments large, subequal, the terminal segment rather pointed; scutellum with evenly spaced hairs continued across meson, the apical pair considerably enlarged, erect, the subapical pair enlarged and partly erect; gaster much shorter than the thorax; ovipositor valves strongly exserted, about as long as gaster, very slender; apical tergite of gaster not produced over the ovipositor valves; middle tarsus thickened, basitarsus long, about as long as the apical four segments combined, basitarsal pad with tubercles in two more or less irregular longitudinal rows over most of the ventral surface; marginal vein distinctly longer than wide but shorter than postmarginal vein, postmarginal subequal to stigmal, stigmal with a distinct spur.

Male.

Body metallic black with slight purple hues; antenna all dark; legs all dark except joints and middle tarsus, less so hind tarsus; tegula dark; mandibles rather dark; wings clear.

Length 1·2 to 1·5 mm.; vertex of head wide, at least as wide as eye width, finely rugoso-punctate, lateral ocelli almost touching eye, slightly wider apart than either is from median ocellus, median ocellus somewhat closer to the eye than to lateral ocellus, about twice its diameter from eye; scrobes deep, clearly defined, converging and meeting above; lower face very similar to that of female; scape somewhat expanded below, widest about the middle, pedicel slightly longer than wide, flagellum clothed in whorls of long hairs, hairs distinctly longer than width of segments, basal four funicle segments subequal, about twice as long as wide, very slightly produced on one side, fifth and sixth funicle segments decreasing, sixth somewhat longer than wide, club large, more than three times as long as wide, as long as the apical two funicle segments combined, tapering to a rather truncately rounded apex; postmarginal vein very slightly shorter than stigmal.

Types.—Holotype ♀, allotype ♂ and paratypes in the Australian National Insect Collection, C.S.I.R.O., Division of Entomology Museum, Canberra. Paratypes in the British Museum (Nat. Hist.) and the U.S. National Museum.



Figures 1-7. *Echthroplexis psyllae.*—1, Head, dorsal view; 2, Head, frontal view; 3, Scutellum; 4, Basal half of forewing; 5, Middle tarsus, ventral; 6, Female antenna; 7, Male antenna.

Type Locality.—Canberra, Australia (1 Mar. 1954, L. R. Clark), bred from *Spondyliaspis vittiformis* on *Eucalyptus polyanthemos.* Paratypes also from *Spondyliaspis albicollaris* on *Eucalyptus polyanthemos*; *Spondyliaspis albitextura* and *Creiis* sp. *corniculata* group on *Eucalyptus blakelyi*; *Spondyliaspis nigra* and *Spondyliaspis* sp. *bancrofti* group on *Eucalyptus melliodora.*

The species is recorded also from Araluen, New South Wales (29 Apr. 1956, L. R. Clark), bred from *Cardiaspina fiscella* on *Eucalyptus tereticornis*; Taemas Bridge, New South Wales (4 Apr. 1957, L. R. Clark), bred from *Cardiaspina retator* on *Eucalyptus blakelyi*; Benalla-Shepparton, Victoria (15 Apr. 1957, L. R. Clark), bred from *Cardiaspina retator* on *Eucalyptus* ? *camaldulensis*; Benalla-Seymour, Victoria (16 Apr. 1957, L. R. Clark), bred from *Cardiaspina retator* on *Eucalyptus blakelyi*; Heywood Park, South Australia (7 June 1959, R. V. Southcott), bred from *Spondyliaspis albitextura* on *Eucalyptus camaldulensis.*

This species can be distinguished at once from species of *Psyllaephagus* by the venation of the forewing, the structure of the middle tarsus or the hairs on the scutellum.

AUSTRALIAN LIVERWORTS.

I. Haplomitrium intermedium, sp. nov. (Calobryales).

By Geoffrey K. Berrie, Department of Botany, University of Sydney.

(Two Text-figures.)

[Read 25th July, 1962.]

Synopsis.

Haplomitrium intermedium sp. nov. is described. This liverwort has been collected at three localities in New South Wales, and is the first member of the Calobryales to be recorded from Australia. The discovery of this species fills a gap in distribution records for the Order. The systematic position of the new species is discussed, and comment is made on the relationship of mucilage cells to marginal teeth on some of the leaves, such a relationship being previously unrecorded in the Calobryales.

Haplomitrium intermedium, sp. nov.

Dioicum, pallide viride, plantae fertile 5 mm ad 25 mm altae. *Caulis subterraneus* multiramis, rami per substratum oblique currentes; in sectione rotundus, ad 0·6 mm latus; vagina mucilaginis parva vel nulla; in sectione transversa, cellulae 33μ ad 46μ. *Caulis aerius* in sectione rotundus, ad 0·5 mm (♂) vel 0·7 mm (♀) latus; in sectione transversa, cellulae 33μ ad 50μ. *Folia* in seriebus tribus aequis, transverse inserta, saepe 1–4 denticulata in base: ♂—divaricans et ovata, rhombata vel suborbiculata, ad 1·5 mm longa; in regionibus fertilibus ad 2 mm longa; ♀—inferiora divaricans et ovata rhombata vel suborbiculata, ad 2 mm longa; in regionibus fertilibus imbricata, praelonga et parum asymmetrica, ad 3 mm longa. *Cellulae foliorum* variae; apicales ad 87μ × 68μ; medianae ad 78μ × 52μ; basales ad 93μ × 63μ, aliquae elongatae ad 160μ × 52μ. *Antheridia* pedicellata, in axilis foliorum caulium et in dispositionibus terminalibus cum foliis mixta. *Archegonia* ad 580μ longa, in inflorescentiis terminalibus foliis elongatis circumdata et foliis parvis mixta; anacrogyna. *Vestis sporangii* (perigynium et calyptra) ad 4·8 mm longa, ex partibus superioribus duabus calyptra, ex inferiore parte perigynium. *Sporogonium* circa 0·6 mm latum, longitudo incerta. *Sporae* 21μ ad 28μ. *Elateres* ad 230μ, trispirales vel bispirales.

Localities: (i) Between one and two miles along the road from Bilpin to Mount Irvine, Blue Mountains, N.S.W.: on soil with filamentous algae, mosses, *Drosera pygmaea* D.C., *Lycopodium laterale* R.Br. and other small plants on wet sandstone cliff face, in slight shade, altitude about 1,700 feet.

Holotype: Sydney University Herbarium, Bryophyte No. 2/62. *Cotype*: Professor R. M. Schuster Collection No. 50,616.

(ii) Adelina Falls, Lawson, Blue Mountains, N.S.W.: mixed in a dense covering of *Symphyogyna* sp. on wet sandstone cliff face beside waterfall, in slight shade, altitude about 1,800 feet. Sydney University Herbarium, Bryophyte No. 8/61.

(iii) Church Point, near Sydney, N.S.W.: mixed in a dense covering of *Pallavicinia* sp. on shaded sandstone cliff in splash from waterfall, altitude about 100 feet. Sydney University Herbarium, Bryophyte No. 1/59.

Haplomitrium intermedium is dioecious and shows marked sexual dimorphism. Female plants grow taller than male plants, have thicker stems and larger more variable leaves (Fig. 1, *a-m*).

The stem has two distinct regions. Upright leafy stems arise from a basal rhizomatous system which branches through the substrate. The maximum diameter of the aerial stem is about 0·5 mm. in male plants or 0·7 mm. in female plants. All stems are circular in section (Fig. 2*b*). The rhizome is also circular in section (Fig. 2*c*)

and up to 0·6 mm. in diameter in female plants. Many of the branches are much finer, commonly 0·1 mm. and sometimes as little as 0·07 mm. in diameter. The finest branches are very simple in structure, with an outer layer of four rows of cells enclosing an axial

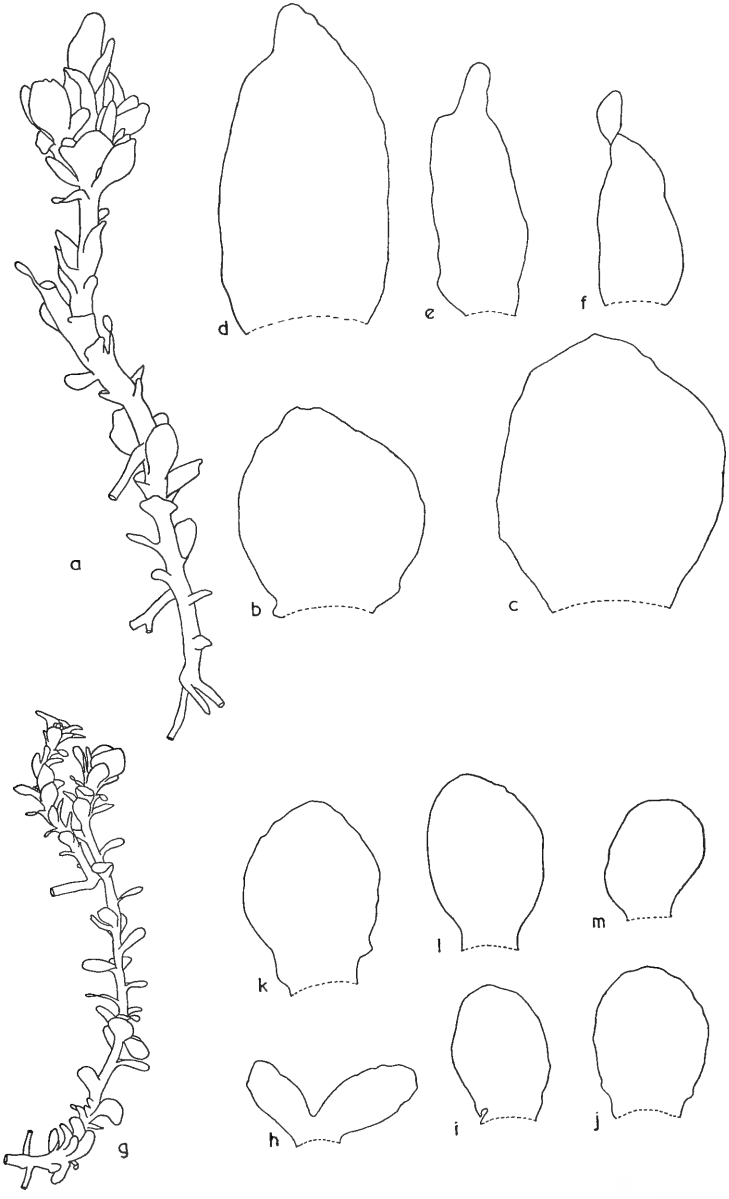


Figure 1. *Haplomitrium intermedium* sp. nov.: *a*, female plant with calyptra (× 4); *b* to *f*, leaves from a female plant (× 20), *b* and *c* from the lower part of the stem, *d* to *f* from the fertile region; *g*, male plant (× 4); *h* to *j*, successive leaves from the lower part of a male plant upwards (× 20).

row of cells. On the surface of the rhizome are mucilage cells which are either sessile or at the tips of short filaments of cells. There is no sheath of mucilage such as that found in *Calobryum gibbsiae* Steph. (Campbell, 1959) and other members of the Calobryales.

The rhizome grows obliquely through the substrate, often reaching a depth of 2 or 3 centimetres below the surface. In plants which are not overshadowed by other vegetation, branching is mostly confined to the rhizome. New leafy shoots are formed

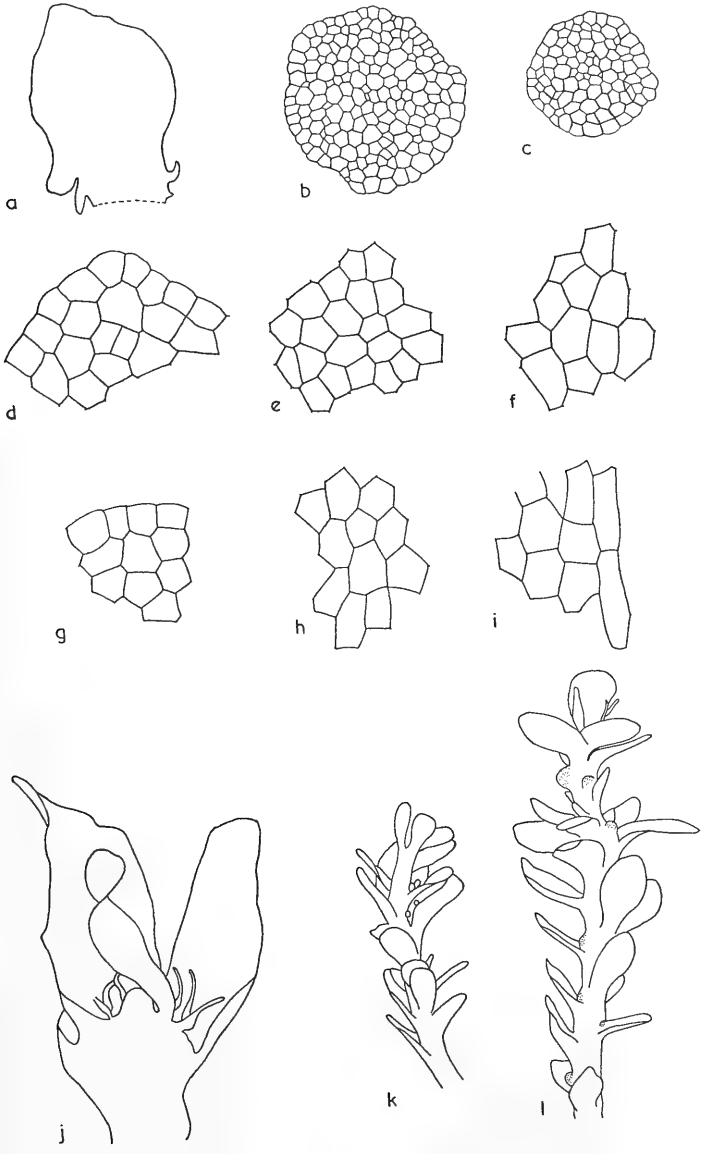


Figure 2. *Haplomitrium intermedium* sp. nov.: *a*, leaf showing four basal teeth (× 20); *b*, T.S. of aerial stem (× 40); *c*, T.S. of rhizome (× 40); *d* to *f*, cells from the tip (*d*), middle (*e*) and base (*f*) of a leaf from a male plant (× 80); *g* to *i*, cells from the tip (*g*), middle (*h*) and base (*i*) of a leaf from a female plant (× 80); *j*, female inflorescence cut longitudinally to show continued growth of the apex (× 8); *k*, small male plant with axillary antheridia (× 8); *l*, female plant showing many lateral branches (stippled) arising between leaves (× 8).

when branches grow vertically upwards, sometimes branching again before or at the surface. Laterals occasionally arise from the aerial stem, in the axils of leaves. Where plants are intermingled with a dense covering of other bryophytes there may be many such branches (Fig. 2*l*).

Since there is complete radial symmetry of the shoot there is no justification for distinguishing between "lateral leaves" and "underleaves", as in other leafy liverworts. In infertile regions the leaves are up to 1·5 mm. long in male plants, and up to 2 mm. long in female plants. The lowest leaves on the stem are small and usually ovate, but occasionally bilobed almost to the base (Fig. 1*h*). Further up the stem the leaves are rhomboid to suborbicular, and stand out from the stem at an angle of 45° or more. In many plants there are 1–4 short marginal teeth near the base of the leaf, one or two on each side close to the insertion (Fig. 2*a*). Toothing is most marked in plants which are slightly etiolated.

Initially, all leaves have six mucilage cells spaced at intervals round the margin. In toothed leaves, each tooth has one of these at or near the tip.

Leaves in fertile regions of male plants are spreading, up to 2 mm. long, and usually slightly asymmetrical. In the fertile regions of female stems the leaves are imbricate, up to 3 mm. long, and variable in shape (Fig. 1, *d-f*). They are usually roughly ovate, often acute at the tip, but sometimes there are one or more linear leaves.

Leaf cells are variable and tend to be larger in female plants than in male plants (Fig. 2, *d-i*). In well-developed female plants there are sometimes a few very elongated cells, up to 160μ × 52μ, at the centre of the base of the leaf (Fig. 2*i*).

Antheridia are always axillary to leaves. In a well-developed male plant the fertile leaves are mostly crowded at the tip of the stem to form a loosely defined inflorescence, but usually there are also leaves lower down the stem with axillary antheridia (Fig. 1*g*). On smaller plants there may be no inflorescence, all the antheridia being in the axils of normal stem leaves (Fig. 2*k*).

The female inflorescence is similarly ill-defined. All archegonia are axillary to leaves, not mixed with mucilage hairs as in *Calobryum* spp. The first formed archegonia are usually in the axils of large asymmetrical leaves, and successive leaves are smaller, giving the female inflorescence a slightly pyramidal shape. Growth of the apex usually continues (Fig. 2*j*), and lateral branches often arise from among the archegonia.

Antheridia, archegonia, and a few sporophytes at various stages of development may be found at any season, but the abundant remains of sporophyte investments were present at the type locality in February, 1962. There is evidently an optimum season for fertilization, resulting in the ripening of capsules and spore discharge in the spring.

The sporophyte is enclosed in a sheath of gametophyte tissue of which the basal third bears old archegonia and is presumably perigynium and the upper part is calyptra. The length of the mature sporophyte is uncertain and the manner of dehiscence unknown. The spores are finely punctate and range in size from 21μ to 28μ. Elaters are trispiral and bispiral, and up to 230μ in length.

Haplomitrium intermedium has been collected from three localities in New South Wales. Elevations of these localities range from about 100 feet to about 1,800 feet. All collections are from lightly shaded cliff faces with a constant supply of water either from seepage or from splash. At the type locality *H. intermedium* grows in soil which has accumulated in irregularities in the cliff face. The soil is consolidated by a rich growth of filamentous algae and a few small mosses, lycopods and flowering plants. At the other localities *H. intermedium* grows intermingled with a dense covering of *Symphyogyna* sp. (Adelina Falls) or *Pallavicinia* sp. (Church Point).

Discussion.

Two genera, *Haplomitrium* Nees and *Calobryum* Nees, are usually recognized in the Calobryales. The distinction between these genera depends upon the disposition of the reproductive organs (Stephani, 1900). In *Calobryum*, antheridia and archegonia are aggregated into terminal inflorescences, each sharply delimited by 3 or 4 distinctive leaves. Archegonia and antheridia are mixed with mucilage hairs or reduced leaves. In *Haplomitrium*, antheridia and archegonia are subtended by stem leaves, not aggregated into inflorescences. In the Australian species male and female inflorescences

are formed, but they are not sharply demarcated. Archegonia are always mixed with leaves within the inflorescence, and also occur in the axils of leaves below the inflorescence and at the bases of innovations which arise from within the inflorescence. Antheridia occur in the axils of leaves below the inflorescence, and in small plants there may be no inflorescence formed, all the antheridia being in the axils of stem leaves as in *H. hookeri*. The condition is therefore intermediate between that of typical *Haplomitrium* and that of typical *Calobryum*. This is the justification for the specific epithet "*intermedium*".

The Australian plant would have been described as a species of *Calobryum* but for a forthcoming publication by Schuster (in press) in which the generic distinction between *Calobryum* and *Haplomitrium* is shown to be invalid. With Professor Schuster's permission, publication of his work has been anticipated, and the species described as *Haplomitrium intermedium*.

The discovery of *H. intermedium* in Australia is important in that it fills a gap in the distribution pattern of the Calobryales between *C. gibbsiae* Steph. in New Zealand and *C. blumii* Nees in Java, Sumatra and New Guinea. *H. intermedium* is probably most closely related to *C. gibbsiae*. It is distinguished from this and other species usually referred to the genus *Calobryum* by its poorly defined inflorescences, smaller leaves, and rhizomes which grow obliquely downwards without forming a horizontal system parallel to the surface of the substrate. It is distinguished from *H. hookeri* by the tendency to form apical groups of antheridia and archegonia and its more robust form.

The relationship of mucilage cells to the teeth present on some of the leaves is interesting. The writer has found the same relationship in cultured material of *H. hookeri* obtained from the University of Cambridge Culture Collection, but teeth have not been recorded in species usually referred to the genus *Calobryum*. The presence of mucilage cells at the apices of these teeth is reminiscent of the occurrence of "hyaline papillae" (mucilage cells) at or near the apices of lobes of the leaf in certain members of the Jungermaniales acrogynae (Greig-Smith, 1958).

Acknowledgements.

Acknowledgements are due to Dr. A. R. H. Martin, of this department, who drew my attention to the Church Point material in 1959, to Miss Helen J. Hewson who made most of the drawings, and to Professor R. M. Schuster of the University of Massachusetts who was first to find *H. intermedium* at what was later chosen as the type locality, and who gave me much valuable advice.

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SOME INSECTS AND TERRESTRIAL ARTHROPODS FROM HERON ISLAND, QUEENSLAND.

By C. E. Chadwick.

[Read 25th July, 1962.]

Synopsis.

A review of the literature relating to insects on coral cays is made and Heron Island briefly described. About 80 species of terrestrial Arthropoda (mainly insects) collected on the island are listed.

The insect fauna of coral cays off the Queensland coast has had very little attention and literature on the subject is scanty.

Apparently the first attempt to list insects occurring on any of these cays was made by Musgrave (1926) who, in November and December, 1925, was among a party of zoologists which visited North-West Islet in the Capricorn Group, forty-seven miles north-east of Gladstone. Musgrave gave a list of thirty-seven named species collected on the islet; a few species could not be identified.

Stephenson, Stephenson and Tandy (1931), describing the results of the British Museum (Natural History) Great Barrier Reef Expedition (1928–9) to Low Isles and other parts of the Great Barrier Reef, state that cockroaches, grasshoppers, beetles, ants, mosquitoes, sandflies, moths and butterflies occur on Low Isles, off Port Douglas, North Queensland, and mention specifically the grasshopper *Valanga irregulare*, the ants *Pheidole variabilis*, *Oecophylla smaragdina virescens* and *Polyrachis sokolova*, the house fly *Musca domestica* and the butterflies *Papilio* (= *Troides*) *priamus euphorion* and *Danaida melissa hamata*. As well as the sand cay of the Low Isles, this survey included the mangrove islet and swamp located on the same coral bank.

Mackerras (1950), when reviewing insects associated with the ocean, included some species occurring on Heron Island. He stated that the Collembola *Axelsonia litoralis* Monz. and *Pseudachorutes* sp. were found in the outer parts of the surrounding reef inside the ramparts, and that the Gerrid *Halobates* lived in the same zone. (However, since then (personal communication, 2/6/1958) Mackerras has advised that the Gerrid was not accurately identified and was probably the same as the species which the present author had determined by Dr. W. E. China.) A spider (possibly *Desis crosslandi* Poc.) was also observed in crevices on the outer parts of coral reefs.

Lee and Reye (1952) recorded the Ceratopogonid, *Culicoides rabauli* Macfie, as being collected on Heron Island by J. L. Wassell in a "tree hole and *Pisonia* tree hole" in May, 1947.

Woodward (1958) mentioned the occurrence of *Omania marksae*, *Halovelia* and "several species of Collembola, mites (*Microtrombidium* sp. and *Eupodes* sp.) and small beetles" on the island.

Heron Island is some forty odd miles in a north-easterly direction from Gladstone. The first naturalist to visit it was J. B. Jukes, in 1843. In his account (Jukes, 1847) he stated: "Both the island and the reef were elongated in an east and west direction, the island itself being half a mile long and not more than 300 yards broad." It is about a mile in circumference, thirty-two acres in area and has a maximum height of fifteen feet; the average height would be only about half this figure. The vegetation is rather scanty, the trees and shrubs being limited to a few species, some of which also occur on Mast-Head Island (Longman, 1913).

Casuarina equisetifolia var. *incana* and *Pandanus pedunculatus* grow in places around the shores. *Pisonia* trees occupy the inner parts of the island, and *Messersmidia* (= *Tournefortia*) *argentea* is much in evidence close by the top of the strand. Some examples of the fig tree *Ficus opposita* are present in the *Pisonia* forest, where their leaves are sometimes affected by the fungus *Trabutia evansii* Theis & Sydow, which

appears as black spots on the leaf surfaces. Another tree, *Celtis paniculata* Planch., grows to a height of 20 or 30 feet. The bush *Boehmeria nivea* is also present and grows to about ten feet in height.

The writer spent the week 2–9th June, 1951, on the islet and in the company of Mr. J. W. T. Armstrong collected a number of insets and other arthropods. This material has been identified as far as practicable. Owing to the uncommon nature of many of the species it was necessary to refer a number of them to various specialists, whose assistance is acknowledged in the text.

Several new species were collected. Mr. Armstrong found numbers of a small Saldid bug in the coral reef. Subsequently Dr. E. N. Marks collected specimens of the same bug at Low Isles in 1954 and Dr. T. E. Woodward secured a further large series on Heron Island in 1957. A year later Woodward (1958) described this bug as the new species *Omania marksae*, and gave an interesting account of its habits and biology. It is of interest to note here that another species, the third of the genus *Omania*, was recently described by Kellen (1960) from Samoa where bugs were found in small holes and crevices in volcanic rocks in the intertidal zone of a shallow, protected lagoon.

Two species of Staphylinidae (apparently belonging to new genera) were also collected, as well as a new Elmid belonging to a new genus which is being studied by Dr. H. E. Hinton and will be described at a later date. Mr. Armstrong found 75 specimens of the latter in consolidated coral rocks taking refuge from the sea water in numerous interstices.

As insects associated with coral reefs Mackerras (1950) noted two species of *Collembola*, a Gerrid bug and the spider *Desis crosslandi* from Heron Island and four species of Chironomidae, described by Edwards from Samoa. To these must now be added beetles belonging to the families Staphylinidae, Melyridae and Elmidae. More intensive collecting on the reefs of Heron Island and other coral cays may well reveal other insects whose bionomics may be of considerable interest.

The collected material also included a species of *Brachymeria*, which E. F. Riek proposes to describe as new, a species of *Microtrombidium*, probably new, and referred to H. Womersley for description; seven species of spider which could only be determined to the genus and could include new species.

Neither house flies nor honey bees were noticed during the week's stay on the islet. The coastal brown ant, *Pheidole megacephala* (F.), was the commonest insect on the island and was found in a great variety of habitats.

A single species of *Planococcus* was collected and subsequently reported on by Miss H. M. Brooks in the following terms (personal communication, 14/9/1960):

"They are *Planococcus*, near *citri* (Risso). They also resemble a new species of *citricus* McConnell which has been collected from a wide variety of hosts in the West Indies, tropical Africa, the Mediterranean region and Hawaii. I cannot positively differentiate between your specimens and *citri*."

Species Collected.

Class INSECTA.

Order THYSANURA.

Family Lepismatidae

Lepisma saccharina L. under bark of *Casuarina equisetifolia* var. *incana*.

Order COLLEMBOLA (Det. H. Womersley).

Family Isotomidae

Axelsonia litoralis Monz. (found on reef).

Family Entomobryiidae

Lepidocyrtinus queenslandicus Wom.

Order ORTHOPTERA.

Family Blattidae

Periplaneta australasiae (F.).

Megamareta verticollis Hebard.

Family Gryllidae

Ornebius australicus Chop.

Family Acrididae

Valanga irregulare (Walk.). On leaves of *Messersmidia argentea*.

Order HEMIPTERA.

Family LYGAEIDAE

Germalus sp. (On *Casuarina equisetifolia* var. *incana*).

Family PENTATOMIDAE

Morna aggressor (F.).

Family MIRIDAE

Campylomma sp.

Family GERRIDAE

Hermatobates weddi China (Det. W. E. China). Found under rock at reef edge.

Family SALDIDAE

Omania marksae Woodward.

Family CICADIDAE

Genus and species unknown (exuviae only collected). Musgrave (1926) recorded *Arunta intermedia* Ashton from North-West Islet.

Family APHIDIDAE

Unidentified species on flower stalk of *Abutilon indicum* var. *australiense*.

Family COCCIDAE (Det. Helen M. Brooks)

Planococcus ? *citri* Risso. (On stem and leaves of *Wedelia biflora*, causing malformation of lower surface of leaves.)

Saissetia coffeae (Walk.). On *Wedelia biflora*.

Order COLEOPTERA.

Family CIIDAE

Cis victoriensis Blackburn. Under bark of dead branches of trees.

Family COCCINELLIDAE

Cryptolaemus montrouzieri Muls.

Platyomus lividigaster Muls.

Family SCYDMAENIDAE

Scydmaenus sp. 1. Under bark of dead branches of trees.

Scydmaenus sp. 2.

Scydmaenus (*Cholerus*) sp. 3.

Family STAPHYLINIDAE (Det. W. O. Steel)

Ctenadropus sp.

Gen. et sp. nov. (*Alaeocharini*).

Gen. near *Quedius*. On upturned coral on outer reef.

Family MELYRIDAE

Dicranolaius alleni (Lea). Larvae and adults on "rocks" around beach.

Family ELMIDAE

Gen. et sp. nov.

Family TENEBRIONIDAE

Hopalocephala pygmaea Champ.

Family SCARABAEIDAE

Protaetia advena Jans. (clinging to stem of *Ficus*).

Family CURCULIONIDAE

Sitophilus oryzae (L.).

Notiosomus rugosipennis Lea.

Order HYMENOPTERA.

Family CHALCIDIDAE (Det. E. F. Riek)

Brachymeria sp. nov. close to *thyma* (Gir.).

Family BETHYLIDAE

? *Sierola* sp. (Det. E. F. Riek).

Family FORMICIDAE

Pheidole megacephala (F.). Found in beds in huts; on flowers, flower buds, leaves, under dead bark on *Messersmidia* (= *Tournefortia*) *argentea* (L.f.) Johnston; around aphids on flower stalk of *Abutilon indicum* var. *australiense*; under bark *Pisonia* sp. (probably *grandis* R.Br.); on the beach; under stones.

Family PSAMMOCHARIDAE

Cryptochilus bicolor F.

Family VESPIDAE

Polistes bernardi Le G.

Order DIPTERA.

Family DOLICHOPODIDAE

Sciapus connexus Walk. (on wild Poinsettia).

Family LONCHAEIDAE

Lonchaea aurea Macq. (on window pane).

Family OTITIDAE

Plagiostenopterina aenea Hend. (collected when emerging from beach sand).

Plagiostenopterina enderleini Hendel. (Det. D. K. McAlpine).

Family MILICHIIDAE

Desmometopa sp.

Milichiella lacteipennis Loew.

Family CHLOROPIDAE

Prohippelates nigricornis flavus (Thompson) (on window pane) (Det. D. K. McAlpine).

Family DROSOPHILIDAE (Det. W. B. Mather)

Drosophila melanogaster Meigen.

Family MUSCIDAE

Caricea sp.

Family TACHINIDAE

Chrysosarcophaga impatiens Walk.

Family HIPPOBOSCIDAE

Unknown species observed on man.

Order LEPIDOPTERA.

Family PYRAUSTIDAE

Hymenia recurvalis (F.).

Family Hypsidae
* *Nyctemera secundiana* L.
Family Noctuidae
Achaea melicerta Drury.
* *Othreis materna* (L.).
Family Pieridae
* *Glycestha java teutonia* (F.).
* *Eurema hecabe sulphurata* Butler.
Family Danaidae
* *Danaus plexippus* L.
* *Danaus hamatus* (Macl.).
* *Euploea tulliolus tulliolus* F.
Family Nymphalidae
* *Acraea andromacha* F.
* *Hypolimnas bolina nerina* F.
Family Satyridae
* *Melanitis leda bankia* F.
Family Lycaenidae
Candalides erinus F.
Zizeeria labradus labradus (Godart.).
* *Cosmolyce boeticus damoetes* (F.).

* Specimens in the collection of Mr. C. Cox, Heron Island; identified by the late A. Musgrave.

Class ARACHNIDA.

Order ACARINA (Det. H. Womersley).
Family Paramegistidae
Promegistus armstrongi Wom.
Family Bdellidae
Biscirus australicus Wom.
Family Trombidiidae
Microtrombidium sp., probably new.

Order ARANEAE (Det. V. V. Hickman).
Family Agelenidae
Desis crosslandi Pocock.
Family Zodariidae
Storena sp.
Family Sicariidae
Scytodes striatipes (L. Koch).
Family Pholcidae
Smeringopus elongatus (Vins.).
Family Argiopidae
Argyope aemula (Wlk.).
Argyope aetheria Walck.
Family Gnaphosidae
Hemicloea sp.
Family Thomisidae
Diaea variabilis L. Koch.
Family Clubionidae
Chiracanthium mordax L. Koch.
Family Salticidae
Cytaea sp.
Hasarius sp.
Homolattus sp.
Ocrisiona complanata L. Koch.
Paraphidippus sp.
Phlegra sp.

Class CRUSTACEA.

Porcellionides pruniosus (Brandt.) (Det. F. A. McNeill).

Acknowledgements.

The author is indebted to Mr. J. W. T. Armstrong for the loan of specimens which have been added to the list and to the various specialists who have identified the more obscure species. Mr. F. A. McNeill has kindly offered certain suggestions with regard to the manuscript.

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STUDIES ON THE INHERITANCE OF RUST RESISTANCE IN OATS.

II. The Mode of Inheritance of Crown Rust Resistance in the Varieties Landhafer, Santa Fe, Mutica Ukraine, Trispernia and Victoria in their Crosses with Susceptible Varieties.

By Y. M. Upadhyaya and E. P. Baker, Faculty of Agriculture, The University of Sydney.

[Read 25th July, 1962.]

Synopsis.

The oat varieties Landhafer, Santa Fe, Mutica Ukraine, Trispernia and Victoria, resistant to the prevalent field races of crown rust in Australia, were studied in crosses with varieties susceptible to certain or all of the following races: 203, 226, 226-2, 237, 237-4, 259 and 286. In the seedling stage resistance was dependent on a single incompletely dominant factor pair in the varieties Landhafer, Santa Fe and Trispernia. These genes also conferred adult plant resistance, but an additional factor pair conditioned the adult plant resistance of Landhafer. Seedling resistance in Mutica Ukraine was likewise due to a single incompletely dominant factor pair; in this case, however, it was ineffective in conferring adult plant resistance. Resistance at this latter stage was due to three independent dominant genes, of which two operated in complementary fashion. The resistance of Victoria was dependent in the seedling stage on two linked dominant complementary factor pairs (with a recombination value of 9·59 ± 1·68 units) and another partially dominant factor pair linked with approximately 10 per cent recombination with its inhibitor. These latter linked genes in addition conditioned adult plant resistance; at this stage two additional dominant factor pairs, one linked with the two complementary factors for seedling resistance and showing about 10 per cent recombination with the proximal gene, were also operative. These studies confirmed the earlier observations made on the variety Garry deriving its crown rust resistance from Victoria.

Stem rust resistance of the variety Burke, due to the factor pair Rd_1 Rd_1, was found to be independent of the factors for seedling resistance in the five varieties and of the factors for adult plant resistance in the variety Victoria.

Introduction.

The advent of new physiologic races of crown or leaf rust of oats (*Puccinia coronata* Cda. var. *avenae* Fraser and Led.) and changes in the prevalence of certain races involve the oat breeder in a continual search for new sources of resistance to counteract the variability of the pathogen. In this connection the experience in Australia has followed that in other countries. Although little work has been done locally in breeding specifically against crown rust, the organism concerned has shown great pathogenic variability. This has become clear from physiologic race surveys in which variants have been found virulent on varieties resistant to the more widespread races.

The varieties Bond and Victoria have been the sole sources of resistance used in the breeding of improved varieties in Australia. As indicated by Baker and Upadhyaya (1955), these varieties no longer offer protection against certain field collections of crown rust. Following North American experience the varieties Landhafer, Santa Fe, Mutica Ukraine (Ukraine) and Trispernia were considered possibly to offer satisfactory new resistance sources. The relative merits of varietal sources of resistance depend upon the genetic diversity they afford and the genetic basis for their resistance. To facilitate the breeding programmes information is required in addition on the mode of inheritance of the resistance.

Although information on certain of these points was available from North American results, the investigations to be presented in this paper were undertaken to obtain similar information on these important varietal sources of resistance to

Australian races of crown rust. Almost certainly local rusts represent distinctive and peculiar pathogenic entities, although on a broad race designation basis they may conform to similar overseas categories. The genotype which a variety manifests may vary with the genotype for pathogenicity against which it is tested. For local breeders to proceed with utmost efficiency, therefore, local data are imperative.

All the resistant varieties on which inheritance studies are reported in this publication are also included in the current international differential set for race identification. To understand the significance of, and basis for, pathogenic variability it is obvious that a knowledge of the genotypes of the varieties in the differential set is essential in this respect. Ultimate refinement in race identification and designation depends upon the use of single genes rather than varieties for this purpose. This was a further impetus to the currently reported studies.

The first paper currently presented will deal with the mode of inheritance of resistance of the five resistant varieties, Landhafer, Santa Fe, Mutica Ukraine, Trispernia and Victoria, as revealed in their crosses with susceptible varieties. A subsequent paper will deal with information revealed by intercrossing them.

Literature Review.

This review of the literature on crown rust inheritance will be restricted to that pertinent to the five resistant varieties studied in these investigations in their crosses with susceptible varieties.

In the case of the variety Landhafer, Litzenberger (1949) was the first to report the presence of a single dominant gene for resistance to races 1 and 45 in the seedling as well as the adult plant stage. Kehr and Hayes (1950) confirmed these observations and found that the same factor conditioned resistance to races 1, 3, 4, 5, 6, 33, 45, 57 and 68. The operation of a single factor against races 1 and 101 was also reported by Simons (1953) and Simons and Murphy (1954). According to them dominance of resistance varied with the cross studied. In the cross with Reselect Clinton resistance was recessive while in others it was dominant. In crosses with Santa Fe–Clinton and Trispernia, transgressive segregation resulting in higher resistance than either parent was reported. Griffiths (1953) and Finkner (1954) also reported the operation of a single factor for resistance in Landhafer.

The variety Santa Fe has been found to show a simple or somewhat complex mode of inheritance according to different investigators even when segregating generations were tested with pathogenic entities of similar race designation. Litzenberger (1949) Maung (cited by Osler and Hayes, 1953), Osler and Hayes (1953), Griffiths (1953) and Finkner (1954) concluded that resistance depended on a single dominant factor pair. Three of the races used in certain of these reports were 1, 45 and 57. Litzenberger (1949), however, reported that in some crosses two factors in Santa Fe were operative against race 1. When crosses were tested with races 45 and 101, Simons (1953) found the resistance to depend on two dominant linked factor pairs with 23 per cent recombination. Simons and Murphy (1954) similarly reported linkage. Finkner (1954) when using race 57 found that in some cases two dominant linked factor pairs were operative with an estimated recombination value of 22·84 $\pm$ 0·04 per cent. Those cases in which only a single factor was operative were explained by assuming that Santa Fe was heterogeneous and varied in its genotype for rust resistance in different lines. Finkner, Atkins and Murphy (1955) concluded that two linked factor pairs were involved with 28·8 $\pm$ 0·8 per cent recombination in tests with races 57 and 109. At the University of Minnesota Maung in 1950 (cited by Finkner, Atkins and Murphy, 1955) found divergent results with Santa Fe. He concluded that inheritance in some cases was complex and that resistance depended on a single dominant factor in addition to two complementary factor pairs when tested against race 1. A similar genotype was proposed by Osler and Hayes (1953) using the same race.

In the case of the variety Mutica Ukraine (henceforth abbreviated to Ukraine), Weetman (1942) using a biotype of race 1 found that the adult plant resistance of

Ukraine was conditioned by two dominant complementary factor pairs. Finkner (1954) concluded that the genotype of the variety had as a basis duplicate dominant linked factor pairs with 23 per cent recombination using race 57 as the pathogen. Finkner, Atkins and Murphy (1955) stated that resistance to this race and susceptibility to race 109 were governed by the same single gene in Ukraine. They concluded that the varietal strain used in their investigations carried only one of the two linked genes reported by Finkner.

In the variety of Trispernia, Simons and Murphy (1954) found resistance dependent on a single dominant factor pair on the basis of tests with races 1 and 101. Finkner (1954), however, was forced to conclude when race 57 was used that the variety was heterogeneous for genetic factors involved. He postulated that resistance depended on from one to three factor pairs.

The literature pertinent to studies involving the variety Victoria has been reviewed by Upadhyaya and Baker (1960). This showed that various investigations indicated that from one to three factor pairs may be involved. Their own studies in crosses of the variety Garry, deriving its crown rust resistance from Victoria, revealed that to races 1, 6, 46 and 57, certain of which were subdivided into further additional pathogenic entities by the use of supplemental differentials, seedling resistance was conditioned by two linked dominant complementary factors (with a recombination value of 9·59 $\pm$ 1·68 units) and another partially dominant factor linked with approximately 10 per cent recombination with its inhibitor. The latter group conditioned adult plant resistance also. Apart from this group two more dominant factors conditioned adult plant resistance only and one of these was linked with the two complementary factors for seedling resistance. Recombination with the proximal gene was about 10 per cent.

Burke was found to possess a single factor (Rd_1) for stem rust resistance to races 2 and 12 (Upadhyaya and Baker, 1962). Litzenberger (1949) reported that this same factor in the variety Richland was independent of the factors for crown rust resistance in Landhafer and Santa Fe. The factor in Burke was independent of the crown rust resistance of Garry (Upadhyaya and Baker, 1960).

Materials and Methods.

The F_1, F_2 and F_3 generations of the following crosses involving the five crown rust resistant varieties under study were investigated:

Landhafer with Fulghum, Algerian, Burke, Bond and Victoria.

Santa Fe with Fulghum, Algerian, Ukraine, Bond and Victoria.

Ukraine with Algerian and Burke.

Trispernia with Fulghum and Burke.

Victoria with Fulghum, Algerian, Burke, Bond, Landhafer and Santa Fe.

The crown rust races used in the studies were 203, 226, 226-Anz-2, 237, 237-Anz-4, 259 and 286. These were from field collections and are described by Baker and Upadhyaya (1955). Race numbers with no additional designation correspond to the Anz-1 type described in this publication in each case. Races 226-Anz-2 and 237-Anz-4 are subsequently abbreviated to 226-2 and 237-4 respectively.

In the crosses with the five varieties under study Fulghum, Algerian and Burke were susceptible to all races. Bond was susceptible only to race 203, Victoria to race 259, Landhafer and Santa Fe to race 286 and Ukraine to races 203, 226, 259 and 286 in the seedling stage.

Field inoculum of crown rust used in tests was sampled from time to time, and found to comprise race 226 and 237 types on the differential set.

The races of stem rust (*Puccinia graminis avenae* E. and H.) used to determine independence or otherwise of the genetic factors conditioning stem and crown rust resistance in appropriate crosses were 2 and 12 following the key of Newton and Johnson (1944).

The experimental procedure was as described by Upadhyaya and Baker (1960).

TABLE 1.

Parental and F_1 Reactions in Crosses of the Resistant Oat Varieties Landhafer, Santa Fe, Mutica Ukraine (Ukraine), Trispernia and Victoria in Crosses with Susceptible Varieties, when tested with certain Crown Rust Races and Field Inoculum in Seedling and Mature Plant Stages.

Parent or Cross.	Reactions in Seedling Stage. Race 203.	226.	237.	237–4.	259.	286.	Reactions in Adult Stage. Race 203.	226.	237.	237–4.	259.	Field Inoculum.
Landhafer*	; − 1=	; − 1=	; − 1=	; − 1=	; − 1=	4	I	I	I	I	I	I
Santa Fe	; − 1=	; − 1=	; − 1=	; − 1=	; − 1=	4	I	I	I	I	I	I
Ukraine	4	4	; − 1=	; − 1=	4	4	R	I	I	I	R − MR	I, R − MR
Trispernia	1+	1+	1+	1+	1+	4	—	—	—	—	—	R
Victoria	1n	1n	1n	1n	3	1n	R	I	R	R	S	I (98%)
Fulghum	4	4	4	4	4	3	S	S	S	S	S	S
F_1 (*a*)‡ ..	1−	; − 1	2=	2=	;	—	—	—	—	—	—	R
(*b*) ..	1−	; − 1	2=	2=	;	—	R	R	R	R	R	R − MR
(*d*)	—	3c	—	—	2− − 3c	—	—	—	—	—	—	MR
(*e*) ..	2− − 2n	1n − 2n	1n	1n − 3 − n	—	3 − n	R	R	R	R	—	R − MR
Algerian	4	4	4	4	4	3	S	S	S	S	S	S (98%)
F_1 (*a*)	;	; − 1	2−	1=	; − 1	—	R	R	R	R	R	R
(*b*) ..	1	; − 1	; − 1	; − 1	; − 1	—	R	I	MR	R	R	MR
(*c*) ..	—	—	—	3 − c	—	—	—	—	R − MR	R − MR	—	—
(*e*) ..	1n − 2 − n	2 − n	1n	1n	—	1 − 2 − n	R	I	R	R	—	R − MR
Burke	4	4	4	4	4	3	—	—	—	—	—	S
F_1 (*a*)	2− − 2	1	—	—	—	—	—	—	—	—	—	MR
(*c*) ..	—	—	—	—	—	—	—	—	—	—	—	MR
(*d*)	—	—	—	—	2+	—	—	—	—	—	—	MR
(*e*) ..	0†	—	—	—	—	—	—	—	—	—	—	R

* 1=reactions observed at high temperatures (75–85° F.).

† Two seedlings inoculated but probably escaped infection.

‡ (*a*) indicates F_1 of susceptible parent in preceding line in table with Landhafer.
(*b*) ,, ,, ,, ,, ,, ,, ,, ,, ,, Santa Fe.
(*c*) ,, ,, ,, ,, ,, ,, ,, ,, ,, Ukraine.
(*d*) ,, ,, ,, ,, ,, ,, ,, ,, ,, Trispernia.
(*e*) ,, ,, ,, ,, ,, ,, ,, ,, ,, Victoria.

(I=immune, R=resistant, MR=moderately resistant, S=susceptible.)

Experimental Results.

(*a*) Reactions of parents and F_1s.

The parental and F_1 reactions are presented in Table 1. The reactions of the susceptible parents are indicated above the appropriate F_1s. Crosses (a), (b), (c), (d) and (e) are those involving the susceptible parent in crosses with Landhafer, Santa Fe, Ukraine, Trispernia and Victoria respectively.

From Table 1 it will be observed that the seedling reaction type of the resistant parent was dominant only in the following cases: Fulghum × Landhafer and Santa Fe (tested with race 259), Algerian × Landhafer (race 103), Algerian × Victoria (races 237 and 237–4) and Fulghum × Victoria (race 237). Also in the adult plant stage the F_1 usually exhibited a higher reaction type than the resistant parent, particularly in field tests.

Table 2.

F_2 Seedling Segregation in Crosses Involving the Resistant Variety Landhafer with Susceptible Varieties tested with certain Crown Rust Races.
(Expected values in brackets.)

Cross.	Race Used.	F_2 Reaction Types. ;	1	2–	3–4	Total.	Hypothetical Ratio.	Probability.
Fulghum × Landhafer ..	203*	—	26	1	77 (78·0)	104	1R. : 3S.	0·9 –0·8
	259	34 (33·0)	68 (66·0)	—	30 (33·0)	132	1R. : 2I. : 1S.	0·9– 0·8
Algerian × Landhafer ..	203*	—	7	11	95 (84·8)	113	1R. : 3S.	0·05–0·02
	259*	—	54	7	156 (162·8)	217	1R. : 3S.	0·3 –0·2
	259	28 (26·5)	52 (53·0)	—	26 (26·5)	106	1R. : 2I. : 1S.	0·95–0·9
Burke × Landhafer ..	203	52 (45·8)	91 (91·5)	—	40 (45·8)	183	1R. : 2I. : 1S.	0·5 –0·3
	226†	121 (182·3)	68	—	54 (60·8)	243	3R. : 1S.	0·5 –0·3
	237	36 (37·0)	60 (74·0)	16	36 (37·0)	148	1R. : 2I. : 1S.	0·99–0·95
Victoria × Landhafer ..	259	64 (52·5)	102 (105·0)	—	44 (52·5)	210	1R. : 2I. : 1S.	0·2 –0·1

* Tested at temperatures above 80° F.
† Reactions read two days earlier than normal, and then seedlings inoculated with race 203.
(R.=resistant, I.=intermediate reaction type, S.=susceptible.)

(*b*) F_2 segregation.

(i) Seedling tests.

F_2 segregation data on crosses pertaining to the five resistant varieties are presented in Tables 2–6 inclusive. Table 2 involves results with Landhafer.

From Table 2 at lower temperatures (below 75° F.) an F_2 segregation of 1 resistant : 2 intermediate : 1 susceptible plant was observed. This substantiated the F_1 behaviour in crosses involving Landhafer which indicated that resistance was partially dominant. At higher temperatures (above 85° F.) the class intermediate at lower temperatures apparently was susceptible and the results were therefore indicative of a 1 resistant : 3 susceptible ratio. On the other hand with race 226, in the cross Burke × Landhafer, the intermediate class numbered fewer than the resistant. These reactions were recorded two days earlier than normal and full development of pustules had not taken place. The fit to a 3 resistant : 1 susceptible F_2 ratio was good, confirming the operation of a single factor for seedling resistance. Tests on the second leaf of the same seedlings with race 203 gave the characteristic three class segregation.

The totals in crosses classified at lower temperatures and tested to a 1 resistant : 2 intermediate : 1 susceptible F_2 ratio were 214, 389 and 176 plants respectively, giving a P value of ·3—·2. Similarly at higher temperatures with the hypothetical ratio of 1 resistant : 3 susceptible the totals were 106 and 328 respectively, the P value being ·8—·7. These results indicated the operation of a single factor pair in the variety Landhafer conditioning resistance which was incompletely dominant.

The data relevant to Santa Fe are set out in Table 3.

TABLE 3.

F_2 Seedling Segregation in Crosses Involving the Resistant Variety Santa Fe with Susceptible Varieties tested with certain Crown Rust Races.

(Expected values in brackets.)

Cross.	Race Used.	F_2 Reaction Types. ;	1	2–, 3–*c*	4	Total.	Probability. 1R. : 2I. : 1S.	3R. : 1S.
Fulghum × Santa Fe ..	203	109 (104·5)	108 (209·0)	1	100 (104·5)	418	0·9 –0·8	0·7 –0·5
	226	90 (56·8)	79 (113·5)	1	57 (56·8)	227	<0·001	0·99–0·95
	237–4	45 (51·0)	103 (102·0)	3	53 (51·0)	204	0·7 –0·5	0·8 –0·7
	259	86 (62·5)	85 (125·0)	18	61 (62·5)	250	0·01–0·001	0·9 –0·8
	259*	26 (35·8)	23 (71·5)	58	36 (35·8)	143	0·2 –0·1	0·99–0·95
	Total ..	356	579		307 (310·5)	1242	—	0·9 –0·8 (χ^2=0·052)
Algerian × Santa Fe ..	203*	—	10 (7·8)	13 (15·5)	8 (7·8)	31	0·7 –0·5	0·95–0·9
	259*	—	29 (40·0)	84 (80·0)	47 (40·0)	160	0·2 –0·1	0·3 –0·2
	Total ..	—	39 (47·8)	97 (95·5)	55 (47·8)	191	0·3 –0·2 (χ^2=2·72)	0·3 –0·2 (χ^2=1·37)
Santa Fe × Bond.. ..	203	126 (89·5)	143 (179·0)	—	89 (89·5)	358	<0·001	0·99–0·95
Santa Fe × Ukraine ..	203	75 (66·3)	136 (132·5)	—	54 (66·3)	265	0·2 –0·1	0·1 –0·05
	226	177 (170·3)	—	—	50 (56·8)	227	—	0·5 –0·3

* Tests carried out at temperatures above 80° F.

(R.=resistant, I.=intermediate reaction type, S.=susceptible.)

The F_1 behaviour indicated partial dominance of resistance in the seedling stage, and good agreement between observed figures and the expected 1 : 2 : 1 ratio on this basis was found in six of the ten cases. In the other cases the number of resistant plants was in excess of that expected. However, a satisfactory fit to a 3 (resistant-intermediate) : 1 susceptible ratio was obtained, confirming the operation of a single factor pair. In the case of the cross Santa Fe × Ukraine tested against race 226, the ";" and "1" type of reactions were not separately classified, and the second leaf subsequently inoculated with race 203, where a non-significant deviation from a 1 : 2 : 1 ratio was observed. The results in the cross Fulghum × Santa Fe tested with race 237 were also obtained on the second leaves of plants in which the primary leaves were used in tests with race 203. Apart from the results secured on secondary leaf inoculations, there were 448 susceptible plants in a total population of 1,788 in all crosses involving Santa Fe; this number deviates by only one from the 447 expected on the single gene hypothesis.

A chi-square test also showed the data to be homogeneous, the value of 2·97 (6 d.f.) having a P value greater than ·8. The factor in Santa Fe was obviously more completely dominant in inheritance than the Landhafer factor since a higher proportion of plants with the fleck (";") reaction type were evident in the F_2 population.

Data involving Ukraine in its crosses with Algerian and Fulghum are set out in Table 4.

TABLE 4.

F_2 Seedling Segregation in Crosses Involving the Resistant Variety Ukraine in Crosses with the Susceptible Varieties Algerian and Burke, tested with Crown Rust Races 237 and 237–4.
(Expected values for 3R. : 1S. ratio in brackets.)

Cross.	Race Used.	F_2 Reaction Types. ; – 1=	2–	3–4	Total.	Probability.
Algerian × Ukraine ..	237	111	—	32 (35·8)	143	0·7 –0·5
	237–4	73	12	37 (30·5)	122	0·2 –0·1
	Total ..	196		69 (66·25)	265	0·7 –0·5
Burke × Ukraine	237	222	—	65 (71·8)	287	0·5 –0·3
	237–4	119	11	63 (48·25)	193	0·02–0·01
	Total ..	352		128 (120·0)	480	0·5 –0·3

These results indicated that a single almost completely dominant factor pair conditioned the resistance of Ukraine to both races 237 and 237–4. A good fit to a 3 resistant : 1 susceptible hypothetical F_2 ratio was obvious in all cases except for the cross Burke × Ukraine tested with race 237–4. The total of the two tests in this cross,

TABLE 5.

F_2 Seedling Segregation in Crosses Involving the Resistant Variety Trispernia in Crosses with the Susceptible Varieties Fulghum and Burke, tested with Crown Rust Races 226 and 259.
(Expected values for 1R. : 2I. : 1S. ratio in brackets.)

Cross.	Race Used.	F_2 Reaction Types. 1	1+, 2–	2+, 3c	3+c, 4	Total.	Probability.
Fulghum × Trispernia..	226*	46 (45·8)	85 (91·5)	—	52 (45·8)	183	0·7–0·5
	259†	24	63	59	78	225	<0·001
		(56·3)		(112·5)	(56·3)		
Burke × Trispernia ..	226*	41 (40·8)	74 (81·5)	—	48 (40·8)	163	0·5 –0·3
	259†	6	51	92	49	198	0·5 –0 3
		(49·5)		(99·0)	(49·5)		

* Tests carried out in the temperature-controlled room at 65±2° F.
† Tests carried out in the glasshouse at temperatures between 75° F. and 80° F.

however, gave a satisfactory fit to the expected ratio and it was considered that a single factor pair conditioned resistance to the two races. The P value for the total in crosses involving Ukraine was ·3–·2 on this hypothesis.

F_2 seedling data pertaining to Trispernia in its crosses with Fulghum and Burke in tests with races 226 and 259 are presented in Table 5.

In view of the partial dominance of resistance in the F_1 in Trispernia crosses the hypothesis of 1 resistant : 2 intermediate : 1 susceptible F_2 plant was adopted and the data obviously do not deviate significantly from it except in the cross Fulghum × Trispernia when tested with race 259. Tests with race 226 were carried out in a temperature-controlled room at 65 ± 2° F., whilst those with race 259 were conducted in a glasshouse at high temperatures between 75 and 80° F. At higher temperatures relatively fewer plants gave a "1" reaction type and two intermediate group classifications were necessary to characterize the segregating population adequately. One of these tended toward the resistant class whilst the other was more closely akin to the

TABLE 6.

F_2 Seedling Segregation in Crosses Involving the Resistant Variety Victoria with Susceptible Varieties tested with certain Crown Rust Races.

(Expected values for 28·1 per cent susceptible plants in brackets.)

Cross.	Race Used.	F_2 Reaction Types. 1n	2—n	3n	3–4	Total.	Probability.
Fulghum × Victoria ..	203	94	47	31	57 (64·3)	229	0·3–0·2
	226	19	8	1	9 (10·4)	37	0·7–0·5
	286	119	20	—	42 (50·8)	181	0·2–0·1
	Total ..		329		108 (125·6)	447	0·1–0·05
Algerian × Victoria ..	226	73	43	4	35 (43·6)	155	0·2–0·1
Burke × Victoria ..	226*	105	—	—	46 (42·4)	151	0·7–0·5
	286	143	39	—	55 (66·6)	237	0·1–0·05
	Total ..		287		101 (109·0)	388	0·5–0·3
Bond × Victoria ..	203†	18	55	—	24 (27·3)	97	0·5–0·3
Landhafer × Victoria	286	70	6	—	29 (29·5)	105	0·9–0·8

* Tests carried out in the temperature-controlled room at 65 ± 2° F.

† Tests carried out at temperatures 80–85° F.

moderately susceptible class. In particular the separation of the latter intermediate class from the susceptible class was somewhat difficult on a single plant basis. Although reactions were checked five days after the first reading and subsequently at transplanting, it will be obvious from the F_3 behaviour of classified F_2 plants to be presented later that errors in F_2 classification had occurred.

The F_2 segregation data in crosses of Victoria against races to which only Victoria was resistant are presented in Table 6.

These results taken alone may be explained on the basis of a single incompletely dominant gene, the grand total figures also agreeing with this simple hyothesis. However, since data from crosses involving Garry (deriving its crown rust resistance from Victoria) as published by Upadhyaya and Baker (1960) and F_3 segregation

behaviour to be later presented in this paper were best explained by invoking four genes in two linkage groups, $\frac{Vc_a\ Vc_b}{9{\cdot}6}$ (complementary in action) and $\frac{IVc_2\ Vc_2}{10}$, this more complex hypothesis was adopted. This would give a hypothetical F_2 seedling ratio of 71·9 resistant : 28·1 susceptible.

All F_2 tests fitted this hypothesis statistically. This included those involving Victoria in crosses with Bond and Landhafer, which latter varieties were susceptible only to specific races—203 and 286 respectively. At the highest temperature in which segregation was studied (80–85° F.), the number of plants with an intermediate ("2–n") reaction type was large; at the lowest temperature range (65 ± 2° F.) no such segregates were observed.

TABLE 7.

F_2 Adult Plant Segregation in Crosses Involving the Resistant Oat Varieties Landhafer, Ukraine, Trispernia and Victoria with Susceptible Varieties to Field Inoculum of Crown Rust.
(Expected values in brackets.)

Cross.	Adult Plant Reactions.						Expected Ratio.	Probability.
	I	R	MR	MS	S	Total.		
Fulghum × Landhafer* ..	136	57	39	—	18 (15·7)	250	15·1	0·5–0·3
Algerian × Landhafer* ..	77	6	23	—	6 (6·9)	111	„	0·5–0·3
Burke × Landhafer	35	67	16	3	23 (27·0)	144	13 : 3	0·9–0·8
Algerian × Ukraine	79	34	—	10	3 (13·8)	126	57 : 7	0·9–0·8
Burke × Trispernia	—	23 (23·0)	51 (46·0)	18 (23·0)		92	1 : 2 : 1	0·5–0·3
Fulghum × Victoria	31	81	34	14		160	94·1 : 5·9	0·2–0·1

* Data recorded in the summer of 1955, others recorded in winter 1954.
(I = immune, R = resistant, MR = moderately resistant, MS = moderately susceptible, S = susceptible.)

In all cases there was a slight deficiency in the number of observed susceptible plants on the hypothesis adopted. This amounted to a significant deficiency in the grand total ($\chi^2 = 5{\cdot}13$, P = ·05 – ·02). However, with closer linkage than 9·6 units between the complementary factors Vc_a and Vc_b, the deviation would have been non-significant. Such an amended linkage value would have fallen within that permissible from the standard error of ± 1·68 units.

(ii) Adult plant tests.

In Table 7 are given the F_2 adult plant reactions in crosses of Landhafer, Ukraine, Trispernia and Victoria with susceptible varieties, when grown at the Castle Hill Research Station in 1954 and 1955. The expected frequencies of the susceptible class on the hypothesis adopted are given in brackets. From certain of these data it was clear that more factors were involved in the resistance of adult plants than that of seedlings. In the varieties Landhafer two factors were operative and in Ukraine results were best explained by invoking three factor pairs. Landhafer in crosses with Algerian and Fulghum possessed two dominant factors. In the cross Burke × Landhafer a single factor hypothesis would have been barely non-significant at the 5 per cent probability level. However, the segregation approximated closely to a 13 : 3 ratio as indicated in Table 7. This suggested the action of a recessive factor in addition to one dominant. The operation and behaviour of the former factor were substantiated by F_3 seedling tests on the progenies of these plants reported below.

With Ukraine a two dominant factor hypothesis in F_2 (producing a 15 resistant : 1 susceptible ratio) gave a P value of ·1 – ·05 and hence is a somewhat dubious fit statistically. A more complex hypothesis invoking three factors (two being complementary in action) with a resultant 57 resistant : 7 susceptible F_2 ratio gave a P value of ·9 – ·8. Data to be presented in a subsequent paper involving a cross Santa Fe × Ukraine could not refute either hypothesis. However, data as yet unpublished from a study of an F_2 population of a cross involving Bond × Ukraine indicated complementary gene action in the adult plant stage due to factors derived from Ukraine and the three-factor hypothesis is accepted on this evidence.

In Trispernia a single factor pair conditioned adult plant resistance and inheritance was no more complex than in the seedling stage.

Segregation was explained satisfactorily in the cross Fulghum × Victoria on the basis of four factors $\overline{Vc_1}$, $\overline{Vc_3}$ and $\overline{IVc_2\ Vc_2}$ indicated previously to be operative in Garry.

Crosses involving Santa Fe were transplanted after recording and classifying seedling reactions and are appropriately reported in detail later. The correlated behaviour shown made it evident that the same factor in Santa Fe conditioning seedling resistance also conferred adult plant resistance, and no additional factors were operative at the latter stage.

TABLE 8.

F_3 Seedling Segregation in Crosses Involving the Resistant Oat Variety Landhafer with the Susceptible Varieties Burke and Victoria tested with Crown Rust Races 203 and 259 respectively.

(Expected values for 1 resistant : 2 segregating : 1 susceptible line in brackets.)

Cross.	Race Used.	Nature of F_2.	F_3 Behaviour. Res.	Seg.	Sus.	Number Tested.	F_2 Total.	Probability.
Burke × Landhafer ..	203	Random ..	13 (12·8)	26 (25·5)	12 (12·8)	51	—	0·99–0·95
		Seedling classd.	41·0 (37·0)	73·6 (74·0)	33·4 (37·0)	59	148	0·9 –0·8*
		Field classd.	23·5 (36·0)	85·5 (72·0)	35·0 (36·0)	59	144	0·3 –0·2*
Victoria × Landhafer	259	Random ..	31 (28·5)	54 (57·0)	29 (28·5)	114	—	0·9 –0·8

* Based on sample tested.

(Res. = resistant, Seg. = segregating, Sus. = susceptible.)

(*c*) F_3 segregation.

(i) Seedling tests.

F_3 studies were carried out with material which was either taken at random or phenotypically classified for crown rust resistance in the F_2. Since only representative samples were drawn from the classified F_2 material the observed frequencies of F_3 lines were calculated on the basis of the original F_2 numbers of each class of reaction for comparative purposes; however, chi-square values were calculated legitimately on the actual samples tested. The data are presented in Tables 8, 9, 10 and 11 for the different resistant parents involved.

In crosses of varieties other than Victoria a monogenic F_3 ratio of 1 resistant : 2 segregating : 1 susceptible line was expected; in crosses involving Victoria as the resistant parent the expected ratio in percentage was respectively 20·5 : 51·4 : 28·1. The 28·1 per cent susceptible lines included those segregating with a preponderance of susceptible plants.

From Table 8, except for a doubtful fit to a 1 : 2 : 1 ratio for field classified F_2 material of the cross Burke × Landhafer, all tests confirmed the operation of a single factor for resistance in Landhafer.

In crosses pertinent to Santa Fe set out in the data of Table 9, F_3 analyses were carried out in five tests involving three different crosses. Statistically satisfactory fits

to a 1 resistant : 2 segregating : 1 susceptible line were obtained in two cases only. In the other sets no consistent behaviour of any class was shown. In one case the susceptible class was close to that expected, in another the homozygous resistant group closely approximated its expected value, whilst in the third case all of the frequencies deviated widely from the calculated values. In the crosses of Santa Fe with Victoria

TABLE 9.

F_3 Seedling Reactions in Crosses Involving the Resistant Variety Santa Fe with Susceptible Varieties tested with certain Crown Rust Races.

(Expected values for 1 resistant : 2 segregating : 1 susceptible line in brackets.)

Cross.	Race(s) Used.	Nature of F_2.	F_3 Behaviour. Res.	Seg.	Sus.	Number Tested.	Total F_2.	Probability.
Fulghum × Santa Fe	203	Seedling classd.	82·3 (62·5)	106·7 (125·0)	61·0 (62·5)	117	150	0·2 –0·1*
Santa Fe × Ukraine	226 & 226–2	Seedling classd.	50·7 (54·5)	127·4 (109·0)	39·9 (54·5)	86	218	0·3 –0·2*
		Field classd.	17·7 (17·3)	35·0 (34·5)	16·3 (17·3)	60	69	0·99–0·95*
Santa Fe × Victoria	259	Seedling classd.	35·0 (56·0)	93·0 (112·0)	94·0 (56·0)	72	222	<0·01*
		Field classd.	27·7 (27·8)	58·9 (55·5)	24·4 (27·8)	49	111	0·9–0·8*

* Based on sample tested.

(Res. = resistant, Seg. = segregating, Sus. = susceptible.)

and Ukraine the progenies from F_2 field classification showed good agreement with theoretical values, whereas the same material from seedling tests in F_2 did not behave as expected. No satisfactory explanation can be advanced for these inconsistencies.

Seedling F_3 tests relevant to crosses involving Trispernia and Ukraine given in Table 10 indicate good agreement between observed and expected ratios, except for the behaviour of progenies from seedling classified F_2 plants in the cross Burke × Ukraine.

TABLE 10.

F_3 Seedling Reactions in Crosses Involving the Resistant Varieties Trispernia and Ukraine with Susceptible Varieties tested with certain Crown Rust Races.

(Expected values for 1 resistant : 2 segregating : 1 susceptible line in brackets.)

Cross (Race(s) Used).	Nature of F_2.	F_3 Behaviour. Res.	Seg.	Sus.	Number Tested.	F_2 Total.	Probability.
Fulghum × Trispernia (R203)	Random*	35 (40·8)	91 (81·5)	37 (40·8)	163	—	0·5– 0·3
Burke × Trispernia (R226) ..	Random*	47 (38·5)	70 (77·0)	37 (38·5)	154	—	0·3– 0·2
Algerian × Ukraine (R237 & R237–4)	Seedling classd.	25·0 (28·0)	51·0 (56·0)	36·0 (28·0)	70	112	0·5–0·3†
	Field classd.	27·9 (31·5)	68·4 (63·0)	29·6 (31·5)	61	126	0·8–0·7†
Burke × Ukraine (R237 & R237–4)	Random	31 (28·3)	62 (56·5)	20 (28·3)	113	—	0·3–0·2
	Seedling classd.	45·1 (48·3)	82·8 (96·5)	65·1 (48·3)	96	193	0·2–0·1†

* Seedlings classified in F_2 and all used for testing progeny behaviour.

† Based on sample tested.

(Res. = resistant, Seg. = segregating. Sus. = susceptible.)

Since random material of the same cross showed good agreement it can be assumed that only a single factor pair was operative in the resistance of Ukraine. This was substantiated when, in the cross Algerian × Ukraine, 1,421 plants in 71 segregating lines were classified for rust reaction and 374 found to be susceptible. The probability of chance deviation on a single factor hypothesis basis was greater than ·2.

In the case of crosses where Victoria was the resistant parent the fit to a ratio of 20·4 resistant : 51·4 segregating : 28·1 susceptible lines was good in F_3 progeny tests of its crosses with Fulghum, Burke and Santa Fe. In the cross Victoria × Landhafer, however, there was an excess of susceptible lines. The proportion of lines resistant to those segregating with a preponderance of resistant plants did not deviate significantly from the expected value, the P value being greater than ·3. The same F_3 lines were also tested with race 259 (Table 8) and a good fit to the expected monogenic segregation

TABLE 11.

F_3 Seedling Reactions in Cross Involving the Resistant Variety Victoria with Susceptible Varieties tested with certain Crown Rust Races.

(Expected values for 20·4 resistant : 51·4 segregating : 28·1 susceptible lines in brackets.)

Cross (Race Used).	Nature of F_2.	F_3 Behaviour. Res.	Seg. R : S	Seg. S : R	Sus.	Number Tested.	Total F_2.	Probability.
Fulghum × Victoria (R286)	Seedling classd.	55·3 (47·0)	120·2 (117·7)	13·3	40·3 (64·3)	152	229	0·5 –0·3*
Burke × Victoria (R203)	Random	29 (29·8)	81 (74·5)	2	33 (40·7)	145	—	0·7 –0·5
(R226)	Random	45 (37·0)	87 (92·4)	1	47 (50·6)	180	—	0·5 –0·3
(R286)	Seedling classd.	31·2 (31·0)	75·5 (77·7)	3·9	40·4 (42·3)	102	151	0·99–0·95
Victoria × Landhafer (R286)	Random	21 (23·3)	43 (58·6)	12	38 (32·1)	114	—	<0·001
Sante Fe × Victoria (R286)	Random	40 (35·7)	90 (89·4)	8	36 (48·9)	174	—	0·7 –0·5

* Based on sample tested.

(Res. = resistant, Seg. R : S = segregating with preponderance of resistant plants, Seg. S : R = segregating with preponderance of susceptible plants, Sus. = susceptible.)

of the Landhafer factor was obtained. This indicated the entirely random nature of the F_3 lines and the excess of susceptible lines in tests with race 286 is difficult to explain. The presence of segregating lines showing a preponderance of susceptible plants in each cross pointed to the operation of the factor Vc_2 with its linked inhibitor IVc_2.

(ii) Adult plant stage.

Of 117 F_3 lines in the cross Burke × Victoria 54 were resistant (R), 56 segregated with a preponderance of resistant plants (designated as R : S), three segregated with a preponderance of susceptible plants (designated as S : R), and four were fully susceptible (S). On combining the latter two classes and fitting to the expected ratio 43·8 R : 50·2 R:S : 5·9 S:R and S the probability of chance deviation was greater than ·8. This confirmed the operation of two major factors $\overline{Vc_1}$ and $\overline{Vc_3}$ for adult plant resistance together with the linked factors $\underline{IVc_2\ Vc_2}$ which were also operative in conditioning seedling resistance.

(*d*) Relationship of reactions to different races and between seedling and adult plant reactions.

(i) F_2 seedling (race 203) versus F_2 seedling (races 226 or 237–4).

In certain instances F_2 seedlings were tested with one race in the primary leaf stage and then, after recording reaction types and labelling appropriately, these leaves were clipped off and the secondary leaf inoculated with another race. Such tests were carried out in the crosses Burke × Landhafer, Fulghum × Santa Fe and Santa Fe × Ukraine, and the results are presented in Table 12.

Thirty-eight out of 90 plants of the fleck (";") reaction class to race 226 in the cross Burke × Landhafer gave a "1" reaction type to race 203, and similarly in the cross Santa Fe × Ukraine 69 seedlings classified as showing ";" or "2–" reaction types

TABLE 12.

Relationship between F_2 Reaction Types on Identical Seedlings in Crosses Involving the Resistant Varieties Landhafer and Santa Fe with Susceptible Varieties Tested with certain Combinations of Crown Rust Races.

F_2 Reaction Types to Race 203.	F_2 Reaction Types to Race 226.			F_2 Reaction Types to Race 237–4.				F_2 Reaction Types to Race 226.	
	(;)	(1)	(4)	(;)	(1)	(2–, 3–c)	(4)	(; and 2–)	(4)
	Burke × Landhafer			Fulghum × Santa Fe.				Santa Fe × Ukraine	
(;)	52	—	—	45	—	—	—	37	—
(1)	38	53	—	—	103	1	—	69	—
(2–, 3–c)	—	—	—	—	—	1	—	—	—
(4)	—	—	40	—	—	1	53	—	18

exhibited a "1" reaction type to these respective races. This indicated their heterozygous nature. In the former cross reactions on the primary leaves were taken two days before full expression, whilst in the latter, seedlings were not classified separately for ";" and "2–" reaction types to race 226 on the secondary leaves. In the cross Fulghum × Santa Fe, of three seedlings with a "2–, 3–c" reaction type to race 237–4, one was more resistant ("1" reaction type), one gave a comparable reaction and the third was susceptible, the remaining classes behaving identically. Reactions to paired races were thus found to be controlled by the same factors in the two varieties.

TABLE 13.

Relationship between Seedling Reaction Types to Crown Rust Race 259 and Adult Plant Reactions to Field Inoculum of Crown Rust in the Cross Fulghum × Trispernia.

Seedling Reaction Types to Race 259.	Adult Plant Reactions to Field Inoculum.		
	MR	Int	S
1	15	2	—
2–	7	41	—
2	1	35	—
3c	—	5	—
3+, 4	—	5	50

(MR = moderately resistant, Int = intermediate reaction, S = susceptible.)

(ii) F_2 seedling versus F_2 adult plant.

In certain cases it was possible to study correlated seedling and adult plant behaviour. In these instances seedling classified F_2 material was transplanted to the field at the Castle Hill Research Station and reactions recorded on adult plants. In the cross Fulghum × Santa Fe 124 seedlings were thus treated. The field reactions of the various classes conformed closely to the seedling reactions, all but one of the highly resistant seedlings being immune, and susceptible seedlings showed susceptibility

in the field. Seedling intermediate types were resistant to moderately resistant in the adult plant stage apart from three such seedlings which were moderately susceptible as adult plants. It was thus evident that the same factor conditioned both seedling and adult plant resistance.

In the cross Fulghum × Trispernia correlated seedling reaction types to race 259 and adult plant reactions to field inoculum are shown in Table 13.

Adult plants showing an intermediate reaction were not well defined, but showed early teleutospore formation in contrast to the susceptible group. It can be deduced from this table, however, that the factor conditioning adult plant resistance was identical with that for seedling resistance in Trispernia.

In the cross Burke × Victoria, seedlings after classification for reaction to race 226 were transplanted and adult plant reactions are shown in Table 14. The expected frequencies for the resistant and susceptible seedling classes were calculated on the assumption of the operation of the factors $\underline{Vc_a\ Vc_b\ Vc_1}$, $\underline{IVc_2\ Vc_2}$ and $\overline{Vc}_3$ (Upadhyaya and Baker, 1960).

The differences in correlated behaviour were not significant and the hypothesis that Victoria possessed two factors for adult plant resistance, one of which was linked with the two linked complementary factors conditioning only seedling resistance, was confirmed.

TABLE 14.

Relationship between Seedling Reaction Types to Crown Rust Race 226 and Adult Plant Reactions to Field Inoculum of Crown Rust in the Cross Burke × Victoria.

(Expected values in brackets—for expected ratio see text.)

Field Reactions.	Seedling Reaction Types to Race 226.*	
	1n	3–4
Immune	68	9
Resistant	1	17
Moderately resistant	2	8
Total	71 (70·75)	34 (33·35)
Moderately susceptible, susceptible	1 (1·25)	6 (6·7)
χ^2 and P value ..	0·051 (0·9–0·8)	0·088 (0·8–0·7)

* Seedling reactions corrected from F_3 behaviour in seedling stage.

In crosses involving Ukraine and Landhafer, classified seedlings were transplanted to the University plot in the metropolitan area where little crown rust developed, as is usual in this environment.

(iii) F_2 seedling versus F_3 seedling.

In Table 15 is given the behaviour in F_3 of seedlings raised from F_2 plants classified for reaction to certain races as seedlings.

From Table 15 it will be seen that there was almost perfect agreement between the F_2 reaction types and F_3 breeding behaviour in the crosses of Landhafer and Santa Fe on the hypothesis of a single factor in each case. With Ukraine only one line in the cross Burke × Ukraine from a resistant F_2 plant gave a homozygous susceptible F_3 line and this was probably an error in F_2 classification or transplanting. In crosses involving Trispernia and Victoria the agreement was not entirely satisfactory. This may have been due to difficulties in F_2 classification which are based on a single plant and to variation arising from environmental effects. Reading of reactions in the crosses except at lower temperatures was difficult, especially in relation to the intermediate type of reactions. Despite rechecking F_2 reactions in the cross Burke × Trispernia three times at one to two days intervals certain plants from the "2–" and "2+" reaction classes gave

susceptible F_3 lines. Light intensity was also low in the glasshouse during the period of development of the rust on F_2 plants. Some effect of environment on the resultant reaction type was clear from the fact that in the cross Burke × Victoria there was much closer agreement than in the cross Fulghum × Victoria. The former F_2 was

TABLE 15.

Relationship between F_3 Seedling Behaviour of F_2 Plants Classified for Seedling Reaction Types to one Crown Rust Race, tested with a second Race, or Mixture of Races in Crosses Involving the Resistant Varieties Landhafer, Santa Fe, Ukraine, Trispernia and Victoria with Susceptible Varieties.

Cross.	F_2 Reaction Types.	F_3 Behaviour. Res.	Seg.	Sus.
	Race 237.		Race 203.	
Burke × Landhafer	;	17	—	—
	1	1	23	—
	2−	—	4	—
	4	—	—	14
	Race 259.		Race 203.	
Fulghum × Santa Fe ..	;	45	2	—
	1	—	49	—
	2−, 3c	—	10	—
	4	—	—	11
	Race 237–4.		Races 237 and 237–4.	
Algerian × Ukraine	; − 1=	14	23	—
	1	—	5	—
	4	—	—	28
Burke × Ukraine	; − 1=	21	35	1
	1	1	8	—
	4	—	—	30
	Race 259.		Race 203.	
Fulghum × Trispernia ..	1	14	3	—
	2−	17	28	4
	2+ − 3−c	3	35	4
	3+c − 4	1	25	29
	Race 259.		Race 226.	
Burke × Trispernia	1	6	—	—
	2−	33	4	1
	2+ − 3−c	8	62	5
	3+c − 4	—	4	31
	Race 226.		Race 286.	
Fulghum × Victoria	1n	21	34	2
	2−n	8	19	3
	3n	5	17	3
	3 − 4	—	9	31
Burke × Victoria	1n	21	44	1
	3 − 4	—	3	33

tested in the light and temperature controlled room, whereas the latter was studied under glasshouse conditions.

That these discrepancies were due to difficulties associated with F_2 classification was evident from studies where F_3 lines were tested against the same race as the F_2

population. Information on this point is contained in Table 17. The almost perfect correlation shown when identical F_3 lines in crosses involving Trispernia and Victoria were tested with two different races indicates that greater emphasis must be placed on the validity of F_3 data. This is perhaps obvious since F_3 lines permit behaviour to be assessed on several plants rather than one in F_2 classification.

(iv) F_2 adult plant versus F_3 seedling.

In the crosses Burke × Landhafer and Algerian × Ukraine the progenies of plants classified in the field were tested for their behaviour to different races in the seedling stage and the results are presented in Table 16. Only a random sample of each F_2 phenotype was tested in most cases and the figures were then adjusted to the total number of F_2 plants for comparative purposes.

TABLE 16.

Relationship between F_2 Adult Plant Behaviour to Field Inoculum and F_3 Seedling Behaviour to certain Crown Rust Races in Crosses involving the Resistant Varieties Landhafer and Ukraine with Susceptible Varieties.
(Expected values in brackets.)

Cross.	Race.	Field Reactions.	Seedling Behaviour. Res.	Seg.	Sus.	Number Tested.	Total F_2.
Burke × Landhafer ..	203	I	5	10	—	15	35
		R	3	13	1	17	67
		MR	—	11	5	16	16
Total (calculated) ..	..	.. ..	23·5	85·5	9·0 (9·1)		118
		MS–S	—	—	11	11	26
Algerian × Ukraine ..	237 & 237–4	I	11	19	4	34	79
		R–MR	—	9	8	17	34
Total (calculated) ..	..	.. ..	25·6 (28·3)	62·1 (56·5)	25·3 (28·3)	—	113
		MS–S	2 (2·3)	6 (4·5)	1 (2·3)	9	13

(I=immune, R and Res=resistant, MR=moderately resistant, MS=moderately susceptible, S and Sus=susceptible, Seg=segregating.)

In both crosses some resistant F_2 adult plants bred true for susceptibility in F_3. In the cross Burke × Landhafer one out of 13 lines showed such behaviour indicating that one of the genes conditioning adult plant resistance was operative in the seedling stage, whilst the other, almost entirely recessive in inheritance, was ineffective for seedling resistance. On this hypothesis 9·1 such lines would have been expected whilst 9 was the number calculated for the whole F_2 from the samples tested. No statistical chi-square tests were permissible on the data from the manner in which it was computed.

In the cross Algerian × Ukraine, however, in both the resistant and susceptible F_2 segregates a good fit to a 1 resistant : 2 segregating : 1 susceptible ratio was observed in F_3, indicating that the factor for seedling resistance was independent of the factors for adult plant resistance.

(v) F_3 seedling (races 203 or 237) versus F_3 seedling (race 286 or mixture of races 226, 237, 237–4 and 259).

In certain crosses F_3 lines tested to one race were reinoculated on the secondary leaves with a second race or a mixture of other races in a manner similar to corresponding F_2 tests. In other cases a further sample of seed drawn from the same F_3 line was inoculated at the primary leaf stage with a second race or mixture of races. The relationship of such reactions to different races is presented in Table 17.

From this table it is evident that, apart from minor discrepancies indicated with an asterisk, the reactions of the F_3 lines were identical. Certain lines classified as

resistant to one race were segregating to the second; with a population of approximately twenty plants in each line used in these tests, such resistant lines to one race may have been wrongly classified due to sampling errors in which susceptible plants were absent. Due to chance one such line would occur in approximately 100 segregating lines. The two plants in the Victoria crosses which each gave a S : R progeny to one race and a susceptible progeny to the other may be explained by similar errors. With these reservations and possible other errors in classification, it was concluded that the same factors conditioned resistance to the different races with which they were tested.

TABLE 17.

Relationship between Seedling Behaviour of F_3 Lines of Crosses involving the Resistant Varieties Landhafer, Santa Fe, Trispernia and Victoria with Susceptible Varieties tested with Different Crown Rust Races or Mixture of Races.

Cross.	F_3 Behaviour to Race.	F_3 Behaviour to Race/Races.		
		Res.	Seg.	Sus.
	203.	Races 226, 237, 237–4, 259.		
Burke × Landhafer ..	Res.	39	—	—
	Seg.	1*	86	—
	Sus.	—	—	43
Fulghum × Santa Fe ..	Res.	45	—	—
	Seg.	—	61	—
	Sus.	—	—	11
Fulghum × Trispernia	Res.	33	2*	—
	Seg.	—	92	—
	Sus.	—	—	37
	237.	286.		
		R	R : S	S : R	S
Fulghum × Victoria ..	Res.	28	—	—	—
	Seg. R : S	—	63	1*	—
	Seg. S : R	—	1*	6	1
	Sus.	—	—	1	27
	203.	286.			
Burke × Victoria ..	Res.	25	2*	—	—
	Seg. R : S	3*	78	—	2*
	Seg. S : R	—	—	2	—
	Sus.	—	2*	—	27

* Behaviour not correlated in two tests.
(Res. = resistant, Seg. = segregating, Sus. = susceptible.)

In the crosses of Ukraine with Algerian and Burke a mixture of two races was used. As previously, no mixed reaction types were noted on leaves in any line indicating the operation of the same factor against the two races.

(vi) F_3 seedling (race 226) versus F_3 adult plant (field inoculum).

F_3 tests were conducted in the cross Burke × Victoria on seedlings and a further sample of each line was then sown in the field to classify for adult plant reactions. The relationship between the behaviour of F_3 lines in such tests is set out in Table 18. The expected frequencies were calculated on the assumption of factors previously indicated and on the basis of a table of expectancies given by Upadhyaya and Baker (1960).

From Table 18 the probabilities of chance deviation were in this case less than between 50 and 30 per cent, confirming the operation of the factors $\underline{Vc_a}$ $\underline{Vc_b}$ $\underline{V\bar{c}_1}$, $\underline{IVc_2}$ $\underline{Vc_2}$ and $\underline{V\bar{c}_3}$ with the appropriate and previously indicated linkage values. The chi-square

value for association or interaction, based on 2 d.f., was calculated by grouping the expected classes 5 and 1 and also 38 and 0 as is conventionally done to make all expected classes greater than 5.

Sowings of F_3 lines in other crosses were made in an out-of-season summer sowing at the Castle Hill Research Station and crown rust did not develop sufficiently for intelligent notes to be taken. It was thus not possible in the cross Burke × Landhafer to confirm the homozygosity for adult plant resistance of certain adult plant resistant F_3 plants giving susceptible F_3 lines in the seedling stage.

TABLE 18.

Relationship between Seedling Behaviour to Crown Rust Race 226 and Adult Plant Behaviour to Field Inoculum of Crown Rust of F_3 lines of the Cross Burke × Victoria.

Seedling Behaviour to Race 226.	Behaviour in the Adult Stage to Field Inoculum.			
	Res.	Seg. R : S.	Sus. (incl. Seg. S : R).	Total.
Res.	23	5[1]	1[1]	29
	(20·5)	(3·4)	(0·1)	(24·0)
Seg. R : S	21	38[1]	0[1]	59
	(21·8)	(36·8)	(1·4)	(60·1)
Sus. (incl. Seg. S : R)	10	13	6	29
	(8·9)	(18·5)	(5·5)	(32·9)
Total ..	54	56	7	117
	(51·3)	(58·8)	(6·9)	

χ^2 for seedling reactions 1·72 P=0·5–0·3.
χ^2 ,, adult plant reactions 0·28 P=0·9–0·8.
χ^2 ,, association (2 d.f.) 1·94 P=0·5–0·3.
(Res.=resistant, Seg. R : S=segregating with preponderance of resistant plants, Sus.=susceptible, Seg. S : R=segregating with preponderance of susceptible plants.)

[1]Expected values grouped for χ^2 analysis.

(vii) Relationship between factors for stem rust resistance in the variety Burke and factors for crown rust resistance in the seedling stage in the varieties Landhafer, Trispernia and Victoria and adult plant resistance in the variety Victoria.

The crosses of Burke with the varieties mentioned above were also tested for reactions to races 2 and 12 of stem rust to which Burke is resistant. Studies on the inheritance of resistance in relation to stem rust in Burke have been published by Upadhyaya and Baker (1962). The reactions to the two rusts are set out in Table 19. From these data it is clear that the reactions were independent of each other.

TABLE 19.

Relationship of Reactions to Stem and Crown Rusts in Crosses of the Stem Rust Resistant Variety Burke with the Crown Rust Resistant Varieties Landhafer, Trispernia and Burke.

Cross.	Generation Studied		Factors.		N.	D.F.	Chi-square.	P.
	Stem Rust.	Crown Rust.	S.R.	C.R.				
Burke × Landhafer	F_2	F_3	Rd_1	Ld_1	243	2	1·35	0·7–0·5
Burke × Trispernia	F_3	F_3	,,	Sf_1''*	148	4	3·30	0·7–0·5
Burke × Victoria	F_3	F_3	,,	Vc_a, Vc_b, Vc_2	190	4	4·53	0·5–0·3
	F_3	F_3 (field)	,,	$V\bar{c}_1$, $V\bar{c}_3$, Vc_2	99	4	5·16	0·2–0·1
	F_3	F_3 (field)	,,	Vc_3	20	4	2·72	0·7–0·5

* Designated Sf_1'' as allelic with gene in Santa Fe (unpublished data).
(S.R.=stem rust, C.R.=crown rust.)

Discussion and Conclusions.

From these studies it has been established that resistance to certain Australian races of crown rust, included among which are those most commonly found in the field, is simply inherited in the seedling stage in the varieties Landhafer, Santa Fe and Trispernia, being dependent on a single factor pair in each case. Each factor pair was found to be incompletely dominant at normal glasshouse temperatures (75° F.) and above. The operation of two linked factors in the variety Santa Fe reported by various investigators, including Simons (1953) and Finkner, Atkins and Murphy (1955), was not revealed in the present studies. Similarly, there was no evidence of the complex mode of inheritance to local races shown to be operative in the variety Trispernia in certain cases to North American race 57 by Finkner (1954).

The factors in each of these varieties for seedling resistance was also operative in the mature plant stage. In addition an adult plant factor pair in the variety Landhafer, not previously reported by workers in other countries, conditioned resistance against Australian races.

In the case of the variety Mutica Ukraine a single factor pair, also incompletely dominant, was operative in the seedling stage, but was ineffective in conferring adult plant resistance. Resistance at the latter stage was conferred apparently by three dominant factor pairs, two operating in complementary fashion. Although a satisfactory fit to a simpler hypothesis based solely on dominant duplicate factors was also obtained, evidence for complementary gene action was secured from as yet unpublished data from the cross Bond × Ukraine when an appropriate category of segregates was tested at an advanced stage of growth. Evidence for complementary factor interaction at the adult plant stage in this variety was also obtained by Weetman (1942). To confirm the hypothesis currently adopted, however, it is clear that more critical analyses based on larger segregating populations carried through more generations must be undertaken.

The factors for seedling resistance in the varieties Landhafer and Trispernia were independent of the stem rust resistant factor (Rd_1) to races 2 and 12 in Burke. Investigations to be presented in a subsequent paper will show that the genes for seedling resistance in the varieties Santa Fe, Ukraine and Trispernia form an allelic series and hence it can be assumed that these three factor pairs are all independent of Rd_1.

The current investigations confirm the presence of the six factor pairs conditioning seedling and/or adult plant resistance in the variety Victoria. This hypothesis was established previously from studies involving Garry which derives its crown rust resistance from the parent Victoria. Similarly the current investigations confirm the independence of the factors for crown rust resistance in Victoria and the stem rust gene Rd_1.

A catalogue of the varieties with regard to their crown rust genotypes will be postponed and presented in a subsequent paper where analyses of data obtained by studying intercrosses between them will be set out.

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ALAN NEVILLE COLEFAX, 1908–1961.

(*Memorial Series No. 20.*)

(With portrait, Plate iv.)

With the tragic death on December 7th, 1961, of Alan Neville Colefax, Australian Zoology lost one of its foremost representatives, and the University of Sydney one of its most accomplished and popular lecturers.

Alan Colefax was born at Moruya, New South Wales, in July, 1908, one of a large family of boys and girls, and the sense of unity and affection engendered by this wide family circle remained with him throughout his life.

He went to the Moruya Public School until he was twelve years of age, when he gained a bursary to Sydney High School. On the small country boy, this change to city life and the sudden transfer from the shelter of his home and primary school to higher learning and discipline, made deep impressions. At Sydney High School he developed a keen interest in Science and in Languages, and in his Leaving year he won a scholarship to the University of Sydney after having gained one of the top places in the State in German.

He entered the Faculty of Science at the University in 1926 with the intention of making his favourite subject, Chemistry, his chosen field. By chance, however, one of his first year subjects was Zoology, a science completely new to him, but one which excited the country boy and opened his eyes to many things he realized he had seen but never appreciated or understood. As a result, although he retained a very keen interest in Chemistry throughout his life, in his senior years he chose Zoology as his major subject, and in 1930 graduated with First Class Honours in Science and the University Medal in Zoology. This achievement was all the more noteworthy in that his final examinations were all taken in hospital where he was recovering from a bad accident after crashing from his motor-cycle.

After graduation he was granted a C.S.I.R.O. Research Studentship in Zoology at the University. In those early post-depression years Science posts were not easy to find, but fortunately a junior lectureship in the Department of Zoology became vacant and in 1931 Alan was appointed to the staff as Lecturer and Demonstrator by the then head of the department, the late Professor W. J. Dakin.

The impact of Professor Dakin's personality and scholarship, his lecturing ability and his enthusiasm, made a deep and lasting impression on the young lecturer and moulded his many talents into something Alan Colefax was to remain for the rest of his life—a true zoologist who, in spite of necessary specialization in research and pressure of teaching, never lost touch with his science as an entity.

Faced with new responsibilities he accepted more; few knew of his struggle on a meagre salary to provide for and educate a younger brother whose death almost at the completion of his education was a tragic loss to Alan.

Right from the beginning of his career as a lecturer he was vitally interested in his students, in finding the best approach to them and to their problems. At all times he tried to establish a close personal contact with them, freely inviting later discussion of any problems occurring during his lectures. His brilliant and delicate technique with his dissecting instruments was a by-word with his colleagues, and the superb artistry with which he conveyed his dissections to the blackboard became a tradition with the generations of students who passed through his classes. His mechanical bent and his skill with his hands also enabled him to invent and make many gadgets facilitating dissection, drawing and display or general preparation of zoological material.

But foremost always in his mind was the desire to make his lectures stimulating, to interest his students and always to keep them up to date with modern trends. To this end he gradually accumulated an extensive library and his reading covered a wide range of subjects, greatly helped by his knowledge of the French and German languages. His well-known skill as a raconteur, his delightful sense of humour and extraordinarily retentive memory enlivened many an otherwise dull lecture topic and enabled him always to get enthusiastic response from his audiences.

Alan's earliest research interests were in Marine Biology, and part of his first year as a research scholar in 1930 was spent at sea on an investigation of the natural history of the Tiger Flathead, at that time the chief food fish of New South Wales. It speaks volumes for his courage and determination that he continued this particular investigation, and later published two papers on his results, for he was a victim of sea-sickness in its worst form, a condition certainly not helped by the ever-pervading smell of dead fish and the cramped living space on the small trawlers in which he sailed.

He also joined in the Plankton programme under Professor Dakin, his chemical knowledge being of special value in the analyses of the various seawater components. Alan's chief interest, however, was the fascinating and very important group of planktonic organisms, the Copepoda. A number of papers on various aspects of the Plankton were published as a result of this team work and the culmination was a large monograph on the Plankton of New South Wales waters which, even today, is still the only standard reference available for the Pacific Ocean and in demand from scientists of many nations.

But his ever-active mind roved over a far wider variety of interests—from lino- and wood-cuts, and the design of stage settings and the colour printing of fabrics, to motor-cycles and speed car races, and the turning out of exquisite precision pieces on his workshop lathe. He taught himself an appreciation of classical music and slowly built up a collection of records which, played on his self-made gramophone, were his constant delight. But it was perhaps with his hand-made fishing rod in his hand along the seashore or the river bank that Alan found his happiest relaxation.

During the years of World War II, with a reduced departmental staff, Alan's teaching load was very considerably added to, and there were many occasions when his special qualifications were enlisted in other fields, and in giving courses to army and civilian groups. He was responsible for the organization of classes for instruction in the voluntary making of camouflage nets for the Services, an art he had learnt among the trawler fishermen, and with needles he turned out in his own workshop. Later he published a small booklet on the making of these nets.

The large classes and small staff of the post-war years of the 1940s compelled Alan to confine most of his attention to teaching, but when he was able to find time he gradually turned his attention to new fields of research and became particularly interested in the embryology and life history of the frogs. Then in 1957 he was able to achieve one of his life-long dreams—a visit overseas, where he worked in Professor Abercrombie's laboratories at University College, London. Whilst there he studied the latest developments in experimental embryology and once again his skill was quickly recognized, for, when he left, a complete copy of his notes and techniques was taken for incorporation into the routine procedures of the laboratory.

His reputation as a lecturer meant that he was always in great demand and his kindly nature never allowed him to say "no" to any appeal. He gave University Extension Board lectures in many parts of the State.

But it was possibly by his broadcasts in the A.B.C.'s Children's Hour that he became so well known and loved by thousands of Australians, both young and old, as "Tom, the Naturalist". For some fourteen years he gave weekly talks on some aspect of Science, and there must be very many students who can thank his inspired enthusiasm for their introduction into a world of vast interest.

In addition there was his long association with the New South Wales Department of Education. From the year 1936 until 1943 he acted either as Assessor or Assistant Examiner with Professors Dakin and Briggs for the Leaving Certificate Zoology

Examination, and from 1944 till 1961 he was Chief Examiner. And in the Leaving Certificate Biology he had been an Assistant Examiner from the inception of that subject until the time of his death. Many teachers will remember with gratitude his ever-ready response to their appeal for advice. For some years also he was a member of the Council of Frensham School.

Alan Colefax was elected a member of the Linnean Society of New South Wales in 1931, was President in 1951, and was a member of Council from 1943 until the time of his death.

But regardless of all other commitments, even through the last and most difficult year of his life when he was never free from suffering, and completely regardless of his ill-health, Alan always found time to help his students, his colleagues and his friends. Nothing was ever too much trouble for this gentle, kindly man. To enter his room was to be met with a wide smile and the "what can I do for you . . ." which was ever his characteristic greeting.

The loss sustained by the University, the community and Alan's friends and colleagues, who knew and loved him well, is small, however, compared to the gap left in his own family circle. To his wife, Una, and his three young children, Hilary, Catherine and Jamie, we who mourn him offer our deepest sympathy, loyalty and affection.

I.B.

List of Publications, by A. N. Colefax.

1934. A Preliminary Investigation of the Natural History of the Tiger Flathead (*Neoplatycephalus macrodon*) on the South-eastern Australian Coast. I. Distribution and Supply; Length Statistics. Proc. Linn. Soc. N.S.W., lix, 1-2: 71-91.

1938. A Preliminary Investigation of the Natural History of the Tiger Flathead (*Neoplatycephalus macrodon*) on the South-eastern Australian Coast. II. Feeding Habits: Breeding Habits. Proc. Linn. Soc. N.S.W., lxiii, 1-2: 55-64.

1940. An Australian Species of *Acetes* (Crustacea, Macrura, Sergestidae), with remarks on the Distribution and Literature of the Genus. *Rec. Aust. Mus.*, xx, 5: 341-353.

1952. Variations on a Theme. Presidential Address. Proc. Linn. Soc. N.S.W., lxxvii, 1-2: viii-xlvi.

1955. New Information on the Corroboree Frog (*Pseudophryne corroboree* Moore). Proc. Linn. Soc. N.S.W., lxxx, 3: 258-266.

A. N. Colefax and I. M. Thomas:

1940, 1941. The Making of Nets. 20 pp. *Govt. Printer, Sydney.*

W. J. Dakin and A. N. Colefax:

1933. The Marine Plankton of the Coastal Waters of New South Wales. I. The Chief Planktonic Forms and their Seasonal Distribution. Proc. Linn. Soc. N.S.W., lviii, 3-4: 186-222.

1934. The Eggs and Early Larval Stages of the Australian Pilchard. *Rec. Aust. Mus.*, xix, 2: 136-140.

1935. Observations on the Seasonal Changes in Temperature, Salinity, Phosphates, and Nitrate Nitrogen and Oxygen of the Ocean Waters on the Continental Shelf off New South Wales, and the relationship to Plankton Production. Proc. Linn. Soc. N.S.W., lx, 5-6: 303-314.

1936. *Ctilopsis*, a Rare Pelagic Nudibranch of the Family Phyllirhoidae (Bergh). *Proc. Zool. Soc. Lond.*, 1936, 455-460.

1937. A Pelagic Nudibranch of the Family Phyllirhoidae from the Waters of New South Wales: A Note on the Subgenera *Ctilopsis* and *Cephalopyge*. *Ann. Mag. Nat. Hist.*, 10, xix, (Feb.): 266-271.

1940. The Plankton of the Australian Coastal Waters off New South Wales. *Univ. of Sydney, Dept. of Zoology*, Monograph I: 1-215.

G. P. Whitley and A. N. Colefax:

1938. Fishes from Nauru, Gilbert Islands, Oceania. Proc. Linn. Soc. N.S.W., lxiii, 3-4: 282-304.

REVISION OF THE THYNNIDAE. PART V.

A Contribution towards a Knowledge of the Thynnidae of the Philippines, Indonesia, New Guinea, The Solomons, New Caledonia and Lord Howe Island.

By K. E. W. Salter, Department of Zoology, the University of Sydney.

(Plates v-viii; thirty-four Text-figures.)

[Read 25th July, 1962.]

Synopsis.

From the islands 37 species are listed and a comparison made of the taxonomic characters of 31 authentically identified specimens. The phylogenetic relationships are indicated between continental and island species. Their taxonomy is traced and notes are made on individual variation. The retention is briefiy discussed of the taxonomic category Family Thynnidae, Shuckard, 1841, rather than Subfamily Thynninae, Pate, 1947. *Thynnus placidus* Smith, 1864, and *Zaspilothynnus cheesmanae* Turner, 1940, are conspecific and are combined as *Zaspilothynnus placidus* (Smith). *Zaspilothynnus lasius* Montet, 1922, is synonymous witn *Zaspilothynnus campanularis* (Smith), 1868. *Spilothynnus thalluse* Montet, 1922, is not a New Caledonian species. *Phymatothynnus zenis* Montet, 1922, and *Eucyrtothynnus ichneumoneus* (Klug), 1842, South Brazil, are conspecific.

Species of Thynnidae Described from this Region.

[1] Species omitted owing to lack of material.
[2] Species incorrectly recorded from these territories.
[3] Australian species.
[4] Whereabouts of Smith's type is unknown.
[5] *Thynnus placidus* and *Zaspilothynnus cheesmanae* Turner, 1940, are synonymous.
[6] Recorded from Monte Bello Island near to Australian mainland.

Introduction.

The relationship between the fauna occurring on a continent and the fauna which is found upon its adjacent islands has captured our interest ever since Darwin's *Origin of Species* in 1859 and his fascinating account of the fauna of the Galapagos Islands. From the continent of Australia approximately 456 species are recognized, while in this vast assemblage of islands extending northwards to the Philippines there are at least thirty-seven species. Of these tropical species it is interesting to note that the first

specimens brought home to England were collected by Alfred Russell Wallace and a hundred years have passed since the publication of the first description. A short account of this early work is given here and the literature is listed in the attached bibliography. Since the original publications, little has ever been contributed on these insects.

Of the Thynnidae ranging through these numerous islands, there is much that remains to be discovered. As a prerequisite, a series of specimens of authentically paired males and females from many localities is an essential, and at present these extensive collections of specimens are unavailable. Therefore, it is not possible to complete all aspects of this investigation at this stage.

There are thirty-seven species recorded from this region and reference has been made in the present paper to only thirty-one of these, as six species have had to be omitted. A series of reasonable size has been available in only four species. In twenty-three species, small samples varying from one to eight specimens have been studied. For the remaining four species use has been made of photomicrographs or original descriptions. Many of the specimens on which this contribution is based are either holotypes, cotypes or homotypes. Some of these species are separated by characters which are not clearly defined and the original descriptions fail to differentiate between them. Certain species are recognized by characters which are well within the scope of potential, individual, variation in Thynnidae. It is difficult, therefore, to be certain as to the validity of such species, and it is quite obvious that unless authentically identified material is available, the correct determination of such species would be an impossibility. Unfortunately, type material is not always readily accessible for identification purposes. Furthermore, individual variation may be so excessive in some species that their representation by a single specimen only would be inadequate. Without a series, information is unavailable on the constancy of the taxonomic characters selected, and the presentation of an infallible definition in such cases is most difficult. Sufficient evidence on the scope of individual variation is necessary, prior to the sinking of such variables as synonyms.

An attempt has been made in the present paper to establish the identity of many of these little-known species and to record all relevant information from this valuable material. In the future, when large samples of the thynnid population can be obtained, it is hoped to make a further investigation regarding the authenticity of doubtful species. Its second objective is to determine, where possible, the actual mainland species from which the island species could have been evolved; and to illustrate some of the morphological differences which have arisen between geographically isolated species living under varying ecological environments.

History.

The thynnids in the Wallace collection from these tropical islands were described by Frederic Smith between 1859 and 1879. Thus the oldest known to science are: *T. tenuicornis* (1859), *erraticus* (1861), *atratus* and *vagans* (1862), *T. lugubris*, *insularis* ♀, *placidus*, *pullatus*, and *comatus* (1864), *T. atratus* ♀, *laevissimus* ♀, *abductor*, and *fragilis* (1865), and finally, *candidus* (1879). Ritsema (1876) described *flavopicta* and the turn of the century was marked by Sharp's illustrated presentation of *serriger* ♀. Meanwhile, Oliff (1889) had made an expedition to Lord Howe Island, and discovered the presence there of *Diamma bicolor* Westwood, 1835, and also *Zaspilothynnus campanularis* (Smith), 1868.

Cameron (1906) described *albopilosellus* and (1911) *Tachynomyia atrata*. Rohwer (1925) gave us *bakeri* and *cyaneiventris*. Cockerell (1929) contributed *superstes*, and lastly, Williams (1945) added *neocaledonica*. All other species of the Thynnidae have been described by Rowland E. Turner; in thirty-three years (1907–1940) he erected seventeen new species from the various collections he examined from these islands and in addition described the opposite sexes of five other species. Turner's species, and all literature ever published on the Thynnidae from this region, are listed in the bibliography. Much in the older works is very brief, and many distinguishing characters necessary for determination were entirely omitted.

The Retention of the Category Family Thynnidae.

It is obvious that a close phylogenetic relationship exists between the Thynnids, Bradynobaenids, Myrmosids, Anthoboscids, Tiphiids, Myzinids, Methochids and Brachycistidids. It is equally apparent that separating each group are taxonomic characters of a considerable order of magnitude. What then is the most satisfactory application of the taxonomic hierarchy to express a basic kindred affinity and yet to maintain the co-existence of taxonomic individuality? Should accentuation be placed upon mutual resemblance or upon differentiation? In the selection of the most suitable taxonomic category, it is important to recognize that it would be very misleading to place undue emphasis upon the relationships existing between the various units of the Tiphioid Complex.

In the division of a family into its appropriate subfamilies, the systematic characters used are relatively trivial, and a multitude of examples could be assembled to verify this statement. Therefore, as a direct result of customary usage of the word in the Insecta, the accepted meaning implied by this category is that the distinctions involved are of *little consequence*. Considering its relative importance, there is hardly scope for much extension beyond the family level in the study of general entomology. The current tendency today is to increase, rather than decrease, the number of higher taxonomic units amongst insects (Kevan, 1961).

Contrasted with the trifling nature of criteria used in separating subfamilies, the units in the Tiphioid Complex differ one from another by characters of a magnitude which is relatively much greater than is usual at the subfamily level. Morphologically, the units in this Tiphioid Complex are perfectly distinct, and the demotion of such a large group as the Thynnids to subfamily rank (Pate, 1947) fails to stress the importance of the various contrasted anatomical features characterizing such groups. Furthermore, this demotion to subfamily status would definitely express a very much stronger phylogenetic relationship than exists in actual reality.

The taxonomic category *family* is a basic unit in modern classification and, in an attempt to be consistent, it has been defined as: "A systematic category including a genus or a group of genera of common phylogenetic origin which is separated from other groups by a decided gap and it is suggested that the size of the gap be in inverse ratio to the size of the family." (Mayr, 1953.) Morphologically, a decided gap exists in both sexes, involving anatomical features of some consequence. The fourth largest family in Tillyard's list of 64 families of Australian Hymenoptera is the Thynnidae. Therefore, the family category is applicable according to Mayr's definition.

The antiquity and geographical distribution of these wasps should be taken into account. The Hymenoptera arose in the Jurassic Period, and from the Miocene shales of Florissant, Colorado, four fossil species were described by Cockerell (1906–1927) as *Geotiphia*. This genus was referred by Turner (1912) to *Anthobosca*. Primitive features are in evidence in the wing-venation of the Thynnidae. The geographical distribution of these wasps is of particular interest. The Thynnidae have survived in the geographically isolated territories of Australasia and South America. The Bradynobaenidae is a small group of peculiar Chilean forms; the Myrmosidae are Holarctic; Anthoboscidae are Australasian, Ethiopian, South American, and they are also found in California. The Tiphiidae, Myzinidae and Methochidae are represented in all major zoogeographic regions with the exception of the Australian realm. The Brachycistididae are restricted to western U.S.A. and more especially to desert areas (Pate, 1947).

To submerge this large group into a subfamily of Tiphiidae exaggerates their relationship to a degree which is scarcely justifiable. Conversely, to establish their obvious individuality by the retention of the category *Family* places appropriate emphasis on their various dissimilarities, and is an expression which has greater consequence. The thynnids are one of eight discrete units, and a classification which maintains this distinctness at the family level is of significance. Other means are available to demonstrate their kindred affinities.

Individual Variation.

"It is estimated that more than half of all synonyms owe their origin to an underestimation of individual variation" (Mayr, 1953). In the Thynnidae it will be essential to make comparative studies of variability in long series of specimens of as many species as possible. Furthermore, a knowledge of the biology of these insects is fundamental.

An illustration of the importance of an examination of a long series, wherever closely related species are involved, is provided by observations on *Dimorphothynnus fimbriatus* (Smith) 1859.* The puncturation of clypeus, pygidium and form of mandibles varies and, as a consequence, its synonymy is confused. Four specific names were involved which Turner sank in 1916 and he left a series of the variants for reference in the British Museum. The appropriate characters of the four original species were well illustrated (Given, 1958*a*). Recently, these illustrations were compared with a series of thirty-one specimens of *fimbriatus*, and it was found that fourteen agreed with the characters of one "species" and five with another, but that the remaining twelve specimens were intergrades and showed combinations of the diagnostic characters of each.

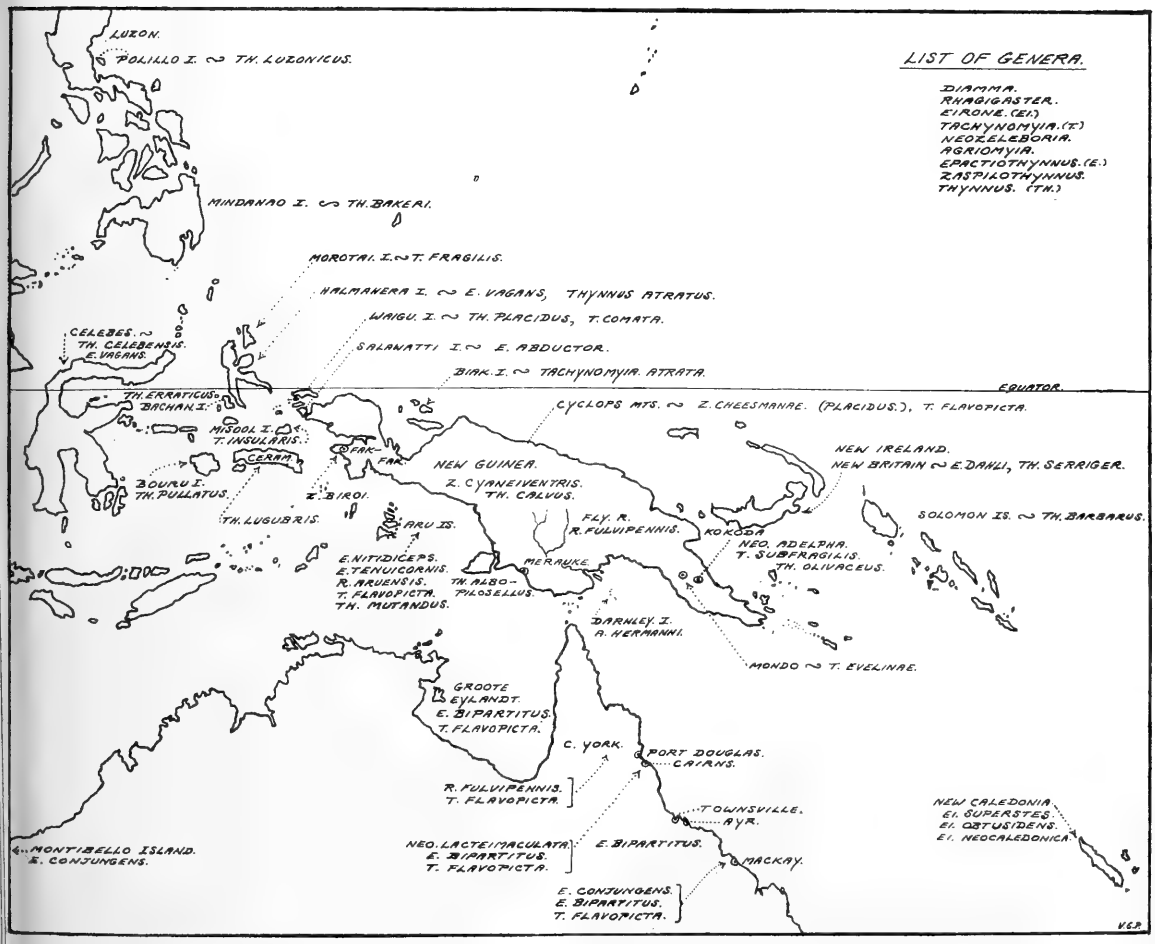
A study of the Thynnidae in general indicates that there is considerable diversity in size, colour, puncturation, relative dimensions of certain structures, and the extent of development of crests, ridges, spines and outgrowths. Specimens of *Hemithynnus apterus* from the same locality can be arranged in a sequence according to the extent of their yellow colour pattern. In the geographical races of *Diamma bicolor*, the males differ in colour, puncturation, hair density, the shape of the inner margins of the eyes and the proportions of the abdomen. In some species, measurements made of particular structures in a large number of individuals fail to yield consistent ratios. The presence of a crest on the clypeus in *Rhagigaster fulvipennis* separates it from *R. aruensis*. The supra-antennal crests vary considerably within a species, e.g., *Neozeleboria lacteimaculata*. The puncturation of the clypeus, the form and puncturation of a fossa on the frontal prominence, and the puncturation of the mesoprescutum, provide the only means of distinction between six male specimens which represented four species: *Thynnus pullatus*, *lugubris*, *barbarus* and *atratus*. From experience, these characters stand well within the range of individual variation. These four species are entirely black except for a fine yellow line behind each eye, but they are closely related to a yellow and black form, *olivaceus*. The females of *olivaceus*, *serriger*, *celebensis*, *calvus*, *lugubris*, *pullatus* and *atratus* may be recognized by the development of paired sulci on the head arising from the antennal bases, and the frontal prominence between them; the presence of a cline may be revealed when the females of the remaining five species are examined. The post-ocular rim in *Tachynomyia flavopicta* is often modified or even aborted and this is sometimes associated with the size of the individual. The hypopygium in some species may be constant, while in other species the extent of development of its spines is very variable.

That many of these diverse forms are cephalic is of classical interest, and these variants could be examples of allometric growth (Rensch, 1959). In some species such variations seem to be associated with the size of the individuals. The Thynnidae are parasitic, and larval nutrition may have an influence upon the development of superficial adult structures. Consequently, the size attained by the adult wasp, its puncturation, sculpture, and the configuration of various protuberances, may all be subject to modifications according to the size and species of the original host, and also perhaps by the presence of more than one thynnid parasite on the body of the host. These protuberances of the exoskeleton are all formed late in the pupal stage, and it is possible that the imago may become more or less fully developed prior to the completion of these excrescences. The migrants from the arid Australian mainland would have to adapt themselves to a very different environment in these tropical islands. It is possible that host-determined variation could account for some of the minor differences observed in these species.

* Further investigations will be necessary before its correct name can be established.

The Distribution of Island Thynnidae and their Phylogenetic Relationship with Mainland Species.

It is recorded here that, in the lists of specimens tabulated for each species dealt with in the present paper, the collector's spelling on the locality label has been used. With the exception of *Diamma bicolor* and *Zaspilothynnus campanularis* from Lord Howe Island, the type localities are shown in Text-fig. 1.



Text-fig. 1.—The type localities in The Philippine Islands, Indonesia, New Guinea, The Solomons, and New Caledonia of species of *Rhagigaster, Eirone, Tachynomyia, Agriomyia Epactiothynnus, Zaspilothynnus* and *Thynnus*. The regions are also indicated on the Australian mainland where closely related species have been found.

1. *Diamma bicolor* has a range extending through Tasmania, Kangaroo I., South Australia, Victoria, N.S.W., and it has also crossed some 374 miles of ocean to Lord Howe Island. Its migration to Lord Howe I. is of particular interest as the male is smaller than the female and a nuptual flight does not occur. The female is sometimes referred to as The Blue Ant; she is particularly tenacious, and has long and powerful legs.

2. *Rhagigaster fulvipennis* is found both on the Australian mainland and in New Guinea. It has been recorded from Port Douglas and various unspecified places on Cape York and also from Kiunga, Fly Rv., New Guinea.

3. *Rhagigaster aruensis* from Aru Island closely resembles *R. fulvipennis* and obviously has been derived from it.

4. *Eirone obtusidens* and 5. *E. superstes* from New Caledonia are both difficult to associate satisfactorily with any particular mainland species. 6. *E. neocaledonica* was unavailable.

7. *Tachynomyia flavopicta* has a very wide range. It is recorded from Brisbane, Mackay, Meringa, Cairns, Kuranda, Groote Eylandt, Thursday Island, Aru Island (Ritsema), Cyclops Mts. It is a very variable species and occurs in at least four distinct forms: Groups i-iv. *Group i*: measures 15·0 mm.; the occipital region is rounded and fully developed; hypopygium with three cusps. *Group ii*: is smaller in size and the longitudinal to transverse axes of the head do not agree with Group i. In *Group iii*: the size of the specimens from Australia does not exceed 9·5 mm., the occipital rim is aborted, and the hypopygium is devoid of spines. Finally, *Group iv*: has a well-developed occipital rim forming a straight, transverse line, and the hypopygium has three very much reduced cusps. Considering the parasitic mode of life-history this seems to be an example of host-determined variation.

8. *Tachynomyia comata*, Waigu; 9. *T. fragilis*, Morotai; 10. *T. evelinae*, Mondo; and 11. *T. subfragilis*, Kokoda. From the single ♂ specimen examined of each, there are differences, but the four species are closely allied and the differences are chiefly in size, colouring, puncturation, relative dimensions, and the development of the supra-antennal crest. Such features are susceptible to individual variation. Furthermore, *T. flavopicta* seems closely related to *comata*, *fragilis*, *evelinae* and *subfragilis*, and it is the probable species from which these island forms have evolved.

12. *Tachynomyia insularis* ♀, Misol I., and 13. *T. atrata* ♂, Biak. Unfortunately, it has not been possible to include these two species in the present paper.

14. *Neozeleboria adelpha*, Kokoda, New Guinea, is very closely allied to *lacteimaculata* from Kuranda, North Queensland, and it would be excusable to regard them as one and the same species. It appears that in the south, Lower Plenty, Victoria, and Champion Bay, Western Australia, there is a species, *trivialis*, which is not far removed from the northern, continental form, *lacteimaculata*; and that still further north, in New Guinea, is the third form, *adelpha*. Illustrations are given of the minor differences between these so-called species.

15. *Agriomyia hermanni*, Darnley Island, Torres Strait. This species is closely allied to the mainland forms of *Agriomyia*, but its particular affinities cannot be established until material is available from Darnley. It can readily be identified from a set of eight photomicrographs of the type.

16. *Epactiothynnus nitidiceps*, Aru Island. Specimens have only recently become available and its relationship to the mainland *Epactiothynnus* have not as yet been ascertained.

17. *Epactiothynnus vagans*, Celebes, Morotai, Batian; 18. *E. abductor*, Salawatti, Morotai, Cyclops Mts., Kokoda, Astrolabe Bay; 19. *E. dahli*, Ralum, New Britain. These three species may be distinguished by the form of the fore-coxae, the puncturation of the mesonotum and the shape of the head of the female. They are closely related one to another and to the widespread mainland species *E. bipartitus* which ranges from Cairns and Mackay on the east coast to Groote Eylandt in the Gulf of Carpentaria. There seems little doubt that the island forms have evolved from the continental species *E. bipartitus*.

20. *Epactiothynnus tenuicornis*, Aru Island, was the first species to be described from the East Indies; however, the type has long since disappeared and Smith's brief description of it leaves much in doubt.

21. *Zaspilothynnus campanularis*, N.S.W. and Lord Howe Island. 22. *Zaspilothynnus biroi*, Sattelberg, Huon Gulf; *Z.b. pratti*, Fakfak, New Guinea. On Lord Howe Island, *campanularis* appears to be more colourful than on the mainland, and there are minor differences in the shape of the propodeum. *Z. campanularis* is related to *interruptus*, N.S.W. and Southern Queensland and also to *stratifrons*, Stradbroke Island, Moreton Bay. *Z. biroi* is a northern representative of this complex and an interesting parallel

exists between the Lord Howe Island variety of *campanularis* and this tropical New Guinea species, *Z. biroi*. Both share the extensive yellow markings and a propodeum which is rounded laterally, and they could be examples of habitat variation. *Z. b. pratti* shows a greater development of the yellow markings, and a narrower form of hypopygium. 23. *Z. placidus* (= *cheesmanae*), Waigu I. and Cyclops Mts., New Guinea. 24. *Z. cyaneiventris*, New Guinea (omitted).

25. *Thynnus erraticus*, Bachan & Halmaheira. 26. *Thynnus olivaceus*, Kokoda; 27. *T. serriger*, New Britain, Hollandia, New Guinea, New Ireland, Mindanao; 28. *T. mutandus*, Aru; 29. *T. luzonicus*, Polillo, Luzon; 30. *T. calvus*, ♀, Mafor, New Guinea; 31. *T. pullatus*, Bouru; 32. *T. lugubris*, Ceram; 33. *T. celebensis*, Celebes; 34. *T. barbarus*, Solomons; 35. *T. atratus*, Gilolo, Morotai; 36. *T. albopilocellus*, Merauke, New Guinea; 37. *T. bakeri*, Mindanao, Philippines (Nos. 36 and 37 omitted).

The phylogenetic relationships between species 23 to 37 and the mainland species of *Zaspilothynnus* and *Thynnus* will be discussed in a subsequent paper when an examination has been made of further material.

Acknowledgements.

This presentation owes its existence to the wonderful co-operation received by the author from every possible source, and its preparation is an answer to the obligation which this magnificent assistance necessarily entails. The assemblage of a communication on the Thynnidae of these territories has been made possible only by access to, or the loan of, collections from fourteen Museums, and all of this material is most valuable.

In particular, the author wishes to express his sincere thanks to Dr. I. H. H. Yarrow and the Trustees of the British Museum for permission to study the Thynnidae in their Collections; for the privilege of working in the Hymenoptera Section of the British Museum for thirteen months (1958–1959); and for authorizing the loan of material for further studies in Australia.

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Illustrations.

In the present paper, and also in the third contribution of this series (1957), the illustrations were prepared by the present author with the exception of the map showing type localities. In making drawings of taxonomic characters, an eye-piece graticule and squared paper were used. Some of the photomicrographs are mosaics because the accommodation of various planes of focus was a necessity, as a camera of short focal-length (a Contaflex IV, *f* 1 : 2·8, F = 50 mm.) was used in conjunction with a microscope. In particular, the author wishes to thank Miss Gay Plowman firstly for her annotated map (Text-fig. 1) and also for her meticulous care in the assembling of all appropriate portions of the photomicrographs.

Genus Diamma Westwood, 1835.

Westwood, 1835: 53. *Psamatha*, Shuckard, 1837: 68. *Tachypterus*, Guérin, 1838: 217, 234. *Psamatha*, Westwood, 1844: 103. *Tachypterus*, Smith, 1859: 64–65. *Diamma*, Ashmead, 1903: 157; Turner, 1907*a*: 212. Turner, 1910*c*: 3.

In the genus *Diamma*, considerable difference exists between its wing-venation and that found in all of the other 489 species of the Thynnidae. Firstly, the cross-vein rm_1 (Tillyard, 1926) which is characteristic of all other Thynnidae is absent altogether here. Secondly, the position of mcu_3 differs completely from every other species in the family. Thynnid wing-venation is illustrated, and in *Diamma* the aberrant situation of the cross-vein mcu_3 on the cell *1m* rather than upon the customary *2m* is shown (Salter, 1957: 342). This modification may not appear excessive, but it is in marked contrast to a very large volume of species in all of which the particular cross-vein is received more distally upon the cell *2m*. There are other contrasted characters to be summarized later. The female is larger than the male and the genitalia of both are unsuited for a nuptial flight.

Considering the Family Thynnidae, the three most constant features are: Firstly the presence of paired laminae overlying the bases of the second coxae. Secondly, a wing-venation which is constant within a very slight range of variation as in illustrations (Salter, 1957). Thirdly, with the exception of *Diamma*, the wingless females are smaller in size than the winged males and so are carried on a prolonged nuptial flight.

Diamma differs from the true Thynnidae in both wing-venation and in the size and morphology of the female. These differences are phylogenetic, and these marked dissimilarities can best be shown by the division of the Family Thynnidae into two subfamilies Diamminae and Euthynninae. To minimize the obvious set of differences which separate the Diamminae from all other thynnids by the reduction of their taxonomic status merely to tribal rank fails to place appropriate emphasis upon a set of inequalities which merits the fullest consideration.

In the Subfamily Diamminae one species only, *Diamma bicolor*, is known, which is divisible into three geographical races.

1. Diamma bicolor, Westwood, 1835.

Westwood, 1835: 53 (♀), New Holland. *Psamatha chalybea*, Shuckard, 1837: 68–9 (♂). Sydney. *Tachypterus fasciatus*, Guérin, 1838: 217 (♂), Ile des Kanguroo; Guérin, 1842: 3, Pl. 99, figs 7–13 (♂); Westwood, 1844: 19–21. *T. australis*, Saussure, 1868: 109 (♂) Sydney. *T. albopictus*, Smith, 1868: 237 (♂), Australia. *D. bicolor*, Olliff, 1889: 98. *D. bicolor*, Hardy, 1952: 46.

Specimens examined: A. (i-xviii) Race of *D. bicolor* from Lord Howe Island. B. (xix-xxviii) Race of *bicolor* similar to *chalybea* Shuckard, N.S.W. C. (xxix-xli) Race of *bicolor* as in *fasciata* Guérin, Kangaroo Island, Tasmania, South Australia and Victoria. D. (xlii-xliv) Intergrades between B & C, Victoria; Dromana 3/11/31, Heathmont 24/10/27, Fern Tree Gully 23/11/27. A. N. Burns.

Somehow this earthbound thynnid has succeeded in crossing at least 374 miles of Pacific Ocean from New South Wales to Lord Howe Island and there it became established. This race is closely allied to the form described by Shuckard as *Psamatha chalybea* from Sydney in 1837. It was found subsequently to be the male of Westwood's *Diamma bicolor* described in 1835. *Tachypterus fasciatus* Guérin is another distinct form of this species. Turner in his revision states: "The colour of the legs in the males is very variable; the variations in this respect may prove to be local, but as I can detect no differences in the females from different localities, I prefer to sink all into one species." An examination of 54 males of *D. bicolor* shows that at least four different forms can be distinguished one from another. Firstly, a geographical race is found in the vicinity of Sydney which agrees with Shuckard's description and for convenience is referred to here as *D. b. chalybea*. Secondly, its nearest relative is the race established in Lord Howe Island. Thirdly, there is a distinct geographical race which includes all forms so far collected from Kangaroo Island, South Australia and Tasmania; this agrees with Guérin's *Tachypterus fasciatus* and for convenience his name *D. b. fasciata*

is applicable to this particular form of *Diamma bicolor*. Lastly, there is a very interesting geographical race which occurs in parts of Victoria in which some of the characters of both *chalybea* and *fasciata* are combined and it is definitely intermediate between these two subspecies. As there is no nuptial flight in *Diamma*, and their migratory powers are limited to the distribution of their host, the mole-cricket, and also to the walking distance covered by a female during her life-time, the northern and southern geographical races are in all probability isolated one from another by a broad zone occupied by a hybrid population. If such a zone exists, it could effectively absorb and eliminate any migration of one of these mainland subspecies into territory occupied by the other.

The geographical race of *Diamma bicolor* which is now established in Lord Howe Island is not far removed from *D. b. chalybea* and has less resemblance to *fasciata*. Eighteen males and three females from Lord Howe were compared with seven males and ten females of *chalybea* from the Sydney district. The differences which have evolved are of interest. In the males from Lord Howe, differences in puncturation have arisen on head and thorax and there are modifications in the shape of the abdomen. In the race found on Lord Howe Island, the abdomen has become relatively longer and more strongly lanceolate. Intersegmental constrictions do not occur and its yellow markings are reduced to narrow bands (Text-fig. 2).

Genus Rhagigaster Guérin, 1842.

Guérin, 1838: 214. Guérin, 1842: 2, Pl. 99, f. 2. Westwood, 1844: 104. Saussure, 1867: 110. Ashmead, 1903: 157. Turner, 1907: 214. *Rhytidogaster*, Turner, 1907: 229.

Type species, *Rhagigaster unicolor* Guérin, 1838.

The form of the hypopygium in *Rhagigaster* and in *Dimorphothynnus* is of considerable interest. It differs completely from all other thynnids and thus the recognition of these two genera is considerably simplified. From about the centre of its ventral surface, it bears an aciculus which projects posteriorly and is curved upwards.

In *Rhagigaster* there are forty-four species described. *R. aruensis* is known so far from Aru Island alone while *R. fulvipennis* ranges from the mainland into New Guinea.

2. Rhagigaster fulvipennis and 3. R. aruensis.

2. Rhagigaster fulvipennis Turner, 1907.

Turner, 1907: 224 (♂♀). Cape York. Type: B.M. 15/438 a & b.

3. Rhagigaster aruensis Turner, 1912.

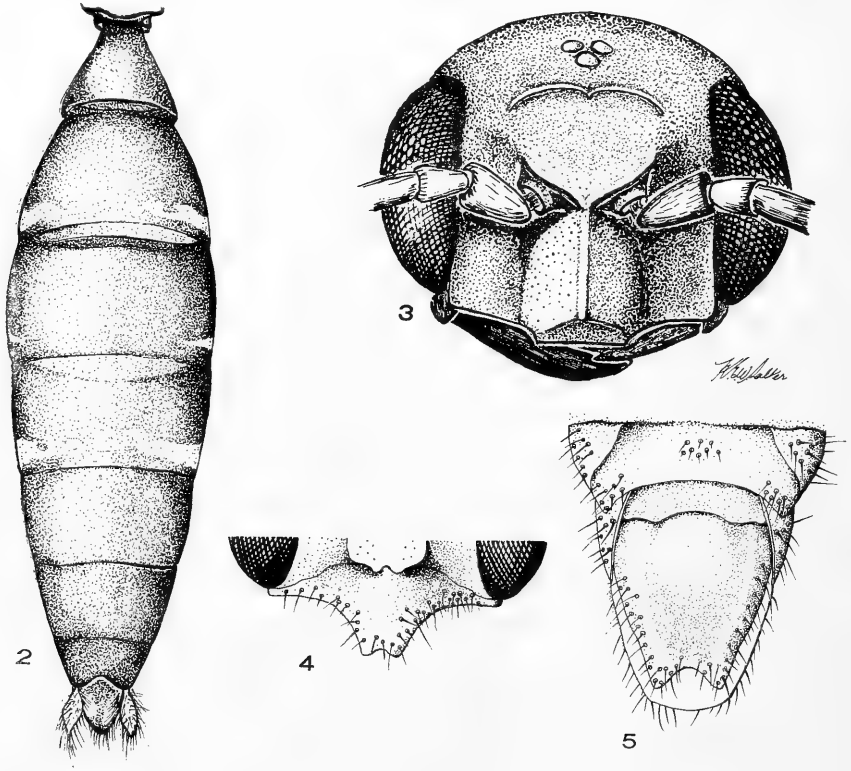
Turner, 1912*b*: 533 (♂♀). Aru Island. Type: B.M. 15/433 a & b.

Specimens examined: *R. fulvipennis*: (i) Cape York, H. Elgner, R. E. Turner 1910, from W. W. Froggatt, 1910–225. B.M. (ii) New Guinea: Papua, Kiunga, Fly Rv. IX/1–3/1957. W. W. Brandt, B. P. Bishop Museum. (iii) New Guinea: Papua, Kiunga, Fly Rv. X/21–24/1957. W. W. Brandt, B. P. Bishop Museum Collector. (iv) Port Douglas, coastal scrub, Oct. 1–6, 1956. J. Baldwin, South Australian Museum. (v-vi) Port Douglas, coastal scrub, June 7th to July 7th, 1956. (vii-viii) New Guinea: Papua, Oriomo Government Station, 26–28. X/1960. J. L. Gressitt Collector. (ix) ♀ New Guinea: Papua, Kiunga, Fly Rv. IX/9/1957. *R. aruensis*: (i) Aru Island Elgner 1911. 32t. Turner Coll. 1912–111. British Museum.

Turner, in his comments on *Rhagigaster aruensis* states: "It is nearest to *fulvipennis* Turn., from Cape York, but differs both in sculpture and colour." The differences in sculpture referred to by Turner consist of crests on clypeus, frons, and propodeum, which are present in *fulvipennis* but absent or weakly developed in *aruensis*. Except for these crests, however, the form, colour, and puncturation of these specimens are very similar.

A comparison has been made between the eight specimens of *fulvipennis* and the single specimen of *aruensis*. The length of *fulvipennis* varies from a maximum of 17 mm. to a minimum of 11 mm. while *aruensis* measures 12·5 mm. The figures for *fulvipennis* are as follows: (i) 17 mm. (ii) 14 mm. (iii) 15 mm. (iv) 15 mm. (v) 12 mm. (vi) 11 mm. (vii) 13 mm. (viii) 11 mm. (Average 13 mm.)

In all of the *fulvipennis*: (*a*) Irrespective of size, the ridged clypeus bears a median longitudinal crest which is most distinct, uniting with the prominent supra-antennal crests to form the letter 'Y'. (*b*) The pre-ocellar crest may form inverted crescents with their inflected ends turned towards the antennal bases, or by their fusion, form a single transverse crest (Text-fig. 3). (*c*) The propodeum, in Froggatt's specimen, shows a tendency to develop very slight median and lateral angles and to be faintly truncate. In all the smaller specimens its appearance is more rounded. (*d*) The leg colour varies: In Froggatt's specimen from Cape York the legs are yellow-brown; those from Port Douglas have black legs. Both variants occur in New Guinea.



Text-fig. 2.—*Diamma bicolor* Westwood, from Lord Howe Island. The abdomen in this race is relatively longer and more strongly lanceolate than in the various races occurring on the mainland.

Text-fig. 3.—*Rhagigaster fulvipennis* Turner, head. The clypeus bears a distinct, median, longitudinal ridge continuous on the frons with the supra-antennal crests, thus having the appearance of the letter Y. On the frons, in front of the ocelli, is a pair of fused crescent-like ridges.

Text-fig. 4.—*Eirone superstes* Cockerell. The clypeus is shaped like a broadly based triangle; its median apex is notched and consequently appears bilobed.

Text-fig. 5.—*Eirone superstes*. Hypopygium with emarginate apex.

In the single specimen, *aruensis*, (*a*) The ridged clypeus does not bear a crest. (*b*) An incipient tendency to form a pre-ocellar crest is apparent. (*c*) The propodeum differs from the larger *fulvipennis* (measuring 17 mm.) but does not vary appreciably from the specimens of comparable size. (*e*) The legs are bright yellow.

That there is no relationship between the size of the individual and the development of the crests on clypeus and frons is evident from an examination of this series of eight *fulvipennis*. Considering the range of variation in the sculpture of the clypeus of *Dimorphothynnus fimbriatus*, a decision as to whether *aruensis* is a subspecies of *fulvipennis*, or a valid species, should be based on a larger series of specimens.

Genus Eirone Westwood, 1844.

Westwood, 1844: 144. Ashmead, 1903: 157. *Aelurus* Turner, 1907*a*: 258 (*nec* Klug). *Eirone* Turner, 1910*c*: 8. Given, 1958: 321.

Type species, *Eirone dispar* Westwood.

Eirone is a large genus including at least 48 described species and there are a number of new species to be added to this list.

4. Eirone obtusidens Turner, 1919.

Eirone obtusidens Turner, 1919, 236 (♂), Noumea. Type: B.M. 15/362.

Photomicrographs and specimens examined: (i) Four colour transparencies and one photomicrograph of type (Pl. v, figs 1–2). (ii) New Caledonia: Houailou, 9/23/25. W. H. Ford Collector. B. P. Bishop Museum. (Received on loan: 22/3/62.)

(i) Photographs of type: Anterior margin of clypeus nearly straight, bearing a median, triangular projection which is approximately one-fifth the width of the clypeus. Scutellum with a single large, undivided, apical, yellow macula, propodeum yellow entirely on dorsal surface, abdominal tergites 2–4 yellow with light brown, intersegmental bands which appear black in the illustration. The tergites are fringed with a single row of short, stiff, black bristles.

(ii) Specimen: Appreciable differences exist between the Houailou specimen and the photomicrographs of Turner's type. Anterior margin of the clypeus with a pair of broad, lateral emarginations on either side of a slight median projection. The 2nd coxae with prominent, posterior, apical spines. Propodeum black on anterior third. Abdominal segments 2–5, also pygidium and hypopygium, yellow dorsally and ventrally; each is crossed anteriorly by a strong, black band. The tergites are fringed along the apical impression by one row of brown bristles. The hypopygium is elongate and truncate posteriorly.

5. Eirone superstes Cockerell, 1929.

Cockerell, 1929: 239–42 (♂). Bourail, New Caledonia. Type: U.S. Nat. Mus.

Specimens examined: 43 males and 22 females, St. Lewis Valley, New Caledonia, Mar. 20–3, 1945, H. E. Milliron (on leaves of fig tree). Bernice P. Bishop Museum.

With this large series of individuals, it is possible to assess the potential range of individual variation occurring within a species. This species, like *E. obtusidens*, is another black and yellow thynnid; and although in this series there are slight variations noticeable in the extent of colouring, certain features have been found to be constant. The margin of the clypeus is extended anteriorly forming a broadly based triangle; its median apex is notched and consequently bilobed (Text-fig. 4). The puncturation on the mesonotum and the form and depth of the parapsidal sutures are apparently constant. The scutellum in 43 ♂♂ with paired, unfused, apical, yellow maculae, propodeum entirely black. Abdominal segments variable, 2nd to 5th (usually) ferruginous, with hairs of a similar colour. Hypopygium is not broadly rounded; here its apex is emarginate (Text-fig. 5).

6. Eirone neocaledonica Williams, 1945.

Williams, 1945: 418–20 (♂). Near St. Louis, New Caledonia. No material available.

This species is entirely black except for the apices of the mandibles which are rufous. Puncturation is generally sparse. The clypeus is produced and subtruncate. The propodeum with dorso-lateral tubercles and a triangular depression extending as a median groove with sparse punctures on either side. Hypopygium is rounded (Williams, 1945). Recognition of this species from *obtusidens* and *superstes* should present no difficulties on account of the lack of the conspicuous yellow coloration and secondly, the unspecialized nature of the clypeus.

4. *Eirone obtusidens*, 5. *superstes* and 6. *neocaledonica*. How closely related are the three New Caledonian species and from which of the 45 mainland species of *Eirone* could they have evolved? Unfortunately, without any specimens of *obtusidens** and

* A further investigation of a specimen received 22/3/62 was not possible prior to going to press.

neocaledonica their relationships are impossible to assess. In *Eirone superstes*, the clypeus and hypopygium differ completely from both *obtusidens* and *neocaledonica*, and a comparison has been made of these two structures in as many other *Eirone* as possible. Of what phylogenetic value are these taxonomic characters? The bifid clypeus of *superstes* has been compared with identified specimens of thirty-seven Australian species of *Eirone* and also with colour transparencies of six others which are known from only single specimens in the British Museum. The evolution of this bifid clypeus can be traced in other species of *Eirone* and an illustrated account of this sequence is now in preparation as part of the revision of this genus. *E. schizorhina* is another example of the ultimate in a split clypeus which is virtually bidentate at the apex. Comparisons between hypopygia were limited to identified specimens and no other example of an emarginate hypopygium has been found.

Genus Spilothynnus Ashmead, 1903.

Ashmead, 1903: 103. Turner, 1910*c*: 18.

Type species, *S. laetus* (Klug), 1842. Chile.

This genus is South American, and its inclusion here is due to an error in the recording of the correct locality of two females which apparently belong to this genus. Its characters are defined by R. E. Turner in his *Genera of Thynnidae*.

Spilothynnus thalluse Montet, 1922.

Montet, 1922: 184–6 (♀). New Caledonia (*in error*). Type: Muséum d'Histoire naturelle de Genève.

Montet's description of *Spilothynnus thalluse* states: "Deux exemplaires ♀. Australie. Nouvelle-Calédonie. Cette espèce est voisine du genre australien *Phymathothynnus* Turner et, en particulier, de *Phymatothynnus pygidialis* Turner. Elle possède aussi certains caractères du genre américain *Spilothynnus* Turner. Comme, d'une part, certains groupes animaux de la Nouvelle Calédonie présentent des affinités avec des genres américains, que, d'autre part, il y a toujours possibilité d'erreur dans l'indication des localités, nous plaçons provisoirement cette espèce dans le genre *Spilothynnus*."

That some of the thynnids examined by G. Montet had been incorrectly localized and identified by former collectors was unfortunate. It is a tribute to the clarity of his work that his descriptions are so explicit that any such irregularities can be rectified without difficulty.

Naturally, the occurrence of a South American genus in New Caledonia would excite very considerable interest and speculation. After a lapse of forty years, however, this record seems still to be unconfirmed and doubts as to its validity have been raised by various authors. An examination of this type has not been made.

In Montet's collection, some of which is on loan to me at present for study, is a male of *Eirone superstes* Cockerell, 1929. This specimen bears no locality label, but the species is known only from New Caledonia, and as it is one of the species with a clypeus which resembles *Spilothynnus*, it may explain how this error in locality could have originated. An abbreviation of the relevant sections of the first five contrasted characters in Turner's Generic Key (1910*c*) to the males would read: (1) South American species. (2) Mandibles bidentate and (3) curved. (4) Clypeus not broadly emarginate, but (5) narrowly and deeply emarginate:

(6) Three apical joints of maxillary palpi moderately elongate; antennae rather short; hypopygium straight and narrow ..... Genus 4. Spilothynnus.
Three apical joints of maxillary palpi very long; antennae long; hypopygium rounded ..... Genus 2. Dolichothynnus.

Two labels are borne by the pin of *E. superstes* (♂), one in Montet's handwriting, stating: "Genus?"; the second, an older but neatly folded note, reading: "Cette esp. [èce] rappelle *Dolichothynnus*, mais le manque d'indication de provenance complique la détermination. Les prol. [ongements] du mésosternum entre les coxae interm. [édiaires] sont remplacé[s] par des rebords membraneux. Peut-être pas une Thynnidae?" Evidently the cleft clypeus of *Eirone superstes* has led incorrectly to its classification

into a South American genus and hence the male from New Caledonia may have been grouped with the two females from South America, on the assumption that they were all *Spilothynnus*. Representatives of the South American genera were determined at the B.M. by the present author (Salter, 1960), including a ♂ & ♀ *in cop.* of *S. bituberculatus* Turner, 1908. A comparison of these two species shows that although a deeply emarginate clypeus is a feature common to both species, the structure of the mandibles, coxae, abdomen and hypopygium is in sharp contrast.

Comparison of the female of *S. bituberculatus* with Montet's description of *S. thalluse* ♀ shows that he was undoubtedly describing a member of this genus, and as there are at least ten species, the validity of *S. thalluse* as a genuine South American species requires investigation. Not the slightest resemblance exists between the females of *S. bituberculatus* and *E. superstes*.

Whether Montet's specimen of *Eirone superstes* had any bearing on the incorrect locality given for *S. thalluse* is a matter for conjecture. It seems most improbable that in 1922 such a common species from a French possession had escaped his notice. As he was uncertain of its correct genus he apparently refrained from describing it as a new species. Montet would have been confronted with a male and two females possessing generic characters which, according to Turner's key, would lead him to conclude that they had some degree of affinity, and hence perhaps to the assumption that *Spilothynnus thalluse* came from New Caledonia. His contribution also contained the descriptions of four new thynnids from South America and *S. thalluse* will in due course be recorded from that country. The locality label is missing from *E. superstes*; was it accidentally transferred to one of the females of *S. thalluse*?

The relationship between *S. thalluse* and *Phymatothynnus* has been investigated. Firstly, Montet's type of *Phymatothynnus zenis* (1922: 200) has been examined. He states: "3 exemplaires ♂. Australie (sans indication plus précise). Cette espèce n'a pas les antennes longues, le labium frangé, et le clypeus étroit des *Phymatothynnus* typiques. Elle possède cependant plusieurs caractères de *P. pygidialis* Turner, quoique en différant d'autre part par sa taille plus grande, sa couleur différente, son clypeus sans carène et sa nervation. *P. nitidus* Sm. possède également les antennes et le clypeus courts." The type on loan from Geneva agrees with his description, but it also corresponds exactly with specimens of *Eucyrtothynnus ichneumoneus* (Klug) 1842 from South Brazil! Montet's *fig. 21 P. zenis* ♂ Tête, and *fig. 22. a.* Hypopygium; *b*, Epipygium, all agree with *Eucyrtothynnus ichneumoneus* and differ completely from *Phymatothynnus*. Further comments on *P. zenis* will be made in my revision of that genus. It is even more difficult to understand the confusion between *Phymatothynnus* and *Eucyrtothynnus* in view of the fact that Montet described in this paper three new species from South America: *Eucyrtothynnus trezen* Montet, 1922; *E. tetreus* Montet, 1922; and *E. phyllis* Montet, 1922. Secondly, the female of *Spilothynnus bituberculatus* was also compared with the females of *Phymatothynnus aratus* (Turner), 1908, *P. monilicornis* (Smith), 1859, *P. pygidiophorous* Turner, 1915, *P. tonsorius* Turner, 1915, and *P. victor* Turner, 1940, and no close phylogenetic relationship is recognizable between the South American *Spilothynnus* and the Australian *Phymatothynnus*. The type of *P. pygidialis* Turner, 1913, is in the Victorian National Museum; there are no determined specimens of *pygidialis* in the British Museum, and it is probable that the specimen examined by Montet had been previously misidentified.

Lastly, it would be appropriate to mention here that *Zaspilothynnus lasius* Montet 1922 (p. 223), is synonymous with *Z. campanularis* (Smith), 1868.

Tachynomyia Guérin, 1842.

Tachynomyia, Guérin, 1842: 6. *Aelurus*, Westwood, 1844: 122. *Tachynomyia*, Saussure, 1868: 124. *Pseudaelurus*, Ashmead, 1903: 99. *Tachynomyia*, Turner, 1907*a*: 276.

The type species is *Tachynomyia abdominalis* (Guérin), 1842. This species had been described by Guérin as *Agriomyia abdominalis* and also as *A. spinolae* in his *Magasin de Zoologie*; as a footnote he proposed the name *Tachynomyia* for this genus.

The genus is distinct from all other Thynnidae and in earlier days received three separate generic names. In Smith's "Catalogue" (1859), *Aelurus* was one of the nine genera included in the Family Thynnidae, and with *Anthobosca*, *Rhagigaster*, *Diamma* etc., it was considered as a genus distinct from the whole of *Thynnus*.

Thirty-four species have been described. Of these, twenty-seven species occur in Australia, and from New Guinea, Waigu, Morotai and Misol six others are recorded; there is also another species common to Australia, New Guinea and Aru Island. The occipital region of the head is unique, as the whole of its postero-ventral surface is completely taken up by an extensive, saucer-like concavity which is bounded by a narrow rim. This rim forms a thin ridge extending behind the eyes and the vertex, and appears to be bounded by the occipital suture. The rim is referred to here in general as the *occipital rim*, while only that portion which lies immediately behind the eyes is referred to as the *post-ocular rim*. In Thynnidae, the size of the occipital concavity is governed by the distance between the occipital suture and the foramen. Its maximum size is attained in *Tachynomyia* (Salter, 1957, Text-fig. 7).

7. Tachynomia flavopicta (Ritsema), 1876.

Aelurus flavopictus, Ritsema, 1876: 185 (♂), Aru. Type: U.S.A. *Tachynomyia flavopicta*, Turner, 1907*a*: 289 (♂ & ♀), Mackay, Cairns, Cape York, Queensland. Turner, 1940*a*: 92, Cyclops Mt., New Guinea.

Specimens examined, Series A: *Group I*: (i) Mackay, 6/2/28, A. N. Burns (908) (agrees with Turner's det.); (ii & iii) Cairns, 7/1/53, A. N. Burns (984). *Group II*: (iv & v) Cairns, 26/1/50, Cairns, 22/1/53; (vi) Kuranda, 9/2/51, A. N. Burns (1124); (vii-ix) Meringa, 5/9/25, (923), (3 ♂ and 3 ♀); (x-xii) Macleay Mus. *Group III*: (xiii) Brisbane, 29/11/22 (935); (xiv) Brisbane, 3/12/22; (xv) Brisbane, 12/3/23, A. N. Burns, Vict. Nat. Mus. *Group IV*: (xvi-xviii) Groote Eylandt, N.T., N. B. Tindale, S. Aust. Mus.; (xix) Thursday Island, N. B. Tindale, S. Aust. Mus.; (xx-xxi) Mackay, Queensland, G. Turner, 1892–16, 1907–244 (442–B.M.).

A comparison of the width and form of the post-ocular rim, the shape of the hypopygium and the length of the maxillary palps in the above series of twenty-one *T. flavopicta* shows that at least four distinct forms of this species occur. In *Series* A the extent of development of these various structures seems to be associated with individual size (Table 1), although in *Series* B no such correlation is evident. In

Table 1.
Length Compared in Seventeen Specimens of T. flavopicta *in Groups I–IV.*

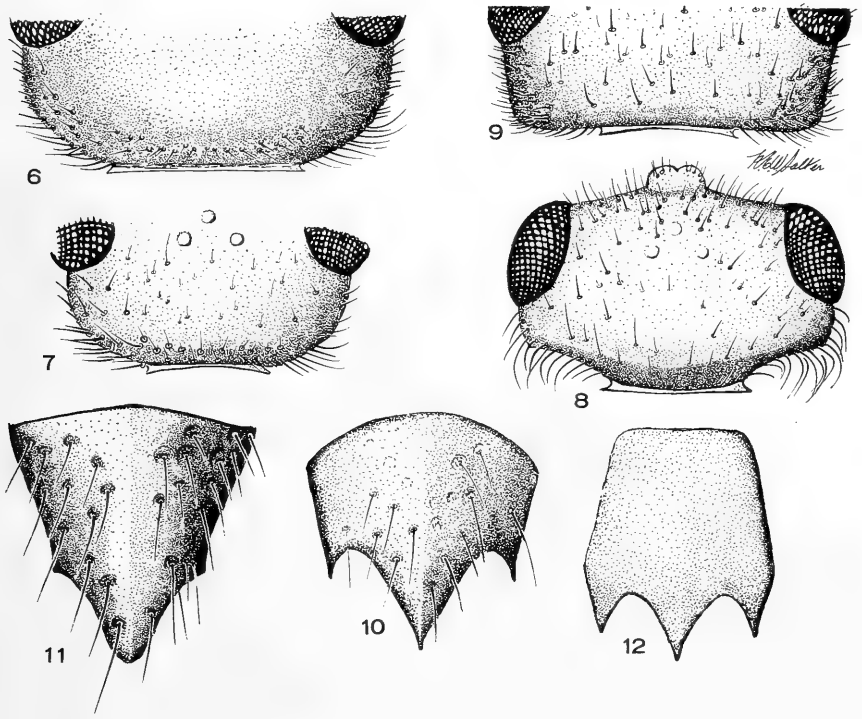
Group.	Number of Specimens Measured.	Maximum and Minimum Length.	Average Length.
I	3	15·0–12·5 mm.	13·8 mm.
II	6	12·5–10·0 „	11·25 „
III	3	11·5– 9·5 „	10·6 „
IV	5	11·5– 9·0 „	10·1 „

Series A, it appears that in larger specimens the post-ocular rim, the hypopygium and its associated spines are developed to a relatively greater extent than in the smaller individuals. There seems to have been an inhibiting factor which has retarded the growth of these structures in the smaller specimens. The size of the adult wasp and the development of these various superficial outgrowths may be related to the nutrition available to the developing parasitic larva. These features have been illustrated as they give some idea of the range of form occurring in one species of thynnid (Text-figs 6–12).

Examination of other structures shows that: (i) The size and proximity of puncturation is slightly variable. (ii) The shape of the supra-antennal ridge is

moderately uniform but slight differences are noticeable in the ratio between its transverse width and the distance between the compound eyes. (iii) The distance between the ocelli varies from once to twice the diameter of the median ocellus (Text-fig. 13). (iv) The size of the eyes, and the extent to which they are elevated over the surface of the head is also slightly variable. (v) The ratio between the longitudinal and transverse axes of the pronotum is not constant, and there are several examples in which the prothorax is expanded at the sides.

Group I: This group agrees with Turner's determined specimens in the B.M. They are large in size and the occipital rim is developed to its maximum, thus forming a broad, post-ocular rim which is continuous behind the vertex and rounded at the sides (Text-fig. 6). The maxillary palps are short enough to be contained easily within the occipital concavity. The hypopygium is broad and bears three cusps (Text-fig. 10); the median cusp forms an equilateral triangle and on either side of it is a small lateral cusp.



Text-fig. 6.—*Tachynomyia flavopicta* (Ritsema). Occipital region of the head in Group I showing the broadly rounded post-ocular rims arising from the genae; its development is variable in this species.

Text-fig. 7.—*Tachynomyia flavopicta,* occipital region in Group II. The post-ocular rim is also broad and rounded, but Groups I and II differ in the ratio between their longitudinal and transverse axes.

Text-fig. 8.—*Tachynomyia flavopicta,* occipital region in Group III. The post-ocular rim arising from the gena is aborted.

Text-fig. 9.—*Tachynomyia flavopicta,* occipital region in Group IV. Here the rim instead of being rounded or undeveloped is expanded and the posterior boundary of the head forms a straight line.

Text-fig. 10.—*Tachynomyia flavopicta,* hypopygium of Group I. It is broad at the apex and bears three cusps, the central cusp being the largest.

Text-fig. 11.—*Tachynomyia flavopicta,* hypopygium in Group III. It is narrowed and devoid of lateral cusps.

Text-fig. 12.—*Tachynomyia flavopicta,* hypopygium in Group IV, bearing three cusps of almost equal size.

Group II: The specimens in the second group resemble those in the first (Text-fig. 7), but are smaller in size than in Group I, and they differ in the ratio between their longitudinal and transverse axes.

Group III: The maximum reduction in the depth of the post-ocular rim characterizes these specimens (Text-fig. 8); thus there is no posterior extension arising from the junction of the gena with the occipital concavity to form the post-ocular rim (Plate vi, fig. 12). The palps are lacking in pigment and they are so elongate that they extend beyond the first-coxae. The hypopygium is atypical, its lateral cusps are represented by narrowed shoulders which support a small, median, apical triangle (Text-fig. 11). Their average length is less than in Group II.

Group IV: In contrast with Group III, these specimens from Groote Eylandt have a very well-developed occipital rim which posteriorly forms a straight line (Text-fig. 9). The maxillary palps extend beyond the fore-coxae. The hypopygium is also atypical; here it consists of three cusps of almost equal size, but in the three specimens from Groote Eylandt, a slight variation is apparent in the width of the median cusp (Text-fig. 12).

Specimens examined, Series *B**: *a*. (xxii) New Guinea: Papua, C. Dist., Otomata Plant'n, 1 m. E. of Moresby, 2.xi.1960, Malaise Trap, J. L. Gressitt; (xxiii-xxvi) New Guinea: Papua, W. District, Oriomo Govt. Sta., 26–28.x.1960, Malaise Trap, J. L. Gressitt; *b*. (xxvii-xxviii) as in (xxii) above; (xxix-xxx) as in (xxiii) above; *c*. (xxxi-xxxii) New Guinea, NE. Turricelli Mts., Siaute, Sea lev., xi.9–17.1958, W. W. Brandt, Collector, Bishop.

Examination of the eleven specimens in *Series* B from New Guinea shows that, unlike the mainland *Series* A, no correlation is evident between individual length and the development of the post-ocular rim, maxillary palps and hypopygium.

(*a*) In five specimens, the length of one from Otomata is 13 mm. and four from Oriomo are approximately 12 mm. They all correspond closely to Group II.

(*b*) In four others, two from Oriomo and one from Otomata are 11 mm. in length; one from Otomata measures 10 mm. In general, they have a more delicate appearance than the examples in (*a*). A slight reduction is evident in the size of the post-ocular rim, the maxillary palps are very long and the hypopygium is minute

(*c*) The two specimens from Torricelli are at least 12 mm. in length and more robust than are the preceding ones in (*b*). The post-ocular region is even more strongly excised than in Group III. The maxillary palps are conspicuously elongated and brownish; the hypopygium varies, one specimen resembling Text-fig. 12, the other Text-fig. 18.

From this series of thirty-two individuals, it is evident that no standard correlation exists between the size of the specimen and the development of the occipital-rim, palps and hypopygium. Only a study of the biology of this species could establish the nature of these variations.

8. Tachynomyia comata; 9. T. fragilis; 10. T. evelinae and 11. T. subfragilis.

The range of *Tachynomyia flavopicta* extends from Brisbane, Thursday Island, Groote Eylandt, to New Guinea. A strong resemblance exists between *flavopicta* and four other species found in New Guinea and its adjacent islands, namely, *T. comata*, *fragilis*, *evelinae* and *subfragilis*. The characters separating them one from another are very slight and it is considered that a knowledge of the potential variation in *flavopicta* could be of some assistance in assessing the values of the various features used for their separation.

8. Tachynomyia comata (Smith), 1864.

Aelurus comatus Smith, 1864: 27 (♂), Waigiou, Malaya. Type: Oxford University Museum. *Tachynomyia comata* Turner, 1910*a*: 122.

* From a collection of 139 specimens received on loan on 22nd March, 1962, from the Bernice P. Bishop Museum.

9. Tachynomyia fragilis (Smith), 1865.

Aelurus fragilis Smith, 1865a: 78 (♂). *Tachynomyia fragilis* Turner, 1907: 290 (♂), Morty Island. Type: Oxford University Museum.

10. Tachynomyia evelinae Turner, 1940.

Turner, 1940*a*: 95 (♂), Mondo, Papua.

11. Tachynomyia subfragilis Turner, 1940.

Turner, 1940*a*: 95 (♂), Kokoda, Papua.

Specimens examined: 8. *T. comata*: (i) Smith Coll. Pres. by Mrs. Farren White, 99–303 Mysul, New Guinea (Agrees with Type); (ii) Sattelberg, Huon Gulf, N. Guinea, Biro 1900. Det. Turner. 9. *T. fragilis*: (i) Type: Morty Island, (Wallace), W. W. Saunders coll. 1830–1873, Purchased and pres. '73 by Mrs. F. W. Hope. (*Anthobosca fragilis* teste F. Smith.) 10. *T. evelinae*: (i) Co-type Mondo, Papua, 5,000 ft.; (ii) 1934 L. E. Cheesman, B.M. 1934–321. 11. *T. subfragilis*: (i) Co-type as above, 1/ix/1933, 1,200 ft., L. E. Cheesman, B.M. 1934–321.

A study of the four species *Tachynomyia comata*, *T. fragilis*, *T. evelinae* and *T. subfragilis* has had to be made from seven specimens only and so a knowledge of the possible range of individual variation is non-existent. These species are very similar one to another and all have a strong resemblance to this widespread species, *Tachynomia flavopicta*. *T. flavopicta* with its latent capacity for variation, allometric, host-determined or otherwise, extends into New Guinea and Aru Island. Nothing has yet been discovered of its biology, host specificity, or the number of eggs deposited by the female upon the host and consequently the supply of food available to the developing larva.

It is interesting to note that, in the four type-specimens which represent *T. comata*, *T. fragilis*, *T. evelinae* and *T. subfragilis*, structural modifications are to be found in the occipital rim, the maxillary palps and in the hypopygium. These are in fact the same features set out above which vary in the four groups of *T. flavopicta*. The post-ocular region of the rim varies from groups III to IV, the maxillary palps are elongate, while the hypopygium is more or less spinescent.

In these four island species, the compound eyes protrude over the general surface of the head to a very marked extent and are larger relatively in size than in *T. flavopicta*. Furthermore, in *Tachynomyia flavopicta* (i) The supra-antennal crest is not completely divided; (ii) The post-ocelli are separated by a space which exceeds the diameter of median ocellus (Text-figs 7–8–13); (iii) The pronotum is slightly emarginate anteriorly.

A brief comparison is presented here of characters noted in *T. comata*, *fragilis evelinae* and *subfragilis* and these are summarized in Table 2. Comparisons of the shape of such structures as the supra-antennal crest can be confusing as, in profile, the outline is readily affected by the angle at which the head has been examined. Obviously, if tilted only slightly upwards or downwards the ratio between the antero-posterior and lateral axes can be considerably modified. This was especially noticeable in a re-examination of the supra-antennal crest of *T. evelinae*. It is most doubtful whether this structure has any real taxonomic value in *Tachynomyia* and it is to be investigated when that genus is revised. This variant has been noted in *Tachynomyia agilis*. The form of the structure is recorded here so that it may at least be considered in subsequent comparisons.

1. In *Tachynomyia comata*, the puncturing on the vertex and propodeum is medium sized (Pls v, vi, figs 3, 13), deep, circular and in contact. The supra-antennal crest consists of two conjoined arcs (Text-fig. 14); there are no distinct parapsidal sutures, and the hypopygium is trispinous. The length of the spines on the hypopygium varies from 0·2 to 0·4 mm.

2. *Tachynomyia fragilis* is an outstanding species and its golden colour is distinctive (Pl. vi, fig. 9). In the single specimen which is known to science, the punctae on the vertex are minute and separated by a space equal to the diameter of the punctures.

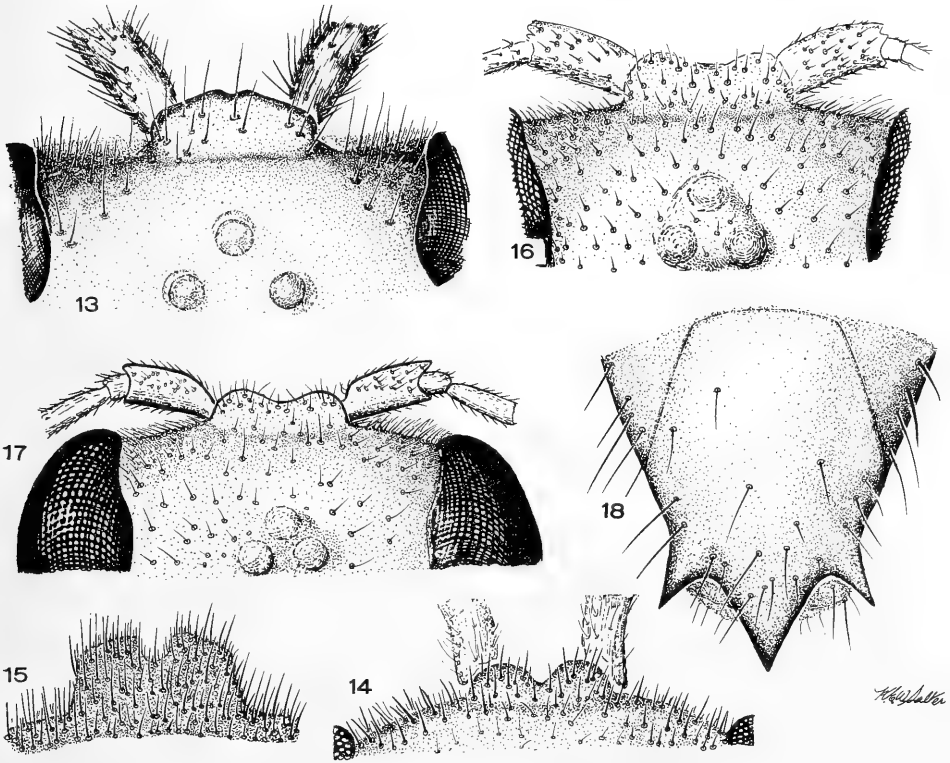
TABLE 2.

A Comparison of the Taxonomic Characters Separating Tachyomyia comata, T. fragilis, T. evelinae *and* T. subfragilis.

Taxonomic Character.	*flavopicta.*	*comata.*	*fragilis.*	*evelinae.*	*subfragilis.*
Puncturation and hair on vertex and propodeum :	(Pl. vi, fig. 12.)	(Pl. v, fig. 3.)	(Pl. vi, figs. 9–11.)	(Pl. v, figs. 4–5.)	(Pl. v, figs. 6–7.)
Shape and size on vertex.	Variable, large and small.	Medium sized, deep, circular, uniform.	Minute.	Medium sized, deep, irregular.	Medium sized, deep, polygonal.
Distribution on vertex	Scattered irregularly, not in contact.	All in close contact.	Each separated by a space equal to its diameter.	Confluent as dissepiments disappear.	Irregularly distributed, some in contact, many separated.
Shape and size on propodeum	Large, deep, polygonal.	Medium sized, deep, circular, uniform.	Minute, deep, circular, uniform.	Small and faint, shallow.	Very small.
Distribution on propodeum	Close contact.	All in close contact.	Each separated by space equal to its diameter.	Irregularly spaced, and separated by 2 to 3× diameter.	Scattered, far apart, separated by 6 to 10× diameter of punctae.
Hair on vertex ..	Sparse, transparent.	Closely covered with fine hairs of medium length.	Clothed with short, dense, golden fur, which is compact and even throughout.	Well covered with fine, transparent, brownish hairs of medium length.	Loosely covered with transparent, brownish hair of medium length.
Hair on propodeum	Sparse, long, transparent.	As above, but longer at sides.	As above.	Loosely covered with faint, transparent, silvery hairs of medium length.	Sparsely covered with fine transparent hairs of medium length.
Supra-antennal crest ..	Unite widestd, centrally with rudimentary notch.	Two conjoined arcs.	Rounded and divided by deep notch.	Bi-lobed.	One bi-lobed projection.
Space separating posterior ocelli.	Greater than diameter of median ocellus.	Less than diameter of median ocellus.	Less than diameter of median ocellus.	Less than diameter of median ocellus.	Less than diameter of median ocellus.
Post-occipital rim ..	Variable, see account of Groups I–IV.	As in *flavopicta* but intergradient between Groups III and IV.	As in *flavopicta*, Group III.	As in *flavopicta*, Group III.	As in *flavopicta*, Group IV.
Maxillary palp ..	Variable, see account of Groups I–IV. ..	Extends as far as 1st pair of coxae.	Extends half-way between 1st and 2nd coxae.	Extends beyond the 2nd pair of coxae.	Extends only beyond the 1st pair of coxae.
Pronotum	Slightly emarginate anteriorly, with collar. Rounded at sides.	Rounded at the sides.	Straight anteriorly, and angular at sides.	Rounded at the sides.	Rounded at the sides.
Parapsidal sutures ..	Present but not very distinct.	Indistinct.	Hidden beneath dense covering of hair.	Reasonably visible, and emphasized by row of hairs.	Very faintly visible.
Scuto-scutellar suture ..	Definite.	Present.	As above.	Very evident and almost as wide as the tegula.	Present and of normal width, less than half the width of tegula.
Hypopygium	Variable, see account of Groups I–IV.	Trispinous. Spines needle-shaped, median spine variable, may be excessively elongate.	Trispinous. Spines needle-shaped, median spine excessively elongate, 6× length of lateral spines.	Tridentate, as in *flavopicta*, Group I.	Tridentate, the median apex is laterally emarginate.

The size of the punctae may be assessed by the size of the crest which surrounds the foramen magnum and measures 0·8 mm. (Pl. vi, fig. 11, *a*—*a*). The head and thorax are covered by a short, close, lemon-coloured "fur" which is unique. The supra-antennal crest is rounded, but it is divided centrally by a deep, median notch (Text-fig. 15). The pronotum is quite straight along its anterior margin, and it is not rounded at the sides. The hypopygium is trispinous, the median spine arising from a triangle and extending six times the length of the laterals (Pl. vi, fig. 10).

3. On the vertex of *Tachynomyia evelinae*, the punctures are medium in size and deep (Pl. v, fig. 5), but their shape and size is not uniform as in *T. comata*. On the propodeum, the punctures are small, but as each is situated in a shallow depression,



Text-fig. 13.—*Tachynomyia flavopicta*. The supra-antennal crest is not completely divided and the post-ocelli are separated by a space exceeding the diameter of the median ocellus.

Text-fig. 14.—*Tachynomyia comata* (Smith). The supra-antennal crest consists of two flattened, conjoined, arc-shaped outgrowths.

Text-fig. 15.—*Tachynomyia fragilis* (Smith). The supra-antennal crest is rounded, but is divided centrally by a deep, median notch.

Text-fig. 16.—*Tachynomyia evelinae* Turner. The supra-antennal crest consists of two separate arcs.

Text-fig. 17.—*Tachynomyia subfragilis* Turner. The supra-antennal crest forms a single bi-lobed projection.

Text-fig. 18.—*Tachynomyia evelinae*. The hypopygium is broad and bears three cusps.

the lighting in this photograph is deceptive. Their size is better illustrated in the highlights than in the shadows (Pl. v, fig. 4). These punctures are scattered irregularly and could be as much as two or three diameters apart. The supra-antennal crest is bilobed (Text-fig. 16) as in *T. subfragilis*. The parapsidal sutures are visible and emphasized by a distinct row of hairs, while the scuto-scutellar notch is particularly well developed. The hypopygium in *evelinae* (Text-fig. 18) is somewhat similar to *flavopicta*, Group I (Text-fig. 10).

4. Unlike the three preceding species, in *Tachynomyia subfragilis* the punctures on the vertex are deep and polygonal, their distribution is irregular and they may or may not be in contact (Pl. v, fig. 6). On the propodeum, the punctures distinguish this species from the four other species as they are very small and scattered a considerable distance apart (Pl. v, fig. 7). The supra-antennal crest is bi-lobed (Text-fig. 17), as in *T. evelinae*. The parapsidal sutures are faintly visible (Pl. v, fig. 6). The reddish colour of the abdomen of the co-type is a colour not commonly found in thynnids.

12. Tachynomyia insularis (Smith), 1864.

Thynnus insularis, Smith, 1864: 26 (♀). D.T. 1897: 109. *Tachynomyia insularis* Turner, 1907: 290, Misol Island. Type: Oxford University Museum.

This specimen was collected by A. R. Wallace on Misol Island, west of New Guinea, and its description by Smith in 1864 is inadequate.

Turner in 1907 placed Smith's species in the genus *Tachynomyia*. No male partner has yet been found for Smith's *insularis* and the females of *atrata*, *fragilis*, *comata*, *subfragilis* and *evelinae* are so far unknown. As *T. flavopicta* (Ritsema) 1876 has a wide range, a female specimen from Meringa, North Queensland, was compared with Smith's description of *insularis*. Although Smith's description certainly differs from Turner's description of the female of *flavopicta*, any final decision as to the identity of the female of *insularis* would still be quite impossible from the writings of these two authors. Thus a century has passed and little has been contributed towards our knowledge of this species. Further collecting in Misol Island is most necessary.

13. Tachynomyia atrata (Cameron), 1911.

Aelurus atratus, Cameron, 1911: 197 (♂), Bivak Island, New Guinea.

No specimens were available of this species.

Neozeleboria Rohwer, 1910.

Rohwer, 1910: 347. *Zeleboria* Turner, 1910*c*: 32. (Not *Zeleboria* Saussure or Ashmead.)

Type species: *Neozeleboria sexmaculata* (Smith), 1859.

There are 19 species in this genus, and its complete revision is necessary. The maxillary palp with its three apical joints moderately elongate, the fourth joint the longest, as set down in Turner's key, 1910, is illustrated (Salter, 1957: 339).

14. Neozeleboria adelpha Turner, 1940.

Turner, 1940*a*: 94 (♂), Kokoda, New Guinea, Type: B.M. 15/268.

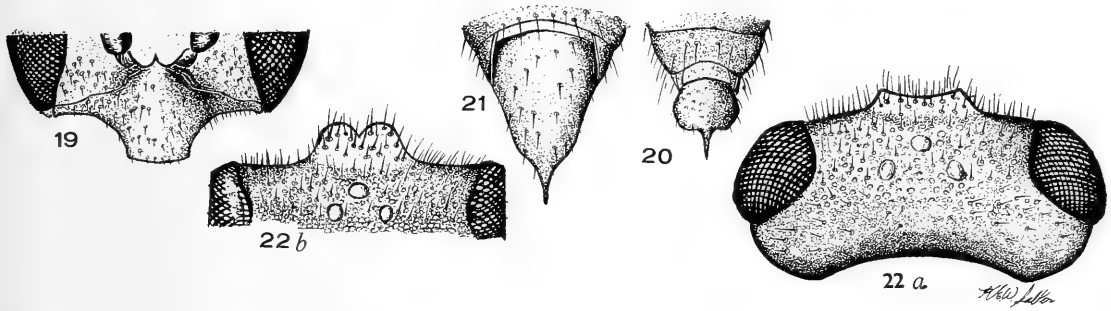
Specimen examined: (i) Papua, Mondo. 5,000 ft. Feb. 1934. L. E. Cheesman. B.M. 1934—321.

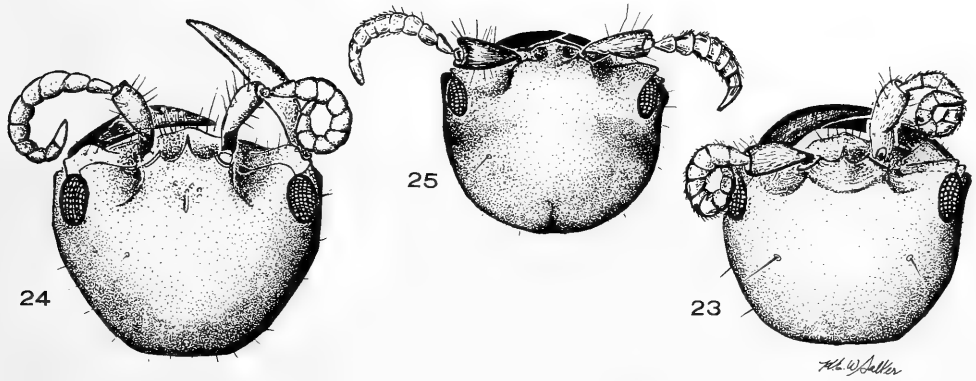
According to Turner (1940), his *Neozeleboria adelpha* is "very near some of the Australian species of the genus such as *N. trivialis* Smith". *N. trivialis* is a variable species which had also been described by Smith as *A. fulvifrons*, and as *T. impatiens*. To test Turner's statement, a comparison with all other *Neozeleboria* has been made and it was found that *adelpha* is actually much closer to *lacteimaculata* Turner, 1913. This latter species is found at Kuranda, north of Cairns, Queensland, while *trivialis* comes from Victoria and Western Australia.

The taxonomic characters which separate the single specimens of *adelpha* and *lacteimaculata* are not easy to define with any degree of precision, and to regard them as one and the same species would be excusable. The search for some reliable means of differentiation at the species level only emphasizes the closeness of this alliance. There is little doubt that *lacteimaculata* and *adelpha* are closely related species, and that *adelpha* is a northern extension of the range of *lacteimaculata*. Both are recorded from mountains of 3–4,000 feet. It is feasible to assume that *trivialis* could even represent the southern limit of the range of this species complex.

The hypopygium in *Adelpha* is expanded and rounded laterally and is broader than the ultimate (7th) sternite; it is heart-shaped and bears a median spine. By contrast, in *lacteimaculata* this structure does not increase greatly in width from the seventh

sternite and, narrowing gradually, it curves slightly, and becomes acute at its apex (Text-figs 20, 21). That this is a constant taxonomic character remains to be proved by the examination of a series of these two so-called species. Considering the variability of this structure in *Tachynomyia flavopicta* and in *T. comata* (Text-figs 10, 11, 12), it is quite probable that the hypopygium is also equally subject to individual variation in *Neozeleboria*. With only a single specimen of each, it is impossible to decide whether the differences observed are specific are subspecific. This is also applicable to the





Text-fig. 19.—*Neozeleboria adelpha* Turner, 1940. The clypeus is more or less truncate.

Text-fig. 20.—*Neozeleboria adelpha*. The hypopygium is expanded and rounded laterally and is broader than the ultimate (7th) sternite; it is heart-shaped and bears a median spine.

Text-fig. 21.—*Neozeleboria lacteimaculata* Turner. The hypopygium is not expanded and heart-shaped; it narrows gradually and terminates in an apical spine.

Text-fig. 22.—*Neozeleboria trivialis* (Smith). The supra-antennal crest. (*a*) It is not elevated in Smith's *trivialis* and it does not project anteriorly over the bases of the antennae. (*b*) In a form *impatiens* (Smith) 1879, regarded by Turner as a synonym, these crests are united at their bases and separated apically by a V-shaped incisure; they protrude beyond the median clypeal protuberance and antennal bases as in *N. adelpha*.

Text-fig. 23.—*Epactiothynnus dahli* (Turner), head of female. The shape of the occipital region is intermediate between *E. abductor* and *E. laevissimus*. There is a depression situated anteriorly between the antennae, thus a crescent-shaped crest is formed on the frons giving rise to a pair of prominences surmounting the antennal bases.

Text-fig. 24.—*Epactiothynnus abductor* (Smith), head of female. It is relatively narrower at the occipital end in this species than in *laevissimus*.

Text-fig. 25.—*Epactiothynnus laevissimus* (Smith), head of female. Lateral depressions are present behind the eyes which extend dorsally, and there is also a median posterior sulcus faintly indicated above the neck region. *E. laevissimus* was considered by Turner to be conspecific with *abductor*.

differences recorded in size, coloration and the boldness of the puncturation on thorax and abdomen. The individual variation in leg colouring shows that in this group of species this character is also of little value. In the specimen of *adelpha*, the legs are almost black and in *lacteimaculata*, the femur, tibia and tarsus are ferruginous. Reading Turner's description we find that the "Fore and intermediate tibiae and tarsi . . . are pale ferruginous".

N. adelpha is only 11 mm. in length, the black colour as described by Turner exceeds the yellow, puncturation on the thorax is not as strongly emphasized here as in the other species, and the abdominal tergites are sparsely punctate. The ratio of the postocellar line (POL) to the ocular-ocellar line (OOL) is: POL : OOL = 9 : 15 (Obj. × 40) or 60%. Although *lacteimaculata* is only a little larger, i.e. 14 mm., it is considerably more robust and its puncturation is much more strongly emphasized. The abdominal tergites are shallowly punctate and spaced 3–4 times their diameter apart. The POL : OOL ratio is as 13 : 18 or 72%.

In *adelpha*, *lacteimaculata*, and the various forms of *trivialis*, a comparison was made of such variables as the apex of the clypeus, and the supra-antennal crest.

Firstly, the clypeus: In the northern forms, the apex of the clypeus is more or less truncate in *adelpha* (Text-fig. 19) and slightly emarginate in *lacteimaculata*. In the southern species, *trivialis*, the tip of the clypeus is either truncate as in *N.t. impatiens* or rounded as in *N.t. trivialis*. The ratio between its apex and base differs considerably (Table 3).

TABLE 3.

A Comparison of the Ratios between Apical and Basal Dimensions of the Clypeus in Certain Species of Neozeleboria.

Neozeleboria sp.	Dimensions of Clypeus at:		Ratio of Apex to Base as a Percentage.
	Apex.	Base.	
	mm.	mm.	
adelpha	0·52	1·68	30·94
lacteimaculata	0·38	0·78	48·70
trivialis trivialis	0·40	1·95	20·51
t. impatiens	0·64	2·18	29·35

Secondly, the supra-antennal crest: In *adelpha* and *lacteimaculata*, the supra-antennal crests are united at their bases and separated apically by a V-shaped incision, and in lateral view the combined crests protrude above the base of the median clypeal protuberance and the antennal sclerites. These crests differ in *N.t. trivialis* and in *N.t. impatiens*; in the former, the crest is not elevated and does not project anteriorly above the bases of the antennae, while in the latter form of *trivialis*, the crests are united at their bases and separated apically by a V-shaped incision, just as in the northern species, *N. adelpha*. Obviously, series of these northern species are required to test the possible range of form (Text-figs 22*a*, 22*b*).

In *N. trivialis*, the POL : OOL ratio is as 18 : 20, i.e., 90%, and in *N.t. impatiens*, this ratio is 12 : 21, i.e. 57%. The head and thorax are very closely punctate and there are no spaces separating individual punctae. The abdominal tergites are devoid of puncturation. The hypopygium is narrower than the ultimate (7th) sternite; it narrows still further and becomes rounded at the apex and bears a median spine.

AGRIOMYIA Guérin, 1838.

Guérin, 1838: 218. Saussure, 1868: 116. *Agriomyia* and *Cephalothynnus* Ashmead, 1903: 100. *Agriomyia* Turner, 1908: 155. Turner, 1910*c*: 33.

Type species: *Agriomyia maculata* Guérin, 1838.

The first sternite of the abdomen bears an almost vertical tubercle which is an important feature in the recognition of the genus *Agriomyia* (Salter, 1957: Text-fig. 20).

15. AGRIOMYIA HERMANNI Turner, 1910.

Turner, 1910*e*: 408 (♂♀), Darnley Island, Torres St. Type: B.M. 15/150 (unduplicated).

Photomicrographs: Eight photomicrographs of the type represent the only material available.

This species is closely allied to the mainland forms but, without specimens to work on, its affinities with any particular species cannot be established. Identification of specimens should be possible from these Islands as there are four photomicrographs in colour, and four in monochrome of the type specimen, in the collection of illustrations made by the present author while in London.

EPACTIOTHYNNUS Turner, 1910.

Turner, 1910*c*: 37.

This genus was described by Turner in his *Genera Insectorum* and the type species selected was *E. crabroniformis* (Smith). There are twenty-three species described, and of these, five are recorded from the islands north of Australia. As in *Diamma*, *Rhagigaster* and *Tachynomyia*, it is not difficult to trace the affinities of the island species of *Epactiothynnus* to a particular species from the mainland, which could have given rise to these introductions. In contrast to the other genera from these regions, *Epactiothynnus* is characterized by the absence of any very pronounced taxonomic features, although the hypopygium and wing-venation are useful criteria. Firstly, the hypopygium is triangular and pointed, with prominent basal spines, and secondly, in that part of the vein M_{3+4}, bounded by the cell 2m (Tillyard, 1926), the ratio of its shorter component cut off by the cross-vein mcu_3 to the whole is approximately 13%. This is described as "very near" the base of the cell 2m (Salter, 1957: Text-fig. 17, p. 342).

16. EPACTIOTHYNNUS NITIDICEPS Turner, 1912.

Turner, 1912*b*: 535 (♂♀), Aru Island. Type: B.M. 16/204 *a* & *b*.

Specimens and photomicrographs examined: (i-ii) New Guinea, Papua, W. District, Oriomo Govt. Sta. 26–28.x.1960. Malaise trap, G. L. Gressitt. Seven monochromes and three colour photographs of the type (photographed 15/8/59).

The facial dimensions and the puncturation of the mesonotum are sufficiently distinct to separate this species from *abductor*, *dahli* and *vagans*. Further, if its size is of any real significance, *nitidiceps* measures only 7 mm., while the other three species vary from 10 to 15 mm. in length. The face of the type is illustrated (Pl. vi, fig. 14).

17. EPACTIOTHYNNUS VAGANS, 18. E. ABDUCTOR and 19. E. DAHLI.

17. EPACTIOTHYNNUS VAGANS (Smith), 1862.

Thynnus (*Agriomyia*) *vagans*, Smith, 1862: 51 (♂), Celebes. Type: (♂ & ♀), Oxford University Museum. Smith, 1877: 83 (♀). Schulz, 1906: 161. *T.* (*Aeolothynnus*) *vagans*, Turner, 1908*a*: 252.

18. EPACTIOTHYNNUS ABDUCTOR (Smith), 1865.

Thynnus abductor, Smith, 1865*a*: 78 (♂), Salwatty & New Guinea. Type: Oxford University Museum. *Thynnus laevissimus*, Smith, 1865*a*: 77 (♀). Type: Oxford University Museum. *T. candidus*, Smith, 1879: 171 (♂), Morty Island. Type: B.M. 15/208. *T. papuanus*, Cameron, 1911: 197 (♂). Type: B.M. 16/209. *Epactiothynnus abductor*, Turner, 1940*a*: 93 (♂♀).

19. EPACTIOTHYNNUS DAHLI (Turner), 1910.

Turner, 1910*b*: 278 (♂♀). Ralum, New Britain. Type: Berlin Museum.

Specimens examined: 17. *E. vagans*: (i) The type (♂), Gil.; (ii-iv) Three duplicates, N. Mollucas, O.m., South Batjan, vi-viii-1953, AMR Wagner Museum, Leiden. 18. *E. abductor*: (v) Papua, Kokoda, 1,200 ft., ix/1933. L. E. Cheesman, B.M. 1934—321. (Homotype) (♂); (vi) New Guinea, Cyclops Mts., Sabron, 930 ft., v.1936. L. E. Cheesman, B.M. 1936–271. (Homotype) (♂♀); (vii) Moluccas, 1953, W. Obi, viii-ix, Kasowari, 0–50 m. AMR Wegner (♂), Museum Leiden v.d.V. 55; (viii) N. Guinea, Biro

1899, Erima, Astrolabe Bay. *abductor* det. Turner, 103 Hungarian National Museum (♂♀). 19. *E. dahli*: (ix) *T.* (*Aelothynnus*) *dahli*, Turner, Type: (♂♀) New Britainnier, Ralam F. Dahl S.

The male specimens of *abductor* and the types of *Epactiothynnus dahli* and *vagans* are separated by only minor differences. The synonymy shows that *candidus* and *papuanus* were sunk by Turner as colour varieties and thus, unless very definite morphological criteria exist, it seemed extraordinary that this new species *dahli* was added in 1910. As time on sabbatical leave was extremely limited, the types of *E. dahli* and *E. abductor* were not exhaustively compared; however, the identity of the above specimens collected by L. E. Cheesman and listed here as numbers (v) and (vii) was verified.

(1) *The Clypeus*: The ratio between the width of the clypeus at apex and base in the specimens of *abductor* and the types of *dahli* and *vagans* is set out in Table 4. It is apparent that there is no difference between the facial features of *E. dahli* and *vagans*, but in the specimens identified as *E. abductor* the clypeus is relatively a little broader at the apex than it is in either of the former species.

TABLE 4.

A Comparison of the Ratios between Apical and Basal Dimensions of the Clypeus of Epactiothynnus vagans, E. abductor *and* E. dahli.

Epactiothynnus sp.	Dimensions of Clypeus at:		Ratio of Apex to Base as a Percentage.
	Apex.	Base.	
	mm.	mm.	
17. *E. vagans*			
(ii)	0·50	2·25	22·2
(iii)	0·50	2·125	23·5
(iv)	0·55	2·25	24·5
18. *E. abductor*			
(v)	0·70	2·12	33·0
(vi)	0·62	1·75	35·5
(vii)	0·42	1·55	29·0
(viii)	0·55	1·87	29·3
19. *E. dahli*			
(ix)	0·55	2·00	27·5

(2) *The First Pair of Coxae*: The determination of *E. vagans* from both *E. dahli* and *E. abductor* can be made by an examination of the fore-coxae, and in fact they provide the only real means of distinction. In *E. vagans* these structures are normally developed, they are rounded and roughly convex in shape and do not extend laterally beyond the edges of the proepisternum. In this species, the coxae are lightly covered with fine hairs (Pl. vi, fig. 16). By contrast, in the type of *E. dahli* and in the specimens of *abductor*, the procoxae are compressed and concave ventrally; they are extended laterally beyond the margins of the proepisternum. The ventral surface is densely covered with long, silvery-white hairs which have a brush-like appearance (Pl. vi, fig. 15).

(3) *Puncturation*: Smith's type of *E. vagans* (Pl. vi, fig. 17) is a little more robust and heavily chitinized than its duplicates from Bachan. A comparison of the puncturation of the mesoprescutum of *vagans*, *dahli* and *abductor* shows that the size of the punctae is uniform, and while the punctae are fairly closely crowded in *vagans*, they tend to become more diffuse in both *dahli* and *abductor*. In *vagans*, the punctae on the mesoprescutum are spaced roughly their diameter apart, leaving few open spaces which exceed twice the diameter of the punctae. By contrast, in *dahli* and *abductor*, the punctae are scattered unevenly on the anterior region of the mesoprescutum, leaving several gaps which may be as much as five times the width of the punctae. It is by no means certain that puncturation is a reliable taxonomic character.

(4) In describing the female of *abductor*, Turner (1940*a*) states: "Should this female prove to be identical with *laevissimus* that name having page priority must be used for the species." His description (1910*b*) of *dahli* concludes with: "The male is very near *abductor* Sm. and *vagans* Sm., but the female differs from that of *vagans* in the shape of the head and in the number of carinae on the second dorsal segment; in the latter character it also differs from *laevissimus* Sm., which is probably the female of *abductor*. The median segment is rather shorter and more rectangular than in either of the two species mentioned." The female of *vagans* was not available to the present author at the time of writing. The following comparison of the female specimens of *abductor* (B.M. 1936—271), *laevissimus* (Hungarian National Museum) and *dahli* (Berlin Museum), shows that: (i) In the females of *abductor* and *laevissimus* the overall length is 10 mm. and so they are both a little larger than *dahli* which is only 6 mm.; but size alone is not necessarily a taxonomic character. (ii) The head in the female of *abductor*, quoting from Turner (1910*a*), is: "Broader in the middle than long, gradually narrowed posteriorly and rounded at the posterior angles", and the same phrase naturally would apply equally well to the female specimens of both *laevissimus* and *dahli*. In *abductor*, the head is relatively narrower at the occipital end than it is in *laevissimus*. The shape of the occipital region in *dahli* is intermediate between *abductor* and *laevissimus* (Text-figs 23, 24 and 25). Other differences are apparent in the heads of these three female specimens. It is hoped that when long series are available, it will be possible to decide whether these species are valid or whether they are further examples of individual variation. Firstly, in the female of *E. laevissimus*, the head bears lateral depressions behind the eyes, which are extended towards the dorsal surface. There is also a median posterior sulcus faintly indicated above the neck region; these features do not occur in either *dahli* or *abductor*. Secondly, the female of *E. dahli* has a depression which is anteriorly situated between the antennae. The edge of this depression forms a crescent-shaped crest on the frons which gives rise to a pair of prominences surmounting the antennal bases. Such a feature is not present in either *laevissimus* or *abductor*. Thirdly, in both *dahli* and *abductor*, the clypeus bears a median vertical ridge extending laterally to the antennal bases; this crest is not strongly developed in *laevissimus*. (iii) In the three female specimens, the number of strong and weak carinae borne by the second abdominal tergite varies. In *abductor* there are five strong carinae and a weaker one hidden by the overlapping first tergite. In *laevissimus* and *dahli* only four strong carinae occur and, similarly, there is a weak carina hidden by the preceding tergite (Pl. vi, fig. 18). (iv) The pygidium in *abductor* is somewhat truncate; it terminates in small median and lateral lobes. By contrast, in *dahli*, it is elongate-ovoid, broader apically with a ratio of 15 : 37 between its axes; it is bounded laterally by a mass of long, golden hair.

The final determination of the relationship between *laevissimus* (female) and *abductor* (male) can only be made by reference to the types which are in Oxford and London. Miss Cheesman's specimen of the female of *abductor* does not agree with the specimen determined by Turner as *laevissimus* which was collected by Biro in 1899. Compared with the type-female of *dahli* there are many points of resemblance, but whether or not these two female specimens are conspecific cannot be fairly determined at this stage with so few specimens. There is no proof that the female collected by Biro was actually taken in copulation with his male specimen of *abductor*, nor has it been proved that it agrees with the female of Smith's original type in Oxford. Should *abductor* and *dahli* be sunk as synonyms of *vagans* (Smith) 1962? As separate species, no adequate picture is given of their close relationship and from a phylogenetic standpoint it seems preferable to regard them as subspecies.

The nearest relative to *abductor*, *dahli* and *vagans* in Australia is *Epactiothynnus bipartitus* (Turner), 1908. This species has a wide range and has been taken from Cairns, Ayr, Gordonvale, and Mackay in North Queensland, and from Groote Eylandt in the Gulf of Carpentaria. It is interesting to note that in *E. bipartitus* both the shape of and pubescence on the procoxae are intermediate between *vagans* and *abductor*.

It is very probable that this species extended its range from the Australian continent into Aru Island, New Guinea and the Celebes and gave rise to such forms as *abductor*, *dahli* and *vagans*.

EPACTIOTHYNNUS CONJUNGENS (Turner), 1908.

Thynnus (*Aeolothynnus*) *conjungens*, Turner, 1908*a*: 139 (♂♀). Mackay, Queensland, nec *productus* Montague, 1914: 649.

A report was presented to the Zoological Society of London by P. D. Montague on the fauna of the Monte Bello Islands in 1914. These islands form an archipelago off the coast of Western Australia from North West Cape to Port Walcott in a shallow sandy sea. They are visible from the low, swampy foreshores of the mainland, and consequently their fauna would not exhibit any marked insular characters. The list of Hymenoptera identified by Mr. Meade-Waldo is provisional; it includes *Epactiothynnus productus* (Turner), 1908, from Hermite Island. The collection on loan from the Western Australian Museum contains a specimen from Monte Bello Islands, No. 8566, but is undated. It was identified in the British Museum by the present author (1958–9) as *Epactiothynnus conjungens* (Turner), 1908.

20. EPACTIOTHYNNUS (?) TENUICORNIS (Smith), 1859.

Myzine tenuicornis, Smith, 1859*b*: 151 (♂). Aru Island. Type: Lost. *Epactiothynnus* (?) *tenuicornis* Turner, 1910*c*: 38.

Unfortunately, Smith's type cannot be located either in the British Museum or at Oxford, and nothing is known of this species. Its identity cannot be established from the description and it was listed in this genus with a query in the *Genera Insectorum*, 1910. It could be merely a colour variant of *abductor*.

ZASPILOTHYNNUS Ashmead, 1903.

Zaspilothynnus, Ashmead, 1903: 90.

Type species: *Zaspilothynnus interruptus* (Westwood), 1844.

This is a particularly large genus and its revision is essential. There are thirty-nine species and one, *Z. campanularis* (Smith), 1868, is found in both New South Wales and Lord Howe Island; three others are known from New Guinea, *Z. biroi* (Turner), 1910, *Z. placidus* (Smith), 1864 (= *Z. cheesmanae* Turner, 1940) and *Z. cyaneiventris* Rohwer, 1925.

The two genera *Thynnus* and *Zaspilothynnus* are closely related and can easily be recognized from other genera so far recorded from the islands. In both genera, the *clypeus* is considerably enlarged, the *frontal prominence* is conspicuous, the *sixth sternite* of the gaster bears a pair of postero-lateral spines and the *pygidium* is produced backwards into a flattened, plate-like crest (Salter, 1957: 348).

In the northern islands, the thirteen species of *Thynnus* and the three species of *Zaspilothynnus* can easily be distinguished. In *Zaspilothynnus*, the males do not have the combination of characters as detailed for *Thynnus* and, in the females, the absence of paired frontal sulci and the intervening frontal prominence seem to be reliable features for their separation.

21. ZASPILOTHYNNUS CAMPANULARIS (Smith), 1868.

Thynnus campanularis, Smith, 1868: 232 (♂), Sydney, Lord Howe Island. Type: B.M. 15/20. *T. leachiellus*, Olliff, 1889: 98. *Z. campanularis*, Turner, 1913: 616. *Zaspilothynnus lasius*, Montet, 1922: 223 (♂). Type: Muséum d'Histoire Naturelle de Genève.

Specimens examined: (i) Smith Coll. pres. by Mrs. Farren White, near Sydney. B.M. Duplicate 99–303; (ii) N.S.W. 1453, Macleay Mus.; (iii) N.S.W. 1454, Macleay Mus.; (iv) *Z. lasius*, N.S.W. Montet's Type; (v-xii) Lord Howe Island, Macleay Mus.; (xiii) Lord Howe Island, A. M. Lea, South Aust. Mus.

Colour alone is the only means of distinguishing Montet's *lasius* from the above series of specimens of *Zaspilothynnus campanularis* and, as no morphological differences exist, this species is considered to be conspecific with *campanularis* (Smith), 1868. In *lasius* the black pigment on the abdomen is represented by a rusty brown which could have resulted from chemicals used in killing bottles.

Z. campanularis is a most interesting species. It is closely related to *Z. interruptus* (Westwood), 1844, which was split by that author into a second species, *leachiellus*, in the same publication. The Lord Howe Island form of *campanularis* has evolved its own colour pattern and certain minor morphological differences. Also, it is closely related to a tropical species *Z. biroi*, the details of which are set out in the section which follows (Table 5). Thus in this complex, differentiation at both intraspecific and interspecific levels is illustrated. Furthermore, there is an interesting similarity between the geographically isolated forms, *biroi* in New Guinea and the Lord Howe Island race of *campanularis*.

On Lord Howe Island, the *campanularis* are more colourful than on the mainland; there is additional yellow on the anterior and posterior margins of the pronotum, and also on the prescutum, scutellum and episternum. Their coloration closely resembles *Z. biroi* from New Guinea, and these two species look so superficially alike that they could easily be confused. The possible range of individual variation in morphology between the mainland and island races of *campanularis* is demonstrated. There are slight differences in the relative dimensions of the components of the thorax, the propodeum, the gaster and the hypopygium. *Firstly*, in the three mainland specimens: (*a*) The propodeum is slightly angular between the sides and the concave posterior portion; (*b*) The sides of the gaster are almost parallel as far as the penultimate segment; (*c*) The hypopygium arises from a broad base and is extended laterally into acute cusps and centrally into a median triangular acumination, which is shorter than the space between the basal cusps. *Secondly*, by contrast in the Lord Howe Island forms: (*a*) The propodeum is rounded at the sides; (*b*) The gaster definitely narrows at the apex from the second segment; (*c*) The median acumination of the hypopygium forms a spine which is longer than the space between the basal cusps.

22. Zaspilothynnus biroi (Turner), 1910.

Thynnus biroi, Turner, 1910*a*: 117 (♂), Sattelberg, Huon Gulf, New Guinea, Biro, 1899; Turner, 1911*a*: 302. Type: Hungarian National Museum. *Z. biroi* subspecies *pratti*, Turner, 1912*a*: 51 (♂), Facfac, S.W. New Guinea.

Specimens examined: (i) The type, Sattelberg, Huon Gulf. (ii-vi) Wareo, Finsch Haven, New Guinea, Rev. L. Wagner, South Australian Museum (five duplicates).

Zaspilothynnus biroi is a yellow and black species which closely resembles such mainland species as *Z. campanularis*, *Z. stratifrons* Turner, 1917, and *Z. interruptus* (Westwood), 1844. Available records of the distribution of these three species show that they have been found principally in New South Wales and Southern Queensland, and *Z. biroi* appears to be a northern form of this complex. It does not seem to be related to *Z. vernalis* (Turner), 1908, which occurs in Mackay, North Queensland. A comparison is set out in Table 5 of the characteristic features separating *biroi* from *campanularis* and *interruptus*. There appears to be a close parallel in shape and colouring between the Lord Howe Island variety of *campanularis* and the tropical species, *Z. biroi*. These two species may both be examples of habitat variation. Of the subspecies, *pratti*, Turner states: "♂. Differs from the typical form in the narrower hypopygium, and in the greater development of the yellow markings." Thus, there is some evidence of variability within this species.

Z. biroi, *Thynnus olivaceus* and *Thynnus celebensis* have a colour pattern which is more or less similar, but to confuse them would be impossible, as the generic characters are distinguishable. The propodeum and first segment of the gaster in *biroi* have no resemblance to *Thynnus dentatus*, the type species. Further, the median sulcus on the frons, which is so distinct in *T. olivaceus*, is absent in *biroi*. The hypopygium is not pentaspinous as in typical *Thynnus* but resembles *T. erraticus* (Text-fig. 28). As in *Zaspilothynnus placidus* there is a transverse preocellar crest joining the inner margins of the eyes, while in contrast to *placidus*, the parapsidal sutures form deep clefts and no transverse ridge is present on the propodeum. In *biroi*, there seems to be a tendency for the episternal region to be dilated and cut across by a furrow; the first, second and third tergites of the gaster are slightly constricted.

TABLE 5.

A Comparison of the Clypeus, Frontal-prominence, Mesoscutum, Mesepisternum, Metanotum, Propodeum, Pygidium and Hypopygium of Zaspilothynnus biroi, Z. campanularis *and* Z. interruptus.

	Z. biroi.	*Z. campanularis.*	*Z. interruptus.*
Clypeus	Punctate and intermittently striate.	Punctate and distinctly striate.	Sparsely punctate; evenly and strongly striated.
Frontal prominence	Linear puncturation with a clear, smooth, non-punctate longitudinal area.	Closely punctate with pronounced median, longitudinal, elevated ridge, which meets the supra-antennal crests forming an anchor-like structure.	Closely punctate with median, longitudinal striation meeting antennal crests.
Mesoscutum: edges of parapsides and the scuto-scutellar suture.	Meet at an angle.	Form a curve.	Meet at an angle.
Mesepisternum	Strongly inflated and slightly furrowed.	Neither strongly inflated nor furrowed.	Not strongly inflated, with a short, clear, non-punctate linear mark.
Hairs on metanotum	Golden-brown.	Silvery.	Transparent and colourless.
Propodeum	Rounded, dorsally and ventrally.	Posterior surface flattened and slightly concave but not expanded transversely or inflated. (*a*) Mainland form angular at junction of sides with posterior concavity. (*b*) Island form rounded at junction of sides and rear surface.	Posterior surface flattened and expanded transversely, giving slight lateral bulges and inflated sides.
Pygidium	Bluntly rounded and intermittently striated.	Sharply rounded; finely and evenly striated.	Sharply rounded; finely and evenly striated.
Hypopygium	As in *T. erraticus* (Text-fig. 28).	Narrowly produced to apex, with strong basal cusps.	Triangular, with strongly pronounced median and basal spines.

23. ZASPILOTHYNNUS PLACIDUS (Smith), 1864 and ZASPILOTHYNNUS CHEESMANAE (Turner), 1940.

Thynnus placidus, Smith, 1864: 26 (♂), Waigiou. Type, Oxford University Museum; Turner, 1908*a*: 251 (♂). *Zaspilothynnus cheesmanae* Turner, 1940*a*: 92 (♂), B.M. 15/226.

Specimens examined: (i) *Thynnus placidus*, Type: Waigiou Island (Wallace) W. W. Sunders coll. (1830–1873). Purchased and pres. '73 by Mrs. W. F. Hope, Oxford University Museum; (ii) *Zaspilothynnus cheesmanae*, Co-type: New Guinea, Cyclops Mts., Mt. Lina. 3,500 ft. 1936. L. E. Cheesman, B.M. 1936—271, (Turner) British Museum 15/226.

Thynnus placidus was placed by R. E. Turner at the end of his revision of 1908 with other thynnids occurring beyond Australia. In the *Genera Insectorum*, 1910, it was listed again in the genus *Thynnus*. That this species did not conform to the generic characters given appears to have been overlooked. The hypopygium is triangular with two basal spines and a median apical spine; the propodeum is not vertically 'truncate' and the scutellum here bears no resemblance to the type species *Thynnus dentatus*. The frontal-sulcus found in *Thynnus* is absent.

Text-fig. 26.—*Zaspilothynnus placidus* (Smith), profile of portion of the thorax. The scutellum is strongly convex and rounded and elevated into a little hump.

Text-fig. 27.—*Thynnus erraticus* Smith, portion of thorax in profile. The scutellum is elevated above the mesoprescutum; it is also convex and rounded, but does not form a hump.

Text-fig. 28.—*Thynnus erraticus*, hypopygium. Here the structure is atypical as the characteristic pair of sub-apical spines are represented by lateral expansions on either side of the median, apical spine.

At the end of Turner's very valuable series of contributions, which extended over a period of more than thirty-three years, *Zaspilothynnus cheesmanae* was described. Except for the lemon yellow colour present on the clypeus, the supra-antennal ridge and the ant-orbital margins, its co-type would be quite indistinguishable from Smith's type of *Thynnus placidus*. There is no doubt that *T. placidus* and *Z. cheesmanae* are conspecific and that *placidus* has the characteristic features of the genus *Zaspilothynnus*, and could not therefore be confused with any of the species listed in this paper. As in all *Zaspilothynnus*, the frontal region, when examined laterally, does not form a continuous curve extending from the apex through to the vertex, and no hairless prominence is developed from the median ocellus to the supra-antennal ridge. Instead a transverse crest crosses the frons in front of the median ocellus, and surmounting the supra-antennal ridge there is a tuft of long yellowish-brown hairs. Unlike *Thynnus erraticus*, the angle subtended by the supra-antennal ridges and the median vertical axis is about 63°. The parapsidal sutures also help to distinguish *Zaspilothynnus placidus* (Smith) from *Thynnus erraticus*. In *Z. placidus*, the suture lies in a shallow depression which is closely punctate. The scutellum in profile is strongly convex and rounded and is elevated into a little hump (Text-fig. 26).

24. Zaspilothynnus cyaneiventris Rohwer, 1925.

Rohwer, 1925: 416, Pl. i, F. 2–3 (♂♀), New Guinea. Types: U.S. National Mus. Omitted, as no specimens were available.

Thynnus Fabricius, 1775.

Thynnus Fabricius, 1775: 360. *Myrmecodes* Latreille, 1809: 118. *Homalothynnus* Enderlein, 1904: 466.

Type species: *Thynnus dentatus* Fabricius, 1775.

The characters of the specimens examined from these territories are: *Male*: *Antennae* shorter than thorax. *Propodeum* with median axis considerably reduced. Consequently, its surface is nearly vertical and may be either flattened or slightly rounded. *Abdomen*, with first tergite truncate and a tendency, which varies, towards a conical shape. *Female*: *Frons* with longitudinal, median prominence separating a pair of smooth, lateral sulci, which encompass the antennal bases.

One of the species listed by Turner as in the genus *Thynnus* has been removed and placed in *Zaspilothynnus*. This species is *placidus* (Smith) 1864, as its characters agree with *Zaspilothynnus* rather than *Thynnus*, and, furthermore, it also corresponds very closely with Turner's *Zaspilothynnus cheesmanae*. Thus the total number of species in *Thynnus* now stands at twenty-five.

Specimens of *Thynnus albopilosellus* Cameron, 1906 (♂) from New Guinea and *T. bakeri* Rohwer, 1925 (♂♀), Mindanao, have had to be omitted owing to lack of material. The male of *T. calvus* Turner, 1910, is not so far established and the species is known from the female only.

According to the literature, thirteen of the twenty-five species of the genus *Thynnus* range through these northern islands and there are twelve species found on the Australian continent. Nine of these mainland forms are limited to Queensland, Northern Territory and north-west Australia. There are three species, whose range extends from the north to the south. These are *pulchralis* Smith, 1859, Adelaide to Cooktown, *ventralis* Smith, 1865, King George Sound to north-west Australia, and *zonatus* Guérin, 1838, Swan Rv. to north-west Australia.

A study of the specimens, photomicrographs or descriptions of the males of twelve species of the genus *Thynnus* recorded from this region shows that there are four species which are almost black and so similar in form that they may be considered conspecific. They are: *T. pullatus* from Bouru Is., *lugubris* from Ceram, *barbarus* from The Solomons and *atratus* from Gilolo. As these species are so very similar, this group is referred to in the present paper as the *atratus* complex. There are such species as *olivaceus*, New Guinea, *luzonicus*, Luzon Is., and *mutandus*, Aru, which are also closely allied to this *atratus* complex, but owing to their distinctive, yellow colour pattern they are recognizable at first sight as superficially differing from the wasps which are almost black. Closer examination shows that there is little morphological difference separating the yellow and black forms from species without the yellow ornamentations. There are two other species which are similarly marked with yellow following the same distinctive pattern; these are *serriger* Sharp, 1900, New Britain, and *celebensis* Turner, 1910*a*, Celebes; both these two species differ by recognizable characters from all of the foregoing. Although it is acknowledged that colour is a most unsatisfactory means of discrimination in these insects, the forms which are ornamented with yellow are considered together merely for convenience as the *serriger* group. These two groups are simply used as terms of reference, and it is hoped that a sufficiently large series will be examined in order to establish the true phylogenetic relationship existing between this assemblage of thirteen species. Whereas the presence or absence of a conspicuous, yellow, colour pattern in the males, easily distinguishes four plain from five ornate species, no such differentiation is apparent in the six corresponding females available for examination. The females so far studied can be arranged in a sequence according to the form of the frontal structures and it is anticipated that an investigation of the remainder may reveal the existence of a cline.

Specimens of *luzonicus* and *mutandus* are not available at present and, instead, a series of photographs have had to be used.

25. Thynnus erraticus Smith, 1861.

Smith, 1861: 114 (♂), Batchian. Type: Oxford University Museum. Turner, 1908: 251.

Specimens examined: (i) *T. erraticus*, Smith: Type, teste F. Smith, in coll. W. W. Saunders, 1830–1873. Purchased and presented '73 by Mrs. F. W. Hope, Oxford University Museum. (ii) Isl. Halmaheira, Kau (sea level) 26, 31–X–1951.

Thynnus erraticus is intermediate between *Thynnus* and *Zaspilothynnus*, and it could be regarded as a link between these two genera. In Turner (1910*c*), the presence or absence of a pentaspinous hypopygium was the taxonomic character used in his generic key as a couplet for their separation. In the type of the genus, *Thynnus dentatus*, five distinct spines are visible, whereas in *T. erraticus* the pair of subapical spines is represented by lateral expansions situated on either side of the median apical spine (Text-fig. 28). Other species of *Thynnus* in which the typical penta-spinous hypopygium does not occur are *T. brenchleyi*, *T. darwiniensis* and *T. zonatus*. More reliance can be placed on the facial features viewed in profile. In common with all other examples of the genus, this profile follows an almost continuous curve from the clypeal apex, through the epistomial bridge, the supra-antennal crest and the frontal prominence, to the ocelli on the vertex. The epistomial bridge and the supra-antennal crests are on the same level, and the angle subtended by the sides of the supra-antennal crests and the median axis is about 45°. The frontal prominence is devoid of a sulcus, although there is a median glossy line extending faintly from the ocellus, and there are brownish hairs scattered sparsely over its surface. A slight ocellar pyramid is present on the vertex.

In the thorax, the parapsidal sutures are deep, with sixteen little cross-connections, and the general distribution of the puncturing closely resembles *Thynnus barbarus*. The scutellum differs from *Thynnus dentatus* as, instead of the typical flattened and almost horizontal mesonotal surface, in *T. erraticus* the scutellum (Text-fig. 27) is elevated above the mesoprescutum; it is convex and rounded, but does not form a hump as in *Zaspilothynnus placidus*. The scuto-scutellar suture is very deep. The reduction of the longitudinal axis of the propodeum which is characteristic of the genus *Thynnus* is not excessive in this species. The colour of the legs tends to vary, as in Smith's type specimen they are a rusty-brown, while the specimen from Halmaheira has black legs.

26. Thynnus olivaceus; 27. T. serriger; 28. T. mutandus; 29. T. luzonicus; 30. T. calvus and 33. T. celebensis.

26. Thynnus olivaceus Turner, 1908.

Turner, 1908*a*: 251 (♂); Turner, 1940*a*: 91 (♀), New Guinea. Type: British Museum 15/2 a & b.

27. Thynnus serriger Sharp, 1900.

Sharp, 1900: 388 (♀); Turner, 1908: 251; Turner, 1910*a*: 119 (♂), New Britain. Type: British Museum 15/3 a & b.

28. Thynnus mutandus Turner, 1912.

Turner, 1912*b*: 544 (♂♀), Aru Island. Type: British Museum 15/4 a & b.

29. Thynnus luzonicus Turner, 1908.

Turner, 1908*b*: 65 (♂); Rohwer, 1925: 419 (♀), Albany, Polillo Island, Luzon. Type: British Museum 15/1.

30. Thynnus calvus Turner, 1910.

Turner, 1910*a*: 121 (♀) (♂ unknown), Mafor. Type: Hungarian National Museum.

33. THYNNUS CELEBENSIS Turner, 1910.

Turner, 1910*a*: 122 (♂♀), North Celebes. Type: Hungarian National Museum.

Specimens examined: 26. *T. olivaceus*: (i) Roon, Ex. coll. Fruhstorfer (♂) (det. by Turner); (ii, iii) (♀) Mt. Lamington, N.E. Papua, 1300–1500 ft. C. T. McNamara, South Australian Mus. 27. *T. serriger*: (i) Finschhafen, N.G., Sept.-Nov. 1943, (♂), D. H. Colless; (ii) N. N. Guinea, Hollandia, Bylslag, xii-1937, (♂), M. E. Walsh, Museum Leiden; (iii) Nieuw Guinea, Bijlslag bij Hollandia, (♂), J. v. d. Vecht, Museum Leiden; (iv) New Ireland (SW), Ridge above Camp Bishop, 15 km. up Kait R., 250–500 m. VII–11–1956, (♂). Bishop Museum; (v) New Ireland (SW), "Camp Bishop", E. J. Ford Jnr., Collector, 15 km. up Kait R., 125 m. VII–11–1956, (♀). Bishop Museum. 28. *T. mutandus*: One monochrome and four colour slides of B.M. type 15/4 (♂). 29. *T. luzonicus*: Three monochromes and four colour slides of B.M. type 15/1 (♂). 30. *T. calvus*: (i) Type, (♀), Mafor, Fruhstorfer. 33. *T. celebensis*: (i, ii) Type and co-type, (♂♀); (iii) Co-type, (♂), Nord Celebes, Toli Toli, Nov.-Dec., 1895, H. Fruhstorfer, Hungarian National Museum; (iv) N. Celebes, Mahasa Batoer, 7/vii/1941, F. Dupont, (♂), leg. Museum Leiden.

Thynnus olivaceus, *serriger*, *mutandus*, *luzonicus* and *celebensis* are large wasps with a similar pattern of yellow markings. They have been referred to by Turner as the *serriger* group. In contrast, is a second group, the *atratus* complex, which includes four almost entirely black species. This colour distinction is only superficial and, as far as is known, does not apply to the females. The male of *calvus* has never been described. At present, the construction of a key is impracticable, as this contribution is based on identified specimens of three species only, *olivaceus*, *serriger* and *celebensis*. *Thynnus mutandus* and *luzonicus* are represented here by a series of twelve photographs of B.M. types 15/1 and 15/4 taken by the present author while in London.

As a means of separating these species, the shape and puncturation of the gaster could be of some value. The relative width of the abdominal segments separates (i) *T. serriger* and *celebensis* from (ii) *T. olivaceus*, *mutandus* and *luzonicus*. Furthermore, in (i) *serriger* and *celebensis*, the first segment of the gaster is slightly wider than the second to the fifth segments, while, by contrast, in (ii) *olivaceus*, *mutandus* and *luzonicus*, the first segment of the gaster is not as wide as the second.

In (i) *serriger* may be recognized from *celebensis* by both the shape of the gaster and puncturation. In *serriger*, the width of the abdomen decreases evenly from the second segment to the apex, and thus the gaster is conical in shape. By contrast, in *celebensis* the second and third segments are about equal in width and the abdomen narrows posteriorly from the middle of the fourth segment. If puncturation is a reliable taxonomic character, then *celebensis* stands out distinctly from *serriger* and also from *olivaceus*, *mutandus* and *luzonicus*. The punctae in *celebensis* are spaced apart by a distance equal to or less than their diameter. In the four other species, the space between the abdominal punctae is greater than the diameter of the punctae.

As regards (ii) *olivaceus*, *mutandus* and *luzonicus*, their discrimination is difficult from photographs. If, however, the details of the puncturation and parapsidal sutures on the mesonotum have any taxonomic significance, then an examination of the colour slides of *T. mutandus* and *luzonicus* shows: Firstly, that in *mutandus* the parapsidal sutures form very distinct grooves which bend near the posterior third towards the median axis and, also, that the punctae on the parapsides are not evenly and densely crowded. Secondly, in *luzonicus*, the parapsidal sutures are comparatively straight and the punctae on the parapsides are evenly and densely crowded. Thirdly, a comparison of these features with the specimen of *olivaceus* shows that the parapsidal sutures do not resemble *mutandus* and have a tendency to curve outwards rather than inwards, and also that the parapsides are closely and evenly punctate.

Of *mutandus*, Turner writes: "This belongs to the group of *T. serriger*, Sharp, and is nearest to *T. celebensis*, Turn., from which the male differs in the sparser puncturation, in which it approaches more closely to *T. olivaceus*, Turn. From both of these species it differs in the truncation of the hypopygium."

31. THYNNUS PULLATUS; 32. T. LUGUBRIS; 34. T. BARBARUS; 35. T. ATRATUS.

31. THYNNUS PULLATUS Smith, 1864.

Smith, 1864: 26 (♂♀), Bouru Island. Type: Oxford University Museum; Turner, 1908: 251.

32. THYNNUS LUGUBRIS Smith, 1864.

Smith, 1864: 25 (♂), Ceram. Type: Oxford University Museum; Turner, 1908: 250; Turner, 1910*a*: 118 (♀), Ceram. Hungarian National Museum.

34. THYNNUS BARBARUS Turner, 1910.

Turner, 1910*d*: 72 (♂♀), Solomon Islands. Type: B.M. 15/5 a & b.

35. THYNNUS ATRATUS Smith, 1862.

Smith, 1862: 51 (♂), Gilolo. Type: Oxford University Museum; Smith, 1865*a*: 77 (♀), Gilolo. Type: Oxford University Museum; Turner, 1908: 250.

Specimens examined: 31. *T. pullatus*: (i) (♂♀), Bouru Island. W. W. Saunders coll. (1830–1873). Purchased and presented '73 by Mrs. F. W. Hope. 32. *T. lugubris*: (i) (♂♀), Ceram. Jllo. C. Ribbe 1884. 781.18 Turner coll. 1909–49. Hungarian National Museum. 34. *T. barbarus*: (i-ii) W. W. Froggatt, Solomon Isl. Jul.-Aug. 1909. (Co-type ♂), B.M. & C.S.I.R.O.; (iii) Sneillius Exp., Ambon 18. Oct. 1930 (♂), Leiden Museum. 35. *T. atratus*: (i) det. Smith (♂), Gilolo. Smith coll., pres. by Mrs. Farren White, 99–303. B.M.; (ii) Bernstein, Morotai. (♂); (iii) Morty Isl. S. (♀); (iv) Bernstein, Galela, Halmah. (♀), Leiden Museum.

Thynnus atratus (♂♀), *T. pullatus* (♂♀) and *T. lugubris* (♂) were described from the collections made by Alfred R. Wallace, while *Thynnus barbarus* was described from several specimens from the Solomons, which Walter W. Froggatt of the N.S.W.D.A. sent to R. E. Turner for identification. The four species are represented in the British Museum, the Oxford University Museum, the Hungarian National Museum, and the Leiden Museum, by only ten males and six females; there is also a specimen of *T. barbarus* in the possession of C.S.I.R.O. Suitable diagnostic characters are not included in earlier literature.

The males of this group closely resemble one another. The differences separating them are very slight, and it is conceivable that when large series of specimens are available from various islands it may be decided that *pullatus*, *lugubris* and *barbarus* are subspecies of *atratus*. It has been found that differences in individual variation may be actually greater, within a single thynnid species, than the features which distinguish the males of this group of four species. Large samples of this population complex are required. The retention of specific status, however, is supported by a study of the females; *T. pullatus*, *lugubris* and *atratus* are quite distinct and have been considered with the females of *olivaceus*, *serriger* and *celebensis*. It is appreciated that some of these specimens were collected a hundred years ago and it has not so far been finally proved that all were authentically paired.

A comparison has been made of minor dissimilarities recognizable in the few available males: (i) the shape of the abdomen, (ii) and (iii) slight differences in form and puncturation of the frontal prominence, (iv) and (v) insignificant differences in puncturing of clypeus and mesoprescutum. It has already been noted that, in the Thynnidae, puncturation and sculpture are subject to individual variation. In taxonomy, these features may have as little value as colour variants.

(i) *The Abdomen*: In *atratus* and *barbarus*, the gaster is truncate anteriorly and conical in shape; the first and second segments are equal in width as in *serriger* and *celebensis*. By contrast, in *pullatus* and *lugubris*, it is truncate and rounded anteriorly; the first segment is slightly narrower than the second and curves inwards, as in *olivaceus*.

(ii) *The Frontal Prominence*: In the genus *Thynnus* this is a feature which is usually present. It is an extension of the vertex to form an elevated portion of the frons. It is continuous with the supra-antennal crests overlying the antennal bases and,

in profile, the head presents an uninterrupted curve from the clypeal apex to the ocelli on the vertex. In *Thynnus* there are a number of species in which this frontal prominence bears a median sulcus between the anterior ocellus and the antennal bases (Pl. vii, figs 21–24).

In the *atratus complex* modifications in the frontal prominence are related to the depth and breadth of this median sulcus. In the type specimen of *Thynnus pullatus*, this sulcus forms a deep cleft with walls which are fairly steep and, as a consequence, the prominence in this species is partly divided to form two longitudinal crests (Pl. vii, fig. 21). Comparison between *Thynnus lugubris* and *T. pullatus* shows that the breadth of the median sulcus is practically the same in each case. However, in *T. lugubris* it does not seem to be as deep (Pl. vii, fig. 22). The shape of the median sulcus in *T. barbarus* and *T. atratus* distinguishes these two species from both *T. pullatus* and *T. lugubris*. The sulcus in both *barbarus* and *atratus*, instead of being comparatively deep and narrow as in *pullatus*, is represented here by a broad and relatively shallow fossa with boundaries which are ill-defined (Pl. vii, figs 23–24). In order to differentiate between these specimens a comparison has been made of the structure of the frontal prominence.

TABLE 6.

A Comparison of the Details of Surface Puncturing of the Frontal-prominence of the Males of Thynnus pullatus, T. lugubris, T. barbarus *and* T. atratus (Pl. vii, figs. 21–24).

	31 *T. pullatus.*	32 *T. lugubris.*	34 *T. barbarus.*	35 *T. atratus.*
Shape and size of punctures:	Amorphous, rounded to elongate.	Amorphous, rounded to elongate.	Two sizes, medium and small. *Medium:* On elevated regions, circular, oval and confluent with a tendency to form rows. *Small:* On median sulcus, three rows on each side of median, glossy line. (Solomon Islands.)	Two sizes, medium and small. *Medium:* On elevated regions, oval, sparse and scattered. *Small:* Floor of median sulcus, three rows on either side of groove.

T. pullatus: In *pullatus*, the frons extends from the vertex as two longitudinal crests which terminate in the ridges overlying the antennal bases. These crests are separated by a deep cleft forming a fossa with almost vertical walls. This cleft is more or less open near the anterior ocellus and closed towards the antennal crests. Along the floor of this fossa is a distinct crease (Pl. vii, fig. 21).

T. lugubris: The extension of the frons resembles *pullatus*, but the median fossa is not as deep and the central crease is absent. The edges of this fossa are clearly designated, and the fossa is closed definitely at each end (Pl. vii, fig. 22).

T. barbarus: This species has a general similarity to both *pullatus* and *lugubris* but the boundaries of the fossa are not so sharply defined. There is a visible, central crease (Pl. vii, fig. 23).

T. atratus: Here the fossa is broad, shallow and open, and is quite distinct from the other examples (Pl. vii, fig. 24).

(iii) *Puncturation of the Frontal Prominence*: A comparison of the dimensions of the punctae on the frontal prominence in *T. lugubris* and *T. pullatus* shows that in these two species no significant difference exists in the size, shape, or even perhaps distribution, of the punctae on this region. In *barbarus* (Solomons), the median sulcus is dotted with evenly distributed micro-punctae (Table 6).

In three specimens of *T. barbarus*, the puncturation of the frontal prominence is not constant. In Froggatt's specimen (Pl. vii, fig. 23) the seven or eight rows of medium-sized punctae lie parallel to the median axis of the head, whereas, in the specimen from Leiden, the punctae are fused longitudinally to form a series of grooves

and intervening ridges. Froggatt's specimen from C.S.I.R.O. resembles *lugubris*. The two specimens of *atratus* differ and in both examples there appears to be a reduction in the size and number of punctae by comparison with the other specimens in this complex. The specimen from Gilolo is less punctate than the specimen from Morotai.

(iv) *The Surface Puncturing of the Clypeus*: It is most doubtful whether this character has any systematic value, as an examination of large series of individuals of the same species shows that it is variable. This is well illustrated by the sculpture of the clypeus in *Dimorphothynnus fimbriatus* (Smith), 1859. The following table is included here with the illustrations in Plate vii for the sake of completeness. There is a tendency for a linear arrangement of these punctae and their intervening ridges to develop, and this feature could separate *barbarus* from *pullatus*. Between these two examples, however, is *lugubris* which seems to combine the characters of both these species. As regards *atratus*, the two specimens examined differ. The specimen of *atratus* from Gilolo agrees with *barbarus*, while the Morotai specimen has a sparse puncturing intermingled with a series of concentric ovals which seem to be centred medianly along the clypeus and roughly following its longitudinal axis (Pl. vii, figs 21–24), (Table 7).

TABLE 7.

A Comparison of the Details of Surface Puncturing of the Clypeus of Thynnus pullatus, T. lugubris, T. barbarus *and* T. atratus (Pl. vii, figs. 21–24).

	31 *T. pullatus.*	32 *T. lugubris.*	34 *T. barbarus.*	35 *T. atratus.*
Shape of punctae:	Shallow, broad and more or less rounded.	Shallow, broad and rounded.	Deep, narrow and oval shaped.	Shallow and amorphous.
Distribution and pattern of puncturing.	Discrete, non-confluent, in contact but separated by a rounded dissepiment. The punctae tend to form rows both laterally and at anterior margin of clypeus.	Some are discrete but many are confluent forming rows which extend longitudinally.	The lateral extremities of the punctae give rise to a series of little, parallel, linear ridges which run towards the anterior margin of the clypeus.	Elongate ridges and grooves which may form a pattern of irregular concentric ovals.

(v) *The Puncturing of the Mesoprescutum*: It is very doubtful if a future systematist could ever separate a long series of *pullatus* from *lugubris* by means of the mesoprescutum alone. Yet the types are different, as indicated by the accompanying illustrations (Pl. viii, figs 25–28). In the types, the punctae in *lugubris* are a little more uniformly rounded and evenly spaced than those of *pullatus* and, furthermore, per unit area there is a higher density of puncturation in *lugubris* than in *pullatus*. In *pullatus* most of the punctae are separated by a space which is twice to three times the diameter of the punctae. In *lugubris*, the average spacing apart of the punctae would be roughly equivalent to the diameter of the punctae and so a slight tendency to the formation of ridges results. Two specimens of *barbarus* show that the puncturation is not constant. The specimen from Ambon resembles *pullatus*, while the co-type from the Solomons shows an antero-median region in which a reduction in puncturation density occurs. In this respect *barbarus* resembles *atratus*. The specimen from Morotai also shows a thinning of the puncturation density in the central region of the mesoprescutum and this feature seems further accentuated in the one collected at Gilolo.

With only seven males available, it is difficult at present to decide whether they represent (i) four valid species or (ii) merely individual variants. The puncturation cannot always be regarded as a constant character, especially in the larger thynnids. Subsequently, it will be interesting to discover whether the modifications of the frontal prominence form a cline ranging from *pullatus* to *atratus*.

TABLE 8.

A Comparison of Diagnostic Characters in the Females of Thynnus.

	olivaceus.	*serriger.*	*calvus.*	*celebensis.*	*lugubris.*	*atratus.*
Paired frontal fossae	Contact eyes at clypeus, and extended as far as back of eye. Semi-circular on vertex. Rear edge clearly defined.	Contact eyes antero-dorsally, not extended as far as their posterior margin. Rounded posterior boundary obscured by punctae.	Not extended laterally to eyes, but separated by crest and elevation. Extended back beyond eyes about half eye-length. Rounded and open to punctae posteriorly.	Separated from eyes by unelevated boundary. Broadly rounded posteriorly, but without raised, crested edges. Extended a little past eyes.	Contact eyes and extend beyond them. Rounded and closed posteriorly. Edges raised laterally into tuberculate crest.	Form isosceles triangles with raised postero-lateral crests, and apices open to vertex.
Frontal prominence	Oval; median to basal ratio about 10 : 25. Bounded by crested, elevated ridge. Setigerous punctae parted medianly by clear space which is divided by groove. Setae form 4 rows, dense apically and extended behind fossae.	Elevated, slightly rounded, with lateral cornua. Median to basal ratio 1 : 1. Divided obscurely by median elevated groove joining faint ridge from vertex. Setigerous, except for ridging: 4 rows of hairs extend around fossae.	Elongate, sides parallel, curving to apex; long axis twice transverse (15 : 34). Edges of fossae raised, and crested laterally. Grooved ridge, apex to vertex, divides it into 2 channels, each with 25–30 fine setae, denser at apex.	Elongate, elevated high above fossae. Sides parallel, tapered to apex, forming raised crests. Ratio 12 : 29. Distinct median grooved ridge, apex to vertex. Hairs coarse and dense on sides but not at apex: continuous behind fossae.	Narrow, elongate, but not elevated as in *celebensis* Raised, lateral crests not tuberculate. Median "rise" continuous with vertex, divides rows of fine setae which follow around fossae.	Forms isosceles triangle with upraised, lateral sides and apex. Median ridge with groove meets triangular raised portion from vertex. Paired channels with 8–12 stiff setae discontinuous with 3–9 post-ocular setae.
Pronoum	Shallowly emarginate and undivided. Punctae shallow, definite, separate and setigerous. (Hair half length of notum.) Sides straight.	Emarginate and undivided by tubercle. Punctae shallow, broad, indefinite, separate and hairless (except at edges). Sides straight.	Emarginate and faintly divided. Punctae shallow, definite, some in contact and not setigerous (except 12 setae on anterior ridge). Sides curved posteriorly.	Deeply emarginate, with obscure median division. Punctae shallow, large, some fused. Hairless, except anterior edge: front angles prominent; sides curved posteriorly.	Emarginate and undivided. Punctae either large and confluent or small and discrete. Hairless, except antero-laterally. Sides with prominent antero-lateral angles and curved posteriorly.	Strongly emarginate, divided by tubercle. Punctae large, shallow, amorphous. Hairless except for 12 very long setae on anterior margin. Sides curved, produced antero-laterally.
First tibia lateral expansion	Channelled on abaxial surface; with prominent spur, 4 spines.	Produced distally into prominent spur, with 3 spines.	Not produced as a spur but projection bears 6 spines.	Reduced distally and bears a group of 5 spines on margin.	Not produced as a spur but projection bears 4 spines.	Reduced distally and bears 3 spines on outer margin.
Mesonotum	About 15 delicate setae.	Setae: sparse, long and fine.	Hairless.	Numerous fine setae.	11 very delicate setae.	With 25 setae on apex.
Propodeum	Lateral setigerous punctae.	Almost hairless.	Hairless.	As in mesonotum.	A few dorso-laterally.	Hairless.

TABLE 8.—*Continued.*

A Comparison of Diagnostic Characters in the Females of Thynnus.—Continued.

	olivaceus.	*serriger.*	*calvus.*	*celebensis.*	*lugubris.*	*atratus.*
First tergite	Setae dense except for clear, median, anterior "V". Striae: 2–3 on sides only.	Projects medianly; hair dense in centre but thins laterally. Striae: 2–3 on sides only.	Hairless, except for 4–5 at sides. Median striae 6–7 on three-quarters of tergite.	Densely setigerous, entire. Striae absent.	Densely setigerous, entire. Striae absent.	Median tubercle present. Hair dense in centre only, with 2–3 striae on sides.
Pygidium	Truncate, narrower above than below. Small d. and v. tubercles turned forwards.	Shallowly emarginate, apices acute. Lower apex points downwards.	Narrowly emarginate; apices acute, lower apex pointing downwards.	Emarginate, apices rounded.	Shallowly emarginate; apices acute, with dorsal one curved forwards.	Notched but reduced. Apices acute; dorsal turned forwards, ventral horizontal.
Hypopygium ..	Small cleft; weakly serrate.	Deeply divided; 14 serrations.	Notch prominent: 17 teeth.	Shallow notch: 9 teeth.	Notch deep; finely serrate.	Notch deep; non-serrate.

A comparison of the females of: 26. *Thynnus olivaceus*, 27. *T. serriger*, 35. *T. atratus*, 33. *T. celebensis*, 30. *T. calvus*, 32. *T. lugubris* and 31. *T. pullatus* (see Table 8).

Female specimens* available were limited to examples of seven species of the total of thirteen listed; obviously, a key applicable to so few would be of no value. The females of *erraticus* Smith, 1860, and *albopilosellus* Cameron, 1906, are unknown. Specimens of the females of *barbarus* Turner, 1910, *bakeri* Rohwer, 1925, *luzonicus* Turner, 1908, and *mutandus* Turner, 1912, are at present unavailable in Australia. As a contribution towards the ultimate completion of this investigation, certain features which appear to be characteristic of each of these described species are presented here, and it is hoped to simplify the recognition of at least seven of these females.

The structures of taxonomic importance are: The dimensions of the head, the frons, prothorax, first tibia, mesothorax, first and second tergites, pygidium and hypopygium. It is interesting to find that in the female, just as in males, the frontal prominence is one of these variables. Also, that there is a pair of lateral fossae originating around the antennal bases, which varies in all these females. Generalizations at this stage are impossible and large series of specimens should be examined in order to determine whether the various features discussed in the present paper are actually constant characters. The possibility that allometric growth could have some bearing on these various cephalic structures cannot be overlooked (Rensch, 1951). The colour pattern of the seven species seems to be very uniform; unlike the males, to separate the females into such divisions as the *atratus* and *serriger* groups would not be possible. In fact, an examination of the seven females illustrates that the use of the presence and absence of an abundance of yellow markings as a method of grouping the males is superficial and irrelevant. An examination of the head structures shows: (i) that its median and transverse dimensions, frontal prominence and sulci are developed to a greater or lesser degree; (ii) that the seven species can be arranged in sequence according to the extent of development of these structures. This suggests the possibility of a cline. To such a sequence, it would be interesting to establish the relationships of the females of *bakeri*, *luzonicus*, *mutandus* and *barbarus*.

The features which distinguish the seven species are as follows:

1. It is possible to separate *olivaceus* from the six other females listed here, as the head is twice as broad as its medial axis. It has a median frontal groove, as already mentioned in the males, and the frontal prominence bears two separate sets of setigerous areas (Text-fig. 29). The hairy nature of the pronotum, continuing laterally along the edges of the propodeum, is unique.

2. As the frontal prominence in *serriger* is quite short and broad, this species can be distinguished from the remaining five (Text-fig. 30). It is evenly covered with hair and differs from *olivaceus*.

3. Elimination of *atratus* is easy, on account of the form of the frontal fossae as described in Table 8 (Text-fig. 34). The triangular nature of these structures is not shared by *celebensis*, *calvus*, *pullatus* or *lugubris*.

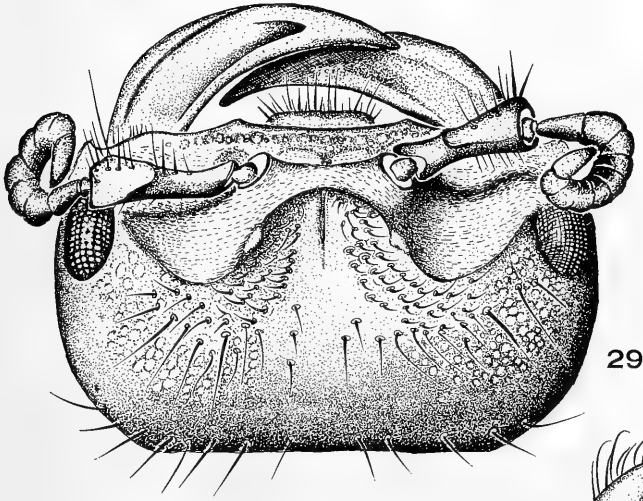
4. In *celebensis*, the ratio of the width of the head to the pronotum is significant. In this species the head is narrower than the pronotum and it is actually received into its deeply concave, anterior surface. In *calvus*, *pullatus* and *lugubris*, the head is broader than the prothorax, and the front of the pronotum is not deeply recessed.

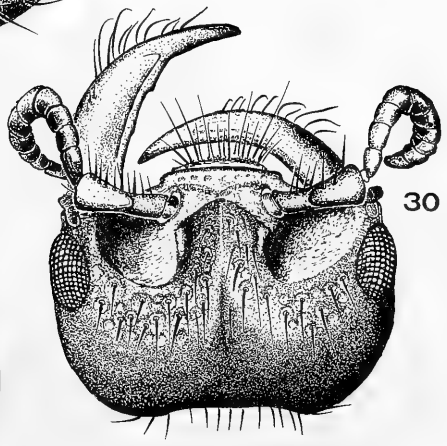
5. The affinities of *calvus* (Text-fig. 31) lie more strongly with *lugubris* and *pullatus* than with the species in the *serriger* group. It can readily be distinguished from *lugubris* on account of the shape of the thorax. The first tergite of the gaster is hairless in *calvus*, but in *lugubris* this tergite is thickly covered with hair. Dorsally, in *lugubris*, the pronotum is parallel sided, curving posteriorly towards the mesonotum. This is not so in *calvus*; the sides of the pronotum are quite straight, but they are set at an angle of 8° to the median axis, and thus they taper inwards posteriorly to the mesonotum at about one unit in every six. The frontal structures are relatively more

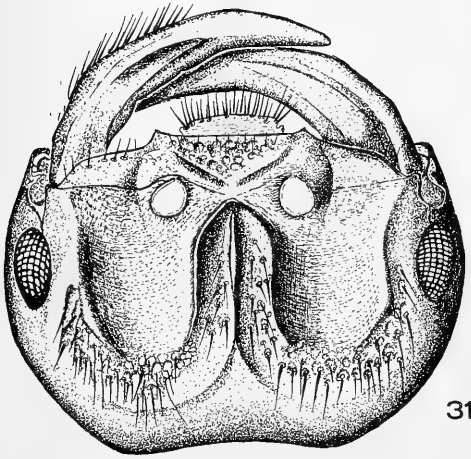
* It is assumed that the males and females had been authentically paired by the original workers.

strongly accentuated in *calvus* than in either *lugubris* or *pullatus* (Text-figs 32–33), and so the fossae appear to be more deeply gouged and the median prominence more elevated. In the gaster, the first tergite seems unique in being hairless in *calvus*, but in the other specimens it is thickly covered with hair. After forty years, the male of *calvus* has not as yet been established, and it would be interesting to know whether the males are entirely black or marked with yellow.

6. There is a similarity between *pullatus* and *lugubris*, but they can be distinguished by the head, pygidium and hypopygium. In *pullatus*, a frontal fossa does not greatly





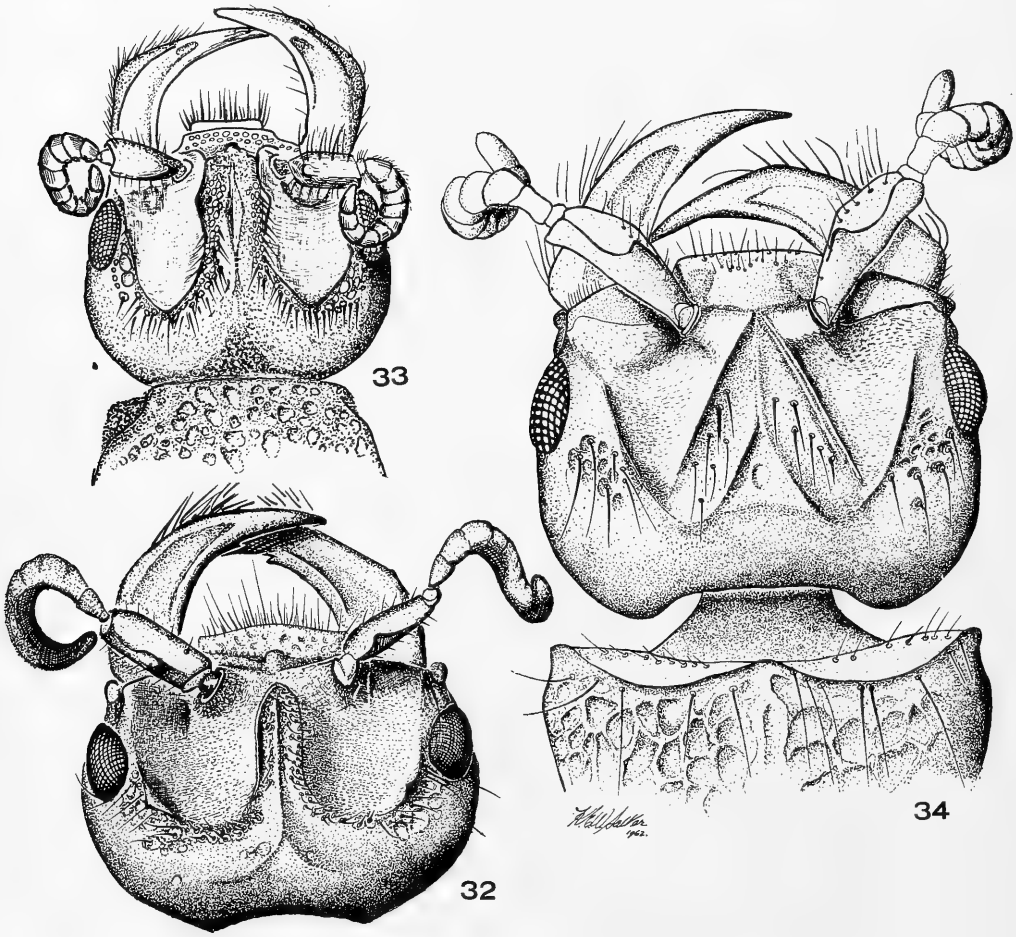


Text-fig. 29.—*Thynnus olivaceus* Turner, 1908, head of female. The clypeus broadly emarginate, with single row of setigerous punctae; paired fossae extending as far as posterior margins of eyes. Frontal prominence roughly semi-circular, with setigerous punctae parted medianly by clear space.

Text-fig. 30.—*Thynnus serriger* Sharp, 1900, head of female. Clypeus broadly truncate, punctae not forming distinct marginal band. Fossae not reaching as far back as posterior of eyes. Prominence extends broadly with lateral cornua; it is divided by an obscure median carina.

Text-fig. 31.—*Thynnus calvus* Turner, 1910, head of female. Clypeus broadly truncate and strongly punctate. Fossae deep, extended beyond eyes; sides elevated. Prominence edged by raised boundaries of fossae forming crests towards apex; it is divided into paired channels by distinct median carina.

exceed the prominence in width, and is somewhat oval posteriorly. The sides of the protuberance are raised and bear tubercles (Text-fig. 33). The antero-dorsal margin of the pronotum is straight and its lateral angles depressed; the mesonotum is hairless. The first tergite is densely covered from side to side with a thick coat of long hair, and lateral striae are absent. Its posterior margin bears a faint suggestion of the median structure found in *atratus*. The second tergite has 12 striae. Pygidium is deeply and narrowly notched laterally, thus forming two prominent rounded teeth on each side; unlike the other specimens listed here, its median posterior lobe bears a fine ridge following closely beside its edge. The hypopygium is shield-shaped and



Text-fig. 32.—*Thynnus lugubris* Smith, 1864, head of female. Clypeus broadly truncate with marginal punctae. Fossae shallow, broadly rounded posteriorly and extended beyond eyes with postero-lateral tuberculate crests. The prominence not strongly elevated but with crested anterior edges; narrowly elongate, length 3× breadth. A fringe of hair continuous with rounded edges of fossae.

Text-fig. 33.—*Thynnus pullatus* Smith, 1864, head of female. Paired, oval, frontal-fossae extended beyond the eyes; their elevated edges margined with hairs and punctae. The prominence is a little narrower than the fossae; its upraised edges form paired lateral tubercles.

Text-fig. 34.—*Thynnus atratus* Smith, 1862, head of female. The fossae and prominence are triangular with raised edges. The channels made by the median carina bear a few scattered setae which are discontinuous with those behind the eyes.

almost semi-circular, with a basal to longitudinal ratio of 7 : 6; the apex is notched and there are about 15 distinct serrations on either side (Pl. vii, fig. 20).

The hypopygia differ in each species and diagrams of this structure would be of value in identification (Sharp, 1900).

36. THYNNUS ALBOPILOSELLUS Cameron, 1906.

Cameron, 1906: 215 (♂), Merauke, New Guinea.

37. THYNNUS BAKERI Rohwer, 1925.

Rohwer, 1925: 418, Pl. 1, f. 4–5 (♂♀), Philippine Islands (Luzon?). Type: U.S. Nat. Mus.

These two species were omitted owing to lack of material.

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EXPLANATION OF PLATES V-VIII.

Plate v.

Fig. 1. *Eirone obtusidens* Turner, 1919. New Caledonia. The distinctive colouring and very stiff black abdominal bristles separate this species from *E. superstes* and *E. neocaledonica*.

Fig. 2. *E. obtusidens*, face. The anterior margin of clypeus is bright yellow and its unique triangular projection is clearly recognizable. (From colour slides.)

Fig. 3. *Tachynomyia comata* (Smith), 1864. Waigiou Is. The puncturing on the vertex is medium-sized, deep, circular, and in contact. The parapsidal sutures are indistinct.

Figs 4, 5. *Tachynomyia evelinae* Turner, 1940. Mondo, New Guinea. On the vertex, the punctures are medium in size and deep, but their shape is not as uniform as in *comata*. On the propodeum, the punctures are small, but as each is situated in a depression, the lighting in this photograph is deceptive. The parapsidal sutures are clearly visible, and emphasized by a distinct row of hairs. The scuto-scutellar notch is particularly well developed.

Figs 6, 7, 8. *Tachynomyia subfragilis* Turner, 1940. Kokoda, New Guinea. The punctures on the vertex are deep, polygonal, and irregular in distribution, and many are not contiguous. On the propodeum, the puncturing distinguishes this species from the other four, as it is very small and diffuse. The parapsidal sutures are faintly visible. Hypopygium is tridentate.

Plate vi.

Figs 9, 10, 11. *Tachynomyia fragilis* (Smith), 1865. Morty Is. Golden in colour, the head and thorax are densely covered with short, lemon-coloured hair. The front of the pronotum is straight and is not rounded at the sides. The punctae on the vertex are minute and not contiguous; scale-line $a — a = 0{\cdot}8$ mm. Hypopygium is trispinose.

Fig. 12. *Tachynomyia flavopicta* (Ritsema), 1876. Aru Is., New Guinea, and Queensland. The vertex is lightly covered with hair and the punctae are deep, polygonal, and separated by pronounced dissepiments. Group III with aborted post-ocular rim.

Fig. 13. *Tachynomyia comata* (Smith), 1864. Frons with its light covering of fine hair and medium-sized, deep, concentrated puncturation. Smooth areas border the visual sides of the ocelli.

Fig. 14. *Epactiothynnus nitidiceps* Turner, 1912. Aru Is. The transverse axis of the head exceeds its longitudinal median axis.

Fig. 15. *Epactiothynnus abductor* (Smith), 1865. Salwatty and New Guinea. The pro-coxae are compressed and concave ventrally; they extend laterally, beyond the pro-episternum, and are densely covered with long, silvery-white hair.

Figs. 16, 17. *Epactiothynnus vagans* (Smith), 1862. Celebes. The pro-coxae are rounded and not concave; they are not extended beyond the pro-episternum, and hair is diffuse. The puncturation on the frons is coarse, uniform and concentrated.

Fig. 18. *Epactiothynnus dahli* (Turner), 1910. Ralum, New Britain. Gaster of female. On the second abdominal tergite, four strong carinae occur in addition to the recurved edge of the tergite.

Plate vii.

Fig. 19. *Thynnus luzonicus* Turner, 1908. Polillo, Philippine Islands. The first segment of the gaster is not as wide as the second, and the parapsidal sutures are comparatively straight.

Fig. 20. *Thynnus pullatus* Smith, 1864. Bouru Is. In the female, the pygidium is deeply and narrowly notched laterally, thus forming two prominent teeth on each side.

Fig. 21. *Thynnus pullatus* Smith, 1864. Bouru Is. Illustrating the ocelli, frons, median frontal sulcus, supra-antennal crest, and clypeus. In this instance the median frontal sulcus forms a deep cleft with steep walls, partly dividing the frontal prominence to form two longitudinal crests. The sulcus is more or less open near the anterior ocellus and closed towards the supra-antennal crests. Along its floor is a distinct crease.

Fig. 22. *Thynnus lugubris* Smith, 1864. Ceram. This appears to be the second example in a graded series. The median frontal sulcus is not as deep as in *pullatus* and the central crease is absent. Its edges are clearly defined and it is closed at both ends.

Fig. 23. *Thynnus barbarus* Turner, 1910. Solomon Islands. Although there is a general similarity here to both *pullatus* and *lugubris,* the median frontal sulcus is broad and relatively shallow, with boundaries which are ill defined. There is no visible central crease, and obvious differences are apparent in the size and arrangement of the punctae.

Fig. 24. *Thynnus atratus* Smith, 1862. Gilolo. In this sequence, at the opposite end from *pullatus,* is *T. atratus.* Here, the median frontal sulcus forms a broad, shallow, open depression on the surface of the frontal prominence.

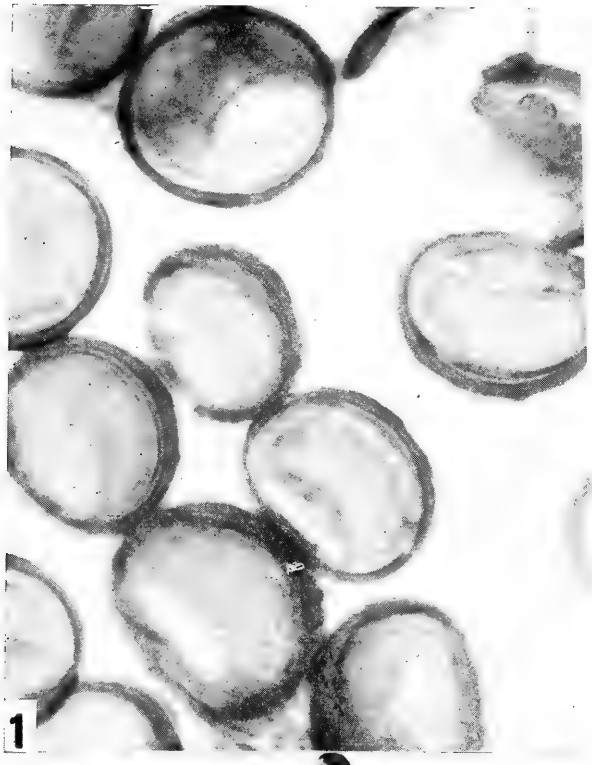
Plate viii.

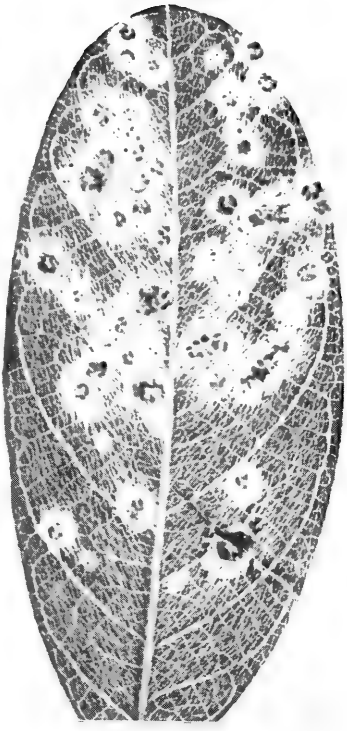
Fig. 25. *Thynnus pullatus.*

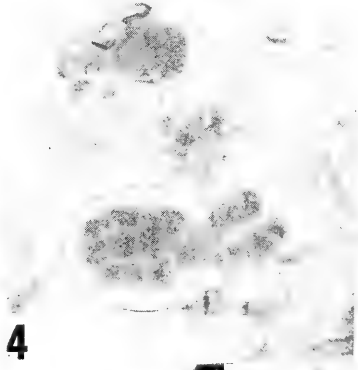
Fig. 26. *Thynnus lugubris.*

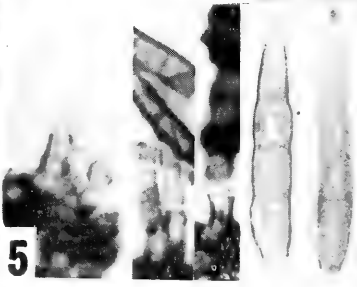
Fig. 27. *Thynnus barbarus.*

Fig. 28. *Thynnus atratus.* A comparison is presented here of the various forms of puncturation on the pronotum, mesoprescutum and parapsides, and also the shape of the parapsidal sutures in three of Smith's and one of Turner's species.



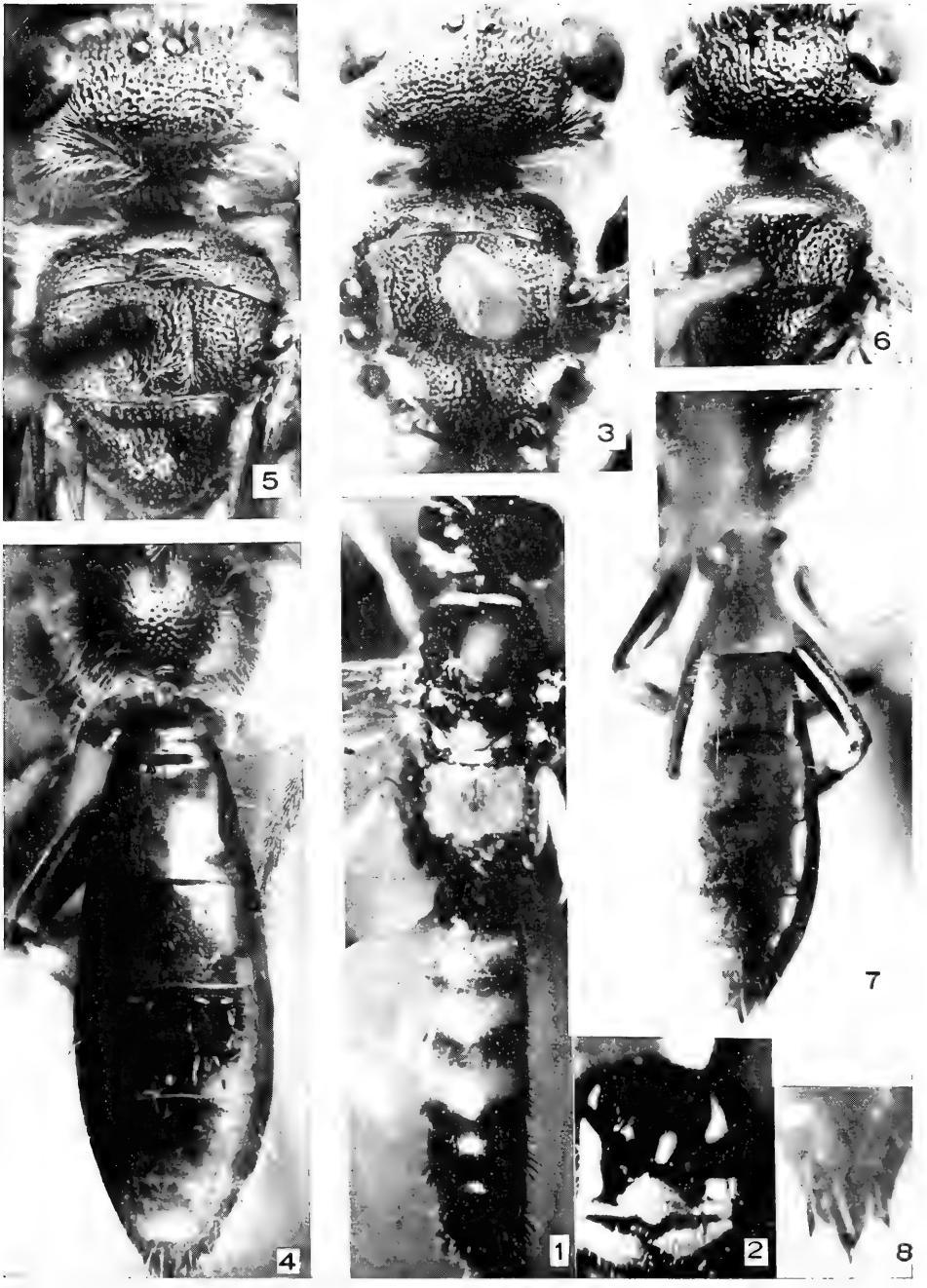






Plant parasitic fungi.

A. N. Colefax.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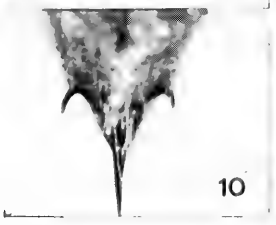
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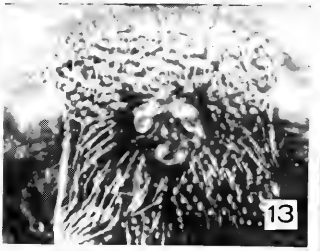
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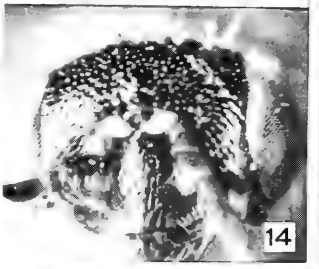
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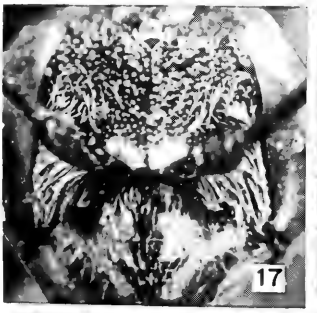
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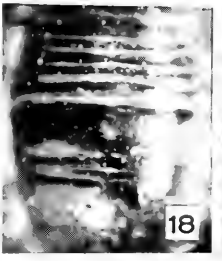
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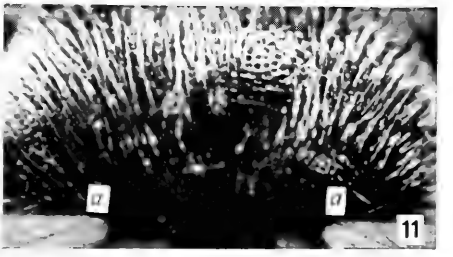
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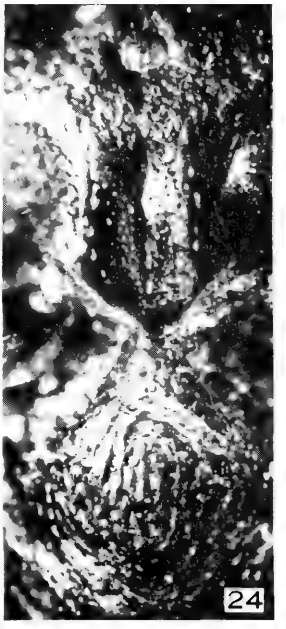
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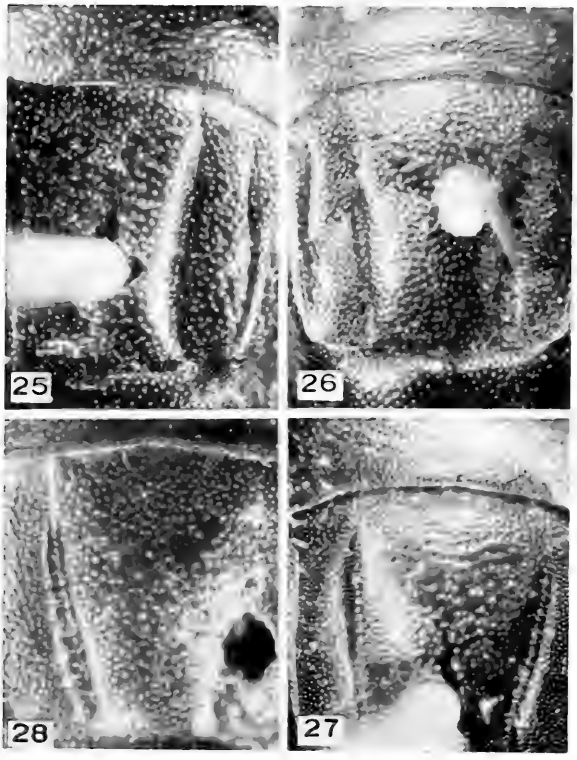
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SIR WILLIAM MACLEAY MEMORIAL LECTURE, 1962.*

LIVING MEMBRANES — FRONTIERS OF RESEARCH AT THE BOUNDARIES OF LIFE.

R. N. Robertson, Department of Botany, University of Adelaide.

(Plate ix and two Text-figures.)

Almost exactly one hundred and twenty-four years ago, a young medical student of the University of Edinburgh embarked in the vessel *Royal George* on a voyage to Australia which was going to have great consequences for science in general, for science in Australia in particular, and, least in general importance but subjectively of great importance, to me! That 19-year-old medical student, William Macleay, was travelling with his cousin William Sharp Macleay, a man of 46 years, son of Alexander Macleay, the Colonial Secretary of New South Wales. Like his father, William Sharp Macleay was an enthusiastic naturalist, a Council Member of both the Linnean and Zoological Societies of London, a past president of Section D of the British Association and a friend of Cuvier, Lamarck, Darwin, T. H. Huxley and other notable biologists. There is little doubt that the long voyage—from November, 1838, to March, 1839—gave time for the older man to have a profound influence on the interests and knowledge of William Macleay to the lasting benefit of science.

On arrival in Sydney, William stayed in his uncle's home at Elizabeth Bay House, but before long took up a property — later known as Kerarbury — on the lower Murrumbidgee near Wagga, where his uncle, and another cousin, George, already had property. There he must have been familiar with characteristic Australian scenes—the domestic animals of his property, the wild life of the area. For 15 years he lived a squatter's life on his property, but election, at the age of 35, to the old Legislative Assembly as member for the Pastoral Districts of Lachlan and Lower Darling, necessitated more frequent visits to the city. Two years later he married and from 1857 onwards made Sydney his permanent home. At that time this great University was five years old, the main building was being fashioned to the design of E. T. Blacket from the sandstone from Pyrmont and two years later this magnificent hall was opened officially.

Residence in Sydney, resulting in more frequent contact with his cousin and other local and visiting naturalists, stimulated Mr. Macleay to fresh activity in natural history, and like his uncle and his cousin he became a private collector. Like them, too, he was associated with the early days of the Australian Museum. In 1862 he arranged the meetings which resulted in the formation of the Entomological Society and in 1874 he took the steps which led to the foundation of the Linnean Society of New South Wales. In the same year he resigned from Parliament to give his attention wholly to natural history and the improvement of his Museum. On the deaths of his uncle and cousin he had moved into the famous old family home, Elizabeth Bay House, and used that as a centre to stimulate interest in natural history in its scientific aspects. He was a member of the Senate of this University from 1875 until his death at the age of 72 in 1891.

I cannot detail all the activities of this remarkable man; they have been well covered in the records of this Society, particularly by Fletcher (1920, 1929), Walkom (1942) and by Abbie (1958), the first Memorial Lecturer. So great was this man's love of knowledge of natural history that he not only devoted a large amount of time to its pursuit, but also much of his income and property while he was alive and most of his estate on his death. In all, his munificence to the Society amounted to about £70,000, which in the latter half of the 19th century was a fortune indeed.

* Delivered 23rd August, 1962, in the Great Hall of the University of Sydney during the thirty-sixth Congress of the Australian and New Zealand Association for the Advancement of Science.

Sir William Macleay, as he became in 1889, was a far-sighted man; he combined interest and enthusiasm with the means of implementing them. In two respects he was great in his conception of how to use his fortune. First, he saw that the sciences of natural history—and here he took a broad view including not only geology, botany, zoology and entomology, which would have been first in the minds of scientists of his day, but also biochemistry and physiology—were in need of financial support which would lead science graduates to adopt the scientific study of natural history as a career. To this end he endowed the Linnean Macleay Fellowships with sufficient capital to provide four fellowships—at what was until recent years the princely sum of £400 per annum, a provision that started many biologists who had graduated from this University on their careers. No one is more grateful to Sir William than I. Twenty-nine years ago I received a degree in this hall and started research during the latter part of the depression on a Science Research Scholarship at £120 per annum. The comparative affluence of appointment in the next year to a Macleay Fellowship enabled me to save half of it and subsequently to use this for the expenses of broadening my scientific knowledge and acquaintances in Europe and Britain. The success of those who have benefited from this endowment would, I think, have been of satisfaction to our benefactor. The list of former Linnean Macleay Fellows includes such well-known names in Australian geology and biology as Petrie, Walkom, L. A. Cotton, Benson, Tillyard and Lilian Fraser.

In another way, Sir William had remarkable prescience. You will remember that he died in 1891, and would have made his will some time before. He specified that either the University or the Linnean Society should receive £12,000 for the establishment of a fund for the employment of a competent bacteriologist to conduct original research in that subject. He died aged 72 in 1891; the Oxford Dictionary records the first use of the word bacteriology in English as 1884. Furthermore, so impressed was Sir William with the need for understanding the new science, that he made this endowment to the University conditional upon its requiring all science students to take a course in bacteriology. Eventually the Linnean Society took responsibility for the Macleay Bacteriologist, and now the arrangement has become a joint University and Linnean Society responsibility. The scientist of today will reflect with admiration on this man in his late sixties who was prepared to back this new science with so large a slab of his fortune and on how well history has approved his foresight. You will see that I, indirectly a beneficiary under his will, have some enthusiasm for accepting the honour of remembering our distinguished, far-sighted champion of natural history. Would that I had the ability to justify the honour with something of the oratory which has been heard in this Great Hall from time to time.

I have chosen to talk to you on the living membrane—a subject near the frontiers of research of the present day. In this subject the boundaries of life—in two senses—are concerned; first, because the living membranes are important boundaries of the living cell and its constituents, and second, because the reactions which occur in or on these membranes are themselves the reactions at the boundary of the living and non-living. Furthermore, this part of biology is seeing such rapid advances that I believe it to be an appropriate subject for 1962 to honour an amateur scientist who before he left this world in 1891 was far-sighted enough to recognize the coming importance of bacteriology.

You will notice that I am not using a new and fashionable term "molecular biology", though I shall be talking about the relation between living activity and molecular structure. When I hear a new word coined to describe some aspect of science which is not in itself new, I am reminded of the young man from outback Australia who said that he did not understand what was prose and what was poetry. When the difference was explained he exclaimed: "Well, ain't that wonderful! Here I've been speaking prose all my life and never knew it." The father of physiology, Claude Bernard, defined its objectives quite clearly in 1878, and every true physiologist has been striving towards the present happy conjunction of chemistry and biology at all levels—molecular biology is only a new name for a specific aspect of these general studies.

My other reason for talking about living membranes is that I believe we are about to reach one of those unifying hypotheses which simplify, from time to time, the apparently increasing complexity in science, and that, in consequence, elementary knowledge of what happens in biological membranes may become part of the stock in trade of the educated man. Doubtless this Great Hall has heard many words on the theme of what should be known by an educated man. Starting in the days when it was scarcely necessary to know anything other than the writings of the Hebrews and the Greeks, passing to the days towards the end of the century when the Darwinian theory of evolution must have been understood, to the twenties of this century when Rutherford had altered an element and Eddington and Jeans were trying to explain the Universe on a theory of its continuous expansion, we have seen the knowledge of science increasingly included in the stock in trade of the educated layman. Most laymen know now that they themselves are composed of cells, as are plants and other animals, that they carry chromosomes as a guide to future generations and that these inherited characters are associated with genes—a household word. I venture to suggest that a further unification of knowledge is imminent with the realization that the important reactions of life take place in or on the membranes of the cell.

If I show you some pictures* of living organisms, you will not be in the least surprised if I describe them as assemblages of many millions of cells, but let me orientate your thinking correctly by describing them as assemblages of membranes. All organisms—a baobab tree, a small barrel cactus of the Californian desert—are organized membranous structures. A beached collection of marine animals on a Hawaiian beach, thanks to a Hawaiian boy's art in spear fishing, or a delightful little ground squirrel living at about 10,000 feet in the high Sierra, and even very distinguished biochemists are all examples of the complex organization of membranes which make life possible.

What is a membrane? Literally the word membrane comes from a Latin word meaning that which covers the members or organs of the body and the word is frequently applied to any thin structure in an organism. Now, however, I want you to realize that the word has a special significance in modern biology and in particular that when we talk of a "unit membrane" we are talking of a very definite structure which seems to have much to do with the organization within all living cells—not a uniform structure in function or in composition, but bearing very definite resemblances in different organisms. Let me be more specific.

About 30 years ago, not more than 50 yards from this place, I heard a professor of biochemistry ask a senior physical chemist whether he thought there was anything in the suggestion that the membrane responsible for the semipermeable properties of the living cell might be only one or two molecules in thickness and would never be resolvable with the microscope. The physical chemist replied that he would be surprised if the membrane were more than two, three or four molecules thick and that its structure would have to be inferred from its properties. So we physiologists had a mental picture of a thin unresolvable membrane which had important properties in controlling what entered and left the living cell, but we could not see it with a microscope. Its properties led to its description which, as we shall see, was fairly accurate, but eventually the advent of the electron microscope and especially of the techniques for cutting very thin sections showed the definite structure occurring at cell surfaces, only a few molecules thick. Let me put this in proper perspective for you in relation to some typical cells, but of very different organisms. Compare the cells of the ordinary tissue of a carrot with the secretory cells of frog's stomach. Both are about the same size, i.e., about 50 microns in diameter (about 1/20 of a millimetre). Within these cells we find with the electron microscope definite membrane structures—one on the outside, and one on the inside of the stomach wall, one all round the cytoplasm of the plant cell and another on the inside of the cytoplasm against the vacuole. These cells contain very definite bodies, the mitochondria. These mitochondria

* The lecture was illustrated by a number of slides which it is not possible to reproduce here.

are also made up of definite membrane structures. We must bear in mind that all these membranes are only about 100 Å thick, i.e., very thin compared with the diameter of the cell—actually about 1/5,000 of the diameter of the cell.

It is important for you to have an idea of this dimension. Let me illustrate this by reference to this Great Hall. Suppose that we could enlarge the cell so that it is as large as this hall—so that we have a cell which is about 45 feet wide, 45 feet thick and about three times that length. If that were the size of a cell, the membrane that I am talking about would be about 1/10 of an inch on the same scale, a very thin membrane in comparison with the size of the cell. My first point then is that this unit membrane structure, about 100 Å in real units, is very thin compared with the dimensions of the cell. These unit membranes often occur in pairs.

What about the nature of these membranes? As I have said, long before we were able to see any membranes with electron microscopy, physiologists had deduced that the permeability properties of the cell, i.e., the powers of the cell to admit or exclude substances, were due to membranes of this kind. Here our knowledge had been put on a sure foundation by the techniques developed by the great physicist, Irving Langmuir, for studying the way molecules spread and pack themselves together, particularly on a water surface in air. Long-chain molecules were shown to have the capacity for arranging themselves in perpendicular arrays—the parts of the molecules with affinity for water with their heads in the water and the other parts of the molecule which had no affinity for water holding each other together by weak forces in the air. Langmuir himself (1942) thought that he had for the biologist "the tools for finding out certain things he wants to know". From the application of such ideas to what was being deduced about the cell surface membrane, we arrived at the classical picture of a living membrane consisting of two layers of long molecules stuck together almost like a lot of parallel sticks forming what we call a bimolecular leaflet. The probable kinds of molecules for such membranes are long organic molecules of fats or fat-like substances called lipids, each containing about 20 carbon atoms.

In 1925 Gorter and Grendel had shown that in the membrane of the red cell there are just enough molecules if pushed together in this way to account for a bimolecular leaflet and the classical concept of the living membrane was developed in detail by Davson and Danielli (1943) in the 1930s. They also pointed out that some spreading of protein on the surface seemed to be necessary as well as the packing of the lipids. Such membranes were formed artificially and were shown to have properties similar to those of the unseen but inferred membranes of the cell. These, then, are non-aqueous membrane structures in the cell and recent interpretations of membranes seen with the electron microscope agree with the classical concept shown in Figure 1 (J. D. Robertson, 1960).

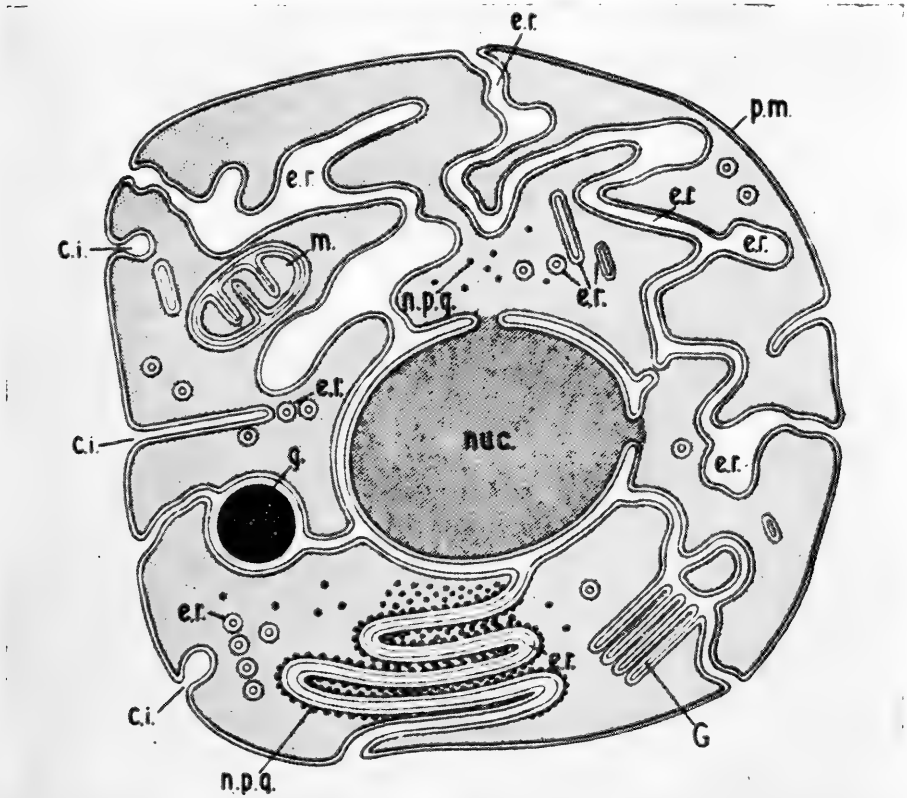
What are their properties?

1. A fair degree of stability. Such membranes, though composed of molecules held together by weak forces, are flexible, and are not easily destroyed by mechanical forces because they bulge or alter with the change of the shape of surface where they occur.

2. While rather permeable to small molecules of water, they are very impermeable to most substances which dissolve in water. They act therefore as splendid barriers at the boundaries of cells and prevent substances from going through indiscriminately. Why? Because the forces, though individually weak, are collectively strong enough to stop molecules or ions from breaking them by collisions. We have a term for this; we speak of the permeability of a membrane and we can show that such a membrane as this may be as much as 100 million times less easily penetrated than the same area/distance of water. It is difficult to give you an accurate picture of what that means, but perhaps this simplification is legitimate: suppose that we liberated a bunch of molecules at a point and let them diffuse through a watery space in the cell until half of them had filled that space in about one second; now suppose that we interpose a membrane with these low permeability properties, it would take up to four days for

the molecules to diffuse across in the same quantity. So these membranes are extremely effective barriers to movement within the cell.

3. They are very effective insulators; these quite thin structures relative to the cell can maintain an electrical potential difference between one side and the other. The best known of these is, of course, the way in which the surface membrane of a



Text-fig. 14. Diagram of a hypothetical cell illustrating relationships of the cell membrane to various cell organelles. The cell membrane is shown as a pair of dense lines separated by a light interzone. The invaginations of the cell surface known as caveolae intracellularis (c.i.) are indicated in several areas. Some of these extend for a considerable distance into the cell and they may connect with the endoplasmic reticulum (e.r.). The nuclear membrane is composed of flattened sacs of the endoplasmic reticulum, and by means of the nuclear pores nucleoplasm (nuc.) is in continuity with cytoplasm. The Golgi apparatus (G) is here shown as a modified component of the endoplasmic reticulum. Secretion granules (g.) are shown as dense aggregates contained within membranes of the endoplasmic reticulum. Nucleo-protein granules (n.p.g.) are shown scattered through the cytoplasm and in some regions attached to the cytoplasmic surfaces of membranes of the endoplasmic reticulum. In some regions the endoplasmic reticulum is shown as tubules, either in longitudinal section or cross-section. It is not clear on present evidence how many of these round membranes are transected tubules and how many, if any, represent isolated vesicles. One mitochondrion (m.) is shown with its cristae formed by invagination of its inner membrane.

Figure 1.—(From J. D. Robertson, 1960.)

nerve cell maintains an electrical difference. The nerve impulse which is a purely electrical phenomenon goes along that imperfect cable because it has an automatic mechanism of amplification built into the surface membrane. The surface membrane by itself around our cell represented by the Great Hall would not be a good enough

conductor or cable to carry a message from the window of the founders of the Oxford Colleges at the west end to that of the founders of the Cambridge Colleges at the east end, because an electric pulse fed in at one end would lose most of its amplitude within a few millimetres. But because this good insulator maintains an electrical potential difference across it, an electric signal triggers off a discharge of electrical energy across the membrane which triggers off an adjoining discharge and so on, so that this succession of discharges gives amplified electrical messages passing along the length of the membrane (Katz, 1962).

4. The membranes are very much under control of the cell. They can be increased by the cell by putting more molecules into the system or can be destroyed by bringing them back into the metabolism. The right stimulus in one part of a cell will bring them back into activity.

5. A relatively impermeable membrane allows for control of most of the entering substances. If substances cannot penetrate easily, then a specific substance may be allowed to enter by combining with some specific substance in the membrane. The entering substance combines on one side of the membrane and is given off on the other side after a chemical change in the carrier. Carriers of this type are known as permeases.

We had deduced that these were the properties of the membranes which separated the outsides of cells from their insides; we had also speculated on whether such membranes separated one part of the cell from another. When sections of fixed and embedded tissue suitable for the electron microscope became available, we were able to see these membranes occurring not only at the surfaces of cells but also through the cytoplasm and round the organelles. If we look at typical young plant cells such as those of the pea seed or the maize seedling (electron micrographs kindly lent by Professor Mercer, Miss Bain and Miss Nittim) we see the unit membranes which go to make up the mitochondria (Plate ix, figs 1 and 2). A single mitochondrion which may be about one micron wide and one and a half microns long, consists of a smooth outer membrane surrounding a very much convoluted inner membrane—each of the thickness of a unit membrane. Mitochondria in all cells of plants and animals control the energy supply which brings about the chemical reactions of the cell. It is now clear that some of the reactions of respiration which liberate the chemical energy for other living processes take place actually in or on the mitochondrial membranes. There, for instance, occur the series of oxidations which convert the chemical energy from sugar molecules into the form of phosphorylated compounds. The occurrence of these important reactions on the membranes of mitochondria has been clearly demonstrated by the experiments of Green, Watson and Siekevitz, Lehninger and others, and we are now familiar with the idea that the unit membrane is important not only to separate one part of the cell from another, but also to guide the course of a reaction by holding the essential molecules in the correct order in an array.

The importance of this idea was further emphasized by the discovery of membranes orientated in various directions in the cytoplasm, often unit membranes in pairs. Furthermore, it was discovered that when a cell was forming protein in large quantity either for secretion to the exterior as in the pancreas (Palade and Siekevitz, 1956) or for accumulation in the cell as in the pea seed (Bain, personal communication), the protein made its appearance between a pair of unit membranes. If secretion to the exterior occurred, the unit membranes could be traced to a gap or pore in the external cell membrane. Across the unit membranes from the protein, ribonucleic acid granules or ribosomes, each about 250 Å in diameter, or about twice the thickness of the membrane, were seen to align themselves, and we believe that the protein synthesis is the result of the combined activity of the ribosome and the unit membrane in its vicinity.

The nucleus, too, is surrounded by membranes of about the same dimensions as the unit membrane, but these membranes are interrupted by wide pores through which the ribosomes, formed in the nucleus and perhaps in the nucleolus, pass out into the cytoplasm to align themselves on the membranes of the cytoplasmic reticulum. These

ribosomes thus convey the information from the nucleus as to what protein is to be synthesized. The cell is a system of compartments, separated by unit membranes which carry the enzymes and align the reactive components in proper sequence for orderly living processes. An animal cell (J. D. Robertson, 1959) is shown diagrammatically in Figure 2. Some other parts of the endoplasmic reticulum where ribonucleic acid granules are not present are thought to be associated with steroid synthesis, glyceride synthesis and detoxication reactions.

For a long time the true structure and function of the Golgi bodies, which are just large enough in some cells to be seen with the light microscope, have defied elucidation. The electron microscope reveals that these bodies are specially shaped assemblages of unit membranes which appear to have some function in forming and secreting substances within the cell. In some preparations the swollen Golgi bodies can be seen with their characteristic unit membranes widely separated with a secreted substance filling the space between them (Mollenhauer, Whaley and Leech, 1961).

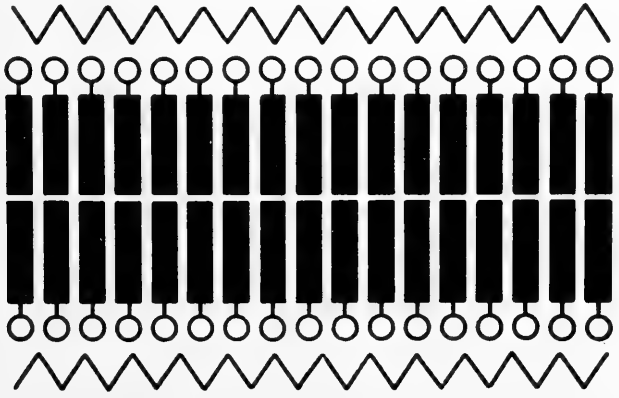


Fig. 66. Diagram representing the molecular organization of the cell membrane. The core of the membrane consists of a bimolecular leaflet of mixed lipids with their non-polar chains (bars) oriented toward one another and their polar groups (circles) directed outwards. The polar surfaces are covered by monolayers of unfolded proteins, the backbone chains of which are indicated by the zig-zag lines. The side chains of the protein components are not shown in this highly schematic drawing.

Figure 2.—(From J. D. Robertson, 1959.)

In plant cells, the plastids represent an elaborate form of specialized membranes. The lamellae of the plastids correspond in dimensions with those of unit membranes and there is evidence that the chlorophyll molecules are spread as a monomolecular film of orientated molecules. Studies of the development of chloroplasts may give an important clue to the formation of such membranes since, in young plastids, the electron microscope shows a distinct crystalline body from which the lamellae appear to originate.

The membrane structures in cells are certainly not static and, as predicted earlier, are quickly formed or destroyed with changing activity in the cell. As reported at this Congress, the change from aerobic to anaerobic conditions is accompanied both in yeast (Dr. Linnane) and in higher plants (Professor Mercer and Miss Rathgeber) by the disappearance of mitochondria and the increase in an extensive endoplasmic reticulum membrane. Calcium has long been known to be necessary to stabilize membrane activities in cells, but only recently have experiments on calcium deficiency in barley seedlings demonstrated the almost complete lack of membrane structure in the deficient cells (Marinos, personal communication).

The rapid accumulation of data by many workers with the improved techniques of electron microscopy shows that unit membranes are of universal occurrence in plants and animals and associated with such wide varieties of activity as the conduction of nerve impulses, secretion of bile in liver, secretion of hydrochloric acid in stomach and energy mobilization for flight muscles in insects. Still more refined techniques should reveal the connection between the molecular orientation of these membranes and the processes in which they participate. We can hope for continuation of cell biology studies in which activity is co-ordinated with changes in membrane structure as revealed by the electron microscope, biochemical studies on isolated organelles whose structure is known, and physical studies, using the techniques of solid state physics to investigate the minute structures of the mixed crystals which probably give the correct orientation to the guided chemical reactions characteristic of living cells.

If we see these membranes not only as the important barriers of the cell, but also as the organized, process-guiding molecular arrays, we might be able to speculate on the first living reactions. Some people thinking about the origin of life from the primeval brei in which many organic molecules might have occurred, have been unduly concerned with the origin of the cell. The real problem may have been the origin of the membranous structure only a few molecules thick but in an orderly arrangement. The Greeks, who were so often right for the wrong reason, may have been right again in subscribing to Anaximander's idea that the action of the sun's heat on moisture caused the membranes from which living things evolved (Whitley, 1962).

In this lecture, I have tried to catch your interest in this exciting development of biology which may be about to produce a unifying and simplifying generalization about how living beings function at the molecular level. Had Sir William Macleay been alive today I am sure that he, a man who thought so much of bacteriology in the 1880s, would have been aware of and excited by these latest revelations of biology.

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EXPLANATION OF PLATE IX.

1. Electromicrograph of Pea Root. × 8,000.

2. Electromicrograph of Maize Coleoptile. × 8,000.

CW, cell wall; N, nucleus; NM, nuclear membrane; M, mitochondrion; P, plastid; G, Golgi apparatus.

BAT TICKS OF THE GENUS *ARGAS* (IXODOIDEA, ARGASIDAE).

5. Description of Larvae from Australian and New Guinea Carios-Group Populations.[1]

By Harry Hoogstraal[2] and Glen M. Kohls.[3]

(*Communicated by Dr. Bruce McMillan.*)

(Twelve Text-figures.)

[Read 26th September, 1962.]

Synopsis.

In literature reviewing the ticks of Australia and New Guinea, larvae presumed to be *Argas* (*Carios*) *vespertilionis* (Latreille, 1802) have occasionally been mentioned as occurring in Australia, but no ticks of the genus *Argas* were reported for New Guinea. Recently, the present authors have described a remarkable new Australian species, *Argas* (*Carios*) *australiensis*, from a single male and nymph, the only specimens thus far known to have been collected. In order to stimulate further search and study, larvae, which may be the same species as those referred to as *A. vespertilionis* by previous authors, are described from Australia and New Guinea. Very slight differences between these and Egyptian samples are noted, but it is suggested that populations from Africa and from Australia and New Guinea may nevertheless differ taxonomically and that in this subgenus (as in the bat-infesting subgenus *Chiropterargas*), adults rather than larvae may be more lucid indicators of separate species. It is impossible at this time to state whether these larvae are *A.* (*Carios*) *australiensis*, *A.* (*C.*) *pusillus* Kohls, 1950, as yet definitely known only from the Philippines and Malaya, or an undescribed species. Hosts are a variety of insectivorous bats (Microchiroptera).

Introduction.

Surprisingly few *Argas* ticks have been collected from bats in Australia and none has been reported from these or other hosts in New Guinea. Taylor (1913) recorded larvae of "*A. vespertilionis*" from "*Vesperugo* sp." from Townsville. Ferguson (1925) and apparently Fielding (1926), too, repeated this record, but it was not mentioned by Taylor (1946) in his review of Australian ticks. Kohls and Hoogstraal (1962) described *Argas* (*Carios*) *australiensis* from a male and a nymph from a house presumed to be bat-infested in Hammondville, New South Wales. The present study of larvae kindly presented to us by Dr. F. H. S. Roberts of the Veterinary Parasitology Laboratory, Yeerongpilly, Queensland, Dr. Bruce McMillan of the School of Public Health and Tropical Medicine, Sydney, New South Wales, and Dr. L. W. Quate of the Bernice P. Bishop Museum, Honolulu, Hawaii, is published with the hope that it will stimulate further search for specimens to indicate the biological characteristics and taxonomic status of Australian and New Guinea populations of argasid bat parasites. Whether or not these *vespertilionis*-like larvae are those of *A.* (*C.*) *australiensis* cannot be determined until the latter species has been reared in the laboratory.

We are grateful to Drs. Roberts, McMillan and Quate for the privilege of studying these specimens, to Dr. Karl F. Koopman of the American Museum of Natural History, New York, and to Mr. John H. Calaby, Wildlife Survey Section, C.S.I.R.O., Canberra, for information on the chiropteran hosts of these ticks.

[1] From Research Project MR005.09-1402.3, Bureau of Medicine and Surgery, Navy Department, Washington 25, D.C. The opinions and assertions contained herein are the private ones of the authors and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

[2] Head, Department of Medical Zoology, United States Naval Medical Research Unit Number Three, Cairo, Egypt, U.A.R.

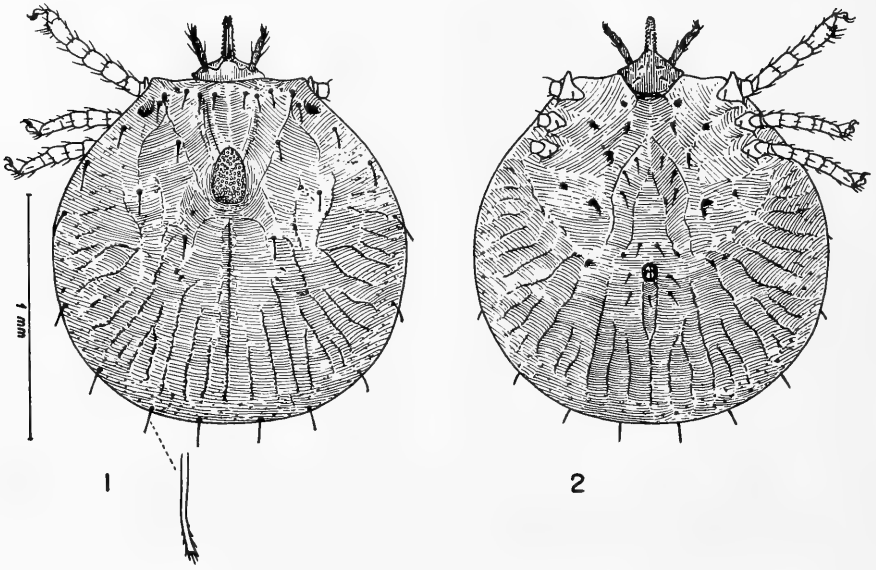
[3] Sanitarian Director, United States Department of Health, Education, and Welfare, Public Health Service, National Institutes of Health, National Institute of Allergy and Infectious Diseases, Rocky Mountain Laboratory, Hamilton, Montana, U.S.A.

ARGAS (CARIOS) (VESPERTILIONIS GROUP) SP. (Figs 1–12.)

Material examined. Numerous larvae, data under *Hosts and Distribution* below.

Description.

Body (engorged) varying from subcircular (as in fig. 1) to elongate in outline, subcircular specimens measuring from approximately 1·0 to 2·0 mm. in diameter, elongate specimens measuring approximately 1·5 mm. in width and 3·0 mm. in length; anterior margin in all specimens truncate and capitulum situated anteriorly. *Squamous area* on dorsal surface bullet-shaped, elongate with blunt posterior margin and parallel lateral margins anteriorly converging to a narrowly rounded apex. *Setae* on body dorsally typically numbering 10 or 11 pairs laterally, rarely as many as 14 pairs, and 3 pairs submedianly; ventrally numbering 3 intercoxal pairs, 3 circumanal pairs, and in most specimens a single seta in the groove immediately posterior to the anus (one pair of anal setae and each coxa with a pair of setae). Setae with minute fringing apically (fig. 1).



Figs 1, 2. *Argas* (*Carios*) *vespertilionis* group, larva from Tooloom, New South Wales. Dorsal and ventral views.

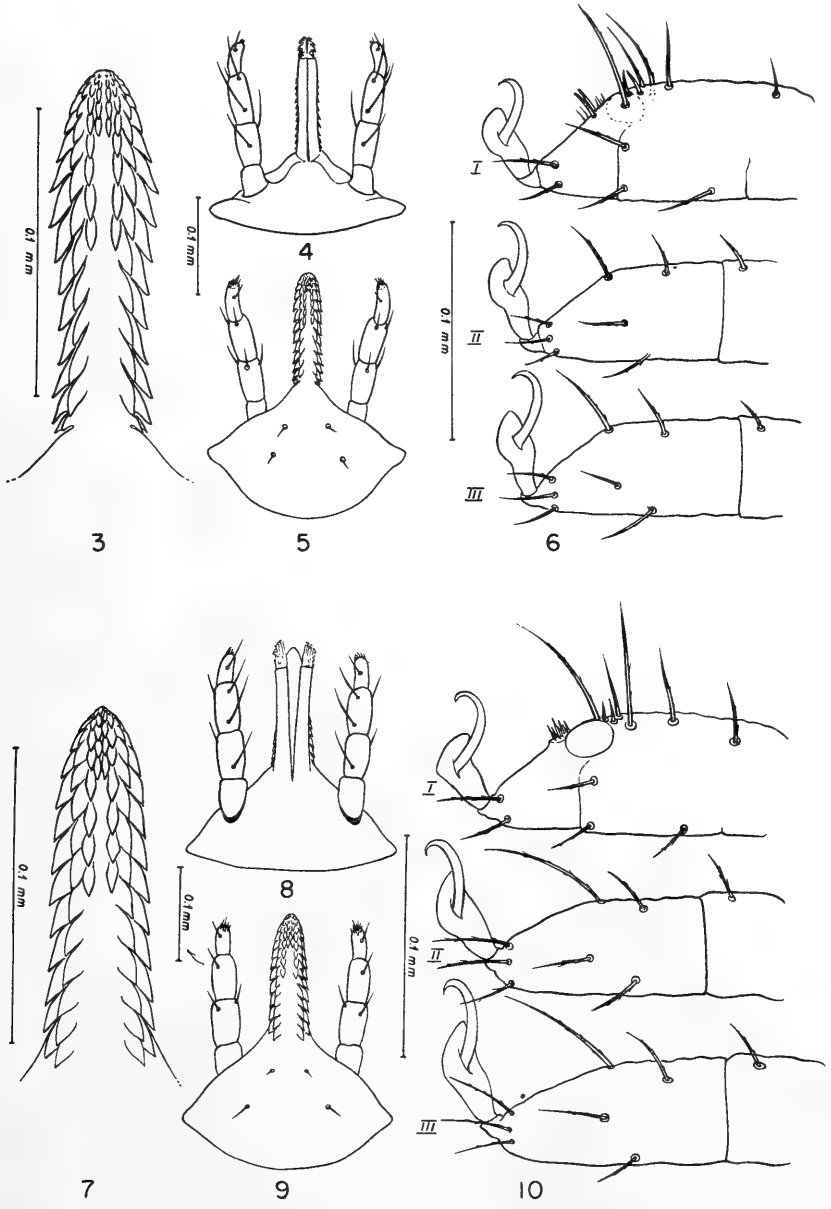
Capitulum (figs 3–5). *Basis capituli* with outline as illustrated; with two pairs of short bristles on the ventral surface. *Hypostome*, from basal denticles almost four times as long as greatest width, gradually tapered anteriorly to a narrow, bluntly rounded apex with a very small corona of a few, minute hooklets. Dentition 2/2 for length of shaft; anteriorly 4/4 with a short inner file of approximately four denticles and an outer file (approximately half the length of the shaft) of approximately eight denticles. *Palpi* extending to apex of hypostome; segments 1 and 4 subequal in length; segments 2 and 3 either subequal in length or 3 very slightly longer than 2; palpal setae as illustrated.

Legs moderately long and narrow. *Tarsi* (figs 6, 11) gradually tapered distally, lacking dorsal protuberances; tarsi II and III each with seven setae visible from lateral view; tarsus I with setae in lateral view (fig. 6) and in dorsal view associated with Haller's organ (fig. 11) arranged as illustrated. *Pads* (pulvilli) comparatively large; *claws* comparatively small.

RELATED SPECIES.

In the subgenus *Carios*, larvae of *A.* (*C.*) *vespertilionis* (Latreille, 1802) are known chiefly from a large number of wild and reared Egyptian specimens; larvae of *A.* (*C.*)

pusillus Kohls, 1950, a species known only from the Philippines and Malaya, from more than 100 wild specimens from the Philippine Islands; and larvae of Australian and New Guinea populations described herein from more than 260 wild specimens. It will probably remain exceedingly difficult to assess critical differences in larvae of this complex until long series of laboratory-reared specimens from many parts of the world have been obtained for comparative study. Adults of numerous *A.* (*C.*)

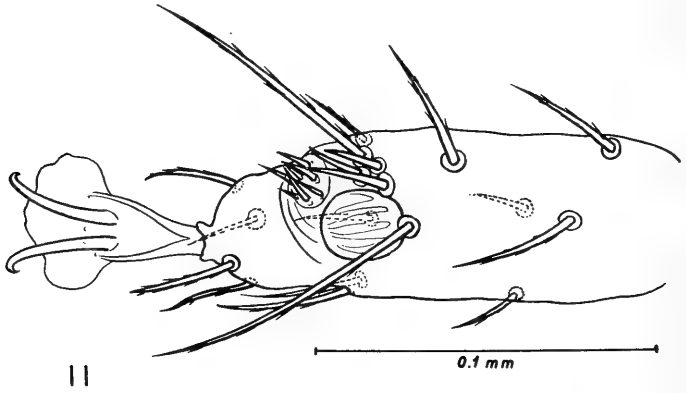


Figs 3-6. *Argas* (*Carios*) *vespertilionis* group, larva from Tooloom, New South Wales: 3, hypostome, ventral view; 4, 5, capitulum, dorsal and ventral views, respectively; 6, tarsi I to III, lateral view.

Figs 7-10. *Argas* (*Carios*) *vespertilionis* (Latreille, 1802), larva from Abu Rawash, Giza, Egypt (NAMRU-3 rearing number 315F_1): 7, hypostome, ventral view; 8, 9, capitulum, dorsal and ventral views, respectively; 10, tarsi I to III, lateral view.

vespertilionis specimens from Egypt (Hoogstraal, 1958) show considerable variation in body size and shape; equally variable adults available in very small series from numerous other localities in Europe, Asia and Africa are provisionally lumped as *vespertilionis*, though separate taxa among these populations may be recognized when adequate comparative material has been collected.

As mentioned below, the larvae described herein differ from Egyptian *vespertilionis* larvae in only minute details and to no greater degree than Philippine *pusillus* larvae differ from Egyptian *vespertilionis* larvae. Adults of *pusillus*, however, are comparatively easily distinguished from adults of Egyptian *vespertilionis*. We therefore



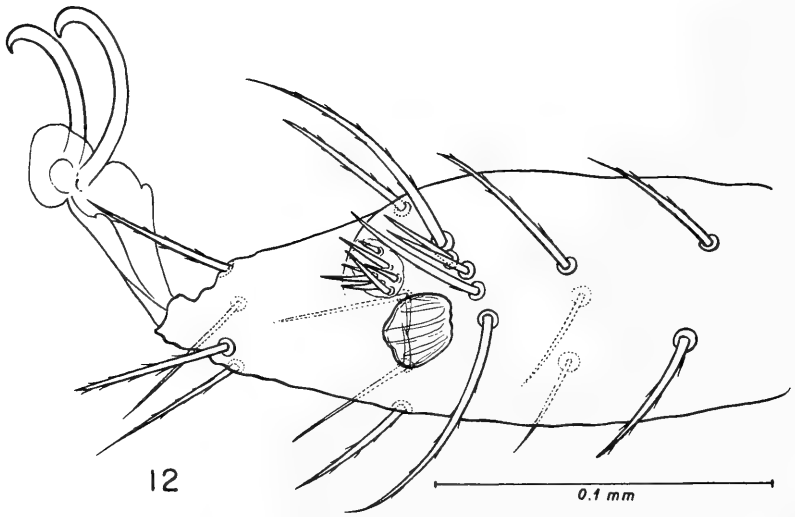


Fig. 11. *Argas* (*Carios*) *vespertilionis* group, larva from Tooloom, New South Wales. Tarsus I, dorsal view.

Fig. 12. *Argas* (*Carios*) *vespertilionis* (Latreille, 1802), larva from Abu Rawash, Giza, Egypt. (NAMRU-3 rearing number 315F_1.) Tarsus I, dorsal view.

assume that the Australian and New Guinea larvae referable to this group are not those of *vespertilionis*, and while they may possibly be larvae of *australiensis* or *pusillus* or an undescribed species we hesitate to claim so at present. With regard to *pusillus*, it may be significant that a single early stage nymph strongly suggestive of the adults of *pusillus*, a species whose nymphs are as yet unknown, was present among the larvae in lot RML 37514 from New Guinea (data under *Hosts and Distribution* below).

It is noteworthy that larvae of the two species in another bat-infesting *Argas* subgenus, *Chiropterargas* (Hoogstraal, 1955), are also exceedingly similar, but their adults are quite dissimilar in general appearance and in critical structural details. On the other hand, larvae of a number of species in the bird-infesting subgenus *Argas*, presently being studied by the writers, differ from each other in easily delineated combinations of characters and adults of the same species are more or less readily differentiable from each other.

In order to illustrate clearly the structural similarity of Egyptian *vespertilionis* larvae and larvae of this group from Australia and New Guinea, details of larvae from the former area are also presented here (figs 7–10, 12).

No significant differences can be detected in engorged body shape of larvae of *pusillus*, *vespertilionis* and Australian–New Guinea populations, though it appears that *pusillus* larvae may generally be considerably smaller than those of the other two forms. Dorsal body setae of *vespertilionis* total 14 (rarely 13) pairs, of *pusillus* 12 to 15 pairs, and of Australian–New Guinea populations, 13 or 14 pairs, exceptionally 17 pairs; ventral body setae are the same in each form.

The basis capituli of each of these three forms appears to differ very slightly in outline, but larger comparative series of reared specimens are needed to determine the constancy of this character. Posthypostomal bristles are all essentially the same. The shape of the hypostome of each form and the dentition of *vespertilionis* and Australian–New Guinea populations is the same in all specimens examined. Many *pusillus* larvae have an extra, short inner file of anterior denticles, but this feature is variable, and dentition of other *pusillus* specimens conforms to that of Egyptian and Australian–New Guinea populations. Palpal characters are similar in each form or differ so minutely that they appear to fail to serve as taxonomic criteria.

The legs of each form and the numbers and position of setae of each leg are essentially the same. Slight differences in length of individual setae probably are not significant. Haller's organ of each form differs very slightly as does the position of associated setae, but better and larger comparative series of specimens are needed before these characters can be evaluated.

Hosts and Distribution.

Collecting data for the larvae described herein are as follows:

Australia: Thirteen specimens, most of them from one of a colony of eight *Tadarida norfolkensis* Gray, 1839, found in a hollow tree at Tooloom, New South Wales, 24 March 1961, J. H. Calaby *legit* (Hoogstraal collection). The ticks were attached to the legs and ear bases. One specimen from ear of *Nycticeius ruppellii* Peters, 1866, at Peacock Creek, Bonalbo, New South Wales, 21 March 1961, J. H. Calaby *legit* (Hoogstraal collection). The bat was shot while flying at dusk. Six specimens from *Chalinolobus gouldii* (Gray, 1841), at Canberra, Australian Capital Territory, 14 November 1957, G. M. Dunnet *legit* (RML 36953). Ten specimens from "bat", Queensland, 2 March 1947 (RML 36952). Thirty-two specimens from *Taphozous flaviventris* (Peters, 1866), at Muralambeen Farm near Ingham, North Queensland, 5 October 1961, K. L. S. Harley *legit* (RML 37779).

New Guinea: One specimen from "*Pipistrellus* bats" at Merauke, Dutch New Guinea, 27 January 1960, T. C. Maa *legit* (RML 37513). Approximately 190 specimens from "*Miniopterus* bats" at Suanimbu, near Maprik, Sepik Subdistrict, Northeast New Guinea, 15 January 1960, T. C. Maa *legit* (RML 37514 and 37515). Sixteen specimens from *Pipistrellus papuanus* (Peters and Doria, 1881), two from Gali, Madang District, and 14 from Roinji, Finschhafen Subdistrict, Northeast New Guinea, October 1961, Bruce McMillan *legit* (Hoogstraal collection).

The following information on known host species is noteworthy. *Tadarida norfolkensis* ranges through eastern Australia from Victoria to northern Queensland. Small colonies roost in tree hollows, caves and buildings. *Nycticeius ruppellii*, the Greater Broad-nosed Bat, rather common where it occurs, appears to be confined to eastern New South Wales and south-eastern Queensland; no information on roosting

habits of this species is available. *Chalinolobus gouldii*, Gould's Wattled Bat, is widely distributed in Australia, including Tasmania and Norfolk Island. This solitary bat roosts in tree hollows or among leaves of eucalyptus in semi-arid and timbered country; little is known of its habits. *Taphozous flaviventris*, the Yellow-bellied Bat, widely distributed on the Australian mainland, apparently roosts in hollow trees. *Pipistrellus papuanus*, a common bat in New Guinea, also occurs in the surrounding islands (but not the Bismarcks), Moluccas, and probably Celebes; it appears to roost only in tree holes.

The earliest record of larval "*Argas vespertilionis*" from Australia appears to be that of Taylor (1913) from "*Vesperugo* sp." from Townsville, Queensland. Fielding's (1926) report of "*Argas vespertilionis*" from "*Vesperugo* spp." apparently stems from Taylor's record, and the descriptions and illustrations included are obviously from Nuttall and Warburton's Monograph of Ticks and from other non-Australian literature. "*Vesperugo* sp." of early twentieth century authors referred to any one of the following currently recognized species of bats: *Pipistrellus tasmaniensis*, *P. regulus*, or *Eptesicus pumilus*.

It is of interest that *Argas* parasites of bats are not mentioned in Dumbleton's various recent reports of ticks of the New Zealand Subregion and that the present records are the first of this genus to be reported for New Guinea.

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A NEW GENUS OF GALL-FORMING BRACHYSCELIDIPHAGINE PTEROMALIDAE (HYMENOPTERA, CHALCIDOIDEA) FROM WESTERN AUSTRALIA.

By E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

(Five Text-figures.)

[Read 26th September, 1962.]

Synopsis.

Alyxiaphagus picturatus, gen. et sp. nov., was reared from galls on *Alyxia buxifolia*.

Most Pteromalidae are parasites or hyperparasites, but the Brachyscelidiphagini have the unusual habit of forming galls on various plants or, in one case, of living in apiomorpha galls (*Brachyscelidiphaga*). The different genera of gall-formers are each more or less limited to one host plant genus. The Brachyscelidiphagini are best developed in Australia where there are about twenty genera. Many species form galls on *Eucalyptus* and *Acacia*, but there are also species attacking *Brachychiton*, *Casuarina*, *Callistemon*, *Syncarpia*, *Ficus* and possibly *Citriobatus*.

A new genus has been reared from galls on *Alyxia buxifolia*. Two species of the genus are known to form galls on this one host plant, but the material of the second species is inadequate for specific description. As is the case with the species of *Decatomothorax* which attack *Brachychiton*, the different species form distinctive galls on different parts of the plant.

Genus Alyxiaphagus, gen. nov.

Genotype, *Alyxiaphagus picturatus*, sp. nov.

Similar to *Encyrtocephalus* and *Neorileyella* in having a relatively large pronotal collar and with a sharply angled bend in the submarginal vein, but the head not compressed or linear at vertex and the hind femur not expanded.

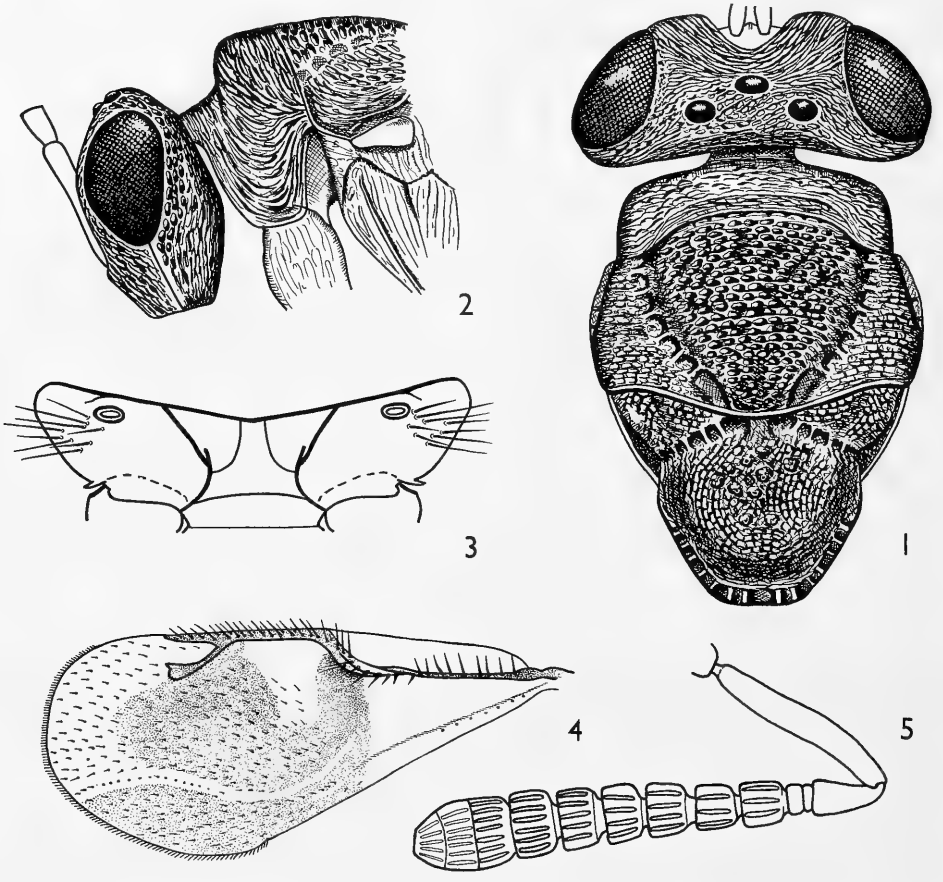
Head wider than high, but malar space a little more than half eye-length; vertex rather rounded above, not carinate even between the lateral ocelli; head with a distinct, though strongly sloping, post-ocular region so that the caudal margin of the eye does not protrude; hind femur not expanded, only as wide as fore femur, without an enlarged tooth; postmarginal vein well developed, as long as the stigmal; stigmal vein curved; antenna 13-segmented, with two ring segments; scutellum not produced over the metanotum.

Alyxiaphagus picturatus, sp. nov.

Female: Body dull red-brown, with gaster darker brown; legs similar but coxae, especially fore coxa, paler and tibiae, especially hind tibia, darker; hind coxa with a small white patch above; antenna with scape and pedicel pale, flagellum blackish but club white; ovipositor valves white except for extreme tip which is black; forewing deeply infuscated in a wide zone from the bend of the submarginal vein to the apex of the stigmal vein except for a small clear area below and bordering the marginal vein.

Length 3·0 mm.; head wider than high, vertex finely rugulose, lower face almost glabrous, mesal margin of eyes diverging below, lower margin of face transverse, malar space clearly somewhat more than half eye-length, malar groove distinct only at upper third; lateral ocelli slightly closer to eye than to median ocellus; scape long, not expanded, pedicel clearly longer than wide, two ring-segments, small, distinct, transverse, first funicle segment, after the ring-segments, quadrate, succeeding segments decreasing very slightly and widening very little, club three-segmented, not expanded, segments all short; funicle segments with distinct glume-like tubercles reaching almost to the apices of the segments; dorsal thorax rugulose, rather transversely so on scutum; pronotal collar distinct, relatively large but about five times as wide as long, caudal margin almost transverse; axillae slightly advanced beyond the caudal margin of the scutum, together forming a gently curved line; axillae almost touching at meson; with distinct large foveae between axillae and scutellum; rim at apex of scutellum

distinct, foveate above, extended only slightly over the metanotum; propodeum with a median pair of fine carinae, diverging very strongly in the middle to join the more distinct longitudinal, laterad carina; propodeum laterally with rather dense long hairs; lateral thorax mostly glabrous; gaster large, not laterally compressed; caudal margin of first three tergites of gaster clearly emarginate at meson, first tergite glabrous, second and third mostly so except antero-laterad, laterally with spaced long setae, succeeding segments with ornamentation and setae extending across meson, apical two segments very small, cerci of apical segment with five long setae, ovipositor valves slightly exserted, with short curved setae at apex; forewing with long setae along the venation,



Figures 1-5. *Alyxiaphagus picturatus*.—1. Dorsal view of head and thorax, × 50; 2, Lateral view of head and pronotum, × 50; 3, Propodeum, × 50; 4, Forewing, × 25; 5, Antenna, × 80.

except stigmal vein; discal ciliation virtually limited to apical half of wing, absent, except for an upper row, between postmarginal and stigmal veins and almost so below the proximal two-thirds of the marginal vein; with a single row of cilia, on lower surface, in the anal groove.

Male: Similar to female, but abdomen small and forewing not as deeply infuscated; glume-like tubercles of antenna denser, particularly on more basad segments; club not as clearly white as in female. Length little more than 2·0 mm.

Types: Holotype ♀, allotype ♂ and paratype ♀♀ in the Western Australian Museum. Paratype ♂, ♀♀ in the Australian National Insect Collection, C.S.I.R.O. Division of Entomology Museum.

Type Locality: Pt. Peron, W.A. (May, 1959, L. N. McKenna), 17 specimens reared from galls on *Alyxia buxifolia*.

A NEW ENCYRTID (HYMENOPTERA, CHALCIDOIDEA) GENUS OF PARASITES OF LERP-FORMING PSYLLIDS ON EUCALYPTUS.

By E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

(Seven Text-figures.)

[Read 26th September, 1962.]

Synopsis.

Two species of *Anisodromus*, a new genus of encyrtid parasites of lerp-forming psyllids on eucalypts, are described.

The encyrtid parasites described in this paper form one of the lesser groups of parasites of lerp-forming psyllids on eucalypts. They can be distinguished from the more abundant species of *Psyllaephagus* at once by the structure of the antennae. The antennae are similar in both sexes and the swollen club is strongly, obliquely acuminate. In this respect they somewhat resemble *Isodromus* and *Homalotylus*, but the club is three-segmented and not solid. Wing-venation too is distinct. The species of *Isodromus* are parasites of neuropterous (chrysopid and hemerobiid) larvae and those of *Homalotylus* parasitize coleopterous (coccinellid) larvae.

Baeoanusia, bred from chrysomelid eggs, is similar only in the shape of the female antenna and structure of the mandibles. (The African species, *oleae* (Silvestri) and *minor* (Silvestri), placed in *Baeoanusia* by Compere are generically distinct from *Baeoanusia*, differing among other characters in wing venation and the shape of the mandibles.) The antenna of the male in *Baeoanusia* is plumose and differs markedly from that of the female.

The genus differs from *Psyllaephagus* only in the structure of the antennae.

Genus Anisodromus, gen. nov.

Genotype, *Anisodromus tarsius*, sp. nov.

Female. Head lenticular, the caudal margin concave, subcarinate, hemispherical in lateral view; antennae inserted towards the mouth, short, flagellum expanding markedly to the obliquely acuminate club, antenna 11-segmented, the club three-segmented but the apical segment small, scape not markedly expanded; mandibles with the upper teeth developed into a broad cutting edge; scutellum with the apical three pairs of hairs enlarged, erect; axillae just meeting at meson; middle tarsus with basitarsus large, expanded, about as long as the following three segments combined, apical segment small, somewhat longer than the fourth segment but very much shorter than the basitarsus, basitarsal pad with numerous irregularly placed tubercles extending almost to base, with a short apical row; forewing with very short marginal vein, no longer than wide, stigmal vein well developed, diverging strongly from wing margin, postmarginal vein only slightly shorter than stigmal.

Male. Very similar to female, distinguishable mainly on genitalia; postmarginal vein slightly shorter than in female.

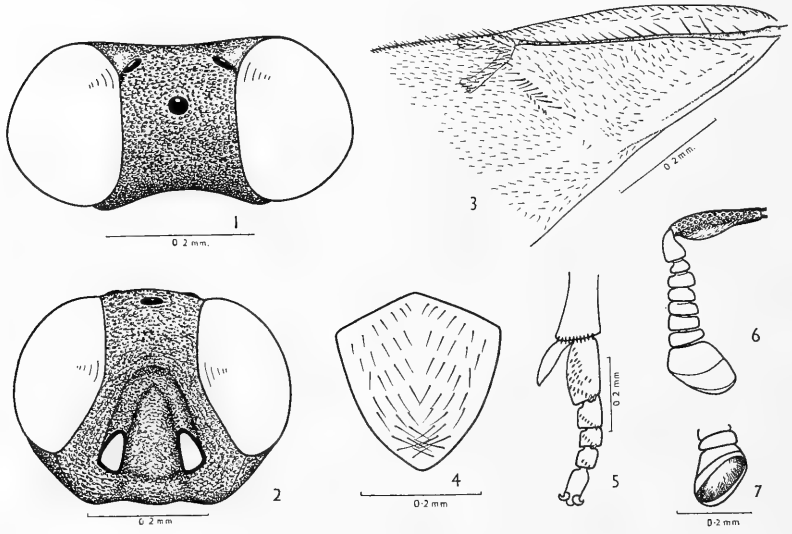
Key to species of Anisodromus.

1. Scape pale at base; apex of middle femur, tibia and most of tarsus and mesal surface of fore tibia and femur in part, pale; tegula reddish-brown; median ocellus about as far from eye as from lateral ocellus ..... *tarsius*, sp. nov.
— Scape all dark; legs, except middle tarsus in part, all dark; tegula whitish at basal half; median ocellus distinctly closer to eye than to lateral ocellus ..... *niger*, sp. nov.

Anisodromus tarsius, sp. nov.

Female. Body very dark metallic green with coppery and purple reflections; scape dark except at extreme base, pedicel dark except narrowly at apex, flagellum mostly dark; legs mostly dark, tarsi and joints paler; tegula pale, reddish-brown; caudal margin of prepectus widely pale; wings clear.

Length 1·6 to 1·9 mm.; vertex of head wide, as wide as eye width, very finely, evenly, rugoso-punctate, lateral ocelli less than half their diameter from eye, much further apart than either is from median ocellus, median ocellus about as far from eye as from lateral ocellus; scrobes clearly defined, deep, converging and meeting above in a rounded point, well removed from eye margin; area between scrobes slightly raised; silvery hairs of lower face rather short and sparse, continued to the upper limits of the scrobes; antennal insertions only slightly further apart than either is from eye, not quite as far from lower border of clypeus as from eye; scape somewhat expanded below over apical half, narrowed and rounded at base, pedicel relatively large, distinctly longer than wide, funicle segments all small, expanding, first segment much narrower than pedicel, subquadrate, second segment widening rapidly, slightly wider than long, following segments subequal in length to second segment but widening, club large, markedly expanded, obliquely acuminate from near base, about half as long as funicle segments combined, club three-segmented, first segment largest, apical segment very



Figures 1-7. *Anisodromus tarsius*.—1, Head, dorsal view; 2, Head, frontal view; 3, Basal half of forewing; 4, Scutellum; 5, Middle tarsus, ventral; 6, Antenna; 7, Club of antenna, ventral.

small; scutellum with hairs rather long and dense, covering most of the dorsal surface, at least the apical three pairs enlarged and erect; basitarsal pad of middle tarsus with numerous tubercles including a short apical row; gaster clearly shorter than the thorax; ovipositor not exserted; hairs under submarginal vein evenly spaced except for a small clear area towards base; postmarginal vein very slightly shorter than stigmal.

Male. Almost indistinguishable from female apart from genitalia.

Types: Holotype ♀, allotype ♂ and paratypes in the Australian National Insect Collection, C.S.I.R.O., Division of Entomology Museum, Canberra. Paratypes in the British Museum (Nat. Hist.) and the U.S. National Museum.

Type locality: Canberra, Australia (30 Aug. 1953, L. R. Clark), bred from *Spondyliaspis nigra* on *Eucalyptus melliodora*. Paratypes also from *Spondyliaspis* sp. *bancrofti* group and *Creiis ? liturator* on *Eucalyptus melliodora*, Mt. Franklin, Australian Capital Territory (2 Mar. 1949, E. F. Riek), bred from finger-like psyllid gall on *Eucalyptus* sp.

The species is also recorded from Bright, Victoria (24 Feb. 1949, E. F. Riek), bred from finger-like psyllid gall (? *Choiza* sp.) on *Eucalyptus niphophila*.

The species is short and stocky and of rather dark colouring, appearing black to the naked eye.

ANISODROMUS NIGER, sp. nov.

Female. Body very dark metallic green with purple and coppery reflections; scape all dark, flagellum mostly dark; legs dark except middle tarsus and joints very narrowly; tegula pale, whitish at base, reddish-brown at apex; caudal margin of prepectus widely pale; wings clear.

Length 2·0 to 2·3 mm.; vertex of head wide, not quite as wide as eye width, very finely, evenly, rugoso-punctate, mesal margins of eyes subparallel, lateral ocelli less than half their diameter from eye, much further apart than either is from median ocellus, median ocellus distinctly somewhat closer to eye than to lateral ocellus; scrobes clearly defined, deep, converging and meeting above in a rounded point, well removed from eye margin; area between scrobes only slightly raised; silvery hairs of lower face rather short and sparse, continued to the upper limits of the scrobes; antennal insertions only slightly further apart than either is from eye, distinctly closer to lower border of clypeus than to eye; scape slightly expanded below over apical half, narrowed and rounded at the base, pedicel relatively large and stout but clearly longer than wide, funicle segments all small, expanding, first funicle much narrower than pedicel, sub-quadrate, second funicle considerably wider, a little wider than long, following segments subequal in length but widening, the sixth funicle about one and a half times as wide as the second, club large, markedly expanded, obliquely acuminate from near base, about half as long as funicle segments combined, club three-segmented, first segment largest, apical segment very small; scutellum with hairs rather long and dense, covering most of the dorsal surface, at least the apical three pairs enlarged, erect; basitarsal pad of middle tarsus with numerous tubercles, the apical row with few tubercles; gaster clearly shorter than thorax; ovipositor not exserted; hairs under submarginal vein somewhat irregularly placed; postmarginal vein as long as the stigmal.

Male. Not known.

Types: Holotype ♀ and two paratype females in the Australian National Insect Collection.

Type locality: Canberra, Australia (2 Dec. 1952, L. R. Clark), bred from *Lasiopsylla* sp. *rotundipennis* group on *Eucalyptus blakelyi*. Paratypes, same data except 11 Nov. 1953 and 22 Oct. 1954.

GYNODIOECISM IN *LEUCOPOGON MELALEUCOIDES* A. CUNN.

By Alison McCusker, Department of Botany, University of New England.

[Read 26th September, 1962.]

Synopsis.

Leucopogon melaleucoides (Epacridaceae) is found to be strictly gynodioecious. The relative frequencies of male-sterile and hermaphrodite plants in the population are estimated, and male-steriles are found to set more fruit than hermaphrodites. The nature of the sex determining mechanism is discussed briefly.

Introduction.

In the family Epacridaceae, many species show deviations from the normal pattern of hermaphroditism which is characteristic of the majority of flowering plants. Bentham (1869) recorded that the flowers were "often more or less unisexual" in the genus *Monotoca* and noted an approach to unisexuality in *Leucopogon hookeri* and "a very few other species" of *Leucopogon*. Smith-White (1959) cited several cases of dioecism and partial dioecism in the family. *Leucopogon melaleucoides* is the only species which is so far known to be gynodioecious. Only female and hermaphrodite plants are produced, and there is no breakdown of the separation such as Yampolsky (1919) observed in *Mercurialis annua* where male or hermaphrodite flowers were often formed on old female plants.

Several species in which gynodioecism is a feature of the breeding system in nature are now known, e.g., *Satureia hortensis*, *Salvia pratensis* and many other labiates, *Cirsium oleraceum*, *Geranium silvaticum*, *Plantago lanceolata* (Correns, 1928), several species of *Hebe* (Frankel, 1940), *Origanum vulgare* (Lewis and Crowe, 1956), *Arundo richardii* (Connor and Penny, 1960). Clearly, this type of sexual dimorphism is not confined to a group of closely related taxa, and has probably arisen many times in the evolution of the angiosperms.

Lewis (1941) discussed the mechanisms by which an equilibrium might be maintained between females and hermaphrodites in natural populations. He showed that, in cases of genic control of male-sterility, a substantial selective advantage favouring the female plants is required, and in the case of cytoplasmic determination a slight advantage of the females is necessary.

It is the purpose of this paper to suggest the nature of the advantage which enables female plants of *Leucopogon melaleucoides* to be maintained at relatively high frequencies in natural populations.

Material.

Leucopogon melaleucoides is "an erect, robust shrub of several feet" (Bentham, 1869). It produces abundant flowers borne in short axillary racemes and maturing in early spring. The fruit is approximately 4 mm. in diameter, drupaceous, developing from a 2–5 locular ovary containing one ovule per loculus and ripening 4–5 months after flowering. Cross-pollination of the flowers is carried out chiefly by bees.

Three populations have been examined, at Gibraltar Range, Torrington and Baldersleigh, all in the New England Region of New South Wales. Gynodioecism has been observed at each of these localities. Gibraltar Range was chosen as the site for more detailed studies.

Male-sterility.

The proportion of male-sterile plants at Gibraltar Range was estimated by taking a belt transect 20 feet wide and approximately 600 yards long (see Table 1).

In a sample of 16 plants examined at Torrington, six were male-sterile (0·375).

Seed Set.

Young fruits were harvested from a sample of four male-sterile and four hermaphrodite plants about three months after flowering, and the percentages of developing seed were compared (Table 2).

These figures show no significant difference in seed set between the two groups of plants.

Embryos from apparently good seeds were tested for viability by the tetrazolium staining technique (Hyde, 1955). None of the embryos gave a positive reaction in the short time (six hours) specified by Hyde for rye-grass seeds, but all the embryos tested had stained brightly after 15 hours, either at 30° C. or at room temperature (approximately 10° C.). Several attempts to germinate seeds dissected from ripe fruits were unsuccessful.

Table 1.

Proportions of Male-sterile and Hermaphrodite Plants in Gibraltar Range Population.

	No.	Proportion.
Male-sterile plants	100	0·392
Hermaphrodite plants	155	0·608

Fruit Set.

In order to determine the percentages of fruit set by the male-sterile and hermaphrodite plants under various conditions, branches were bagged during the flowering season and harvested 14 weeks later for scoring. Six treatments were set up in order to ascertain:

(i) the comparative efficiencies of hermaphrodite and male-sterile plants in setting fruit following pollination and fertilization under normal field conditions;

(ii) whether self-pollination of hermaphrodite plants leads to effective fertilization;

(iii) whether apomixis may occur in the species in the event of pollen being unavailable to the flowers;

(iv) whether the technique used for emasculation of hermaphrodite flowers—viz., removal of the corolla tube bearing the anthers—causes sufficient damage to the flower to inhibit the setting of fruit.

Table 2.

Percentage Seed Set in Male-sterile and Hermaphrodite Plants.

	Male-sterile Plants.				Hermaphrodite Plants.			
	1	2	3	4	1	2	3	4
No. of loculi examined ..	179	158	64	192	139	185	123	152
No. of seeds developed*	128	151	55	184	123	149	109	86
Percentage seed set ..	71·5	95·6	85·9	95·8	88·5	80·5	88·6	56·6

* Seeds which were white and turgid, filling the loculus, were counted as good. Undeveloped seeds were brown and shrivelled, and the loculi often compressed to narrow slits in transverse section.

Details and results of the six treatments are given in Table 3.

Statistical analyses have shown that the differences between (A) and (B) and between (A) and (C) are highly significant, and that between (A) and (F) is significant at the 2% level.

Two conclusions may be drawn from treatments (A) to (C):

(i) since fruit is set in both (B) and (C), both outcrossing and selfing may lead to effective fertilization in the species;

(ii) since fruit set in (C)<(A)<(B), outcrossing is more effective than selfing.

The figures obtained in treatments (D) and (E) strongly suggest that apomixis is not a normal or even a possible means of reproduction in the species. If it is assumed that the single fruit formed in treatment (D) was the result of experimental error, it can be stated that neither type of plant set fruit in the absence of pollen. The

possibility of apomictic development stimulated by contact of pollen grains with the stigma cannot be ruled out. However, it seems unlikely that such a mechanism operates in view of the significantly higher fruit set in male-sterile plants (B), where pollination is dependent upon external agents, than in hermaphrodite plants (A) in which abundant pollen is shed directly onto the stigma. Such a mechanism should result in practically 100% fruit and seed set in hermaphrodite plants.

The difference between the figures obtained for treatments (A) and (F) may indicate that some degree of mechanical damage is caused by emasculation, or it may be due to the treatment in (F) having been set up before pollination of some flowers had been effected. Newly opened flowers were used so that side effects of emasculation in this treatment might parallel those in (E) as closely as possible.

Discussion.

It has been shown that male-sterile plants gain a selective advantage over hermaphrodites by higher seed set, although this was not revealed by the technique of comparing the seed contents of a given number of matured fruits, which Lewis and Crowe (1956) employed for *Origanum vulgare*. Table 3 shows that when selfing is enforced, only 20% of hermaphrodite flowers set fruit. Even many of these may have been outcrossed under natural conditions. It is probable, then, that most of the seeds of hermaphrodite parents, scored in Table 2, are the results of outcrossing and that a large number of non-viable seeds formed on these plants were not scored because the fruits which contained them failed to develop.

Table 3.

Fruit Set Data.

	No. of Flowers Bagged.	No. of Fruits Set.	Percentage of Fruit Set.
(A) Open hermaphrodite flowers	351	152	43
(B) Open male-sterile flowers ..	211	130	62
(C) Hermaphrodite buds	469	94	20
(D) Male-sterile buds	264	1	0·004
(E) Emasculated hermaphrodite buds	121	0	0
(F) Emasculated hermaphrodite flowers	208	71	34

Thus it may be assumed that, if a hermaphrodite flower is cross-pollinated before selfing has been effected, a high seed fertility will result. If it is not, there is a high probability (0·8) that no fruit will be set. It is clear that early cross-pollination occurs frequently because open-pollinated hermaphrodite flowers set twice as much fruit as those bagged in the bud (Table 3).

Cross-fertilization may be assisted by a mechanism such as differential pollen-tube growth, but no experimental evidence has been obtained on this point.

Because of failure to germinate seeds, it has not been possible to gain any information regarding the mode of inheritance of gynodioecism in this species. Correns (1928) found that both female and hermaphrodite plants bred true in *Satureia hortensis* and *Cirsium oleraceum*, and suggested therefore that male-sterility was under the control of a cytoplasmic factor. East (1934) stated that genic control could not be ruled out in these two species, but that it would require peculiar types of balanced lethals and hence a high degree of sterility, which was not in accordance with the observations. In *Leucopogon melaleucoides*, however, a high level of sterility has been observed. Figures given in this paper show a high degree of abortion of embryo sacs and/or young zygotic stages in both types of plants, and the pollen of the species is of the variable tetrad type (the "A-type" of Smith-White, 1955, first described by him (1948) in *Astroloma pinifolium*), with a total fertility of the order of 60%. Thus the possibility of control of the sex balance by a complex genic mechanism must be left open. If a single genetic

factor is responsible for sex determination, a second major selective advantage must favour the female plants, since the higher seed set determined here falls short of the twofold advantage which Lewis (1941) has shown to be necessary for their maintenance in the population.

Acknowledgements.

This work was commenced during my tenure of a Linnean Macleay Fellowship in Botany in 1959.

My thanks are due to Dr. S. Smith-White of the Botany Department, University of Sydney, for guidance during the early stages of the work, to Associate Professor G. L. Davis, Department of Botany, University of New England, for reading the manuscript, and to Miss Gwenda J. Cane, Department of Mathematics, University of New England, for help with the statistical analysis of the results.

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AMENDMENTS TO THE DISPOSAL OF TYPE SPECIMENS OF SPECIES OF *CULEX* (*LOPHOCERAOMYIA*) FROM NEW GUINEA.

By Donald H. Colless, Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

[Read 24th October, 1962.]

In a previous paper (Proc. Linn. Soc. N.S.W., 84: 382) describing four new species of mosquito from New Guinea, I notified my intention of placing the primary types in the British Museum (Nat. Hist.). This has not yet been done, and I am now of the opinion that such types could be more conveniently located in an Australian institute. I therefore announce herewith the following amended disposition of types.

Culex (*Lophoceraomyia*) *atracus* Colless.

Holotype male (Kavieng, N. Ireland, F. H. Taylor, CH101, CT506) and five paratype males in the Australian National Insect Collection, Canberra; two paratype males each in the British Museum (Nat. Hist.) and the United States National Museum.

C. (*L.*) *pseudornatus* Colless.

Holotype male (Edie Ck., N. Guinea, F. H. Taylor, CH87, CT505) and allotype female in the Australian National Insect Collection, Canberra; one male and one female paratype in the British Museum (Nat. Hist.).

C. (*L.*) *petersi* Colless.

Holotype male (N.G. 12; Minj, N. Guinea, 1958, W. Peters; CH81, CT499) and allotype female, both with associated larval and pupal skins, and three morphotype larvae, in the Australian National Insect Collection, Canberra; paratype series, each of one male and one female, both with associated larval and pupal skins, in the British Museum (Nat. Hist.) and the United States National Museum.

C. (*L.*) *christiani* Colless.

Holotype male (N.G.5; Minj, N. Guinea, 1958, W. Peters; CH80, CT498) and allotype female, both with associated larval and pupal skins, and 10 morphotype larvae, in the Australian National Insect Collection, Canberra; paratype series, each of one male with associated larval and pupal skins, and four morphotype larvae, in the British Museum (Nat. Hist.) and the United States National Museum.

NOTES ON AUSTRALIAN MOSQUITOES (DIPTERA, CULICIDAE).

VI. Five New Victorian Species and a Description of the Larva of Aëdes milsoni (Taylor).

By N. V. Dobrotworsky, Zoology Department, University of Melbourne.*

(Five Text-figures.)

[Read 24th October, 1962.]

Synopsis.

Adults, larvae and pupae of *Culiseta antipodea,* n. sp., *Aëdes imperfectus,* n. sp., and *Aëdes subbasalis,* n. sp., are described and figured. *C. antipodea* is placed in the subgenus *Climacura*; the other species of this subgenus is distributed in the Eastern and Central United States. *Aë. imperfectus* is closely related to *Aë. burpengaryensis* (Theobald), and *Aë. subbasalis* to *Aë. rupestris* Dobrotworsky. Descriptions are given of the adults of *Masonia variegata,* n. sp., the female of *Masonia aurata,* n. sp., and the larva of *Aëdes milsoni* (Taylor).

Culiseta (Climacura) antipodea, n. sp.†

Types: The holotype, allotype and seven paratypes were bred from larvae collected by the author 23.1.62 at Cann River, Victoria; 13 paratypes were bred from larvae collected by G. W. Douglas 15.9.54 at Wilson's Promontory and from an egg raft collected 5.3.54 at the same locality. The holotype, allotype and 10 paratypes have their associated larval and pupal skins. The holotype male, allotype female, five paratype males and five 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.

Material Examined: 30 ♂♂, 25 ♀♀.

Distinctive Characters: Adult: Forked upright scales on vertex black. Scutum, tergites and sternites black scaled. Tarsi black. Male terminalia: Coxite with black setae; basal lobe small with 2–3 strong setae and several finer ones. Phallosome smooth. Larva: Brown. Siphon with ventral row of setae. Lateral comb composed of single row of scales.

Holotype Male. Head: Vertex clothed with narrow curved pale scales and black forked scales. Proboscis black scaled. Palps about as long as proboscis with labella, black scaled; terminal segment not swollen. Antennae plumose, hairs of verticils evenly spread round the segments. Thorax: Integument dark brown. Scutum sparsely clothed with narrow curved dark-bronze and black scales. Scutal bristles black. Scutellum with a few narrow dark scales. Posterior pronotum with a few hair-like scales. One small black spiracular bristle. Sternopleuron with a few black bristles. One lower mesepimeral bristle and 2–3 narrow pale scales towards middle. Wing length: 2·7 mm. Legs: Black scaled, femora pale below. Fore and mid claws toothed, hind simple. Abdomen: Tergites and sternites black scaled; scales on VIIIth sternite paler. Terminalia (Fig. 1, *a*): Coxite about three times as long as broad, with black bristles. Basal lobe about one-fifth of length of coxite, with 2–3 long strong setae and several finer ones at tip. Style narrow, slightly less than half length of coxite, with three minute setae spaced along it and three at tip. Terminal appendage small. Paraproct with three strong teeth. Phallosome simple, smooth. Lobes of IXth tergite flat, each with 5–6 setae.

* This work was supported in part by a grant from the Trustees of the Science and Industry Endowment Fund of the Commonwealth Scientific and Industrial Research Organization.

† The generic name *Theobaldia* Neven-Lemaire being preoccupied by *Theobaldia* Fischer, 1885. Mosquitoes of the genus are now renamed to *Culiseta* Felt.

Allotype Female. This differs from the holotype as follows: Palps about one-fifth length of proboscis. Scutal scales narrow, curved, black. There are more narrow curved scales on posterior pronotum. Three lower mesepimeral bristles and patch of pale hairs towards middle. Wing length: 3·8 mm. All tarsal claws simple.

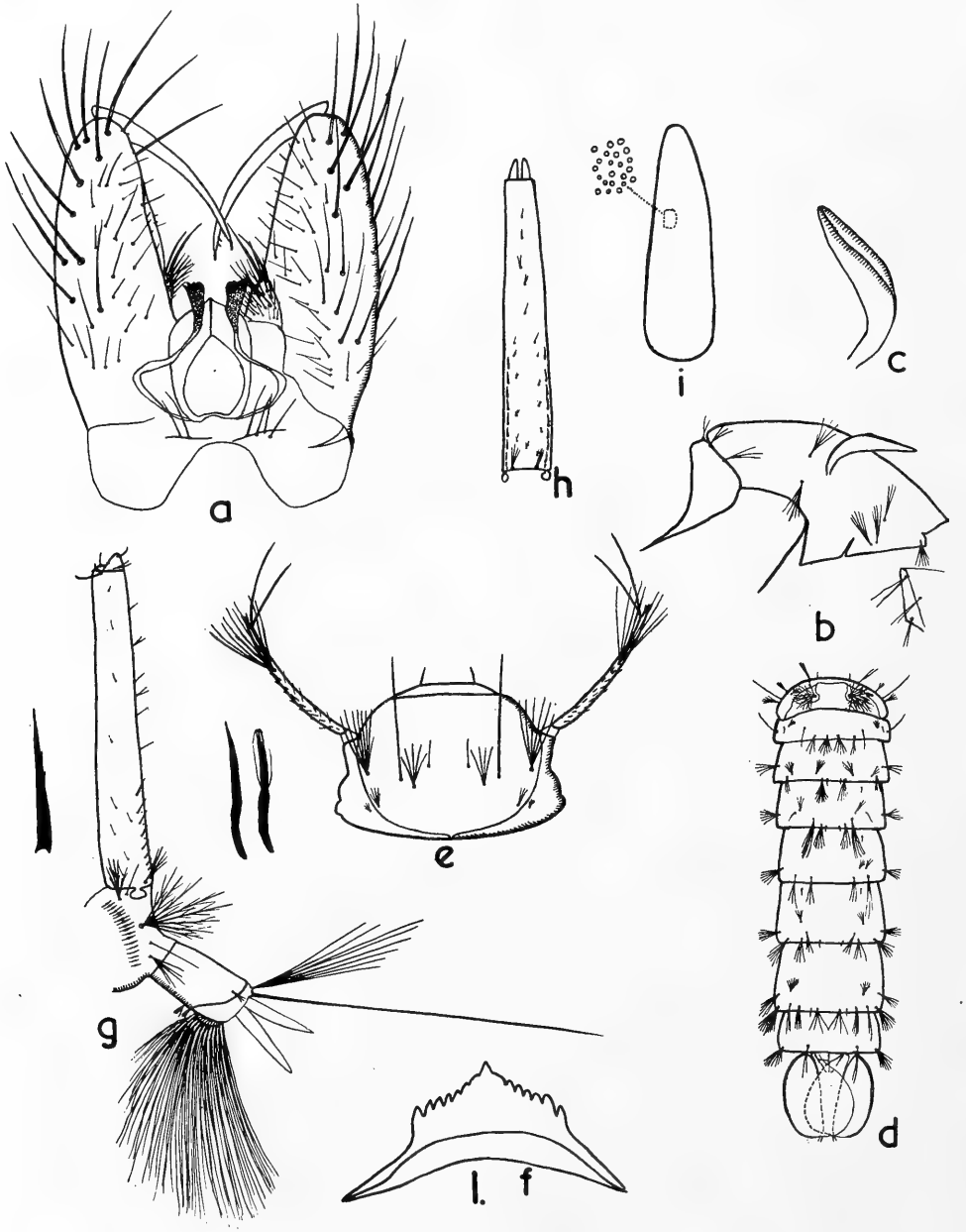

Fig. 1. *Culiseta antipodea*, n. sp. *a*, ♂ terminalia, left coxite sternal aspect, right tergal aspect; *b*, *c*, pupa; *b*, cephalothorax and metanotum; *c*, trumpet; *d*, abdomen; *e*, *f*, *g*, *h*, larva; *e*, head; *f*, mentum; *g*, terminal segments; *i*, eggs.

Paratype Males and Females. The series of 10 paratype males and 10 paratype females do not show significant variations. Wing length in males varies from 2·8 mm. to 3·7 mm., in females from 3·3 mm. to 3·6 mm. There are from 1 to 3 spiracular

bristles and from 1 to 3 lower mesepimeral bristles. Some females have a few narrow pale scales among pale hairs of mesepimeron towards the middle.

Pupa: Details shown in Figure 1, *b*, *c*, *d*.

Larva (Fig. 1, *e*, *f*, *g*, *h*): Brown. Head broad. Head setae 4 and 6, single; 5, 4–5 branched, about ¼ length of seta 6; 7, 6–8 branched; 8, 3–5 branched; 9, 4–6 branched. Antenna long, curved, about as long as head; seta 1 with about 30 branches. Mentum with broad central tooth and 6–7 lateral teeth on each side. Thorax: Prothoracic setae 1, 2, 4 and 6, single; 3, 2 branched; 4, 4–7 branched. Abdomen: VIIIth segment: Lateral comb of 14–21 scales in single row. Seta 1, 5–9 branched; 2 and 4, single; 3, 6–9 branched; 5, 4–5 branched. Syphon long, slightly tapering, index 6·1–7·5, mean 6·8. Pecten of 6–9 spines. Basal siphonal seta, small, 3–5 branched; 7–8 minute lateral setae along siphon; 10–12 minute setae on ventral side between pecten, and row of 5–6 single or two branched, longer, fine setae in single row above pecten. Anal segment: Saddle complete ring; seta 1, small, 3–4 branched; 2, 6–10 branched; 3, single; 4 (ventral brush) of 14 tufts. Anal papillae narrow, pointed, about as long as saddle.

Eggs (Fig. 1, *i*): An egg raft found in a Teatree swamp at Wilson's Promontory, Victoria, by Mr. G. W. Douglas 5.3.54 consisted of 102 eggs. Several adults were reared from it.

Biology: In Queensland it breeds in Teatree swamps and semi-permanent pools 2–3 feet deep, in coastal heath country (E. N. Marks). In Victoria also it was found breeding in Teatree swamps with a dense growth of tall *Gleichenia dicarpa*, *Cladium tetragonum* and *Restio tetraphyllus*. In the swamp near Cann River the vegetation was so dense and entangled that movement through it was possible only by following animal tracks. There the larvae of *C. antipodea* were associated with larvae of *C. fergusoni* (Taylor), *C. orbostiensis* Dobr., *C. inconspicua* (Lee) and *A. atratipes* Skuse. Adults have not been collected in the field.

Biting Habits: *C. antipodea* does not attack man and nothing is yet known about the blood sources of this species.

Distribution: *C. antipodea* was found breeding in Queensland: Caloundra 13.VIII.45, F. A. Perkins & J. L. Wassell; Victoria: Wilson's Promontory 5.III.54, 15.IX.54, G. W. Douglas; Cann River 23.I.62, 20.III.62, N. V. Dobrotworsky.

Discussion: Within the genus *Culiseta*, recognition of subgenera on adult characters is notoriously difficult. Edwards (1932), with only adult specimens available, placed the four Australian species known at the time in the subgenus *Climacura*, but on larval characters (Dobrotworsky, 1954, 1960) three of these species have since been placed in other subgenera.

The subgenus *Climacura* is characterized by the row of ventral tufts along the siphon and by the arrangement of the lateral comb scales in a single row. These features are found in only two species: the North American *C. melanura* (Coquillett), for which the subgenus was established, and the present species *C. antipodea*. The two are remarkably similar. In the adults of both, the antennae are of the *Culex* type and the palps of *Aëdes* type and with the terminal segment not swollen. The male terminalia show little difference.

As far as the larvae are concerned there is a strict correspondence in the setae of the head of the two species and in the structure of the terminal segments of the abdomen.

The similarity of these species becomes more remarkable when it is realized that the subgenus is not known from any parts of the world other than North America, New Zealand and Australia.

Mansonia variegata, n. sp.

Types: The type series was collected at Cann River, Victoria. Holotype male 23.I.62; allotype and two paratype females 6.II.61. The holotype and allotype are in the collections of the National Museum, Melbourne. One paratype female is in the collections of C.S.I.R.O., Division of Entomology, Canberra, and the second in the University of Queensland, Brisbane.

Material Examined: 1 ♂, 3 ♀♀.

Distinctive Characters: Proboscis more or less mottled. Wing with broad scales, mottled. Femora and tibiae mottled; hind femora and tibiae with preapical creamy patch. Tarsi with apical creamy bands.

Holotype Male. Head: Vertex with narrow curved pale scales; upright scales pale medially, black laterally and towards neck. Palps exceed length of proboscis with labella, by terminal segment. Proboscis black, slightly mottled with pale scales. Thorax: Integument dark brown with some lighter areas on pleura. Scutum clothed with narrow curved light-golden and black scales; front and lateral margins have more light-golden scales than black. Scutellum with narrow curved light-golden scales and darker border bristles. Posterior pronotum with narrow curved light-golden scales. Pleura with two patches of broad scales on sternopleura. Lower mesepimeral bristles

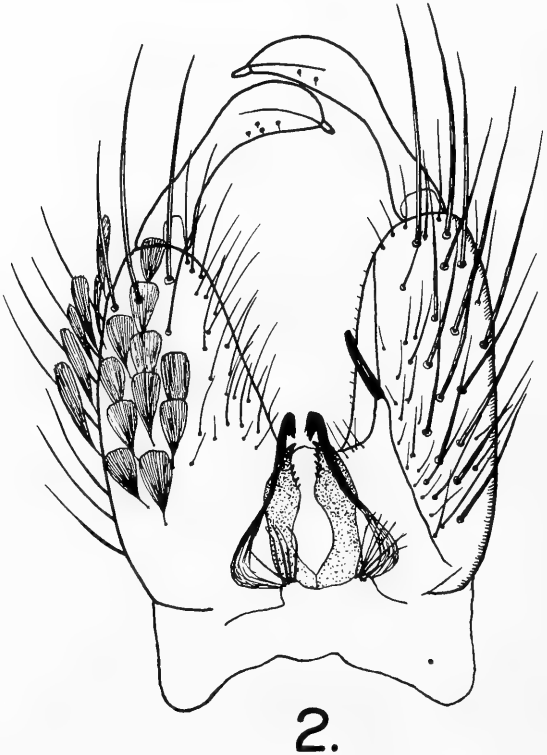

Fig. 2. *Mansonia variegata,* n. sp. ♂ terminalia, left coxite sternal aspect, right tergal aspect.

absent. Wing mottled, scales broad. Wing length 3·7 mm. Knob of halters pale scaled. Legs: Femora and tibiae mottled, with preapical patch of pale scales most conspicuous on hind legs. Knee spots white. First three tarsal segments of fore and mid legs with creamy apical bands. Hind tarsi with four apical bands. Fore and mid tarsal claws toothed, hind claws simple. Abdomen: Tergites black scaled with white basal lateral patches. Sternites white, with large triangular black patch toward apical border. Terminalia (Fig. 2): Coxite slightly more than twice as long as broad; sternally and laterally with broad scales, tergally and laterally with long setae. Basal lobe with long blunt spine. Style swollen distally, with small appendage. Paraproct with four strong teeth. Phallosome scoop-shaped with thickened margins and teeth along each side. Lobes of IXth tergite small, with five setae.

Allotype Female. This differs from the holotype as follows: Proboscis creamy scaled, except for black-scaled base and tip. Palps about one-quarter length of proboscis, black scaled, with a few white scales dorsally. Pleura with distinct dark

band extending from upper part of mesepimeron to posterior pronotum. Two strong lower mesepimeral bristles. Wing length 3·6 mm. Upper fork cell slightly longer than stem. All claws simple. Eighth tergite with pale scales. Sternites black, with small lateral patches of white scales.

Paratype Females. The two paratype females are similar to the allotype. Wing length 3·6 mm.

Biology and Habits: Mating has been observed just after sunset; it is initiated in flight, and completed on grass. It is a man-biting species. All specimens were collected, after sunset, near a permanent Teatree swamp.

Distribution: *M. variegata* is known only from the type locality, Cann River, Victoria, 6.II.61 and 23.I.62, N. V. Dobrotworsky.

Discussion: The holotype male and one paratype female have one spiracular bristle, which are absent in all other species of the genus.

It is difficult to assign *M. variegata* to any one of the subgenera recognized by Edwards (1932). On the characters of the male terminalia and palps, seventh abdominal segment of the female which is large, and the absence of post-spiracular bristles it appears to belong to *Coquillettidia*, but the wing scales are broad, not "rather narrow (lanceolate to almost linear)", as is characteristic of this subgenus. It is better not to assign this species to a subgenus until the larva is discovered.

Mansonia aurata, n. sp.

Types: The type series was collected at Cabbage Tree Creek, Victoria. Holotype female and 10 paratype females, 16.XII.59. The holotype and five paratypes are in the collections of National Museum, Melbourne. One paratype is 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.

Material Examined: 46 ♀♀.

Distinctive Characters. Proboscis black. Scutum uniformly clothed with light-golden scales. Wing with narrow dark scales. Hind tibia black. Tarsi with basal creamy bands. Tergites black, unbanded; sternites pale with a few dark scales.

Holotype Female. Head: Vertex with narrow curved light-golden scales and upright light-golden scales, becoming black laterally. Proboscis black. Palps dark, with some pale scales dorsally. Thorax: Integument brown; scutum with light-golden scales; most bristles black. Posterior pronotum with narrow curved light-golden scales. Scutellum with narrow scales. Post-spiracular area with patch of elongate pale scales. Sternopleura and mesepimeron with patches of broad pale scales and light-golden bristles; three lower mesepimeral bristles. Wing length: 4·0 mm. Wing with narrow dark scales with violet-pink reflections. Upper fork cell about twice length of its stem. Knob of halters dark, pale scaled. Legs: Fore and mid femora dark scaled with admixture of pale scales above, pale scaled below. Hind femora pale except for dark tip on distal quarter, extending toward base dorsally. Knee spots light-golden. Fore and mid tibiae dark above, pale below; hind tibiae black, with violet reflections. First segment of all tarsi creamy below for about half length. Fore tarsi with two basal creamy bands, mid and hind with four. All claws simple. Abdomen: Tergites black scaled, with violet reflections, unbanded; basal lateral spots creamy. Sternites pale scaled, with a few dark scales medially.

Paratype Females. The series of ten paratypes does not show much variation. In some specimens the number of dark scales on sternites is increased and they then form an inconspicuous band towards the apical border. Wing length varies from 3·5 mm. to 4·2 mm.

Biting Habits: A day biting species which attacks man.

Distribution: *M. aurata* has been collected in east Gippsland, Victoria, east of Orbost. Specimens have been examined from the following localities: Cabbage Tree Creek, 5.XII.57, 16.XII.59, 7.II.61, 22.I.62; Cann River, 6.II.61, 22.I.62; Genoa, 7.II.61, N. V. Dobrotworsky.

Discussion: *M. aurata* has no post-spiracular bristles and has narrow wing scales. On these characters it appears to be *Coquillettidia*, but should not be assigned to this subgenus until the male is discovered.

Aëdes (Ochlerotatus) imperfectus, n. sp.

Types: The type series was bred from larvae and pupae collected at Woori Yallock, Victoria, 16.IX.58. Holotype, allotype, two paratype males and four paratype females have their associated larval and pupal skins. The holotype male, allotype female, five paratype males and five 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.

Material Examined: 15 ♂♂, 102 ♀♀.

Distinctive Characters. Adult: Scutum light-golden, with two dorso-central black stripes. Hind femora in females, white with black scales at tip making a ring, broken below. Tergites usually unbanded, with large lateral patches of creamy scales extending to dorsal side. Larva: Only first stage larvae have detached pecten teeth beyond seta 1. Fourth stage larva: Head setae 5 and 6 single. Lateral comb of 10–14 spines arranged in single row.

Holotype Male. Head: Vertex with narrow curved and upright scales creamy. Proboscis and palps dark scaled. Palps longer than proboscis without labella by about length of terminal segment. Thorax: Integument black. Scutum clothed with light-golden scales becoming paler around bare area. Posterior pronotum with narrow curved creamy scales. Pleura with patches of broad creamy scales and bristles. No lower mesepimeral bristles. Wings dark scaled; wing length: 4·6 mm. Knob of halters dark with white scales. Legs: Fore and mid femora black anteriorly, pale posteriorly, unmottled. Hind femora white on basal three-quarters, black dorsally with dark dorsal line on apical half. Tibiae and tarsi black with dull violet reflections. Fore and mid claws toothed; hind claws simple. Abdomen: Tergites black scaled with violet reflections; basal lateral patches large, creamy. Sternites pale scaled with apical black bands and some black scales medially. Terminalia (Fig. 3, *a*, *b*): Coxite with short setae tergally and a few long setae laterally and apically. Sternally coxite with scales and long and medium setae. Basal and apical lobes small. Basal lobe with large patch of short, fine setae and one long seta near tergal edge. Apical lobe pointed, with one long curved, flattened seta and a few shorter ones at base. Style widening in middle; on apical third more slender and with four small setae; appendage long. Harpago long, with pilose subbasal thumb on inner side, bearing terminal seta about as long as thumb. Appendage with curved pointed tip and fimbriated distal margin. Paraproct with single tooth. Lobes of IXth tergite with 7–8 stout setae.

Paratype Males. The series of ten paratype males does not show much variation. Wing length varies from 3·4 mm. to 4·3 mm. Sternites in some specimens have more black scales medially and these may join the apical black band forming triangle.

Allotype Female. This differs from the holotype male as follows: Palps about one-fifth of proboscis with labella. Four lower mesepimeral bristles. Wing length: 5·0 mm. Upper fork cell is less than twice its stem. Hind femora white with black scales dorsally and laterally on distal quarter and forming a dorsal line for three-quarters of length. All hind claws except one toothed. First tergite with some white scales; second to sixth with line of pale scales at base and large lateral triangular spots of creamy scales. Seventh tergite mostly pale scaled. Sternites white scaled, becoming creamy towards apical border.

Paratype Females. The series of ten paratype females does not show much variation. The number of lower mesepimeral bristles varies from two to five. Wing length from 3·3 mm. to 5·0 mm. On the hind femora the area covered by dark scales may be reduced to a dorsal line on the distal half, broadening toward the tip. Hind claws in

some specimens all simple, in others from one to three claws may be toothed. Most specimens have no pale scales at base of tergites. Sternites may have scattered black scales or an inconspicuous apical black band.

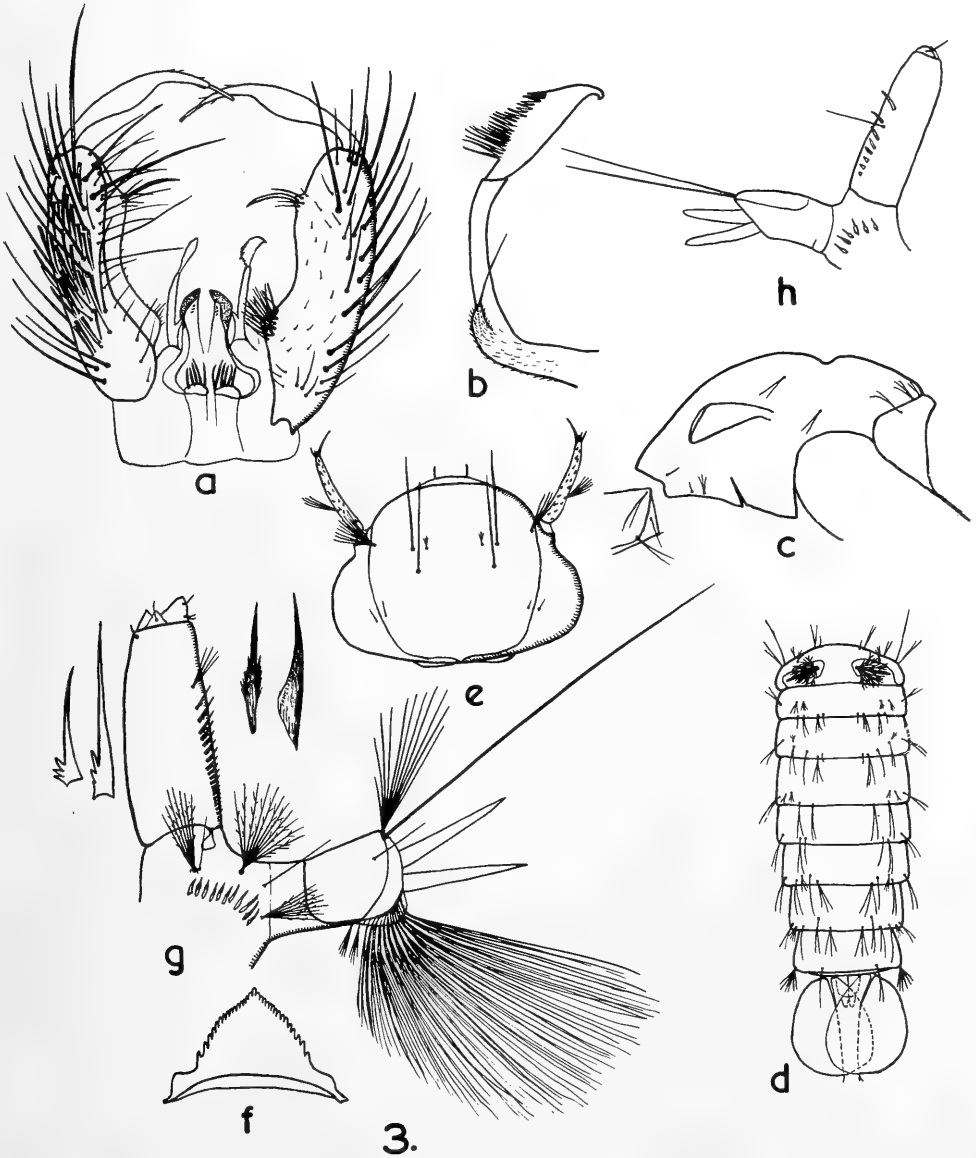

Fig. 3. *Aëdes imperfectus,* n. sp. *a, b,* ♂ terminalia: *a,* left coxite sternal aspect, right tergal aspect; *b,* harpago; *c, d,* pupa: *c,* cephalothorax and metanotum; *d,* abdomen; *e, f, g,* IVth stage larva: *e,* head; *f,* mentum; *g,* terminal segments; *h,* 1st stage larva: terminal segments.

Larva: Fourth stage (Fig. 3, *e, f, g*): Head broad, seta 4, small, 2–6 branched, 5, 6 and 8, single; 7, 4–10 branched; 9, 2–3 branched. Antenna short, about half length of head; seta 1, 4–7 branched. Mentum with 14–15 lateral teeth on each side. Thorax: Setae 1, 2, 4, 5 and 6 single; 3 single or 2 branched; 7, 3 branched. Abdomen. VIIIth segment: lateral comb of 10–14 spines; seta 1, 5–8 branched; 2 and 4, single; 3, 9–12 branched; 5, 6–8 branched. Siphon short and stout, index from 1·9 to 2·3,

mean 2·1. Seta 1, arising two-thirds of length from base of siphon, 3–5 branched; pecten of 18–24 spines; no detached teeth beyond siphonal seta 1. Anal segment: Saddle almost complete ring; seta 1, single; 2, 8–12 branched; 3, single; 4 (ventral brush) of 14–16 tufts. Anal papillae longer than saddle, narrow, pointed.

First Stage Larva (Fig. 3, *e*, *f*, *g*): Siphonal seta 1, single; pecten of 7–8 spines, two detached teeth beyond siphonal seta 1.

Pupa: Details shown in Figure 3, *c*, *d*.

Biology: This species breeds in partly shaded ground pools filled, usually, by flood waters. Small numbers of adults can be collected at any time from September to April, but peaks of abundance are reached during periods following flooding of rivers in the area. This may occur at different times of the year. Thus in the Woori Yallock area, in 1957, the specimens were abundant during the second half of November, but in 1961 it was rarely found during the spring and summer and reached its peak in March (1962). In Victoria it was found associated with *Aë. alboannulatus* (Macquart) and *Aë. rubrithorax* (Macquart).

Habits: It is a very vicious day-biting mosquito near breeding grounds during its peak period. It has been recorded attacking man and cows.

Distribution: It is distributed in eastern Australia from South Queensland to Victoria. Specimens have been examined from the following localities: Queensland: Pine Creek, Mt. Pleasant, April, 1955, M. C. Coy. New South Wales: Merricumbene, 10.III.55, 21.III.55, 22.III.55, A. L. Dyce and E. O'Sullivan, 14.IV.55, R. Lewis; Colo Vale, 27.2.56, K. O'Gower. Victoria: Cabbage Tree Creek, 19.I.56, 22.II.56, 12.IV.61, 20.III.62, N. V. Dobrotworsky; Leongatha, 26.X.53, G. W. Douglas; Woori Yallock, 14.XI.57, 21.XI.57, 15.IX.58 (larvae only), 9.XII.60, 26.III.61, N. V. Dobrotworsky; Watson's Creek, 24.X.53, A. Neboiss; Lyonville, 9.III.55; Beaufort, 3.X.59 (larva), N. V. Dobrotworsky.

Discussion: Adults of *Aë. imperfectus* closely resemble *Aë. burpengaryensis*, but lack the intense violet reflections which are so characteristic of the latter species. Also, in *Aë. imperfectus* the ring of dark scales at the tip of the hind femur is incomplete, being interrupted ventrally by pale scales. On the characters of the male terminalia, the species should be placed in the Burpengaryensis Section of the subgenus *Ochlerotatus*. The fourth stage larva, it is true, has no detached pecten teeth beyond siphonal seta 1, but such detached teeth are present in the first stage larva.

Aëdes (Finlaya) subbasalis, n. sp.

Types: The holotype, allotype and 20 paratypes were bred from larvae collected by A. L. Dyce 28.2.62 at Ginninderra Falls, New South Wales. All have their associated larval and pupal skins. The holotype male, allotype female, five paratype males and five paratype females are in the collections of the C.S.I.R.O., Division of Entomology, Canberra. One paratype male and one paratype female are in each of the following collections: National Museum, Melbourne; School of Public Health and Tropical Medicine, Sydney; University of Queensland, Brisbane; British Museum (Natural History), London; U.S. National Museum, Washington.

Material Examined: 29 ♂♂, 54 ♀♀.

Distinctive Characters. Adult: Scutum bronze scaled with admixture of white scales. Prescutellar area with narrow curved scales. Tibiae black scaled with subbasal pale ring which may be incomplete. Tarsi banded. Sternites in female with apical black bands. Larva: Head setae 4, 5 and 6 with their bases on almost a straight line. Prothoracic seta 4, single; 5, 2 branched. By these traits larvae of *Aë. subbasalis* may be distinguished from all other members of *alboannulatus* group except *Aë. rupestris* Dobrot.

Holotype Male. Head: Narrow curved white scales on vertex forming a broad triangular patch. Upright forked scales black. Palpi slightly shorter than proboscis without labella, black scaled with white patches at base of segments 2–5. Proboscis black. Thorax: Integument dark, almost black. Scutum clothed mostly with bronze scales with golden reflections; white scales on front and lateral margins, around bare area and forming two short dorso-central lines. Scutellum with narrow white scales.

Posterior pronotum with broad white scales below, narrow curved black scales in middle and narrow curved white scales above. Pleura with usual patches of broad white scales and pale bristles. Wing length 3·7 mm. Knob of halters white scaled. Legs:

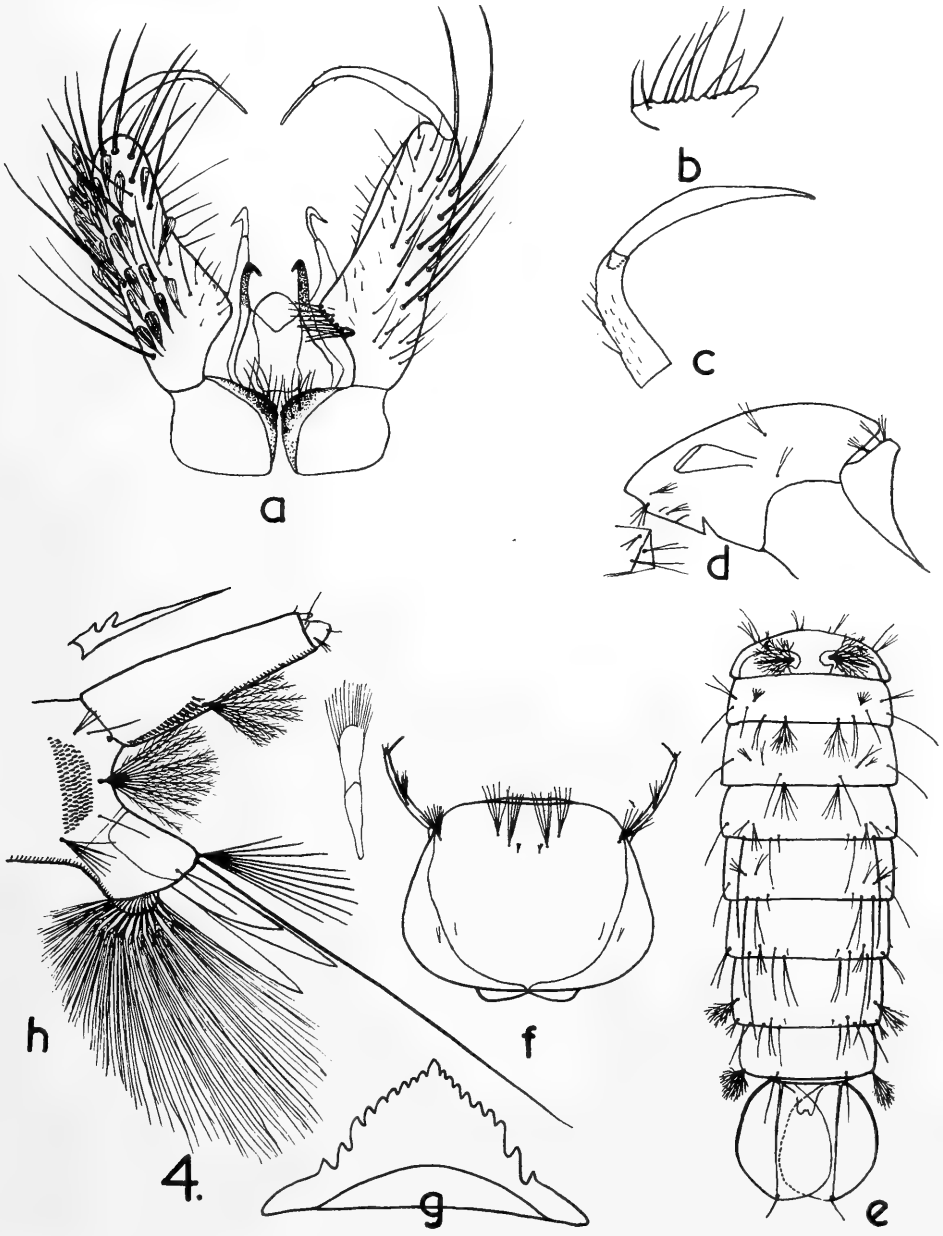

Fig. 4. *Aëdes subbasalis*, n. sp. *a, b, c,* ♂ terminalia: *a,* left coxite sternal aspect, right tergal aspect; *b,* basal lobe of coxite; *c,* harpago; *d, e,* pupa: *d,* cephalothorax and metanotum; *e,* abdomen; *f, g, h,* larva: *f,* head; *g,* mentum; *h,* terminal segments.

Fore and mid femora black, mottled with white scales; fore tarsi with two basal bands, mid tarsi with three. Hind femora white with black mottling on distal half. All tibiae black scaled with incomplete subbasal pale ring. Hind tarsi with four white basal bands. Knee spots white. Abdomen: Tergites black scaled with white basal

bands, except on the first. Sternites black scaled with white lateral basal patches. Terminalia (Fig. 4, *a*, *b*, *c*): Coxite black scaled with some white scales basally, and long and short setae laterally. Basal lobe of coxite narrow, transverse, with row of about 10 long setae along edge. Style about half length of coxite narrow, curved, with 2–3 preapical setae; terminal appendage straight and long. Harpago stout, with fine setae at base; appendage longer than harpago. Paraproct with single tooth. Ninth tergite with large lobe bearing 4 setae.

Paratype Males. The series of 10 paratype males does not show much variation. The scutal scales in some specimens with golden reflections. Length of wings varies from 3·3 mm. to 3·7 mm. Lobes of IXth tergite with 3–8 setae.

Allotype Female. This differs from the holotype as follows: Palps about one-fifth length of proboscis, with white scales at base of second segment and at base and apex of third. Torus and first flagellar segment of antenna with white scales. First tergite with a few white scales, second with basal band not joining lateral spots, third–seventh with constricted laterally bands. Sternites white scaled with apical bands joined to elongate median patch of black scales. Wing length: 4·0 mm. Upper fork cell about twice the length of its stem.

Paratype Females. The main variations in a series of 10 females are: The triangular pale scaled area on the vertex in some specimens is reduced to a narrow median patch. The scutal scales may be golden. The dorso-central white lines on the scutum are sometimes reduced to two patches. The intensity of mottling of femora is variable. The basal bands on the tergites, in some specimens, are straight, in others all are constricted laterally. Wing length: 3·0 mm. to 4·0 mm.

Larva (Fig. 4, *f*, *g*, *h*): Head only slightly wider than long. Seta 4 small, 3–5 branched; 5 and 6, 5–6 branched; 7, 6–9 branched; 8, single; 9, 2–3 branched. Setae 4, 5 and 6 with bases almost in a straight line. Mentum with 9–11 lateral teeth on each side. Prothoracic setae: Seta 1, single or 2 branched; 7, 3 branched. Abdomen: VIIIth segment: seta 1, 2–5 branched; 2 and 4, single; 3, 9–12 branched; 5, 4–6 branched. Comb of more than one hundred scales. Siphon index from 3·0 to 3·6, mean 3·3; seta 1, 7–11 branched; pecten of 17–21 spines. Anal segment: saddle covering about one-third of the segment. Seta 1, single, rarely 2 branched; 2, 10–12 branched; 3, single; 4 (ventral brush) of 14–16 tufts. Anal papillae long, slightly less than twice length of saddle.

Pupa: Details shown in Figure 4, *d*, *e*.

Biology: The breeding places of *Aë. subbasalis* are rock pools in river and creek beds. Usually they are exposed to sun, but may be partly shaded. The water may be light-brown coloured or clear, with decayed leaves and debris on the bottom.

In Queensland it was found in association with larvae of *C. halifaxii* Theob., *Aë. notoscriptus* (Skuse) and *A. annulipes* Walker. In New South Wales with *Aë. notoscriptus*, *Aë. alboannulatus*, *Aë. rubrithorax*, *C. p. australicus* Dobr. and Drumm, and *A. annulipes*. In some pools in New South Wales it was the dominant species. In Victoria where it is less common it was found breeding mostly in association with *Aë. rupestris*.

Habits: *Aë. subbasalis* is a day-biting mosquito, often attacking man in bright sunlight.

Distribution: *Aë. subbasalis* is distributed in eastern Australia and has been collected from Kuranda (N.W. of Cairns) in Queensland to the Cann River–Buchan area in Victoria. Specimens have been examined from Queensland: Kuranda, 22.VI.46, E. N. Marks; Stannary Hills, 30.X.08, T. L. Bancroft; O'Connell River, 7.X.47, J. L. Wassell; Broken River, alt. 2,000′, 27.VII.56, T. E. Woodward; Koumala, 18.XI.45, B. Atherton, 11.XII.45, A. Price; Nambour, 14.VIII.45, F. A. Perkins & J. L. Wassell, 25.IV.45, J. L. Wassell; Egan's Creek nr. Crow's Nest, 21.VII.57, M. Loveday; Canungra, 13.III.55, M. J. Mackerras. New South Wales: Wallangra, 16.I.53, E. N. Marks; Bendimeer, 30.IX.50, I. M. Mackerras; Bundarra, 18.VIII.54, 31.VIII.54, 6.X.54, E. J.

Waterhouse; Gata River, Armidale, 20.V.49; Ginninderra Creek, Sept. 1952, R. Mykytowycz, 24.IV.58, N. V. Dobrotworsky, 28.II.62, A. L. Dyce. Victoria: Tubbot, 17.II.56; Little River, Gippsland, 17.II.56; Weeragua, 24.I.62, N. V. Dobrotworsky.

Discussion: *Aë. subbasalis*, *Aë. milsoni* and *Aë. rupestris* have apical black bands on the sternites. *Aë. milsoni* has a prescutellar patch of broad scales, but in the other two species there are only narrow, curved scales.

The larvae of these three species are very similar, but the setae of the head and prothorax indicate that *subbasalis* is more closely related to *rupestris* than to *milsoni*. The bases of head setae 4, 5 and 6 in *subbasalis* and *rupestris* are on a straight line; prothoracic seta 5 is 2 branched in both. The bases of these head setae in *milsoni* are arranged to form the apices of a triangle and prothoracic seta 5 is single.

In Victoria where *Aë. subbasalis* breeds together with *Aë. rupestris* no intermediate forms have been collected and because of this *Aë. subbasalis* should be regarded as a species.

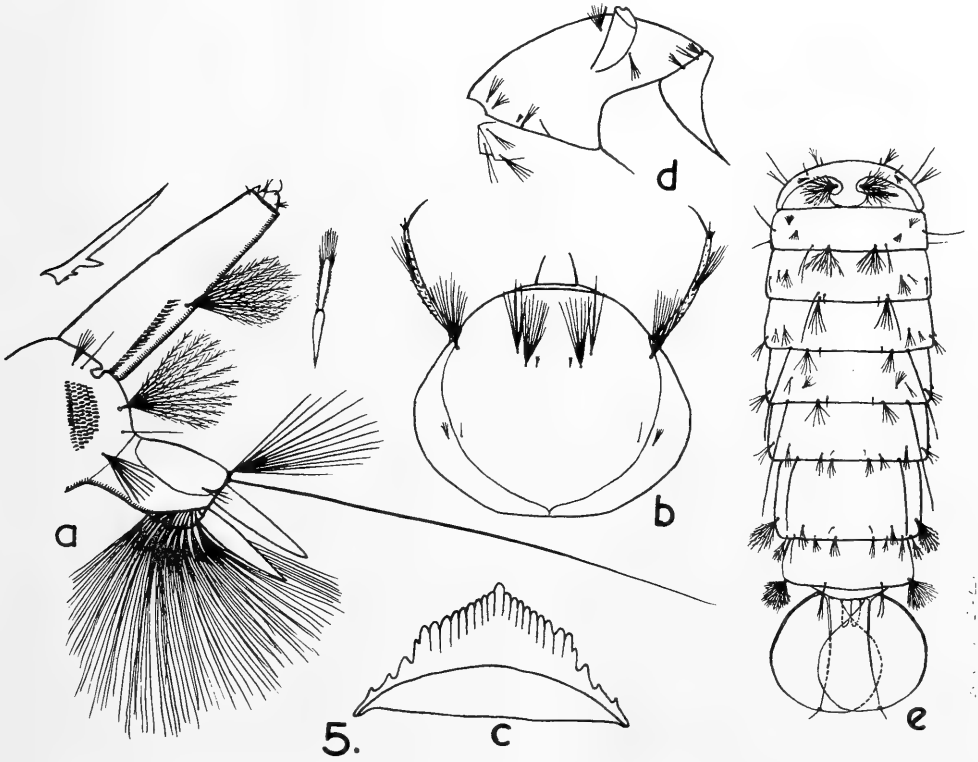

Fig. 5. *Aëdes milsoni* (Taylor). *a*, *b*, *c*, larva: *a*, terminal segments; *b*, head; *c*, mentum; *d*, *e*, pupa: *d*, cephalothorax and metanotum; *e*, abdomen.

Aëdes (Finlaya) milsoni (Taylor).

Culicada milsoni Taylor, 1915, Proc. Linn. Soc. N.S.W., 40: 179.

Description of Larva (Fig. 5): Head only slightly wider than long. Seta 4, small, 5 branched; 5, 7–10 branched; 6, 3–5 branched, usually with one branch much thicker than others; 7, 12–15 branched; 8, single; 9, 4–5 branched. Mentum with 11–13 lateral teeth on each side. Antenna short, about half length of head; seta 1, 5–7 branched. Prothoracic setae: Seta 1, 2 branched; 2, 5 and 6, single; 3, 7–12 branched; 4 and 7, 3 branched. Abdomen: VIIIth segment: Seta 1, 5–6 branched; 2 and 4, single; 3, 11–13 branched; 5, 6–7 branched. Siphon index 3·0–3·3; pecten of 25–26 spines; seta 1, 9–10 branched, Anal segment: seta 1, 3 branched; 2, 12–13 branched; 3, single; 4 (ventral brush) of 14 tufts.

Pupa: Details shown in Figure 5, *d*, *e*.

The larva has been described and the pupa figured from larvae and pupae collected at Salisbury, Queensland, 15.X.46, L. Angus.

Biology: In Queensland it breeds in partly shaded ground and rock pools, with leaves on bottom. The water was clear or, in some pools, discoloured.

Distribution: It is a northern species recorded in Queensland and New South Wales. In Victoria three females have been collected at Maryborough, I.X.60, N. V. Dobrotworsky.

Acknowledgements.

Thanks are expressed to Dr. E. N. Marks, Queensland University, for loan of specimens from University collections; Mr. G. W. Douglas, Department of Crown Lands and Survey, Melbourne, for providing specimens of *C. antipodea* from Wilson's Promontory; Mr. A. L. Dyce, C.S.I.R.O., Canberra, for larvae and adults of *Aë. subbasalis*; and Mr. D. J. Lee, School of Public Health and Tropical Medicine, Sydney, for consenting to the publication of the description of latter species. The author is grateful to Dr. F. H. Drummond for assistance in preparation of the manuscript.

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NEW SPECIES OF *OHAKUNEA* EDWARDS AND A RELATED NEW GENUS WITH NOTES ON THE RELATIONSHIPS OF *HETEROTRICHA* LOEW. (DIPTERA).

By Donald H. Colless, Division of Entomology, C.S.I.R.O., Canberra.

(Two Text-figures.)

[Read 24th October, 1962.]

Synopsis.

The genus *Ohakunea,* previously known only in New Zealand and South America, is recorded from Australia as *O. australiensis,* sp. nov. A related genus is also described, with a single species *Colonomyia albicaulis,* gen. et sp. nov. The family relationships of these genera and the apparently related *Heterotricha* are discussed. It is concluded that the latter belongs in the Mycetophilidae, subfamily Diadocidiinae, while the others are retained for the present in the Sciaridae.

Recent collections of Diptera from New South Wales and Victoria have included two peculiar species of small Nematocera, one rather uncommon and the other distinctly rare. Both were taken by sweeping foliage in rain-forest or wet sclerophyll, in moist, shady places, and most records are from the colder, more mountainous areas. One, the rarer of the two, can be placed in the genus *Ohakunea* Edwards, previously known only from New Zealand and southern South America; the other, although apparently related to *Ohakunea,* clearly requires a new genus. Both are with some difficulty referable to the family (or subfamily) Sciaridae, but, as discussed below, they differ markedly from most of its members, and *Colonomyia,* gen. nov., seems to show some slight relationship with *Heterotricha* Loew. The family status of all three genera is discussed below.

Genus Ohakunea Edwards.

Edwards and Tonnoir, 1926; *Trans. N.Z. Inst.,* 57: 799 (Type species, *O. bicolor*).

The Australian species, known so far from three male specimens only, agrees well with the original description of this genus, and with that of *O. chilensis* (Freeman, 1951). I prefer, however, to regard the palp as 4-segmented, rather than 3-segmented plus palpiger. The diagnostic characters of the genus, within the Mycetophiloidea, would appear to be as follows: Eyes bare, or nearly so, partially bridged dorsally. Ocelli in a flat triangle, the lateral ones nearly touching the eye margin. Antennae long, with 16 segments, these cylindrical, elongate, and progressively shorter towards the apex. Labium short; palpi 4-segmented (seg. 2 with a sensory area in *O. australiensis,* sp. nov.). Thorax of much the same shape as described below for *Colonomyia,* gen. nov., with relatively high postnotum and pleurosternite; the latter only slightly convex. No mid-pleural pit. Legs slender, without strong spines or bristles; coxae markedly elongate; tibial spurs short, one on fore-tibia, two each on mid- and hind-tibiae; apex of fore-tibia without any sensory area; tarsal claws small to minute, simple.

Wing with minute microtrichia and profuse, long, curved macrotrichia on the membrane. Venation as in Figure 1*a*; costa not produced; Sc evanescent apically. Sc_2 present but weak (see note under *C. albicaulis*); r-m very long; base of Rs transverse, short, beyond middle of wing; M_{3+4} rising near base of wing; M and basal portions of its branches very weak, represented mainly by folding of the membrane.

Abdomen with seven distinct pregenital segments. Male terminalia: ninth tergite large, with strong bristles or spines; tenth segment overlying a chitinous armature apparently derived from basal processes of the coxites and the parameres; coxites with a strong, bristly or spinose apical lobe, with the slender, pointed, rather sinuous style rising from near its base.

OHAKUNEA AUSTRALIENSIS, sp. nov.

Types. Holotype male (Mt. Dom-Dom, Vic., 22 Oct. 1961, D. H. Colless) and two paratype males (Macquarie Pass, N.S.W., 2.xi.1960, and Palm Ck., R. Nat. Pk., N.S.W., 29.xii.1960, D. H. Colless; latter mounted on slide) in the Australian National Insect Collection, Canberra.

Type locality: Mt. Dom-Dom (Black Spur), Maroondah Highway, Victoria.

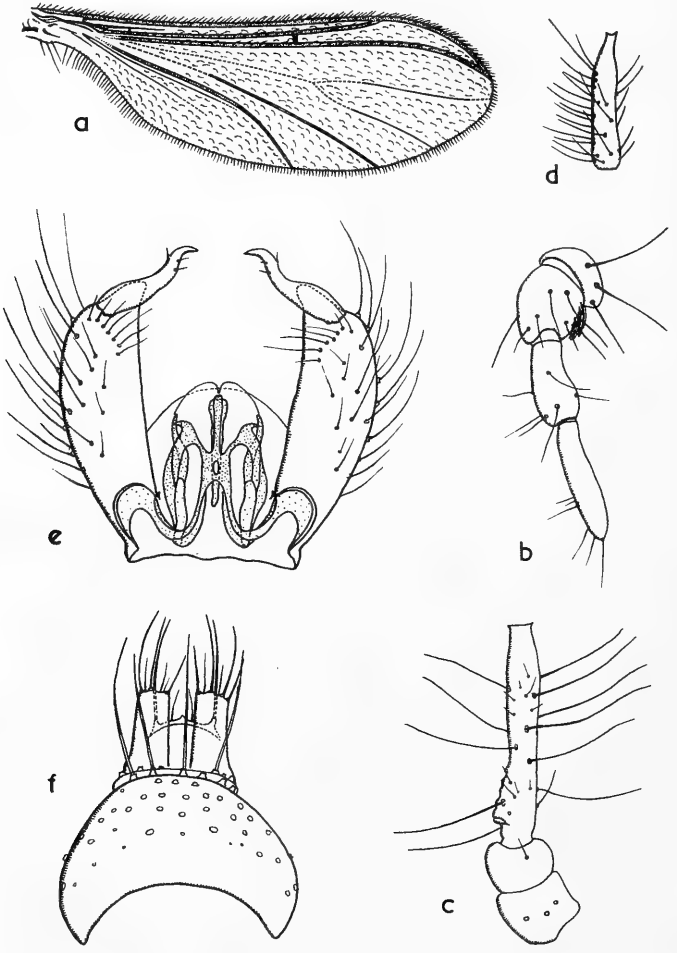

Fig. 1. *Ohakunea australiensis*, sp. nov. (*a*) Wing; (*b*) Palp; (*c*) Antenna, segs. 1-3; (*d*) Antenna, seg. 12; (*e*) Male terminalia, dorsal (9th and 10th segments removed; apical lobe dotted, its setae not shown); (*f*) 9th tergite and anal segment (scale slightly larger than in *e*).

Male.

Head black above, face yellowish, mouth parts and palps brown. Eyes with scanty fine hairs (visible clearly only in balsam mounts); dorsal bridges short, widely separated, their apices lying opposite the centre of the antenna bases and below the lateral ocelli. Antenna longer than body, almost as long as wing, segs. 1 and 2 yellowish-brown, flagellum dark brown; flagellar segments (Figs 1*c*, 1*d*) irregularly cylindrical, with long necks and numerous, long, outstanding hairs, most profuse on the ventral sides, their lengths about equal to those of the segments; lengths of segments 3, 9, 12 and 16 in the ratio 9:7:6:4. Maxilla represented by a weak blade, fringed apically and along internal margin; palp (Fig. 1*b*) 4-segmented, seg. 2 with a lateral area of blunt-tipped sensillae.

Mesonotum arched anteriorly, rather dark brown, slightly paler laterally; most setae rubbed from my specimens, but dorso-centrals and acrostichals present; scutellum with a pair of strong bristles centrally and weaker ones laterally. Propleuron with several bristles dorsally. Ventral lobes of prosternum triangular, rather unusually prominent. Mesopleura greyish-brown, apparently bare, but a balsam mount shows a patch of 3–4 minute setae immediately below the haltere base. Halteres dark brown, with rather profuse, fine pubescence dorsally on the knob, continuing along most of the stem. Coxae elongate, mid-coxa about as long as the distance from its base to the wing root. Lengths of femur, tibia and tarsus respectively: fore-leg, 21, 32, 47; mid-leg, 23, 34, 48; hind-leg, 29, 38, 38 (units of 0·04 mm.). Tarsal claws minute, barely discernible

Wing length 2·5–2·8 mm., venation as illustrated (Fig. 1*a*) and described above; membrane greyish.

Abdomen dark brown with erect dark setae; ninth tergite rather paler. Terminalia partially rotated in one specimen at least; structure as in Figures 1*e*, 1*f*; ninth tergite prominent, strongly convex, with an apical row of very strong bristles; lobes of tenth tergite projecting well beyond the sternite; the latter with a pair of strong, incurved lateral setae and a small sub-median pair. Tenth segment overlying a complex chitinous armature with latero-apical hooked processes. Central rod of mesosome (ejaculatory apodeme) simple. Apical lobe of coxite with strong bristles (not shown in figure) but no spines.

Female. Not known.

Specimens seen: Type series only.

Genus Colonomyia nov.

Type species. C. albicaulis, sp. nov.

Generally similar to *Ohakunea*, but of rather stouter build and differing as follows: Eyes abundantly haired. Ocelli set in a more obvious triangle, the anterior one between the internal dorsal angles of the eyes. Palp segment 2 without patch of sensillae. Mesonotum evenly arched; postnotum almost vertical, very high, almost as long as the mesonotum (Fig. 2*b*); pleurotergite similarly high, bulging laterally. Coxae less markedly elongate; apex of fore-tibia with depressed area, containing numerous sensory hairs, on inner surface. Wing (Fig. 2*a*) with straight macrotrichia; costa produced almost to apex of M1; Sc_2 absent (see note below); R1 ending only a little past centre of wing; Rs base before the centre of wing; Cu_1 rather sharply angled. Terminalia as figured (Figs 2*e*, 2*f*, 2*g*) and described below.

Colonomyia albicaulis, sp. nov.

Types. Holotype male (Rutherford Ck., Brown Mt., N.S.W., 10.iii.1961, D. H. Colless), allotype female (Mt. Dom-Dom, Vic., 22 Oct. 1961, D. H. Colless), 10 male and five female paratypes, in the Australian National Insect Collection, Canberra. Also, one paratype of each sex to be lodged in the British Museum (Nat. Hist.), the United States National Museum, and the Bishop Museum, Hawaii.

Type locality: Rutherford Creek, Brown Mountain, Bega District, N.S.W.

Male.

Head very dark brown, mouth parts brown. Antenna dark brown, except for seg. 2, which is yellowish; flagellar segments (Figs 2*c*, 2*d*) cylindrical, with dense, fine, short pubescence, the more apical segments with short necks; segs. 3–9 in ratio 10:8:7:6:5:5:4, segs. 9–16 of about the same length; whole antenna about two-thirds the length of the wing. Maxilla represented by a narrow, fringed rod; palps curved back laterally in dried specimens, 4-segmented, of much the same form as in *Ohakunea*.

Thoracic setae dark, integument uniformly dark brown, except the dorsum of the prothorax, which is yellowish; the adjacent margin of the mesonotum, and the ventral margin of the propleuron, also slightly yellowish. Dorso-central and acrostichal setae present, but minute anteriorly. Scutellum with posterior fringe of some 10 setae, the central pair longer and stronger. Pleura with sutures weakly marked, propleuron with minute setae, otherwise bare; posterior part of pleurotergite and lateral areas of postnotum minutely pubescent. Halteres prominent, with pale stem and dark knob,

the latter with several fine setae. Coxae completely pale; mid-coxa a little shorter than distance from its base to the wing root; femora rather pale, darkening apically; tibiae and tarsi dark; fore- and mid-legs about 2·5 mm. long, hind leg about 2·8 mm. Tarsal claws small, simple; empodium and pulvilli weakly developed.

Wing as illustrated (Fig. 2*a*), rather short and broad; the base distinctly pale as far as the humeral crossvein; anterior veins brown, membrane greyish; length 2·6–3·0 mm.

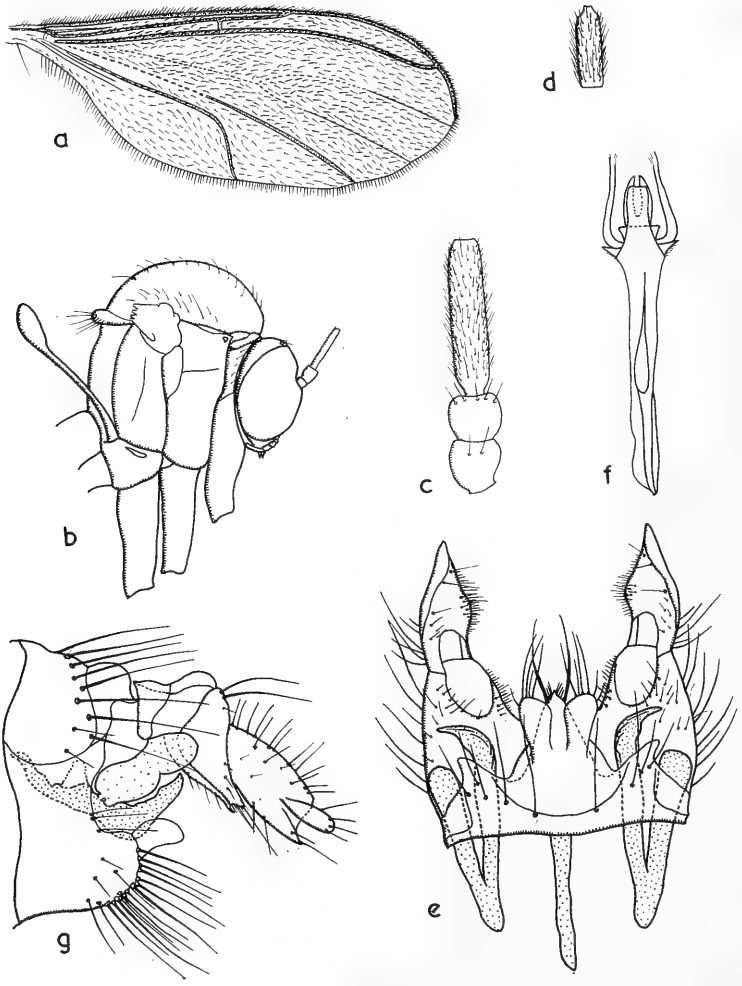

Fig. 2. *Colonomyia albicaulis*, sp. nov. (*a*) Wing; (*b*) Thorax, lateral; (*c*) Antenna, segs. 1-3; (*d*) Antenna, seg. 12; (*e*) Male terminalia, dorsal; (*f*) Central rod (ejaculatory apodeme) of male mesosome; (*g*) Female terminalia, lateral.

Abdomen with integument and setae all dark brown, except for tenth segment, which is pale brown. Terminalia as in Figures 2*e*, 2*f*, rather complex; ninth tergite narrow centrally, broadening to a pair of blunt lateral lobes; beneath them, a pair of bi-ramous processes, the inner limbs long, pointed, and curved outwards; ninth sternite rather large, fused between the coxites. Styles stout, pointed. Mesosome with central rod (Fig. 2*f*) of very complex structure apically, with a pair of dorsal arms, a simple median lobe, and a bifid ventral lobe.

Female.

Resembling the male, but antennal segment 2 usually pale-brown, rather than yellowish, and knob of haltere more pubescent. Terminalia as in Figure 2*g*; eighth sternite almost completely divided into two lateral lobes which are produced dorsally; apical segment of cercus very small, borne subapically in a depression on the much larger basal segment.

NOTE: I have above described the wing venation as lacking Sc_2. There is, in fact, a distinct connection between Sc and R at the extreme base, just distal to the humeral crossvein, but this does not appear to be analogous to the vein usually described as Sc_2; e.g., *Ohakunea* and *Diadocidia* have both this basal connection and a normal Sc_2. Such a basal connection can be found in a number of Mycetophiloid genera, e.g., *Scythropochroa*, *Australosymmerus*, *Mycetophila*, while it is absent in others, e.g., *Orfelia*.

Specimens seen: *N.S.W.*: Mt. Wilson, 23.ix.1961, D. K. McAlpine, 1♀; Macquarie Falls, 14.xi.1960, 2 ♂♂; Upper Kangaroo Valley, 21.xi.1960, 1 ♂; Rutherford Ck., Brown Mountain, 19.i., 10.iii., 15.iii., and 11.xi., 1961, 9 ♂♂, 6 ♀♀ (including holotype); Geehi R., 9.xi.1961, 1 ♂. *A.C.T.*: Bendora, 14.xii.1960, 2 ♂♂. *Victoria*: Mt. Beauty, 21.x.1961, 1 ♂; Nowa-Nowa, 28.x.1961, 1 ♂, 1 ♀; Mt. Dom-Dom, 22.x.1961, 4 ♂♂, 2 ♀♀ (including allotype); Cement Ck., 27.x.1961, 5 ♂♂, 3 ♀♀. (All but the first, coll. D. H. Colless.)

DISCUSSION.

The discovery of *Ohakunea* in south-eastern Australia is not surprising, and provides another example of the so-called Antarctogaean distribution pattern. It is interesting to note that *O. australiensis* resembles the Chilean *O. chilensis*, rather than the New Zealand *O. bicolor*, particularly as regards the antennae and male terminalia. *Colonomyia* is probably an endemic genus, related to *Ohakunea* and resembling it closely in wing venation and the structure of eyes and thorax. The resemblance in the shape of thorax, with high, almost vertical postnotum, is particularly striking. Its male terminalia, however, are quite distinctive, and seem in some ways more like those illustrated (Freeman, 1951) for the aberrant genus *Heterotricha*. The latter genus, not so far known to occur in Australia, is found in Chile, New Zealand and South Africa.

All three of these genera are difficult to place in any currently recognized family. Both *Ohakunea* and *Heterotricha* have been placed in the Sciaridae, mainly because of their venation and partially bridged eyes; *Heterotricha* also has a mid-pleural pit (Freeman, 1951). This latter genus, however, was placed by Tonnoir and Edwards (1926) in the Diadocidiinae and I am strongly of the opinion that this was correct. Although I have only published descriptions to go by, comparison with undescribed species of Australian *Diadocidia* shows no difference that could be considered significant at the subfamily level. One of our two species (that referred to by Tonnoir, 1929) has an incomplete, dorsal eye-bridge of an extent greater than in some species of *Heterotricha*, and has a rudimentary mid-pleural pit which is, I suspect, at least the equivalent of that found in some species of that genus. Moreover, a similar pit is present in various genera of Mycetophilidae (*Australosymmerus*, *Mycomyia*, *Exechia*). The venation of *Heterotricha* differs but slightly from that of *Diadocidia*, while there are distinct resemblances in structure of the antennae and male terminalia. There would therefore appear to be no grounds for placing *Heterotricha* anywhere but in the Diadocidiinae, where the rather similar *Pterogymnus* is already lodged (Freeman, 1951).

The position of *Ohakunea* and *Colonomyia* is more difficult to judge, even though their wing venation closely resembles that found in the Sciaridae. They lack the strongly developed mid-pleural pit so characteristic of that family and the presence of an incomplete eye bridge cannot be considered very significant, for reasons discussed above. Also, the long coxae of *Ohakunea*, and the shape of the thorax in both genera, show a closer resemblance to Mycetophilidae such as *Neoaphelomera* and *Austrosynapha*.

Their male terminalia are totally different from the rather uniform pattern found in the Sciaridae, particularly in the chitinous armature which lies below the tenth segment. This seems to be derived from basal processes of the coxite, and/or the parameres; rather similar structures occur in various Mycetophilidae but, as far as I know, not in the Sciaridae. The female terminalia of *Colonomyia* are also not of the Sciarid type.

Pending a thorough investigation of the Mycetophiloidea as a whole, I propose for the present to leave both genera in the Sciaridae. It seems, however, that this may necessitate reduction of that family to its original status, as a subfamily of Mycetophilidae. Alternatively, the Mycetophilidae may have to be split into some 6–8 families, as is done by some European authors.

Acknowledgements.

I am indebted to Miss Neel Key for the figures of the wings.

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NOTES ON AUSTRALASIAN TANYDERIDAE, WITH DESCRIPTION OF A NEW SPECIES OF *RADINODERUS* HANDL. (DIPTERA).

By Donald H. Colless, Division of Entomology, C.S.I.R.O., Canberra.

(One Text-figure.)

[Read 24th October, 1962.]

Synopsis.

Radinoderus ochroceratus, sp. nov., is described from the Solomon Isiands and notes given on three other Australian species of Tanyderidae.

The Australian National Insect Collection, Canberra, includes a number of specimens of Australian Tanyderidae and a single specimen of an apparently new species from Bougainville, in the Solomon Islands. The latter, which is closely allied to *Radinoderus holwayi* Alex. from Guadalcanal, is described below together with notes on the Australian specimens.

Radinoderus ochroceratus, sp. nov.

Type. Unique holotype female (Bougainville, 2.iv.45, F. N. Ratcliffe) to be placed in the Bishop Museum, Hawaii.

Type locality. Bougainville, Solomon Islands.

Female. Wing length 18·9 mm.; abdomen 18·2 mm. Closely resembling *R. holwayi* (see Alexander, 1946), differing as follows:

Antenna with 24 segments, flagellum pale yellow, the segments minutely darkened apically; segment 2 brown; segment 1 dark-brown.

Pronotum uniformly brown. Mesonotum more or less uniformly brown, the stripes faintly differentiated by a median, and two sublateral, slightly paler broad lines; lateral lobes (immediately behind wing roots) greyish pruinose; scutellum dark centrally and posteriorly, with a pair of antero-lateral grey spots which extend onto the scutum. Pleura with small grey area across the posterior margin of the sternopleurite, immediately below the mid-pleural pit, and another larger grey area dorsally on the pteropleurite; pleurotergite slightly greyish dorsally; postnotum more or less uniformly brown, slightly paler at the antero-lateral angles.

Wing as in Figure 1*b*; costal cell with median pale area (opposite fork of R_s) shorter than adjacent dark areas; crossvein m angulated, with a basally directed spur. The forked apex of vein R_1 suggests that the anterior portion may actually represent the free tip of Sc_2, and the spur, the true apex of R_1.

Abdomen brown, darker on the apical segments. Tergite 1 with a pair of grey, latero-basal spots and a faint, greyish, subapical band; tergites 2–5 each with a pair of grey lateral spots, placed a little short of the centre, and a pair of rather larger sublateral spots, placed a little past the centre; tergite 6 similar, but the lateral spots subbasal. Cerci dark brown.

Some of the above features no doubt represent individual variation only; the essential differences are the yellow antennae, and abdominal tergites with four pale spots instead of two. The close resemblance to *holwayi*, and the apparent geographic separation, suggest that *ochroceratus* may eventually prove to be a subspecies, but, lacking more detailed data, I prefer to treat it for the present as a species. These two forms, and *R. pictipes* Alex. of New Guinea, form a group characterized by the unusually conspicuous convexity in the apex of cell Rs.

Specimen seen. Holotype only.

RADINODERUS OCCIDENTALIS (Alexander).

Alexander, C. P., 1925; Insec. Inscit. Menst., 13: 32. *Tanyderus* (*Radinoderus*) *occidentalis*. Swan River, W. Australia.

The original description was based on a rather imperfect, unique female specimen. I now have three additional females, one in perfect condition. These show a distinctly yellowish-grey pruinose ground colour on the mesonotum and scutellum, and have the postnotum pale laterally. Also, the hypopleuron is greyish, the colour extending down onto the postero-lateral surface of the hind coxa. The legs, which are intact, show that it is the mid-leg which has the most conspicuous dark band on the femur; the tibial spurs are brown, contrasting sharply with the yellow ground colour, while the apical tarsal segments are all brown, rather than yellow.

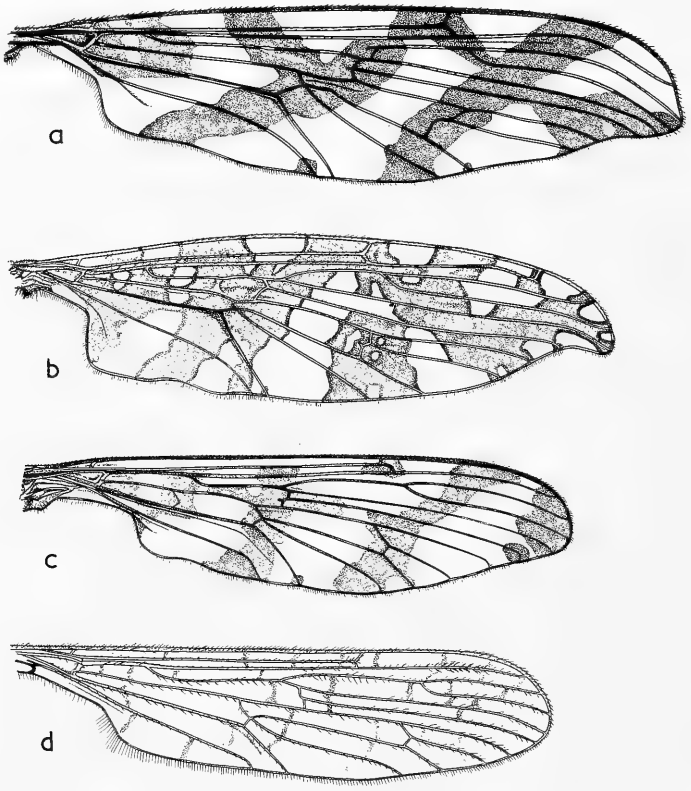

Fig. 1. Wings. (*a*) *Radinoderus occidentalis* (Alex.). (*b*) *R. ochroceratus*, sp. nov. (*c*) *Eutanyderus oreonympha* Alex. (*d*) *E. wilsoni* Alex. (*a-c*, female; *d*, male).

The wing is illustrated in Figure 1*a*. Two of the three specimens have dark spots at the apices of Cu_1 and M_3 and one of these also has a small dot at the apex of R_1. One specimen, perhaps teneral, has the dark markings very weakly developed, many of them grey centrally with brown borders.

The abdominal pattern is as follows: general colour brown; tergite 1 with a pair of conspicuous latero-basal yellowish spots; tergites 2–7 each with a pair of elongate, roughly oval yellowish spots, slanted downwards anteriorly, and each surrounded by an irregular zone of dark, velvety brown; the spots are placed a little distad of the centre on segs. 2 and 3, becoming progressively more basal on the posterior segments. Sternites 3–6 (and sometimes 7) with small sublateral spots, placed opposite the tergal spots; sternites 3–5 (and sometimes 6) with a weaker median subapical spot. Ninth sternite pale brown; terminal segments and cerci otherwise black.

The type specimen is now in the Macleay Museum, Sydney University.

Specimens seen: *Western Australia.* Pemberton, 24.xi and 6.xii.1936, K. R. Norris, 2 ♀♀; Beedelup Falls, 13.xi.1958, E. F. Riek, 1 ♀.

EUTANYDERUS OREONYMPHA Alexander.

Alexander, C. P., 1938: *Philipp. J. Sci.*, 66: 221. Mt. Kosciusko, N.S.W.

I have a single female specimen, collected on the same date, and in the same general locality, as the holotype male (presumably by A. L. Tonnoir, whose handwriting is on the label). This shows the following features: Wing 16·2 mm.; abdomen 12·9 mm. Antenna with apical segment subspherical, about one-third the length of the penultimate segment. Wing as illustrated (Fig. 1*c*), the basal markings differing slightly from the original description. Abdomen generally as described for the male, but better described as follows: tergite 1 brown, vaguely grey on the lateral thirds; tergites 2–6 dark velvety brown, with large, roughly rectangular, sublateral grey patches which extend from base about three-quarters the distance to apex; tergite 7 similar, but the spots just reaching the apex. Sternites grey, on segs. 2–6 with apical dark bands produced medially. Cerci rather pale brown, ninth sternite orange-brown.

Specimens seen: N.S.W. Sawpit Ck., Mt. Kosciusko, 4,000′, 11.xii.1931. 1 ♀.

EUTANYDERUS WILSONI Alexander.

Alexander, C. P., 1928: PROC. LINN. SOC. N.S.W., 53: 371. Millgrove, Victoria.

A male specimen in the collection has the wing markings greatly reduced, only their brown borders being clearly developed (Fig. 1*d*). Placed beside a female, with its strong wing pattern, it is at first difficult to believe them conspecific. However, Alexander's male specimen, with the markings faintly differentiated from the ground colour, shows that such sexual dimorphism is a characteristic feature of the species.

Specimens seen: *Victoria.* Mt. Dom-Dom (Black Spur), 22.x.1961, 1 ♀; Cement Ck., 27.x.1961, 1 ♂; both coll. D. H. Colless.

Acknowledgement.

I am indebted to Miss Neel Key for the figures of the wings.

Reference.

ALEXANDER, C. P., 1946.—Notes on the Tanyderidae of the Australasian Region (Diptera). Pt. 1. *Pan-Pacif. Ent.*, 22: 51.

NOTES ON THE TAXONOMY OF THE *AËDES SCUTELLARIS* GROUP, AND NEW RECORDS OF *A. PAULLUSI* AND *A. ALBOPICTUS* (DIPTERA: CULICIDAE).

By Donald H. Colless, Division of Entomology, C.S.I.R.O., Canberra.

(One Text-figure.)

[Read 24th October, 1962.]

Synopsis.

A Malayan form of *Aëdes "scutellaris"* is shown by hybridization experiments to be fully interfertile with the type form from New Guinea. It is described as *A. s. malayensis,* subsp. nov., and it is proposed that *A. hensilli* of the Carolines be also considered a subspecies of *A. scutellaris.* Records are also given of *A. paullusi* from North Borneo and *A. albopictus* from New Guinea.

In an earlier paper (Colless, 1957), a form of *Aëdes "scutellaris"** was recorded from Singapore. The form was there identified as *A. hensilli* Farner and it was noted that it also appeared to be conspecific with the Philippine form, described as *A. scutellaris* by Knight and Hull (1952). It was thought at that time that it might be a recent immigrant into Malaya, established in only the one locality, but there are now records from two other localities: Pulau Jarak, a small island in Malacca Strait, and Kuantan, on the east coast. The form is therefore distributed right around Malaya, although its foothold seems rather precarious; it is probably restricted to the offshore islands and the immediate coast, by competition from the widespread and abundant *A. albopictus.*

A study has been made of the identity and taxonomic status of this form and hybridization tests have been carried out with *Aëdes scutellaris scutellaris* from New Guinea. The results and taxonomic conclusions are discussed below. Records are also given of another member of the group from North Borneo, and of the related *A. albopictus* from New Guinea.

A. Hybridization Experiments.

Material and Methods.

Colonies of the Malayan form from Singapore, and *A. s. scutellaris*, from Hollandia, New Guinea, were established from eggs kindly supplied by Mr. W. Chellapah and Dr. R. Sloof respectively. Crosses were made in both directions, using newly emerged adults (sexed in the pupal stage), held on 80° F. and *circa* 80% R.H., in cages of 1 cub. ft. capacity. One cross was made with *scutellaris* as the male parent and two in the reverse direction. Some 50–100 males were used in each experiment, and a similar number of females of the Malayan form. Difficulties with the parent colony allowed the use of only five female *scutellaris* in one cross, and 12 in the other, but clear-cut results were obtained. Eggs were kept moist for 48 hours and then dried, usually for about one week, but up to six weeks in one instance. F2 adults were obtained from each cross, but no backcrosses were attempted. All colonies were held in the same room, but no evidence of cross-contamination appeared in the results.

Results.

Detailed quantitative records were not kept, but the results are simply presented in the statement that the cross appeared to be a complete success in both directions. Egg production, hatching percentages, sex ratios, and vigour of adults and larvae showed no apparent deviation from normal; in fact, the hybrid colonies flourished better than those of the *scutellaris* parent, which, for some unknown reason, were difficult to maintain.

* I am following the convention of Reid (1950), of using the species-group name in inverted commas for members whose precise identity is in doubt.

The only obvious morphological difference between the parent forms lies in the shape of the basal lobe of the male coxite, a stable and very distinctive character (Figs 1*a*, 1*c*). In F1 progeny from all crosses the form of the lobe was intermediate, with perhaps a slightly stronger resemblance to the Malayan form. Moreover, in some 20 specimens dissected, it showed very little variation. In the F2 progeny, there was obvious segregation into a variety of forms, some approaching those of the parents and F1, others of various intermediate types (Figs 1*d*, 1*e*, 1*f*). Subjective estimates of shape are difficult, but I would say that none (of some 30 specimens dissected) was absolutely identical with *scutellaris* and few, if any, with the Malayan form. The character is obviously determined by a number of genes.

Discussion.

No genetic barrier could be demonstrated between the two forms and, in view of their allopatric distributions, sub-specific status seems appropriate for the Malayan form. The question remains of its relationship to other Malaysian forms and the very similar *A. hensilli* of the Caroline Islands. From Knight and Hull (1952), it appears to be identical with their "*A. scutellaris*" from the Philippines, and the male terminalia seem identical with those of *A. hensilli* (Bohart and Ingram, 1946; Bohart, 1956). The latter is distinguishable, however, by having hind tarsal segment V partly black, and segment IV at least half black, although there is a variant population in Truk in which some 50% have segment V all white (Bohart and Ingram, *op. cit.*). Clearly, *hensilli* has evolved from an isolated eastern population of the Malayan form, and some of the Truk specimens may not be distinguishable from it. (It is not clear whether such variant specimens occur in Palau, to the west.)

A. s. scutellaris is known to occur in the south-western islands of the Carolines and it is worth noting that such specimens (as figured by Bohart, *op. cit.*) have the apex of the basal lobe more prominent and rounded than usual. It is, in fact, very similar to that seen in some of the above hybrids. One of the lobes figured for *A. hensilli* (Bohart, *op. cit.*, fig. 10*g*) is also rather reminiscent of certain segregants. It is, then, plausible that some degree of hybridization has occurred in these islands. It is also conceivable that the variation in colour of tarsal scaling in *hensilli* is the result of secondary intergradation, i.e., introgression of genes from *scutellaris* or, in Truk, from the local *scutoscriptus*. In any case, *hensilli* would seem to be better treated as a subspecies of *scutellaris*.

It seems therefore that, in addition to the Australian *A. s. katharinensis*, three distinct subspecies can be recognized: *s. scutellaris*, extending into, perhaps, the Moluccas, and north into the Carolines; *s. hensilli* of the Carolines, typically represented on Ulithi, and with variant forms, possibly due to hybridization, on other islands; and another subspecies in Malaya, the Philippines, and other islands of the archipelago (probably including Sumatra). The western limits of the type form and eastern limits of the Malayan form are not yet known, and zones of intergradation or clinal variation may yet be discovered. Formal recognition of these forms is proposed in the next section.

B. Systematics.

Aëdes (Stegomyia) scutellaris scutellaris (Walker).

Culex scutellaris, Walker, 1859; *Proc. Linn. Soc. London*, 3: 77. (Aru Islands.) (For full synonymy, see Bohart, *op. cit.*)

Full descriptions are given by previous authors (see Bohart, *op. cit.*), but only Marks (1954, p. 372) discusses the critical features of the basal lobe of the coxite. This has a very characteristic truncate appearance as follows: Expanded portion, in lateral view, with sides more or less parallel, sternal angle rather sharp; modified setae usually 4–6 in number, set on a slight prominence; apical portion of the lobe only slightly rounded or almost square, the inner face with the long setae concentrated near the apex (see Fig. 1*c*, and Marks, 1954, Plate 18).

Also, hind tarsal segment IV has the pale band covering about 0·7 of its length.

Distribution: New Hebrides; Rennell and Bellona Is.; New Guinea; Australia (Cape York); Carolines (Palau and western atolls); Aru; probably also some islands of the Moluccas.

AËDES (STEGOMYIA) SCUTELLARIS MALAYENSIS, subsp. nov.

Types. Holotype male, allotype female (both from laboratory colony), and 10 paratypes of each sex, in the Australian National Insect Collection, Canberra. Paratype series also to be lodged in the British Museum, United States National Museum, and the Bishop Museum, Hawaii.

Type locality: Pulau Hantu, Keppel Harbour, Singapore (see Colless, 1957, for exact locality).

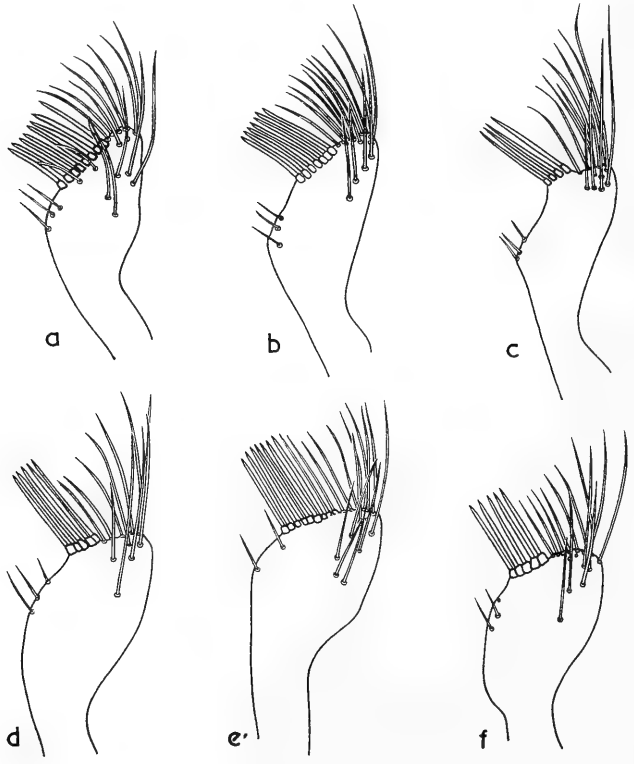

Fig. 1. Basal lobes of male coxites. (*a*) *A. s. malayensis*, (*b*) F1 hybrid, (*c*) *A. s. scutellaris*, (*d-f*) F2 hybrids.

Adult. Differs from *A. s. scutellaris* only as follows: Basal lobe of male coxite with the expanded portion subtriangular in lateral view, not truncate, the sides not parallel but tapering, sternal angle rounded; modified setae usually 7–10 in number, forming a more prominent row, not set on a prominence; inner face with long apical setae extending further basally.

Specimens examined: *Singapore*: Numerous specimens from the type locality, and their descendants in laboratory culture; collections in 1954, 1957, 1960 (W. Chellapah). *Malaya*: Kuantan, 6 ♂♂, 6 ♀♀ (R. H. Wharton); Pulau Jarak, 3 ♂♂, 5 ♀♀, 4.xi.1958 (W. W. Macdonald). Also known from the Philippines.

AËDES (STEGOMYIA) SCUTELLARIS HENSILLI Farner.

Aëdes hensilli, Farner, 1945; *Proc. biol. Soc. Wash.*, 58: 59. (Ulithi Atoll, Carolines.) (See Bohart, *op, cit.*, for other references.)

Adult. Closely similar to *A. s. malayensis* in almost all respects, including the male terminalia. Differing from that form, and *A. s. scutellaris*, as follows: Hind tarsal segment V black on about the apical half; segment IV with the pale band covering only about 0·4–0·6 of its length.

Variant populations are known, in which a proportion of specimens have segment V all white, but this condition has not been recorded from the type locality.

Distribution. Generally throughout the Caroline Islands, as far east as Nukuoro Atoll.

AËDES (STEGOMYIA) PAULLUSI Stone & Farner.

Aëdes paullusi, Stone & Farner, 1945; *Proc. biol. Soc. Wash.*, 58: 155. (Samar, Philippines) Knight & Hull, 1952, *Pac. Sci.*, 6: 178.

Originally described from the Philippines, this species has also been reported from various Indonesian islands. Marks (1954) pointed out that, with the exception of Sangir Is., some of these records may refer to *A. alorensis*. It can now be reported with certainty that *paullusi* is widespread in North Borneo; I have specimens from both east and west coasts and the interior. Strangely enough, all were reared from larvae taken in tree holes, bamboo stumps, etc.; none was ever taken biting around the breeding places.

The species is readily recognized by the pale anterior stripe on the mid-femur, the antero-lateral stripe on the scutum, and the characteristic male terminalia.

Specimens seen: *North Borneo*: Tawau, Feb., 1960, 3 ♂♂, 5 ♀♀; Keningau, Aug., 1956, 9 ♂♂, 2 ♀♀; Jesselton, Sept., 1945, 1 ♀, and July-Aug., 1956, 7 ♂♂, 7 ♀♀ (all coll. D. H. Colless).

AËDES (STEGOMYIA) ALBOPICTUS (Skuse).

Culex albopictus Skuse, 1894, *Indian Museum Notes*, 3: 20. (Calcutta.)

This widespread species has been reported on a number of occasions from New Guinea, but such records have generally been considered doubtful, and possibly referring to the closely related *A. scutellaris*. *A. albopictus* can now be recorded with confidence from Hollandia, Western New Guinea, as it was present as a contaminant in a batch of *scutellaris* eggs received from that area. The specimens have been checked thoroughly, including the male terminalia, and their identity is certain. It is not known, however, how widespread the species is around Hollandia, nor how long it has been there.

Acknowledgements.

I am deeply indebted to Mr. W. Chellapah and Dr. R. Sloof, who supplied the eggs from which my colonies were established, and to Dr. R. H. Wharton for specimens from Malaya; also to Miss Neel Key for assistance with the figures; and to Dr. A. R. Woodhill, who initiated the hybridization experiments, but was prevented by ill health from performing them.

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THE BIOLOGY OF *ROESELIA LUGENS* (WALK.), THE GUM-LEAF SKELETONIZER MOTH, WITH PARTICULAR REFERENCE TO THE *EUCALYPTUS CAMALDULENSIS* DEHN. (RIVER RED GUM) FORESTS OF THE MURRAY VALLEY REGION.

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

(Plate x; seven Text-figures.)

[Read 24th October, 1962.]

Synopsis.

The gum-leaf skeletonizer moth *Roeselia lugens* (Walk.) is an economically important defoliator of *Eucalyptus* sp., particularly of the *E. camaldulensis* Dehn. (river red gum) forests of the Murray Valley region. Plague numbers of this insect have been recorded from time to time in these forests and high numbers were last present in 1957-58. The biology of this insect was studied and its mortality factors recorded. The flooding responsible for and necessary to the growth of these forests appears to influence some of the mortality factors and the fluctuations in numbers of *R. lugens*.

Introduction.

Roeselia lugens (Walk.), the gum leaf skeletonizer moth, is an important defoliator of the *Eucalyptus camaldulensis* Dehn. (river red gum) forests of the Murray River region. High numbers of this insect which defoliated large areas of this forest were first recorded by Froggatt (1900), and since then there have been at least ten outbreaks of varying severity. The most recent was in 1957–58, during which about 100,000 acres of forest were defoliated.

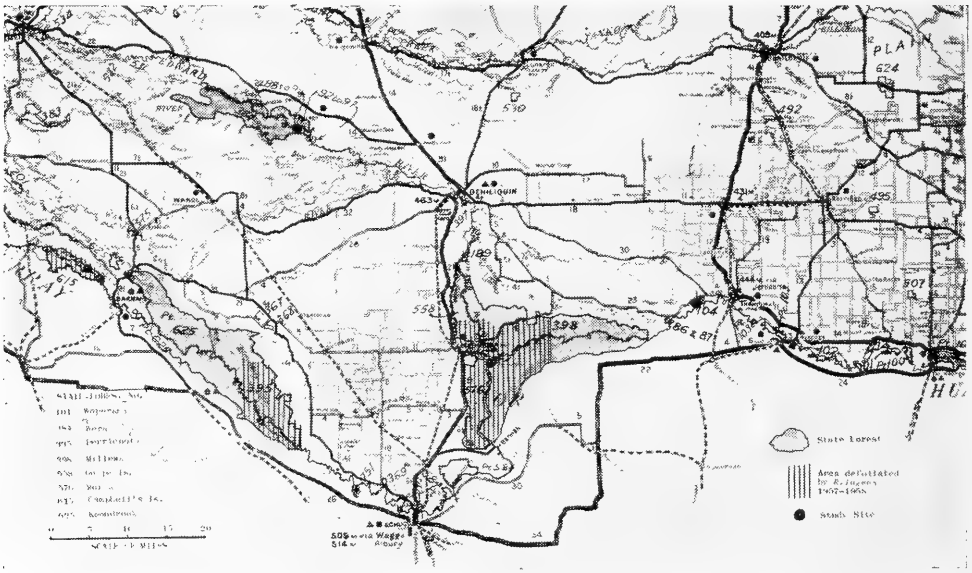

Fig. 1. Map of River Red Gum Forests.

The river red gum forests are unique ecologically amongst the broad-leaved forests of the Australian continent, being composed almost exclusively of a single woody species, *E. camaldulensis*. Small patches of *E. largiflorens* F. Muell. (black box) occur on localities less liable to flooding and *E. melliodora* A. Cunn. (yellow box) fringes the forest where flooding does not usually reach. These forests are situated on a series of flood plains which are generally flooded during the winter period each year. The main

flood plain forest has developed around a series of anabranches of the Murray River between Tocumwal and Wakool Junction nearly 200 miles to the west. These forests form a major but not the sole habitat of *R. lugens* as sporadic outbreaks have occurred in forests of the Southern Highlands and along the coast around Sydney in New South Wales and in parts of Victoria, South Australia and Queensland.

The *R. lugens* population of the highland forests exhibits minor behaviour differences from those of the inland and coastal populations, although the adults are morphologically similar.

This insect was first described by Walker (1863) as *Uraba lugens* (Arctiidae-Nolinae) from specimens collected in Tasmania in the collection of the British Museum. He later described this species, also from Tasmania, as *Coesa viduella* (Walker, 1866). Felder and Rogenhofer (1874) described the insect as *Toxoloma australe* Felder, apparently being unaware of Walker's description of the holotype in the British Museum collection. Meyrick (1886) in his revision of Australian Lepidoptera (Arctiidae) describes this moth as *Nola lugens* Walk.

Lucas (1890) in his work on Queensland and other Australian Macrolepidoptera describes it as *Sorocostia interspersa* and includes *Nola metallopa* (Meyr.) and *Mosoda jucunda* Walk. in his synonymy. *N. lugens* and *N. metallopa* had previously been separated (Meyrick, 1886) and there is now no doubt that they are distinct species. Strand (1920) refers to the insect as *N. lugens* and Baldwin (1928) as *N. lugens* (Walk.) the "social caterpillar". Turner (1926) raised the subfamily Nolinae to family status and (1944) placed the species in the genus *Roeselia*.

The fully grown larva is 20–25 mm. in length, cream ventrally and pink with yellow and dark brown markings dorsally. It bears a characteristic "head dress" composed of successive moulted head capsules and prothoracic skins which are retained by the prothoracic setae instead of being shed with the remainder of the exuviae; up to six head capsules may be retained.

Each body segment, except those bearing legs or prolegs, has two small tubercles ventrally, each tubercle being surmounted by a small rosette of grey setae. Laterally each segment bears two tubercles, the upper and larger being clothed with a rosette of barbed grey setae about twice as long as those borne by the lower.

Dorsally each segment bears four tubercles each surmounted by a small rosette of brown tipped setae, those setae present on the tubercles of the ninth abdominal segments, one of both types, some short and brown tipped and others long and barbed; some of the latter are grey, the others dark brown.

Prolegs are present on abdominal segments 4, 5, 6 and 10. Small tubercles bearing grey setae are borne just above the crochets, those setae on segments 4, 5 and 6 being clubbed. The insect is commonly known as the "gum-leaf skeletonizer moth" (C.S.I.R.O., 1955).

R. lugens is first recorded as an important defoliator of *E. camaldulensis* (= *E. rostrata* Schlecht.) by Froggatt (1900). He refers to the insect as *Nola metallopa* Walk., but describes the characteristic larva and pupa and damage caused by *R. lugens*. The moth is accurately described by him separately (Froggatt, 1923). French (1911) records this insect as severely defoliating *Eucalyptus* spp. in Victoria. There is no doubt that the larva reported and figured by Froggatt (1923) as defoliating 100,000 acres of river red gum in the Murray Valley region in 1919 is that of *R. lugens*.

Since that time reports of defoliation by this insect have been received by the Forestry Commission of New South Wales and Forests Commission of Victoria, but these give little information. During 1944–45 (unpublished report on file F.C. N.S.W. = K. L. Taylor) and again during 1949–50 (unpublished report on file F.C. N.S.W. = P. Hadlington) extensive defoliations by this insect were reported.

In 1957 extensive defoliation again occurred and the writer carried out a survey to determine the extent and severity of damage caused by this insect. As a result of this survey it was determined that an area of approximately 60,000 acres had been defoliated and that the potential population, present as eggs at the time of survey, was estimated to be great enough to cause further severe damage in 1958.

General Biology.

(1) *Seasonal Cycle.*

Two generations of *R. lugens* may occur during the one year and these will be designated in this paper the (*a*) "winter" and (*b*) "summer" generation respectively. Adults of the summer generation emerge from pupation during the period March, April and early May and copulation takes place soon after emergence.

(*a*) *Winter Generation.*

Oviposition, usually on fresh or undamaged foliage, commences about ten days after emergence of the adults. Eggs are laid in more or less parallel rows which are spaced about one egg diameter apart; this formation will be referred to hereafter as an "egg mass"; eggs are seldom laid on damaged leaves.

Eggs hatch in May and June, and once the eggs of one egg mass begin to hatch the larvae from that mass all eclose within approximately a day. Young larvae exhibit overt gregariousness, and at first feed together in aggregations on the leaf surface on which the egg mass has been laid. During the 4th or 5th stadia the larvae begin to feed alone or two or three to a leaf.

After the fifth stadium* the head capsules and prothoracic skins are not shed during ecdysis with the remainder of the exuviae, but remain attached above the prothorax by means of the setae. This process is continued at successive ecdyses and when the larva is fully grown as many as five or six head capsules and prothoracic skins may be borne by the larvae. This "head dress" is characteristic of the larva of *R. lugens* (see Plate x).

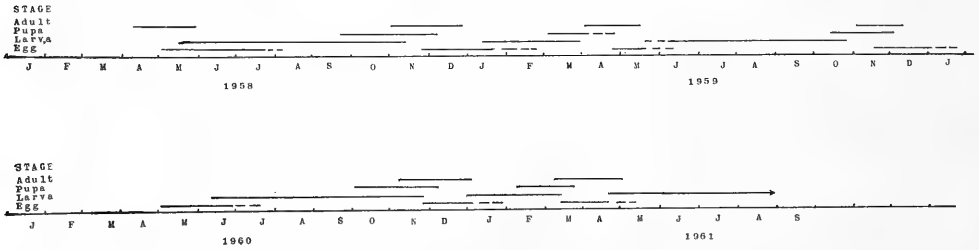

Figure 2.

The larvae pass through eleven stadia in this stage, which occupies the period between late May and early December in the Murray Valley Region. When about to pupate the larvae seek sheltered places in which to spin their cocoons, which are characterized by having the "head-dress" woven into the outer silk. Pupation sites are on the small twigs of the crown, the upper trunk, but mainly beneath flakes of bark on the rough lower trunk, or beneath litter on the forest floor. Moths of the winter generation emerge from pupation during December and early January.

(*b*) *Summer Generation.*

Eggs are laid during the period December to early February. The larvae begin to hatch during January and feed gregariously until the 4th or 5th stadium, after which they feed one or two to a leaf. The larval stage is completed by early March.

Pupation occurs during mid-March to early April. The moths emerge from pupation during the period March, April and early May.

No apparent diapause supervenes in any part of the life cycle of either the winter or summer generations of *R. lugens* in the Murray Valley Region.

Figure 2 is a diagram showing the duration of various stages of the life cycle between 1958 and 1961 in the Murray Valley Region.

(2) *The Adult Stage.*

(*a*) *Behaviour.*

The behaviour of adults of the winter and summer generations is similar.

* "Stadium" is used to denote the interval between moults of larvae instead of "instar" because of the arguments presented by Hinton (1958).

(i) *Emergence of Adults.*

Prior to emergence the pupa becomes active and makes an opening at the anterior end of the cocoon by means of a raised ridge-like process on the head. The pupal skin splits and the adult moth emerges. After an hour or so, during which the wings enlarge and dry, the moth flies upward to the nearest foliage.

(ii) *Copulation.*

When coupled the male and female face in opposite directions with the male uppermost, its wings partially covering those of the female. The moths are not readily disturbed and the dark markings on the forewings of both males and females blend

TABLE 1.

Number of Egg Masses Collected on Foliage—Gulpa Is. State Forest—14/5/1958.

No. of Samples per 10 Chains.	No. of Egg Masses Collected.		Total No. of Egg Masses.
	Below 7 Feet.	Above 7 Feet, but Below 20 Feet.	
25	44	0	44
16	26	11	37
21	40	0	40
25	87	5	92
12	13	18	31
21	17	32	49
25	10	2	12
10	24	0	24
15	6	9	15

together giving the appearance of a single individual with a shape quite unlike that of a moth at rest. This may have some protective function against possible predators. Both emergence and copulation take place during the early hours of darkness.

(iii) *Oviposition.*

Fresh undamaged foliage is usually available in abundance during the periods the adults emerge. This consists mainly of epicormic shoots, of which the crowns of *E. camaldulensis* are largely composed, often because of recurrent defoliation by *R. lugens.*

TABLE 2.

Number of Eggs per Female Moth.

Ex Millewa S.F. 10/12/58.	Ex Campbell's Is. S.F. 9/12/58.	Ex Fairfield 25/11/58.
389	506	609
586	235	507
533		662
		479

This foliage is favoured for oviposition sites, especially if it is situated near the ground, though eggs are laid occasionally higher in the crown.

As shown in Table 1, foliage less than seven feet from the ground appears to be more favoured than foliage between 7 and 20 feet from the ground. Samples were taken in a transect 85 chains long by 5 chains wide. Five samples were taken per chain in crowns between 0 and 20 feet above the ground, a sample consisting of a branchlet 15 inches long including the leaves. Twenty feet was the highest which could be conveniently sampled from the ground using secateurs; trees were felled separately, but very few egg masses could be found higher than this in the crowns.

Several females were dissected to determine the number of eggs an individual moth might be capable of laying. The results are given in Table 2.

It is apparent that all the eggs a moth is capable of laying are not always deposited in the one mass. Occasionally several egg masses may be laid in close proximity, giving the appearance of one large mass. However, slight asymmetry is usually discernible, and unless the masses are laid at nearly the same time the larvae of one egg mass will eclose before those of another. The green eggs are clearly visible through the ventral cuticle of the abdomen and are ready for fertilization and oviposition at emergence. Female moths do not appear to fly far from the point of emergence prior to oviposition; the males appear to be much stronger fliers than the females and in high density populations failure of eggs to develop because of non-fertilization is probably rare.

Viability of eggs collected at different times is shown in Table 3.

TABLE 3.
Viability of Eggs.

	Site.			
	Campbell's Is.	Woperana.	Werai.	Millewa.
(*a*) *High Density Population*—August, 1958.				
No. of egg masses examined	87	79	16	75
Total no. of eggs	6906	7517	999	6855
Total no. of eggs which failed to hatch..	160	538	5	471
Percentage which failed to hatch ..	2·3	7·1	0·5	6·9
(*b*) *Low Density Population*—February, 1959.				
No. of egg masses examined	5	57		10
Total no. of eggs	440	4048		967
Total no. of eggs which failed to hatch	122	1665		386
Percentage which failed to hatch ..	27·7	41·1		39·9
(*c*) *Low Density Population*—June, 1960.				
No. of egg masses examined	2	5		4
Total no. of eggs	321	554		267
Total no. of eggs which failed to hatch	5	14		10
Percentage which failed to hatch ..	1·5	2·5		3·7

This behaviour may be significant in limiting the rapid increase in numbers to areas where host trees are in suitable density and where adequate oviposition sites are available. These conditions are satisfied by the higher site-quality stands of the riverine red gum forests of the Murray River, its tributaries and distributaries.

(3) *Egg Stage.*

The eggs are laid on either side of a leaf blade. Except rarely, only leaves undamaged by any destructive agency and which have developed fully in size, but are still young, are favoured oviposition sites. Despite this, eggs which are not laid on such leaves can develop normally and hatch. This may occur even if the leaf dies subsequent to oviposition, though survival of the eclosing larvae is naturally dependent on living foliage being available nearby.

The eggs are flattened, cylindrical, and about 0·5 mm. in diameter by 0·25 mm. high. They are laid in parallel rows which are composed of eggs laid successively, the margin of one egg touching that of the next. The rows are usually about one egg diameter apart, but the symmetry may be disturbed for the reasons mentioned previously when describing the behaviour of adult females during oviposition (see Plate x).

The dimensions of the eggs and distance between rows of eggs in an egg mass are shown in Table 4.

The number of eggs per egg mass is variable and has been determined for various sites. The figures are presented in Table 5.

It is not uncommon for more than one egg mass to be laid on a leaf, and Table 6 shows the number of egg masses laid on 45 leaves taken at random.

The transparent chorion of the egg renders embryonic development visible. The contents are at first green, but darken as development proceeds constantly without the supervention of any diapause.

The developmental period of the eggs is about five weeks during autumn and less in summer. Shortly after the head capsule is clearly visible within the egg, eclosion of the larva takes place.

TABLE 4.

Table of Egg Dimensions and Egg Mass Dimensions—August, 1960.

Source	Egg Diameter	Egg Height	Operculum Diameter	Distance between Rows
	In Millimetres.			
Woperana S.F.	0·494	0·246	0·368	0·524
	0·496	0·246	0·360	0·516
	0·504	0·247	0·358	0·542
			0·374	0·520
			0·376	
			0·360	
	0·472	0·212	0·368	0·494
	0·474	0·214	0·368	0·482
	0·484	0·216	0·364	0·544
	0·520	0·224	0·384	0·514
	0·524	0·226	0·378	0·480
	0·516	0·216	0·378	0·528
Gulpa Is. S.F.	0·514	0·252	0·370	
	0·506	0·248	0·390	
	0·508	0·246	0·388	
Campbell's Is. S.F. ..	0·514	0·252	0·390	0·494
	0·520	0·262	0·392	0·568
	0·508	0·246	0·372	0·568
	0·534	0·256	0·374	0·572
	0·540	0·248	0·392	0·580
	0·536	0·248	0·406	0·574

(4) *Larval Stage.*

The larva ecloses by pushing off the disc-shaped operculum of the egg to emerge head first and the larvae of one egg mass all emerge within a day or so of one another. The young larvae are overtly gregarious and at first they feed together on the leaf surface close to the egg mass from which they have emerged. Only the palisade layer and spongy mesophyll of the leaf are eaten by the young larvae; the oil cells and veins are avoided. This results in the skeletonizing of the leaf and this habit is referred to in the common name of this insect.

TABLE 5.

Average Number of Eggs per Egg Mass.

		Population Density	Egg Masses	No. of Eggs/ Egg Mass.
8/8/58	Campbell's Is. S.F.	High	78	87± 9·4
10/8/58	Woperana S.F.	High	79	88± 9·6
9/8/58	Werai	Low	16	62±16·4
10/8/58	Millewa S.F.	Medium	75	85± 8·8

Until the larvae have completed the third stadium the egg mass appears to be used as shelter during unfavourable weather conditions or at night. During the 5th and 6th stadia the larval aggregates separate and the larvae feed singly or a few to each leaf. This behaviour is more marked in succeeding stadia when the larvae consume portions of the leaf blade instead of merely skeletonizing it.

The number of larvae in these larval aggregations during the period of overt gregariousness is variable; the mean number has been determined for various areas and is given in Table 7.

The characteristic "head-dress" of the larva has been previously described; the larvae pass through eleven stadia prior to pupation. The duration and number of these is shown in Figure 3.

TABLE 6.

Number of Eggs and Egg Masses per Leaf—Gulpa Island S.F.—April, 1958.

One Egg Mass/Leaf. No. of Eggs/Egg Mass.		More than One Egg Mass/Leaf. No. of Eggs/Egg Mass.		No. of Eggs/Leaf.	
78	71	103	61	216	
100	103	113	78		347
			120		
145	40	53	88	109	
100	99	56			
	72		141		241
48		28	100		
43	94	71		283	
53	101	93	33		
28	91	91	133		380
	115		124		
68		93	90		
224	66	89		256	
181	89	74	100		
			101		
55	85	44	25		374
118	89	104	38		
114	87	37		321	
188	184	36	32		164
			132		
	112	18		80	
		62	84		285
			201		
		147			
		107	50	334	
		80	28		78

The range of the widths of head capsules is significantly different for each stadium. Many head capsules were measured and the results recorded.

It was found that it was possible to determine the stadium of a larva by measuring the greatest width of the head capsule and referring it to Table 8.

TABLE 7.

Number of Larvae per Larval Aggregation.

Site.	Date.	No. per Larval Aggregate (Mean ± Fiducial Limits at 95% Level).	Range	Number of Aggregates Counted.	Population Density.
Campbell's Is. S.F. ..	13/8/58	48 ± 7	5–151	74	High
Woperana S.F. ..	10/8/58	66 ± 11	8–170	76	High
Millewa S.F.	12/8/58	25 ± 5	4–144	75	Medium
Werai S.F.	9/8/58	37 ± 11	18– 86	14	Low

Larval Dispersal.

As mentioned previously, the larvae are at first overtly gregarious, but begin to disperse during the fifth or sixth stadium to feed more or less singly. Movement of larvae from one host tree or sapling to another may take place, but is uncommon unless depletion of the food supply of an individual host occurs and another host is

available close nearby. For larvae to transfer themselves successfully, hosts must be in close proximity (almost, if not actually, in contact).

Usually, unless fallen timbers connect the trunks of nearby hosts, transfer by a larva's own effort is rarely accomplished although, if the population is very dense, larvae may lower themselves on silken threads and be blown a short distance by the

TABLE 8.

Head Capsule Widths.

Stadium.	No. Measured.	Mean Head Capsule Widths mm.	Fiducial Limits 95% Confidence Level—mm.
1	58	0·229±	0·004
2	52	0·285±	0·007
3	70	0·348±	0·003
4	66	0·455±	0·004
5	57	0·545±	0·004
6	81	0·667±	0·016
7	72	0·884±	0·028
8	53	1·079±	0·013
9	38	1·456±	0·024
10	37	1·891±	0·022
11	50	2·367±	0·025

wind. This sort of movement is limited, however, even within a forest stand where trees are relatively close together. Larvae appear reluctant to cross open ground for more than a short distance even under the stimulus of actual starvation.

In the eleventh stadium, when fully fed prior to pupation, the larvae begin to move about the host tree apparently seeking pupation sites. After moving like this for

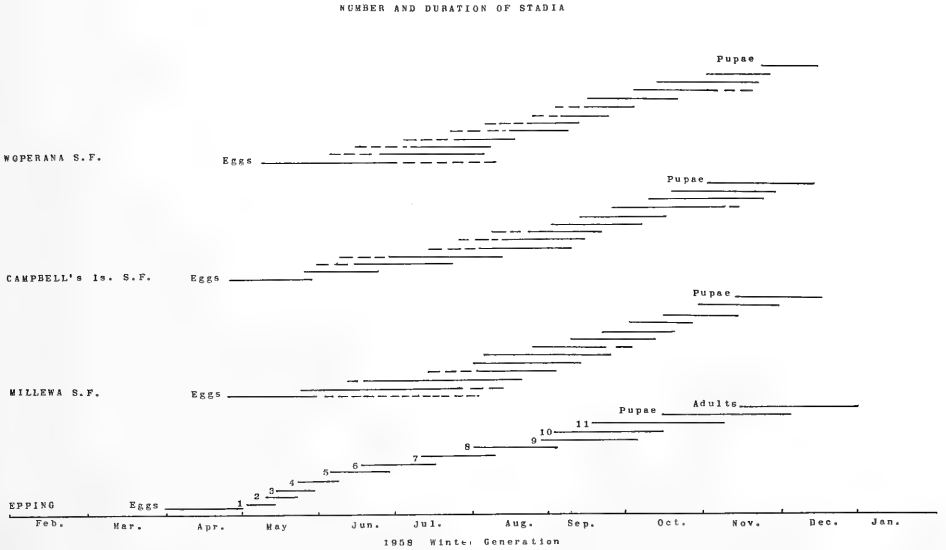

Figure 3.

several hours they exhibit a strong positive-geotaxis and travel toward the base of the tree; however, when the larva arrives at the base it does not immediately seek a pupation site but turns and ascends the trunk. This procedure may be repeated several times.

This behaviour is particularly evident when the forest floor is flooded and the larvae cannot reach pupation sites in the apparently favoured localities—on the lower

trunk and beneath litter on the forest floor. The larvae then wander apparently aimlessly around the twigs and branches of the host tree, finally pupating where they can.

Wherever possible the majority of larvae which have survived to the ultimate larval stadium pupate beneath litter on the forest floor.

TABLE 9.

Date of Pupation, Pupal Period and Number of Male and Female Moths Emerged.

Source.	Date of Pupation.	Date of Emergence of Adults.	Pupal Period.	No. of Moths. Females.	No. of Moths. Males.	Remarks.
Murray River Region.						
Millewa S.F... ..	——	12/4/58	——	3	3	Pupae collected in field.
Finley	21/9–20/10/58	4/11–14/11/58	46–28 days	5	10	Larvae collected in field.
Gulpa Is. S.F. ..	29/9–30/10/58	6/11–23/11/58	40–24 days	27	28	Eggs collected in field 14/4/58. Bred Epping, N.S.W.
Campbell's Is. S.F...	23/11/58	10/12/58	30 days	9	7	Larvae collected in field when fully grown.
Millewa S.F... ..	22/11–7/12/58	10/12/58	19 days	6	10	do.
Woperana S.F. ..	28/11/58	12/12/58	15 days	13	9	do.
		1958 Winter Generation		60	64	
Millewa S.F. (Picnic Point)	4/3/59 (1) 7/3/59 (1) 18/3/59 (12) 25/3/59 (12) 31/3/59 (9) 6/4/59 (5) 14/4/59 (1)*	6/4/59	13 days	2	2	Larvae collected in field and used experimentally.
		1959 Summer Generation ..		2	2	
Campbell's Is. S.F...	16/10–27/10/59	3/11–3/12/59	19–38 days	11	17	Eggs collected in field 14/5/59. Bred Epping, N.S.W.
Millewa S.F... ..	–27/10/59	12/11–27/11/59	–32 days	2	6	do.
Picnic Point (Millewa S.F.)	–13/10/59	4/12/60	–53 days	0	0	Larvae collected in field when fully grown.
		1959 Winter Generation		13	24	
Coastal.						
Fairfield	21/9–20/10/58	6/11–14/11/58	54–26 days	1	2	Larvae collected in field. Bred Epping, N.S.W.
Tea Gardens	——	——	——	1	1	
Cumberland N.F. (Pennant Hills)	27/9–27/10/59	28/10–27/11/59	33–32 days	12	17	Eggs collected in field. Bred Epping, N.S.W.
				14	20	

* Number of pupae—all other pupae except those shown as emerging died as a result of infection of *A. parasiticus*.

(5) *Pupal Stage.*

Having selected a suitable pupation site, the larva commences to spin its cocoon. Fragments of bark, litter or even frass may be woven into the outer silk and the cocoon blends into its surroundings. It is characteristic, however, because the "head dress" of head capsules is usually affixed to the outer silk.

Shortly after the cocoon is complete the larva begins to pupate and assumes the appearance of the obtect pupa. The sex of the insect is then distinguishable.

At the completion of development the pupa becomes active and tears an opening in the anterior end of the cocoon by means of a special ridged process on the vertex.

The pupal skin splits along the epistomal suture and the split continues along the antennal suture; the adult insect emerges through the opening so made.

The pupal period varies from 13 days in the summer generation to 54 days in the winter generation. It is thought that this may be a result of the lower temperature retarding metamorphosis as the pupal period of the winter generation shortens with rising mean daily temperature. Table 9 summarizes this information.

TABLE 10.

Total Number of Pupae. Small Trees not over 25 Feet in Height. 16–18/12/58.

Site.	No. of Trees.	Number of Pupae		
		On Branchlets or Leaves.	On Trunk.	Under Litter.
Campbell's Is. S.F. ..	10	82	—	—
Millewa S.F.	15	32	23	1
Woperana S.F.	15	102	108	375

TABLE 11.

Pupae Collected at Base of Ten Large Trees—16–18/12/58.

Site.	Total Number of Pupae Collected.		
	Trunk to 1 Foot from Trunk Right Around the Tree.	From 1 Foot to 2 Feet from Trunk, etc.	From 2 to 3 Feet from Trunk, etc.
Campbell's Is.	45	12	2
Millewa S.F.	4	5	0
Woperana S.F.	132+7 larvae*	6+2 larvae	0

*1 live, 3 diseased, 3 dead.

TABLE 12.

Pupal Count on Trunk and in Crown of Large Trees—16–18/12/58. Total Number of Pupae Counted.

Height Above Ground—Feet.	Site.			
	Campbell's Is.	Millewa.		Woperana.
		Tree No. 1.	Tree No. 2.	
0– 6	0	4, 1 old*	0	0
6–12	0	1, 1 old	0	0
12–18	0	0	0, 2 old	0
18–24	0	1	0, 1 old	2
24–30	1	1, 1 old	0, 2 old	2
30–36	2	0, 1 old	1	2
36–42	1	0	0	8
42–48	0	Crown 0	0	Crown 17
48–54	1			0
60+	Crown 0			

* Old=not this generation.

In the red gum forests the flood water removes most of the leaves, etc., which provide the ground litter of the area, though branches and logs are often piled against some trees by the flood. At Campbell's Is. no leaf litter remained, at Millewa there was a small amount, and at Woperana this type of ground cover was variable in amount throughout the site. At all sites branches and logs were piled against some trees, but many had no ground litter beneath them following the flood. A count was made of the pupae in the various pupation sites; this is summarized in Table 10.

To obtain information of the pupation sites of *R. lugens*, litter from around the base of several large trees on each study site was examined. Table 11 summarizes the results obtained.

Most pupae were found within a radius of two feet from the periphery of the butts of the trees; few pupae could be found further from the tree—apparently larvae do not move far from the base of a tree when seeking pupation sites.

Four large trees were felled and the number of pupae on various sections of the trunk and crown counted. The results are shown in Table 12.

It is evident that larvae will pupate in the trunk and in the crown of large trees as well as in the litter beneath the trees. However, when numbers are high, a large proportion of pupae occur in the litter.

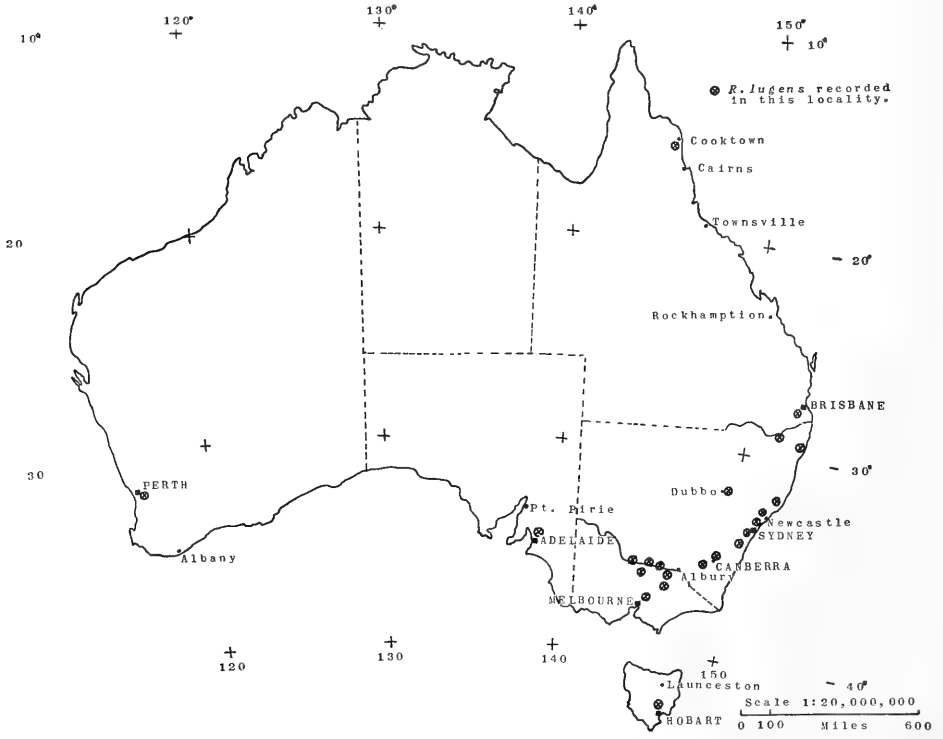

Figure 4.

Distribution.

As far as can be ascertained the distribution of *R. lugens* extends from the south-west of Western Australia, through the south-east of South Australia, through Victoria and eastern New South Wales, and Queensland northwards to Cape York Peninsula. The insect has also been recorded from Tasmania.

Mean annual rainfall throughout the area of distribution is extremely varied, from less than 20 to more than 60 inches. However, the areas in which *R. lugens* is known to reach plague numbers are all characterized by high relative humidity during part of the year. Rainfall is mainly responsible for the high humidity in the alpine and maritime areas, but it is the presence of the large bodies of water represented by the Murray River and its distributaries and tributaries which provide this factor in the dry inland area studied.

There appear to be two forms of the insect, the adults of which are not, so far, distinguishable morphologically. There is at least one major behaviour difference between the form present in the highland region and that which occurs in the inland

or coastal lowland regions. Moths of the coastal and inland lowland form place their eggs in an egg mass composed of parallel lines as described, whereas those of the highland form oviposit theirs in compact masses (see Plate x). It appears that there may be two more larval stadia in this stage of the highland form (personal communication, Mr. K. M. Moore).

Hosts.

R. lugens has been recorded as occurring in plague numbers on *E. camaldulensis* in the Murray River region, on *E. dalrympleana* (mountain gum) in the alpine region and on *E. robusta* (swamp mahogany) in Sydney. It will feed also on a number of other *Eucalyptus* spp. hosts, all hosts so far recorded being within this genus.

The hosts recorded to date are:

Murray Valley Region, N.S.W., Victoria, South Australia: *E. melliodora* A. Cunn. Yellow Box; *E. largiflorens* F. Muell. River Black Box; *E. hemiphloia* F. Muell. Grey Box; *E. camaldulensis* Dehn. River Red Gum.

Goulburn River Area, Victoria: *E. obliqua* L'Hérit. Messmate Stringybark; *E. macrorrhyncha* F. Muell. Red Stringybark.

Canberra, A.C.T.: *E. blakelyi* Maiden. Blakely's Red Gum.

Alpine Region, N.S.W.: *E. dalrympleana* Maiden. Mountain Gum; *E. robertsoni* Blakely. Robertson's Peppermint.

Sydney Area, N.S.W.: **E. stellulata* Sieb. Black Sally; *E. saligna* Sm. Sydney Blue Gum; *E. baueriana* Shauer. Blue Box; **E. andreana* Naudin. River Peppermint; *E. robusta* Sm. Swamp Mahogany.

Boambee, N.S.W.: *E. grandis* Hill. Flooded Gum.

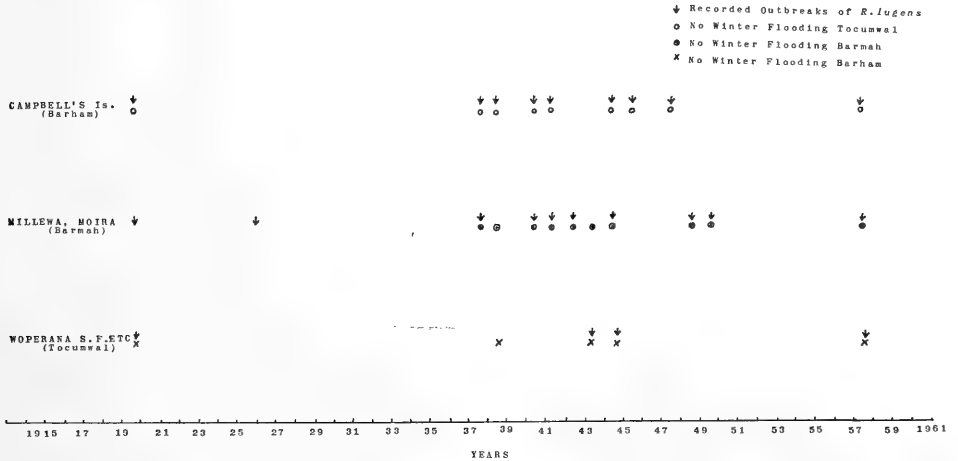

Figure 5.

Investigation of Past Outbreaks.

In order to obtain more evidence as to the probable cause of outbreaks of *R. lugens*, a search was made of past records and inquiries were made from various forestry staff and other workers and residents in the red gum forests. A search was made of the records of the Water Conservation and Irrigation Commission to obtain information of years in which the red gum forests were or were not flooded during the winter and spring (these latter are termed "no flood" years).

The information obtained, which was verified as far as possible by cross checking, is shown in Figure 5. Known occurrences of plague numbers of *R. lugens* in the various red gum forests are plotted on the same graph.

The coincidence of "no flood" conditions and outbreaks of *R. lugens* on the riverine red gum forests suggests that during these periods conditions are unfavourable to the

* Arboretum trees, Cumberland National Forest, Pennant Hills, N.S.W.

mortality factors regulating the increase of the insect. It has been found that high humidity is important to the spread of fungus infections of insects with or without accompanying high temperatures. Hall and Dunn (1957) have described how fungus epizootics among spotted alfalfa aphids have been initiated by irrigating the alfalfa.

1957–58 Outbreak.

Following the record flood of 1956, no winter flooding of the forest took place in 1957 and conditions remained very dry during the summer of 1957–58. Toward the end of 1957 defoliation of large areas of river red gum became apparent. Throughout the entire forest area *R. lugens* was present, the populations being most dense and the defoliation most severe in the higher site-quality areas. In Campbell's Is. State Forest, an area of more than 9,000 acres of high site-quality, practically all the trees were completely defoliated. In New South Wales and Victoria about 100,000 acres of river red gum forest was similarly affected during this outbreak.

The winter generation of this insect was primarily responsible for this defoliation in 1957, but the rapid refoliation characteristic of red gum (Jacobs, 1955) which occurred prior to oviposition ensured that adequate sites were available to the adults of the summer generation of 1958.

Surveys of the egg stage present early in 1958 showed that high numbers of eggs were present throughout the previously defoliated area and counts of these and larvae were carried out at various times throughout the season. Presentation and discussion of these does not come within the scope of the present paper.

Numbers of larvae were high, but some mortality had occurred. Larvae were examined for the presence of endoparasites and it was apparent that at least two species, both hymenopterous, were present. Some predation by crows and currawongs was suspected but could not be verified.

Towards the end of September, 1958, water levels in the Murray River began to rise and the forests were flooded during October. Woperana State Forest (near Tocumwal) was submerged to a depth of several feet, and as the flood moved down the river, Millewa State Forest near Mathoura, Campbell's Island State Forest near Barham and finally Werai State Forest 25 miles west of Deniliquin were inundated. Werai State Forest remained under water until January, 1959, but Woperana was dry by mid-November and Campbell's Island in December.

By November, larval mortality was considerable, but could not be attributed merely to the parasitism measured and observed or to the suspected predation. It may have been attributed to starvation at Campbell's Island or Woperana where defoliation was practically total, but a similar reduction occurred at Millewa where there was generally adequate food for the larvae to complete their development. At this time some larvae appeared abnormal and some were found dead on the ground; it was suspected that a disease might be responsible.

Pupation had commenced in the field by mid-November and, although the flood had subsided in many localities, much of the litter on the forest floor had been removed or redistributed and this had a profound effect on this stage of the insect. Fully grown larvae at Campbell's Island were still confined to their individual host trees by the flood water and were observed to move toward the base of the tree only to turn at the water's edge and move upwards toward the branches again. These trees were completely defoliated and the larvae may have been motivated by the need for more food; however, it has been observed that larvae in cages with abundant food also move about for some time apparently seeking suitable pupation sites. The favoured pupation sites in the field or cages appear to be amongst floor litter.

Pupal mortalities were caused by endoparasites both dipterous and hymenopterous and some appeared to be damaged by a mandibulate predator whose identity could not be established. However the mortality was variable and a proportion survived from which the adults of the next generation emerged.

1959 Summer Generation.

The eggs laid by the emerging adults were nowhere as numerous as those present in early 1958, but by March of this year larval mortalities were extremely heavy and

few could be found even in localities where in the previous generation they had been very numerous. It appeared, at this time, that some larvae were diseased and consequently an experiment was devised to examine the possible causes of this disease.

1959 Winter Generation.

Numbers remained at a very low level and the winter flooding of the red gum forests occurred.

1960 Summer Generation.

Numbers of *R. lugens* were still at a very low level, very few larvae could be found and no noticeable defoliation occurred.

1960 Winter Generation.

The population of *R. lugens* was present at very low density, no perceptible defoliation occurred and the winter flooding took place as usual.

1961 Summer Generation.

Numbers of the insect remained at a very low level and no perceptible defoliation occurred.

1961 Winter Generation.

The population of *R. lugens* remained at a very low level and no perceptible defoliation occurred.

TABLE 13.

Total Number of Eggs and Number Parasitized and Removed by Predators.

	Site.			
	Campbell's Is.	Woperana.	Werai.	Millewa.
Number of egg masses examined	87	79	16	75
Total number of eggs	6906	7517	999	6855
Number parasitized	21	61	0	1
Number removed by predator(s)	47	113	0	106
Number failed to hatch or infertile	92	354	4	364
Number hatched	6746	6979	995	6384

MORTALITY FACTORS.

Parasites and Predators.

(*a*) *Egg Stage.*

The eggs of *R. lugens* are subject to attack by a wasp parasite *Trichogramma* sp. Larval and pupal development of this wasp takes place within the egg, an adult wasp emerging instead of a larva of the moth.

The mite *Microsmaris goannae* Hirst is predatory on the eggs, sucking out their contents. This mite (family Erythraeidae) is recorded also as an egg predator of the moth *Cactoblastis cactorum* (Berg) (Dodd, 1940).

At times a predator is responsible for the removal of complete eggs from the egg mass, though seldom are more than a few taken. The identity of this predator could not be established.

These factors are responsible for the destruction of only a very small percentage of the eggs.

Table 13 summarizes the results obtained from the examination of egg masses taken from the various study sites in August, 1958.

(*b*) *Larval Stage.*

Several endoparasites and one ectoparasite have been found attacking this stage.

Endoparasites.

(i) *Hymenoptera.*

Several species of these have been found, oviposition in most cases occurring in the host's early larval stadia. Development of the parasite larva takes place at the expense of the host, but the latter does not die until the penultimate or ultimate stadium when the parasite emerges to pupate.

In all observations only one parasite has emerged from each host larva, the body contents of which appear to be almost completely consumed. The parasite's cocoon, where present, is constructed beside the body of the host.

These endoparasites are represented by two super-families, the Ichneumonoidea and Chalcidoidea. The Ichneumonid parasites are represented by two major groups. One group constructs a white loosely-woven silken cocoon about 4 mm. in length and 1·5 mm. in diameter in which to pupate. One Braconid and one Ichneumonid are represented in this group. The Braconid is probably a species of *Apanteles*, but this and the Ichneumonid have not yet been determined.

The other group constructs a firm, closely-woven, smooth-surfaced cocoon, silver in colour with dark brown spots 6 mm. in length and 2·5 mm. in diameter. This group is represented by three (probably) species of Ichneumonids. None of these have been determined.

There are also three (probably) species belonging to the super-family Chalcidoidea.

(ii) *Diptera.*

There are two species, one belonging to the family Muscidae and the other to the Tachinidae-Sarcophaginae. In the case of the latter, although parasitization takes place during the larval stage, emergence takes place from the pupa. Neither species has been determined.

TABLE 14.

Total Number of Pupae Found under Bark and in Litter, 16–18/12/1958.

Condition.	Site and Number of Trees.				
	Campbell's Is.		Millewa.	Woperana.	
	Under Bark, 10 Trees.	Under Litter, 6 Trees.	Under Bark, 5 Trees.	Under Bark, 4 Trees.	Under Litter, 3 Trees.
Pupae alive	2	0	2	5	17
,, emerged	5	5	0	1	1
,, dead	3	0	4	2	11
,, parasitized by *Brachymeria* ..	16	1	2	22	23
,, parasitized by other *Hymenoptera*	0	0	0	0	1
,, damaged by unknown predator	4	1	1	0	0

Ectoparasites.

At least one species of Chalcid wasp has been found to be an ectoparasite of *R. lugens*. The larvae are affected in the very early stadia and commence to shrivel, giving the appearance of a disease.

(c) *Pupal Stage.*

The most important pupal parasite of *R. lugens* is *Brachymeria rubripes* Gir., Chalcidae. This wasp overwinters as an adult sheltering beneath flakes of bark and has been taken at light in August. It has been observed to be active during the pupation period of its host.

Cocoons were collected from the study sites from under the flakes of bark on the base of the trunk of trees and from beneath the litter on the ground near the trunk.

Table 14 summarizes the results of examination of these cocoons.

The adults of Tachinid flies emerge from the pupae, but parasitism occurs during the late larval stages. There is also a small amount of parasitism by other hymenoptera (Ichneumonoidea), but only a very small proportion of pupae are affected.

Exhaustion of Food Supply.

In portions of the forest where defoliation was complete and the individual trees were isolated by floodwater, death of the larvae from starvation and/or by drowning occurred when larvae descended the trunk of completely defoliated trees and were washed off. In such situations this was merely incidental, as the immature larvae would not have survived anyway. The mortality attributable to this factor was very

variable, but was greatest at Campbell's Is., where the defoliation was complete in many parts and the flood water persisted during this period.

Larval Dispersal.

After the fifth stadium has been attained larvae move singly about the foliage seeking food. When the population is dense and food supply is being depleted larvae are forced to move about seeking food more frequently. Movement of the branchlets, as by the wind, during this period often results in larvae lowering themselves groundwards on silken threads.

Contact is sometimes made in this way with the lower crown, but often larvae reach the ground. Unless the trunks of host trees, or fallen branches, etc., in contact with such, are adjacent, many larvae die through inability to reach a food supply. Larvae apparently do not or cannot cross open ground with a heavy vegetative cover (grass, etc.) which is common in the red gum areas.

Larvae will transfer from host to host readily if the crowns are interconnected or overlap, or if the trunks are in contact by means of fallen logs or debris forming a "bridge" across which larvae can move unhindered.

If the area is flooded during this period death of such larvae is almost certain and higher mortality will result under such conditions. "No flood" conditions favour survival of larvae.

Trees are generally closer together and the crowns are denser on higher site quality areas, making them more favourable for larval survival under these circumstances.

Adult Dispersal.

The adult moths do not feed, mouthparts being vestigial, and can live and oviposit without access to free water. However, if the latter is available, moths have been observed to imbibe this in captivity and presumably this occurs in nature also.

The oviposition behaviour of the females, that is, the most usual fixing of egg masses onto the first (lowest) available and acceptable foliage (contacted after emergence and copulation), tends to limit the spread of high density populations into surrounding areas if there are large openings in the forest stand or if suitable oviposition sites are readily available.

Young undamaged leaves are preferred oviposition sites. These are most readily available in recently defoliated forest stands which have been refoliated during the period the insect is present as pupa, adult and egg, particularly those of higher site qualities.

Plague numbers tend to be self-perpetuating in this respect as river red gum refoliates readily and strongly by epicormic shoots. The more severe and extensive the defoliation the greater is the number and availability of suitable oviposition sites and the lower the mortality of moths seeking such sites.

Forest Stand Factors.

It has been observed that the higher site quality areas are the most severely defoliated during plagues and it is within these areas that plagues most usually occur.

The forest stand factors favourable to high density populations of this insect are considered to be: (1) Host trees close together with some overlap of crowns or dense areas of small seedling or other regeneration; (2) Abundant fresh undamaged leaves; (3) Continuous canopy of foliage—no large breaks or openings in forest stand.

Open country, sand banks, expanses of water—lagoons and swamps with reed beds and clumps of trees unsuitable as hosts—*Callitris* sp. or *Casuarina* sp. or extensive areas of low site-quality river red gum all appear to act as barriers limiting the dispersal of the moths.

Disease.

The rapid increase in larval mortality toward the end of the 1958 winter generation cannot be accounted for by the observed parasitism or predation. Larvae taken in the field and bred in the insectary at Epping, N.S.W., began to die of a disease caused by a fungus. Larvae bred from eggs collected in the field had a very low mortality rate and were not affected by the fungus even though held in adjoining cages.

Even as early as the end of January, 1959, mortalities in the larval stage of the summer generation of 1959 were widespread and heavy through the river red gum forests. It appeared, at this time, that some larvae were diseased and there was evidence to suppose that this could cause the death of a high proportion of larvae.

Consequently, a number of apparently healthy larvae were collected in the field and transferred to Epping. It was suspected that these larvae might be infected by disease, but until they were subject to some stress, perhaps crowding, the disease would not be manifest and cause mortalities (Steinhaus, 1958).

More than 400 larvae were collected on 12/2/59, mostly at Millewa and Woperana State Forests, four only being collected at Campbell's Is. State Forest. Of these 170 showed some signs of disease and were discarded, the remainder being used experimentally.

Crowding Experiment.

An experiment was designed to attempt to test the effect of a crowding stress on these larvae.

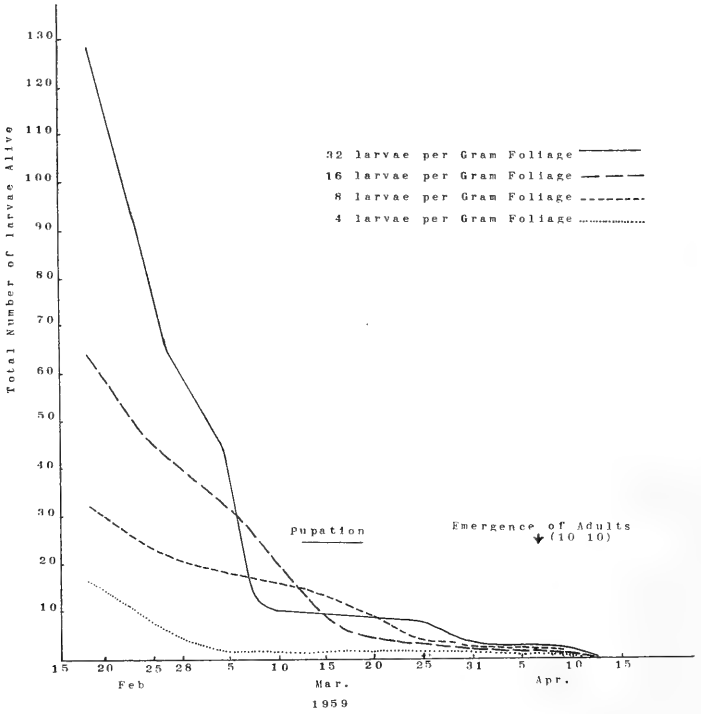

Figure 6.

New clean plastic jars 3½ inches in diameter and 4½ inches high with loose-fitting lids were used as containers. Sixteen such jars were provided with one gram of *E. camaldulensis* foliage, providing for four replications of four treatments. The treatments were groups of 4, 8, 16 and 32 larvae per jar—240 larvae being used altogether.

As the larvae in each jar exhausted the one gram of foliage, this was replaced to prevent dispersal of the larvae; thus the food supply was not a limiting factor. The larvae remained throughout the experiment on the foliage, the 32 larvae, of course, being more crowded than the four larvae per gram of foliage.

The experiment was commenced on 18/2/59 and 50% mortality of larvae had occurred within nine days on the four larvae and 32 larvae treatments, within 14 days in the treatments with 16 larvae, and 17 days in the treatments with eight larvae.

Within 27 days pupation was occurring and within 41 days an average of only one pupa remained alive in each replication. Of a total of 240 larvae, 16 pupated and two moths emerged (one male and one female).

These results are presented in Figures 6 and 7; the conditions of temperature and relative humidity applying during the period of the experiment are also shown.

All larvae which died were submitted for examination; in practically all cases the cause of death was disease caused by *A. flavus* or *A. parasiticus* (personal communication, M. F. Day). Sussman (1952) has found that the *A. flavus/oryzae* group is lethal when injected into the pupae of *P. cecropia*.

It did not appear that severe crowding was necessary for mortality to occur, as the relatively uncrowded larvae (four per gram of foliage) were as badly affected as the severely crowded (32 per gram of foliage), or perhaps four larvae per gram is sufficient crowding to provide this stress.

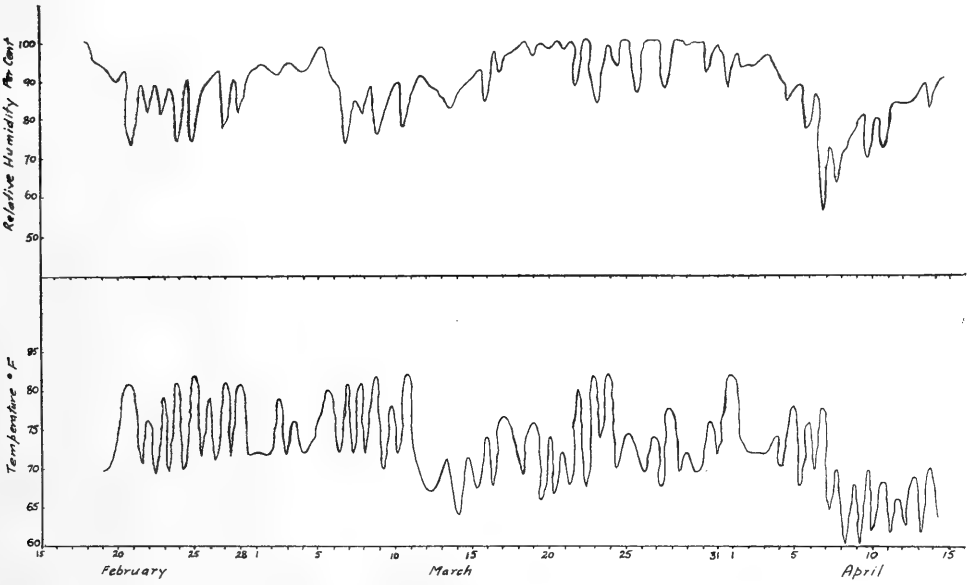

Figure 7.

However, all larvae were subject to high humidity, and it is considered that this was the important factor in permitting the action of the entomogenous fungus.

This factor was present in the redgum forests during the summer of 1959, since free water surfaces were there in abundance in the form of lagoons and swamps following the flooding, and the high temperatures prevailing in the region also provided conditions favourable to the spread of such a disease.

In the field, at this time, the population density was at a very low level and it was difficult to find even a few larvae where recently these had been present. No other factor could be found which would explain this reduction of the population to such a low level.

Non-occurrence of the winter flooding means that lagoons and pools dry up and there is very little free water surface (except in the rivers and its distributaries which, of course, contain relatively little water at such times) and the relative humidity is low. Conditions are then cool and dry in winter and hot and dry in summer and not favourable to the spread of a fungal disease.

Survival of a high proportion of larvae (which would otherwise be killed by disease) and subsequent adults provides the nucleus for a rapid increase in numbers in the next generation. This increase continues until the onset of favourable conditions for the spread of the fungus and the mortality of the dense population is consequently very great, which restores numbers to a low level.

Defoliation Studies.

In order to study the damage caused by defoliation due to *R. lugens*, three branchlets were selected and tagged on each of the sample trees on each study site. All the leaves present on each of these branchlets were counted and recorded. To obtain a figure which could be used for comparison, 50 leaves were taken from each tree at random and weighed, once before any serious defoliation occurred and again at the end of feeding of the larval stage.

Variable defoliation of trees from total to moderate occurred on the same site at Woperana S.F. and Table 15 illustrates the results obtained.

TABLE 15.

Tree No.	20/9/58.		18/11/58.				Remarks—Condition of of Foliage.
	Number of Leaves.	Weight 50 Leaves (Gms.).	Number of Leaves.		Weight of 50 Leaves (Gms.).		
			Old.	New.	Old.	New.	
T1 A	126	19	141	—	24·5	—	Defoliation only moderate.
B	117		195	—		—	
C	253		338	—		—	
T2 A	181	18	149	—	6	22·7	Defoliation severe, most leaves almost completely skeletonized.
B	364		450	—			
C	346		408	26			
T3 A	76	13		—	0	—	Defoliation extreme, all leaves skeletonized.
B	110			—		—	
C	248			—		—	
T10 A	141	9	34	—	16	—	Defoliation moderate.
B	200		49	—		—	
C	374		440	—		—	
T11 A	326	8	244	—	10	—	Defoliation moderate.
B	350		308	—		—	
C	370		397	—		—	
T13 A	210	19	176	—	14	—	Defoliation severe, most leaves almost completely skeletonized.
B	68		249	—		—	
C	181		154	—		—	
T14 A	147	14	190	—	13	—	Defoliation moderate.
B	43		139	—		—	
C	179		140			—	
T15 A	140	18	185	—	23	—	Defoliation moderate.
B	141		251	—		—	
C	134		222	—		—	

Although the leaves were being consumed by the larvae, other leaves were growing, and in a number of instances there were more leaves when the larvae pupated than when they commenced feeding and, except in the cases of severe defoliation, the leaves were of larger average size.

This no doubt is attributable to the stimulus provided by removal of some of the leaves. It is a characteristic of *E. camaldulensis* to refoliate rapidly. This, of course, results in the diversion of energy normally available for height and diameter growth being expended on leaf growth, to the detriment of the tree. Such foliage is largely composed of epicormic shoots which are usually replaced by normal foliage when such defoliation ceases.

A transect across the Woperana site from east to west, a chain wide, was traversed. This was done at the end of the larval stage when most defoliation had occurred.

The degree of defoliation of each tree was observed; the results are summarized in Table 16.

Although all classes of trees may be severely defoliated or only slightly affected there appeared to be a definite grouping of defoliated trees. The more dense populations of *R. lugens* appeared to occur in areas of high density of saplings or young trees occurring in belts, a characteristic resulting from the establishment of regeneration in flooded areas with debris providing optimum conditions for such establishment (Jacobs, 1955).

Large trees are more severely defoliated, i.e., have high populations of the insect when these have low branches. Quite often these branches may be completely defoliated, whereas the remainder of the foliage is only slightly damaged. The oviposition behaviour of the female moth is thought to account for this pattern of attack and the subsequent larval behaviour for the "grouping" of the defoliation.

Defoliation of the tree is significant for several reasons. Firstly there is the removal of "normal" foliage and its replacement by epicormic shoots which are temporary and will be replaced in turn by the normal foliage when the stimulus of defoliation has ceased.

TABLE 16.

Classification.

Tree Class.
S = Sapling.
Y = Young tree.
M = Mature tree.
V = Veteran.

Defoliation.
N = Negligible.
S = Slight.
M = Moderate.
H = Heavy (= Severe).

Tree Class.	Degree of Defoliation.	Tree Class.	Degree of Defoliation.
M	S	S	H
M	H	S	H
M	M	S	H
Y	H	S	H
M	S	S	M
Y	S	S	H
Y	M	Y	M
Y	M	S	H
M	M	Y	M
Y	H	Y	H
Y	H	M	H
M	S	M	S
M	S	S	H
V	H	S	S
S	S	S	H
S	N	M	H
Y	H	M	H
M	M	S	H
M	M		

The immediate result of this is the diversion of energy ordinarily used in the apical and lateral growth of the tree to the growth of foliage, causing a loss of wood increment.

A secondary result is the development of faults within the wood caused by growth of the epicormic shoots. Gum flecks are common, and as the shoots are unstable and easily broken this may provide access to wood-destroying organisms, both insects and pathogens.

Another less obvious result of the replacement of the normal crown by epicormic shoots is the loss of production of buds and flowers. Production of flowers may be delayed for several years after the normal foliage is regained and is probably a result of depletion of starch reserves of the tree caused by the defoliation and forced refoliation.

This, of course, affects seed production and the resultant regeneration, so that the effects of severe defoliation may be long term and exercise a profound influence in the forest.

Discussion.

R. lugens is an economically important defoliator of the *E. camaldulensis* forests in the Murray Valley Region. Since 1919 there have been at least eleven recorded outbreaks of this insect with up to 100,000 acres of forested lands defoliated on at least two occasions.

The major "legislative" factor (Nicholson, 1954) considered to be responsible for the control of *R. lugens* appears to be the winter-flooding which normally occurs over the flood-plain on which the red-gum forests grow. This flooding which ensures high humidities and moderate temperatures within the forest stand is thought to favour the spread of an entomogenous fungus, *Aspergillus flavus* or *A. parasiticus*, which maintains the population of *R. lugens* at a low density.

The larval and pupal stages are affected indirectly by the winter-flooding. Flooding removes much of the litter from the forest floor so that favourable pupation sites are limited. Pupae in unfavourable situations may be more readily found by the parasite *B. rubripes*, resulting in a higher proportion of mortalities from this cause.

Failure of winter-flooding results in dry conditions on the flood-plain which are unfavourable to the spread of the fungus. This may permit a greater survival of the larval stage of the winter generation of this insect. Favourable pupation sites are abundant in dry conditions; lower parasitism of the pupae ensues resulting in a greater survival and emergence of adults.

Abundant oviposition sites—fresh undamaged leaves—are readily available to the adult female moths, particularly in the high site-quality areas of the forests. It is usually on these sites that population increases first occur and to which they may be limited if the outbreak is not extensive.

The stand factors which favour population increases are: (1) Abundant fresh undamaged leaves; (2) Low-hanging branches; (3) Trees close together with crown peripheries adjacent or overlapping; (4) Dense young regeneration; (5) Abundant litter on the forest floor.

The winter-flooding usually does not persist into the summer period, but leaves the flood-plain saturated with water. The lagoons are full and conditions are still very humid. The young larvae of the summer generation suffer mortalities caused by the entomogenous fungus which is considered to maintain the population at a low-density level.

Failure of the winter-flooding not only favours an increase in the winter generation directly affected, but may also permit a much greater increase—an "explosion"—in the population during the summer period. This population is usually maintained at a high level in the winter generation following until flooding of the forest area provides conditions in which heavy mortality occurs and the numbers are reduced to a low level.

Thus a single failure of a winter-flooding may result in three successive defoliations of a red-gum area, the first usually small and localized, the second and possibly the third extensive and severe. Despite serial defoliation, recovery of the crown of the river red gum is rapid and such refoliation may favour population increase. The duration of the pupal period is usually sufficient for recovery of the crown to occur and abundant fresh undamaged leaves, favoured as oviposition sites, are readily available to the emerging adults.

The epicormic shoots produced following destruction of the normal crown foliage are often produced low down in the stem and are usually pendant. The oviposition behaviour of the female, in which the eggs are deposited on the lowest available suitable foliage, is thus given opportunity for full expression and more eggs per female may be laid.

The ecological conditions which favour the establishment of the river red-gum forests on the flood-plains of the Murray River have provided *R. lugens* with abundant hosts and stand factors which may permit its population density to reach a very high

level. This may not occur, however, unless the usual winter-flooding, so important in the establishment and maintenance of the forest, is absent. Then, the disease, favoured by the usual humid conditions resulting from floodings, is rendered relatively ineffective and the insect may take advantage of the favourable habitat and increase in numbers.

Damage to the host trees, though often severe, is seldom prolonged enough to cause widespread death of the trees. The condition of winter-flooding is present more often than not and the trees recover rapidly. However, the growth rate of *E. camaldulensis* is affected and it is considered that *R. lugens* is one of the prime agencies contributing to the slow growth of this tree species, especially in the high site-quality areas where this growth rate would be expected to be the greatest, but where it is much reduced because of this defoliator. The importance of the insect in this respect may be judged from the fact that there have been up to ten outbreaks within a period of twenty years in some localities.

Acknowledgements.

The writer is grateful to Mr. L. R. Clark, Dr. P. B. Carne and Messrs. E. Lewis and A. R. Helman of the Division of Entomology, C.S.I.R.O., for their helpful assistance during these investigations. The assistance given by officers of the Wagga Wagga Forestry district from time to time is gratefully acknowledged. The criticism of the manuscript by my colleagues Messrs. P. Hadlington and K. M. Moore is much appreciated. The photographs 1–9 were taken by Mr. P. Hadlington.

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EXPLANATION OF PLATE X.

Figs 1 and 2. Male and female *R. lugens* from Murray River region.
Figs 3 and 4. Male and female *R. lugens* from Pennant Hills, N.S.W.
Figs 5 and 6. Male and female *R. lugens* from Bago S.F. near Batlow, N.S.W.
Fig. 7. Egg masses of *R. lugens* on *E. camaldulensis* leaf.
Fig. 8. Cocoon of *R. lugens*—note head capsule affixed to silk.
Fig. 9. "Head-dress" of serial head capsules of larva of *R. lugens*.
Fig. 10. *E. camaldulensis* (river red gum) of high site quality defoliated by *R. lugens* (Campbell's Is. S.F., near Barham, N.S.W.).

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

Part ix. The Genus Macrurohelea.

By David J. Lee.

(Five Text-figures.)

[Read 24th October, 1962.]

Synopsis.

The genus *Macrurohelea*, previously known only from South America, has recently been found in Australia. A new species, *M. commoni*, is described.

Genus Macrurohelea Ingram & Macfie.

Ingram, A., & Macfie, J. W. S., 1931. "Ceratopogonidae" in "Diptera of Patagonia and South Chile", Part II, fascicle I. (British Museum, Natural History): 203.

Generic Characters.

Wing with costa extending at least two-thirds of wing length, with two very distinct radial cells, the second much longer than the first, median fork distinctly petiolate; surface of wing with microtrichia but macrotrichia absent; anal angle pronounced, approximately rectangular. Eyes rather widely separated; antennal segments not elongated other than 11–15 which do not exceed 2–4 times their width. Thorax without tubercles or humeral pits. Legs with no segment swollen or armed; claws equal, not elongated. Abdomen of female with tenth segment long and cylindrical and bent forward (this character is unique to the genus); lamellae well developed. The genus belongs to the tribe Stilobezziini of Wirth (1952) and would fall in the *Stilobezzia* group of Lee (1948).

Macrurohelea commoni, n. sp.

Types: Holotype ♀ and 6 ♀♀ paratypes in SPHTM except for two paratypes, one each in CSIRO and USNM.

Type Locality: All of the type series from Clyde Mountain, New South Wales (2,400 feet), taken in light trap, 21.ix.1960, I. F. B. Common and M. Upton.

Description (Female).

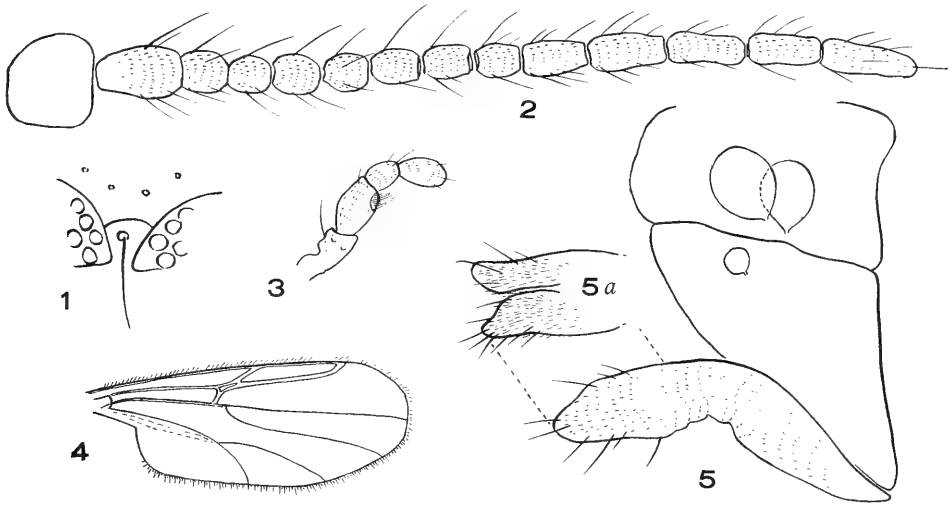
Head: Eyes rather widely separated (Text-fig. 1); antennae (Text-fig. 2) with segment 3 a little more than twice as long as 4, segments 4–10 barrel-shaped, tending to become slightly vasiform in the more distal segments, 11–15 together slightly shorter than 3–10 together. Mouth parts short, less than half height of head; palpi with third segment only slightly enlarged, bearing a shallow sensory pit distally (Text-fig. 3).

Thorax: In the mounted specimens this appears to be uniformly brown with pale halteres. Legs brown, without markings, unmodified except for bilobed fourth tarsal segments, and fifth twice as long as fourth; although the fifth segments are narrowed basally they are not obviously swollen distally; claws simple. Wings as illustrated (Text-fig. 4).

Abdomen: Uniformly brown with tenth segment elongated and bent forward (Text-fig. 5); lamellae pronounced, about equal in length to tenth segment and usually bent at an angle to the tenth segment, away from the body. Two subequal and subspherical spermathecae with only rudimentary ducts; a third small spermatheca is present in the holotype (Text-fig. 5) but absent in the paratypes.

Measurements: (from holotype): Wing length 1·4 mm. Antennae, segments 3–10, 252μ, 11–15, 228μ. Segments of palp: 2, 30μ; 3, 36μ; 4, 21μ; 5, 30μ. Hind leg: femur, 456μ; tibia, 468μ; tarsal segments 1–5 respectively, 180μ, 84μ, 48μ, 30μ, 60μ, claw 36μ. Spermathecae: 36 × 36μ, 36 × 30μ, 12 × 12μ.

Differentiation from other species: Of the two known species of *Macrurohelea* from the south of South America *M. thoracica* I. & M. is distinctly larger and lighter in colour than *M. commoni*. The new species is closest to *M. caudata* I. & M, but differs in the absence of the intercalary fork and of well-developed ducts on the spermathecae. In



Text-figures 1-5. 1, Interorbital space. 2, Antenna. 3, Palp. 4, Wing. 5, Apex of abdomen including spermathecae. 5*a*, Lamellae in ventral view. All × 425 except wing, × 30.

addition its lamellae are longer, almost equal in length to the tenth segment instead of about one-third that segment and the fourth tarsal segments are bilobed instead of obliquely truncated.

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ON A COLLECTION OF PLANTS OF PERMIAN AGE FROM BARALABA, QUEENSLAND.

By J. F. Rigby, B.H.P. Central Research Laboratories, Shortland, N.S.W.

(Plates xi-xii.)

[Read 24th October, 1962.]

Synopsis.

A collection of fossil plants of Permian age from Baralaba, Queensland, is described. It is similar to other Permian floras from the same district and to the flora of the Raniganj Stage of India.

It includes *Raniganjia indica*, n. comb., and *Plumsteadia microsacca*, n. gen. et. n. sp.

Introduction.

This paper concludes the description of a flora from the roof of the Dawson Seam, Baralaba, Queensland. The previous part discussed "The Taxonomic Position of *Actinopteris indica* Srivastava" (Rigby, 1962).

All species found have been included in the systematic descriptions given below, but the existence only of the specimens is noted where there are only a few imperfect specimens, or where specimens conform exactly to other illustrated specimens.

The numbers of the specimens are those of the Museum of the Geology Department, University of Queensland. Fragmentary specimens have not been numbered.

Description of the Flora.

Cyclodendron leslii (Seward) Kräusel. (Pl. xi, fig. 4.)

This species has previously only been reported from South Africa, Uganda, Tanganyika, Congo and Brazil.

Specimens: F42606, F42645.

Phyllotheca australis Brongniart. (Pl. xi, fig. 1.)

A single leaf whorl (no. F21832) of calamitalean foliage was included in the collection. It was catalogued as a *Neocalamites*. In appearance *Neocalamites* was similar to *Annularia*, but the leaves were completely free, whereas in *Annularia* they were united basally. In this specimen they are united basally. The union of the leaves is atypical of *Annularia*, but typical of *Phyllotheca*.

In both *Annularia* and *Phyllotheca* the leaf whorl is confined to a single plane. As Elias (1931) has pointed out, leaves of the *Annularia* type are found in association with both Equisetalean cones and seed-bearing fructifications, but *Phyllotheca* is restricted entirely to typical Equisetalean plants. Elias listed three types of *Annularia* leaf based on external morphological characters. These characters were: (1) The degree of definition of the midrib; (2) The presence or absence of lateral grooves parallel to the margin; (3) The nature of minute striations occurring on the leaf blade. He considered these striations to have reflected the presence of leaf hairs.

The species typical of each leaf type are: (1) *Annularia stellata* (Schlotheim) Potonié; (2) *Annularia westphalica* Stur; (3) *Annularia zalesskii* Elias.

Annularia zalesskii appears to be a nomen nudum, with *Annularia lanceolata* Radchenko 1934 representing the first valid description of this species.

In midrib and lateral groove character, specimen F21832 resembles *Annularia lanceolata*, but the minute striations are not apparent. This could be due to the state of preservation of this specimen, although the writer considers that these striae are absent.

Phyllotheca species usually do not have striated leaves, although they are prominent in *Phyllotheca etheridgei* Arber.

Annularia is not common in Australia, having only been reported by Walkom (1916, 1941). This in no way precludes its occurrence at Baralaba.

This specimen had 12 leaflets in the whorl, otherwise is closely similar to many illustrated in the literature (e.g., Feistmantel, 1890, Pl. XIV, fig. 2) and described as *Phyllotheca australis*. The nature of the united part of the leaf bases was not apparent until the specimen was examined under the binocular microscope. It may be seen quite clearly on Plate xi, fig. 1.

Some isolated fragments of leaf similar to the leaves of this whorl were found, but because they were so fragmentary, they have not been considered as undoubted specimens of any particular plant.

There are also a number of equisetalean stem fragments present, such as No. F42621.

Raniganjia, n. gen.

Equisetalean foliage having leaves united for most of their length to form an almost flat, but open conical, slightly elliptical verticil, verticils not ensheathing, large number of leaves per verticil. Each leaflet with a single median vein and bluntly acute, rounded apex.

The genus has been erected to contain certain species previously included in the genus *Actinopteris* Schenk, a genus originally erected for the reception of certain Mesozoic fern-like foliage.

Type species: *Actinopteris bengalensis* Feistmantel.

Doubts have been expressed by a number of investigators (Zeiller, 1902; Arber, 1905; Dolianiti, 1953) that *A. bengalensis* was a fern. They thought that it was probably a new genus of the Equisetales. Srivastava (1954) reviewed all previous evidence and concluded from the absence of a resistant cuticle that it may have been a fern after all. Rigby (1962) considered that *Actinopteris indica* Srivastava represented the foliage of a calamite, basing his conclusion on a large number of specimens in this collection.

Rigby (1962) suggested that the stem of *A. indica* was either a pith cast or a protostele that had shrunk in thickness on fossilization. It is now realized that a third interpretation is possible; that is, that the stem on the fossil represented the almost full thickness of the living plant. If this were so, then the stem was most unlikely to have been rigid. The plant then would have been a creeper hanging from other plants similar in habit to that usually accepted for *Sphenophyllum*. A strong objection to this view of its habit is the longitudinal ribbing on the "stems". If it were a creeper, one would expect the ribbing to spiral around the "stem". If the verticils were on a pendulous stem, one would expect, but not categorically, that the verticils would be in inverted order to that as illustrated by Rigby (1962, Text-fig. 1).

Part of the reasoning for the inclusion of *A. indica* in the Equisetales was based on the absence of a cuticle resistant to acid maceration. Without comparing the action of acid maceration on other plant groups from the same area, this fact has little value as it is possible that no cuticles had been preserved, because of, say, metamorphic activity.

The nature of the Canada balsam transfers themselves of the proposed genus *Raniganjia* differed from those of *Spenopteris*, *Glossopteris* and *Dictyopteridium* even before maceration was carried out. *Raniganjia* gave rise to a thin, membranous film, whereas the other three gave rise to firm masses of tissue. Unfortunately these masses of tissue broke up into very fine needles of material during maceration. The needles of *Glossopteris* and *Dictyopteridium* tissue could withstand maceration, but the tissue of *Raniganjia* could not. The needles of macerated tissue were too thin to show anything of the cuticular structure of their respective plants.

Irrespective of whether the plant be a member of the Calamitaceae, or the Equisetaceae or the Sphenophyllaceae, it was certainly equisetalean. Because of this a new genus for its reception must be erected, but its correct taxonomic position will not be determined until after the finding of fructifications.

The genus has been named *Raniganjia* as both of its known species occur together only in the Raniganj Group of India, and both species were first discovered there. Undoubted specimens have been reported only from the Permian of India and Australia. A doubtful specimen has been reported from Brazil.

RANIGANJIA BENGALENSIS (Feistmantel), n. comb. (Pl. xii, figs 8, 9.)

1876. *Actinopteris bengalensis* Feistmantel, *Rec. geol. Surv. India*, 9 (3): 76.
1876. *Actinopteris bengalensis* Feistmantel, *J. Asiat. Soc. Bengal*, 45 (2): 377.
1880. *Actinopteris bengalensis* Feistmantel, *Flora Gondw. Syst.*, 3 (2–3): 115, Pl. XIXA, figs 1, 1a
1902. *Actinopteris bengalensis*, Zeiller, *Palaeont. indica*, n.s., 2 (1): 28–29.
1905. (*Actinopteris*) *bengalensis*, Arber, *Glossopteris Flora*, Brit. Mus. (N.H.) Catalogue, p. 14–16, text-fig. 5.
1954. *Actinopteris bengalensis*, Srivastava, *Palaeobotanist*, 3: 75–76, Pl. 1, fig. 9. Reference very doubtfully belonging to this species.
1953. *Actinopteris bengalensis*, Dolianiti, *Not. Prelim. Estud.*, 62: 1–3, Pl. 1.

Holotype: No. 5185, Geological Survey of India, Calcutta.

RANIGANJIA INDICA (Srivastava) Rigby, n. comb. (Pl. xii, fig. 10.)

1954. *Actinopteris indica* Srivastava, *Palaeobotanist*, 3: 72, fig. 4; 74–76, Pl. 3, fig. 26.
1962. *Actinopteris indica*, Rigby, PROC. LINN. SOC. N.S.W., 86 (3): 299–304, Pl. XA, text-figs 1–3b.

Holotype: No. 8663, Birbal Sahni Institute of Palaeobotany, Lucknow, India.

SPHENOPTERIS POLYMORPHA Feistmantel.

The collection contained approximately 24 fragments of fronds, of which four were fertile. Venation extends into all pinnae including the apical pinnule. Three fertile specimens were exposed along the dorsal surface and the fourth along the ventral surface. From the fourth specimen, F42619, it was possible to determine the arrangement of the sporangia. These are spherical bodies up to 0·3 mm. diameter, one per secondary vein in each pinna. The sporangia were generally within one sporangium-diameter of the midrib of the pinna. Upon development of the sporangia, the secondary venation on the underside of the pinnule appeared to become very indistinct, although it remained quite clear on the upper surface.

Specimens: F31983, F36714, F36717, F36718, F42602, F42608, F42619, F42620, F42625, F42626, F42643.

VERTEBRARIA INDICA (Royle).

Typical specimens were found in the collection, e.g., F42604.

GLOSSOPTERID FRUCTIFICATIONS AND LEAVES.

These are described in the following order: Leaf with attached fructification; Detached fructification; Leaves.

There has been some discussion as to the nature of these plants. This has been either on the question of the rank of the taxon in which they should be placed, or on their position in the plant kingdom.

The first question has been discussed by Archangelsky (1958*a*), who suggested that the name of the class into which they should be placed might be called Glossopteropsida. Lam (in Plumstead, 1956*a*) suggested that they might be included in the class Glossopteridales in the order Pteropsida.

The second question cannot be settled until more is known of the true nature of the fructifications. Various suggestions have been made. Plumstead (1956) suggested that they bore a closer relationship to the angiosperms than to the gymnosperms.

Melville (1960) considered that *Glossopteris* must have been very close to the pro-angiosperm stock. Plumstead (1952) originally considered them to be pteridosperms, a suggestion supported by Thomas (1958) in his finding of *Lidgettonia*. Sen (1959) has summarized the case for a gymnospermous affinity.

PLUMSTEADIA, n. gen.

Diagnosis: Fructification attached to the midrib of a glossopterid leaf by a short petiole; consists of two parts, adnate organ non sac-bearing, free organ sac-bearing with sacs facing the adnate organ, adnate organ developed from expansion and rupture of the midrib.

Type Species: *Plumsteadia microsacca*, n. sp.

The genus has been named for Dr. Edna Plumstead, University of the Witwatersrand, Transvaal, who first recognized and described the fructifications of glossopterid leaves.

Discussion and Comparison: *Plumsteadia* is erected to receive a certain fructification that on first sight appeared to be *Lanceolatus* in that one-half of the cupule was adnate to the supporting leaf and the other half of the cupule is free. The distinguishing feature is that the free half of the cupule is sac-bearing and the adnate half is not. This is the reverse to the position in *Lanceolatus*. The adnate organ appeared to have faint ribbing, and also to show the midrib of the leaf.

In this discussion "glossopterid" means "similar to *Glossopteris*, *Gangamopteris* or *Palaeovittaria*". The word "cupule" has been used in the same sense as used by Plumstead (1952).

PLUMSTEADIA MICROSACCA, n. sp. (Plate xi, fig. 5.)

1962. *Lanceolatus* sp., Rigby, *Nature*, 195: 196–198, fig. 1.

Possibly belonging to this species:

1955. *Glossopteris* sp. in association with a fructification, Sen, *Bot. Notiser*, 108 (2): 245–6, figs 2, 3.

Diagnosis: Fructification of the *Plumsteadia* type borne on a leaf described below as *Glossopteris* cf. *communis*.

The fructification is in two parts, a sac-bearing organ and an adnate organ. The sac-bearing organ is attached to the midrib by a short, stout petiole. It is represented only by an impression on shale enclosed between the two organs with occasional fragments of carbon still adhering to the shale. The sac-bearing organ has the structure of a *Dictyopteridium*, differing only slightly from a *Dictyopteridium sporiferum* described below. The impressions of sacs throughout most of the half cupule retained are similar in size and shape, being hemispherical, and are tightly packed. The marginal sacs are arranged in a single marginal row; the body sacs appear to be arranged in rows that correspond in curvature and angle to the midrib of the secondary venation of the supporting leaf. The sacs visible on the exposed surface are only a reflection of the sacs originally present. Some of the sacs were exploded.

The adnate organ appeared to have developed by splitting along the midrib of the upper epidermis, and then expansion of the split zone to expose the mesophyll. The midrib appears as strong in the adnate organ as in the leaf above the adnate organ. Leaf venation starts just inside the adnate organ, passes over the top of the marginal rim and continues unbroken to the margin of the leaf. There is a suggestion of the structure illustrated by Plumstead (1958) particularly as the immature male half of a cupule of *G. stricta* (Plate XIX, fig. 1a).

Holotype: No. F31956, Geology Department Museum, University of Queensland.

Age and Locality: Permian. Roof of the Dawson Seam, Baralaba, Queensland.

Discussion and Comparison: This species fits in with the same basic pattern for known glossopterid fructifications in that it consists of a sac-bearing organ attached to the midrib of a leaf. It differs in that the sac-bearing organ is facing a second organ adnate to the leaf, in the reverse way to that usual for these fructifications. In

Lanceolatus the adnate organ is sac-bearing. This is the only other genus that is closely similar to *Plumsteadia*. The question arises as to whether Plumstead (1952, 1958) had similar fructifications to *Plumsteadia*, but had not recognized the true nature of them because of inferior material. This postulate is dismissed in the case of *Lanceolatus lerouxides* as her illustrations (1952, Pl. LI–LII) show where the sac-bearing organ has developed as the adnate organ, not on the cupule.

Dimensions of the holotype are: Length 27 mm., width 9 mm., height of marginal rim 0·4 mm., width of midrib 1·9 mm.

Sac-bearing organ: Length unknown, width 9·7 mm., length of petiole 0·7 mm., width of petiole 2·1 mm., width of midrib below petiole 2·1 mm., thickness of carbonaceous matter 0·05 mm. approx.

Dimensions of sacs: Towards margin in centre of organ, length 0·6–0·9 mm., average 0·8 mm., breadth 0·5 mm. Towards base near petiole, length 1·4 mm. maximum, breadth 0·7 mm. maximum. Height of sacs not greater than 0·03 m. Sacs along the margin of the organ 14/cm.

Leaf: Width at top of adnate organ 16 mm., thickness of midrib 1·5 mm., density of venation at margin parallel to margin 36/cm., density of venation along top of rim of adnate organ 32/cm., angle secondary venation makes with midrib 45°.

Dictyopteridium sporiferum Feistmantel. (Pl. xi, fig. 3.)

1881. *Dictyopteridium sporiferum* Feistmantel, *Flora Gondw. Syst.*, vol. iii, pts 2–3, pp. 7, 14, 34, 47, Pl. XXIIIA, figs 4–6, 14, 14a.
1886. *Dictyopteridium* sp., Feistmantel, *Ibid.*, vol. iv, pt. 2, p. 34, Pl. VA, fig. 3.
1902. *Dictyopteridium* sp., Zeiller, *Pal. indica*, n.s., vol. 2, p. 24, Pl. IV, fig. 4.
1905. *Dictyopteridium sporiferum*, Arber, *Glossopteris Flora*, Brit. Mus. (N.H.), p. 224, fig. 51.
1922. *Dictyopteridium sporiferum*, Walkom, *Publ. geol. Surv. Qd.*, 270, p. 36, Pl. 9, fig. 48.

Some glossopterid fructifications have been placed in this species. The most entire specimen is illustrated. This specimen is 35 mm. long × 9 mm. at its widest. It is the negative image of a sac-bearing organ. Although it is a negative image, it consists of a more or less uniform layer of carbonaceous material. The other specimens are fragmentary, and are generally the negative images of the sac-bearing organ rather than the sac-bearing organ itself. The impressions of the sacs show that they were of two types: (1) A swollen rounded body with a hemispherical top. These are called "unexploded sacs". (2) The above type of sac, but having a central depression with a single boss in the centre of the depression. Crowding tended to make these depressions angular. These are called "exploded sacs".

The distribution of these sacs was into three broad regions.

(*a*) The sacs arranged around the margin of the fructification. Rigby (1962*a*) has called these the marginal sacs. They appeared larger than the remaining sacs, the body sacs, although they were similar to the body sacs in all other respects.

The body sacs could be divided into two types; the difference was probably a function of the development of the fructification. These were:

(*b*) the majority, small sacs hemispherical if unexploded or centrally depressed if exploded;

(*c*) some towards the petiole, similar to the body sacs above except that they have been compressed on the fructification.

Dimensions of some of these sacs are: Marginal sacs at apex 1·0 mm. × 0·7 mm., range (·75–1·12) × (·57–·90); near base 1·2 mm. × 1·2 mm.; largest 1·4 mm. × 0·9 mm. opposite the figure 1 on the illustration; exploded sac 1·2 mm. × 1·1 mm. near apex; diameter at rim 0·9 mm.; depth of depression made by sac 0·2 mm.; height of rim 0·2 mm.; diameter of central boss 0·08 mm. (this was elongated in a direction at 30° to the axis of the fructification); body sacs (normal) 1·0 mm. × 0·6 mm.; elongated body sacs 1·8 mm. × 0·3 mm.

Only two elongated sacs appear exploded, and these are intermediate between normal elongated and body sacs. Almost all the body sacs, other than the elongated body sacs, are exploded. The distribution of the unexploded sacs is completely random, although there tend to be more towards the apex. About half of the marginal sacs are exploded. The majority lie in the middle half of each side. No significant conclusion can be drawn from the arrangement of these sacs.

A section cut through another specimen along the axis of the fructification and at right angles to the plane containing the fossil showed some details of the elongated body sacs. The sacs were about three times as long as broad and lay so as to cover partly the lower part of the next sac higher up towards the apex. The sacs further from the petiole did not appear to be thus elongated.

The section was cut in the following manner: A balsam transfer was prepared of the specimen under examination. The specimen was removed from the slide by leaving the slide inverted over a watch glass containing xylol for a period of some hours. This dissolved away the Canada balsam, thus freeing the specimen from the slide. The specimen floated down in the xylol and came to rest at the bottom of the watch glass. It was then set in a polyester resin block. The resin block was sectioned for examination.

The petiole of the illustrated specimen extends 8 mm. below the specimen. It is striated longitudinally with five ribs over its width of 1·2 mm.

Specimen F21411 showed a microstructure on each sac of small rounded protuberances; one sac had approximately 40 of these protuberances. These are reminiscent of the hyaline swollen epidermal cells of succulent xerophytes such as are found on leaves of some members of the Aizoaceae. No similarity to these cells is suggested; they have been cited only as an example of the appearance of the sac surface.

Earlier (Rigby, 1962*a*) it was thought that these fructifications could have formed from either compression of a bilateral organ or of a radially symmetrical organ similar to a strobilus, but it is now realized that there must have been at least some bilateral symmetry present because of the larger size of the marginal sacs. A transfer of a sac-bearing organ showed the sacs as swollen bodies on both surfaces.

These specimens differ from the sac-bearing organ of *Plumsteadia microsacca* in being very much larger; each sac is at least twice as large.

The name *Dictyopteridum* is here retained for isolated sac-bearing organs that may have been derived from the unwinged glossopterid fructifications *Lanceolatus*, *Cistella* or *Plumsteadia*. These sac-bearing organs may also have been derived from a *Glossopteris* leaf in the same way as described by White (1962) for *Glossopteris angustifolia*.

Specimens: F21411, F31955, F31957, F31959, F31960, F31988, F42629, F42632, F42639, F42640, F42641, F21623 (considerably distorted, and may represent a winged fructification).

Glossopteris browniana Brongniart.

Some specimens with a venation conforming closely with Zeiller's (1896), Fig. 8, p. 363, have been included in this species.

Specimens: F42611, F42614, F42615, F42635, F42636, ?F31984.

Glossopteris indica Schimper.

A few pieces of leaf similar to Walkom's (1922), Pl. 2, figs 11, 11a, have been included in this species.

Specimens: F21622, F31963, F31964, F31966, F31989, F36715, F36716, F42607, F42609, F42610, F42613, F42616, F42617, F42623, F42628, F42633, F42634, F42637, F42638, F42642, F42644, ?F31971.

Glossopteris (?) damudica Feistmantel.

The writer is convinced that *G. damudica* Feistmatnel and *G. ampla* Dana occur together in Australia, and is endeavouring to find suitable material for cuticular

preparations to confirm this. Archangelsky (1957) has reported finding both in Argentina. Part of leaf F42622 resembles the leaf illustrated by Feistmantel (1881) as Pl. XLA, fig. 6. The fragment of leaf is not large enough to allow a positive comparison, so it has been included here only with hesitation.

GLOSSOPTERIS cf. COMMUNIS Feistmantel. (Pl. xi, fig. 7.)

These specimens appear to have characters of *G. intermittens*, *G. indica* and *G. communis*. They have been compared with *G. communis* as they seem closer to this species than to either of the others.

Specimens: F31962, F31965 (2 specimens), F31981, F42627, F42630, F42631.

These leaves are linear lanceolate with an acute apex, midrib strong and thin, secondary venation straight, making an angle of 40° to the midrib, dichotomous near the midrib, occasional anastomosing. The illustrated specimen, No. F31962, is a typical fragment.

In this leaf there are 10 veins per cm. at the midrib, and 22 per cm. at the margin at the lower end of the leaf. The midrib is 1 mm. wide, and the leaf 18 mm. wide.

The longest leaf fragment in the collection is the same width, and 95 mm. long. It had narrowed perceptibly at each end. A basal fragment, apparently of this species, shows a gradual thinning to a thicker petiole about 2 mm. wide. These leaves never appear to be wider than 20 mm.

Feistmantel (1880) described *G. intermittens* in the following way: "The secondary veins pass out somewhat thickish and with a slight curve from the midrib at an angle of about 45°, then continue more straightly to the margin. Most of the veins are dichotomous close to the midrib and form here and there anastomoses, producing elongated narrow nets." He also remarked on the *Taeniopteris*-like character of the leaf. The specimens agree with this description, but not with the illustrations. These show a leaf with a broadly rounded apex and roughly twice as long as broad.

G. indica is typically a linear-lanceolate leaf with an acute, slightly rounded apex. The secondary venation makes an angle of 30° to 45° to the midrib. Zeiller's illustrations (1896, figs 11 and 12) of the type specimens nominated by Schimper show a leaf having frequent anastomoses in the secondary venation, and tending to a more arched venation than in our specimens although the leaf shape is identical. The Baralaba specimens appear to be the same as described as the fertile leaf of *G. indica* by Plumstead (1952). She limited her specimens to those with a taeniopteroid tendency.

Feistmantel (1876) distinguished *G. communis* from *G. indica* in that "the areoles are all pretty equally oblong and very narrow (while in *G. indica* they are more polygonal and larger next to the rhachis), reaching to the margin".

Zeiller (1902) considered that Feistmantel had confused these species in his application of names. Srivastava (1956) has shown that their cuticles are quite distinct, possibly sufficiently distinctive to be of generic rank (Surange and Srivastava, 1956).

G. communis is normally a large, ovate leaf. The leaves do not have the broad midrib of *G. longicaulis*.

From the above discussion, it appears difficult to say which species these leaves should be placed in. They have been compared with *G. communis*. Probably these leaves should be placed in a new species, but as they are so similar to other species, it would be unwise to erect a new species without more evidence as to its validity.

GLOSSOPTERIS TAENIOPTEROIDES Feistmantel. (Pl. xi, fig. 2.)

1878. *Glossopteris taeniopteroides* Feistmantel. *Palaeontographica*, Supplement vol. 3, p. 92, Pl. ix, figs 1, 1a.

1890. *Glossopteris taeniopteroides* Feistmantel. *Mem. geol. Surv. N.S.W.*, Palaeont., 3: 128, Pl. XVIII, figs 1, 1a.

(This paper represents a revision of the 1878 paper.)

1956. *Glossopteris taeniopteroides*, Srivastava, *Palaeobotanist*, 5, pt. 1: 17–19, Text-figs 20, 21, Pl. 7, figs 48, 49, Pl. 8, figs 50–52.

The illustrated specimen, F42624, is quite small, 22 mm. wide × 28 mm. long, but it is so characteristic that it has been included in this species without hesitation. Of Feistmantel's (1890) illustrations, it more closely resembles *G. parallela* (Pl. xviii, fig. 4 only) than *G. taeniopteroides* (Pl. xviii, figs 1, 1a), but it has not been included in *G. parallela* because it differs markedly from Feistmantel's other illustrations of *G. parallela* (Pl. xviii, figs 2, 3) which show more of the leaf. The fragment is almost identical with the specimen used by Srivastava (1956, Pl. 7, fig. 48) in his study of the cuticles.

The leaf has a broad, longitudinally striated midrib. The longitudinal striations extend a short distance on either side of the midrib. The secondary venation arises from these marginal striations and passes out at an angle between 70° and 85°. Long, narrow meshes formed by the secondary venation become smaller towards the margin.

Specimens: F42603, F42624.

Glossopteris stipanicicii Archangelsky. (Pl. xi, fig. 6.)

1958. *Glossopteris stipanicicii* Archangelsky, *Acta geol. Lilloana*, 2: 64, Figs 47, 48.
1958*a*. *Glossopteris stipanicicii* Archangelsky, *Rev. Asoc. geol. Argent.*, 12 (3): 153, Pl. VIII, fig. 1.

Some specimens of this species have been identified. The best, F31969, has been illustrated. They are fragmentary, but appear quite characteristic of the species. Archangelsky (1958) considered this species to have venation characters intermediate between those of *Glossopteris wilkinsoni* Feistmantel and *Glossopteris taeniopteroides* Feistmantel.

Darrah (1941) reported the presence of *Sagenopteris* cf. *longicaulis* from South America. Thomas (1952) redescribed this species as *Glossopteris verticillata*.

Specimens of *G. verticillata* have been found by myself (Rigby, 1961) in Australia, and these differ markedly from the specimens listed here, although it is realized that fragmentary specimens of either species could be confused with the other. It is possible that Darrah's specimens were also of *G. stipanicicii*. In larger specimens, these two species are quite distinctive.

Specimens: F31969 (3 pieces), F42606.

Glossopteris scale-leaf.

Specimen F31990 is a poorly preserved scale-leaf. No sori were found in association with it. (See Arber, 1905*a*; Thomas, 1958; and White, 1962.) The anastomosing venation was rather faint.

Wood.

A considerable number of impressions of bark are present. They are unidentifiable, but conform to the texture of the bark of *Dadoxylon*.

Comparison with Other Floras.

Walkom (1922) included descriptions of specimens and a tabulation of the flora from the Baralaba district. This flora has been included with that described in this paper in Table 1.

These two floras are more closely analogous than they would at first sight appear. Arber had revised the *Glossopteris* flora (1905) and had combined a number of Feistmantel's species with earlier named species as he considered they were not sufficiently distinct or were based on insufficient evidence to warrant separate names. These were: *Glossopteris damudica* with *G. ampla* Dana; *Glossopteris communis* with *G. indica* Schimper; *Glossopteris taeniopteroides* with *G. indica* Schimper.

Walkom (1922) based his determinations on the species that Arber had concluded were validly erected. Since then these species have again been separated on their cuticular differences (for *G. indica*, see Zeiller, 1896; for other species, see Srivastava, 1956).

A comparison of this flora with the floras of the various Indian stages of the Lower Gondwanas is given in Table 1. The Indian floras are based on published lists of Jacob (1952), Srivastava (1954, 1956) and Surange and Lele (1956). It must be remembered that these other floras also contained other species that do not appear in Table 1 as they have not been found at Baralaba.

TABLE 1.

Comparison between Floras of the Baralaba District, Queensland, and the Various Indian Stages.

(Species not reported from Queensland have been omitted.)

	Baralaba District.		India.				
					Damuda Series.		
	Rigby (this paper).	Walkom (1922).	Talchir Series.	Karharbari.	Barakar Stage.	Raniganj Stage.	Panchet Series.
Cyclodendron leslii	x						
Phyllotheca australis	x	x					
P. robusta		x				?	
Phyllotheca sp.		x					
Raniganjia indica	x					x	
Cladophlebis roylei		x				x	
Sphenopteris polymorpha	x	x			x	x	
S. lobifolia		x				x	
Vertebraria indica	x	x	x	x	x	x	?
Plumsteadia microsacca	x						
Dictyopteridium sporiferum	x	x			x	x	
Glossopteris browniana	x	x			x	x	
G. indica	x	x	x	x	x	x	x
G. damudica	?					x	
G. communis	cf.		x	x	x	x	x
G. taeniopteroides	x					x	
G. tortuosa		x				x	
G. stipanicicii	x						
Nummulospermum bowenense		x					
Noeggerathiopsis hislopi		x	x	x	x	x	
Samaropsis dawsoni		x					
Glossopteris scale-fronds	x	x					
Dadoxylon arberi		x					
Wood fragments	x						

From the table, it appears that the Baralaba flora had more in common with the flora of the Raniganj stage than with other Indian floras. This means that climatic conditions during the deposition of the bed containing the Baralaba flora were similar to those that occurred during Raniganj times in India, and it does not necessarily mean that both floras occurred at the same time.

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The examination was made partly at the University of Queensland and partly at the B.H.P. Central Research Laboratories. The writer's indebtedness to Dr. A. B. Walkom for suggestion that the writer might be allowed to examine this material is also acknowledged.

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EXPLANATION OF PLATES XI-XII.

Plate xi.

Fig. 1. *Phyllotheca australis* Brongniart. Specimen F21832, × 4. This shows the united basal portion of the leaf whorl.

Fig. 2. *Glossopteris taeniopteroides* Feistmantel. Specimen F42624, × 2.

Fig. 3. *Dictyopteridium sporiferum* Feistmantel. Specimen F31957, × 2½. The larger marginal sacs are more clearly shown on the left hand side of the fructification. Body sacs with an apparent double margin are exploded.

Fig. 4. *Cyclodendron leslii* (Seward) Kräusel. Specimen F42645, × 4.

Fig. 5. *Plumsteadia microsacca*, n. gen., n. sp. Specimen F31956. The short petiole of the saccate organ is attached to the leaf where it enters the shadow.

Fig. 6. *Glossopteris stipanicicii* Archangelsky. Specimen F31969, × 2.

Fig. 7. *Glossopteris* cf. *communis* Feistmantel. Specimen F31962, × 2.

Plate xii.

Figs 8, 9. Type specimen of *Actinopteris bengalensis* Feistmantel. Geological Survey of India Type No. 5185. This specimen is here designated as the holotype of the genus *Raniganjia* as *Raniganjia bengalensis* (Feistmantel). Fig. 8, natural size, fig. 9, × 2½.

Fig. 10. *Raniganjia indica* (Srivastava). Part of specimen F31979, × 2½. A suggestion of the small swellings at the leaf bases mentioned previously (Rigby, 1962, p. 301) that are thought to represent swellings in the vascular bundles where leaf branching occurs may be seen.

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

Part X: Additional Australian Species of Culicoides.

By David J. Lee and Eric J. Reye.

(Plate xiii; 55 Text-figures.)

[Read 28th November, 1962.]

Synopsis.

The present paper describes twelve new species of *Culicoides* from eastern Australia and introduces new synonymy for two other species from the same region. Two species previously known only from the New Guinea area are also recorded from north Queensland.

Introduction.

In the course of our continuing studies of Australian biting midges we have found that as more and more collecting is done occasional specimens of relatively rare species are taken, until eventually a series sufficient for reasonable description is acquired. In other cases species we have known to exist from one specimen only may eventually be taken in numbers when a new locality or habitat is explored. Although most of the new species herein described are relatively rare in our collections, this is more than likely to be due to a failure to use the most suitable methods of collection in the most favourable habitats.

Illustrations are given of the interorbital spaces, palpi, segments 9–12 of the antennae, and spermathecae of all species and of the male genitalia when this sex is available. Wings are reproduced photographically for all species. All measurements are given in Table 1.

Apart from the primary division into species with apex of second radial dark or pale, the species are described in the order of increasing complexity of wing pattern.

(*a*) *Descriptions of New Species.*

(i) *Species with second radial cell dark.*

Culicoides smeei Tokunaga.

Tokunaga, M., 1961. *Akitu*, 9: 73. Tokunaga, M., 1962. *Pacific Insects*, 4: 462.

This species was originally described from Keravat, New Britain. In general appearance it is similar to *C. immaculatus* L. & R., but differs particularly in the restriction of the macrotrichia to the distal quarter of the wing, the contiguous eyes, and the more elongated distal antennal segments.

Distribution: Queensland, Mackay, Pioneer R., 10:v:1955, E. J. Reye; Townsville, Belgian Gardens, 17:xi:1955, A. K. O'Gower.

Culicoides purus, n. sp.

Types: Holotype ♀, allotype ♂ and 1 ♂ and 1 ♀ paratype. All in S.P.H.T.M.

Type Locality: Hornsby, New South Wales. All from light trap, D. J. Lee. Holotype 24:x:1956, the rest 31:x:1956.

Distinctive Characters: A species without markings on the wing which could only be confused with *C. immaculatus* in which the sensory pit of the third segment of the palp is less than a quarter the length of the segment instead of almost half. *C. purus* is a slightly larger species with a close affinity to *C. immaculatus*.

Description: From the type series, all mounted specimens. Measurements from holotype ♀ and 1 ♀ paratype and allotype ♂.

TABLE 1.

Measurements of Various Species of Culicoides.

		purus.[1]	*marginalis.*	*leanderensis.*[1]	*mackerrasi.*	*narrabeenensis.*	*interrogatus.*[2]	*sigmoidus.*[4]	*mykytowyczi.*	*henryi.*	*hornsbyensis.*[1]	*fulbrighti.*	*pallidothorax.*[3]
♀♀													
Wing length	Holotype	1·18 mm.	0·89 mm.	0·91 mm.	1·06 mm.	1·14 mm.	1·18 mm.	1·37 mm.	1·39 mm.	1·22 mm.	1·22 mm.	1·71 mm.	0·97 mm.
	Average of selected series	1·20 mm.	0·97 mm.	0·89 mm.	1·08 mm.	1·12 mm.	1·20 mm.	—	1·35 mm.	1·16 mm.	1·14 mm.	1·52 mm.	0·99 mm.
	Range in above	1·18–1·23 mm.	0·89–1·04 mm.	0·87–0·91 mm.	1·06–1·14 mm.	1·04–1·20 mm.	1·10–1·33 mm.	—	1·3 – 1·4 mm.	1·14–1·22 mm.	1·14–1·22 mm.	1·33–1·71 mm.	0·91–1·03 mm.
Antenna	Holotype, 3–10	336μ	192μ	276μ	360μ	240μ	276μ	240μ	336μ	288μ	288μ	336μ	252μ
	,, 11–15	360μ	192μ	240μ	324μ	360μ	324μ	300μ	336μ	324μ	360μ	384μ	276μ
	Average of selected series												
	3–10	324μ	192μ	240μ	348μ	216μ	293μ	—	300μ	264μ	264μ	312μ	258μ
	11–15	360μ	228μ	204μ	312μ	354μ	342μ	—	300μ	324μ	312μ	384μ	276μ
Palp	Holotype, segment 2	60μ	36μ	48μ	84μ	42μ	72μ	60μ	120μ	96μ	60μ	60μ	66μ
	,, ,, 3	84μ	48μ	60μ	90μ	60μ	72μ	72μ	108μ	84μ	96μ	72μ	66μ
	,, ,, 4	30μ	24μ	30μ	36μ	24μ	30μ	24μ	36μ	30μ	24μ	24μ	24μ
	,, ,, 5	24μ	18μ	30μ	36μ	24μ	30μ	18μ	36μ	24μ	18μ	24μ	18μ
Hind leg	Holotype, femur	444μ	276μ	360μ	444μ	348μ	408μ	384μ	504μ	420μ	396μ	444μ	348μ
	,, tibia	468μ	276μ	372μ	444μ	360μ	324μ	432μ	480μ	396μ	396μ	480μ	336μ
	,, tarsus I	204μ	132μ	180μ	228μ	168μ	192μ	192μ	216μ	180μ	180μ	240μ	144μ
	,, ,, II	120μ	60μ	96μ	114μ	72μ	96μ	108μ	108μ	84μ	96μ	120μ	60μ
	,, ,, III	72μ	36μ	60μ	66μ	42μ	60μ	66μ	72μ	60μ	60μ	78μ	42μ
	,, ,, IV	48μ	54μ	48μ	54μ	30μ	36μ	42μ	60μ	36μ	48μ	54μ	36μ
	,, ,, V	60μ	36μ	48μ	60μ	36μ	48μ	54μ	60μ	48μ	48μ	60μ	48μ
	Average of selected series												
	Tarsus I	204μ	144μ	168μ	240μ	156μ	174μ	—	204μ	180μ	180μ	228μ	168μ
	,, II	120μ	60μ	84μ	108μ	67μ	90μ	—	96μ	89μ	86μ	120μ	72μ
Spermathecae	Holotype a	72×60μ	36×36μ	60×36μ	84×48μ	60×36μ	42×42μ	60×42μ	48×48μ	72×60μ	48×48μ	60×48μ	72×60μ
	,, b	60×48μ	36×36μ	48×36μ	48×48μ	42×36μ	42×42μ	54×42μ	48×38μ	72×60μ	48×48μ	60×48μ	72×60μ
	,, c	—	7μ	8μ	—	12μ	—	—	8μ	—	8μ	duct 24μ	18μ
	,, d	—	7μ	8μ	—	—	—	—	—	—	—	duct 12μ	—
♂♂													
Wing length	Allotype	1·08 mm.	—	—	—	0·95 mm.	—	1·27 mm.	—	1·16 mm.	1·1 mm.	1·46 mm.	—
Antennae	Allotype 3–12	324μ	—	—	—	324μ	—	312μ	—	420μ	396μ	420μ	—
	,, 13–15	300μ	—	—	—	252μ	—	252μ	—	288μ	312μ	384μ	—

[1] Instead of average measurements, those of the ♀ paratype are given.

[2] Averages from holotype and 2 paratype ♀♀.

[3] Averages from holotype and 3 paratype ♀♀.

[4] Measurements from holotype and allotype only.

Female.

A uniformly brown species (mesonotal pattern not discernible but certainly not pronounced); legs without distinct markings. Wing membrane with a brownish tinge from C through R to median stem.

Head: Basal flagellar segments longer than wide, 5–10 vasiform, 11 a little less than twice the length of 10. 10–14 equal, vasiform, 15 slightly longer tapering at tip. Antennal ratio 0·9. Palps with segment 3 swollen at middle, pit large, fairly deep, extending from middle almost to apex (almost half as long as segment). Eyes well separated, mouth parts distinctly shorter than height of head.

Thorax: Legs unmodified. Tibial comb 4. Tarsal ratio 1·7. Wings without spots, radial cells subequal, distinct. Macrotrichia strong but not dense.

Abdomen: Two subspherical spermathecae with distinct necks to the ducts.

Distribution: Only known from the type locality. Additional dates 19:xi:1956, 9:1:1957, 23:1:57 and 2:ii:1957 (all light trap, D. J. Lee).

Male.

Similar to ♀, except for sexual differences; genitalia as figured.

Culicoides melanesiae Macfie.

Macfie, J. W. S., 1939. Proc. Linn. Soc. N.S.W., 64: 368 (not *C. melanesiae* of Tokunaga, M., 1962. *Pacific Insects*, 4: 466).

C. melanesiae was described by Macfie from a single female taken at Rabaul, New Britain. Because Macfie stated that the third segment of the palp was without a sensory pit and because the type, mounted under a very small coverglass, has proved very difficult to examine, previous attempts to recognize this species have not been successful.

However, a recent reexamination of the type specimen, under more critical illumination, has revealed its identity with specimens collected on the Queensland coast and with the help of these it is now possible to correct Macfie's misleading statement and characterize the species.

Distinctive Characters: Wing with reduced wing pattern, a pale spot over r-m and another one abutting the end of the second radial cell but not including part of the cell. Macrotrichia are strongly developed and occur over the entire wing surface. The third segment of the palp is elongated, slightly swollen at the middle and with many small, single sensory pores on the under surface for the distal three-quarters.

Distribution: Queensland: Green Island, north Queensland, 1:vi:1955, 1615–1630 hrs., attacking man, M. B. Wilson.

Culicoides marginalis, n. sp.

Types: Holotype ♀ and 7 paratype ♀♀. In S.P.H.T.M., except 1 paratype in each of C.S.I.R.O., U.S.N.M. and B.M.

Type Locality: Hornsby, New South Wales. Holotype and 2 paratypes taken in light trap, D. J. Lee, 2:ii:1957. The rest, same data except 1 paratype on 7:ii:1957, 2 on 8:ii:1957 and 1 on 24:i:1957.

Distinctive Characters: A species with small pale wing spots most of which are marginally arranged leaving a large spot-free area. It is closest to *C. parviscriptus* Tokunaga, from which it differs in having the pale spot at the end of the radius terminating on the lower branch of the intercalary fork instead of on M_1, and in the absence of a pale spot in the middle of the median cell. Wing pattern also not unlike *C. leanderensis*, n. sp., but in this species the pale spot abutting cell R_2 is expanded below this cell and the r-m pale spot does not extend to costa. The interorbital space, palp and spermathecae are also distinct.

Description: From the type series; all mounted specimens. Measurements from holotype ♀ and 8 paratype ♀♀.

Female.

Thoracic markings not available from mounted material. Legs with pale subapical rings on anterior four legs and basal pale rings on all tibiae. Knees very dark.

Head: Eyes separated above, contiguous below. Mouthparts about three-quarters height of head. Basal segments of antennal flagellum about as long as wide, becoming more elongated and narrowing distally. Segment 11 about 1·5 times length of 10. Antennal ratio 0·84. Segments 11–15 subequal, with 11–14 slightly vasiform. Third segment of palp progressively enlarged from base to a maximum in distal half with single, well-developed shallow sensory pit on the distal third.

Thorax: Legs unmodified. Tibial comb 4. Tarsal ratio 2·4. Wings with two distinct radial cells. Spotting of fairly strong contrast but reduced especially in the middle of the wing, there being only a small pale spot at the distal extremity of the median cell. Spot over r-m small, fading to anterior wing margin. Almost entire intercalary area without pale spots except at base and close to wing margin. Macrotrichia not very dense.

Abdomen: Two subequal subspherical spermathecae with short stems, two additional small rudimentary spermathecae.

Distribution: Additional records from the type locality are 25:x:1956, 26:x:1956 and 23:i:1957 (all light trap, D. J. Lee). Also taken from Merricumbene, New South Wales, 5:i:1955 and 5:ii:1955 (A. L. Dyce). The Merricumbene specimens were bred from treeholes situated four to twelve feet above ground level in the trunks of the river oak, *Casuarina cunninghamiana*. Other diptera found breeding in these treeholes have been discussed by English, Mackerras and Dyce (1958).

Culicoides leanderensis, n. sp.

Types: Holotype ♀, 1 paratype ♀ in SPHTM.

Type Locality: Both from Longreach, Queensland, 22:iv:1955, from net over sheep, E. J. Reye.

Distinctive Characters: Closest to *C. mackerrasi*, n. sp., on wing pattern, but lacking the prominent pale spot above Cu_1. An obvious pale area along M_2 and the expansion of the radial spot below cell R_2 distinguish it from *C. marginalis*, n. sp.

Description: From the holotype ♀ and measurements from this and the single paratype ♀.

Female.

Head: Eyes well separated. Mouthparts more than half height of head. Antennal flagellar segments mainly vasiform, segment 11 little different from 10. Antennal ratio 1·17. Palp with third segment swollen, maximum width below half-way. Sensory pit fairly deep, in third quarter.

Thorax: Legs unmarked, knees not dark. Tarsi unmodified. Tarsal ratio 2·0. Tibial comb 4. Wings with macrotrichia moderately developed, majority of pale areas marginal.

Abdomen: Two subequal ovate spermathecae, a minute rudimentary one and an accessory duct.

Distribution: Only known from the type locality.

Culicoides mackerrasi, n. sp.

Types: Holotype ♀ and 25 paratype ♀♀. All in SPHTM, except for paratypes in each of CSIRO, QIMR, USNM and BM.

Type Locality: Yellow Water Lagoon, Roper River, Northern Territory. All taken biting man, A. K. O'Gower, type and 20 paratypes on 29:iv:1957, 2 paratypes with same data except 28:iv:1957 and two others 14:iv:1957.

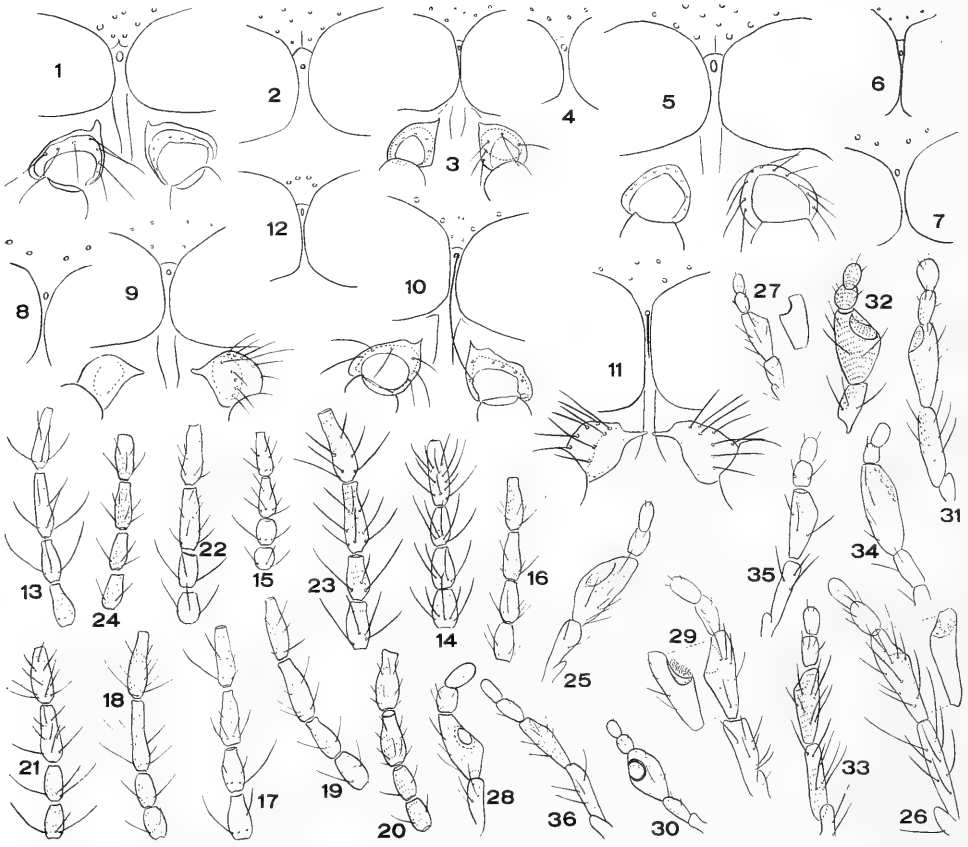
Distinctive Characters: Wing multispotted with radial spot surrounding but not including end of second radial cell; intercalary spot triangular with its broad base along lower branch of intercalary fork and a pale spot on the median fork between

the r-m spot and one close to the wing tip. Other Australian species with somewhat similar pattern either have the distal part of the second radial cell pale or some form of pale area over the central part of the median cell.

Description: Details of coloration not available from mounted material. Measurements from holotype ♀ and 9 paratype ♀♀.

Female.

Head: Eyes separated; mouthparts about three-quarters height of head. Basal flagellar segments vasiform, segments 11–12 elongate vasiform, 13–15 elongate, almost cylindrical. Antennal ratio 1·15. Third segment of palp swollen at middle with large shallow pit at from half to beyond three-quarters length of segment.



Text-figures 1-36. 1-12, interorbital spaces (females). 13-24, segments 9-12 of antenna (females). 25-36, female palp. *C. purus*, n. sp., 1, 13 & 25. *C. mykytowyczi*, n. sp., 2, 14 & 26. *C. marginalis*, n. sp., 3, 15 & 27. *C. leanderensis*, n. sp., 4, 16 & 28. *C. mackerrasi*, n. sp., 5, 17 & 29. *C. narrabeenensis*, n. sp., 6, 18 & 30. *C. interrogatus*, n. sp., 7, 19 & 31. *C. sigmoidus*, n. sp., 8, 20 & 32. *C. henryi*, n. sp., 9, 21 & 33. *C. hornsbyensis*, n. sp., 10, 22 & 34. *C. fulbrighti* n. sp., 11, 23 & 35. *C. pallidothorax*, n. sp., 12, 24 & 36. All × 166 approx.

Thorax: Legs without markings; tarsi unmodified. Tibial comb 4. Tarsal ratio 2·2. Wings with radial cells equal but short; macrotrichia pronounced and moderately dense. Base of first radial cell included in enlarged spot over r-m extending from C to below M_2. Second radial cell dark but apex surrounded by a bilobed spot which extends to M_1. Intercalary spot large, broadly triangular; the only spot in the median cell is near its distal extremity.

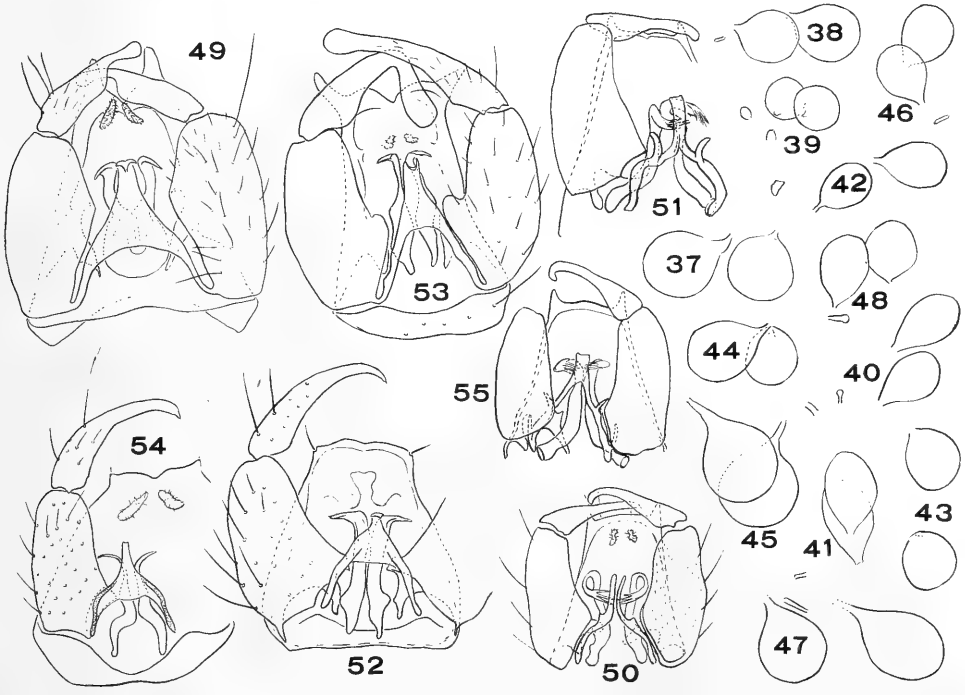
Abdomen: Two subequal ovoid spermathecae with short ducts.

Distribution: Northern Territory: the type locality and adjacent Roper R. Mission, iv:1957 and xi:1957, A. K. O'Gower. Humpty Doo, 9:xii:1956, A. K. O'Gower. All taken attracted to man or biting. Queensland: Eidsvold, 18:iv:1924, T. L. Bancroft.

Culicoides narrabeenensis, n. sp.

Types: Holotype ♀, allotype ♂, 10 paratype ♀♀ and 3 paratype ♂♂. All in SPHTM, except for paratypes in each of CSIRO, USNM and BM.

Type Locality: Deep Creek, Narrabeen, New South Wales, W. W. Wirth, 3:iii:1957, bred from pupa (holotype). Newport, 12:12:1956, light trap, W. W. Wirth (allotype). All paratypes Narrabeen, light trap, W. W. Wirth, 26:x:1956; 9:xi:1956; 8:xii:1956; 13:xii:1956 except one from Warriewood, 23:x:1956, bred from ditch margin, W. W. Wirth. All localities within a radius of 1 mile.



Text-figures 37-55. 37-48, spermathecae. 49-55, male genitalia. *C. purus*, n. sp., 37 & 49. *C. mykytowyczi*, n. sp., 38. *C. marginalis*, n. sp., 39. *C. leanderensis*, n. sp., 40. *C. mackerrasi*, n. sp., 41. *C. narrabeenensis*, n sp., 42 & 50. *C. interrogatus*, n. sp., 43. *C. sigmoidus*, n. sp., 44 & 51. *C. henryi*, n. sp., 45 & 52. *C. hornsbyensis*, n. sp., 46 & 53. *C. fulbrighti*, n. sp., 47 & 54. *C. pallidothorax*, n. sp., 48. *C. bunrooensis* Lee & Reye, 55. All × 122 approx.

Distinctive Characters: Wing pattern not unlike *C. williwilli* L. & R. and *C. bunrooensis* L. & R., but distinct from both of these because the intercalary pale area does not extend above the upper branch of the fork. Similar to *C. williwilli* in details of interorbital area and palp but median processes of aedeagus short instead of extremely long.

Description: From the type series and unmounted material from Narrabeen. Measurements from holotype ♀, allotype ♂ and 9 paratype ♀♀.

Female.

Uniformly dark brown except for very distinct pattern of white spots on mesonotum, pale preapical rings on anterior four legs, present but less marked on posterior legs, and pale basal rings on all tibiae; knees very dark; halteres dark basally, white above. On the mesonotum there are irregular submedian white spots about the middle, horse-shoe-shaped white spots on either side of the prescutellar area, four small rounded spots towards the lateral margins, the first close to the humeral angle and two more

down each side of the mesonotum and an additional one between the second of these and the humeral pit. There is a less marked pale area at the posterolateral margin of the mesonotum which extends to cover the lateral quarters of the scutellum.

Head: Eyes separated above, contiguous below. Mouthparts about half height of head. Basal flagellar segments barrel-shaped, 9 and 10 very slightly longer, 11–15 distinctly elongated, 11 twice as long as 10. Antennal ratio 0·61. Palpi with third segment swollen at middle with large sensory pit from half-way almost to apex.

Thorax: Pattern as described above. Legs unmodified. Tibial comb 4. Tarsal ratio 2·3. Wings of complex pattern, radial cells distinct, about equal; macrotrichia largely restricted to distal half of wing. Basic pattern of the wing similar to that of *C. williwilli* but spots not quite so marked. The intercalary spot lies wholly within the intercalary fork and may be divided (as illustrated) or occasionally the two divisions are linked along the lower branch of the intercalary fork.

Abdomen: Two subequal, subspherical spermathecae with distinct ducts and an additional small rudimentary duct.

TABLE 2.
Characters Differentiating C. bunrooensis, C. interrogatus *and* C. sigmoidus.

	C. bunrooensis.	*C. interrogatus.*	*C. sigmoidus.*
Wing:			
Pale area between cell R_2 and intercalary stem.	Present.	Absent.	Present.
Pale area between intercalary fork and M_1.	Present.	Present.	Absent.
Pale stripe on Cu_1	Absent.	Present.	Absent.
Leg:			
Pre-apical pale band on hind femur ..	Distinct.	Not distinct.	Fairly distinct.
Pre-apical pale band on hind tibia ..	Absent.	Present.	Absent.
Head:			
Antennal ratio	1·07	0·85	0·8
Antennal segment 11/10	1·0	1·9	1·6
Palp 3, length/width	2·3	2·5	1·7

Male.

Resembles the ♀ in all but sex differences. Genitalia with complex harpes, ninth tergite with apico-lateral processes and aedeagus with a short median spur-like process on each side.

Distribution: Taken from the type locality in all months from October to March. Also South Creek, Deewhy, 28:ii:1957, W. W. Wirth; Careel Bay, 3:xi:1956, 20:ii:1958, 15:iii:1958, 27:iii:1958, all light trap, D. J. Lee. Hornsby, 5:i:1957, 23:i:1957, 31:1:1957, 2:ii:1957 and 7:ii:1957, all light trap, D. J. Lee.

CULICOIDES INTERROGATUS, n. sp.

Types: Holotype ♀ and 3 paratype ♀♀. All in SPHTM.

Type Locality: Colo Vale, New South Wales. Holotype 3:iii:1956; A. K. O'Gower, 1 paratype on 25:i:1956, D. J. Lee, 1 on 24:ii:1958, 1 on 25:ii:1958, both A. L. Dyce.

Distinctive Characters: A species with many small pale wing spots of which the dumbbell-shaped spot over the intercalary area is the most striking. Distinct from *C. bunrooensis* L. & R. and *C. sigmoidus*, n. sp., as shown in Table 2.

Description: All specimens mounted, so no thoracic colour pattern available. Legs with preapical rings on anterior four femora, not distinct on posterior femora, basal rings on all tibiae.

Female.

Head: Eyes separated; mouthparts at least as long as height of head. Basal flagellar segments slightly vasiform, 11 about 1·75 × 10, 11–15 subequal, narrowing slightly distally. Antennal ratio 0·85. Palp with third segment elongated, broadest beyond midpoint with sensory pit from broadest point almost to tip, fairly small.

Thorax: Legs unmodified. Tibial comb 4. Tarsal ratio 1·93. Wings with macrotrichia well developed over most of wing surface. Radial cells about equal, distinct. Membrane brownish in area from C to median fork over R. Wing pattern of good contrast. Spot over r-m narrow and extending to C. Spot adjoining cell R_2 not returning below the cell. Intercalary spot narrow, somewhat dumbbell-shaped. A small spot below the post-radial one between the lower branch of the intercalary fork and M_1. Another small spot near base of median cell and a larger one about two-thirds length of cell. The narrow pale area along Cu_1 is unusual. Additional spots as illustrated, but those mentioned above are all of some diagnostic value.

Abdomen: Two subequal spherical spermathecae with broad but very short ducts.

Distribution: Apart from the type locality only known from Merricumbene, New South Wales, 14:xii:1954, A. L. Dyce; 14:i:1955, M. N. Dennis. All specimens have been taken attracted to man.

Culicoides sigmoidus, n. sp.

Types: Holotype ♀, allotype ♂ in CSIRO.

Type Locality: Holotype, Black Mountain, Australian Capital Territory, light trap, 7:xi:1960, I. F. B. Common. Allotype from Minnamurra Falls, New South Wales, 16:xi:1960, I. F. B. Common and M. Upton.

Distinctive Characters: The differential characters of the three most similar species are presented in Table 2.

Description: From the types. Measurements from holotype ♀ and allotype ♂. All specimens mounted.

Female.

Head: Eyes narrowly separated; mouthparts about three-quarters height of head. Antennal flagellar segments 4–10 slightly longer than wide and narrowing slightly distally; segments 11–14 distinctly vasiform with swollen bases and narrowed subapically. Antennal ratio 0·8. Third segment of palp considerably swollen at two-thirds from base, prominent sensory pit in apical third.

Thorax: Mesonotum with pale spots at least anteriorly, but detail not available from mounted material. Legs with preapical pale rings on femora and basal pale rings on tibiae. Tarsi unmodified. Tarsal ratio 1·77. Tibial comb 4. Wing very similar to *C. interrogatus*, n. sp., but there is a pale spot below cell R_2, the one below the base of the intercalary fork is absent, the intercalary spot is double-curved and Cu_1 is not distinctly pale.

Abdomen: Spermathecae two, subspherical and subequal with short ducts.

Male.

Similar to ♀ in all but sex differences. Genitalia as figured.

Distribution: Apart from the type series further specimens come from Colo Vale, 18:xi:1954, light trap, and Merricumbene, 14:xii:1954, light trap, both A. L. Dyce.

Culicoides bunrooensis Lee & Reye.

Due to an oversight the male allotype of this species was not figured in the original description (Lee and Reye, 1955). A figure of the genitalia is herein presented.

(ii) *Species with distal part of second radial cell pale.*

Culicoides mykytowyczi, n. sp.

Types: Holotype ♀ and 25 paratype ♀♀. In SPHTM, except for paratypes in each of CSIRO, QIMR, USNM and BM.

Type Locality: All of type series from Colo Vale, New South Wales. Holotype, 3:iii:1956, A. K. O'Gower. Paratypes, 4:iii:1956, 5:iii:1956, 6:iii:1956, 28:ii:1956 and 29:ii:1956 (A. K. O'Gower, A. L. Dyce, E. O'Sullivan). All attracted to man.

Distinctive Characters: Not to be confused with any other Australian species with distal part of cell R_2 pale because of the reduction of spotting to two spots, one over end of cell R_2 and one over r-m.

Description: From the type series, all mounted. Measurements from holotype ♀ and 9 ♀♀ paratypes.

Female.

Head: Eyes separate. Mouthparts at least equal to height of head. Basal flagellar segments uniform, about 1·5 times longer than wide, slightly vasiform; segment 11 about 1·75 × 10, segments 11–14 about equal, slightly vasiform, 15 pointed. Palp with segments 2 and 3 rather long and about equal, the third expanding slightly to its greatest width at three-quarters from base where a subterminal shallow sensory pit is situated.

Thorax: Legs uniform brown with pale knees and pale bases to mid and hind tibiae. Tibial comb 4. Tarsi unmodified, tarsal ratio 2·1. Wings as described under distinctive characters.

Abdomen: Two spherical spermathecae with short distinct ducts and a vestigial third.

Distribution: All known specimens from type locality including the Nattai River. Taken attracted to man in November and February to April.

Culicoides henryi, n. sp.

Types: Holotype ♀, allotype ♂ and 10 paratype ♀♀. In SPHTM, except paratype in each of CSIRO, QIMR, USNM and BM.

Type Locality: Lota, south-east Queensland. Holotype, allotype and 7 paratypes, 11:ii:1955, E. J. Reye. The other paratypes with same data except 12:ii:1955 and 13:ii:1955.

Distinctive Characters: Closest to *C. victoriae* Macfie, but with wing spotting less pronounced. Pale spot over cell R_2 extending below base of intercalary fork; both branches of M dark. In *C. victoriae* the lower branch of the intercalary fork is dark towards the base and the basal pale spot in the median cell extends over both M_1 and M_2. In addition the pale spot in the intercalary area does not extend to the wing margin. The absence of apico-lateral processes on the ninth tergite is a major point of distinction of the male from that of *C. victoriae*. See also under *C. hornsbyensis*, n. sp.

Description: From the type series. Measurements from holotype, allotype and 9 ♀♀ paratypes. Unmounted material for description of thorax from Careel Bay, New South Wales.

Female.

Head: Eyes narrowly separated. Mouthparts about equal to height of head. Basal flagellar segments mostly vasiform, distal ones noticeably longer but still vasiform except 15. Segment 11 about twice length of 10. Antennal ratio 0·81.

Thorax: Brown, mesonotal pattern not of distinct spots but somewhat vague due to variation with light incidence. A large pale area centrally from level of humeral pits to distal part of prescutellar area surrounded by dark brown which includes scutellum. Additional irregular pale areas from humeral pits to margin of scutum but not including humeral corners and latero-median pale areas. Prescutellar sensory areas (Wirth and Blanton, 1959) black. Legs brown, distal tarsi paler. Femora paler preapically on anterior legs, not on hind pair; all tibiae pale subbasally; knees very dark. Tarsi unmodified, tarsal ratio 2·0. Tibial comb 4. Wings with macrotrichia moderately dense over distal half and lower part of anal cell. Radial cells well developed, second larger than first. Pattern as illustrated, differential points given above.

Abdomen: Two subequal subspherical spermathecae with very distinct necks and ducts.

Male.

Similar to ♀, except in characters of sex difference. Genitalia as illustrated.

Distribution: The type locality (in Moreton Bay) in Queensland. New South Wales: Careel Bay, light trap, 16:xi:1957, 27:xi:1957, 20:ii:1958, 19:iii:1958, 15:xi:1957, 18:xi:1957, 25:xi:1957, all D. J. Lee, and 20:x:1956, 30:x:1956, 3:xi:1956, 21:xii:1956, all light trap, W. W. Wirth; Berowra, 6:iii:1956, D. J. Lee; Cowan Cr., 29:x:1949, B. McMillan.

Culicoides hornsbyensis, n. sp.

Types: Holotype ♀, allotype ♂ and 1 ♂ and 1 ♀ paratype. In SPHTM.

Type Locality: Hornsby, New South Wales, in light trap, D. J. Lee, 25:x:1956 for holotype and paratype ♂, 10:x:1956 for allotype and 24:x:1956 for paratype ♀.

Distinctive Characters: Wing with basic similarity to *C. henryi*, n. sp., but the third segment of the palp is similar only to *C. bancrofti* L. & R. which is a larger species with long vasiform basal antennal segments.

Description: From the types. Measurements include holotype, allotype and 1 ♀ paratype.

Female.

Head: Eyes separated. Mouthparts about equal to height of head. Antennae with basal segments barrel-shaped, 11–14 vasiform, segment 11 twice length of 10, antennal ratio 0·84. Palp with third segment enlarged, ovoid, its length slightly more than twice its width, extensively covered with small sensory pits.

Thorax: Brown with lighter brown areas, halteres pale. Legs uniformly light brown, no obvious markings. Tarsi unmodified, tarsal ratio 2·0. Tibial comb 4.

Abdomen: Two subequal, subspherical spermathecae with very short ducts and an accessory duct.

Male.

Similar to ♀ apart from sex differences, except wings with less strongly contrasting pattern and pale areas tending to be larger. Palp smaller but of similar form. Genitalia as illustrated.

Distribution: In addition to the type series this species has been taken in the same locality (Hornsby) on 29:i:1957, 7:ii:1957 and 8:ii:1957, all light trap, D. J. Lee.

Culicoides fulbrighti, n. sp.

Types: Holotype ♀, allotype ♂, 16 ♀♀ paratypes and 6 ♂♂ paratypes. All in SPHTM, except paratypes in CSIRO, QIMR, USNM and BM.

Type Locality: Hornsby, New South Wales. All specimens from light trap, D. J. Lee, holotype and 1 paratype ♂ 4:x:1956, allotype and 1 ♂ paratype and 16 ♀♀ paratypes 6:x:1956, the remaining four ♂♂ paratypes 8:x:1956, 10:x:1956, 24:ix:1956 and 28:ix:1956.

Distinctive Characters: Although the distribution of pale spots is very similar to that of *C. victoriae*, all spots are larger and the dark areas greatly reduced. The r-m pale spot and the one over cell R_2 converge below the junction of the two radial cells. The male genitalia are intermediate between *C. victoriae* and *C. henryi*. In the latter the ninth tergite has no apico-lateral prolongations, in *C. fulbrighti* short prolongations are present and in *C. victoriae* they are long. See also *C. pallidothorax*, n. sp.

Description: From the type series. Measurements from holotype, allotype and 9 ♀♀ paratypes.

Female.

Head: Eyes narrowly separated. Mouthparts slightly less than height of head. Antennal flagellar segments vasiform, except apical one which tapers slightly. Segment 11 about 1·75 × 10. Antennal ratio 0·81. Palp with segment 3 slightly expanded at two-thirds from base; shallow sensory pit occupying distal third.

Thorax: Legs with broad pale areas at apices of femora and bases of tibiae; knees dark. Tarsi unmodified, tarsal ratio 2·2. Tibial comb 4. Wings with macrotrichia moderately well developed. Radial cells relatively large, both pale except for narrow dark area at junction of the two cells. Pale areas extensive, those on anterior half of wing almost coalescing.

Abdomen: Two subequal, ovate spermathecae with distinct ducts and two rudimentary ducts (one of these forms a third small spermatheca in one of the paratypes).

Male.

As for ♀ except for sex differences. Genitalia as figured.

Distribution: The type locality all months from September to February, always from light trap. Other localities from New South Wales are Careel Bay, November, February and April; Newport, December; Colo Vale, March.

CULICOIDES PALLIDOTHORAX, n. sp.

Types: Holotype ♀ and 4 paratype ♀♀. In SPHTM, except one paratype in each of CSIRO and USNM.

Type Locality: All of type series from Humpty Doo, Northern Territory, 29:xi:1956, A. K. O'Gower.

Distinctive Characters: Superficially very similar to *C. fulbrighti*, n. sp., on wing pattern but very distinct on coloration. *C. pallidothorax* is a pale yellowish species and considerably smaller than *C. fulbrighti*. Both of these species have much in common in wing pattern with *C. tritenuifasciatus* Tokunaga, but in both there are dark areas over the distal portions of M_1, M_2 and Cu_1, these being absent in *C. tritenuifasciatus*. However, the similarity of genitalia between *C. fulbrighti* and *C. tritenuifasciatus* does suggest a close affinity for these species.

Description: From the type series, measurements from holotype ♀ and 3 paratype ♀♀.

Female.

Head: Eyes separated above, almost touching below. Mouthparts equal to height of head. Basal flagellar segments barrel-shaped, becoming vasiform; 11–14 vasiform. Antennal ratio 0·93. Palpi pale, slender, segment 3 elongated but not conspicuously expanded, with small sensory pit about distal one-fifth.

Thorax: Brown around anterior and lateral margins to about half-way from anterior end. Just before scutellum, the scutellum itself and the postscutellum brown, the rest of the dorsal thorax yellowish. Lateral thorax with broad yellowish band across upper half, rest brown, legs pale with paler apices to femora and bases to tibiae; knees pale. Tarsi unmodified. Tarsal ratio 2·3. Tibial comb 4. Wings extensively pale, the distribution of pale areas very close to that of *C. fulbrighti*, n. sp.

Abdomen: Two subequal, subspherical spermathecae and a minute rudimentary one.

Distribution: Only known from the type locality.

(iii) *New Synonymy.*

CULICOIDES BREVITARSIS Kieffer.

Kieffer, J. J., 1917. *Ann. Nat. Mus. Hung.*, 15: 187.

New Synonymy:

Culicoides robertsi Lee & Reye 1953.

Dr. P. Freeman of the British Museum was kind enough to arrange with Dr. Mikaly, of the National Museum of Hungary (Budapest), for the loan of certain Kieffer types for examination by himself and Dr. B. McMillan. The type of *C. brevitarsis* was compared with a paratype of *C. robertsi* and no important distinctions could be detected. Our original reluctance to recognize any Australian species as *C. brevitarsis*, due to the

description stating that the $M_{3+4} - Cu_1$ fork was immediately below the distal extremity of R_{4+5} no longer held because this is not so in the holotype. All characters which could be determined with confidence in the Kieffer type as well as measurements indicate the need for the synonymy proposed above.

The above comparison was made in September, 1955. It is possible, following the disastrous fire in the Hungarian National Museum in October, 1956, that the type of *C. brevitarsis* is no longer in existence, in which case the type of *C. robertsi* would be available as a neotype.

CULICOIDES VICTORIAE Macfie.

Macfie, J. W. S., 1941. *Proc. R. Ent. Soc. Lond.* (B), 10: 67.

New Synonymy:

Culicoides magnimaculatus Lee & Reye 1953. PROC. LINN. SOC. N.S.W., 77 (1952): 388.

In our earlier papers on Australasian *Culicoides* Macfie's *C. victoriae* was inadvertently overlooked. Shortly after we became aware of its existence Dr. B. McMillan compared the type of *C. victoriae* with a paratype of our *C. magnimaculatus* and considered them to be identical.

However, in view of the absence of the distal antennal segments on the type of *C. victoriae* and because the large amount of material we have examined has shown evidence of geographic variation in wing pattern we hesitated to propose the synonymy given above. In the intervening time we have been unable to relate the wing pattern differences with any other characters, particularly of male genitalia, and our present view is that *C. victoriae* will eventually prove to be a species complex. Even though a number of segregates may emerge from this complex it now seems doubtful that *C. magnimaculatus* will be one of these.

A full biological investigation of this complex appears to be warranted as it is unlikely that any clarification will emerge from haphazard collecting.

Acknowledgements.

We wish to record our indebtedness to the co-operation of Dr. W. W. Wirth of the United States Department of Agriculture during his sojourn with us as a Fulbright Fellow in 1956–57 and to Mr. Ian Roper of the C.S.I.R.O. McMaster Animal Health Laboratory, University of Sydney, who prepared the wing photographs.

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EXPLANATION OF PLATE XIII.

Figures 1-12. 1, *C. purus*, n. sp. 2, *C. mykytowyczi*, n. sp. 3, *C. marginalis*, n. sp. 4, *C. leanderensis*, n. sp. 5, *C. mackerrasi*, n. sp. 6, *C. narrabeenensis*, n. sp. 7, *C. interrogatus*, n. sp. 8, *C. sigmoidus*, n. sp. 9, *C. henryi*, n. sp. 10, *C. hornsbyensis*, n. sp. 11, *C. fulbrighti*, n. sp. 12, *C. pallidothorax*, n. sp. All × 66 approx.

"SANDFLIES" AS POSSIBLE VECTORS OF DISEASE IN DOMESTICATED ANIMALS IN AUSTRALIA.

By D. J. Lee,[1] E. J. Reye[2] and A. L. Dyce.[3]

[Read 28th November, 1962.]

Synopsis.

The known data, much of which has not previously been reported, relating to the distribution and feeding habits of individual species of Ceratopogonidae (biting midges), Simuliidae (blackflies) and *Phlebotomus* (sandflies) are herein reported.

Some emphasis has been placed on the results of precipitin tests since in important instances, such as feeding on sheep, this has been the only method so far employed which has yielded positive evidence of attack.

The veterinary diseases known to occur in Australia, which are probably transmitted by one or other of these groups of flies, are discussed even though the incrimination of vector species remains to be accomplished.

Some stress is given to the recording of feeding of biting midges on sheep and cattle. These observations have not previously been published and have an important bearing on the potential threat of blue-tongue virus to the sheep industry.

Early interest in the transmission of bovine onchocerciasis and ephemeral fever was faced with frustration due to very inadequate knowledge of the biting midges. The taxonomic and biological data accumulated in the past fifteen years now make further investigation of the transmission of these diseases a more feasible proposition.

Introduction.

The use of the common name "sandfly" in Australia is at variance with the rest of the world. In coastal Australia "sandfly" refers to the Ceratopogonidae, in inland New South Wales, Queensland and New Zealand it refers to the Simuliidae. Elsewhere in the world "sandfly" implies the genus *Phlebotomus* of the family Psychodidae. Since consistency is desirable, and Australia is at fault, the adoption of "biting midge" for Ceratopogonidae, "blackfly" for Simuliidae and "sandfly" for *Phlebotomus* is proposed. These are the accepted common names overseas.

All these groups have been incriminated in the transmission of diseases of domesticated animals, and of man, in other parts of the world. However, being small and often inconspicuous they have received far less attention as potential vectors of disease than the larger, more obvious mosquitoes, march flies, stable flies and tse-tse flies.

Biting midges of the genus *Culicoides* are now known to transmit *Onchocerca reticulata* of horses in England (Steward, 1933, as *O. cervicalis*), *Onchocerca gibsoni* of cattle in Malaya (Buckley, 1938), *Haemoproteus nettionensis* of ducks in Canada (Fallis and Wood, 1957), *Leucocytozoon caulleryi* of chickens in Japan (Akiba, 1960) and *Hepatocystis kochi* of monkeys in Africa (Garnham *et al.*, 1961). Although not of veterinary significance this parasite has a counterpart (*Hepatocystis pteropi*) in flying foxes in Australia. Up to the present attempts to find a vector for this have failed (Bearup and Lawrence, 1947), but *Culicoides* have not been investigated. Evidence of the feeding of *Culicoides* on flying foxes is presented in Tables 1 and 3 and in Reye and Lee (1961).

The viruses of blue-tongue of sheep and African horse sickness (du Toit, 1944) are also *Culicoides* transmitted. In addition Karstad *et al.* (1957) reported the recovery of eastern equine encephalomyelitis from *Culicoides* sp. in Georgia and cite a private

[1] School of Public Health and Tropical Medicine. [2] One time of School of Public Health and Tropical Medicine, University of Sydney. [3] C.S.I.R.O. Division of Wildlife Research, Canberra.

communication from R. Levi-Castillo stating that Venezuelan equine encephalomyelitis had been isolated from *Culicoides* in Ecuador during an outbreak affecting both man and horses. Tokunaga (1937), quoting an earlier publication of Shiraki, reported *Culicoides* to be able to transmit fowlpox virus, apparently on the purely presumptive evidence of the breeding of *Culicoides* in fowl pens.

Species of *Simulium* and *Eusimulium* are known to transmit several species of *Leucocytozoon* affecting poultry (fowls, ducks, turkeys, geese and other birds) in North America (Johnson *et al.*, 1938; Fallis *et al.*, 1956; Karstad *et al.*, 1957; Fallis and Bennett, 1958), *Onchocerca gutturosa* of cattle in England (Steward, 1937) and *Ornithofilaria fallisensis* of domestic and wild ducks (Anderson, 1956). Although Dalmat (1955) states that Simuliidae "have also been incriminated in the transmission of *Setaria equina* of horses" we are not aware of evidence to support this.

Phlebotomus spp. are vectors of *Leishmania donovani* of dogs in Mediterranean countries and China (reviewed by Adler and Theodor, 1957).

In relation to animal diseases in Australia Cleland (1912) observed *Culicoides* attacking cattle but, after careful consideration, practically dismissed them as possible vectors of bovine onchocerciasis. However, he was unaware of the later finding (Heydon, 1927) of the concentration of microfilariae in the skin rather than in circulating blood vessels. Cleland undoubtedly influenced the thinking of workers in this field for many years and subsequent investigations of transmission did not include biting midges although they are mentioned (Cleland, 1914; McEachran and Hill, *c.* 1915; Dickinson and Hill, 1916; Cleland *et al.*, 1916; Hill *et al.*, 1917; Henry, 1927).

Mackerras *et al.* (1940) gave serious consideration to biting midges as possible vectors of ephemeral fever, but their experimental work was interrupted by the outbreak of war. More recently, during a brief outbreak in southern Queensland in 1956 Reye (unpublished) was hampered by technical difficulties of handling the insects when he unsuccessfully attempted to implicate *Culicoides brevitarsis* in the transmission of ephemeral fever. Finally, the condition, Queensland itch of horses, has been shown to be an allergic response to the bites of *Culicoides brevitarsis* (Riek, 1954, as *C. robertsi*).

The Simuliidae have not been investigated as possible animal disease vectors in this country except in the case of myxomatosis in rabbits (Mykytowycz, 1957). Expressions of opinion relating to onchocerciasis have appeared in Blacklock (1927), Cleland (1927) and Roberts (1938).

Phlebotomus spp. have never been considered as animal disease vectors in Australia.

Recent opinion relating to the Ceratopogonidae and Simuliidae as vectors of both onchocerciasis and ephemeral fever is reviewed in Seddon (1950, 1951, 1952) and Roberts (1952). These authors emphasize the possible role of Ceratopogonidae in relation to both diseases. This change of emphasis owes much to the dramatic epidemic of ephemeral fever which swept eastern Australia in 1936–1937. Faced with the necessity to postulate likely insect vectors, workers at that time found that existing knowledge of blood-sucking flies was inadequate for the formulation of hypotheses covering the epidemiological picture. The then possible conclusions are summarized by Mackerras *et al.* (1940). This inadequacy stimulated a period of basic research which has continued to the present time; furthermore this stimulation has been reinforced by the later need to understand the epidemiology of myxomatosis, Murray Valley encephalitis, fowlpox and the potential threat of diseases such as blue-tongue.

Outline of Investigations.

The observations reported herein result from three lines of investigation.

(i) Taxonomic studies of Australian biting midges (Lee, 1948*a*, *b*, *c*, *d* and *e*; Lee, 1963; Lee and Reye, 1953, 1955, 1963; Wirth and Lee, 1958, 1959; Wirth, 1960), blackflies (Wharton, 1949; Mackerras and Mackerras, 1948, 1949, 1950, 1952 and 1955) and of *Phlebotomus* sandflies (Fairchild, 1952).

(ii) Studies of the epidemiology of arthropod-borne virus diseases in Australia since 1950. Relevant data on host relationships arising from this work have already

appeared in Lee *et al.* (1957), Lee *et al.* (1958), Reye and Lee (1961) and Dyce and Lee (1962). This work contributes to the overall conclusions presented herein, but further important data stem from Dyce's studies at Moree (1951–1953) and Merricumbene (1956–1958), those of Waterhouse in the Armidale area (1954–1959), and of Reye in Queensland and the Northern Territory (1950–1960).

(iii) Deliberate studies of biting midges in the vicinity of stock, especially by Reye in inland and coastal Queensland.

All these studies have contributed to the general finding that the three blood-sucking groups of flies in question are more common and far more widely distributed over the continent than had previously been supposed and certainly meriting consideration in the epidemiology of diseases with an obscure ætiology. While some species appeared to be rare and of limited distribution there were others which were found to occur in high densities and over large areas of Australia. (See Table 3.) Evidence of their attack on animals has been obtained either by direct observation or by precipitin testing of the stomach contents of captured engorged specimens (see Lee, 1954, for techniques).

Investigation of Feeding Activities.

None of the "sandflies" are as easy to observe in the act of feeding as are mosquitoes. Diurnally active species may be recognized from characteristic flight behaviour by some observers. Observations of mass attack by Ceratopogonidae and Simuliidae on a variety of animals contribute to the emphasis we place on particular species. Since animals are not always co-operative and because nocturnal attack is also important, various methods of recovery of engorged specimens for subsequent precipitin tests have also been employed, e.g., (i) adventitious collection in the course of general studies of biting fly activity, including collections from man, and from light traps; (ii) sweep netting over and around animals, usually penned for this particular purpose; (iii) light trapping in close proximity to bait animals; (iv) the use of a tent trap adjacent to a bait animal; and (v) cone drop traps (Dyce and Lee, 1962) baited with rabbit.

The results of all precipitin tests performed are presented in Table 1 wherein attention is drawn to the following points.

(i) Negative precipitin tests are not entered. Imperfect technique was responsible for negatives in some early series. Others were due to the small blood meals which severely limited the number of tests which could be performed.

(ii) These results are in no way an indication of relative frequency of attack by different species, nor are they indicative of abundance. The high recordings of man positives for *Culicoides victoriae* is a reflection of the frequent use of a particular microhabitat in which this species is common.

(iii) The antisera for marsupial and bird were prepared from possum and fowl respectively, but both were capable of yielding positive results over a fairly wide range of marsupials or birds and cannot be regarded as species specific.

(iv) The results for sheep, ox, flying fox and bird are regarded as particularly significant and in the case of the first three would not have been obtained if deliberate efforts to prove feeding on these animals had not been made.

It is of interest that Jones (1961) first demonstrated field feeding of *Culicoides variipennis* (Coq.) on sheep in 1960 despite the fact that this species has been regarded as a proven vector of blue tongue in the U.S.A. for at least six years. The following observations demonstrate the need for the development of satisfactory techniques for the recovery of fed material in serological investigations.

(*a*) In a comparison of net sweeping with light trapping over stock the ratio of fed to unfed specimens captured varied widely. In one series the percentage of engorged to total *Culicoides marksi* varied from 2% to 5% when netted, but reached 60% from light traps; on the other hand *C. brevitarsis* rarely yielded 1% engorged in either case.

TABLE 1.

Complete Results of Precipitin Tests.

	Man.	Sheep.	Ox.	Horse.	Dog.	Rabbit.	Marsupial.	Flying Fox.	Bird.	Total.
CERATOPOGONIDAE										
Leptoconops stygius ..	4					7				11
Lasiohelea townsvillensis	1	1			5	3				10
Culicoides antennalis ..	5									5
Culicoides austropalpalis								1	45	46
Culicoides dycei ..	2		3							5
Culicoides mackayensis ..									1	1
Culicoides magnesianus									2	2
Culicoides victoriae ..	82		8			10	1			101
Culicoides marksi ..	1	13	21						1	36
Culicoides marmoratus ..	1	7								8
Culicoides molestus ..	3	5				6		7	23	44
Culicoides nattaiensis ..	1									1
Culicoides ornatus ..	6							80		86
Culicoides parvimaculatus	2									2
Culicoides brevitarsis ..		11	16							27
Culicoides subimmaculatus	6	4	11			1		44		66
SIMULIIDAE										
Austrosimulium bancrofti	3			2		1				6
Austrosimulium furiosum	5					3				8
Austrosimulium sp.* ..				5						5
Cnephia spp.†	1					5				6
PSYCHODIDAE										
Phlebotomus spp. ..	1					1			2	4
Totals	124	41	59	7	5	37	1	132	74	480

* Either or both *A. bancrofti* or *A. torrentium*.

† Both *C. terebrans* and an undescribed *Cnephia* sp.

TABLE 2.

Two-Hour (1800–2000 hrs.) Light Trap Catches over Different Animals.

	Culicoides marksi.			*Culicoides brevitarsis.*		
	Total ♀ ♀	Engorged.	Precipitin Test Positive.	Total ♀ ♀	Engorged.	Precipitin Test Positive.
Ox	34	21	21	1896	20	11
Sheep ..	4	—	—	203	3	2

(*b*) Comparable two-hour light trappings over sheep and ox at Longreach were indicative of very different types of activity on the part of these two species. (See Table 2.)

As the significance of an individual positive precipitin test varies greatly with the circumstances under which it is collected so the records of observed attack on particular hosts vary with the circumstances of observation. The relative importance of species as pests or potential vectors of disease must include consideration of geographic range, relative abundance and characteristic environments as well as hosts attacked. In presenting a summary of the accumulated information of attack on animals for each "sandfly" species (Table 3), due regard has been given to the above variables.

Discussion Relating to the Insects.

(*a*) *Ceratopogonidae* (Biting Midges).

Within the Ceratopogonidae five blood-sucking genera are known to occur in Australia: *Austroconops*, *Styloconops*, *Leptoconops*, *Lasiohelea* and *Culicoides*. Of these the last three are known to attack stock. *Leptoconops* and *Lasiohelea* are both less adequately known than *Culicoides*, one reason being the fact that light traps have not been of material assistance as they have been in the case of *Culicoides*. The brief seasonal incidence of *Leptoconops* spp. would militate against their being of epidemiological significance, but the genus warrants further study to elucidate the frequency with which mass attacks may occur.

The pest status of *Lasiohelea townsvillensis* to man has at times been obvious in Queensland, but its more usual behaviour is of a cryptic character. Methods of detection so far employed have not been satisfactory for this species. Special studies will be necessary to divulge its host relationships and full range.

Species of the genus *Culicoides* may be divided into four categories on the basis of known host relationships and distribution.

(i) Species of the coastal estuaries which are best known as a serious nuisance to man (*C. subimmaculatus*, *C. ornatus*, *C. marmoratus* and *C. molestus*).—These species appear to be opportunist feeders and attack stock quite readily in those limited areas where they are coincident. That these species may possibly be involved in the dissemination of disease through the dispersal of stock from coastal saleyards should not be overlooked.

(ii) Species of subcoastal and inland distribution known to attack stock (*C. dycei*, *C. victoriae*, *C. marksi*, *C. brevitarsis*).—Most of these species have also been known to attack man, but this is relatively insignificant; indeed they often occur in districts regarded by man as being "sandfly" free. *C. brevitarsis* has been intensively studied as the cause of Queensland Itch in horses, but it is also more commonly taken attacking cattle by stock inspectors than any other species. All the above deserve special study from a primarily stock-feeding angle.

(iii) Species restricted to avian feeding (*C. austropalpalis* and possibly *C. mackayensis* and *C. magnesianus*).—Opportunist feeding on birds may also be a feature of the species listed under category (i). The evidence suggests that *C. austropalpalis* feeds on both native birds and domestic poultry, and some significance in the latter field could be disclosed.

(iv) A considerable number of apparently rare species which, on grounds of limitation of distribution and density, do not appear to have any significance.—For some of these species further study is bound to reveal special points of ecology or behaviour which will raise them to a more important category.

(*b*) *Simuliidae* (Blackflies).

Information on blood feeding relationships of members of this family in Australia has been slow to accumulate and significant evidence of stock feeding has been limited to three species (*Austrosimulium pestilens*, *A. bancrofti*, *A. furiosum*). *A. pestilens*, although most spectacular in its attacks on animals during its short period of occurrence over a more limited range, is considered of secondary importance to the

Table 3.

Distribution and Known Feeding Activity of Blood Sucking "Sandflies" Occurring in Australia.

Species.	Summary of Data from all Sources.	Remarks.
CERATOPOGONIDAE.		
Leptoconops grandis Cart.	Originally recorded attacking man near Perth, W.A. (W. J. Dakin, pers. comm.; not interior of W.A. as stated by Carter, 1921). No additional information.	No significant data.
Leptoconops longicornis Cart.	Well-known as a pest of man in south-western W.A. Also recorded attacking man at Noosa, Q'ld. Diurnal.	No significant data.
Leptoconops stygius Sk.	A common pest species in sandstone gullies in the Sydney area and Blue Mountains usually only appearing in late Spring. Known to attack man, horse, ox, dog, rabbit and fowl. Sometimes causes "bung-eye" in man (Lee, 1958). Heavy biting of the ears of horses and calves causes a hard thickening. *Leptoconops*, at present indistinguishable from *stygius*, have also been taken in several inland N.S.W. localities. At Moree attacks on man and horse have been observed. This species has also been tentatively identified from W.A. Diurnal.	Although attacking stock with some intensity its brief seasonal incidence would probably reduce its epidemiological significance (cf. *Austrosimulium pestilens*).
Leptoconops woodhilli Lee.	Known to attack man in the N.T.	No other data.
Leptoconops sp.	S. Davies (pers. comms.) reported vicious attacks on man about 500 miles north-east of Perth in W.A. during a brief period following summer rains. J. Calaby has reported similar attacks in June. Diurnal.	No other data.
Styloconops australiensis Lee.	Pest of man on some beaches in northern Australia but known to occur as far south as Sydney on the east coast and Roebourne in W.A.	No other data.
Austroconops mcmillani Wirth & Lee.	Limited records of attack on man near Perth, W.A.	No other data.
Lasiohelea townsvillensis (Tayl.)	The known range of this species includes most of Q'ld. and N.S.W. to south of Sydney. Also recorded from the Roper R. in N.T. Known to attack man, horse, ox, sheep, dog, goat, rabbit and wallaby. Intense attacks on man have been observed at Longreach and parts of the Q'ld. coast. Observed attack on cattle in Q'ld. has also been heavy. Diurnal and crepuscular.	Suspected of being a more important pest of stock than has been revealed by methods of investigation so far employed.
Lasiohelea sp.	An undescribed species is known to attack man in north-western W.A.	No other data.
Culicoides angularis L. & R.	South-eastern Australia to southern Q'ld.; known only from bred material.	No data.
Culicoides antennalis L. & R.	Not abundant although collected with reasonable frequency in sub-coastal and tableland areas of N.S.W. Diurnal to crepuscular. Attacks man.	Apparently a mammalian feeder but important blood sources are not known.
Culicoides austropalpis L. & R.	An abundant species in coastal and inland eastern Australia from Cape York to southern N.S.W. Nocturnal, common in light traps. An avian feeder, the only known exception being one record from flying fox.	Almost exclusively an avian feeder; the evidence implicates both native and domestic birds.
Culicoides bancrofti L. & R.	Occurs with *C. antennalis* but less abundant. Vic. to southern Q'ld. Diurnal and perhaps crepuscular. Occasionally attacks man; one record of attack on cattle. Most recorded attacks are by single specimens.	Apparently a mammalian feeder.
Culicoides brevitarsis Kieff. (syn. *C. robertsi* L. & R.).	A very common species over most of Q'ld. extending as far south as Sydney in N.S.W. Known to attack man (single record), horse, ox and sheep. Active between dusk and dawn.	An important species very commonly recorded attacking horses and cattle. In view of the considerably greater difficulties in proving feeding on sheep, the positive precipitin tests for this host must be considered highly significant.

TABLE 3.—*Continued.*

Distribution and Known Feeding Activity of Blood Sucking "Sandflies" Occurring in Australia.—Continued.

Species.	Summary of Data from all Sources.	Remarks.
CERATOPOGONIDAE.—*Continued.*		
Culicoides bundyensis L. & R.	Rare species from northern N.S.W. and southern Q'ld.	No data.
Culicoides bunrooensis L. & R.	Rare species from northern N.S.W. and southern Q'ld.	No data.
Culicoides coronalis L. & R.	Torres Sts. islands only. Possibly attacks man.	Data inconclusive.
Culicoides cuniculus L. & R.	Apparently rare, from central southern Q'ld.	No data.
Culicoides dycei L. & R.	A reasonably common species extending from northern Q'ld. to southern N.S.W. and into western N.S.W. Known to feed on man, ox, horse and rabbit. Late afternoon to crepuscular. Common in light traps.	A mammalian feeder persistently recorded attacking livestock.
Culicoides fulbrighti L. & R.	Sydney area, N.S.W.	No data.
Culicoides henryi L. & R.	Coastal, southern Q'ld. to central N.S.W.	Occasionally attacking man.
Culicoides hornsbyensis L. & R.	Only known from the Sydney area.	No data.
Culicoides immaculatus L. & R.	A strictly coastal species common from Darwin to Townsville; less frequently recorded south to Moreton I. A minor pest to man.	Important blood sources not known.
Culicoides interrogatus L. & R.	Eastern N.S.W. Rare.	Does attack man.
Culicoides leanderensis L. & R.	Only known from Longreach, Q'ld.	Only capture has been close to sheep.
Culicoides mackayensis L. & R.	Strictly coastal in central Q'ld. Nocturnal. Only record of attack is on bird.	Apparently an avian feeder.
Culicoides mackerrasi L. & R.	N.T. and Q'ld.	Attacks man but inadequately known.
Culicoides magnesianus L. & R.	Strictly coastal, Torres Sts. to Moreton Bay in Q'ld. Known to feed on birds, a single record of attack on man. Nocturnal.	Presumably an avian feeder.
Culicoides marginalis L. & R.	A tree hole breeding species (in river oaks), N.S.W.	No data.
Culicoides marksi L. & R.	Widely distributed east of a line through Darwin and Adelaide, subcoastal and inland but especially important west of the Dividing Range. Attacks on man, horse, ox, sheep, dog and bird have been recorded. Diurnal to crepuscular, but particularly the latter.	Attacks on sheep and cattle are unquestionably significant.
Culicoides marmoratus (Sk.)	A strictly coastal species from Townsville to southern N.S.W. There have been frequent observations of dispersal for three or four or even ten miles from its estuarine breeding areas. Known to attack man, horse, sheep and wallaby. The observed attack on wallaby would indicate a primary native host. Crepuscular activity more important than diurnal.	On ecological grounds we consider this is likely to prove an opportunist feeder attacking the most readily available blood sources. Although the recorded attack on sheep is apparently heavy, this took place in a coastal slaughteryard.
Culicoides mcmillani L. & R.	The limited records indicate a range from southern Q'ld. to Vic. in coastal areas only. Diurnal attack on man has been recorded.	No significant data.
Culicoides melanesiae Macfie.	Only known from New Britain and Green I., north Q'ld.	Known to attack man.
Culicoides molestus (Sk.).	A commonly recorded strictly coastal species from Townsville, Q'ld., to Gippsland in Vic., but not found in the same high densities as *C. subimmaculatus*. Known to attack man, sheep, rabbit, bird and flying fox. Diurnal and crepuscular.	Considered to be an opportunist feeder on the same grounds as *C. marmoratus*.
Culicoides moreensis L. & R.	This is a rare inland species taken only from southern Q'ld. and northern N.S.W. Diurnal attack on man has once been recorded.	No significant data.
Culicoides multimaculatus Tayl.	Vic. only. Known to attack man. Crepuscular.	No significant data.

TABLE 3.—*Continued.*

Distribution and Known Feeding Activity of Blood Sucking "Sandflies" Occurring in Australia.—Continued.

Species.	Summary of Data from all Sources.	Remarks.
CERATOPOGONIDAE.—*Continued.*		
Culicoides mykytowyczi L. & R.	Does attack man.	Southern tableland, N.S.W. Rare.
Culicoides narrabeenensis L. & R.	No data.	So far only known from Sydney area: coastal.
Culicoides nattaiensis L. & R.	Known from the southern tablelands of N.S.W., attacks man in a very minor way. Crepuscular.	No significant data.
Culicoides ornatus Tayl.	A strictly coastal species ranging from southern Q'ld. around the northern coastline to Port Samson in W.A. and the most important pest species of the estuaries within the tropics. Known to feed on man, horse and flying fox. Diurnal and crepuscular; very common in light trap catches.	This should certainly prove an opportunist feeder which may be expected to attack stock within its habitat.
Culicoides pallidothorax L. & R.	N.T. only.	Known to attack man.
Culicoides parvimaculatus L. & R.	A subcoastal and tableland species from southern Q'ld. to southern N.S.W. Although taken with some frequency attacking man even moderate densities have never been encountered. Attack on dog has also been observed. Diurnal and crepuscular.	No significant data.
Culicoides purus L. & R.	Apparently rare; only known from vicinity of Sydney.	No data.
Culicoides rabauli Macfie.	Only Australian record from Heron I. off the Q'ld. coast.	No data.
Culicoides sigmoidus L. & R.	A.C.T. to adjacent coast.	No data.
Culicoides smeei Tokunaga.	Originally described from the New Guinea area, this species is now known to occur in coastal Queensland.	No data.
Culicoides subimmaculatus L. & R.	A strictly coastal species ranging along the eastern coastline from Thursday Is. through to S.A. The most important estuarine species south of southern Q'ld. Known to attack man, ox, sheep, rabbit and flying fox. Diurnal to crepuscular. Very common in light trap catches.	This is apparently an opportunist feeder which may be expected to attack a wider range of hosts.
Culicoides victoriae Macfie (syn. *C. magnimaculatus* L. & R.).	A very common species from central Q'ld. to Tas. and S.A., both coastal and inland. Known to attack man, horse, ox, dog, rabbit and marsupials. Its attacks on rabbit appear to be rare and although it worries man with some severity in favourable habitats, man is not usually available in these. Observed attacks on cattle are suggestive and an observed attack on the ears of a wallaby are probably indicative of a native host. Diurnal and crepuscular and very common in light trap collections.	This is considered to be essentially a mammalian feeder whose native hosts are probably marsupials. Among the domestic animals cattle at least may be important.
Culicoides waringi L. & R.	As yet only known from Rottnest Is., W.A.	No data.
Culicoides williwilli L. & R.	A rare species taken occasionally from southern Q'ld. to southern N.S.W.	No data.
SIMULIIDAE.		
Cnephia aurantiacum (Tonn.).	Southern Q'ld. to Tas., mainly a tableland species.	No data.
Cnephia fergusoni (Tonn.).	Found in N.S.W., Vic. and S.A., but records infrequent. An old record of injury to horses and cattle (Lea, 1917) is referred to by Mackerras and Mackerras (1949) and Seddon (1951). Attack on man once recorded (Tonnoir, 1925).	Attack on stock requires confirmation.
Cnephia fergusoni var. of Mackerras & Mackerras (1949).	W.A. only. Known to attack man.	No significant data.
Cnephia strenua M. & M.	Q'ld. only.	No data.

TABLE 3.—*Continued.*

Distribution and Known Feeding Activity of Blood Sucking "Sandflies" Occurring in Australia.—Continued.

Species.	Summary of Data from all Sources.	Remarks.
SIMULIIDAE.—*Continued.*		
Cnephia terebrans (Tonn.).	Limited records in N.S.W. and Vic. Recorded attacking man and a positive precipitin test for rabbit was recently obtained at Mt. Flora, N.S.W. Diurnal.	No significant data, although the rabbit-positive precipitin test is suggestive (Dyce & Lee, 1962).
Cnephia tonnoiri (Drum.)	Ranging from Q'ld. to Tas., also W.A.	No data.
Cnephia umbratorum (Tonn.).	Vic. only.	No data.
Cnephia sp. A. of Mackerras & Mackerras (1949).	W.A. only. Possibly attacking man.	No data.
Cnephia sp. undescribed from Mt. Flora, N.S.W.	Taken with *C. terebrans*. Precipitin tests have been positive for either man or rabbit, or both.	As for *C. terebrans*.
Simulium aureonigrum M. & M.	Northern Q'ld. only.	No data.
Simulium clathrinum M. & M.	Central Q'ld. to Sydney in N.S.W.	No data.
Simulium faheyi Tayl.	Northern Q'ld. and N.T. Occasional man biter (Mackerras & Mackerras, 1950).	No significant data.
Simulium inornatum M. & M.	Southern Q'ld. to Vic. A species of the *clathrinum* group, probably *S. inornatum*, was recorded attacking man near Sydney (McMillan, pers. comm.).	No data.
Simulium melatum Wh.	Q'ld. to Vic. Known to attack rabbits (Mykytowycz, 1957). Attracted to man (Dyce & Lee, 1962).	Rabbit feeding is significant.
Simulium nicholsoni M. & M.	Southern Q'ld. to Vic. Occasional records of attack on man.	No significant data.
Simulium ornatipes Sk.	Fairly frequently recorded as larvae in all States except Tas. and the N.T. Recorded as a pest by Taylor (1944) but this is discounted by Mackerras & Mackerras (1948). Sometimes collected attracted to man but not known to feed.	No significant data.
Simulium peregrinum M. & M.	Far north Q'ld. only.	No data.
Simulium torresianum M. & M.	Torres Sts. islands.	No data.
Simulium sp. undescribed.	Roper R., N.T. Attacks man.	No other data.
Simulium sp. undescribed.	A different species from Kalumburu, W.A., known to attack man.	No other data.
Austrosimulium bancrofti (Tayl.).	Fairly frequently recorded in all States except S.A. and the N.T. Known to attack man, horse, dog, rabbit, kangaroo, wombat and eagle. Swarming attack has been observed on man, horse, rabbit, kangaroo and wombat. Diurnal.	Second in importance to *A. pestilens* as a pest as it does not occur in such enormous swarms. However, its wider distribution and independence of flood conditions, coupled with its range of attack on stock, would suggest it to be the most important species for epidemiological consideration.
Austrosimulium cornutum (Tonn.).	Limited records from N.S.W., Vic. and Tas.	No data.
Austrosimulium crassipes Tonn.	Southern Q'ld. to Vic. Few records.	No data.
Austrosimulium fulvicorne M. & M.	Only recorded from Fraser Is., Q'ld.	No data.
Austrosimulium furiosum (Sk.).	Known in all States except the N.T. Recorded attacking man, horse, ox, dog and rabbit. Occasional instances of vicious attack on man, horse and ox. Diurnal.	Could possibly be important in relation to stock but its erratic feeding behaviour requires explanation. See also *A. victoriae*.

TABLE 3.—*Continued.*

Distribution and Known Feeding Activity of Blood Sucking "Sandflies" Occurring in Australia.—Continued.

Species.	Summary of Data from all Sources.	Remarks.
SIMULIIDAE.—*Continued.*		
Austrosimulium magnum M. & M.	Northern Q'ld., limited records only.	No data.
Austrosimulium mirabile M. & M.	Southern Q'ld., limited records only.	No data.
Austrosimulium montanum M. & M.	N.S.W. and Vic., a mountain species.	No data.
Austrosimulium pestilens M. & M.	Central and south-western Q'ld. and north-western N.S.W. This species appears in immense swarms in the Dawson R. and western rivers after floods. Intense attacks on man, ox, sheep, dog and marsupials are well known. Typical experiences of the Dawson R. are described by Mackerras & Mackerras (1948) and effects on kangaroos and wallabies in the channel country are discussed in McCarthy (1961). Diurnal.	The best known of all Australian Simuliidae with important pest status, but see also remarks under *A. bancrofti*.
Austrosimulium torrentium Tonn.	N.S.W., Vic. and Tas. Only known record of attack was in ears of horse at Tidbinbilla, A.C.T.	No other data.
Austrosimulium victoriae (Roub.).	Southern Q'ld. to Tas. Known to attack man in southern Australia. Has once been taken from a rabbit warren. Diurnal.	In some cases of attack on man identification has not been precise owing to the difficulty of differentiating this species from *A. furiosum* as spirit specimens.
Simuliidae undifferentiated.	Recorded as pests of sheep and other animals in various parts of Q'ld. (Roberts, 1940). The earliest record of bird feeding by Simuliidae in Australia originated in Vic. (T. H. Johnson, unpublished).	
PSYCHODIDAE.		
Phlebotomus brevifilis Tonn.	Known only from Yass and Canberra. Has been experimentally fed on man.	No other data.
Phlebotomus brevifiloides Fair.	Known only from Yass.	No data.
Phlebotomus buccinator Fair.	Cairns only.	No data.
Phlebotomus englishi Tonn.	Yass only. Experimentally fed on lizard.	No other data.
Phlebotomus pexopharynx Fair.	Cairns only.	No data.
Phlebotomus queenslandi Hill.	Cairns only. Subspecies *meridionalis* Tonn. from Yass has been experimentally fed on lizard.	No other data.
Phlebotomus spp. unidentified.	Feeding on man and bird has been proven at Moree, and rabbit feeding at Uralla in N.S.W. Roberts (1952) figured a *Phlebotomus* as a cattle feeding species from Q'ld., but the evidence was circumstantial (Roberts, pers. comm.).	From this limited evidence of feeding it would appear that a variety of hosts are attacked in Australia.
Phlebotomus spp.	The now known range of this genus includes Perth, Adelaide, some ten widely dispersed coastal and inland localities in N.S.W., southern and northern Q'ld., and Darwin, N.T. Collections made at Charleville and Cloncurry, Q'ld., in May, 1955, by E. J. Reye gave a strong indication of an as yet unexplained association with cattle in cattleyards and also with poultry.	Field studies of this genus have been very meagre.

widespread *A. bancrofti* as a potential vector of livestock diseases. With the possible exception of *A. victoriae*, *A. furiosum* and *Simulium melatum*, breeding of other species would appear to be rather too sporadic and localized for them to emerge as significant species. In view of the marked preference of some overseas Simuliids for avian blood the two observations of bird feeding reported here might well point to a similar relationship in this country.

(*c*) *Phlebotomus* (Sandflies).

Although the blood-sucking genus *Phlebotomus* occurs in widely separated parts of Australia our knowledge of it is less than meagre. No observations have been made which would suggest that they deserve immediate investigation in relation to stock. However, in specialized studies of other "sandflies" watch should be kept for the possible presence of *Phlebotomus*.

Discussion Relating to Diseases.

The transmission of any disease of stock or domestic animals by "sandflies" in Australia has not been proven nor has this been seriously attempted.

Worm nodule of cattle (onchocerciasis), known to be *Culicoides* transmitted in Malaya, is widespread in Australia and the presumption that similar vectors will be responsible in Australia is justifiable. When geographic distribution as well as attack on cattle is taken into account possible suspects would be first *C. brevitarsis* and then *C. marksi* and *C. dycei*. *Onchocerca reticulata* of horses may also be presumed to have a *Culicoides* as vector, nor should the possibility of the recently recorded *Dipetalonema* of dogs in Australia (Dunsmore, 1961) being *Culicoides* transmitted be overlooked. Simuliidae, of course, may come into the picture for *Onchocerca gutturosa* of cattle.

The virus of ephemeral fever of cattle is almost certainly transmitted by a blood-sucking fly, but attempts to incriminate mosquitoes have not been successful; nor does the epidemiology fit easily to a mosquito explanation. Our present knowledge of the Ceratopogonidae does suggest that this group should come under suspicion and species such as *Lasiohelea townsvillensis* and *Culicoides brevitarsis* should certainly be investigated. Although the evidence for mosquito transmission of fowlpox is strong (Lee *et al.*, 1958) the further possibility of biting midge transmission is worthy of investigation.

Of the exotic diseases which present a potential threat to Australia, blue tongue virus of sheep is the most important. Known originally in South Africa and later in the U.S.A., in recent years the dramatic spread of this disease through North Africa and easternmost Europe, and later to Japan, is a clear indication that the virus has little difficulty in finding satisfactory indigenous vectors in countries outside its original home. Since sheep feeding by a variety of species of *Culicoides* has now been proven in Australia, potential vectors may well be present. The less intensively studied African horse sickness is another *Culicoides* transmitted virus disease of horses in Africa and India for which potential vectors might reasonably be expected to occur in Australia.

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THE INFLUENCE OF THE TIDE CYCLE ON CERTAIN SPECIES OF *CULICOIDES* (DIPTERA, CERATOPOGONIDAE).

By Eric J. Reye and David J. Lee.

(Ten Text-figures.)

[Read 28th November, 1962.]

Synopsis.

Observations are reported which relate the emergence of *Culicoides subimmaculatus* Lee & Reye and *Culicoides ornatus* Tayl. to the neap-tide periods. An analysis of the tide cycle correlated with this emergence rhythm suggests that the intertidal area from which emergence takes place is the mean neap zone.

Introduction.

Following the finding of the immature stages of *Culicoides subimmaculatus* Lee & Reye in the sand of an estuarine tidal flat (Lee, 1949, as an undescribed species) further attempts have been made to elucidate any rhythms that might be inherent in the long recognized occurrence of the intermittent character of plagues of pest biting midges. Early attempts to correlate information supplied by residents adjacent to areas recognized as being potential breeding grounds were not illuminating, even when the reports received from three areas were noted against a graph of the daily high tide levels. It is now clear that such observations, restricted largely to week-ends, and dependent on the outdoor activities of the observers, and the vagaries of weather in relation to biting midge activity, bore so little relation to population densities of the midges that reliable data could scarcely be expected.

Although it then became obvious that nothing short of a daily, reliable index of *Culicoides* abundance would provide the necessary basic data, means of obtaining this did not become available until 1956 when, through the co-operation of a resident at Careel Bay, on Pittwater just north of Sydney, the use of a light trap in sheltered scrub, fifty feet from the edge of a mangrove flat, was initiated. The suction light trap proved a very successful means of catching the local pest species, *Culicoides subimmaculatus*. Moreover the numbers caught by the single trap, operating through the hours of darkness, varied in such a way that a clear record of population densities could be obtained.

Peak catches were soon correlated with neap-tide periods and nil or meagre catches with spring tides. However, it still proved difficult to attain the ideal of a continuous nightly record due to enforced irregularity of attendance to the trap and it was not until the summer of 1957–1958 that a continuous record covering a six-weeks period could be obtained. However, the discontinuous records of the 1956–1957 season and also of the remainder of the 1957–1958 season showed nothing to conflict with the evidence presented below. Furthermore, one of us (E.J.R.) had the opportunity to conduct a similar series of light trapping in the vicinity of Darwin and obtained a similar relationship to the tide cycle for the northern pest species of estuarine areas, *Culicoides ornatus* Tayl.

Results at Careel Bay, Pittwater, New South Wales.

An attempt to record frequent light trap catches at the same catching point at Careel Bay as was used in the previous season commenced on 26:x:1957. In the early part of the season it was not possible to arrange for setting and clearing the trap every night and morning although more frequent visits, combined with local assistance, did result in a continuous period of 36 days during which single days were missed on only seven occasions. For the period up to the end of 1957 three peaks of emergence of *Culicoides subimmaculatus* were recorded and each of these coincided

with a neap-tide period. No significant catches were recorded at any other times, and although two other neap tides occurred in the period trapping was not effected for one, and for the other insignificant catches were recorded.

The first recorded peak, which followed nil catches for *C. subimmaculatus*, commenced on 31:x:57 and ceased on 3:xi:57, during which period a similar peak of emergence was recorded for *C. ornatus* at Darwin.

The total catch for this first *C. subimmaculatus* peak at Careel Bay totalled 361 for the four days. Of these 25% were males. The capture of males in reasonably high numbers is taken to be a conclusive indication of an emergence peak. The validity of this assumption rests on

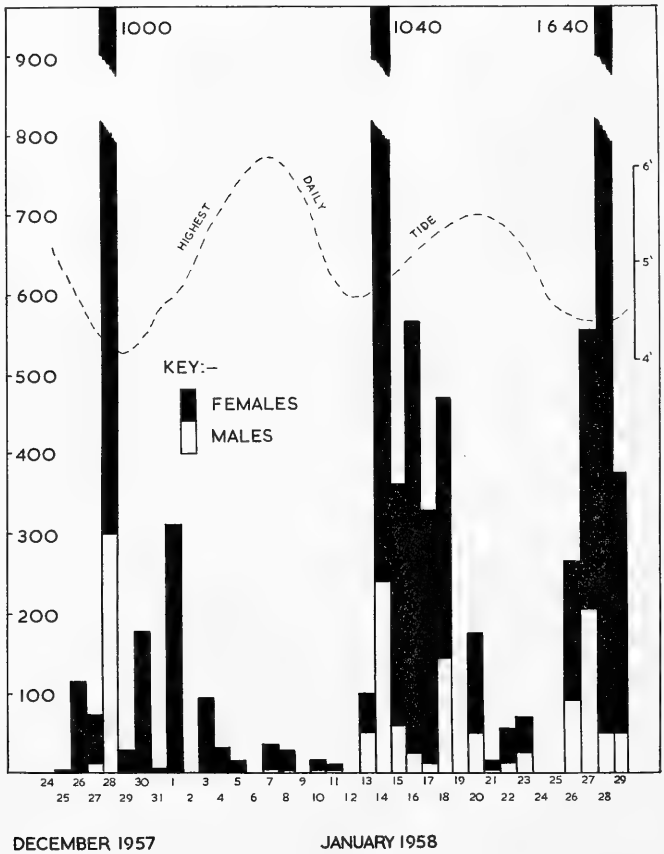


Fig. 1.—Nightly catches of *Culicoides subimmaculatus* in a light trap at Careel Bay, N.S.W. (males and females differentiated).

(i) the fact that reasonable numbers of males are only recorded when high catches of females are taken (in fact during 37 nights trapping at the end of 1957 females were taken on 30 occasions but males on only 9);

(ii) during a period of high catching rates males may be recorded for only the first two or three nights and then disappear, even though females continue to be caught for some time; and

(iii) the general observation that male Nematocera are short-lived.

The Careel Bay catches showed definite periodic peaks during the spring of 1957. They were not as high as those recorded in the exploratory trappings undertaken in the previous spring and without corroborative evidence might still be considered as possibly fluctuating with the varying climatic conditions which can influence trapping levels from night to night. However, the early summer catches, presented as a

histogram in Text-figure 1, strongly suggest a rhythmic pattern of emergence, which, superimposed on a tide graph, demonstrates a concentration of emergence during the neap tide period.

Apart from this neap-tide rhythm the recorded catches appear to show (i) a brief emergence period in the case of the first peak (26:xii:57–1:i:58) as indicated by the presence of males on only two consecutive days, (ii) a longer emergence period in the case of the other two peaks with the possibility of two consecutive periods of emergence in the case of the second (13:i:58–20:i:58), again on the evidence of male abundance. The fact that male numbers are usually well below 50% of the total catch is thought to have no other significance than a reflection of the distance of the catching station from probable emergence areas.

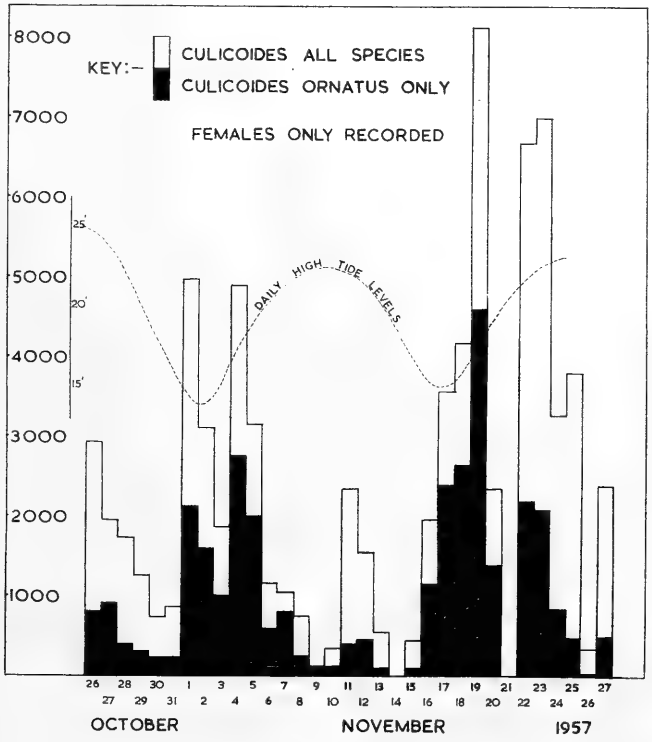


Fig. 2.—Nightly catches of *Culicoides ornatus* and other *Culicoides* in a light trap at the Quarantine Station, Darwin (females only recorded).

The somewhat different character of each of the peaks cannot be explained on the data available although two obvious variables do exist. The examination of the tide sequences does show variations in the character of successive neap periods and weather conditions will have a considerable effect on the survival of adults after each emergence period. The higher rate of catching at the last quarter of the moon at Darwin as compared with the first quarter catches could also reflect another phenomenon we have frequently observed, that light trap catches tend to be greater on moon-free nights than on nights with considerable illumination from the moon. At the last quarter of the moon, moonrise approximates midnight, whereas the moon is in the sky until midnight in the first quarter. Hence a dark sky in the early part of the night at the time of the second quarter neap tide may correlate with a relatively higher catching rate as compared with the first quarter neap.

Other species of *Culicoides*, in particular *C. marmoratus* Skuse, were also taken from time to time, but showed no correlations with the *C. subimmaculatus* catches or with any particular part of the tide cycle.

Results at Darwin, Northern Territory.

As at Careel Bay, a light trap was used to provide an index of *Culicoides* populations. The trap was operated at the Quarantine Station, an area known to be heavily infested by biting midges, from 25:x:57 to 24:xi:57 with the exception of two nights when it was used for exploratory catches elsewhere.

Parallel investigations established that *C. ornatus* was the dominant pest species in this area although several other species were also abundant. The catches in this area were numerically far greater than those experienced at Careel Bay and simply reflect the relative intensity of the pest problem. However, the size of the catches imposed problems of sorting and identification, especially as over 50% of the catches comprised undescribed species. Female midges only were counted and differentiated into *C. ornatus* and other species of *Culicoides*. These results are presented in histogram form in Text-figure 2.

Again there is a distinct coincidence of peaks of abundance of *C. ornatus* with the two periods of neap tides. For the other species of *Culicoides* the results are more complex; one species appears to parallel closely the peaks of *C. ornatus*, but is not a pest of man; two other species appear to have peaks approximating the spring tides, but again these are not pest species.

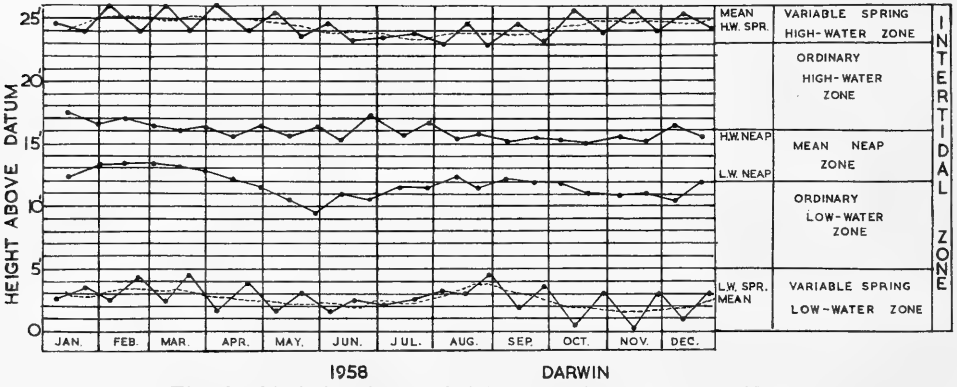


Fig. 3.—Variation in the height of spring and neap tides.

Discussion of the Results of Light Trap Catches.

Since parallel results concerning the pest species, *C. subimmaculatus* at Careel Bay and *C. ornatus* at Darwin, have been obtained correlating mass emergence of these with the period of neap tides it is felt that the ecological circumstances of the dominant estuarine pests of southern and northern coastlines respectively are essentially similar.

A tidal correlation introduces (i) the possibility of prediction of the appearance of pest swarms of these particular biting midges and (ii) the possibility of a theoretical determination of the breeding areas.

In relation to the former appearance in pest numbers of *C. subimmaculatus* may be expected to coincide with neap tides over the spring to autumn period. In Sydney and other southern areas predictions are unreliable to the extent that pest populations fail to appear on many of the neap tide periods; on the other hand they do not appear at other times. In northern areas the appearances of *C. ornatus* are more regular and predictions are less likely to fail. However, this statement is based on the limited observations reported above and a further eight weeks' observations undertaken at Darwin from May to July, 1958; it may not necessarily be true at other times.

In relation to breeding areas an emergence coinciding with one particular part of the tide cycle, from tidal flats, must be indicative of a recurrent feature of the tide cycle determining emergence. To explore this an analysis of tidal fluctuation has been undertaken.

Analysis of the Tide Cycle Relative to Potential Breeding Zones for Culicoides ornatus.

(*a*) *Annual Patterns and Tidal Zonation.*

Since the data on day to day *Culicoides* populations over a continuous period was more complete for Darwin and since the tidal amplitude was far greater (26 feet for Darwin, 6 feet for Sydney) an exploratory analysis of tidal fluctuations was undertaken for Darwin rather than Sydney.

The available data comprised the predictions for times and levels of daily high and low tides prepared by the Admiralty.

In order to arrive at an understanding of the seasonal changes of recognized variables (high-water spring tides, low-water spring tides, high-water neap tides and low-water neap tides) these were plotted on a graph for the 12 months of 1958. This graph (Text-figure 3) then showed a half-yearly variation in the height of the spring

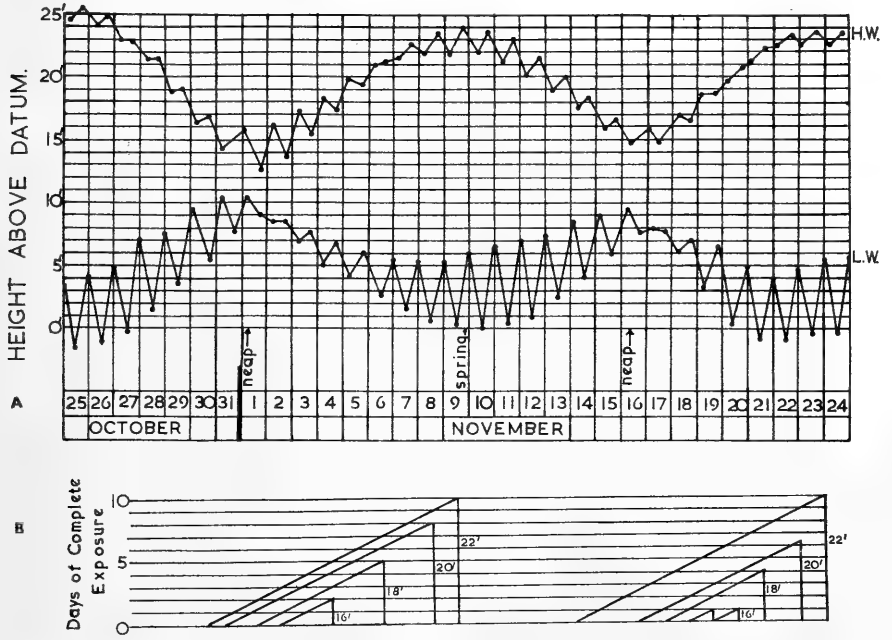
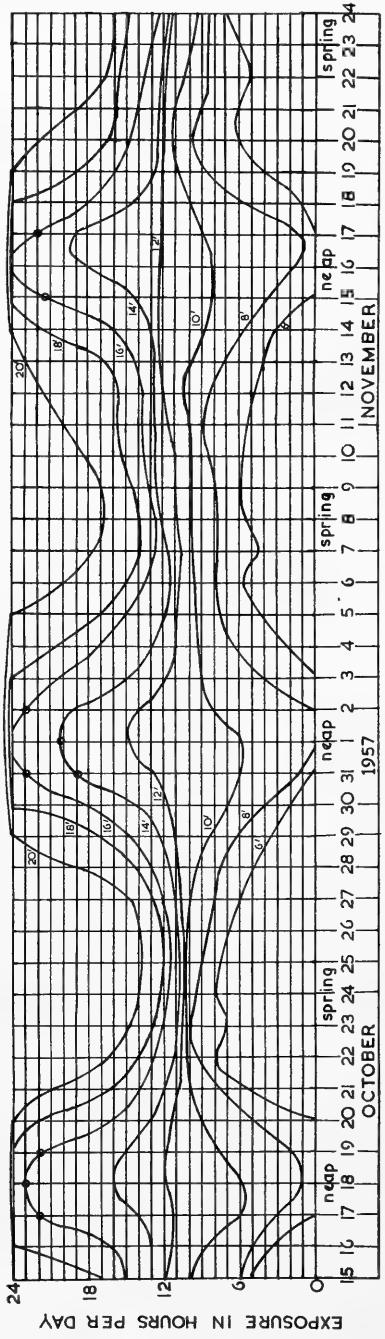


Fig. 4.—(*a*) Heights of high and low water, lunar tide cycle. Darwin, 1957; (*b*) Complete (24 hour) exposure at different levels (the same date scale as (*a*)).

tides. In the year 1958 the mean curve of high water springs reached its maxima about March and October and its minima in January and July with the July minimum the lower, that is, during the southern hemisphere winter. A somewhat similar, but not synchronous, variation occurred with the curve of mean low water springs; this was in fact nearer to the curve for low water neaps. Only slight variation occurred in the mean for high water neaps, and if any correlation does exist this appears to be in opposite phase to the mean for high water springs.

From this graph (Text-figure 3) it may be seen that the entire intertidal zone falls into the five conventionally recognized primary zones the characteristics of which, at Darwin, are as follows:

(i) *Variable Spring High Water Zone, 23′–26′.* The upper part of this (24′–26′) is immersed only around every second spring tide at the maximum of the half-yearly tide cycle and dries progressively as the mean high water spring falls; thus in 1958 the 25′–26′ zone was dry from mid-May to mid-October (5 months) and the 24′–25′ level was dry from the end of May to mid-August (2½ months). The lower part, 23′–24′, on the other hand, is wet by some three-quarters of all spring tides and would never be dry for more than one month at a time.



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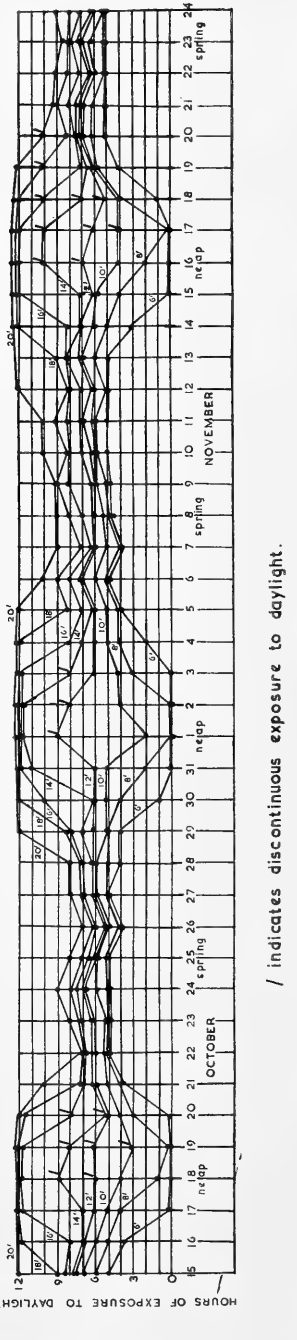

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Fig. 5.—Duration of daily exposure at different levels of inter-tidal zone. Darwin: computed from tide curves based on predicted heights. The plottings for the curves on this graph lay within ±1 hr of the curves.

Fig. 8.—Darwin: Duration of daily exposure to daylight (0700-1900 hrs C.A.T.) at different levels, 15th October to 24th November, 1957.

(ii) *Ordinary High Water Zone, 16′–23′.* This is exposed progressively for increasing periods per day as the fortnightly tide cycle wanes from spring to neap and is progressively immersed as it waxes to spring again.

(iii) *Mean Neap Zone, 12′–16′.* This is immersed and exposed in every tide cycle of approximately 12 hours. Its upper limit varies by ±1′ and its lower limit by ±1·5′, with occasionally greater variation.

(iv) *Ordinary Low Water Zone, 5′–12′.* This is immersed progressively for increasing periods per day as the fortnightly tide cycle wanes from spring to neap and is progressively exposed as it waxes to spring again.

(v) *Variable Low Water Spring Zone, 0′–5′.* This is not exposed by all low water spring tides.

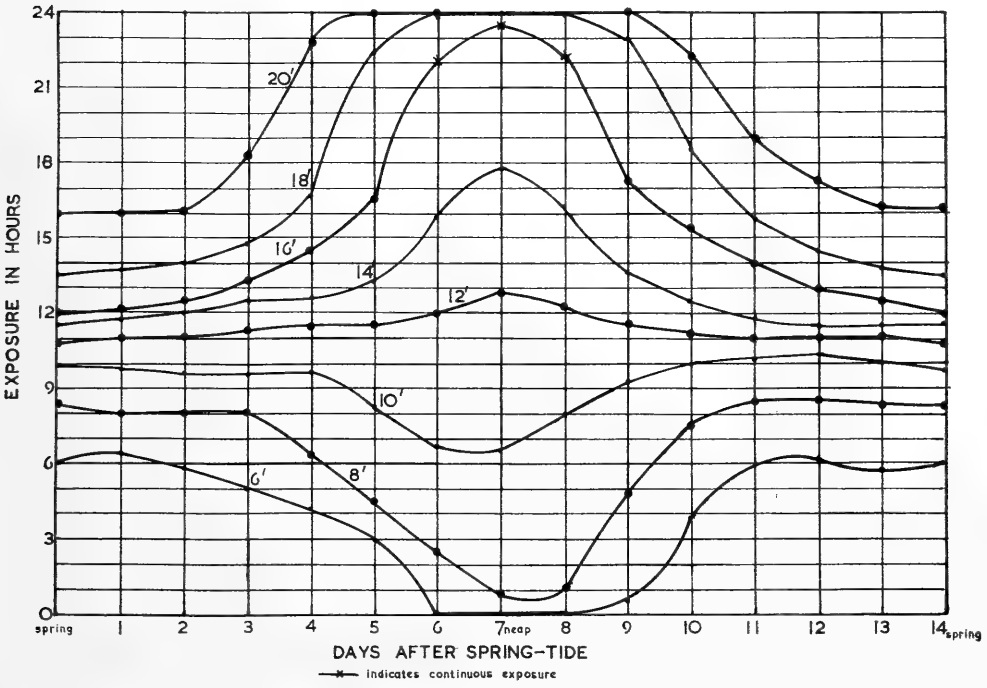

Fig. 6.—Duration of daily exposure at different levels of inter-tidal zone. Darwin: Composite of three cycles, 15th October to 24th November, 1957.

(b) The Lunar Tide Cycle.

The waxing of tide amplitude to spring tides about full and new moon, and its waning to neap tides about the first and last quarter of the moon produce a variation in the extent and duration of immersion and exposure of the intertidal zone, and the times of these vary from day to day. The further variations resultant from local meteorological conditions which may occur from time to time are ignored as the basic data are predicted, not recorded.

Complete (24 hours per day) exposure and immersion of various levels in the intertidal zone can be computed from a simple graph of heights of high water and low water through the cycle (Text-figure 4*a*) and plotted as a series to show duration and position in the cycle. This is done for exposures from 16′ to 22′ at 2′ intervals in Text-figure 4*b* for the period in 1957 during which light trap catches were made.

Incomplete exposures (less than 24 hours per day) can only be computed from curves drawn for each tide since only the times of the extremes (high tide and low tide) are available from prediction tables. A complete continuous graph of the water level at any given time has been constructed for the period 15:x:1957 to 25:xi:1957,

the light trap observation period. Since the rate of rise and fall varies from hour to hour the rough method of computing changes of level applicable to water fairly open to the sea was employed. This involved dividing the predicted rise or fall from a low to the next high tide and vice versa (approximately six hours) into twelfths, then in successive sixths of the time the change will be 1/12, 2/12, 3/12, 3/12, 2/12 and 1/12 of the predicted rise or fall. Freehand curves incorporating this formula were used to derive the continuous graph. This was only feasible on a graph which exceeded four feet in length and it is not reproduced herein as any reasonable reduction makes it impossible to read.

From the curves in this graph it was possible to derive the duration of exposure at different levels for each day. In Text-figure 5 these have been plotted and brought to smooth curves (with a variation of ±1 hour) for contours from 6′ to 20′ with contour intervals of 2′.

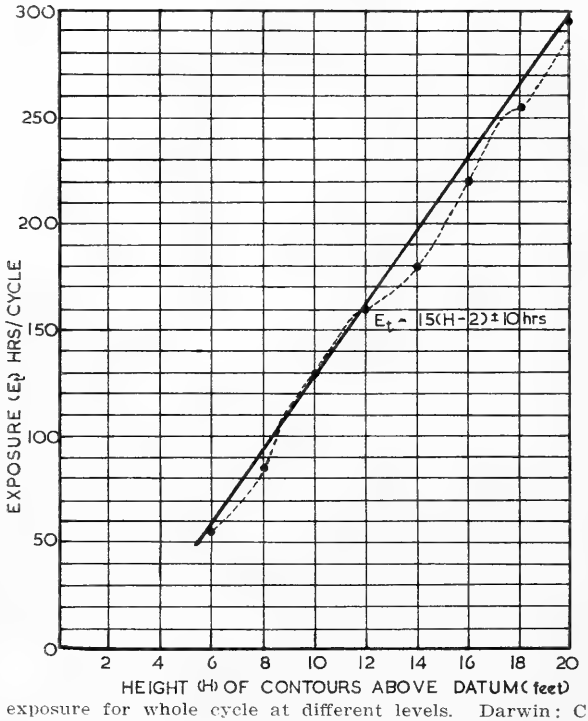

Fig. 7.—Total exposure for whole cycle at different levels. Darwin: Computed from the composite of three cycles.

These exposure curves show a fairly regular pattern of increase and decrease through the cycle spring—neap—spring. The greater exposure of 12′ and 14′ contours about the neap of November 1 as compared with the other two neaps may be due to its preceding the full moon spring of November 8. On the whole, however, the patterns are sufficiently regular for a mean pattern to be drawn from them.

Text-figure 6 shows this mean pattern and it will be seen that there is little variation in exposure through the cycle at 12′, but that exposure increases above 12′ and decreases below 12′ as the neap is approached. From 16′ to 20′ the increases are fairly rapid, beginning for 16′ at 2 to 3 days, for 18′ at 3 to 4 days and for 20′ at 4 to 5 days before the neap. The proportional increase is largest at 16′ where also the exposure on neap −1 to neap +1 days, though less than 24 hours, is for one continuous period, that is, it is washed by only one tide per day at this time and these tides do not immerse it deeply. Below 12′ the 8′ level shows the largest proportional increase in exposure occurring at 1 to 2 days after the neap; for the 6′ level this increase commences 2–3 days after the neap.

From the mean curves the total hours of exposure at different levels for the whole 14 days cycle can be computed and when plotted (Text-figure 7) show a roughly linear relationship to the height of the contour above datum, given by total exposure for 14 days cycle = 15 (contour height − 2′) ±10 hours.

In a similar fashion the continuous tide curves can be used to derive the duration of exposure to daylight for the different contours on each day. When these are plotted (Text-figure 8) it is found that they follow the same general pattern as in Text-figure 3 but with the difference that where most periods of exposure per day (24 hours) of less than 24 hours are made up of two periods, most periods of exposure to daylight are continuous. Discontinuous daylight exposure occurs mostly on the day of the neap and the two following days, and mostly involving the zone 10′–16′. It will be seen in Text-figure 6 that these discontinuous daylight exposures group into patterns of which the 12′, 12′, 14′ sequence occurs in all three and two other sequences (14′, 14′, 16′ and 10′, 12′) occur in the other two. These could be of biological significance, but, in the absence of a similar analysis for the whole year, the only deduction possible at this stage is that, weather permitting, at and following the neap tides there will be a warmer layer of water over the mean neap zone (as it will be a sunlit intrusion of the tide) where this is gently sloped than is likely at other times.

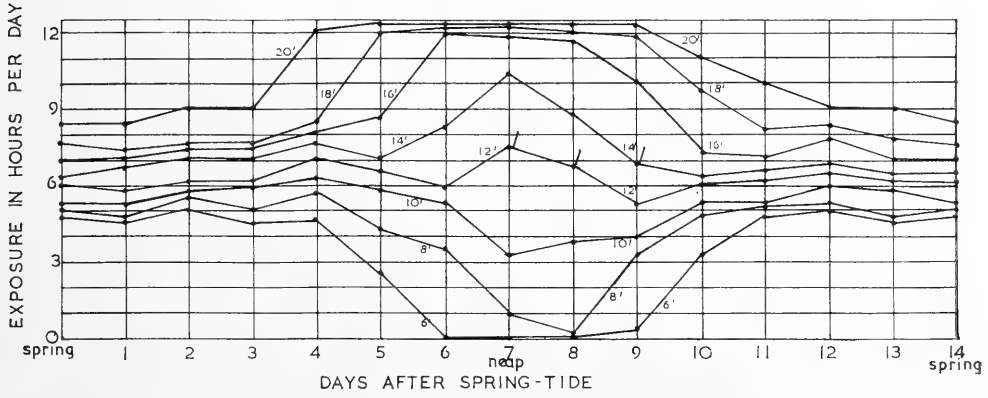

Fig. 9.—Duration of daily exposure at different levels of inter-tidal zone. (Daylight exposure, 0700-1900 hrs C.A.T.) Darwin: Composite of three cycles, 15th October to 24th November, 1957.

The three cycles of exposure to daylight are sufficiently similar to permit the drawing of a mean (Text-figure 9) and the significant increases in exposure to daylight above the 12′ contour bear the same relation to the neap tide as do the exposures per day and are of similar proportional magnitude.

As for total exposure for the 24 hours the sum total of hours exposure to daylight for the whole 14-day cycle can be computed and again there is a roughly linear relationship to contour height (Text-figure 10) given by the formula total daylight exposure per cycle = 7·5 (contour height) ±5 hours.

Application of Tide Cycle Analysis to Culicoides *Breeding.*

Since it has been established that peak emergence of important species of *Culicoides* (*ornatus* and *subimmaculatus*) coincides with the period of neap tide and may continue for up to four days after the neap tide, then decline to nothing at spring tides, some information on the possible breeding zones may be derived from the tide graphs.

This single peak in each 14-days tide cycle indicates that the zone of significance lies roughly between 10′ and 15′ above datum for Darwin. Any other single peak would have to correlate with the spring tide. If the breeding zone lay between 15′ and

24′, or if it lay between datum (0′) and 10′, then the emergence peaks should be bimodal within the 14-day cycle since the tidal phenomena between neap and spring occur twice in each cycle.

Hence it seems reasonable to assume, in the case of Darwin, that the breeding zone lies between the approximate limits of 10′ and 15′ above datum, in other words in the mean neap zone. In the latter terms this assumption may be applied to other areas with tidal amplitudes of considerably less magnitude than Darwin.

The probable exposure of the mean neap zone per 14-day (336 hour) cycle, either total or to daylight only, may be derived from Text-figures 7 and 10. The total exposure of 130–200 hours is roughly 50%, but of this 70–110 hours or roughly 70% of the exposure is in daylight (and conversely it is covered in daylight for 30% of the time). This higher proportion of exposure to daylight may be significant. Moreover the mean neap zone is the one zone which is alternately covered and exposed by almost every tide, while towards the neap tide, when emergence of *C. ornatus* and *C. subimmaculatus* takes place, the depth of cover is decreased and both total and daylight exposure increased.

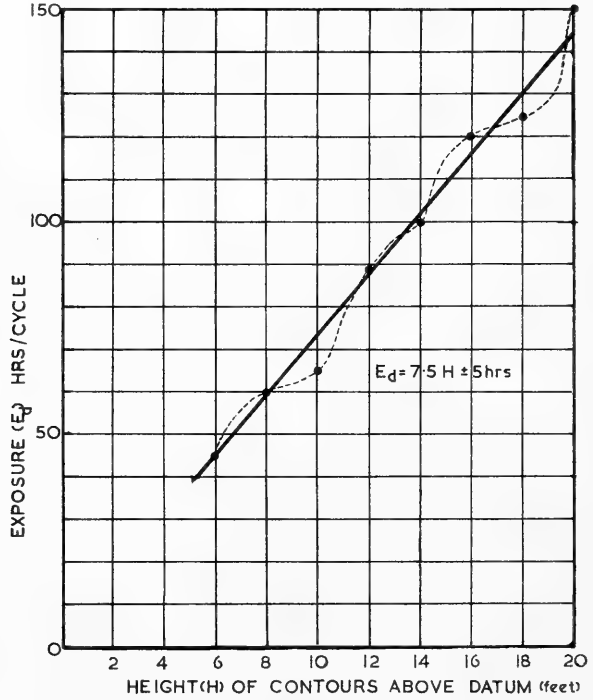

Fig. 10.—Total exposure to daylight for whole cycle at different levels. Darwin: Computed from the composite of three cycles.

Within the zone of tidal influence this mean neap zone would appear to be by far the most suitable zone for insects such as biting midges, which basically require air, water and soil in their breeding medium. Nevertheless field evidence suggests that other zones, superficially less favourable, are also utilized by other species of *Culicoides* which at present are not known to be of primary importance as pests.

The immature stages of *C. subimmaculatus* had proved elusive following the original find of Lee (1949). As knowledge of the species was accumulated it became evident that there was an association with sandy rather than muddy foreshores, and with mangrove. This still left a wide area for search, but with the addition of the correlation of population with the tide cycle it became evident that the search should be directed towards the mean neap zone.

A sandy beach on Karragurra I. in Moreton Bay, Queensland, was selected in 1960 for a rough trial. The beach, of pale brown-white quartz sand, has a low, largely grass-covered dune, behind which is a shallow, slightly muddy sand swampy area flooded at spring high tides, scarcely wet at neap high tides and with scattered small mangroves in it; its outfall passes through a belt of larger mangroves which cover about one-third of the length of the foreshore. Larvae of *C. subimmaculatus* were found in sand samples from the region of neap high water both within the swampy area and on the outside beach, especially in and near the pellets turned up by soldier crabs in the vicinity of their holes where these were near the mangroves or on the beach partly sheltered by mangroves. Samples taken away from these areas (including soldier crab areas), both vertically and horizontally, were barren of larvae of this species.

Soil samples from a soldier crab habitat in mean neap zone at Careel Bay at approximately the same time also yielded a very few *C. subimmaculatus*. These were the only ones taken in the area from a wide range of samples. Adult catches at this time were continuously well below pest proportions so this meagre recovery is taken to confirm the Queensland findings.

The apparent association with soldier crabs may be fortuitous, but at least one undescribed Australian species of *Culicoides* is found most easily in association with crabs. We feel this point is worthy of further investigation as it may provide a readily usable indicator for larval habitats.

Acknowledgements.

We wish to acknowledge the assistance provided by the Commonwealth Health Department at Darwin for the work undertaken in that area, Margaret E. Reye for assistance in the sorting of Darwin light trap catches, the facilities provided by Mr. I. Grinblatt at Careel Bay, and Mr. D. Gibb and Miss J. McDougall for processing many soil samples from Careel Bay.

Reference.

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CHROMOSOME RACES IN *GOODENIA BELLIDIFOLIA* SM.

By W. J. Peacock, Linnean Macleay Fellow of the Society in Botany,
Botany Department, University of Sydney.

(Plates xiv-xv; two Text-figures.)

[Read 28th November, 1962.]

Synopsis.

Goodenia bellidifolia Sm. has several chromosome races. Diploid, tetraploid, hexaploid and octoploid numbers have been found in determinations made on plants from some 130 localities. The chromosome races present a clear-cut distribution pattern on the slopes, highlands and coastal regions of New South Wales and southern Queensland. Despite close contact in several regions the cytodemes remain strictly allopatric. Morphological and cytological data indicate that the various chromosome forms have been generated in an intraspecific process. Evidence of several independent origins of both tetraploidy and hexaploidy is presented.

The restriction of each chromosome race to a major physiographical region has led to the inference that the establishment of cytological complexity and the correlated geographical expansion of the species were directly associated with the late Pliocene uplift of the eastern highlands.

This example of Quaternary evolution is briefly considered in relation to the development of the Australian flora as a whole.

Introduction.

Cytological investigations in the Goodeniaceae, one of the major herbaceous groups in the palaeoaustralian element of the Australian flora, have revealed a pattern of chromosome evolution which differs markedly from that characteristic of the hardwood families (Peacock, 1962; Smith-White, 1959). In particular, the Goodeniaceae exhibits a high incidence of polyploidy both at specific and subspecific levels.

The intraspecific polyploid series of the family may be regarded as being of two types with respect to distributional range—continental or subcontinental. *Goodenia pinnatifida* Schlecht. is diploid in Western Australia and changes across the continent through tetraploidy to hexaploidy in eastern New South Wales. On the other hand *Goodenia bellidifolia* Sm., in which a number of chromosome races have been found, has a subcontinental distribution occurring only on the slopes, highlands and coastal regions of New South Wales and southern Queensland.

Inferences as to past migrations and evolutionary development of taxa can often be made on the basis of distribution patterns of units in a polyploidy series. This is principally because, as Darlington (1956) has pointed out, any form of genetic differentiation is likely to be correlated with geographical and ecological change and delimitation. Stebbins (1950) has emphasized that the availability of new niches is essential for the establishment of a polyploid. As with other mechanisms, evolutionary change by polyploidy relies on the coincidence of opportunity and occurrence.

G. bellidifolia appears to be a case in which the probable historical and geographical development can be inferred from a correlation of the distribution of the chromosome races with major ecological changes of the past. The species, a well-defined member of the Racemosae (Section Eugoodenia), is a perennial herb with radical leaves and unbranched inflorescence scapes.

Methods.

Chromosome determinations were made either from meiotic material or from mitosis in ovule wall tissue. All material was fixed in ethanol-acetic acid (3:1) and stained in aceto-orcein. Ovules were hydrolysed in N HCl for six minutes at 60° C. before staining.

Voucher specimens have been lodged in the herbarium of the Botany Department, University of Sydney.

Observations.

a. Chromosome Numbers.

The basic number in *G. bellidifolia*, in conformity with most other species of *Goodenia*, is x = 8. All chromosomes are metacentric or submetacentric, and are of small and uniform size. One of the chromosomes has a satellite on one arm.

Determinations have been made on plants from 130 localities extending over the full range of the species. Four chromosome races have been identified: diploid, 2n = 16 (32 localities); tetraploid, 2n = 32 (72 localities); hexaploid, 2n = 48 (25 localities); and octoploid, 2n = 64 (1 locality).

b. Characteristics of Meiosis.

Throughout the species chiasma formation is restricted in all chromosomes to the distal region of the chromosome arms. This form of localization is widespread in the Goodeniaceae. Chiasma frequency is low, being only slightly greater than one per bivalent. Summarized data on chiasma frequency for eight plants are presented in Table 1. The means quoted are based on an analysis of at least thirty cells. The data show that there is no significant change in chiasma frequency through the levels of ploidy.

Table 1.

Chiasma Frequencies and Pollen Fertilities.

Plant No.	Locality.	Diploid No.	Mean No. X'ta/cell.	Pollen % Fertility.	Comments.
6012. 3.1	Inverell	16	8·3±0·01	100	Regular rod bivalents.
6111.11.1	Bundarra	16	9·3±0·02	100	0–3 ring bivalents.
5910. 1.1	Willoughby	32	16·0±0·00	95	Regular rod bivalents.
609.50.1	Terry Hills	32	16·9±0·20	41	Quadrivalents in some cells. Br.+f. in most.
6111.18.1	Deepwater	32	17·1±0·25	80	12/52 cells with 2 univalents. 4/52 with quadrivalents.
611. 5.1	Muogamarra	32	16·4±0·18	73	1 or 2 quadrivalents in 8/36 cells. Univalents in 10/36.
611. 3.2	Bulahdelah	48	24·8±0·14	70	Univalents and multivalents. 1 hexavalent in 30 cells.
611.23.1	Morisset	48	25·3±0·31	62	Univalents in 20/32 cells. Rare A_I Br.+f.

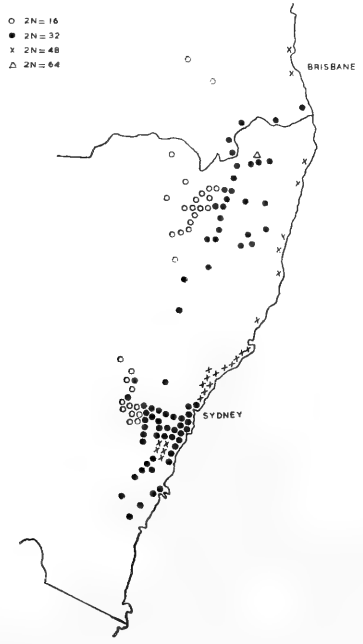
Meiosis is regular in the diploids which show no evidence of structural hybridity. Occasional chromosome loss from the spindle is the only aberration which has been observed. Individual plants differ in chiasma frequency, some having up to three ring bivalents per pollen mother cell, whereas other plants regularly have eight rod bivalents at M_I and only rarely form a bivalent with two chiasmata (Pl. xiv, fig. 1). Such variation can be expected since chiasma characteristics are subject to both genetic and environmental variation (e.g., Rees, 1955; Rees and Thompson, 1956). These inter-plant differences are more marked at the tetraploid level. In some localities, e.g., Willoughby, all plants show regular rod bivalent formation and have an extremely orderly meiosis. Other tetraploids have a higher chiasma frequency, occasional multivalents and univalents at first metaphase, and, consequentially, reduced pollen fertility (Pl. xiv, figs 2, 3, 4, 6, Pl. xv, fig. 1). A low but significant frequency of multivalents and univalents is also characteristic of all hexaploids which have been examined (Pl. xiv, fig. 5, Pl. xv, fig. 2). Univalents generally divide at first anaphase and are often lost in the second division (Pl. 2, figs. 3, 4). Microcytes and restitution dyads have been found in the polyploids, both presumably resulting from meiotic irregularity.

Bridge and fragment configurations have been found in low frequency in a number of tetraploid and hexaploid plants (Pl. xv, figs 5, 6). In one tetraploid plant from Terry Hills (cf. Table 1) and in one from Mt. Victoria, however, almost every first anaphase cell possessed a bridge and fragment. It is not known whether inversion hybridity or breakage and non-sister chromatid reunion is responsible for this unusual

behaviour, but the latter mechanism is favoured. With metacentric chromosomes and a chiasma frequency of approximately one per potential bivalent, it is improbable that, with inversion hybridity, the one chiasma would always form in the one chromosome arm and in the inversion loop. The population frequency of this type of bridge formation in the polyploids is not known.

c. The Distribution of the Chromosome Races.

Text-figure 1 shows the distribution of plants of the various levels of polyploidy. The diploids occur on the western escarpment and slopes of the Great Dividing Range, and are replaced on the Tablelands by the tetraploid form. In the north, the tetraploid is montane, reaching the coast only along the Macpherson Ranges, but in the south it occupies the coastal plains as well as the mountains. Fifty miles north of Sydney a hexaploid race replaces the tetraploid on the coast, and extends as far north as Caboolture in Queensland. A distinct area of hexaploids occurs in the Picton-Bargo district south-west of Sydney. The single octoploid determination was made in a collection from an otherwise tetraploid population between Drake and Tabulam in northern New South Wales.



Text-figure 1. The distribution of chromosome races in *Goodenia bellidifolia*.

There appears to be a discontinuity in the distribution of both the diploid and tetraploid races forming disjunct northern and southern areas, this being particularly marked in the diploid. Inspection of herbarium records has shown that no specimens have been collected from the intermediate region, indicating that the suggested disjunction may be real.

The chromosome races have completely allopatric distributions. Although there are several regions of contact, e.g., diploid/tetraploid on the western side of the central and northern tablelands, tetraploid/hexaploid in the Gosford-Wyong area and in the Picton-Bargo region, no cases of overlap have been discovered. High density sampling of the diploid/tetraploid contact zone in the Hartley-Bell-Mt. Victoria region has revealed a remarkably strict geographic replacement between the cytodemes. The diploid occurs extensively along the base of the western escarpment and extends up the mountains for some distance. Its altitudinal limit is aspect dependent: on north-

facing slopes it does not occur above 2,700′, whereas on southern aspects it extends almost to the plateau at about 3,000′. Collections made on three northern aspect slopes showed that in each case the tetraploid extended from the plateau down to approximately 2,800′, leaving a zone of about one hundred vertical feet where neither chromosome race occurs. No triploids were found during the investigation (approxmately 100 plants in the marginal regions were examined cytologically).

A parallel sharp delimitation of diploid and tetraploid was found to occur in the north of the State near Bundarra, Glen Innes and Emmaville.

The junction of the hexaploid and tetraploid cytodemes north of Sydney does not present such a spectacular situation, but the replacement is just as precise. In this area the cytodemes are separated by a band from 5 to 10 miles wide of unsuitable habitat (either wet sclerophyll forest or swamp lands). Although no intensive collections have been made in the Picton district, the determinations that have been made suggest that the hexaploid has a discrete range. This southern hexaploid race is an aggressive form with highly developed vegetative propagation activity. Large populations occur in disturbed areas and encroachment on surrounding tetraploid territory would seem to be highly probable.

d. Correlation of Morphological Characteristics and Chromosome Number.

No gross differences in overall size exist between plants at different ploid levels, but individual cell size is correlated with chromosome number. This is shown by size of pollen grains and by number of stomates per unit leaf area (Table 2).

TABLE 2.

Pollen Diameter and Stomate Number.

Plant No.	Locality.	Diploid	Mean Pollen Grain Diameter (μ).	Mean No. of Stomates/unit Area.
6112.11.1	Hartley	16	26·48±0·24	12·1
6111.12.1	Bundarra	16	25·71±0·33	—
6012.50.2	Leura	32	31·30±0·34	9·4
611.11.1	Mittagong	32	31·24±0·40	—
611.25.1	Wyee	48	38·38±0·93	—
611.14.1	Bargo	48	34·26±0·30	8·0

Field observations suggested that the northern and southern diploids differ with respect to leaf shape, the leaves of the northern forms being more or less spathulate, whereas those of the southern forms tend to be lanceolate. Data were therefore obtained from herbarium specimens. In the collection of these data plants were classified as northern if collected north of the Hunter Valley–Cassilis Gap, and as southern if collected south of this line. Three fully grown leaves were chosen from each of 143 specimens (35 northern, 108 southern), and two measurements were made on each leaf. These were: the maximum width (Y), and the distance from the leaf apex to the line of greatest width (X). Average $\overline{X}$ and $\overline{Y}$ values for each plant were computed. The data are illustrated in Text-figure 2.

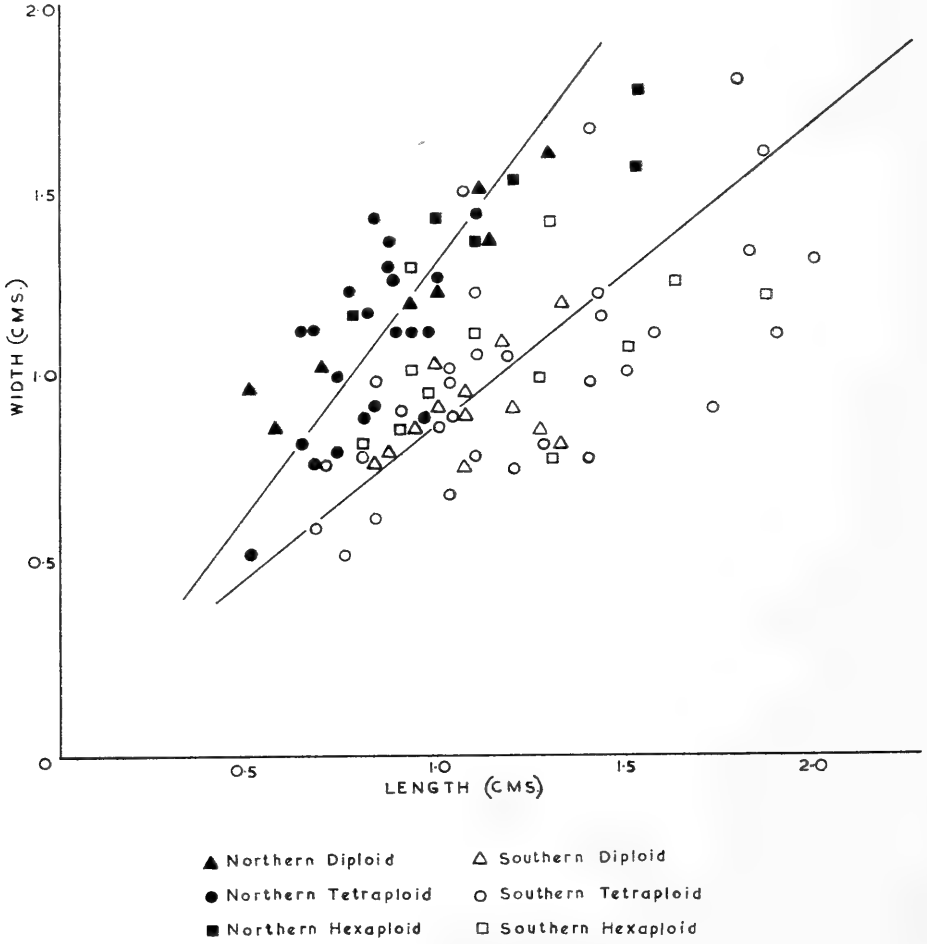
This scatter diagram clearly shows that there is a difference in leaf shape between northern and southern plants irrespective of chromosone number. The line of best fit to each set of points was obtained from an equation incorporating Bartlett's regression coefficient (Simpson, Roe and Lewontin, 1960, p. 232). A summary of this analysis is presented in Table 3.

DISCUSSION.

1. *The Nature of the Polyploid Series.*

a. Morphology. The species, through the different levels of ploidy, is uniform in overall morphology, but the chromosome races can be distinguished on the basis of pollen grain diameter or stomate size since there is a positive correlation between individual cell size and chromosome number.

The analysis on leaf shape has shown that a geographical cline exists and that the cline holds over all levels of polyploidy. This means either that the clinal variation was established at the diploid level before the advent of the polyploid races, or that there has been an identical response to selection by each of the chromosome races in both the northern and southern regions. The improbability of several independent origins of a quantitative morphological characteristic is heightened when the very different ecological situations of the chromosome races are considered. The first



Text-figure 2. Leaf shape in plants from the northern and southern regions.

hypothesis is thus considered to be more likely acceptable. A cline in rosette morphology, which involves leaf-position as well as leaf-shape, could well have been a selective response in the diploid to environmental conditions over the distributional range.

If the origin of the cline is regarded as being a feature of the species prior to the origin of the cytological complexity, then the parallel differences in the tetraploid provide evidence for multiple occurrences of this race. A minimal requirement would be that the northern "spathulate" and the southern "lanceolate" diploids were each progenitors of a tetraploid form. The fact that the tetraploid race occurs in a wide variety of niches over an extensive range is suggestive of a reasonable age of establishment and several occurrences would be highly probable.

At the hexaploid level the marked disjunction, the contrasting ecological niches and the different leaf morphologies argue a strong case for at least two independent origins of this chromosome number.

b. Cytology. The presence of maximum association multivalents in meiosis of the polyploids implies that all the constituent genomes have a degree of homology. Although the frequency of multivalent formation is low, it cannot be argued that the component genomes have only limited homology. With the observed chiasma frequency in the diploid of one chiasma per bivalent only a low frequency of multiple associations would be expected, even in a full autotetraploid.

In general pollen fertility varies inversely with the level of ploidy, but in some localities the tetraploids have very high pollen fertility (Table 1). In these plants there is regular formation of rod bivalents with consequent normal meiosis. This may mean that these tetraploids differ qualitatively from most of the tetraploid race in the degree of homology between their genomes. Alternatively it is possible that in some habitats there has been strong selection for plants tending to form bivalents, thus resulting in "diploidization" of the tetraploid.

TABLE 3.

Summary of Leaf Shape Analysis.

Item.	Southern Localities.	Northern Localities.
Number of plants	N=108	N=35
Mean lengths	$\overline{Y}$ = 95·21 $\overline{X}$ =108·92	$\overline{Y}$ =118·26 $\overline{X}$ = 90·46
Group mean lengths	$\overline{Y}_1$= 69·03 $\overline{X}_1$= 90·44	$\overline{Y}_1$= 88·89 $\overline{X}_1$= 69·17
	$\overline{Y}_3$=124·36 $\overline{X}_3$=134·53	$\overline{Y}_3$=147·25 $\overline{X}_3$=113·00
Variances and covariance ..	S_Y^2 = 718·954	S_Y^2 =786·772
	S_X^2 =1063·161	S_X^2 =654·709
	S_{XY}= 608·324	S_{XY}=594·216
Bartlett's coeff.	B=0·80±0·21	B= 1·34±0·31
Axis intercept	A=8·41±3·94	A=−2·59±6·63
Regression line equation	Y=8·41+0·80X	Y=−2·59+1·34X

Analysis of the chromosome races by karyotype studies is not practicable because of the uniformity of chromosome size and morphology, but mitotic preparations have shown that the satellite chromosome is represented twice in the tetraploid and three times in the hexaploid complements. This evidence supports the inference from meiotic data that some degree of relationship exists between the chromosome sets in the polyploids.

c. Modes of Origin. The tetraploid race of *G. bellidifolia* resembles the diploid very closely in general morphology and it is tempting to suggest that it has arisen from an intraspecific doubling rather than from interspecific hybridization. However, Stebbins (1950) quotes examples of strict alloploids which resemble one or other of the parental species very closely, e.g., *Nasturtium microphyllum* and *Madia citrigracilis*. The formation of multivalents in frequencies that could be expected on the basis of close homology between the chromosome sets would seem to strengthen the case for intra-specific origin, but even chromosome pairing data can lead to false inferences (e.g., *Primula kewensis* and *Lycopersicum peruvianum-esculentum* cited by Stebbins). The evidence of multiple, geographically disjunct occurrences of tetraploidy possibly supports intra- rather than inter-specific origins.

It would be of value to have information from a diploid-tetraploid interbreeding programme, but no such data are yet available. Triploids have not been found in the field, but, of course, may occur occasionally or sporadically.

With the above qualifications in mind, the morphological and cytological data available suggest that the tetraploids are effectively autoploid. This autoploidy may have involved hybridization between different ecotypes of the diploid species so that genic homology may not have been even initially absolute.

The single octoploid plant which was found in a tetraploid population almost certainly resulted from somatic doubling and may be regarded as an auto-tetraploid in origin.

Since the hexaploids are morphologically homogeneous with the diploids and tetraploids, and form multiple associations at meiosis, intra-specific origins may again be inferred with the same reservations as for the tetraploid. Furthermore, since the hexaploids in both of the geographically separated areas are associated only with the tetraploid race and are far removed from the diploids, it seems probable that the union of an unreduced gamete with a normal tetraploid gamete was the mode of genesis of the hexaploid number. However, the possibility that the diploid had a more extensive distribution in the past cannot be completely ruled out, so the hexaploid may have resulted from a somatic doubling of a triploid hybrid.

2. *Interpretation of the Distribution Pattern.*

The clear-cut distribution pattern of the chromosome races may be examined from both a localized ecological level and a wider geographical basis.

a. Ecological. The allopatry of the chromosome forms is emphasized by the strict replacements that have been found in the regions of contact. The precision of the change from diploid to tetraploid over a vertical range of approximately 100′ in the central tablelands is comparable with that described by Lorkovic (1958) between species of the butterfly genus *Erebia.* But whereas in *Erebia* Lorkovic suggests that mutual incompatibility results in elimination of one or other of the species from a particular zone, an ecological discrimination is demanded in plants. It is not known just what factor or factors of the environment operate over such a relatively small region in such a way as to reverse the selective values of the two chromosome races, but presumably a threshold level is established for the ecological tolerances of both the diploid and tetraploid. It is probable that different environmental conditions are limiting at the various contact zones, e.g., on the northern and central tablelands. An ecological and physiological investigation of the species would be extremely valuable.

b. Geographical. A marked geographical pattern holds for the units in the *G. bellidifolia* polyploid series: the distributional range of each chromosome race conforms to a major physiographical and climatological region, these being determined directly and indirectly by the eastern highlands.

Since the various cytodemes have discrete but adjoining ranges, it is probable that polyploidy has enabled extension of the species' distribution by migration. The direction of this migration must have been from west to east rather than the reverse since the development of a polyploid series must always initiate at the diploid level.

There is no evidence that the polyploids have replaced the diploids in their respective areas, but rather that they have been colonizers in regions which were unavailable to the diploid. The southern hexaploid race possibly provides an exception since it appears to be colonizing by direct competition rather than by migration into new niches. An efficient system of vegetative reproduction has apparently conferred competitive superiority over the surrounding tetraploids despite lower fertility in sexual reproduction.

Polyploidy often provides greater potential recombination, and hence an extended or possibly different range of adaptability, on a species. Such would be the case in the *Goodenia bellidifolia* tetraploid if it were an inter-ecotypic autoploid as has been suggested. This new genetic potential, together with any direct *per se* effect of polyploidy, would confer high selective value on a polyploid if the opportunity for utilization of these properties were to arise. The provision of a large new area for colonization would be such an opportunity.

The major change in the topography of eastern Australia at the end of the Pliocene (David, 1950), when uplift of the Great Dividing Range took place, would have provided extensive new montane and radically changed coastal habitats. It is highly probable that this large-scale occurrence of new niches in the early Quaternary was

the evolutionary opportunity for the establishment of cytological complexity and correlated geographical expansion in *G. bellidifolia*. The species provides an example of Quaternary evolution at the subspecific level.

3. *Relation to the Evolution of the Australian Flora.*

Smith-White (1959) has presented a general hypothesis on the evolution of the Australian flora based principally upon patterns of chromosomal change in some hard-wooded palaeoaustralian families and subfamilies. The herbaceous Goodeniaceae has provided supporting evidence for this hypothesis (Peacock, 1962). In the hardwood families, generic levels of evolution are in general early Tertiary, and specific levels later Tertiary, after the establishment of an east-west migration barrier. The available evidence suggests that evolutionary changes in the hardwood groups during the Quaternary have been minor, but Briggs (1960) has been able to show that speciation in the eastern *Darwinias* can be related to Quaternary topographical and climatic changes.

G. bellidifolia provides a demonstration that in herbaceous groups chromosome changes have played a part in Quaternary evolution. The situation in this species parallels rather closely that reported for *Themeda* by Hayman (1960), in which routes of migration within the continent can be traced by an analytical study of polyploid distribution patterns. In both *Themeda* and *G. bellidifolia* chromosome number changes are associated with the eastern highlands.

Other studies which suggest Quaternary chromosomal evolution deal with *Dianella* and *Pultenea* (Curtis, 1952), *Erodium* (Carolin, 1958), *Danthonia* (Brock and Brown, 1961) and *Casuarina* (Barlow, 1958, 1959). In *Ranunculus* in alpine south-eastern Australia, Briggs (1960) has also been able to show that Quaternary speciation has probably been important, although in this case not associated with numerical chromosome change.

Many more detailed studies will be necessary to establish the general patterns of Quaternary evolution in the Australian flora, but it is already evident that substantial evolution may be expected particularly in the herbaceous groups, wherever there is evidence of considerable climatic and topographical changes.

Acknowledgements.

I would like to express my gratitude to the Linnean Society of New South Wales for the support of this work, to Dr. S. Smith-White for valuable discussion, to Professor R. L. Crocker for making the facilities of the Botany Department available, and to Miss J. Jacobs for the preparation of the figures and plates.

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EXPLANATION OF PLATES XIV-XV.

Plate xiv.

Figures 1-6. ×1800. First metaphases in diploids and polyploids.

1. Diploid, showing 7 rod bivalents and 1 ring bivalent. 2. Tetraploid, Glen Innes, showing 16 bivalents. 3. Tetraploid, Bell, with 14 rod bivalents and 2 ring bivalents. 4. Tetraploid, Goulburn. 5. Hexaploid, Bulahdelah, showing 24 rod bivalents. 6. Tetraploid, Leura, showing 1 quadrivalent association.

Plate xv.

Figures 1-6. First metaphases and anaphases in tetraploids and hexaploids.

1. Tetraploid, Glen Innes; M_1 with two quadrivalents. 2. Hexaploid, Yanderra; M_1 with a trivalent and univalents. 3. Hexaploid, Yanderra; A_1 with lagging univalents. 4. Hexaploid, Kurri Kurri; A_1 with univalent division. 5. Tetraploid, Mt. Victoria; Anaphase bridge and fragment. 6. Hexaploid, Morisset; A_1 with bridge and fragment and lagging univalent.

STRUCTURAL GEOLOGY OF PART OF THE TAMWORTH TROUGH.

By Keith A. W. Crook, Australian National University, Canberra.

(Plate xvi; twelve Text-figures.)

[Read 28th November, 1962.]

Synopsis.

Structural analysis of the area between Tamworth, Nundle and Wallabadah suggests that two deformational phases affected the region. In the first, which commenced in the Artinskian, joints were formed early, and were rotated with bedding as plane cylindrical parallel folds formed, with axes regionally horizontal in direction 350°. A fracture cleavage, axial plane for these folds, developed in the mudstones constituting much of the sequence. Cleavage is more prominent towards the east of the area. Thrust faults, often in fold hinges, and subparallel normal faults were formed in the closing stages of this phase.

In the second phase which probably commenced in the Late Permian, wrench faults, accompanied by serpentinite along the Peel Fault System, developed in the eastern margin of the area. They strike 340° and dip steeply eastwards. Late normal faulting in the region of Tamworth is also referred to this phase.

The two phases together constitute the Hunter-Bowen Orogeny, and were completed prior to the intrusion of the Moonbi Granite of Permo-Triassic age.

Introduction.

The stratigraphy of the Devonian and Lower Carboniferous rocks of the Tamworth Trough sequence between Tamworth and Nundle has already been described together with maps and sections showing structural features (Crook, 1961*a-c*). In the present paper some aspects of the structure of this region are described and interpreted. Notes on structural features of the Woolomin Beds are included. This unit of Silurian and possibly older rocks is not considered to be part of the Tamworth Trough sequence, since it is faulted against it along the Peel Fault System.

Woolomin Beds.

The Woolomin Beds consist of slates and phyllites, with occasional jasper bands and rare arenites. Slaty cleavage is well developed in the slates and phyllites. This cleavage is penetrative, and micas have recrystallized in the foliation planes locally imparting a micaceous sheen to the cleavage surfaces. Bedding has not been observed in the slates or phyllites, and may have been obliterated by recrystallization.

Cleavage attitudes (Fig. 1), measured in an area approximately half a mile by three miles extending along the Nundle-Woolomin Road northwards from Anderson's Flat, suggest that the area chosen is statistically homogeneous with respect to cleavage. Qualitative observations elsewhere suggest a similar homogeneity on a larger scale, perhaps up to ten times that of the examined area.

The slates and phyllites are cut by joints with planar surfaces, usually oriented approximately normal to the foliation, which they evidently post-date.

Thirty-eight joints were measured at a locality on the Nundle-Woolomin Road half a mile north of Anderson's Flat. These form three sets (Fig. 2), with each maximum lying on a great circle defined by the average pole of the foliation.

Tamworth Trough Sequence.

There are four major units in the Tamworth Trough Sequence. The oldest, the Tamworth Group, consists dominantly of well-indurated siliceous argillites, with some thick masses of spilite, keratophyre and some arenaceous and rudaceous units. The Parry Group, which overlies the Tamworth Group conformably, is essentially a sequence of moderately indurated mudstones with arenaceous and rudaceous units locally abundant, particularly towards its base. These coarser units do not affect the overall structural response of the sequence.

The Kuttung and Permian units overlie the Parry Group and complete the Tamworth Trough Sequence. The sequence probably exceeded 45,000 ft. in thickness in the region of the Peel Fault System. It thins towards the western margin of the Tamworth Trough.

Joints.

Joints occur throughout the sequence, but are most prominent in the mudstones of the Parry Group. Being both thin bedded and moderately indurated, these mudstones have closely spaced joints, usually in several sets. Strike and dip sets have been observed but are not always present.

Joint surfaces are essentially planar and may transect several sedimentation units, often terminating at a change in lithology. They transgress concretions, pebbles, slumped zones, and diagenetic veins (Crook, 1961*d*). Fine plumose markings (Parker, 1942) have been observed on some joint surfaces. Joints may be partly healed by aggregates of stilbite crystals growing perpendicular to the joint surfaces. Elsewhere plates of heulandite or films of calcite cover the joint surfaces (Crook, 1961*d*).

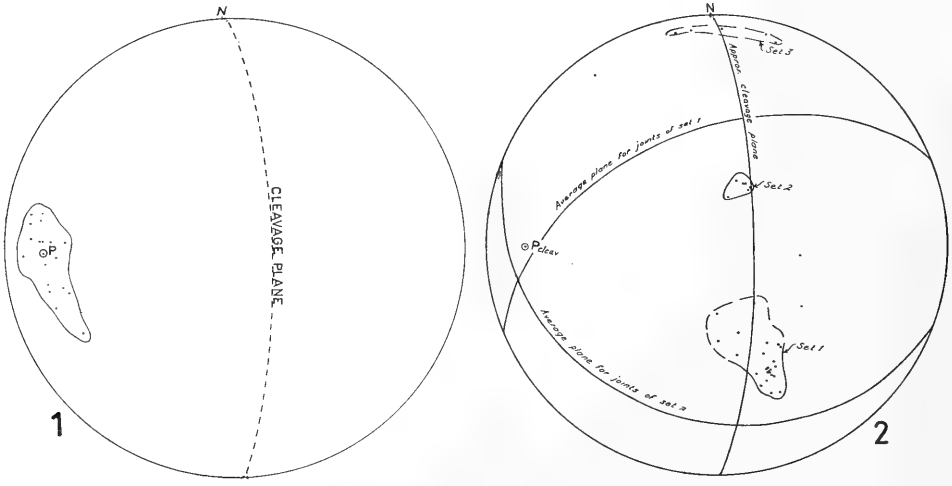

Fig. 1. 18 poles to slaty cleavage, Woolomin Beds. P = Average Pole.
Fig. 2. 38 poles to joints, Woolomin Beds.

Generally the joints are perpendicular to bedding planes or nearly so. Plots, uncorrected for bedding dip, of the attitude of joints in three small areas gave random distributions.

Joints in other parts of the sequence, although less closely spaced, are similar to those in the mudstones. Plumose markings are particularly characteristic of joints in arenaceous units. Joints in the Tamworth Group are usually very regular and plumose markings are less common.

Folds.

East-west sections (Crook, 1961*a*, sections 1, 2, 3) show a number of major macroscopic folds which are described below, from west to east (see Fig. 3).

1. The Gowrie Terrace: This is an area of nearly horizontal strata within the homocline west of Highway 15. It extends from the northern margin of the area southwards and dies out rapidly south of Gowrie.

2. The Goonoo Goonoo Anticline: This major feature is first encountered about 3 miles S.W. of Tamworth where its axial trace strikes south-west. The strike swings to due south and the structure extends southwards almost to Goonoo Goonoo village, where it dies out rapidly and is replaced by two synclines and three anticlines. Of these structures the Wangarang Anticline and the Kiah Syncline continue southwards,

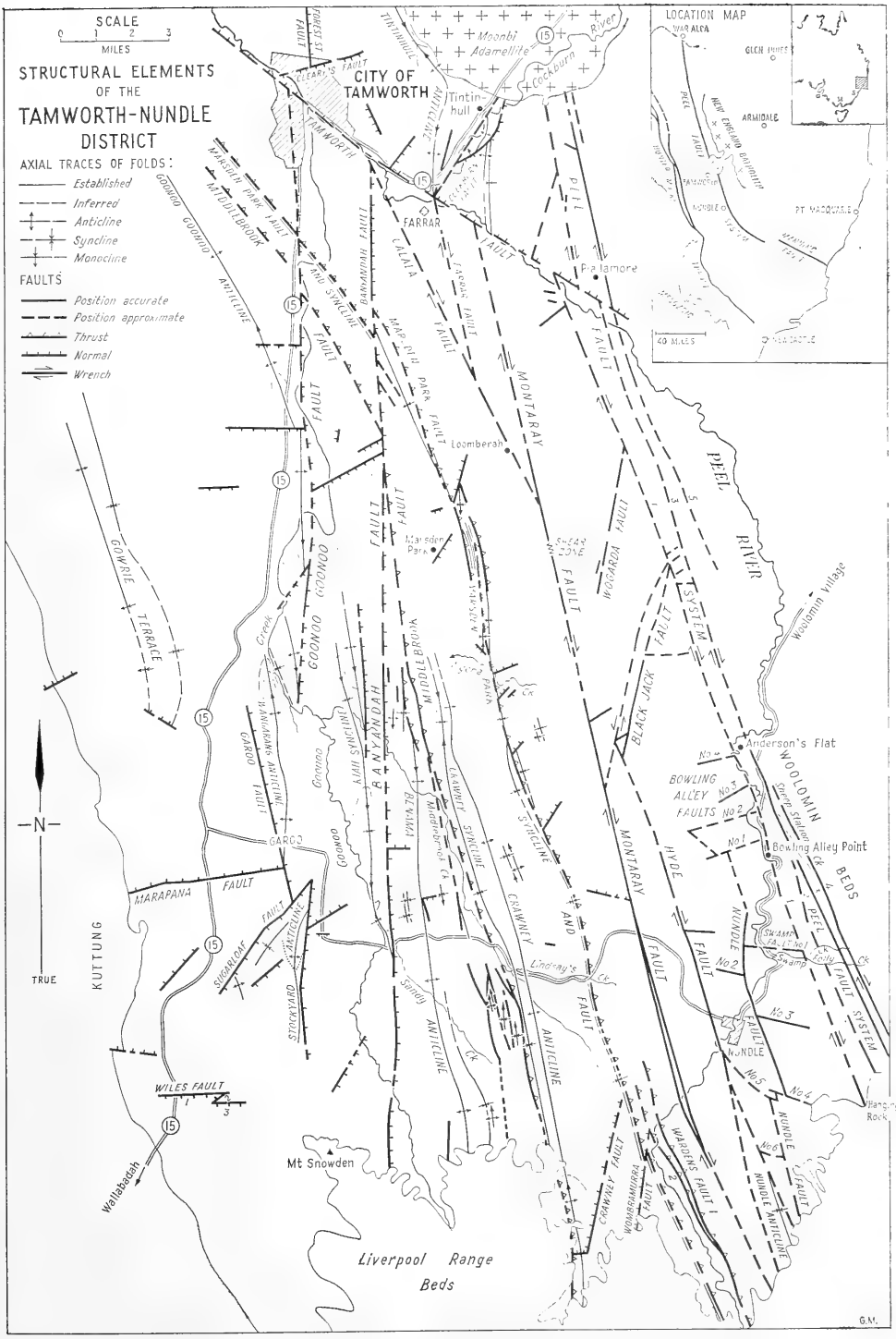

Fig. 3. Structural Elements of the Tamworth-Nundle district.

and the easternmost anticline, which is faulted out immediately south of Middlebrook Creek, develops an analogue a little further east. This analogue, the Benama Anticline, also continues southwards.

Further south in the area the Wangarang Anticline is broken by the Garoo and Sugarloaf Faults. Its analogue south of these structures is the Stockyard Anticline. Both the Kiah Syncline and the Stockyard Anticline die out into an area of gentle southerly dips around Mount Snowdon. The Benama Anticline develops a syncline on its east side near Sandy Creek, and both structures disappear beneath the Liverpool Range Beds on the south margin of the area.

3. The Crawney Anticline and Syncline: The Crawney Anticline is well developed in the Crawney district and is the northern extension of the Timor Anticline of Osborne *et al.* (1950). Traced northwards, this anticline acquires a syncline on its west side near Middlebrook Creek. Further north it becomes of less importance and is last seen as a minor structure near Algona Creek.

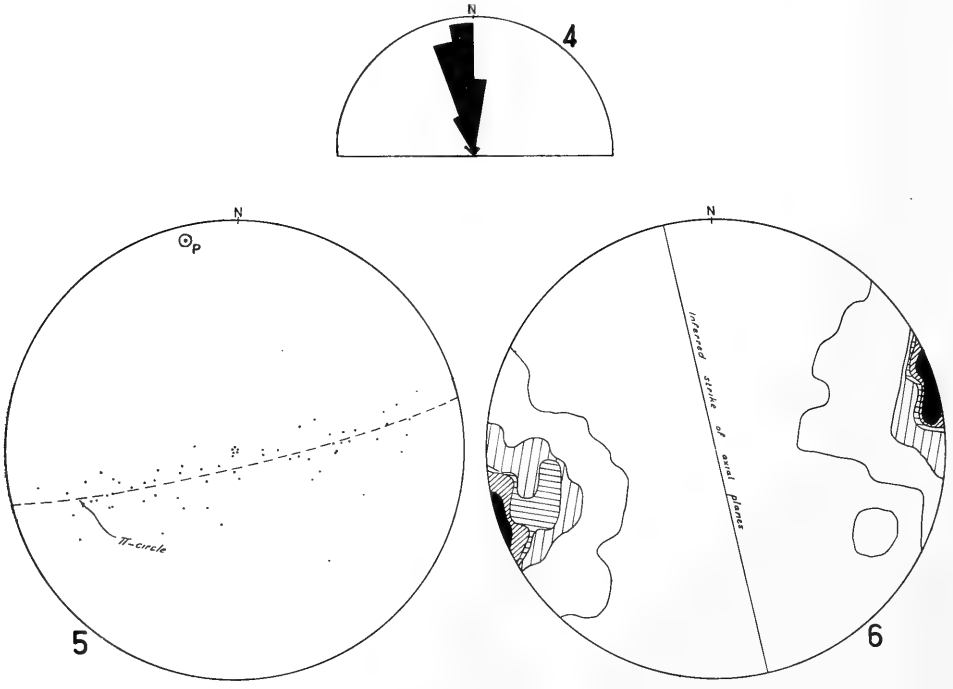

Fig. 4. Rose diagram of trends of 69 axial traces of folds (derived from maps in Crook, 1961*a*, *b*).

Fig. 5. 67 poles to bedding, Lindsay's Creek district. P, Pole of π-circle.

Fig. 6. 200 poles to fracture cleavage. Contours ½-5-6-10-15%.

4. The Marsden Park Syncline: First recognized by Benson (1918, p. 358), this structure has an axial trace striking 320° in the north-west of the area. South of Farrar the strike swings to 345° and the structure continues southwards, with complications near Marsden Park, to pass beneath the Liverpool Range Beds near the head of the Peel River. Probably this major structure reappears south of the Liverpool Range.

5. The Eastern Homocline: The eastern limb of the Marsden Park syncline forms the margin of a homoclinal area of steep dips extending eastwards to the Peel Fault System. Strikes usually lie between 340° and 350° with local variations. From Bowling Alley Point to Swamp Creek there is an anomalous area where east-west strikes are dominant and there is some suggestion of steeply plunging folds. These features have not been interpreted satisfactorily.

6. The Tintinhul Anticline: First noted by Benson (1915, p. 581), this structure lies north of the Peel and Cockburn Rivers to the east of Tamworth. It differs from all other folds in the area in showing considerable variations in strike of axial trace and in plunge. Near Tintinhul the structure is dominantly domal.

7. The Sugarloaf Creek Anomalous Area: Notable departures from the regional pattern of strikes and dips occur along Sugarloaf Creek between the Wangarang and Stockyard Anticlines. These departures are due to a syncline with axial trace striking 33° and many associated mesoscopic folds (Pl. xvi, fig. 1). This syncline sub-parallels, and is apparently related to, the Sugarloaf Fault.

Mesoscopic folds are common, particularly in a zone about one and a half miles wide which straddles the Middlebrook Fault and the west limb of the Crawney Anticline and extends from the edge of the Tertiary northwards to Warrimoo Creek.

The meso- and macroscopic folds are of the plane cylindrical parallel type and have symmetrical limbs. The folds are generally open and hinges are rarely sharp. Axial planes of folds in the west of the area are vertical, but in the east they dip eastwards at angles up to 70°. A plot of the strikes of the axial traces (Fig. 3) shows a pronounced maximum in a direction 340–360° (see Fig. 4).

Locally the macroscopic folds show plunge reversals. Plunges in excess of 15° have not been observed, and values much less than this are generally obtained in cylindrical sub-areas.

The local plunge in the Lindsay's Creek district is estimated to be 6° in a direction of 345° from a π-diagram of bedding attitudes (Fig. 5).

Cleavage.

In the Tamworth Group the rocks are strongly indurated and cleavage is only rarely developed. In contrast, cleavage is well developed in most of the mudstones of the Parry Group. This cleavage takes the form of an anastomosing system of fine fractures, penetrative on the scale of an outcrop, and forming a series of closely spaced, statistically planar, parallel surfaces, which are rarely more than half an inch apart. The cleavage is usually at a high angle to bedding and its trace on bedding planes is often visible. This trace can be termed a lineation only in a statistical sense: it consists of an anastomosing system of sub-parallel fractures so arranged that the average trend is readily apparent, and frequently very strongly developed. There has been no recrystallization of new minerals along the cleavage surfaces, and bedding is not dislocated along them. This cleavage will henceforth be termed *fracture cleavage.*

The fracture cleavage is not uniformly developed. On the western limb of the Goonoo Goonoo Anticline some outcrops show little evidence of cleavage and in others it is only incipient. Eastwards the cleavage gradually becomes more intense and locally, east of the Marsden Park Syncline, it forms a quasi-planar foliation which all but obscures the bedding of the mudstones (Pl. xvi, fig. 2). The starchy fracture of the mudstones, whereby they break into small elongate polygonal fragments on weathering, results from the strong development of this cleavage.

In addition to its development in massive mudstone sequences, fracture cleavage has been noted in large mudstone blocks included in conglomerate units. In such cases the cleavage is morphologically identical to, and parallel with, the cleavage in the mudstones adjoining the conglomerate units.

A plot of cleavage attitudes measured throughout the area shows a very prominent single maximum. This maximum is normal to a plane striking 348° and dipping vertically or steeply north-east (Fig. 6). This relationship suggests a statistical parallelism between the cleavage and the axial surfaces of folds.

Further evidence for this relationship is obtained from a plot of cleavage-bedding intersections measured in the Lindsay's Creek district (Fig. 7). These intersections would define the fold axis if cleavage and axial surfaces were parallel. The value obtained, a plunge of 7° in direction 341°, is in excellent agreement with that obtained from the π-diagram of bedding (Fig. 5).

Faults.

The area has been extensively faulted both on a macroscopic and mesoscopic scale. Mesoscopic normal and reverse faults are particularly common in the mudstones of the Parry Group and generally have a throw of only a few feet. They are often accompanied by fairly intense shearing over a zone a few feet wide. This zone may be veined with laumontite and calcite, and may be extensively slickensided. Laumontite-calcite veins may extend into the unsheared sediments, where they cut stilbite veins filling the joints (Crook, 1961*d*).

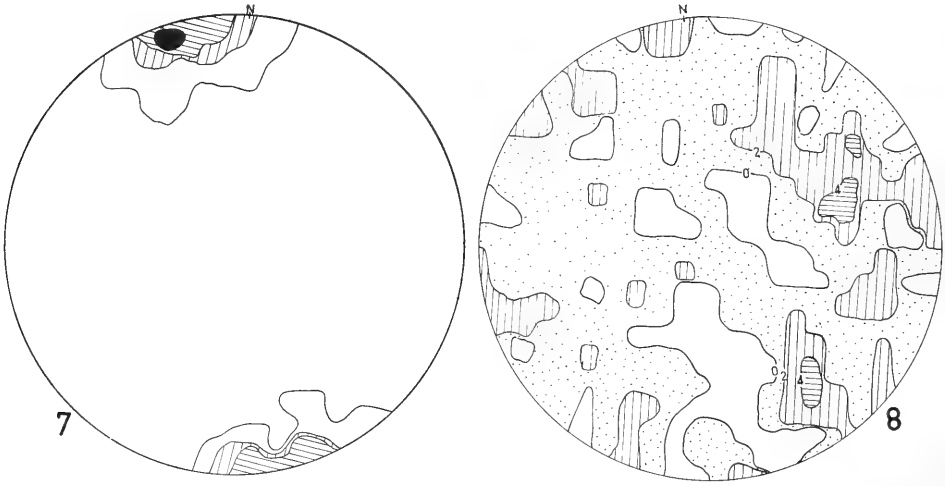

Fig. 7. 53 cleavage-bedding intersections, Lindsay's Creek district. Contours 2-10-20-40%.
Fig. 8. 161 poles to mesoscopic faults. Contours 0-2-4%.

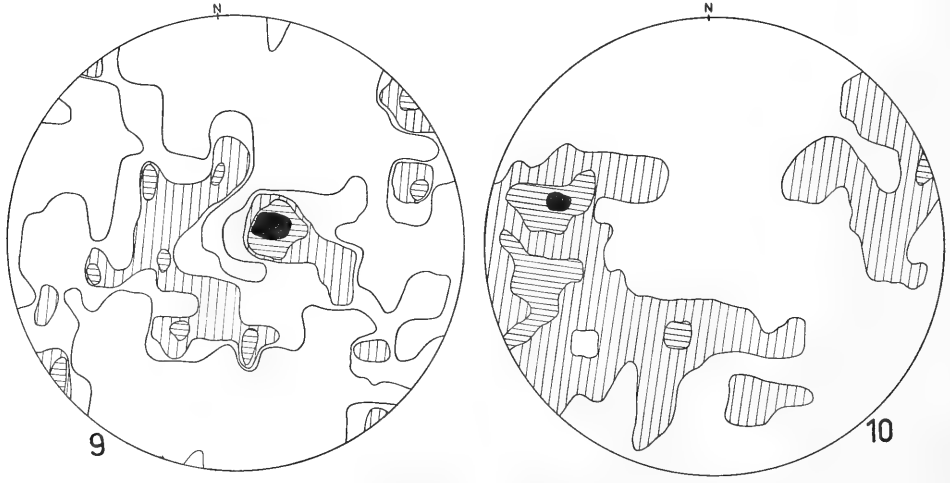

Fig. 9. 64 slickensides. Contours 1½-3-4½-6%.
Fig. 10. 74 S-surfaces, Peel Serpentinite. Contours 1-4-8%.

Faults on a smaller scale have also been encountered in various places in the Parry Group. The throw of these faults is from a few inches to a fraction of an inch. Characteristically they form groups of slickensided surfaces, individual surfaces being a few square inches in extent, and somewhat curved. Generally they are oblique to bedding, but occasional slickensided bedding planes are encountered. These groups of slickensided surfaces are not accompanied by shearing in the surrounding rocks.

A plot of the attitudes of 161 faults and slickensided surfaces (Fig. 8) yielded a near-random distribution. However, analysis of the attitude of slickensides (Fig. 9) showed a maximum plunging at about 75° in direction 075°.

Many macroscopic faults are recognized within the area. Aerial photographs of the regions between Middlebrook and Sandy Creeks along the Nundle-Garoo road show numerous lineaments oblique to the bedding. Both the bedding and these lineaments stand out due to differences in vegetation and soil colour, particularly in freshly cultivated paddocks. The distribution of strike directions of these lineaments is not random; two or three maxima are present.*

These lineaments dislocate beds, the component of throw, as seen on the air photographs, being several tens of feet. They must therefore represent the outcrop of faults, which would be expressed as mesoscopic features in suitably exposed areas.

The structural map (Fig. 3) shows many large macroscopic faults. Their existence has been postulated on the basis of the occurrence of shear zones, and structural and stratigraphic discontinuities, aided by aerial photograph interpretation.

The exact extent and nature of individual faults is a matter of inference, as are the relationships between intersecting faults. Here, as will be apparent from the structural map, the author has been influenced by the wrench faults tectonics concept of Moody and Hill (1957). Four groups of faults are recognized.

Group I: The Middlebrook Fault Nos. 1 and 2, the Marsden Park Fault, the Warden's Fault Nos. 1 and 2, and parallel smaller faults associated with each of these, form this group. All are thrusts, with upthrow on the east. The faults closely parallel the strike of surrounding beds.

The Marsden Park Fault generally follows the hinge of the Marsden Park Syncline, but locally breaks out of it. It is somewhat broken by later faults in the hinge of the syncline near Marsden Park, and is also cut by the Banyandah Fault, as is the Middlebrook Fault.

Group II: To this group belong certain of the longer faults—the Banyandah Fault and the Goonoo Goonoo Fault—and most of the short faults—the Wiles Fault, Stockyard Fault, Sugarloaf Fault, Crawney Fault, Woombramurra Fault, Marapana Fault, Garoo Fault, and faults associated with each of these. All are apparently normal faults.

The two larger faults both strike approximately true north and have downthrow on their east. They appear to cut across both fold hinges and thrust faults.

Group III: This group consists of a number of extensive, very straight, apparently steeply dipping faults, often with upthrow on the east, and with some evidence of lateral movement.

The Peel Fault System, a great structural break clearly recognized by Benson (1913, p. 511), is placed in this group. It lies on the eastern margin of the area and separates rocks of the Tamworth Group from the Woolomin Beds which are older (Crook, 1961*a*). The eastern side of the system is therefore upthrown.

Individual faults in the Peel Fault System are marked by lenses of the Peel Serpentinite. The distribution of the serpentinite suggests a system of several parallel faults: five are recognized by the author. North of Bowling Alley Point the outcrop of the faults may be marked by knobs of secondary jasper.

The faults maintain a remarkably constant strike, trending between 335° and 340° from south of Nundle to Piallamore, to the north of which they trend 345°. This strike is also characteristic of the Peel Fault System from Tamworth north to Warialda, a distance of more than 100 miles (Benson, 1917, Pl. 20).

The attitude of the serpentinite foliation gives the possible dip of the faults. South of Chrome Hill (Pl. xvi, fig. 3) this foliation dips east at about 70°. A similar orientation was obtained from plotting data obtained at Hanging Rock, Folly Creek and Sheep Station Creek (Fig. 10). Unfortunately the serpentinite has yielded few

* Data on this point, since destroyed by fire, have not been recollected.

other mesoscopic structures of significance. North of Attunga a strong lineation was observed on the foliation. This lineation plunged down dip and was formed by small plications having monoclinic symmetry.

Other faults in this group are the Montaray Faults Nos. 1 and 2, Hyde Faults Nos. 1 and 1a, Black Jack Faults Nos. 1 and 2, the Wogarda Fault, Cope Fault, Calala Fault, Farrar Fault, and several small faults, lying east of the Montaray Fault.

The shear zone in the Montaray Fault is exposed at several points along its length. South of Loomberah intense shearing has imparted a strong foliation to the mudstones (Pl. xvi, fig. 4). This foliation shows numerous folds of a few inches' amplitude whose symmetry is generally monoclinic. A β-diagram from this folded foliation (Fig. 11) shows the steep plunge of the fold axes.

The general strike of the foliation in this outcrop is 195°, which differs considerably from that of the Montaray Fault at this point. Exposures elsewhere in the vicinity are very poor or absent, and the divergence of strikes is probably to be

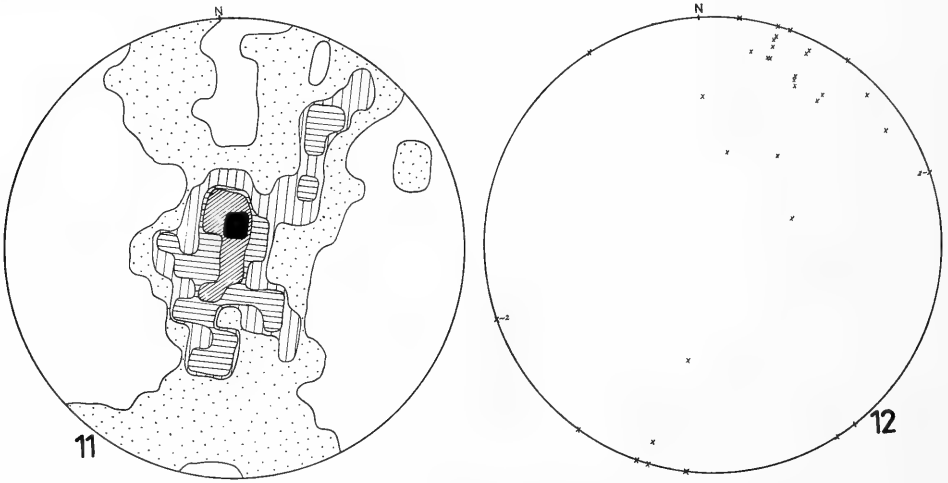

Fig. 11. β-plot of 26 S-surfaces in shear zone of Montaray Fault. Contours ½-3-5-8-10%.
Fig. 12. 28 poles to dykes.

explained in terms of local adjustment in a wider fault zone. The trace of the axial surfaces of the small folds is oblique to the foliation and strikes slightly south of west, suggesting that the block on the western side of the fault has moved south. The overall strike of the Montaray Fault is remarkably constant at 345°, paralleling the Peel Fault system.

Group IV: The Tamworth Fault, which follows the Peel River from Tamworth to Piallamore, is the main fault in this group. Benson (1915, p. 564) suggested its presence, which is now confirmed by the exposure of a zone of intense deformation beneath the bridge at the south-eastern end of Peel Street, Tamworth. The fault appears normal and cuts faults of all groups previously discussed. It marks the south-west margin of an area differing in tectonic style from that further south. In view of this contrast in styles, the faults north of the Tamworth Fault, which are also normal, are grouped with it.

The affinities and nature of the Nundle Fault, Bowling Alley Faults Nos. 1–4 and Swamp Faults Nos. 1–6 are unknown. They are not included in any of the above groups.

Dykes.

Porphyry dykes have been encountered throughout the area, but are most common on its western margin. Both massive and sheared dykes are known. The plot of the attitude of dykes (Fig. 12) yields a pronounced maximum corresponding to a strike of 295° with a steep dip to the south.

Variations in Style of Deformation.

Five regions of different tectonic style can be recognized in a section normal to the regional strike.

a. The Western Homocline: Lying on the western margin of the area, this is a region of generally constant westerly dips with some local nearly horizontal areas. It forms the eastern limb of the Werrie Syncline (Carry, 1934*a*) and passes southwards into a relatively undeformed sub-horizontal area north-west of Wallabadah. Fracture cleavage is absent or only incipiently developed throughout the zone.

b. Zone of Normal Faults and Folds with Vertical Axial Planes: This zone includes the Goonoo Goonoo Anticline on its western margin and extends eastwards to the region of the Banyandah Fault. It contains the major normal faults of the area. Fracture cleavage is present.

c. Zone of Thrust Faults and Folds with Inclined Axial Planes: This zone can be subdivided into two sub-zones. The western sub-zone straddles the Middlebrook Fault and is characterized by intense mesoscopic and small-scale macroscopic folding. The eastern sub-zone, which extends from the Marsden Park Syncline to the Montaray Fault, is more or less homoclinal. Fracture cleavage is prominent throughout both sub-zones.

d. The Eastern Homocline: This zone is characterized by faults of Group III (probably wrenches), and by uniformly steeply dipping strata with few structural irregularities. It extends from the Montaray Fault to the Peel Fault system. Cleavage is well developed in the mudstones and is locally very prominent.

e. The Zone of Slaty Cleavage: This comprises the Woolomin Beds and other rocks east of the Peel Fault System, in which the pelitic rocks, and some arenites, have a prominent slaty cleavage.

Interpretation.

Joints: The joints in the Woolomin Beds post-date the slaty cleavage. The orientation of the joint sets normal to the cleavage suggests a genetic relationship between the two structures. The joints may have formed as an expression of residual elastic strain, remaining in the rock after the formation of the cleavage. If so, it would appear that the axis of minimum strain was approximately vertical while that of maximum strain was approximately horizontal, trending 350°.

The random distribution of attitudes of joints in the Tamworth and Parry Groups, and their relationship to the bedding, suggests that they formed prior to folding and have since been rotated.

The joints post-date the burial metamorphic modification of the sediments, since they cut veins associated with this modification (Crook, 1961*d*). Infilling of the joints with stilbite took place prior to the development of mesoscopic faults, for the laumontite-calcite veins associated with the faults cut the stilbite infillings.

Folds: The folds in the Tamworth and Parry Groups are of the style normally attributed to flexural-slip movement. They have thus been generated by shortening in a direction normal to their axial surfaces, and by elongation in a direction lying in their axial surfaces. Although there is no direct evidence, the direction of maximum elongation probably lies in the axial surfaces normal to the axes of the folds. Thus the axial surfaces of the folds contain both the maximum and intermediate strain axes, the intermediate axis being also the regional fold axis (B_1). The minimum strain axis is the normal to the axial surface.

By plotting normals to axial surfaces throughout the area a regional picture of minimum strain trajectories can be obtained. The trajectories so constructed are horizontal in the western part of the area, but curve and plunge gently westwards as the Peel Fault System is approached.

Cleavage: The fracture cleavage in the Parry Group is axial plane for B_1 folds (Fig. 6). Presumably it developed as a response of the rocks to the strain developed during folding. There seems no doubt that it results from deformation of the mudstones in bulk, rather than from local strains related to movement horizons within

the mudstones. The rarity of such movement horizons, and the development of fracture cleavage in isolated mudstone blocks within conglomerates both suggest that the cleavage is a response to strain affecting a large body of rock.

The slaty cleavage in the Woolomin Beds may be axial plane for a system of folds. If so it could be used to indicate a minimum strain trajectory for that system of folds. The trajectory so determined plunges towards 270° at 20°.

Faults: Assuming they dip eastwards (Sections 1–3, Crook, 1961*a*, *b*), the faults of Group I are thrusts. They appear to have been the earliest formed in the area, being cut by faults of Groups II and IV. Their close relationship to fold hinges suggests that they are contemporaneous with the folds, and resulted from failure of the rocks during shortening.

Cross-sections show that faults of Group II are normal. They often parallel axial traces of folds, and may be located in hinges. Some, however, are cross-cutting. They may result from residual strain present in the folded rock mass at the close of deformation.

Although Benson and several later workers considered some of the faults in Group III to be thrusts, several features suggest that they may all be wrench faults. The faults are extensive and show remarkable constancy of strike for tens of miles. They dip at high angles and have upthrow consistently on one side. The orientation and geometry of mesoscopic folds in foliation within the Montaray Fault shear zone and in the Peel Fault System serpentinite north of Attunga suggests lateral movement.

The Peel Fault System margins the Central Complex (Voisey, 1959) of the Hunter-Bowen orogenic belt, and separates two terrains which are distinct structurally, lithologically and in age. This is a characteristic feature of wrench faults. It seems unlikely that this system is of the "upthrust" type, although it undoubtedly has a component of vertical movement. De Sitter (1956, p. 237) describes, as typical features of "upthrusts", their sinuosity in outcrop and the restricted lateral extent of the individual faults.

Working in the Wood's Reef district, north of the area described here, Osborne (1950, p. 70) and Proud and Osborne (1952) concluded there had been some wrench movement within the Peel Fault System. They presented evidence that the eastern block moved southwards along the fault system during one of their postulated "stress phases".

The general parallelism of the Peel and Hunter-Mooki Fault Systems should not be taken as necessarily indicating both to be thrusts. Carey (1934*b*) showed by construction that movement along the Hunter Thrust near Piallaway, west of the present area, was directed to the south-south-west along a line plunging at 43½° in direction 026°. Homologous movement on the Peel Fault System would cause appreciable lateral movement, the eastern block being displaced south.

Although the Group III faults are older than those of Group IV, their relationship to Groups I and II is not known. The minimum strain trajectories deduced for the deformation which produced the B_1 folds and the thrusts (Group I) are approximately normal to the faults of Group III. It seems unlikely that the wrench faults can have been generated under a strain with the minimum component so oriented. The wrench faults are therefore considered to be later than, and unrelated to, the thrusts.

It seems unlikely also that wrench faults with a thrust component would develop contemporaneously with the normal faults of Group II.

The wrench faults represent, then, a later period of deformation, with a different strain pattern, which does not appear to have produced macroscopic flexural features. A not impossible orientation of minimum strain trajectories for this deformation is NNE–SSW, assuming that they are right lateral wrenches (Moody and Hill, 1956).

The Group IV faults, in particular the Tamworth Fault, are younger than the wrench faults. Constructions suggest that the faults are normal, and this interpretation is possibly strengthened by the dome-and-basin style of the area north of the Tamworth Fault.

It is tempting to consider that these faults developed at the close of the wrench faulting in response to residual strain. The orientation of the Tamworth Fault does not exclude this possibility.

Dykes: The orientation of the dykes is similar to that of the Tamworth Fault, and they may be contemporaneous with it. If so they could be a response to the strain pattern responsible for this fault, coupled with upward directed magmatic pressure (Anderson, 1951, p. 23).

Synthesis.

Two phases of deformation can be recognized in the Tamworth Trough sequence. Joints formed at the commencement of the first phase, and were subsequently rotated with the bedding as folds of flexural-slip type developed. The regional attitude of the fold axis (B_1) for this system is horizontal in direction about 350° (see Table 1). A fracture cleavage, axial plane for B_1 folds, developed in mudstones of the sequence, increasing in intensity eastwards. The minimum strain trajectory for this deformation, determined from attitudes of axial surfaces, was in direction 260°, the plunge varying from 0° in the west to 20° in the east, and 20° in the Woolomin Beds, if these were deformed in this phase.

TABLE 1.

Orientation of Fold Axes of B_1 Folds.

Source.	Figure.	Direction.	Plunge.
Bedding Lindsay's Ck.	5	345°	N. at 6°
Maps (Crook 1961a, 1961b)	3	Average 350°	Variable N. & S. at low angles.
Flow cleavage	1	360°	—
Fracture cleavage	6	348°	—
Cleavage bedding intersection	7	341°	N. at 7°.

Further deformation produced thrust faults, striking parallel to the axial traces of the folds, and often situated in fold hinges. The phase of deformation closed with the formation of normal faults, dominantly parallel in strike to the thrusts, which may have formed in response to residual strain in the rock mass as deformation ceased.

Response to the second phase of deformation was by faulting, the major wrench faults in the east of the area being a product of this phase. The strain pattern which produced these faults is not known, but is unlikely to have been similar to that which was dominant in the first phase, as the faults strike parallel to the axial traces of the B_1 folds. Normal faults, some intersecting the wrench faults at a high angle, formed at the close of this phase, and appear to have been accompanied by dyke intrusion.

West of the present area Carey (1934*a*) has described dome and basin structures along the axis of the Werrie Syncline. These result from variations in plunge of B_1 which may reflect cross-folding of B_1 by a second fold system related to the strain pattern of the second deformational phase.

Time of Deformation.

The two deformational phases together form the culmination of the Hunter-Bowen orogeny of Late Permian age. Osborne (1950) and Voisey (1959) have suggested different ages for various deformational phases within this orogeny. The author's conclusions add little to those of Osborne and Voisey and it is evident that many more data are necessary before finality can be reached.

The Tamworth Trough contains a structurally conformable sequence extending from the Lower Devonian through the Tournaisian (Crook, 1961*a*, *b*) up to the Middle Permian Werris Creek Coal Measures. There may be some minor unconformities within this sequence (Carey, 1934*a*, p. 353). However, as the upper parts of the Tamworth Trough Sequence lie less than 12 miles west of the top of the Parry Group, no significant folding can have occurred until after the deposition of the Werris Creek

Coal Measures. These Coal Measures are correlatives of the Greta Coal Measures (Voisey, 1958), which are probably of Early Artinskian age on data presented by Glenister and Furnish (1961).

At Anderson's Flat, within the Peel Fault System, the ?Lower Permian Anderson's Flat Beds occur faulted against Lower Devonian. This is further evidence for a post-Sakmarian age for the deformation.

An upper limit to the age of the second deformation is set by the Moonbi Adamellite which intrudes Devonian sediments and cuts the Peel Fault System near Kootingal. This mass is part of the New England Batholith which is known to intrude Upper Permian rocks near Drake (Voisey, 1936) and is usually regarded as Permo-Triassic.

Osborne (1950) recognized four episodes within the Hunter-Bowen orogeny. The first, in which folding was initiated, he placed at the end of deposition of the Muree Formation, i.e., about Middle Artinskian. The second, which emphasized previous folding and produced some gravity faults of meridional strike, he placed at the end of deposition of the Maitland Group, i.e., probably Late Artinskian. The third episode, involving strong folding, the production of many thrusts and the injection of peridotites, he placed at the close of the Permian. The fourth episide, involving a "rotational stress influence" and responsible for the Hunter-Mooki Thrust, came later than the third.

Voisey (1959) considered that movements commenced about the end of deposition of the Dalwood Group, i.e., Late Sakmarian, with the main deformation taking place after the Maitland Group had been deposited and culminating in the formation of the Hunter-Mooki Thrust.

In the portion of the Tamworth Trough being described, the author considers deformation did not commence until Middle Artinskian. Deformation may, however, have commenced earlier in other regions, as suggested by Voisey (1959). No time for the end of the first deformational phase can be given. The timing of the second phase of deformation is also problematical and must await geochronological studies. It is, however, likely to be no younger than very early Triassic.

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EXPLANATION OF PLATE XVI.

1.—Mesoscopic syncline in mudstone, Sugarloaf Creek, looking north.

2.—Intense fracture cleavage (right side of photograph) in mudstones south of Montaray.

3.—Peel Serpentinite, view south from Chrome Hill near Bowling Alley Point.

4.—Folded foliation in Shear Zone of Montaray Fault, looking down on outcrop.

ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.

28th March, 1962.

Professor B. J. F. Ralph, President, in the chair.

The minutes of the last Monthly Meeting (29th November, 1961) were read and confirmed.

The Chairman announced that library accessions amounting to 29 volumes, 510 parts or numbers, 9 bulletins, 16 reports and 11 pamphlets, total 575, had been received since the last meeting.

The Chairman announced that the Third Sir William Macleay Memorial Lecture will be delivered by Dr. R. N. Robertson on Thursday, 23rd August, 1962.

PAPERS READ.

1. Selecting for Virulence on Wheat while inbreeding *Puccinia graminis* var. *secalis*. By I. A. Watson and N. H. Luig.

2. A Study of some Smuts of *Sorghum* spp. By R. F. N. Langdon.

3. Studies in Australian Loranthaceae. I. Nomenclature and New Additions. By B. A. Barlow.

4. The Reproduction and Early Life Histories of the Gastropods, *Bembicium auratum* (Quoy and Gaimard) (Fam. Littorinidae), *Cellana tramoserica* (Sower.) (Fam. Patellidae) and *Melanerita melanotragus* (Smith) (Fam. Neritidae). By D. T. Anderson.

ORDINARY MONTHLY MEETING.

18th April, 1962.

Professor B. J. F. Ralph, President, in the chair.

The following were elected Ordinary Members of the Society: Miss Barbara J. Ballantyne, B.Sc.Agr., Rydalmere, N.S.W.; Mr. D. C. Drummond, Sydney University; and Miss Paulette S. McWilliam, Greenwich, N.S.W.

The Chairman announced that the Council had elected the following office-bearers for the 1962-63 session: Vice-Presidents: Professor J. M. Vincent, Dr. T. G. Vallance, Dr. S. Smith-White and Dr. Lilian Fraser; Honorary Treasurer: Dr. A. B. Walkom; Honorary Secretaries: Dr. A. B. Walkom and Dr. W. R. Browne.

The Chairman offered congratulations to Miss Isobel Bennett on the award to her of the first honorary Master of Science degree to be conferred by the University of Sydney.

The Chairman announced that library accessions amounting to 8 volumes, 97 parts or numbers, 8 bulletins, 4 reports and 2 pamphlets, total 119, had been received since the last meeting.

PAPERS READ.

1. A New Species of Trigonalid Wasp parasitic on the Sawfly *Perga affinis* Kirby (Hymenoptera). By E. F. Riek.

2. A New Genus of Australian Stoneflies (Plecoptera, Gripopterygidae). By E. F. Riek.

3. The Host-Plant Relationship of an Australian Swallowtail, *Papilio aegeus*, and its Significance in the Evolution of Host Plant Selection. By George O. Stride and R. Straatman. (*Communicated by Dr. D. F. Waterhouse.*)

4. Galls of Agromyzidae (Diptera) on *Pittosporum undulatum* Andr. By Erich M. Hering. (*Communicated by Mr. C. E. Chadwick.*)

5. A Revised Classification of the Australian Amphiuridae (Ophiuroidea). By H. Barraclough Fell. (*Communicated by Miss Elizabeth C. Pope.*)

NOTES AND EXHIBITS.

Dr. I. V. Newman exhibited five seedlings selected out of forty-one grown from a prostrate individual of the normally erect species, *Acacia spectabilis*. Four were prostrate, or nearly so, one was nearly erect. An exhibit of specimens from an erect plant and the prostrate plant was made at the ordinary monthly meeting on 26th November, 1958. Lantern slides of the prostrate plant and nearby erect plants were shown and reference made to a similar form in a cultivated *A. mollissima* in South Africa, at the ordinary monthly meeting on 25th November, 1959. The plants were growing on the side of a railway cutting in clay near Pymble station (suburb of Sydney). A first attempt to bag inflorescences for selfing and crossing the two forms was unsuccessful, as unknown persons destroyed the bags. At a second attempt on a smaller scale, with the bags hidden, no seed was set — probably due to failure in the attempted pollination.

Seeds of the prostrate plant were collected from open pollination in the 1958 season (about October), kept in pod groups and sown in mid-December, 1961, in pots after being scratched with a file and soaked overnight. There was practically 100% germination of seeds that were not originally shrivelled. Records of the seedlings were kept, leaf by leaf, till the middle of February, 1962, when the maximum number of leaves was about seven, the hypocotyls and stems were still erect in general direction and maximum height of seedlings would have been about 7–9 cm. Teaching-load prevented further recordings till mid-April. The lengths of the plants then ranged from 9 cm. to 34 cm., with most between 20 and 26 cm. Of the 41 plants, 24 were lying in a general direction of 45° or less to the horizontal (some almost parallel with the ground but *not* in contact with it), 10 showed a distinct inclination, and 7 were approximately erect. Four of the erect plants were less than 20 cm. long, and might yet become inclined. The direction of inclination was mostly north of the east-west line, ranging from east to west; one seedling lay towards the south and one towards the south-east. The inclination, therefore, if a phototropic response, is not directly such.

The first basic question is about the genetical status of the parent's prostrate form. The appearance of it in the offspring establishes it as genotypically determined. It would seem to be a new mutation. Mutations are commonly only recessive to the wild form, so this plant may be homozygous for the mutant character. Selfing should then give progeny, all mutants, which cannot yet be denied for this case, as it is still possible that prostrate posture may be assumed by the remaining non-prostrate seedlings. Crossing with homozygous erect plants should give all erect progeny, with heterozygous erect plants should give half-and-half prostrate and erect progeny. The numbers suggest either inbreeding with prostrate habit not yet assumed by all progeny or a slight proportion of outbreeding to the dominant erect form.

The second basic question is the mechanism of the prostrate habit. It is clear that the early growth up to about the seventh leaf, at least, was erect, i.e. for about five or six weeks after germination. Eight weeks later a great number showed a marked tendency to the prostrate habit, with the stem still rather straight in the overall direction and of a more or less definite zig-zag form due to slight changes in direction at the nodes. The inclination seems to be largely due to a bend coming into existence in the previously straight hypocotyl, associated with a lack of positive geotropic response in the stem. Note that the stem is not lax; even stems approaching the horizontal are not supported along the ground, but are held by cantilever mechanics above the ground, at this stage of growth. If reaction wood were involved in the bending, then it would appear to be different in action from the tension wood normally found in Angiosperms.

Work will proceed to test the genetical and physiological situations. The first must await the flowering of these seedlings, which can then be manipulated in conditions free from public interference. The second must await acquisition of more seedlings to provide experimental material, following preliminary anatomical study.

LECTURETTE.

An illustrated lecturette entitled "Some Harmful Marine Invertebrates: A Modern Review" was delivered by Miss Elizabeth C. Pope, Australian Museum, Sydney.

ORDINARY MONTHLY MEETING.

30th May, 1962.

Professor B. J. F. Ralph, President, in the chair.

The following were elected Ordinary Members of the Society: Messrs. P. T. Bailey, Blakehurst, N.S.W.; R. F. G. Swinbourne, Alice Springs, Northern Territory; and M. J. Whitten, Lidcombe, N.S.W.

The Chairman announced that Dr. D. T. Anderson had been elected a Member of Council in place of Dr. I. V. Newman, resigned.

The Chairman on behalf of members expressed congratulations to Dr. S. Smith-White on his election to Fellowship of The Australian Academy of Science.

The Chairman announced that library accessions amounting to 27 volumes, 231 parts or numbers, 9 bulletins, 9 reports and 5 pamphlets, total 281, had been received since the last meeting.

The Chairman drew the attention of members to the fact that there will be no Ordinary Monthly Meeting of the Society in August (usual meeting night, 29th August, occurring during the meeting of A.N.Z.A.A.S.) but that the Third Sir William Macleay Memorial Lecture will be delivered by Professor R. N. Robertson on Thursday, 23rd August, 1962.

PAPERS READ.

1. Observations on some Australian Forest Insects. 12. The Taxonomy of *Zenarge turneri* Rohwer, 1918 (Hymenoptera: Argidae), the Cypress Pine Sawfly. By K. M. Moore.

2. Observations on some Australian Forest Insects. 13. A Comparison of the Biology of the Cypress Pine Sawfly Subspecies. By K. M. Moore.

3. Asexual Intercrosses between Somatic Recombinants of *Puccinia graminis*. By I. A. Watson and N. H. Luig.

4. The genus *Walchiella* (Acarina, Trombiculidae). By R. Domrow.

NOTES AND EXHIBITS.

Mr. G. P. Whitley exhibited H. Irwin's original painting of the holotype of a coral fish, *Chaetodon aphrodite* Ogilby (1889, *Austr. Mus. Mem.*, 2: 55, Pl. iii, fig. 2), until very recently the only known specimen of the species. However, a skindiver, Miss Julie Booth, collected several specimens at Lord Howe Island, the type-locality, this year. The same species was discovered last April at Manly, New South Wales, a new record for Australia. All known specimens of the species are preserved at the Australian Museum, Sydney.

Mr. J. P. F. Hennelly contributed a note on a new Sporomorph from the Avon Coal Measures, N.S.W. Upper Permian.

In the examination of a sample from an outcrop of the Avon Coal Measures, a new *Granulatisporites* species was noted. The specimen of coal came from a location Gloucester 1″ = 1 mile map at 996416. Unfortunately this new form very closely resembles *Verrucosisporites pseudoreticulatus*, an indicator fossil for the Greta Coal Measures. In fact the only distinguishing feature of any reliability is that this new form does not present a pseudoreticulate appearance when viewed slightly below the correct focus. There are other distinguishing features, such as its equatorial compression to the three-vaned form as occurs with occasional specimens of *Granulatisporites trisinus*, but these features are not always necessarily present and it is readily possible to confuse it with the *V. pseudoreticulatus* of the Greta Measures. Samples overlying and underlying the Avon Coal Measures were examined and both found to be components of the Upper Coal Measures, thus excluding any possible link with Greta.

Mr. J. P. F. Hennelly exhibited petrified timber from Aberdeen (Hunter Valley). Transverse thin section shows original more lignified xylem and medullary rays just as in a live specimen, but of little diagnostic value. Longitudinal radial section shows multiseriate bordered pits on side walls of xylem. Diagnosis, *Araucariacites* or *Podocarpites*. Age presumed to be Tertiary.

Mr. M. J. Whitten compared the meiotic behaviour of chromosomes possessing diffuse centromeres as found in the Sternorrhynca (Homoptera) and *Luzula* of the Juncaceae with the meiotic behaviour in the Auchenorrhynca (Homoptera) also possessing diffuse centromeres. The former have auto-orientation of the bivalents on the metaphase plate while co-orientation, as found in organisms possessing localized centromeres, is present in the latter. The significance of the two types of orientation in chromosomes with diffuse centromeres was discussed.

Mr. W. J. Peacock gave a brief account of an occurrence of a ring chromosome in man. The cytological behaviour of the ring was described, and its probable importance in causation of the associated clinical syndrome was discussed. Possible modes of origin of the ring were outlined and it was pointed out that ring chromosomes were of importance in considerations on chromosome structure.

Dr. W. R. Browne gave a short note on the Miocene peneplain in eastern New South Wales.

ORDINARY MONTHLY MEETING.

27th JUNE, 1962.

Professor B. J. F. Ralph, President, in the chair.

Professor M. R. J. Salton, Professor of Microbiology, University of New South Wales, delivered a lecturette entitled "The Anatomy of Micro-organisms".

Mr. I. P. Burgess, B.Sc.For., Dip.For., Taree, N.S.W., and Dr. G. M. Philip, M.Sc. (Melb.), Ph.D. (Cantab.), F.G.S., Armidale, N.S.W., were elected Ordinary Members of the Society.

The Chairman announced that Dr. R. C. Carolin had been elected a Member of Council in place of Dr. Lilian R. Fraser, resigned.

The Chairman offered congratulations to Dr. Joyce W. Vickery on receiving the honour of M.B.E. from Her Majesty the Queen.

The Chairman announced that the Third Sir William Macleay Memorial Lecture, 1962, will be delivered by Dr. R. N. Robertson, F.R.S., F.A.A., Professor of Botany, University of Adelaide, on Thursday, 23rd August, 1962, at 8 p.m. The title of the lecture is "Living Membranes—Frontiers of Research at the Boundaries of Life".

The Chairman announced that library accessions amounting to 8 volumes, 108 parts or numbers, 5 bulletins, 5 reports and 11 pamphlets, total 137, had been received since the last meeting.

PAPERS READ.

1. *Hyla phyllochrous* Gunther (Amphibia) as an Addition to the Fauna of Victoria, with the Description of a New Race and a Note on the Name of the Genus. By Stephen J. Copland.

2. A New Encyrtid Genus parasitic on Bug Eggs. By E. F. Riek.

3. A Trigonalid Wasp (Hymenoptera, Trigonalidae) from an Anthelid Cocoon (Lepidoptera, Anthelidae). By E. F. Riek.

4. Studies on the Inheritance of Rust Resistance in Oats. I. Inheritance of Stem Rust Resistance in Crosses involving the Varieties Burke, Laggan, White Tartar and Anthony. By Y. M. Upadhyaya and E. P. Baker.

ORDINARY MONTHLY MEETING.

25th JULY, 1962.

Professor B. J. F. Ralph, President, in the chair.

Miss Mary C. Flynn, M.A., Sydney, and Mr. J. Rade, M.Sc., Melbourne, Victoria, were elected Ordinary Members of the Society.

The Chairman announced that the Council had elected Mr. S. J. Copland a Vice-President in place of Dr. Lilian Fraser, who had resigned from the Council.

On behalf of members the Chairman congratulated Mr. E. H. Zeck on the award of the Australian Natural History Medallion for 1961.

The Chairman announced that the Third Sir William Macleay Memorial Lecture, 1962, will be delivered by Dr. R. N. Robertson, F.R.S., F.A.A., Professor of Botany, University of Adelaide, on Thursday, 23rd August, 1962, at 8 p.m., in the Great Hall, University of Sydney. The title of the lecture is "Living Membranes—Frontiers of Research at the Boundaries of Life". All interested are welcome.

No Ordinary Monthly Meeting of the Society will be held during August, 1962.

The Chairman announced that library accessions amounting to 22 volumes, 166 parts or numbers, 8 bulletins, 2 reports and 9 pamphlets, total 207, had been received since the last meeting.

PAPERS READ.

1. Notes on Plant Parasitic Fungi. I. By John Walker.

2. The Actual Identity of Captain Cook's Kangaroo. By Tom Iredale and Ellis Troughton.

3. Australian Liverworts. I. A New Species of *Haplomitrium* (Calobryales). By G. K. Berrie.

4. Some Insects and Terrestrial Arthropods from Heron Island, Queensland. By C. E. Chadwick.

5. Zinc Deficiency on the Darling Downs, Queensland. By B. R. Hewitt.

6. A New Species of *Echthroplexis*, an Encyrtid Hyperparasite of Lerp-forming Psyllids on Eucalypts (Hymenoptera, Chalcidoidea). By E. F. Riek.

7. Revision of the Thynnidae. Part V. Contribution towards a Knowledge of the Thynnidae of the Philippines, Indonesia, New Guinea, The Solomons, New Caledonia and Lord Howe Island. By K. E. W. Salter.

8. Studies on the Inheritance of Rust Resistance in Oats. II. The Mode of Inheritance of Crown Rust Resistance in the Varieties Landhafer, Santa Fe, Mutica Ukraine, Trispernia and Victoria in their Crosses with Susceptible Varieties. By Y. M. Upadhyaya and E. P. Baker.

9. The Development of the Polychaete *Galeolaria caespitosa* Lamarck (Fam. Serpulidae). By J. C. Andrews and D. T. Anderson.

ACCOUNT OF PRESIDENTIAL ADDRESS.

Professor J. M. Vincent, who was overseas on 28th March, 1962, gave an account of his Presidential Address entitled "Australian Studies of the Root-nodule Bacteria. A Review".

ORDINARY MONTHLY MEETING.

26TH SEPTEMBER, 1962.

Professor B. J. F. Ralph, President, in the chair.

The following were elected Ordinary Members of the Society: Miss Carina J. Clarke, B.Sc., Gordon, N.S.W.; Mr. W. H. Payne, A.S.T.C., A.M.I.E.Aust., M.A.P.E., Picnic Point, N.S.W.; Miss Valerie E. Sands, M.Sc., Sydney University; Mr. R. Strahan, M.Sc., University of New South Wales; and Mr. A. W. Sweeney, Maroubra, N.S.W.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1963, from qualified candidates. Each applicant must be a member of this Society and be a graduate in Science or Agricultural Science of the University of Sydney. The range of actual (tax-free) salary is, according to qualifications, up to a maximum of £1,600 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 7th November, 1962.

The Chairman offered congratulations to Professor R. N. Robertson on his election as a Foreign Associate of the National Academy of Sciences, Washington, U.S.A.; also to Associate Professor I. A. Watson on his appointment to the Chair of Agricultural Botany (Plant Breeding) in the University of Sydney.

The Chairman announced that library accessions amounting to 41 volumes, 221 parts or numbers, 13 bulletins, 10 reports and 22 pamphlets, total 307, had been received since the last meeting.

The Chairman announced that invitations to members of the Society have been received from the Bouddi Natural Park Trustees to attend the Dedication of "The Dingeldei Memorial Shelter" in the Park on Saturday, 10th November, 1962, at 3 p.m., and to be present at The Sir Edward Hallstrom Faunal Reserve No. 15 (between Berowra and Cowan, off the Pacific Highway) on Saturday, 24th November, 1962, at 3 p.m., when Sir Edward Hallstrom will hand over the key to the Warden/Ranger's cottage to the Chief Secretary.

The Chairman brought to the notice of members a communication from the Adolph Basser Library, Australian Academy of Science, drawing attention to its purposes as a centre for the study of the history of science in Australia; to build up a specialist library of published material relating to the history of Australian science, including Australian scientific journals; and to collect and preserve archival material (or to record the whereabouts of such material) that throws light on the lives and work of Australian scientists and their institutions. The Academy asks the help of anyone able to give it, in tracing such archival material. The Library would also be interested to learn of any work in progress on the history of Australian science.

PAPERS READ.

1. A New Genus of Gall-forming Brachyscelidiphagine Pteromalidae (Hymenoptera, Chalcidoidea) from Western Australia. By E. F. Riek.

2. A New Encyrtid (Hymenoptera, Chalcidoidea) Genus of Parasites of Lerp-forming Psyllids on Eucalypts. By E. F. Riek.

3. Gynodioecism in *Leucopogon melaleucoides* A. Cunn. By Alison McCusker.

4. Bat Ticks of the Genus *Argas* (Ixodoidea, Argasidae). 5. Description of Larvae from Australian and New Guinea *Carios*-group Populations. By Harry Hoogstraal and Glen M. Kohls. (*Communicated by Dr. Bruce McMillan.*)

LECTURETTE.

An illustrated lecturette entitled "Human Chromosomes" was delivered by Mr. W. J. Peacock, Linnean Macleay Fellow of the Society in Botany.

ORDINARY MONTHLY MEETING.

24TH OCTOBER, 1962.

Professor B. J. F. Ralph, President, in the chair.

LECTURETTE.

An illustrated lecturette entitled "Paralysis in Ecology" was delivered by Professor F. L. Milthorpe, School of Agriculture, University of Nottingham.

The Chairman announced that Professor I. A. Watson had been elected a Member of Council in place of Professor R. L. Crocker, who had resigned.

The Chairman offered congratulations to Dr. Aola M. Richards, who recently received the Citation of Merit from the National Speleological Society of U.S.A., for her researches in the cave-biology of New Zealand.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1963, from qualified candidates. Each applicant must be a member of this Society and be a graduate in Science or Agricultural Science of the University of Sydney. The range of actual (tax-free) salary is, according to qualifications, up to a maximum of £1,600 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 7th November, 1962.

The Chairman announced that library accessions amounting to 10 volumes, 124 parts or numbers, 2 bulletins, 3 reports and 9 pamphlets, total 148, had been received since the last meeting.

PAPERS READ.

1. Notes on Australian Mosquitoes (Diptera, Culicidae). VI. Five New Victorian Species and a Description of the Larva of *Aëdes milsoni* (Taylor). By N. V. Dobrotworsky.

2. The Biology of *Roeselia lugens* (Walk.), the Gum-leaf Skeletonizer Moth, with Particular Reference to the *Eucalyptus camaldulensis* Dehn. (River Red Gum) Forests of the Murray Valley Region. By K. G. Campbell.

3. Amendments to the Disposal of Type Specimens of Species of *Culex* (*Lophoceraomyia*) from New Guinea. By Donald H. Colless.

4. New Species of *Ohakunea* Edwards and a Related New Genus, with Notes on the Relationships of *Heterotricha* Loew. (Diptera). By Donald H. Colless.

5. Australasian Ceratopogonidae (Diptera, Nematocera). Part IX. The Genus *Macrurohelea*. By D. J. Lee.

6. Notes on the Taxonomy of the *Aëdes scutellaris* Group, and New Records of *A. paullusi* and *A. albopictus* (Diptera, Culicidae). By Donald H. Colless.

7. Notes on Australasian Tanyderidae, with Description of a New Species of *Radinoderus* Handl. (Diptera). By Donald H. Colless.

8. On a Collection of Plants of Permian Age from Baralaba, Queensland. By J. F. Rigby.

ORDINARY MONTHLY MEETING.

28TH NOVEMBER, 1962.

Professor B. J. F. Ralph, President, in the chair.

The Chairman announced that the Council had appointed Mr. P. J. Dart, B.Sc.Agr., to a Linnean Macleay Fellowship in Plant Physiology for one year from 1st January, 1963.

The Chairman announced that library accessions amounting to 11 volumes, 193 parts or numbers, 9 bulletins, 5 reports and 5 pamphlets, total 223, had been received since the last meeting.

PAPERS READ.

1. Australasian Ceratopogonidae (Diptera, Nematocera). Part X. Additional Australian Species of *Culicoides*. By David J. Lee and Eric J. Reye.

2. "Sandflies" as Possible Vectors of Disease in Domesticated Animals in Australia. By D. J. Lee, E. J. Reye and A. L. Dyce.

3. The Influence of the Tide Cycle on Certain Species of *Culicoides* (Diptera, Ceratopogonidae). By Eric J. Reye and David J. Lee.

4. Chromosome Races in *Goodenia bellidifolia* Sm. By W. J. Peacock.

5. Structural Geology of Part of the Tamworth Trough. By Keith A. W. Crook.

NOTES AND EXHIBITS.

Mr. C. E. Chadwick exhibited specimens and photographs of the Tingid bugs *Stephanitis pyrioides* and *S. queenslandensis*. It is obvious that these two species have been confused for many years.

S. pyrioides (Scott) 1874 was described from Japan, and has been imported into Australia, probably from the Orient, Europe, or U.S.A. It is a pest of azaleas in the Sydney district where mottling of leaves results from their attacks.

S. queenslandensis Hacker 1927 was described from Mt. Tambourine, Queensland, where it was taken from the native plant *Stephania hernandiaefolia* (*Mem. Q'land. Mus.*, ix, 1 (28 April): 19–32, Pl. VII, fig. 8). In the following year Hacker recorded the species from Cairns and Magnetic Island (*Mem. Q'land. Mus.*, ix, 2 (16 June): 174–187, Pls xx–xxiii). Specimens were collected at Gosford by P. C. Hely on 16th March 1953 and at Terrigal on 28th June last when J. G. Gellatley obtained them from the native plant *Sarcopetalum harveyanum*. These are possibly the first authentic records of the species in N.S.W.

The two species are readily distinguishable on microscopic examination as indicated in the following table. Probably the most useful character is the size and form of the lateral carina.

Stephanitis pyrioides (Scott)	*Stephanitis queenslandensis* Hacker
Head mottled; eyes prominent.	Head light in colour; eyes not so prominent.
Head pointed in front; vesicle extends more than half way down pronotal disc.	Head somewhat blunt in front; vesicle extends only about half way down pronotal disc.
Pronotal disc brownish.	Pronotal disc grey.
Lateral carina very short and straight.	Lateral carina long, often curved.
Hemielytra relatively flat.	Hemielytra more corrugated.

The late Anthony Musgrave exhibited specimens of "*Stephanitis queenslandensis*" at the July 1950 meeting of the Linnean Society (Proc. Linn. Soc. N.S.W., lxxv (5–6): p. xxvii). The specimens mentioned in his note were examined at the Australian Museum recently and they, and in fact the whole fifteen specimens in that collection, are undoubtedly *S. pyrioides* in spite of labels (not in Hacker's handwriting) indicating that some were determined by Hacker.

Specimens examined so far indicate that *S. queenslandensis* is an indigenous species attacking native plants and at present known from the Gosford district to Cairns.

S. pyrioides has been definitely determined from azaleas in Sydney suburbs and Canberra, but is probably more widespread. It would be of interest to examine further specimens. The species had obviously been in the Sydney district for well over twenty years as is indicated by the following statement: "An unusually severe infestation of the Lace Bug (*Stephanitis queenslandicus*) occurred on azaleas and rhododendrons, causing much damage in Sydney and Suburban districts." (Noble, R. J., Rep. Dep. Agric. N.S.W., 1941, p. 32.) There is no known indication of the date or method of entry into the State.

Dr. K. P. Lamb, at the invitation of the Chairman, reported the first record of the Order Protura in New South Wales.

The Order Protura includes about 100 species of minute, primitive, apterygote insects which lack antennae and compound eyes. They are widely distributed in leaf mould and in damp situations with a low pH (Tuxen, 1931). Representatives of the Order have been found in Europe, North, Central and South America, South Africa, India, Japan, Indonesia, New Guinea and New Zealand. Because of their small size (less than 2 mm. long) and sluggish movement these insects are often overlooked by collectors.

Womersley (1939) recorded eight species and one subspecies from Australia: five from Western Australia and four from South Australia. All the species described by Womersley were recently examined and redescribed by Tuxen (1961).

Hitherto no Proturans have been recorded from the eastern States of Australia. However, examination of leaf litter collected from a subtropical rain forest remnant at Bulli, N.S.W., on 29th April, 1961, revealed the presence of four specimens, apparently all of the same species. Two of these were identified by Dr. S. L. Tuxen of the Zoological Museum, Copenhagen, Denmark, as immature individuals (maturi juniores) of *Berberentulus capensis* (Womersley, 1931). This species was orginially described as *Acerentulus capensis* Womersley, 1931 from Capetown, South Africa. Dr. Tuxen notes that this species is synonymous with *A. caldarius* Condé and *A. populeus* da Cunha and is thus known from Capetown, Portugal and France. It has not been found before in Australia.

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Mr. M. J. Whitten gave a brief description of a new eye mutant in *Drosophila melanogaster*, and an account of its genetic determination.

Professor J. M. Vincent exhibited colour-transparencies of the garden of Linnaeus at Uppsala, Sweden.

Dr. A. R. H. Martin exhibited a group of photographs of pollen of *Eucalyptus* species from the University of Sydney pollen collection. These illustrate a surprising range of pollen morphology within the genus.

LIST OF MEMBERS.

(15th December, 1962.)

ORDINARY MEMBERS.

(An asterisk (*) denotes Life Member.)

1940 Abbie, Professor Andrew Arthur, M.D., B.S., B.Sc., Ph.D., c.o. University of Adelaide, Adelaide, South Australia.
1940 *Allman, Stuart Leo, B.Sc.Agr., M.Sc., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W.
1959 Anderson, Donald Thomas, B.Sc., Ph.D., Department of Zoology, Sydney University.
1922 Anderson, Robert Henry, B.Sc.Agr., Royal Botanic Gardens, Sydney.
1927 *Armstrong, Jack Walter Trench, "Cullingera", Nyngan, N.S.W.
1952 Ashton, David Hungerford, B.Sc., Ph.D., 92 Warrigal Road, Surrey Hills, E.10, Victoria.
1912 Aurousseau, Marcel, B.Sc., 229 Woodland Street, Balgowlah, N.S.W.

1952 Baehni, Professor Charles, Dr.sc., Conservatoire botanique, Université de Genève, 192, rue de Lausanne, Genève, Switzerland.
1962 Bailey, Peter Thomas, B.Sc., 1 Coogarah Street, Blakehurst, N.S.W.
1961 Bain, Miss Joan Maud, M.Sc., 18 Onyx Road, Artarmon, N.S.W.
1949 Baker, Eldred Percy, B.Sc.Agr., Ph.D., Faculty of Agriculture, Sydney University.
1962 Ballantyne, Miss Barbara Jean, B.Sc.Agr., N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W.
1959 Bamber, Richard Kenneth, A.S.T.C. (Science), 113 Lucinda Avenue South, Wahroonga, N.S.W.
1950 *Barber, Professor Horace Newton, M.A., Ph.D., Department of Botany, University of Tasmania, Hobart, Tasmania.
1960 Barber, Ian Alexander, B.Sc.Agr., Department of Zoology, Sydney University.
1955 Barlow, Bryan Alwyn, B.Sc., Ph.D., Department of Botany, University of Queensland, St. Lucia, Brisbane, Queensland.
1956 Barnard, Robert Alexander Stephen,
1960 Batley, Alan Francis, A.C.A., 123 Burns Road, Wahroonga, N.S.W.
1954 Baur, George Norton, B.Sc., B.Sc.For., Dip.For., 3 Mary Street, Beecroft, N.S.W.
1935 *Beadle, Professor Noel Charles William, D.Sc., University of New England, Armidale, 5N, N.S.W.
1946 Bearup, Arthur Joseph, B.Sc., 66 Pacific Avenue, Penshurst, N.S.W.
1940 Beattie, Joan Marion, D.Sc. (*née* Crockford), 28 Menangle Road, Camden, N.S.W.
1961 Bedford, Miss Lynette, B.Sc., Department of Zoology, Sydney University.
1952 Bennett, Miss Isobel Ida, Department of Zoology, Sydney University.
1960 Berrie, Geoffrey Kenneth, B.Sc., Ph.D., 202 Headland Road, Dee Why, N.S.W.
1948 Besly, Miss Mary Ann Catherine, B.A., Department of Zoology, Sydney University.
1961 Bishop, James Arthur, Department of Zoology, Sydney University.
1958 Blake, Clifford Douglas, B.Sc.Agr., Ph.D., N.S.W. Department of Agriculture, Division of Science Services, 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., Department of Zoology, University of Melbourne, Parkville, N.2, Victoria.
1960 Bourke, Terrence Victor, B.Sc.Agr., c.o. Post Office, Graman 5N, N.S.W.
1946 Brett, Robert Gordon Lindsay, B.Sc., 7 Petty Street, West Hobart, Tasmania.
1960 Brewer, Ilma Mary, D.Sc., 7 Thornton Street, Darling Point, Sydney.
1955 Briggs, Miss Barbara Gillian, Ph.D., 13 Findlay Avenue, Roseville, N.S.W.
1924 Browne, Ida Alison, D.Sc. (*née* Brown), 363 Edgecliff Road, Edgecliff, N.S.W.
1949 Browne, Lindsay Blakeston Barton, Ph.D., C.S.I.R.O. Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1911 Browne, William Rowan, D.Sc., 363 Edgecliff Road, Edgecliff, N.S.W.
1952 Bunt, John Stuart, B.Sc.Agr., Ph.D., School of Agriculture, Sydney University.
1949 Burden, John Henry, 1 Havilah Street, Chatswood, N.S.W.
1931 *Burges, Professor Norman Alan, M.Sc., Ph.D., Professor of Botany, University of Liverpool, Liverpool, England.
1959 Burgess, The Rev. Colin E. B. H., Parks and Gardens Section, Department of the Interior, Canberra, A.C.T.
1962 Burgess, Ian Peter, B.Sc.For., Dip.For., The Forestry Office, Taree, N.S.W.

1960 Cady, Leo Isaac, "Milford", Saddleback Road, Kiama, N.S.W.
1959 Campbell, Keith George, D.F.C., B.Sc.For., Dip.For., M.Sc., 17 Third Avenue, Epping, N.S.W.

1927 Campbell, Thomas Graham, Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
1934 *Carey, Professor Samuel Warren, D.Sc., Geology Department, University of Tasmania, Hobart, Tasmania.
1949 Carne, Phillip Broughton, B.Agr.Sci. (Melb.), Ph.D. (London), D.I.C., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1956 Carolin, Roger Charles, B.Sc., A.R.C.S., Ph.D., Department of Botany, Sydney University.
1957 Casimir, Max, B.Sc.Agr., Flat 2, 36 Benelong Road, Cremorne, N.S.W.
1936 *Chadwick, Clarence Earl, B.Sc., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W.
1956 Chambers, Thomas Carrick, M.Sc. (N.Z.), Ph.D., Botany School, University of Melbourne, Parkville, N.2, Victoria.
1959 Chippendale, George McCartney, B.Sc., Lindsay Avenue, Alice Springs, Northern Territory, Australia.
1947 Christian, Stanley Hinton, Malaria Research Unit and School, Kundiawa, Eastern Highlands, Territory of Papua and New Guinea.
1932 *Churchward, John Gordon, B.Sc.Agr., Ph.D., 6 Kareela Road, Chatswood, N.S.W.
1946 Clark, Laurance Ross, M.Sc., c.o. C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1961 Clarke, Miss Lesley Dorothy, 4 Gordon Crescent, Eastwood, N.S.W.
1947 Clarke, Mrs. Muriel Catherine, M.Sc (*née* Morris), 122 Swan Street, Morpeth, N.S.W.
1901 Cleland, Professor John Burton, M.D., Ch.M., C.B.E., 1 Dashwood Road, Beaumont, Adelaide, South Australia.
1957 Clinton, Kenneth John, School of Public Health and Tropical Medicine, Sydney University.
1956 Cogger, Harold George, M.Sc., 4 Blane Street, Granville, N.S.W.
1946 Colless, Donald Henry, Ph.D. (Univ. of Malaya), c.o. Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
1956 Common, Ian Francis Bell, M.A., M.Sc.Agr., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1942 Copland, Stephen John, M.Sc., 15 Chilton Parade, Warrawee, N.S.W.
1947 Costin, Alex Baillie, B.Sc.Agr., C.S.I.R.O., Division of Plant Industry, P.O. Box 109, City, Canberra, A.C.T.
1908 Cotton, Professor Leo Arthur, M.A., D.Sc., 113 Queen's Parade East, Newport Beach, N.S.W.
1950 Crawford, Lindsay Dinham, B.Sc., 4 Dalton Avenue, West Hobart, Tasmania.
1955 Crocker, Professor Robert Langdon, D.Sc., Department of Botany, Sydney University.
1957 Crook, Keith Alan Waterhouse, M.Sc., Ph.D. (New England), Department of Geology, Australian National University, G.P.O. Box 197, Canberra, A.C.T.

1960 Dart, Peter John, B.Sc.Agr., Department of Botany, Sydney University.
1957 Davies, Stephen John James Frank, B.A. (Cantab.), Emmanuel College, Cambridge, England.
1945 Davis, Professor Gwenda Louise, Ph.D., B.Sc., Faculty of Science, University of New England, Armidale, 5N, N.S.W.
1934 Day, William Eric, 23 Gelling Avenue, Strathfield, N.S.W.
1937 Deuquet, Camille, B.Com., 56 Avenue Eug. Ysaye, Brussels 7, Belgium.
1953 Dobrotworsky, Nikolai V., M.Sc., Ph.D., Department of Zoology, University of Melbourne, Parkville, N.2, Victoria.
1954 Domrow, Robert, B.A., B.Sc., Queensland Institute of Medical Research, Herston Road, Herston, N.9, Brisbane, Queensland.
1960 Dorman, Herbert Clifford, J.P., A.S.T.C. (Dip.Chem.), Dip.Soc. Stud. (Sydney), Rodgers Street, Teralba 2N, N.S.W.
1954 Douglas, Geoffrey William, B.Agr.Sci., 226 Clarendon Street, East Melbourne, C.2, Victoria.
1962 Drummond, David Charles, Department of Zoology, Sydney University.
1946 Durie, Peter Harold, M.Sc., C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Brisbane, Queensland.
1952 Dyce, Alan Lindsay, B.Sc.Agr., 48 Queen's Road, Asquith, N.S.W.

1953 Edwards, Dare William, B.Sc.Agr., Forestry Commission of N.S.W., Division of Wood Technology, 96 Harrington Street, Sydney.
1947 Endean, Robert, M.Sc., Ph.D., Department of Zoology, University of Queensland, St. Lucia, Brisbane, Queensland.
1930 English, Miss Kathleen Mary Isabel, B.Sc., 2 Shirley Road, Roseville, N.S.W.
1957 Evans, Miss Gretchen Pamela, M.Sc., Box 92, P.O., Canberra, A.C.T.
1955 Evans, John William, M.A., D.Sc., Sc.D., 47 Bundarra Road, Bellevue Hill, N.S.W.

1955 *Fairey, Kenneth David, Box 1176, G.P.O., Sydney.
1957 Filewood, Lionel Winston Charles, 62 Dickson Avenue, West Ryde, N.S.W.

1953 Frame, William Robert, Goroka, New Guinea.
1930 Fraser, Miss Lilian Ross, D.Sc., "Hopetoun", 25 Bellamy Street, Pennant Hills, N.S.W.

1959 Gardner, Mervyn John, B.Sc.For., Dip.For., Forest Office, Baradine 6W, N.S.W.
1935 *Garretty, Michael Duhan, D.Sc., Box 763, Melbourne, Victoria.
1958 Green, John William, B.Sc. (Adel.), Department of Botany, University of New England, Armidale 5N, N.S.W.
1944 Greenwood, William Frederick Neville, 11 Wentworth Avenue, Waitara, N.S.W.
1946 *Griffiths, Mrs. Mabel, B.Sc. (*née* Crust), 42 Bellevue Parade, North Curl Curl, N.S.W.
1936 Griffiths, Mervyn Edward, D.Sc., Wildlife Survey Section, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
1939 *Gunther, Carl Ernest Mitchelmore, M.B., B.S., D.T.M., D.T.M. & H. (England), 29 Flaumont Avenue, Lane Cove, N.S.W.

1959 Hadlington, Phillip Walter, B.Sc.Agr., 15 Annie Street, Hurstville, N.S.W.
1952 Hannon, Miss Nola Jean, B.Sc., Ph.D., 22 Leeder Avenue, Penshurst, N.S.W.
1952 *Hansford, Clifford Gerald, M.A., Sc.D. (Cantab.), D.Sc. (Adel.), F.L.S., P.O. Box 66, Uvongo Beach, Natal, South Africa.
1917 Hardy, George Huddleston Hurlstone, "Karambi", Letitia Street, Katoomba, N.S.W.
1960 Hartigan, Desmond John, B.Sc.Agr., 75 Northwood Road, Northwood, Lane Cove, N.S.W.
1958 Hennelly, John Patten Forde, B.Sc., Highs Road, West Pennant Hills, N.S.W.
1951 Hewitt, Bernard Robert, B.A. (Qld.), B.Sc. (Syd.), M.Sc. (N.S.W.), Joint Coal Board, Vincent Street, Cessnock, N.S.W.
1930 Heydon, George Aloysius Makinson, M.B., Ch.M., 9 Sirius Avenue, Mosman, N.S.W.
1938 Hill, Miss Dorothy, M.Sc., Ph.D., Department of Geology, University of Queensland, Brisbane, Queensland.
1943 *Hindmarsh, Miss Mary Maclean, B.Sc., Ph.D., 4 Recreation Avenue, Roseville, N.S.W.
1956 *Holder, Miss Lynette Anne, B.Sc., 48 Rutiedge Street, Eastwood, N.S.W.
1932 Hossfeld, Paul Samuel, M.Sc., Ph.D., 132 Fisher Street, Fullarton, South Australia.
1953 *Hotchkiss, Arland Tillotson, M.S., Ph.D. (Cornell), Department of Biology, University of Louisville, Louisville 8, Kentucky, U.S.A.
1956 *Hotchkiss, Mrs. Doreen Elizabeth, Ph.D., B.A., M.A. (*née* Maxwell), 2440 Longest Avenue, Louisville, Kentucky, U.S.A.
1942 Humphrey, George Frederick, M.Sc., Ph.D., C.S.I.R.O. Marine Biological Laboratory, Box 21, Cronulla, N.S.W.

1960 Ingram, Cyril Keith, B.A., B.Ec., P.O. Box 12, Bathurst, N.S.W.

1938 Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., Australian Forestry School, Canberra, A.C.T.
1961 Jacobson, Miss Constance Mary, M.Sc., 9 Fletcher Street, Bondi, N.S.W.
1960 James, Sidney Herbert, M.Sc., 54 Holmfirth Street, Mt. Lawley, Western Australia.
1960 Jenkins, Thomas Benjamin Huw, Ph.D., Department of Geology and Geophysics, Sydney University.
1952 Jessup, Rupert William, M.Sc., 6 Penno Parade North, Belair, South Australia.
1956 Jobson, Arthur Edgar, 3 Wellington Road, East Lindfield, N.S.W.
1947 Johnson, Lawrence Alexander Sidney, B.Sc., c.o. National Herbarium, Royal Botanic Gardens, Sydney.
1945 Johnston, Arthur Nelson, B.Sc.Agr., 99 Newton Road, Strathfield, N.S.W.
1960 Jolly, Violet Hilary, M.Sc., Ph.D., 1 Twenty-Second Street, Warragamba Dam, N.S.W.
1958 Jones, Edwin Llewelyn, B.A., P.O. Box 196, Leeton 6S, N.S.W.
1930 Joplin, Miss Germaine Anne, B.A., Ph.D., D.Sc., Department of Geophysics, Australian National University, Canberra, A.C.T.
1960 Judd, Howard Kenniwell, Minnamurra Falls Forest Reserve, Box 14, P.O., Jamberoo, N.S.W.

1949 Keast, James Allen, M.Sc., M.A., Ph.D. (Harvard), Professor of Vertebrate Zoology, Queen's University, Kingston, Ontario, Canada.
1951 Kerr, Harland Benson, B.Sc.Agr., Ph.D., 41 Badminton Road, Croydon, N.S.W.
1937 Kesteven, Geoffrey Leighton, D.Sc., c.o. Division of Fisheries and Oceanography, C.S.I.R.O., P.O. Box 21, Cronulla, N.S.W.
1957 Kindred, Miss Berenice May, B.Sc., 58 Caroline Street, Kingsgrove, N.S.W.
1961 King, Miss Dianne, B.Sc., 9 Royce Avenue, Croydon, N.S.W.

1956 Langdon, Raymond Forbes Newton, M.Agr.Sc., Ph.D., Department of Botany, University of Queensland, George Street, Brisbane, Queensland.
1932 Lawson, Albert Augustus, 9 Wilmot Street, Sydney.
1934 Lee, Mrs. Alma Theodora, M.Sc. (*née* Melvaine), Manor Road, Hornsby, N.S.W.
1936 Lee, David Joseph, B.Sc., School of Public Health and Tropical Medicine, Sydney University.
1943 Lothian, Thomas Robert Noel, Botanic Gardens, Adelaide, South Australia.

1957 Luig, Norbert Harold, c.o. Faculty of Agriculture, Sydney University.
1958 Lyne, Arthur Gordon, B.Sc., Ph.D., C.S.I.R.O., Ian Clunies Ross Animal Research Laboratory, P.O. Box 144, Parramatta, N.S.W.

1951 Macdonald, Colin Lewis, Grenfell Road, Cowra, N.S.W.
1948 **Macintosh, Professor Neil William George, M.B., B.S., Department of Anatomy, Sydney University.**
1961 Mackay, Miss Margaret Muriel, B.Sc., Hons. (St. Andrews), M.Sc. (Syd.), M.I.Biol., J.P., "Duncraigon", Cleveland Terrace, Melton Hill, Townsville, Queensland.
1922 Mackerras, Ian Murray, M.B., Ch.M., B.Sc., C.S.I.R.O., Veterinary Parasitology Laboratory, Fairfield Road, Yeerongpilly, 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.
1957 Martin, Anthony Richard Henry, M.A., Ph.D., Department of Botany, Sydney University.
1953 Martin, Mrs. Hilda Ruth Brownell, B.Sc. (*née* Simons), No. 3 Talus Street, Naremburn, N.S.W.
1951 McAlpine, David Kendray, M.Sc., 12 St. Thomas Street, Bronte, N.S.W.
1932 McCulloch, Robert Nicholson, M.B.E., D.Sc.Agr., B.Sc., c/- Board of Tick Control, Lismore, N.S.W.
1957 McCusker, Miss Alison, M.Sc., c/- Department of Botany, University of Ghana, Legon, Accra, Ghana.
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., Agronomy Department, School of Rural Science, University of New England, Armidale 5N, N.S.W.
1948 McKee, Hugh Shaw, B.A., D.Phil. (Oxon.), Division of Plant Industry, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
1957 McKenna, Nigel Reece, 118 Grey Street, South Brisbane, Queensland.
1952 McMichael, Donald Fred, B.Sc., M.A. (Harvard), 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.
1962 McWilliam, Miss Paulette Sylvia, 4 Kingslangley Road, Greenwich, N.S.W.
1944 **Mercer, Professor Frank Verdun, B.Sc., Ph.D. (Camb.), Department of Botany, Sydney University.**
1947 Messmer, Mrs. Pearl Ray, 64 Treatts Road, Lindfield, N.S.W.
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.
1948 Millerd, Miss Alison Adèle, M.Sc., Ph.D., C.S.I.R.O., Division of Plant Industry, P.O. Box 109, City, Canberra, A.C.T.
1947 Millett, Mervyn Richard Oke, B.A., 18 Albion Road, Box Hill, E11, Victoria.
1958 Moore, Kenneth Milton, Cutrock Road, Lisarow, N.S.W.
1960 Moore, Raymond Milton, M.Sc.Agr., 94 Arthur Circle, Forrest, Canberra, A.C.T.
1955 Morgan, Mrs. Eva, M.Sc., 4 Haberfield Road, Haberfield, N.S.W.
1961 Morrison, Gordon Cyril, 21 Urunga Street, North Balgowlah, N.S.W.
1958 Moss, Francis John, 37 Avenue Road, Mosman, N.S.W.
1944 **Moye, Daniel George, B.Sc., Dip.Ed., 6 Kaling Place, Cooma North, N.S.W.**
1955 Muirhead, Warren Alexander, B.Sc.Agr., C.S.I.R.O., Irrigation Research Station, Private Mail Bag, Griffith, N.S.W.
1926 Mungomery, Reginald William, c/- Bureau of Sugar Experiment Stations, 99 Gregory Terrace, Brisbane, Queensland.
1949 Murray, Professor Patrick Desmond Fitzgerald, M.A., D.Sc., Department of Zoology, University of New England, Armidale 5N, N.S.W.

1947 Nashar, Mrs. Beryl, B.Sc., Ph.D., Dip.Ed. (*née* Scott), c.o. 23 Morris Street, Mayfield West 2N, N.S.W.
1925 **Newman, Ivor Vickery, M.Sc., Ph.D., F.R.M.S., F.L.S., Department of Botany, Sydney** University.
1922 Nicholson, Alexander John, C.B.E., D.Sc., F.R.E.S., C.S.I.R.O., Box 109, City, Canberra, A.C.T.
1935 *Noble, Norman Scott, D.Sc.Agr., M.Sc., D.I.C., C.S.I.R.O., 314 Albert Street, East Melbourne, C.2, Victoria.
1920 Noble, Robert Jackson, B.Sc.Agr., Ph.D., 32A **Middle Harbour Road, Lindfield, N.S.W.**
1960 Noffz, Erwin Karl, 6 Church Street, North Sydney, N.S.W.
1912 North, David Sutherland, 42 Chelmsford Avenue, Lindfield, N.S.W.

1948 **O'Farrell, Professor Antony Frederick Louis, A.R.C.Sc., B.Sc., F.R.E.S., Department of** Zoology, University of New England, Armidale 5N, N.S.W.
1950 O'Gower, Alan Kenneth, M.Sc., Ph.D., 20 Gaerloch Avenue, Bondi South, N.S.W.
1961 O'Malley, Miss Doreen Theresa, 100 Hargrave Street, Paddington, N.S.W.

1927 Osborn, Professor Theodore George Bentley, D.Sc., F.L.S., St. Mark's College, Pennington Terrace, North Adelaide, South Australia.
1950 Oxenford, Reginald Augustus, B.Sc., 75 Alice Street, Grafton 3C, N.S.W.

1952 Packham, Gordon Howard, M.Sc., Ph.D., Department of Geology, Sydney University.
1954 Parrott, Arthur Wilson, "Lochiel", Wakapuaka Road, Hira, R.D., Nelson, New Zealand.
1940 *Pasfield, Gordon, B.Sc.Agr., 20 Cooper Street, Strathfield, N.S.W.
1957 Paterson, Miss Betsy Rivers, B.Sc., Ph.D. (Univ. Chicago), Department of Botany, University of New England, Armidale 5N, N.S.W.
1962 Payne, William Herbert, A.S.T.C., A.M.I.E.Aust., M.A.P.E., 250 Picnic Point Road, Picnic Point, N.S.W.
1957 Peacock, William James, B.Sc., Department of Botany, Sydney University.
1922 Perkins, Frederick Athol, B.Sc.Agr., Department of Entomology, University of Queensland, Brisbane, Queensland.
1962 Philip, Graeme Maxwell, M.Sc. (Melb.), Ph.D. (Cantab.), F.G.S., Department of Geology, University of New England, Armidale, 5N, N.S.W.
1947 Phillips, Miss Marie Elizabeth, M.Sc., Ph.D., 4 Morella Road, Clifton Gardens, N.S.W.
1935 Pope, Miss Elizabeth Carington, M.Sc., C.M.Z.S., Australian Museum, College Street, Sydney.
1938 Pryor, Professor Lindsay Dixon, M.Sc., Dip.For., Department of Botany, School of General Studies, Australian National University, Box 197, P.O., City, Canberra, A.C.T.

1960 Racek, Albrecht Adalbert, Dr.rer.nat. (Brno, Czechoslovakia), Department of Zoology, Sydney University.
1962 Rade, Janis, M.Sc., Flat 28A, 601 St. Kilda Road, Melbourne, S.C.3, Victoria.
1956 Rae, Mrs. Clare Annetta, D.Sc., Department of Histology, Sydney University.
1929 Raggatt, Harold George, C.B.E., D.Sc., 60 Arthur Circle, Forrest, Canberra, A.C.T.
1951 Ralph, Professor Bernhard John Frederick, B.Sc., Ph.D. (Liverpool), A.A.C.I., School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W.
1952 Ramsay, Mrs. Helen Patricia, M.Sc. (*née* Lancaster), 34 Haig Avenue, Ryde, N.S.W.
1955 Reed, Mrs. Beryl Marlene, B.Sc. (*née* Cameron), 145 Duffy Street, Ainslie, A.C.T.
1957 Reed, Eric Michael, 145 Duffy Street, Ainslie, A.C.T.
1953 Reye, Eric James, M.B., B.S. (Univ. Qld.), 35 Instow Street, Yeronga, Queensland.
1957 Reynolds, Miss Judith Louise, 118 Homer Street, Earlwood, N.S.W.
1961 Richards, Miss Aola Mary, M.Sc. (Hons.), Ph.D. (N.Z.), School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W.
1946 Riek, Edgar Frederick, B.Sc., Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
1958 Rigby, John Francis, B.Sc., Central Research Laboratories, B.H.P. Coy., Ltd., Shortland 2N, N.S.W.
1936 Roberts, Noel Lee, 10 Kardella Avenue, Killara, N.S.W.
1932 *Robertson, Rutherford Ness, F.R.S., B.Sc., Ph.D., F.A.A., Professor of Botany, University of Adelaide, Adelaide, South Australia.

1957 Sakker, Mrs. Elizabeth Robin (*née* Phillis), Department of Zoology, Sydney University.
1960 Salkilld, Barry William, Dip.Soc.Stud. (Univ. Syd.), 53 Wareemba Street, Abbotsford, N.S.W.
1932 *Salter, Keith Eric Wellesley, B.Sc., Department of Zoology, Sydney University.
1962 Sands, Miss Valerie Elizabeth, M.Sc., Department of Botany, Sydney University.
1919 *Scammell, George Vance, B.Sc., 7 David Street, Clifton Gardens, N.S.W.
1950 *Sharp, Kenneth Raeburn, B.Sc., Eng. Geology, S.M.H.E.A., Cooma, 4S, N.S.W.
1948 Shaw, Miss Dorothy Edith, M.Sc.Agr., Ph.D., Department of Agriculture, Stock and Fisheries, Port Moresby, Papua-New Guinea.
1930 Sherrard, Mrs. Kathleen Margaret, M.Sc., 43 Robertson Road, Centennial Park, Sydney.
1947 Shipp, Erik, 23 Princes Street, Turramurra, N.S.W.
1959 Simons, John Ronald, M.Sc., Ph.D., 242 Kissing Point Road, Turramurra, N.S.W.
1955 Slack-Smith, Richard J., Alice Street, Sassafras, Victoria.
1955 Slack-Smith, Mrs. Shirley Margaret (*née* Ryan), Alice Street, Sassafras, Victoria.
1952 Slade, Milton John, B.Sc., 12 Dobie Street, Grafton, N.S.W.
1953 Smith, Eugene Thomas, 22 Talmage Street, Sunshine, Victoria.
1916 Smith, Miss Vera Irwin, B.Sc., F.L.S., "Loana", Mt. Morris Street, Woolwich, N.S.W.
1943 Smith-White, Spencer, D.Sc.Agr., F.A.A., Department of Botany, Sydney University.
1945 Southcott, Ronald Vernon, M.B., B.S., 13 Jasper Street, Hyde Park, South Australia.
1937 Spencer, Mrs. Dora Margaret, M.Sc. (*née* Cumpston), No. 1 George Street, Tenterfield, N.S.W.
1960 Staff, Ian Allen, B.Sc., Dip.Ed., The Ohio State University, Department of Botany and Plant Pathology, 1735 Neil Avenue, Columbus 10, Ohio, U.S.A.

1926 Stanley, George Arthur Vickers, B.Sc., Post Office Box 378, Port Moresby, Papua-New Guinea.
1932 Stead, Mrs. Thistle Yolette, B.Sc. (*née* Harris), 14 Pacific Street, Watson's Bay, N.S.W.
1956 Stephenson, Neville George, M.Sc. (N.Z.), Ph.D. (Lond.), Department of Zoology, Sydney University.
1949 Stevens, Neville Cecil, B.Sc., Ph.D., Department of Geology, University of Queensland, St. Lucia, Brisbane, Queensland.
1935 Still, Professor Jack Leslie, B.Sc., Ph.D., Department of Biochemistry, Sydney University.
1961 Strong, Philip David, 17 Kennedy Road, Austinmer, N.S.W.
1952 Sullivan, George Emmerson, M.Sc. (N.Z.), Ph.D., Department of Histology and Embryology, Sydney University.
1911 *Sulman, Miss Florence, 11 Ramsay Street, Collaroy, N.S.W.
1955 Sutherland, James Alan, B.A., B.Sc.Agr., "Skye", Galloway Street, Armidale, 5N, N.S.W.
1962 Sweeney, Anthony William, 62 Torrington Road, Maroubra, N.S.W.
1962 Swinbourne, Robert Frederick George, Box 210, Post Office, Alice Springs, Northern Territory, Australia.

1940 Taylor, Keith Lind, B.Sc.Agr., c/- C.S.I.R.O., Stowell Avenue, Hobart, Tasmania.
1950 Tchan, Yao-tseng, Dr., ès Sciences (Paris), Microbiology Laboratory, Faculty of Agriculture, Sydney University.
1950 Thompson, Mrs. Joy Gardiner, B.Sc.Agr. (*née* Garden), 5 Reed Street, Cremorne, N.S.W.
1956 Thomson, James Miln, D.Sc. (W.A.), c.o. C.S.I.R.O., Box 21, P.O., Cronulla, N.S.W.
1960 Thorne, Alan Gordon, 82 Ben Boyd Road, Neutral Bay, N.S.W.
1949 Thorp, Mrs. Dorothy Aubourne, B.Sc. (Lond.), Ph.D., "Sylvan Close", Mt. Wilson, N.S.W.
1944 Thorpe, Ellis William Ray, B.Sc., University of New England, Armidale 5N, N.S.W.
1943 Tindale, Miss Mary Douglas, M.Sc., 60 Spruson Street, Neutral Bay, N.S.W.
1946 Tipper, John Duncan, A.M.I.E.Aust., Box 2770, G.P.O., Sydney.
1921 *Troughton, Ellis Le Geyt, C.M.Z.S., F.R.Z.S., No 1 Hall Street, Bondi Beach, N.S.W.

1952 Valder, Peter George, B.Sc.Agr., Ph.D. (Camb.), Department of Botany, Sydney University.
1949 Vallance, Thomas George, B.Sc., Ph.D., Department of Geology, Sydney University.
1917 Veitch, Robert, B.Sc., F.R.E.S., 24 Sefton Avenue, Clayfield, Brisbane, Queensland.
1930 Vickery, Miss Joyce Winifred, M.B.E., D.Sc., Royal Botanic Gardens, Sydney.
1940 Vincent, Professor James Matthew, D.Sc.Agr., Dip.Bact., Faculty of Agriculture, Sydney University.
1934 *Voisey, Professor Alan Heywood, D.Sc., University of New England, Armidale 5N, N.S.W.

1961 Walker, Donald, B.Sc., M.A., Ph.D., F.L.S., 50 Vasey Crescent, Campbell, Canberra, A.C.T.
1952 Walker, John, B.Sc.Agr., Biological Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W.
1909 Walkom, Arthur Bache, D.Sc., 5/521 Pacific Highway, Killara, N.S.W.
1946 Wallace, Murray McCadam Hay, B.Sc., Institute of Agriculture, University of Western Australia, Nedlands, Western Australia.
1947 Ward, Mrs. Judith, B.Sc., 50 Bellevue Parade, New Town, Hobart, Tasmania.
1930 Ward, Melbourne, Gallery of Natural History and Native Art, Medlow Bath, N.S.W.
1911 Wardlaw, Henry Sloane Halcro, D.Sc., F.R.A.C.I., 71 McIntosh Street, Gordon, N.S.W.
1936 Waterhouse, Douglas Frew, D.Sc., C.S.I.R.O., Box 109, Canberra, A.C.T.
1947 *Waterhouse, John Teast, B.Sc., "Burragillo", Moree, N.S.W.
1927 Waterhouse, Professor Walter Lawry, C.M.G., D.Sc.Agr., M.C., D.I.C., F.L.S., F.A.A., 30 Chelmsford Avenue, Lindfield, N.S.W.
1941 Watson, Professor Irvine Armstrong, Ph.D., B.Sc.Agr., Faculty of Agriculture, Sydney University.
1949 Whaite, Mrs. Joy Lilian, c/- Department of Main Roads, Deniliquin 6S, N.S.W.
1946 Wharton, Ronald Harry, B.Sc., Institute for Medical Research, Kuala Lumpur, Federation of Malaya.
1926 *Whitley, Gilbert Percy, F.R.Z.S., Australian Museum, College Street, Sydney.
1962 Whitten, Maxwell John, 4 Raymond Street, Lidcombe, N.S.W.
1960 Wildon, David Conrad, B.Sc.Agr., Department of Botany, Sydney University.
1954 Williams, John Beaumont, B.Sc., University of New England, Armidale, 5N, N.S.W.
1954 Williams, Mrs. Mary Beth, B.Sc. (*née* Macdonald), 902D Rockvale Road, Armidale 5N, N.S.W.
1960 Williams, Neville John, B.Sc., 56 Karimbla Road, Miranda, N.S.W.
1952 Williams, Owen Benson, M.Agr.Sc. (Melbourne), c/- C.S.I.R.O., The Ian Clunies Ross Animal Research Laboratory, P.O. Box 144, Parramatta, N.S.W.
1950 Willis, Jack Lehane, M.Sc., A.A.C.I., 26 Inverallan Avenue, Pymble, N.S.W.

1959 Wilson, Frank, Australian Scientific Liaison Office, Africa House, Kingsway, London, England.
1947 Winkworth, Robert Ernest, P.O. Box 77, Alice Springs, Northern Territory, Australia.
1949 Wood, Edward James Ferguson, B.A., M.Sc., C.S.I.R.O., Marine Biological Laboratory P.O. Box 21, Cronulla, N.S.W.
1932 Woodhill, Anthony Reeve, D.Sc.Agr., Department of Zoology, Sydney University.

1936 Zeck, Emil Herman, F.R.Z.S., 694 Victoria Road, Ryde, N.S.W.

CORRESPONDING MEMBERS.

1949 Jensen, Hans Laurits, D.Sc.Agr. (Copenhagen), State Laboratory of Plant Culture, Department of Bacteriology, Lyngby, Denmark.

LIST OF PLATES.

PROCEEDINGS, 1962

I.—Wheats inoculated with cultures of *P. graminis*. Galls of *Phytobia pittosporocaulis*.
II.—*Phytobia pittosporophylli* on *Pittosporum undulatum*.
III.—Plant parasitic fungi.
IV.—A. N. Colefax.
V–VIII.—Thynnidae.
IX.—Electromicrographs of: 1. Pea Root, 2. Maize Coleoptile.
X.—*Roeselia lugens*.
XI–XII.—Permian plants from Baralaba, Queensland.
XIII.—Species of *Culicoides*.
XIV.—First metaphases in diploids and polyploids.
XV.—First metaphases and anaphases in tetraploids and hexaploids.
XVI.—Geology of Tamworth Trough.

LIST OF NEW GENERA, NEW SPECIES AND NEW SUBSPECIES.

VOL. 87.

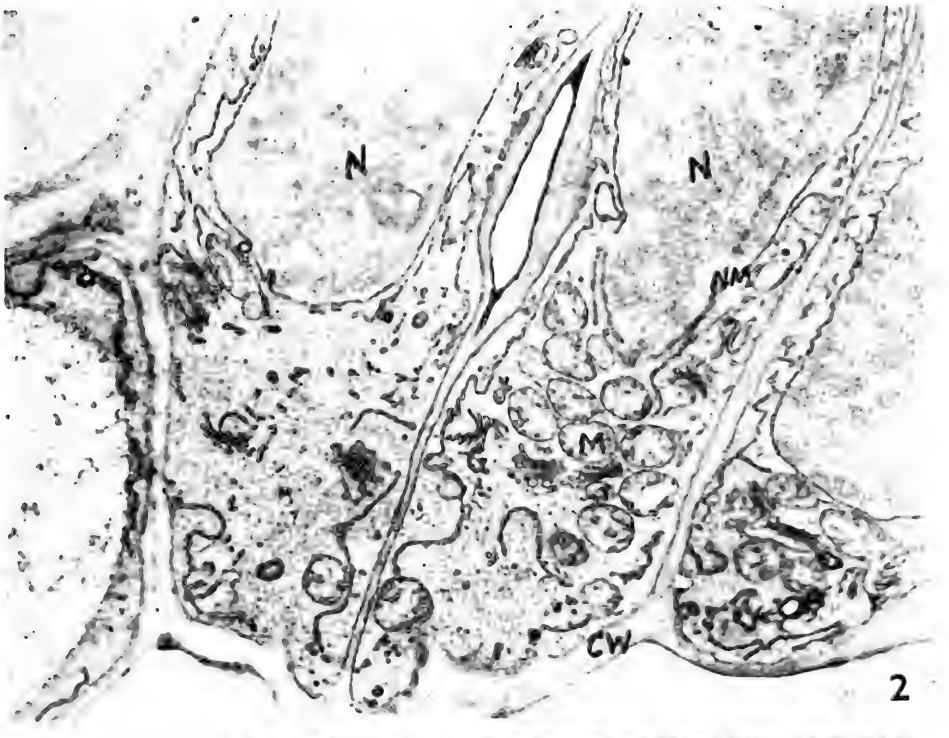
New Genera.

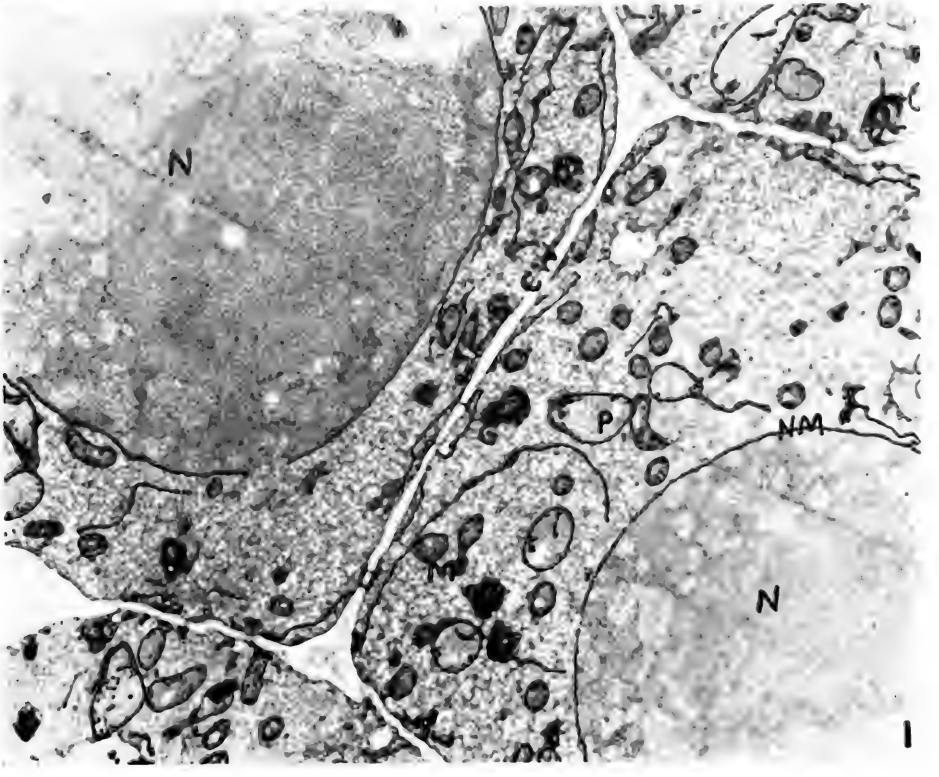
New Species.

New Subspecies.

INDEX.

1962.





Electromicrographs of: 1. Pea Root. 2. Maize Coleoptile.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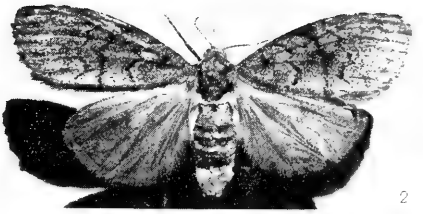
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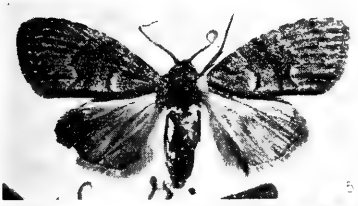
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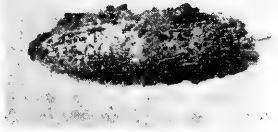


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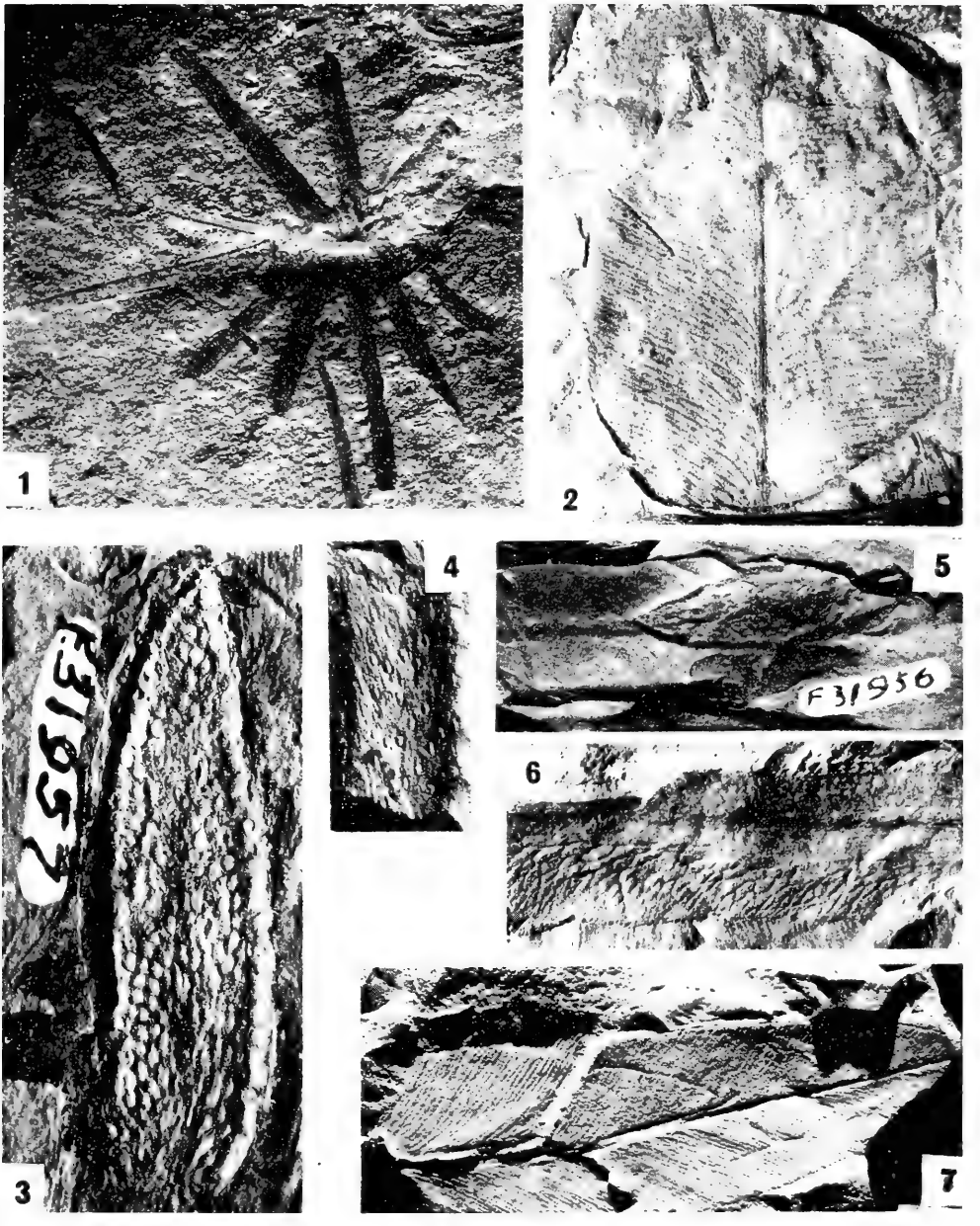
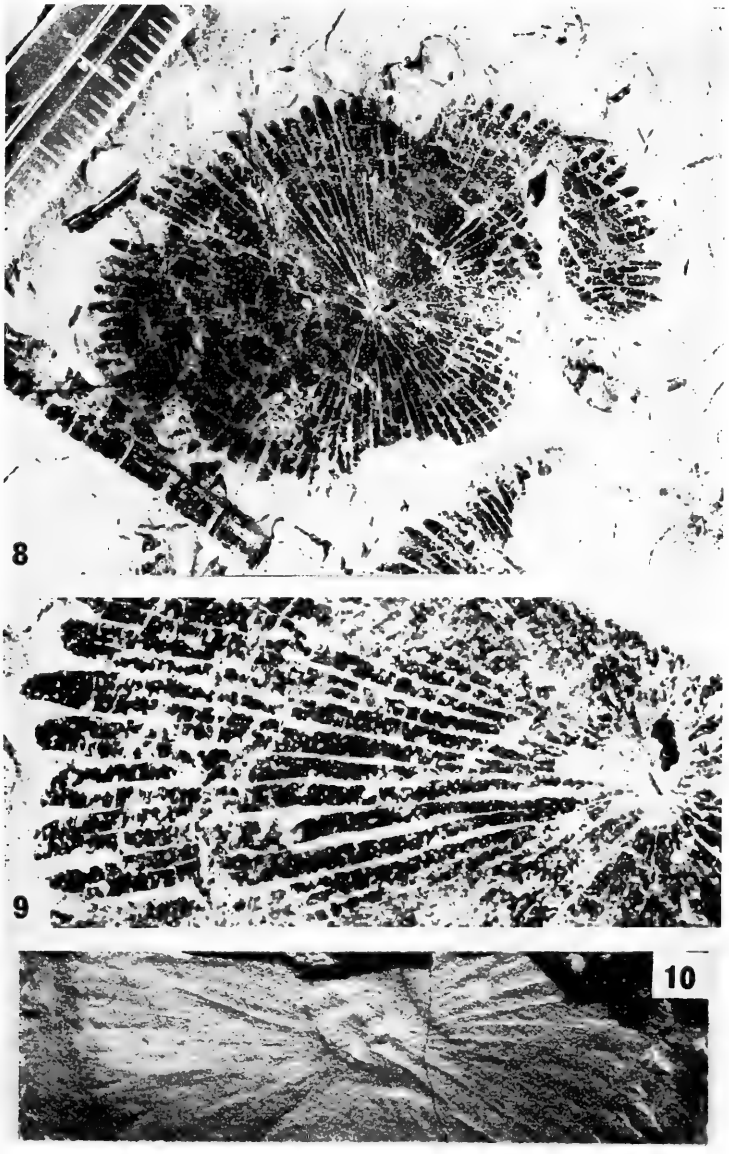
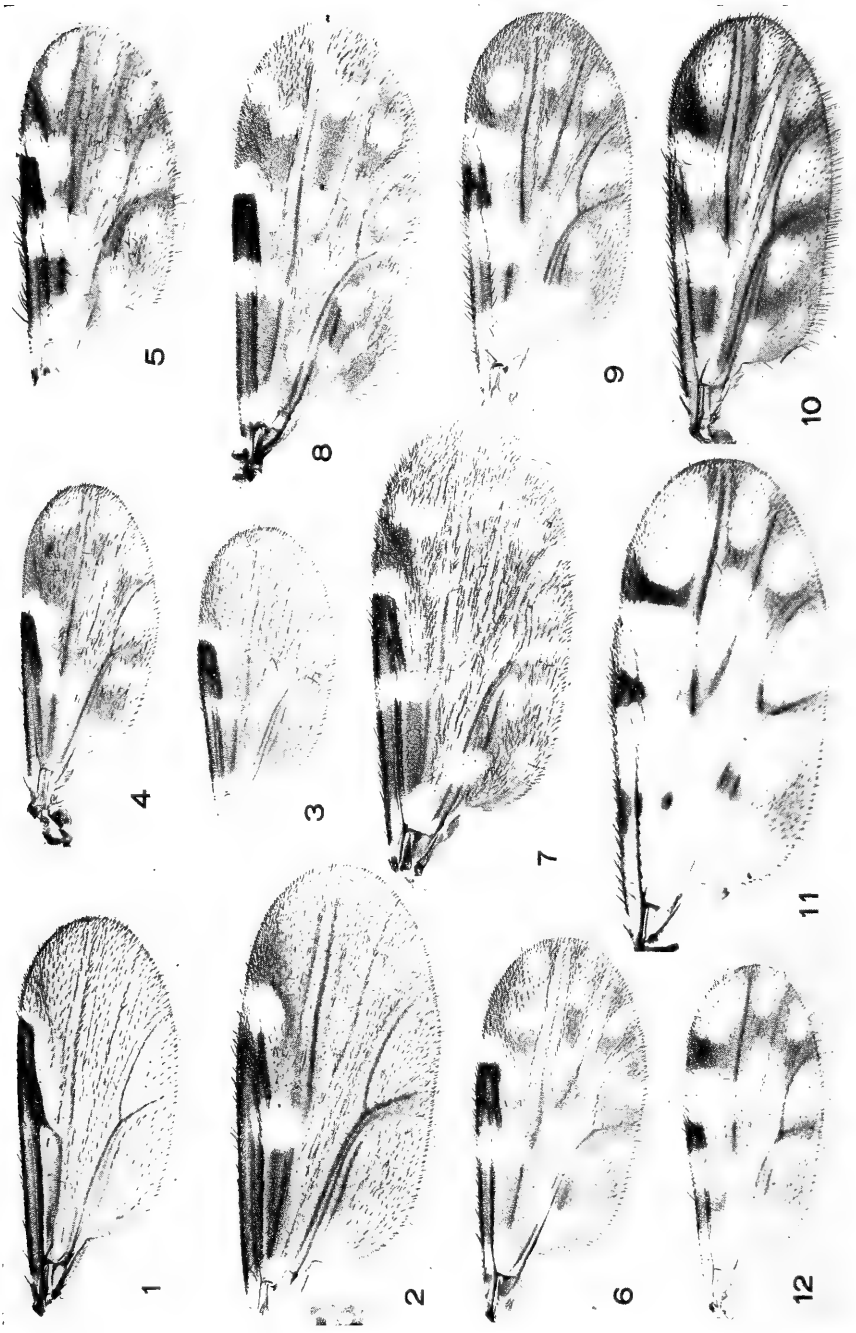
Roeselia lugens.



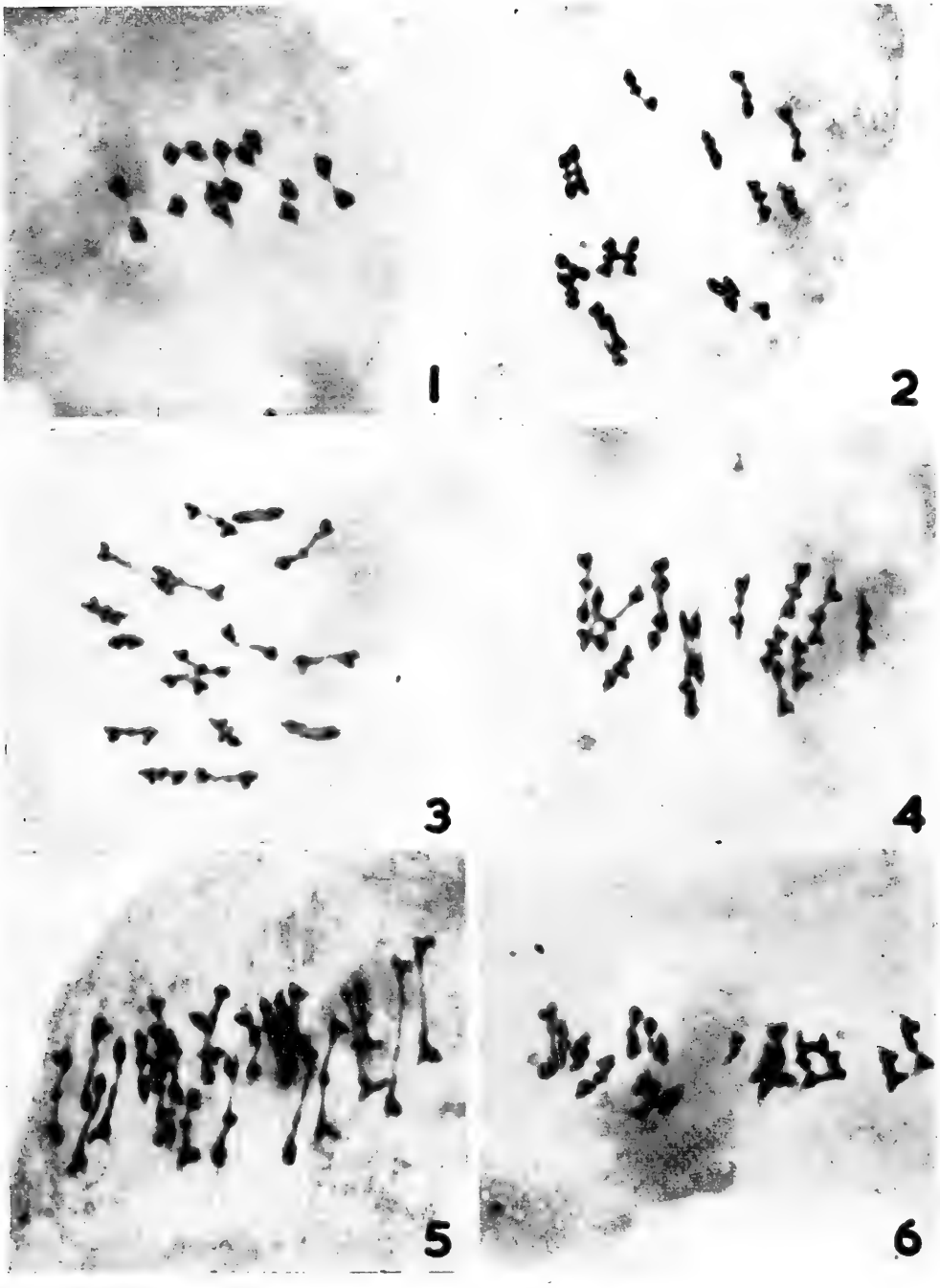
Permian plants from Baralaba, Queensland.



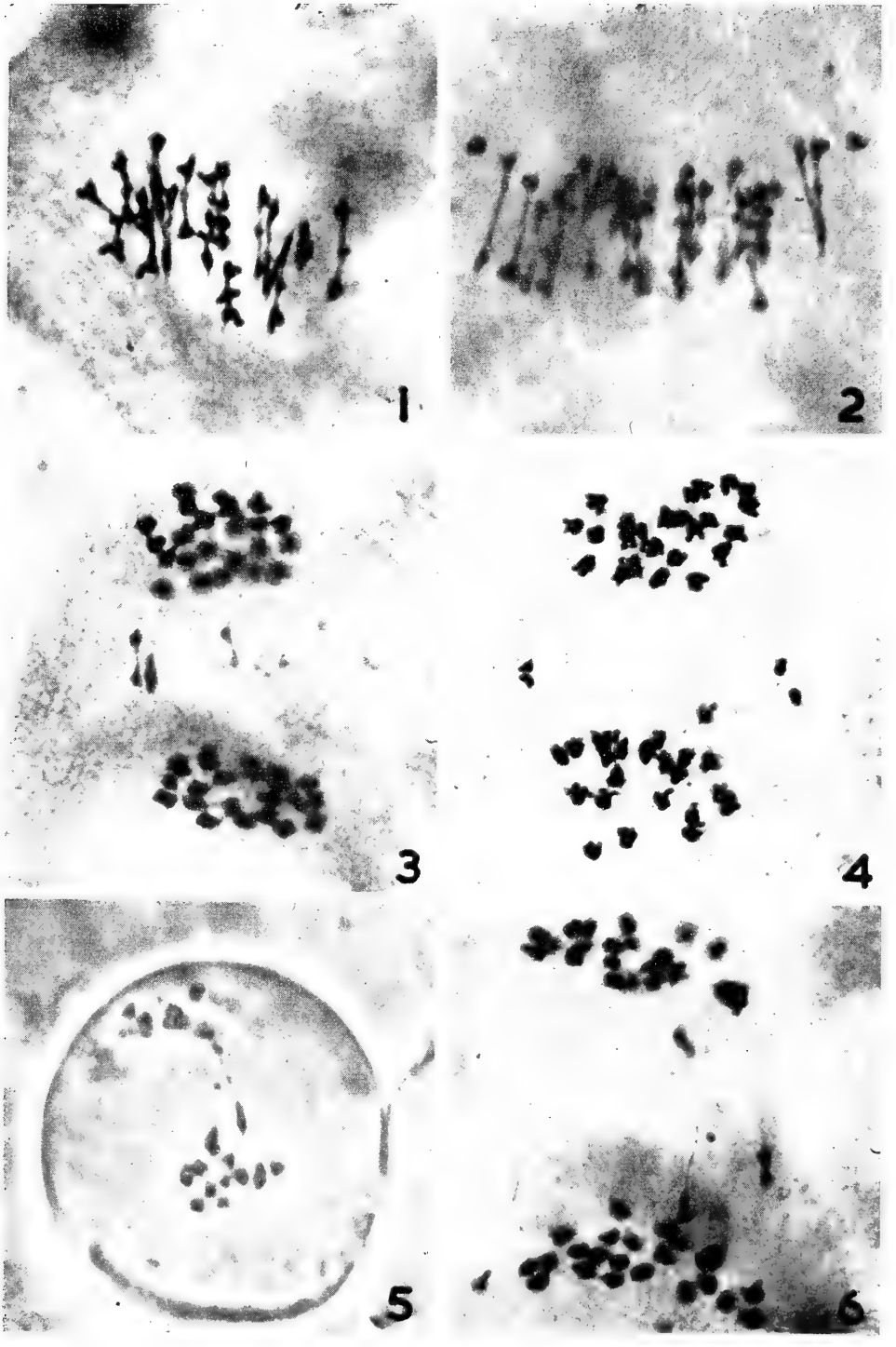
Permian plants from Baralaba, Queensland.



Species of *Culicoides*.



First metaphases in diploids and polyploids.



First metaphases and anaphases in tetraploids and hexaploids.


1


2


3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