Proceedings of the Linnean Society of New South Wales

Issued 5th November, 1965

VOLUME 90
PART 1
No. 407

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The Linnean Society of New South Wales

Founded 1874. Incorporated 1884

"For the cultivation and study of the science of Natural History in all its branches"

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The Society's headquarters are in Science House, 157 Gloucester Street, Sydney N.S.W., Australia

Proceedings of the Linnean Society of New South Wales

VOLUME 90
Nos. 407-409

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PART 1 (No. 407).
(*Issued 5th November, 1965*)
(Presidential Address and Papers read March–April, 1965)

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PART 2 (No. 408).
(*Issued 18th February, 1966*)
(Papers read June–July, 1965)

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PART 3 (No. 409).
(*Issued 22nd July, 1966*)
(Papers read September–November, 1965)

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SYDNEY
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1966

ANNUAL GENERAL MEETING

31st March, 1965

The Ninetieth Annual General Meeting was held in the Society's Rooms, Science House, 157 Gloucester Street, Sydney, on Wednesday, 31st March, 1965.

Miss Elizabeth C. Pope, President, occupied the chair.

The minutes of the Eighty-ninth Annual General Meeting (25th March, 1964) were read and confirmed.

President's Introductory Remarks

It is customary for a retiring president to review the Society's activities during his year of office but in this rather special year, the Society's 90th one, I would like, first of all, to take a brief look forward.

The Council has decided to present our publication, The Proceedings of the Linnean Society of New South Wales, in a new and more modern format. An increase in the size of type used and a number of editorial changes should result in a pleasing layout and make the Proceedings easier to read.

Since 1950, when the annual subscription was raised from £1 1s. to £2 2s., costs of printing and distribution of the Proceedings have risen steeply. About each second year the printer has notified us of the necessity for an increase in printing charges. In 1950 the basic charge was £1 10s. per page and at the beginning of 1965 this had risen to £4 10s. 9d. per page. It has been suggested that the Council should consider a review of membership subscriptions, and that the result of their deliberations be submitted to members in time for any changes to come into effect with the introduction of dollar currency in February, 1966.

The Council is also exploring the possibility of changing the Society's programme of activities to meet the needs and wishes of members. Attendances at Ordinary Monthly Meetings have fallen off so greatly, that it is apparent that this type of meeting is no longer what the members want. This change in the needs of members is being experienced also by many societies abroad —it is a world-wide change. Some groups are meeting the challenge by organizing one or two symposia each year, others by activities of a different nature, and you can rest assured that your in-coming Council will be forward-looking and will aim to introduce new ideas to test the needs of members. Your response to these innovations will determine what the Council finally decides. It could be that our Society may become merely a vehicle for publication of research, and provision of a research library service to members. It is for the members to support or criticize Council's attempts to find what changes should be made so as best to serve the needs of the majority of our members.

Before reviewing the year's activities I should like to express, on behalf of all members, our thanks to that small and devoted group of hard-working people who do so much to keep the Society's affairs running smoothly, as it were, on roller bearings: to Miss G. Allpress, our Assistant Secretary, who continually watches over the welfare of the Society and its members and implements so ably and faithfully the considerable volume of clerical work and the working of the library and its loans and exchanges which the Council and its executive pass on to her. Our debt of gratitude to our Joint Honorary Secretaries, Dr. W. R. Browne and Dr. A. B. Walkom, to whom we owe the smooth running of the Society's affairs in the past year, continues to mount

with each year that they serve in this honorary capacity. Dr. Walkom is also Honorary Treasurer and Editor of The Proceedings, so that we owe him thanks on this score also. We thank them both most sincerely for their services to the Society in the past year. Finally I offer my thanks to my fellow councillors for their help and support during the year and to our Auditor, Mr. S. J. Rayment, F.C.A.

Report on the Affairs of the Society for the Year

The Society's Proceedings for 1964, Vol. 89, Part I was published in 1964 and Parts II and III in 1965. Vol. 89 consists of 398 pages, eight plates and 180 text-figures. An increase in the cost of blocks of about 7½% took place in 1964 and notification was received from the Society's printers of an increase of 10% in printing charges as from 1st January, 1965. An anonymous contribution of £525 was received towards the cost of printing the Proceedings for 1964. Information was received of the death of the Society's agent in London, Mr. David Nutt. Council decided not to appoint another agent. The State Government increased its annual grant to the Society from £200 to £400, on condition that 100 (instead of 60) copies of the Proceedings be made available for governmental distribution. The total net return from the Society's one-third ownership of Science House for the year ended 31st August, 1964, was £1,356 6s. 1d.

During the year twenty-five new members were added to the list, two died, one resigned, and two were removed from the list of members. The numerical strength of the Society at 1st March, 1965, was: Ordinary Members, 265; Life Members, 33; Corresponding Member, 1; total 299.

It is with regret that the deaths of Professor Charles Baehni and Miss Vera Irwin Smith are recorded. (See pages 5–6 for obituary notices.)

A total of 27 papers was read at the Ordinary Monthly Meetings. Lecturettes were given at the following meetings: June, Reptile Collecting in New Guinea, by Mr. H. G. Cogger; July, Some Aspects of Forestry in New South Wales, by Mr. G. Baur; September, Chemistry and Insects, by Associate Professor E. W. K. Cavill, and October, Biological Studies in East Africa, by Mr. H. J. de S. Disney. Interesting discussions followed the lecturettes. A symposium on the Natural History of Kosciusko was held in April, the following speakers taking part: Dr. W. R. Browne, Dr. R. C. Carolin, Mr. D. K. McAlpine and Dr. D. F. McMichael. We are grateful to the lecturers and speakers for their contributions to the interest of the meetings.

On 21st August, 1964, the fourth Sir William Macleay Memorial Lecture was delivered in the Large Hall, Science House, Sydney, by Professor H. G. Andrewartha, Department of Zoology, University of Adelaide, the title of the Lecture being "How Animals can live in Dry Places".

On 15th February, 1965, the resignation from the Council of Professor B. J. F. Ralph was accepted with great regret.

On 24th March, 1965, the resignation of Professor W. L. Waterhouse, as a member of Council, tendered on account of continued ill health, was accepted with great regret and the Council "put on record its high appreciation of Professor Waterhouse's devoted service to the Society as a member of Council since 1930 and as president in 1935".

Library accessions from scientific institutions and societies on the exchange list amounted to 2,222, compared with 2,174 and 1,997 in the years 1963 and 1962 respectively. The total number of borrowings of books and periodicals by members and institutions was 263 for the year. Members and others continued to consult publications in the Society's rooms, and books and periodicals were made available for photographic copying. Council decided that, commencing with Part II of the volume for 1964, all copies of the Proceedings as issued should be despatched directly by post; hitherto certain foreign exchanges

have been sent through the International Exchange Bureau by courtesy of the Public Library of New South Wales. The following requests for exchange of publications were acceded to during the year: Staatliches Museum fur Tierkunde, Dresden, East Germany; Leyden Museum of Natural History, Leyden, Netherlands (Abstract of Proceedings); U.S.S.R. Academy of Sciences, Leningrad (two additional copies of the Proceedings commencing 1965 in exchange for its "Oceanology"); Societas Entomologica Helsingforsiensis, Helsingfors, Finland (Entomological Reprints for "Notulae Entomologicae") and National Institute of Science and Technology, Manila, Republic of the Philippines. Council arranged for a set of the Proceedings from 1941 to be sent to Manila by the Museum of Applied Arts and Sciences, Sydney, as a gift to the National Institute of Science and Technology, to replace volumes destroyed during World War II. The University, Louvain, Belgium, is now forwarding "La Cellule" in exchange for our Proceedings. The Beaudette Foundation for Biological Research, Moss Landing, California, U.S.A., was removed from the Society's exchange list owing to the cessation of its publication "Pacific Naturalist". Mr. K. A. Hindwood presented a reprint of his paper "George Raper: An Artist of the First Fleet" (from *J. and Proc. Roy. Aust. Hist. Soc.*, vol. 50, pt. 1, 1964) and Mr. K. Mair, Director of the Royal Botanic Gardens, Sydney, forwarded a copy of a valuable report by Dr. Joyce W. Vickery on her observations of the behaviour of exotic grasses used for stabilization in disturbed areas of the Snowy Mountains, for inclusion in the Society's library.

During the year the Society: (1) supported the Iluka Softwood Rain Forest Protection Committee in its efforts to prevent destruction of the local native fauna and flora through possible rutile mining; (2) sponsored a Photographic Conservation Exhibition at the Australian Museum; and (3) was represented by invitation at the inaugural meeting in Canberra, on 21st August, of the Australian Conservation Foundation, whose Provisional Council includes two members of the Society. Council also sent two delegates to the Annual Conference of the Nature Conservation Council of New South Wales. Owing to the number of questions relative to Nature Conservation brought before it for consideration, Council set up a Committee to examine and advise on matters coming under this head.

At the Annual General Meeting on 25th March, 1964, the President (Mr. G. P. Whitley) unveiled a framed, enlarged photograph of Dr. A. B. Walkom to mark his 75th birthday and his 45 years of continuous service to the Society. By resolution of Council a copy of the photograph was printed in Part I of the Proceedings for 1964.

A collection of framed photographs, watercolour drawings and maps, a photograph of Alexander Walker Scott, and a watercolour drawing of *Evolvulus alsinoides* by Rev. Julian Tenison-Woods—all of which had long been in the possession of the Society—were presented to the Mitchell Library, the Macleay Museum, and the Royal Botanic Gardens, Sydney, respectively.

Council has been considering the advisability of modernizing the format of the Society's *Proceedings*, and an *ad hoc* Committee has already submitted a report on this matter.

Linnean Macleay Fellowships

In November, 1963, Mr. P. J. Dart, B.Sc.Agr., was reappointed to a Fellowship in Plant Physiology for the year commencing 1st January, 1964. He continued his studies on nodule fine structure within the different legume-*Rhizobium* cross inoculation groups, and his examination of fine structure changes in Mo-deficient nodules. He resigned his Fellowship in May, 1964, to take up a C.S.I.R.O. Overseas Scholarship to study in Denmark and U.S.A.

In November, 1964, Mr. A. J. T. Wright, B.Sc., was appointed to a Linnean Macleay Fellowship of the Society in Palaeontology, tenable for one year from

1st January, 1965. Mr. Wright proposes to continue his studies of the Devonian sediments and faunas of the Mudgee district and of the Capertee Valley area. We offer him our best wishes for a successful year's research work.

Linnean Macleay Lectureship in Microbiology

Dr. Y. T. Tchan, Reader in Agricultural Microbiology and Linnean Macleay Lecturer in Microbiology, University of Sydney, reported on his work for the year ending 31st December, 1964, as follows: Progress has been made on the cytology of *Azotobacter*, particularly on the ultrafine structure of flagella and internal membranous organelles. The interference of Ca in the availability of trace elements in medium for culture of *Beijerinckia* has been investigated. It was found that it is related to the pH of the medium. Progress has also been made on the study of pesticides by algal method. The method proved to be suitable for testing of herbicide in soil.

The Honorary Treasurer (Dr. A. B. Walkom) presented the balance sheets for the year ending 28th February, 1965, duly signed by the Auditor, Mr. S. J. Rayment, F.C.S., and his motion that they be received and adopted was carried unanimously.

Presidential Address

A Review of Australian and some Indomalayan Chthamalidae (Crustacea : Cirripedia)

The review mentioned genera and species of the Family Chthamalidae recorded from Australia and certain collections taken during the Dutch Snellius Expedition of 1929-30, but dealt particularly with species occurring in the upper half of the intertidal zone of the shores round Australia. The possible significance of certain morphological characters as adaptations for feeding at different intertidal heights was discussed from the point of view of the systematics of the Chthamalidae in general. (For full text see pp. 10 *et seq.*)

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

President : D. T. Anderson, B.Sc., Ph.D.

Members of Council : R. H. Anderson, B.Sc.Agr. ; Miss 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.

The President then installed Dr. D. T. Anderson as President.

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

OBITUARY NOTICES

Charles Baehni

Professor Charles Baehni who died suddenly at Geneva on 23rd January, 1964, was elected to membership of this Society in April, 1952. For many years he played a leading part in the life of his native city, Geneva, where he received his early education and where he was destined to occupy high office. Swiss botany has sustained a grievous loss. At the University his first botanical investigations were carried out under his eminent predecessor, Prof. Robert Chodat, and in 1932 he was awarded the degree of Dr. es Sc. In the same year he was appointed as assistant at the Conservatoire et Jardin Botaniques. During 1934-35 he studied in the Botanical Department of the Field Museum of Chicago. He was conservator (1941) and later director (1943-1964) of the Botanic Garden at Geneva. While director of the Gardens he was also professor of systematic botany in the University of Geneva, and for a time in the University of Lausanne. He published more than a hundred scientific papers, his chief interest being in the Sapotaceae, although his contributions extended to other families, including the Ulmaceae, Lacistemaceae and Violaceae. He was a member of the Editorial Committee of the International Code of Botanical Nomenclature from 1950.

A more detailed obituary notice appeared in *Nature*, Vol. 202, No. 4928, April 11, 1964, p. 132.

Vera Adelaide Irwin-Smith

Miss Vera Adelaide Irwin-Smith, B.Sc., F.L.S., who died on 2nd April, 1964, was born in Albury, New South Wales, in November, 1885. She was the daughter of Irwin Smith, a surveyor in the Riverina district, and Adelaide Smith, formerly Adelaide Riches. She was educated at Glenair Ladies' College in Albury. When about 18 years of age she went for a world tour with her paternal grandparents, and this trip evidently instilled in her a love of travel which never left her. About 1910 Mr. Smith moved to Sydney to live, probably for the benefit of the children's education; they lived at first at Northwood, then at Valentia Street, Woolwich. Miss Irwin-Smith had been told that her health would not permit her to undertake a University course so she took a course in architecture at the Sydney Technical College, Ultimo. Having found that she could manage that, she decided to do a science course at the University of Sydney. She commenced the science course in 1912 and, on medical advice, took two years to complete the first year. She graduated B.Sc. in 1916 with First Class Honours in Botany and Second Class Honours in Zoology. She was awarded a University Science Research Scholarship which she held for the years 1916, 1917 and 1918. Miss Irwin-Smith was elected to membership of the Society in 1916. From 1919 to 1923 she held a Linnean Macleay Fellowship of the Society in Zoology, being the first woman to be appointed to a Fellowship. She contributed thirteen papers to the Proceedings.

Miss Irwin-Smith

Her first published paper dealt with some new Chaetosomatidae. Recent ecological studies on the minute animals inhabiting the interspaces between sand grains on the littoral of oceans and lakes has led to a marked revival of

interest in many of the small and more obscure groups of animals. Among these are the free-living worms of the group Chaetosomatidae, Australian specimens of which were described in some detail in 1918 by Miss Irwin-Smith in the Society's Proceedings. Lately many requests have been received from abroad for reprints of her paper, as workers are only now beginning to appreciate the functional significance of many of the minute structures she described in local Chaetosomes. In all she described four new species in two genera, one of which was new.

In 1920 she was Senate representative on the Board of Directors of the Sydney University Women's Union.

During her tenure of a Linnean Macleay Fellowship she continued her study of Nematodes and allied worms, commenced under her Research Scholarship. She had also undertaken the preparation of a report on the collection of parasitic Nematodes brought back by the Australasian Antarctic Expedition. She studied further collections of Nematodes parasitic on Australian hosts, and undertook a series of studies of life-histories of Australian Diptera Brachycera. Of the latter, she investigated Stratiomyiidae, dealing first with *Metoponia rubriceps*, followed by a study of the Asilidae. Her studies of Nematodes included the Nematode parasites of the domestic Pigeon, and also the genus *Physaloptera* with special reference to those parasitic in reptiles. In addition, she made large collections of dipterous larvae, with the object of working out further life-histories, and much interesting information was accumulated. In 1923 she went to England to continue her research work and worked for a time at the Molteno Institute in Cambridge, but family circumstances compelled her to return to Australia. After her return she continued to collect and, in association with the late Mr. Luke Gallard of Epping, Fruit Inspector in the Department of Agriculture, larvae of at least seven families of Diptera were found. Many of these were reared to maturity and records were kept of their development. Her father died shortly after their return from England, and for some years she cared for her mother who became an invalid. Later, her own poor health prevented her from completing any further research work. She spent the latter part of her life in a convalescent home. Miss Irwin-Smith bequeathed in her will the sum of approximately forty thousand pounds to the Australian Academy of Science, Canberra, A.C.T.

GENERAL ACCOUNT. Balance Sheet at 28th February, 1965.

LIABILITIES.	£ s. d.	£ s. d.	ASSETS.	£ s. d.	£ s. d.
Accumulated Funds—			**Fixed Assets—**		
Amount received from Sir William Macleay during his lifetime ..	14,000 0 0		Commonwealth Loans, at Cost ..	15,048 10 0	
Further sum bequeathed by his will	6,000 0 0		Debentures :		
		20,000 0 0	Metropolitan Water, Sewerage and Drainage Board, at Cost ..	10,844 7 6	
Contingencies Reserve		20,962 1 4	Sydney County Council	3,000 0 0	
Current Liabilities—			Science House (one-third share), at cost	14,835 4 4	
Bookbinding Account	912 6 7				43,728 1 10
Income Account	3,858 18 3		**Current Assets—**		
Suspense	8 4 4		Cash in hand	10 0 0	
		4,779 9 2	Commercial Banking Company of Sydney, Ltd.	2,003 8 8	
					2,013 8 8
		£45,741 10 6			£45,741 10 6

INCOME ACCOUNT. Year Ended 28th February, 1965.

	£ s. d.	£ s. d.		£ s. d.	£ s. d.
To Salary		822 0 0	By Balance from 1963–64		4,377 5 7
,, Printing Proceedings	1,717 8 3		,, Subscriptions :		
,, Printing Reprints	637 3 6		1964–65	480 18 0	
,, Illustrations	270 3 0		Arrears	42 0 0	
		2,624 14 9	In Advance	16 16 0	
,, Insurance		13 4 5			539 14 0
,, Postage	126 15 6		,, Entrance Fees		23 2 0
,, Petty Cash	34 18 0		,, Interest		1,406 2 6
		161 13 6	,, Science House		1,356 6 1
,, Audit	16 16 0		,, Rent		17 10 0
,, Printing and Stationery	151 2 6		,, Sales		741 2 7
,, Expenses	145 17 7		,, N.S.W. Government Grant ..		400 0 0
,, Cleaning	70 12 0		,, Fellowships Account (surplus income at 28th February, 1965, transferred)		1,199 8 3
,, Library	101 4 8		,, Sale of Reprints		491 7 3
,, Exhibition	31 17 1		,, Postcard Sales		3 0
,, Macleay Lecture	79 0 6		,, Donation towards Printing ..		525 0 0
		596 10 4			
,, Transfer to Contingencies Reserve		3,000 0 0			
,, Balance to 1965–66		3,858 18 3			
		£11,077 1 3			£11,077 1 3

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1965, 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, 1965, 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, 1965.

A. B. WALKOM,
Hon. Treasurer.

2nd March, 1965.

LINNEAN SOCIETY OF NEW SOUTH WALES.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

Balance Sheet at 28th February, 1965.

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 ..	30,442 15 0	
Surplus Income Capitalized	23,869 16 6	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	
		State Electricity Commission ..	2,500 0 0	
		Loan on Mortgage	6,035 0 0	
				57,798 19 9
		Current Assets—		
		Commercial Banking Company of Sydney, Ltd.		1,070 16 9
	£58,869 16 6			£58,869 16 6

INCOME ACCOUNT. Year Ended 28th February, 1965.

	£ s. d.		£ s. d.
To Salaries of Linnean Macleay Fellows	586 6 10	By Interest..	2,799 8 3
,, Capital Account	1,013 13 2		
,, Balance, being Surplus Income transferred to General Account	1,199 8 3		
	£2,799 8 3		£2,799 8 3

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1965, 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, 1965, 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, 1965.

A. B. WALKOM, Hon. Treasurer.

2nd March, 1965.

LINNEAN SOCIETY OF NEW SOUTH WALES.

BACTERIOLOGY ACCOUNT.

Balance Sheet at 28th February, 1965.

LIABILITIES.	£ s. d.	£ s. d.	ASSETS.	£ s. d.	£ s. d.
Accumulated Funds—			Fixed Assets—		
Amount bequeathed by Sir William Macleay	12,000 0 0		Commonwealth Loans, at cost	15,318 2 6	
Accumulated Income Capitalized	6,310 0 0		Debentures:		
Research Fund	10 0 0		Metropolitan Water, Sewerage and Drainage Board, at cost	800 0 0	
		18,320 0 0	Loan on Mortgage	2,200 0 0	
					18,318 2 6
Current Liability—			Current Assets—		
Income Account at 28th February, 1965		228 16 4	Commercial Banking Company of Sydney, Ltd.		230 13 10
		£18,548 16 4			£18,548 16 4

INCOME ACCOUNT. Year Ended 28th February, 1965.

	£ s. d.		£ s. d.
To University of Sydney (towards salary of Lecturer)	925 0 0	By Balance from 1963–64	230 11 2
,, Balance to 1965–66	228 16 4	,, Interest	923 5 2
	£1,153 16 4		£1,153 16 4

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1965, 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, 1965, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, F.C.A., Chartered Accountant, Auditor.
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Sydney, 9th March, 1965.

A. B. WALKOM,
Hon. Treasurer.

2nd March, 1965.

PRESIDENTIAL ADDRESS

A REVIEW OF AUSTRALIAN AND SOME INDOMALAYAN CHTHAMALIDAE (CRUSTACEA : CIRRIPEDIA)

ELIZABETH C. POPE
*Curator of Worms, Echinoderms, etc., The Australian Museum**

(Plates i and ii)

[Delivered 31st March, 1965]

Synopsis

All species of intertidal barnacles of the Family Chthamalidae known from Australian shores are reviewed and discussed with reference to their geographical distributions and ecological occurrence. Eight species in four genera are included but none is new to science. Considerable extensions of the ranges of *Chthamalus intertextus* to New Guinea and of *Chthamalus malayensis*, *C. caudatus* and *C. withersi* along the northern coast of Australia are recorded.

There are five tropical species in Australia in two genera, of which four are included in genus *Chthamalus* and one in *Octomeris*. Only three species of the family occur in the temperate southern half of the continent, but each belongs to a different genus. Thus *Catophragmus*, *Chthamalus* and *Chamaesipho* are represented. A second species of *Chamaesipho* occurs in New Zealand, but these two species are the sole representatives of the Family Chthamalidae in that region.

Certain species of *Chthamalus* (*C. withersi* and *C. caudatus*) and *Octomeris brunnea* possess structures on their mouth parts and cirri which are believed to be adaptations for capturing particulate food over a relatively short period and in seas showing only slight to moderate degrees of water movement other than tidal flow except, of course, during storms. The remaining five species from three genera have armouries of elaborate hooks or grapples well adapted to the holding of food particles, in the ebb and flow of surf or other considerable water movements. When these hooks, grapples and other food-holding adaptations are catalogued for each species, it will be found that the species constantly subjected to roughest water movements possess a greater variety of such adaptations than species from calmer situations. However, many more Chthamalid species will have to be examined before any conclusions about the phylogenetic significance of these structures, if any, can be drawn.

INTRODUCTION

The following genera have hitherto been included by general consent in the Family Chthamalidae : *Catophragmus*, *Chionelasmus*, *Octomeris*, *Chthamalus*, *Chamaesipho*, *Pachylasma* and its closely related genus *Hexelasma*, and the fossil genus *Tessarelasma*. Of these, four, namely *Catophragmus*, *Chthamalus*, *Chamaesipho* and *Octomeris*, are familiar intertidal dwellers on Australian shores, and *Pachylasma* and *Hexelasma* are represented in the deeper water fauna off our coasts.

Of this deeper water group records are scattered, few specimens are known of each species, and collecting has never been systematically carried out. Just a few specimens have been taken by deep sea expeditions from time to time, or by chance trawling operations, here and there. In these circumstances, little is to be gained by reviewing them, until additional and adequate material is collected. It is proposed here, merely to list the species occurring in Australian waters and to pass on to a more detailed review of the extremely common intertidal species.

The list of deep-water Chthamalidae occurring near Australia is as follows : *Pachylasma scutistriata* Broch, 1922, eastern slopes of Bass Strait, Tasman Sea, 70–160 fathoms ; *P. integrirostrum* Broch, 1931, Kei Islands and

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Amboina, 140 metres; *P. aurantiacum* Darwin, 1854, "New South Wales" i.e., east coast of Australia, "apparently from deep water"; *Hexelasma velutinum* Hoek, 1913, NW. of Timor and Kei Islands, 245–390 metres; *H. arafurae* Hoek, 1913, Arafura Sea, 560 metres.

Of the remaining genera listed in the Family Chthamalidae, *Chionelasmus* (a deeper water form) has not been taken from seas off Australia and the fossil genus *Tessarelasma* has been recorded no nearer to Australia than the Indian subcontinent where it occurs embedded in rocks of the Surma Series (Lower Pliocene) at a depth of approx. 2,000 feet, along the Arakan Coast region of Eastern Bengal, Pakistan.

Terminology used in this review is defined in Pilsbry (1916).

Broadly speaking Australian Chthamalidae may be divided into two groups differing markedly in their ecology, their abundance, and also in several aspects of the basic arrangement of the plates forming their shells. The one group, comprising the genera *Chthamalus*, *Octomeris*, *Catophragmus* and *Chamaesipho*, inhabit rocks or other hard substrates in the upper half of the intertidal zone. Most of them thus spend more time surrounded by air than they do under water. In fact, some individuals of *Chthamalus antennatus* in the temperate zone or of *Chthamalus withersi* in the tropics in Australia spend approximately 95–98% of their time exposed to air while *Chthamalus malayensis* is exposed from 30–90% of the time*.

This is really an extraordinary state of affairs, when one considers that they are marine animals, living cemented to the substrate and therefore entirely dependent on the sea to bring them their food (for they are filter feeders), and to carry away and distribute their planktonic young after they have been brooded for a time. Presumably also fertilization of eggs can only take place during periods when the barnacles are covered by seawater. Their hermaphroditism must also have played a tremendous part in their successful colonization of the high shore rocks. However, it is not intended to enlarge on the mechanisms of reproduction in the Chthamalidae in this review. Also no mention will be made of their respiratory needs since it is obvious that plenty atmospheric oxygen is available to them. Rather their main metabolic problems would appear to be concerned with obtaining sufficient food and the need to conserve moisture during the long periods of subjection to the blazing sunlight and constant high temperatures encountered in their environment.

As mentioned above, the other ecological group within the family inhabits the deeper waters of the ocean which, from the point of view of filter-feeding organisms, presents fewer problems. While it is not intended to review this latter group, certain fascinating questions about their mode of life arise in one's mind. Why, for instance, has the genus *Hexelasma*, in the course of its evolution from an 8-valved ancestral type, reduced its shell plates to 6, by the elimination, through amalgamation of the rostro-lateral pair of compartments with the rostrum, whereas in the 6-valved intertidal genus *Chthamalus*, the reduction from 8 to 6 has been achieved by loss of the carino-lateral pair of plates—at the opposite end of the animal? Another enigma associated with the Chthamalidae is the apparent failure of this otherwise evolutionarily successful family to invade and colonize the lower half of the intertidal zone of the shallower seas of the continental shelf, where the other sessile barnacle family, the Balanidae, has become so successfully established. Whatever the reason for their exclusion from the lower shore, the fact remains that some genera of the Chthamalidae have, in the course of their evolution, become highly adapted to living as marine animals out of water for the greater part of the time. Can we by studying their field occurrence, the geographical and vertical range of the various species, and their morphology learn anything

* From unpublished M.Sc. thesis by Miss Judy Bryan of Townsville University College, Queensland.

about the adaptations that make for success in the high shore environment? The present study is an attempt to make a slight contribution in this field and to arouse interest in these animals, so suitable for experimental studies.

Firstly, however, it is necessary to review the nature and composition of the Australian Chthamalid fauna, for no comprehensive account of the family has appeared since Charles Darwin's Ray Society Monograph of the Sub-Class Cirripedia was published in 1854. It is also apparent that the collections made for, and sent to, Charles Darwin must have completely neglected mainland Queensland in particular, and the tropical half of the continent in general, for his work fails to record *Octomeris brunnea* and three species of *Chthamalus* (which at that period were undescribed) although Barrier Reef species in Family Balanidae were well represented.

The intertidal surveys made by Endean *et al.* (1956, *a* and *b*) revealed for the first time how extensively Indomalayan species of Chthamalidae range along the eastern coast of Queensland and the prominent role they play in the pattern of intertidal zonation. As a direct consequence of their work and because of the zoogeographical importance of this group, collecting of cirripedes in tropical Australia was extended by the author to the northern and western coasts of the continent and the now extensive collections which resulted are housed in the Australian Museum, in Sydney. It is chiefly on these collections that the present study is based. The author has also made many field trips over the years, studying the field occurrence of barnacles along 7,000 miles of coastline.

The practice followed in this study has been to base descriptions on as large a population of each species as possible, using many dissections and also notes made of their field occurrence in varying environments, for slight changes in environmental conditions have been found to cause marked differences in the general appearance of Chthamalid shell plates.

Samples have been examined, wherever possible, in batches collected at approximately hundred mile intervals throughout the Australian ranges of each species. In most cases large Australian individuals in any one species are as much as 1½ to 2 times bigger than any specimen previously recorded and it soon became apparent that the original descriptions of several species had been based on fairly juvenile material—the original authors having been misled into the belief that their specimens were full grown by the fact that they were frequently brooding developing larvae. Pilsbry's description of *Chthamalus withersi* (1916) and Darwin's of *Octomeris brunnea* (1854) are two such cases. If the descriptions of Australian specimens given below differ markedly from the original accounts this is often the reason, for the larger a barnacle grows the more rugged its shell becomes and the more characters appear in the shell and in the internal soft parts.

The following systematic account includes all known intertidal species of the Family Chthamalidae from Australia and New Guinea. They comprise eight species divided between four genera of which only one genus (*Chthamalus*) ranges into both the tropical and temperate areas of Australia and no one species is common to both.

Chthamalidae of Australian Intertidal Zone

Chthamalidae characteristic of the intertidal zone of temperate Australian shores are *Chthamalus antennatus*, *Chamaesipho columna* and *Catophragmus polymerus* and they are listed in the order in which they occur, from the high shore down to mid-tide level. All three are species forming prominent bands in the pattern of intertidal zonation in SE. Australia and all are adapted to living on rocks which are usually subject to regular pounding by surf. To a certain extent their vertical ranges overlap one another, so that *C. antennatus* and *Chamaesipho columna* may be found together, likewise *Chamaesipho* and

Catophragmus may occur in the one area, but only in areas subjected to especially rough seas could *C. antennatus* and *Catophragmus* ever occur together in a circumscribed area on the shore, for the latter could not survive for long on the high level of the rocks frequented by *C. antennatus*.

Tropical species of the family represented on the Australian mainland are *Chthamalus withersi* and *Chthamalus malayensis* on the upper surface of rocks, with *Chthamalus caudatus* and *Octomeris brunnea* occurring either under boulders or in shaded areas among boulders or under overhangs of rock. An area of boulders offering the type of habitat frequented by *C. caudatus* and *O. brunnea* is shown in Plate ii, figure 4, and unless such areas are rather deliberately searched, their occurrence in a locality can easily be overlooked. This probably accounts for the few and scattered references to them in literature and it is likely that they will be found to range more widely through the Indonesian and Philippine Islands when systematic collecting is carried out in such places.

On the rocky shores of Queensland, Endean, Kenny and Stephenson (1956) found a certain degree of interspecific competition between *C. withersi* and *C. malayensis*, the former being favoured in areas subjected to wider fluctuations in salinity and in turbid waters, and *malayensis* tending to be favoured by increased wave action (i.e. less turbid areas) and more stable salinities. Thus *C. withersi* invades the mangrove swamps and settles on the trees near the mouth of coastal streams or colonizes wharf piles in river mouths and, indeed, can occur in these habitats in great numbers, as shown in Plate ii, figures 2 and 5. On rocky reefs, fronting the more open waters, where turbidity is not too high, *C. malayensis* becomes dominant intertidally, as shown in Plate ii, figures 3 and 6.

Where these two species occur together, *withersi* occupies the higher levels, ranging from the high water mark of spring tides down to high water neap tide level, whereas *C. malayensis* ranges from approximately mean high water mark down to high water mark of neap tides. Their vertical ranges thus overlap to a certain extent and their distributions on any particular reef will depend partly on the substrate and partly on the particular microclimates offering within its area. Their occurrence in Queensland has been discussed by Endean *et al.* (1956, both papers). However, along the northern coast of Western Australia, the behaviour of *C. malayensis* apparently differs, judging by collections sent to the author. West of Darwin, Northern Territory, no *C. withersi* have been taken but *C. malayensis* and *C. caudatus* colonize the rocks between the same relative tidal levels as in Queensland but, owing to the enormously greater tidal range (33 feet), the belt of intertidal rocks on which they settle is, of course, much wider. In the absence of *withersi* in the west, *C. malayensis* and *C. caudatus* may colonize the roots and trunks of mangroves. Records of *Octomeris brunnea* also occur on a similar substrate in the New Hebrides and the Santa Cruz Island Group and would seem to indicate either the needs of barnacles in the high tropics to find some degree of shelter from direct sunlight and/or a lack of rocky substrates on which to settle, so that they are driven to colonize tree trunks. The mangroves in these areas occur, of course, on the open coastline in the high intertidal zone and are not confined to the banks of inlets and rivers, where reduced salinities obtain throughout the year.

Chthamalus malayensis and *C. intertextus* are the two species in tropical Australia occurring where the water is consistently rougher. In general, however, at least inside the shelter of the rampart of the Great Barrier Reef of Queensland, much of the mainland coast of Queensland must be judged as relatively little exposed to wave action (except during cyclones).

Octomeris brunnea and *C. caudatus* may occur together in the one locality since they occupy overlapping vertical ranges and tend to settle in shaded areas (in Queensland, at least). The former species ranges from the level of

mean high water to the level of high water neap tides, while *C. caudatus* ranges from the same upper level but extends lower down the shore to approximately mean low water mark.

The remaining tropical species included in this account, *C. intertextus*, has not yet been recorded farther south than the coast of Papua, not far from Port Moresby, and although it occurs in the New Hebrides and Fiji it has not been taken in New Caledonia. Some ecological data of its occurrence and association with *C. malayensis* and *O. brunnea* in the Riu Kiu Islands are recorded by Tokioka (1953) and Utinomi (1954) but no further data have been supplied with the New Guinea material, other than the statement that it occurs on rocks in the mid-tidal zone and *C. malayensis* occurs in the same locality. It apparently is attached both on the open faces of rocks and on shaded areas and under overhangs.

Systematic Account

In general, Australian members of this family have rather drably coloured shells, generally coloured in varying tones of dirty grey, or greenish-grey where erosion discloses underlying layers of horny lamina (in the case of *Chthamalus caudatus* of a bright yellow tone) or where dark corium shows as a series of spots on the upper surface of greatly eroded shells. The only brightly coloured member of the family is *C. intertextus* and then only when erosion reveals the deep violet layers of shell laid down internally, during secondary calcification.

The practice has been followed of giving a table of measurements of a series of barnacles, representative of the population of each species, since maximum and minimum sizes mean little, when one is trying to make an identification. They are given only where Australian material differed considerably in size from previously described specimens.

No new species have been discovered in northern Australia. Those not described by Darwin were described by Henry Pilsbry (1916) in another classic monograph of Cirriped literature. Most of them range widely throughout the Indomalayan Peninsula and Indonesia or the Western Pacific islands and it was from there they were first described.

The following section includes descriptions of all intertidal species of the Family Chthamalidae known to occur on Australian shores :—

Order THORACICA
Sub-order BALANOMORPHA
Family CHTHAMALIDAE

Genus Catophragmus G. B. Sowerby, 1826

Sowerby, G. B. (1826) *Catophragmus imbricatus*, type of genus.—Darwin, C., 1854 ; Pilsbry, H. A., 1916 ; Broch, H., 1922 ; Withers, T. H., 1935.

The genus *Catophragmus* was originally erected by Sowerby for *C. imbricatus* from Antigua in the West Indies.

It now comprises only three species—*C. imbricatus* Sowerby (1826) from Bermuda and the West Indies, *C. polymerus* Darwin (1854) from Australia, with a very doubtful record from "Table Bay" (? South Africa) by Gruvel in his 1905 Monograph, and *C. pilsbryi* Broch (1922) from Tobago, Panama.

Pilsbry (1907) described a fourth species, *C. darwini*, from several fragmentary specimens. However, he was unable to determine the number of plates in the inner whorl of his species and guessed that it would be eight. In a later work (1911) he expressed the opinion that, when whole specimens of *C. darwini* were found, they might indicate the need for a new genus and he felt strongly enough in the matter to suggest a name for the new genus *Chionelasmus* which, meanwhile, he used as a subgenus of *Catophragmus*. When complete specimens

of *darwini* came into the hands of Nilsson-Cantell (1928) and were found to have only six plates in the inner shell whorl, he removed it from *Catophragmus* and used Pilsbry's proposed name, *Chionelasmus*, as the new generic name for it. *Chionelasmus* differs from *Catophragmus* in the number of shell plates in the inner whorl—six and eight respectively—and in the number of whorls of supplementary plates—one in *Chionelasmus* and several in *Catophragmus*. The genus *Catophragmus* is an intertidal one, whereas *Chionelasmus* is a deeper-water species.

Pilsbry (1916) divided *Catophragmus* into three sub-genera *Catophragmus*, *Catomerus* and *Chionelasmus*. This last sub-genus has now been elevated to generic rank and the other two are distinguished from one another by the presence in sub-genus *Catophragmus* of a caudal appendage and its absence in sub-genus *Catomerus*. The Australian species thus falls into the sub-genus *Catomerus*, while *C. imbricatus* and *C. pilsbryi* fall into sub-genus *Catophragmus*, the former having a minute caudal appendage, fide Darwin, and the latter a well-developed one, almost as long as the protopodite of cirrus VI, fide Broch.

In 1935 Withers erected another sub-genus within *Catophragmus*, sub-genus *Pachydiadema* to accommodate his newly-described fossil species *C.* (*Pachydiadema*) *cretaceum* from Ifo in Sweden. In the fossil species which was described from a series of isolated plates, considerable differences in the structure of the opercular valves and the absence of teeth on the basal edge of the shell plates separated it from other species and sub-genera. However, it most resembles the sub-genus *Catomerus* except in the opercular plates which are close to those of pedunculate cirripedes, whereas in *C. polymerus* they are clearly of the balanomorph type. The interest in *C.* (*P.*) *cretaceum* lies in the fact that it is, to quote Withers, " The earliest form, and the only Mesozoic form, which can be regarded as belonging to the Balanomorpha, and shows clearly its origin from the pedunculate stock. It is possibly the ancestor of *Catophragmus* (*Catomerus*), which in turn is the most primitive member of the Balanomorpha ".

Catophragmus (*Catomerus*) *polymerus* is the only species of the genus in Australia and is easily distinguishable from other local intertidal barnacles by the supplementary whorls of shell plates.

This species has a southern distribution in Australia and, in view of this, it is perplexing to find that Broch (1927) regards *C. polymerus* as a representative of the northerly intertidal zone of Australia. Guiler (1952), quoting P. H. Fischer (1940), also lists this species as representing, in Tasmania, the " relic of a tropical fauna ", whereas it is endemic in temperate Australia.

The phylogenetic interest of *Catophragmus* has been discussed by Darwin (1854), Withers (1928 and 1935) and nothing need be added to their statements. The resemblance between a *C. polymerus* growing in its tall, narrow form attached to the mussel *Branchidontes rostratus* and a short stalked species of the Lepadormorph genus *Mitella* is most marked.

The world distribution of living species of this genus shows two isolated groups with *C. polymerus* in Australia and the other two species in the Caribbean Sea and Bermuda in the Atlantic. The fossil species *C.* (*Pachydiadema*) *cretaceum* came from Ifo, Sweden, in Cretaceous rocks. The finding of this last species does not alter Pilsbry's and later Withers's belief that the recent species of *Catophragmus* represent survivors of an ancient genus once widespread in its distribution.

No key to species of the genus *Catophragmus* is considered necessary as Broch (1922, p. 301) makes the differences between the species quite clear. These differences depend on obvious characters, such as the presence or absence of caudal appendages, the sculpturing, and number of the supplementary plates round the main whorl.

Catophragmus polymerus Darwin, 1854

(Plate i, figure 2 ; Text-figures 1,*a*,*b* ; 2,*a*)

Catophragmus polymerus Darwin, 1854 ; Gruvel, 1903, 1905 ; Pilsbry, 1916 ; Broch, 1922, 1927 ; Nilsson-Cantell, 1926 ; Pope, 1945 ; Dakin *et al.*, 1948, 1952 ; Bennett and Pope, 1953, 1960 ; Endean, Kenny and Stephenson, 1956 ; Womersley and Edmonds, 1958 ; Wisely and Blick, 1964.

Catophragmus polymerus, known as the " surf barnacle ", occurs in a well developed horizontal band in the barnacle zone on intertidal rocks along the south-east quarter of the Australian coastline.

In the original description Darwin lists *Tetraclita purpurascens* among other barnacles associated with *Catophragmus* and *T. purpurascens* does indeed often occur in the same locality but is cryptic in habit, and not in an exactly similar niche as the other species listed, e.g. *Balanus nigrescens*, *Chthamalus antennatus* and *Chamaesipho columna*. These all attach to the upper surface of the rocks in the barnacle zone. On the other hand, *Tetraclita rosea* occurs in large numbers among the *Catophragmus* along the New South Wales coast and it is felt that it may be the species Darwin intended to list as an associate of *C. polymerus* or, at least, it should be added to the list he gave.

Tetraclita rosea is favoured by warmer conditions and is able to survive at a slightly higher shore level in New South Wales than *C. polymerus*. The latter, on the other hand, is a southern species that is favoured by cooler conditions. As a result, towards the northern, warmer end of their joint range, notably from Ballina northwards, *C. polymerus* is greatly outnumbered by *T. rosea* and, just north of the New South Wales border, in Queensland, *T. rosea* is the sole barnacle in this shore zone. Again, towards the south of New South Wales, where the environment becomes progressively cooler, the numbers of *T. rosea* fall off and *C. polymerus* becomes dominant. This tendency was noted between Ulladulla and Batemar's Bay. Farther south, at Mallacoota Inlet in Victoria, *T. rosea* is scarce and by Wilson's Promontory it has disappeared from the rocks, so that from there southwards *C. polymerus* competes for settlement space with the mussel, *Brachidontes rostratus*, rather than with another species of cirripede.

Local *C. polymerus*, from Sydney, have been shown to breed throughout the year but peak breeding periods occur in winter and early spring (Wisely and Blick, 1964).

Structure and Appearance of Shell

Darwin's very detailed account of the shell of *C. polymerus* makes it unnecessary to add more than a few comments on the variations seen.

Scutum and Tergum

There is some variation in the shapes of the opercular valves according to the age of the barnacle and the degree of erosion it has experienced, but their structures are basically similar to those shown in Darwin (1854, Plate XX, fig. 4, *e*). The placement of the prominent articular ridge of the scutum may vary from a central position on the tergal margin to a position above this point—the corresponding furrow on the tergum varying in position in consequence. Both tergum and scutum may be more nearly triangular in outline and the tergum is generally somewhat bent about an axis running from the apex to the basi-scutal tip of the valve, so that its two sides are inclined to one another almost at right angles. The number of crests for attachment of the tergal depressor muscles may be of the order of 13–15 in larger individuals.

Soft Body

The body of *C. polymerus* occupies the space immediately below the opercular plates only. The rest of the area of the base between the body and

the outer wall of the shell is occupied by the bases of the successive whorls of supplementary plates and the enclosed spaces filled with corium. This arrangement produces a structure well adapted to withstand severe battering by surf. The basis of the shell is membranous and fairly tough and covers the whole area below the shell. The milky white areas of the basis were tested for the presence of calcium carbonate but none was present. The depressor muscles of the tergum are very large and occupy approximately one-third of the space inside the shell.

In freshly preserved *C. polymerus* the edges of the tergo-scutal flaps are black. The body itself shows a marked contrast in the colouring of the cirri. The first two pairs are a dark greyish-purple from pedicel to the tips of the rami and bear thick bunches of comparatively long, light-coloured bristles on each segment. Cirri III–VI, on the other hand, have dark pedicels and as a rule the rami are much lighter, varying from cream, with a few regular dark patches, to light grey or fawn. Each segment has concentrations of dark pigment cells round the bases of the spines. An occasional specimen has been found with cirri III–VI having the outer third of the rami darker in colour like the pedicels.

Trophi

The shapes of the various mouth parts vary slightly from those depicted by Nilsson-Cantell (1926, text-fig. 2) but not significantly enough to warrant new illustrations.

The main difference noted is, however, considered important since it involves the setation of the trophi. In general, there are many more hairs than are shown in his drawing, for *C. polymerus* is an extremely hirsute species. The *labrum* is bullate and has a wide, deep groove anteriorly carrying along its margins both hairs and a few small teeth (seen only under high magnifications and from certain angles). The setae along the upper border of the *palp* are so thickly bunched they resemble a brush. The *mandible* has three main teeth and a coarsely pectinated lower angle in which the longest spines are at the tip of the jaw. No secondary pectination was seen on teeth 1–3 as shown by Nilsson-Cantell. *Maxilla I* has two distinct notches and a double prominence forming its lower angle. These divide the spines on the anterior border into a number of distinct groups. The two upper pairs of spines are the largest. Just below them, and above the first notch, are 3–4 pairs of considerably smaller spines. Below this notch are 6–7 pairs of medium-sized spines which arise from the anterior cutting edge between the upper and lower notches. The spines on the double prominences of the lower corner of the jaw are much smaller and comparable in size to those just above the first notch. The spines on the upper prominence tend to point downwards, whereas those on the lower one are directed horizontally. *Maxilla II* is somewhat pear-shaped, with a notch in the upper half of the free edge. The notch is free of bristles but numerous longish spines occur along the rest of the border. Those of the ventral surface are about twice as long as those above the notch.

Cirri

Cirri I and II are much shorter than the remaining pairs and bear many bristles on each segment of their rami. Both have unequal rami with the anterior one exceeding the posterior one in length. The longer ramus is notably broader than its fellow. The numbers of segments in the rami of *cirrus I* vary, but they are of the order of eleven in the anterior ramus and 7 or 8 in the posterior one. The terminal segments, as well as several other segments, are furnished with pinnate spines in which the central shaft bears alternating fine side hairs (Text-fig. 1, *b*). These may be the barbed spines to which Darwin (1854, p. 490) and Nilsson-Cantell (1926) refer but should not be confused with the much stouter serrated spines of cirrus II (Text-fig. 1,*a*). *Cirrus II* has

its anterior ramus longer by about 3 of its segments than the posterior one, the actual segmental numbers being of the order of 9–10 (anterior) and 8 (posterior). The 3 or 4 terminal segments of both rami of this cirrus carry a number of very stout and coarsely pectinated spines in addition to the normal and pinnate longer spines. These last tend to be more concentrated in segments below the tips of the rami where the barbed stout spines are absent or few in number. Cirri III–VI are similar to one another in shape and the rami are subequal. The numbers of pairs of major spines on each of their segments is not always 5, as described by Darwin, but varies from segment to segment,

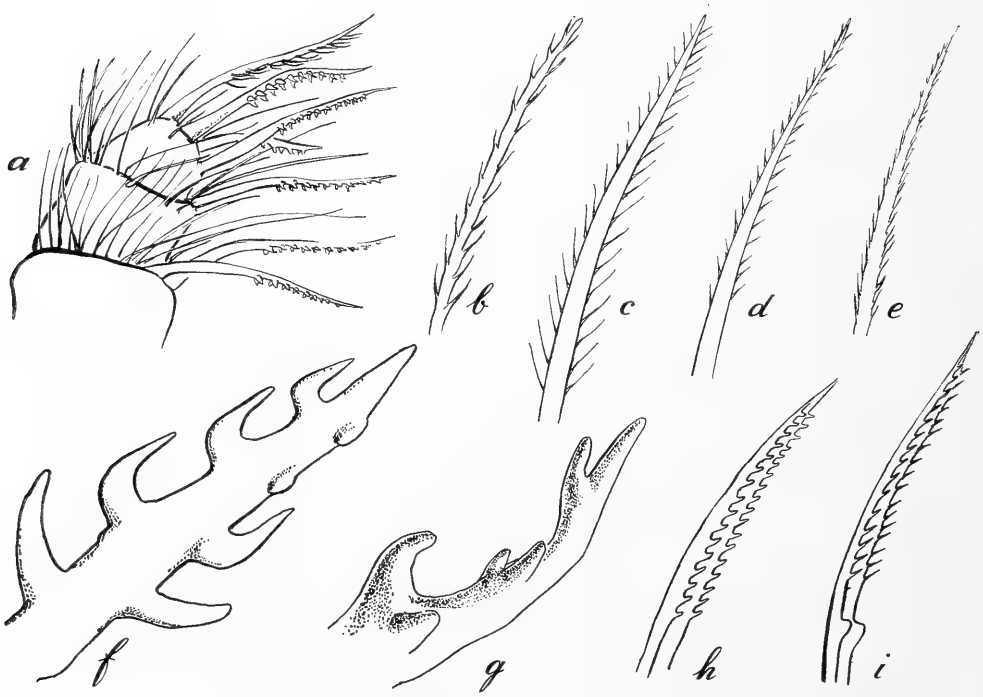

Fig. 1. Shapes of some stout spines and pinnate setae in intertidal Chthamalidae. (*a-b*), *Catophragmus polymerus*. Tip of anterior ramus of cirrus II showing stout serrated spines among pinnate setae (*a*), while in (*b*) a pinnate seta is more highly magnified to show side hairs; (*c*), *Octomeris brunnea*, a stouter pinnate seta from cirrus II; (*d-e*), pinnate setae from terminal segments of cirrus II in (*d*) *Chthamalus withersi* and (*e*) *Chthamalus caudatus*; (*f-g*), stout grapple-spines from distal segments of cirrus II of *Chthamalus intertextus* (*f*) and of *Chamaesipho columna* (*g*); (*h-i*), stout, toothed spines from terminal segments of cirrus II in *Chthamalus antennatus* (*h*) and in *Chthamalus malayensis* (*i*). (Spines in view (*f*) seen from front view, while that in view (*g*) is seen in side view. Their structures are somewhat similar.)

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ramus to ramus, and cirrus to cirrus, even in the one individual. In a specimen from Sydney cirrus III had four pairs on most segments of its rami; cirrus IV had four pairs on its outer ramus and five on the inner one; cirrus V was similar to IV, while the spine pairs varied from four to five per segment on the outer ramus while the inner ones had four pairs of major spines. In another barnacle there were five pairs of spines on the segments of the inner ramus of cirri IV–VI, while the outer ones had four. There is, however, one constant spine character in all cirri from III to VI—namely, the presence of a thick brush-like tuft of small spines of variable length, situated centrally on each segment between the double row of major spines (Text-fig. 2, *a*). This character is shared with the pedunculate species of the genus *Mitella* but is not present in other Australian chthamalids.

The *penis* is comparatively long, and towards its base is marked by a series of narrow, dark rings and has a small tuft of hairs near its tip. There is no *caudal appendage.*

Habitat

The preference shown by *C. polymerus* for areas of rock exposed to maximal wave action has been indicated above. It grows on rocks just above the distinctive *Galeolaria* Worm (Serpulid) Zone, in the upper half of the intertidal zone, above mid-tide level, along with another so-called Surf Barnacle, *Tetraclita rosea* (Family Balanidae) but in Victoria and Tasmania and along the mainland coast westwards from Bass Strait, *C. polymerus* occurs either above or intermingled with bands of the mussel, *Brachidontes rostratus* (Dunker), to which it is often attached. The absolute width of its vertical range varies in Victoria proportionately with the variations in tidal range but it still occupies relatively the same vertical proportion of the tidal range (Bennett and Pope, 1953).

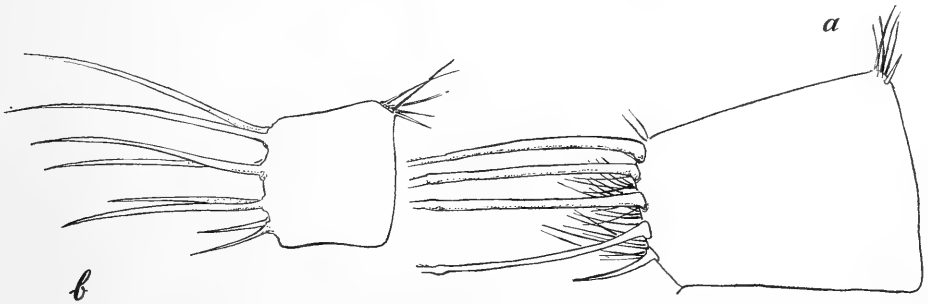

Fig. 2. Central segments of cirrus VI of (*a*) *Catophragmus polymerus* showing small central tuft of spines between bases of major spine pairs, and (*b*) *Octomeris brunnea.*

F. J. Beeman del.

Distribution

Australian : Collections in the Australian Museum show that *Catophragmus polymerus* ranges from Currumbin, near the border between New South Wales and Queensland, southwards through Victoria and round into the eastern half of the Great Australian Bight (Womersley and Edmonds, 1958). It also occurs round Tasmanian shores. However, in Victoria and Tasmania the population numbers may be considerably reduced where conditions favour the growth of the mussel, *Branchidontes rostratus*, which occurs in beds on the shore rocks. A covering of mussels prevents the *Catophragmus* larvae from settling and only a few survive to settle on the shells of the mussels themselves.

Catophragmus polymerus is virtually absent also from approximately 200 miles of the Victorian coast immediately west of Cape Otway and only scattered specimens are found in south-west Tasmania. These areas of coast are subjected to prevailing cold winds from the south in summer, and probably air temperatures are too low for survival of *Catophragmus.* Several other species of intertidal animals are also missing in the same areas. However, insufficient physical data are available to draw any firm conclusions in the matter.

In Darwin's original description the locality " Swan River ? " is given for material in the Cuming collection. However, no examples of *C. polymerus* are to be found today, anywhere in the vicinity of Perth or Fremantle, and it is absent from the southern coast of Western Australia. This anomalous record of Darwin's has always been a puzzle, for it is highly unlikely that the species ever occurred there and it is not one that attaches itself to ships, so it is unlikely that it could have reached the Swan River in this manner. Recent surveys on the intertidal zone in Tasmania, however, suggest how this record may have occurred. Miss Isobel Bennett collected *C. polymerus* on Swan Island in Bass Strait. Since Darwin's original record has a query after the

word " River " he may have been unable to decipher the original label, with the Cuming specimens, and they may actually have come from Swan Island. If this were so, it would fit into the present geographical range satisfactorily and remove the anomalous record for Western Australia. Another unfortunate record occurs in the caption of Figure 468 in Broch's contribution to Kukenthal and Krumbach (1927) where it is stated that " *C. polymerus* is found in the northern intertidal zone of Australia ", whereas it is limited to the southern half of the continent.

As the growth of *C. polymerus* is favoured by exposure to turbulent seas, it is not surprising to find it also missing along the sheltered part of the northern coast of Tasmania where the shores are protected from the full force of oceanic waves and the waters are sometimes turbid (Bennett and Pope, 1960).

World Occurrence: It is considered that Gruvel's (1905) record of *C. polymerus* from " Table Bay " (? South Africa) is probably due to an error of labelling, for there are no subsequent reports of it from any locality outside SE. Australia. Old records show that Mt. Wellington, Hobart, Tasmania, was sometimes called " Table Mountain " and this may account for Gruvel's record.

Genus Octomeris Sowerby, 1825

Nilsson-Cantell, 1921, q.v. for earlier bibliography.

Mention of this genus in connection with the Australian fauna was first made in 1932 by T. H. Withers who recorded the fossil species *Octomeris crassa* from beach-rock from Magnetic Island, North Queensland. However, in 1952, a collection of living *Octomeris*, taken on a beach-rock boulder, from Magnetic Island was brought to the Australian Museum and proved to be mature specimens of *O. brunnea* Darwin.

Subsequent surveys along the Queensland coast by R. Endean, R. Kenny and W. Stephenson (1956) recorded *O. brunnea* from Coral Point (Broad Sound) northwards to the Cooktown area. Field work by the author has extended the range southwards approximately to latitude 23° S.

In all, seven species of this genus have been described since 1825, but later workers reduced the number by synonymy to four: *O. angulosa* Sowerby from southern Africa; *O. brunnea* Darwin from Japan, Formosa, the Philippines, Indo-Malayan Archipelago, Australia, Santa Cruz and the New Hebrides; *O. sulcata* Nilsson-Cantell from Japan and Formosa; and the fossil species *O. crassa* Withers recorded from beach-rock of Magnetic Island, off Townsville in Queensland.

In this present paper *O. crassa* is synonymized with *O. brunnea*, reducing the number of species in the genus to three.

Key to the species of *Octomeris*

1. Mandible with four main teeth and a pectinated lower border on which the lowest spines are the longest. Bristles on the anterior border of Maxilla I divided into only two groups by a single notch. Sutures between shell plates finely toothed. Basis membranous ..... *O. angulosa* Sowerby, 1825.

1*a*. (1). Mandible with three teeth and a pectinated lower corner. Bristles of the anterior margin of Maxilla I in three groups, either because two notches separate them as in *O. brunnea* or, as in *O. sulcata*, because they are arranged in that way, although there is only one notch ..... (2)

2. No caudal appendage, sutures between shell plates coarsely toothed. Basis membranous but with a central hole or thin area ..... *O. brunnea* Darwin, 1854.

2*a*. (2). With caudal appendage. Sutures between plates without teeth. Basis calcareous and thick ..... *O. sulcata* Nilsson-Cantell, 1932.

Octomeris brunnea Darwin, 1854

(Plate i, figures 3 and 6; Text-figures 1,*c*; 2,*b*)

Octomeris brunnea Darwin, 1854; Weltner, 1897; Gruvel, 1903, 1905; Nilsson-Cantell, 1921, 1930; Hiro, 1932, 1939; Utinomi, 1954; Endean, Kenny and Stephenson, 1956; Endean, Stephenson and Kenny, 1956.

O. intermedia Nilsson-Cantell, 1921, 1932, 1938 ; Hiro, 1939.
O. crassa Withers, 1932.
Coronula sp. Longman, 1930.

The comparatively late discovery of living *O. brunnea* on the Queensland coast, by Dr. A. Keast in 1952, is explained by its cryptic habit and the lack of systematic collecting of barnacles in Queensland before that time. The fact that the intertidal surveys of Endean *et al.* (1956) discovered the presence of *O. brunnea* along the east coast of Queensland from Coral Point, N. of Broad Sound northwards to the Cooktown area in any locality offering suitable habitats for its settlement and survival, leads one to believe that careful collecting will reveal its presence throughout the Indo-Malayan Peninsula, the Philippine Islands and south-east Asia from latitude 34° 5′ N., southwards round the Asian coast line to the Mergui Archipelago in the Indian Ocean where it has been recorded as *O. intermedia* by Nilsson-Cantell (1938).

The reasons for synonymizing *O. intermedia* with *O. brunnea* have been set out by Hiro (1939) and it is only necessary to state that the extensive Australian collections of *Octomeris* fully support Hiro's action. There are several series of barnacles from Queensland that were taken in the one locality, sometimes from the same rock, that show individuals with the characters described by Darwin (1854) for *O. brunnea* and others with the appearance of *O. intermedia* of Nilsson-Cantell (1921). There are also intermediates between these two kinds of shell structure.

Examination of the type specimens of both these species in European museums shows them to agree closely with Queensland specimens in the following way—the type of *O. brunnea* being referable to uneroded and generally fairly juvenile barnacles (see Plate i, fig. 6) and that of *O. intermedia*, to older eroded specimens (Plate i, fig. 3).

The soft parts of *O. brunnea* do not grow proportionately with the increase in size of the shell. Their rate is slower than that of the shell plates, the inner basal parts of which thicken greatly, so that the animal occupies only the small central space immediately below the opercular plates. There is a close correspondence in the morphology of mouth parts and cirri in all Australian *Octomeris*, so that there is no doubt that only one species is present in the area.

The fossil species, *O. crassa* Withers (1932), is also included as a synonym of *O. brunnea* for the following reasons :—Examination of the type material of *O. crassa* in the Queensland Museum revealed complete similarity of shell structures between the fossil barnacles from Magnetic Island, Queensland, and specimens of well-grown and somewhat eroded *O. brunnea* growing today on the beach-rock at the type locality of *crassa* (Magnetic Island, Queensland). The " fossil " barnacles show no shell character not present in living *O. brunnea*.

It may be that Withers's estimate that the rock forming the matrix is " possibly of Pleistocene age " is in error for, in the opinion of Dr. Graham Maxwell (in a private communication to the author), the process of beach-rock formation in Queensland has been continuous in geological time right up to the present day and the beach-rock containing the *O. crassa* may, in fact, have been younger than Withers thought. Associated fossil barnacles listed by Withers as " *Tetraclita* sp. and *Chthamalus* sp. " occur in the same rock with his *O. crassa*. These proved upon examination to be *Tetraclita squamosa* Brug. and *Chthamalus caudatus* Pilsbry and to differ in no way from present-day specimens of these two species which are associated with living *O. brunnea*.

A fairly detailed description of the collections of *O. brunnea* in the Australian Museum, Sydney, follows. It is based on a large series of specimens from a wide geographical range.

Appearance and Shell Stuctures

The shell comprises eight sub-triangular plates with crenated sutures between them. In uneroded and juvenile specimens the colour is brown and

the shell plates are finely ribbed (Plate i, fig. 6). There is a persistent brown epidermis which projects as a comb-like row of tiny spines along the horizontal growth-lines on the ribs. Eroded specimens tend to show a general grey colour alternating with wavy dark lines where the dark laminae are exposed (Plate i, fig. 3). In juveniles the orifice is often toothed but erosion leads to the wearing down of the projecting apices and the orifice becomes wider. In eroded specimens traces of the brown rib-folds are often still evident near the base of the shell.

As a rule, the outline of the base is almost circular but a series of measurements shows that the carino-rostral diameter is generally slightly greater than the width of the shell.

The shell has mostly a depressed conical shape except where crowding modifies growth. Crowding tends to cause the shells to grow taller as Table 1 shows. In Table 1 measurements are given of several *Octomeris brunnea* exhibiting different growth habits, as being representative of numerous other specimens that were examined in the present collection.

Table 1

Measurements of O. brunnea *and Shell Appearance*

Locality	Carino-rostral diam. in mm.	Breadth of shell in mm.	Height of shell in mm.	Description of shell
Chinaman's Beach, N. of Cairns, Q.	24	23	5·0	Somewhat eroded normal shape with parietes thickening at base.
,,	12	11	4·5	Uneroded. In a crowded group.
North Keppel Is., E. of Yeppoon, Q.	25	23	5·5	Greatly eroded and parietes much thickened, normal low shape.
,,	18	14	6·0	Uneroded. Shape distorted and tall due to crowding.
Slade Point, near Mackay, Q.	26	22	7·0	Shell eroded; parietes greatly thickened. Distorted by crowding.
,,	20	19	3·1	Shell eroded ; parietes thickened, normal shape.
South of Nasowa, W. Central Maevo, New Hebrides	13	13	3·0	Fairly uneroded shell moderately thickened at base. Shape normal.

The eight shell plates are rarely equal in size, the carino-laterals and the rostro-laterals are, more often than not, smaller than the others. Where shell erosion is severe, it may be necessary to inspect the inner side of the shell to see the crenated sutures. Radii and alae are but little developed and in older specimens consist only of the projecting teeth which interlock with those of adjacent valves. The basis is membranous but does not cover the entire area. Centrally there is a thin patch or lacuna, as shown in Plate i, fig. 3, left specimen.

Hiro (1939, pp. 252–4, fig. 3 and 4) gives an excellent account of the changes occurring in the external appearance of the opercular valves and shell plates with growth and with erosion and there is nothing to add to his description in this respect.

The sheath extends to about half the depth of the shell and is lined by a brown membrane but below the sheath the interior of the parietes is a translucent grey.

Scutum and Tergum

Basically the structures of the scutum and tergum in Australian *O. brunnea* are similar to those depicted in Hiro's paper (1939, fig. 3). However, slight

variations occur in the shapes, articular ridges and furrows of these two valves, for they may sometimes be situated nearer to the apices of the valves or, in older specimens, nearer to the centre of the tergal margin of the scutum or the scutal margin of the tergum. The depth of the scar of attachment for the adductor muscle of the scutum is also variable, as are the number of crests for the attachment of the depressor muscles of the tergum.

Soft Body

The flaps of the tergo-scutal membrane are bordered with white, round the orifice, in newly preserved material and the cirri are light coloured, except in the areas round the bases of the anterior spine pairs and the posterior spine tufts. Here there are concentrations of dark pigment giving a distinctive barred colour pattern to the cirri.

Trophi

The *labrum* has a well-defined wide, shallow groove which in all specimens examined is deeper than that depicted by Nilsson-Cantell (1921, text-fig. 59*a*). It is bordered by a single row of triangular teeth along its entire length. In describing *O. brunnea*, Darwin (1854, p. 485) likened the labrum to that of *O. angulosa* and as therefore having the " Labrum bullate, with the crest hairy and furnished with a few most minute teeth ". It must be remembered that Darwin was describing immature specimens of this barnacle and this may account for the smaller number and size of teeth seen. *Palps.*—The palps of Australian *O. brunnea* bear more bristles along their straight anterior margins and near the tip, than the number shown in Nilsson-Cantell (1921, text-fig. 59–61). Otherwise they are similar to those he described. *Mandible.*—The mandible has three well developed teeth and a pectinated lower angle. There is some degree of variability in the structure of the second tooth for it may carry a few small denticles on its upper margin or be quite smooth. These denticles tend to disappear as the barnacle matures. The third tooth is generally pectinated on its upper side. *Maxilla I.*—Two notches on the anterior border of the first maxilla divide the bristles into three groups—two smaller bundles on either side of a large central one. A pair of large spines and two pairs of smaller spines lie above the first notch. The central group of bristles are second in size only to the large dorsal pair above the first notch. The lower group gives a pectinated appearance to the lower angle of the maxilla. *Maxilla II* is as shown by Nilsson-Cantell (1921, text-fig. 61) but is more hirsute.

Cirri

The first two cirri are considerably shorter than the remaining ones and very setose. In each pair the rami are unequal, the anterior one being longer by approximately two or so segments and about half as broad again as its fellow. In spite of this, the two rami generally have an equal number of segments (from 6 to 7) or occasionally they may differ by one. Many of the longer and broader setae are pinnate as shown in Text-figure 1, *c*. Others are pinnate but finer. In *cirrus I* there are a few of these broader setae on the terminal segment but only a few occur in the segments below it. The pedicel is also hirsute with numerous bristles along its anterior surface. *Cirrus II* resembles I in shape and size but the anterior ramus is not so broad, by comparison with I. Although the segmental numbers of the rami tend to be equal, the anterior one is longer by the length of more than two of its segments. Many of its long setae are pinnate and are so numerous in the terminal segments of the anterior ramus as to form a felted mass and an efficient sieving organ for catching minute food-particles. Similar setae are found in the posterior ramus but they are fewer in number. *Cirri III to VI* differ in shape and are much longer than I and II. The two rami of each cirrus are comparable in breadth and in shape and are almost equal in length except for cirrus III in

which the posterior one may sometimes be slightly the longer. Several of the more basal segments of the anterior ramus of cirrus III carry tufts of pinnate spines. Each segment of the rami has four pairs of stout larger spines anteriorly, of which the distal ones are longest and the proximal pair very much the shortest, while posteriorly there is a small tuft of spines, placed at the junction of adjacent segments (Text-fig. 2,*b*). One pair of spines in this tuft is generally longer than the other ones. Concentrations of dark pigment occur near the bases of all these spines, giving the characteristic darker colour patches posteriorly, near the junction of adjacent segments.

The numbers of segments in the rami of the cirri vary slightly between right and left sides of the same barnacle. Several specimens have been dissected which had damaged cirri—shorn off at varying distances from the pedicel. Damage and regeneration may account for the fact that the numbers of segments making up the rami of right and left cirral pairs in one individual do not always agree.

The *penis* is of moderate length, tapering to a blunt tip. Near the extremity there are a few hairs scattered generally over the surface, with a small tuft of hairs near the tip of the organ. There is no *caudal appendage*.

Habitat

Octomeris brunnea occurs either far back in crevices or on the undersides of small boulders or overhanging rocks where it is sheltered from sunlight. A series of specimens occurs on mangrove roots taken at Carlisle Bay, Santa Cruz Island. Another batch was collected from the walls of an intertidal limestone cave 1½ miles south of Nasowa, W. Central Maevo, in the New Hebrides. It occurs on the higher levels of the shore from approximately the level of mean high water down the shore to the level of high water of neap tides. It is rarely found in large numbers even in favourable localities.

Distribution

Australia and the Pacific: Collecting by the author has extended the known range of *O. brunnea* in Queensland southwards for a further 200 miles to the vicinity of the Keppel Islands in latitude approximately 23° S. There are also specimens from the New Hebrides and Santa Cruz Islands in the Australian Museum. It is not recorded, as yet, along the northern coast of Australia.

World Occurrence: Southern Japan; Formosa; Philippine Islands; Malay Archipelago generally; E. coast of Queensland, south to Tropic of Capricorn; New Hebrides and Santa Cruz.

Genus Chthamalus Ranzani, 1817

Pilsbry, 1916, q.v. for earlier synonymy and references; Nilsson-Cantell, 1921; Hiro, 1932; Kolosváry, 1941; Moore, 1944; Newman, 1961; Davadie, 1963; Zullo, 1963.

From the point of view of taxonomy the genus *Chthamalus* is regarded as a difficult one. Certainly, so far as Australian species were concerned this proved true. While four of the five species, namely *C. antennatus*, *C. withersi*, *C. caudatus* and *C. intertextus*, posed few problems in identification and the patterns of their geographical distributions were clear cut and logical, the fifth, *C. malayensis*, proved most difficult to name. At one stage Australian material of this species was thought to represent at least three distinct populations with confused and overlapping distributions, especially if stress were placed on obvious shell differences, and one of these populations (typified by the shell illustrated in Text-fig. 5,*d*) was not recorded in literature. These three groups ultimately proved to be ecological or age variants of the one widely ranging, polymorphic species, the true nature of which had not been appreciated

by workers on the following important collections :—(1) the Dutch Siboga Expedition ; (2) additional collections from the Dutch East Indies (Indonesia) housed in Dutch Museums ; (3) Dr. Mortensen's Pacific Expeditions (1914–16), and (4) large collections from the Indomalayan area worked by C. A. Nilsson-Cantell which were housed in various European museums. It was not recognized by Darwin (1854) as being distinct from *C. stellatus* but he commented on the pecularities of specimens from the Philippine Islands, although he did not separate them from the European species. In all these earlier collections samples had been taken from widely scattered geographical areas and little notice was taken of any ecological background. Considerable confusion exists in the literature documenting these collections and, even after examining all of the specimens concerned, the author was still left in doubt as to the correct name to apply to the species universally distributed round the tropical Australian coast. However, many doubtful points were clarified when a sufficiently large sample of this wide-ranging population was examined, and the examination of the type of Pilsbry's *C. malayensis* in the United States National Museum in Washington, D.C. in 1963 provided the necessary clues to clear up any doubts about the nomenclature of the northern Australian species. Although the name *C. malayensis* had been applied by the author to material collected during the intertidal surveys in Queensland made by Endean, Kenny and Stephenson, the use of the name was still somewhat tentative at that time. Fortunately it has proved correct so that records of it in their surveys need no emendation. Under the specific description of *C. malayensis* some slight indication is given of the confusion that has occurred in its naming in previous literature and, while the synonymy quoted has been made as complete as possible, carrying on from Utinomi's excellent review (1954), no attempt has been made to take each reference and state the nature of the error it contains. To do so would require more space than is merited in the present review. However, in the synonymy above, with the exception of Stubbings (1963) and Daniel (1956), the actual specimens concerned have been examined by the present author, before the step of synonymizing them was taken.

When large populations of *Chthamalus* from all over the world are examined without regard to names previously bestowed on them, it becomes apparent that confusion of the species is in the literature, rather than inherent in the barnacles themselves, provided that a certain combination of characters of both shell and soft parts is used to determine the species. The chief difficulty in determining the doubtful Australian *Chthamalus* hinged on being able to distinguish with certainty the following closely related species :—*C. stellatus* (Poli) s.s., *C. antennatus* Darwin, *C. challengeri* Hoek and *C. malayensis* Pilsbry. During the present study the following characters were found useful in distinguishing them : the general morphology of the mandible in the region of the comb-like series of spinules ; the type of notching, below the uppermost large spines on the first maxilla, and the crests for attachment of the depressor muscles of the tergum, while the most reliable criteria, in fully mature specimens, proved to be the minute structure of the stout, lanceolate spines associated with the terminal segments of both rami (chiefly the anterior one) of cirrus II and the sculpturing of the pit or depression on the interior of the scutum, where the lateral depressor muscles are attached. These distinguishing characters are tabulated in Table 2 which should assist the renaming of Indomalayan specimens in the collections of various European museums where *C. challengeri*, *C. stellatus* and *C. malayensis* have often been very much confused.

Recent ecological-systematic surveys of cirripedes in the vicinity of Japan and south-east Asia by Utinomi (formerly known as Hiro) have led to the same general conclusions about the distributions of species within genus *Chthamalus* as have emerged from the present study. After due allowance has been made for the taxonomic confusion of the past, it is seen that there is a distinct tropical

TABLE 2

Characters of certain species in stellatus *group of* Chthamalus

Species and geographical distribution	Type of notch in Maxilla I	Features of Tergum	Features of Scutum	Type of lanceolate spine on terminal segment of Cirrus II
C. antennatus Darwin. Temperate Australian shores.	Most distinct. Like a U lying on its side with no spines originating from side walls of notch and obscuring it. (N.B. Tips of a few hairs on the side wall of maxilla may show, but no spines.)	Tergum smooth and flattish internally. Not bent. Two fully developed crests for tergal depressors or there may be an additional third crest partly developed.	Smooth internally and little sculpturing. No obvious pitting. Shallow depression for lateral depressor muscles with two incipient crests (hard to see). Ledge below adductor muscle scar but little developed, or absent.	Lanceolate spines stout and coarsely serrate with a double row of peg-like teeth, the lowest two of which are not separated from the rest by a distinct gap.
C. malayensis Pilsbry. Tropical and sub-tropical regions of Indian and Western Pacific Oceans and Tropical Australia.	ditto	Tergum strongly pitted internally and bent about a central line of pits (or incipient pits) at an obtuse angle. Three or four fully developed crests for tergal depressor muscles—juveniles tending to have three crests and later developing a fourth one.	Internal surface much pitted. Sculpturing more marked than in *antennatus* but less so than in *challengeri*. Pit for attachment of lateral depressor muscles deep but without visible crests. Scar for adductor muscle a deep pit with a small ledge below it—the adductor ridge—not as well-developed as the ridge in *challengeri*.	Lanceolate spines stout and coarse but with side spines stout but pointed (not blunt and peg-like as in *antennatus*). Two lowest spines (which may be worn down to blunt knobs) separated by a distinct space from those in the rows above.
C. stellatus (Poli) s.s. North Atlantic Ocean and Mediterranean Sea.	Notch less distinct, often a wide open V-shaped indentation with a very small notch obscured by spines. Some smaller spines based along the side wall of the notch.	Tergum slightly pitted internally and broad above and bent about a central groove at least in its lower half. Four crests for depressor muscles often associated with pits, or they may be worn and irregular in shape.	Somewhat pitted internally but with less distinct sculpturing than *challengeri* or *malayensis*. Pit for attachment of lateral depressor muscles distinct but shallow, and without any crests and not deep, as in *malayensis*.	Stout spines with a double row of fine, often almost hair-like, side teeth but without large teeth below separated from the serrate teeth by a space.
C. challengeri Hoek. Japanese mainland waters. (N.B. Records by Nilsson-Cantell in Malayan Seas probably erroneous.)	Notch less distinct than in *antennatus* and *malayensis* and not U-shaped, but more clearly defined than in *stellatus*. It is generally V-shaped and furnished with spines along its upper border. (See Hiro, 1932, Text-fig. 2.)	Tergum slightly pitted internally and bent about a central groove in its lower, narrower section. Three to four crests (according to age) for attachment of the depressor muscles. They may be regular or very irregular in outline. Lower part narrower than in *malayensis*.	Scutum slightly pitted internally and with a shallower pit for attachment of the adductor muscle. The ridge below this pit is, however, very strongly developed. Pit for attachment of lateral depressor muscles well developed and with three or four small crests in it, clearly visible.	Stout spines with a double row of fine, hair-like serrations, slightly coarser than those of *C. stellatus* and some with the lowest pairs of teeth larger and separated from the fine teeth by an appreciable gap.

fauna common throughout the Indomalayan region which has its northern boundary in the southern regions of Japan and SE. Asia in approximately the latitude of Taiwan.

This same fauna has now been found to range south of the equator into the northern region of Australia and, in fact, colonizes the coasts of the northern half of the continent. It contains no species of *Chthamalus* endemic to the region but is characterized by *C. malayensis*, *C. caudatus*, and to the east by *C. withersi* also. To the north in New Guinea *C. intertextus* also occurs.

In the more temperate seas of Japan a different group of species in genus *Chthamalus* is represented on the upper shore, namely *C. pilsbryi* Hiro, *C. dalli* Pilsbry and *C. challengeri* Hoek. In temperate Australia the genus is represented by a single species, *C. antennatus*, and the rest of the upper shore Chthamalids belong to different genera, namely *Chamaesipho* and *Catophragmus*. There is thus a marked falling off from four species to one in the genus *Chthamalus* on the southern half of the Australian coastline and corresponding levels of the upper shore, while still occupied by representatives of the family, are relatively poorly supplied with species of this genus. The sole representative, *C. antennatus*, is, however, endemic to southern* Australia and does not range across the Tasman Sea to New Zealand where there is no representative of the genus in the intertidal fauna. Earlier records of genus *Chthamalus* in New Zealand by Cranwell and Moore (1938) have been subsequently shown by one of them (Moore, 1944) to be juveniles of a second species of *Chamaesipho*—(*C. brunnea*).

The geographical distribution of Indomalayan and Pacific species of *Chthamalus* can now be clearly defined, and Kolosváry's (1941) arrangement of them into formenkreise is found to be inaccurate as there is little tendency for overlapping in the distributions of tropical and temperate species from one major zoogeographic area to another. This author's records of *C. stellatus* in New Guinea, *C. malayensis* from Victoria, and *C. moro* from New Zealand in his 1943 work should also be disregarded in the light of the present survey.

Among Australian species, *C. withersi*, *C. intertextus* and *C. caudatus* show affinities in some of their structures, habitat preferences and feeding adaptations with *Octomeris*, whereas *C. antennatus* and *malayensis* have corresponding structures and adaptations more aligned with those of the most primitive of all living genera, *Catophragmus*. *Chthamalus intertextus* also has features relating it with both the three- and four-toothed groups of species within the genus *Chthamalus* and also with *Chamaesipho*, since the structures of its short stout spines on cirri II and III are almost identical in shape with those described by Moore (1944) for *Chamaesipho brunnea*. Zullo (1963) indicated in a paper read before the XVI International Congress of Zoology that it was his intention to divide the former genus *Chthamalus* into two, resurrecting Conrad's name *Euraphia* for the group of species with tridentate mandibles (Nilsson-Cantell's *hembeli*-group) and restricting the genus *Chthamalus* s.s. to those species with quadridentate mandibles, of which *C. stellatus* is a typical example. Since Zullo's paper is not yet published the matter must be considered under review. The present study has, however, shown that the line dividing species hitherto characterized as having tri- and quadri-dentate mandibles is by no means so clearly defined as was thought by Pilsbry (1916) and Nilsson-Cantell (1921). The finding of large individuals of certain Australian species in which normally 4-toothed species have developed only 3 teeth, or conversely, of 3-toothed species with 4 teeth, is going to make the drawing of distinctions between Zullo's proposed generic groups somewhat difficult. Moreover, if *Chthamalus intertextus* is included with the *hembeli*-group of species (to which it shows

* The unfortunate use of geographical terms such as " South and West " in the names of certain Australian States can lead to confusion in discussions of distributions. The present author's practice is to use term " southern " for the whole coast of the continent south of approximately the latitude 30° S., and not just restricted to the State of South Australia.

undoubted affinities) the relating of the genus *Chamaesipho* more directly to the *stellatus*-group by Zullo will require some explanation, since the structure of its short stout spines on cirri II and III and tendency of the sutures between its shell plates to become obliterated and overgrown by later calcification would seem to indicate certain affinity with species like *Chthamalus intertextus*.

No published key to species of *Chthamalus* satisfactorily differentiates *C. malayensis* from closely related forms and the key in Nilsson-Cantell's 1921 monograph omits it. The following full synopsis and key to Australian and New Guinea species has therefore been prepared and since it will largely be used by non-systematists, unfamiliar with the vagaries and difficulties associated with the characters used to differentiate species in the genus *Chthamalus*, a rather full series of warnings and notes are appended in the form of footnotes. With the aid of these, identification of Australian species of *Chthamalus* should present little difficulty.

Key to Australian and New Guinea species of genus Chthamalus

1. (1*a*). *Chthamalus* with much flattened shells without distinct ribs and having a mandible generally with only three major teeth* above a coarsely and irregularly pectinate section forming the lower tip of the jaw, with the longest spine generally at the tip of the jaw. Teeth 2 and 3 often with secondary side teeth. Labrum generally not bullate but flattened above the palps or developed as a muscular, semicircular funnel-like organ (see Text-fig. 3,*d*). Rami of cirrus II without stout serrated, lanceolate spines on their terminal segments except for *C. intertextus*†. Pinnate setae very numerous ..... (2)

1*a*. (1). *Chthamalus* with shells generally taller and of truncated conical shape which, under conditions of crowding, may become tubular. Rarely flattened but in such individuals ribbing generally more distinct than in species in group 2. Mandible with four major teeth (occasionally five) of which the fourth is generally doubled*. Lower tip of jaw generally armed with several (from two to four) spines of even size and distinct from the other spines above them. Between these and tooth four, straight-edged, groups of closely packed spinelets generally form comb-like sections as illustrated by Utinomi (1959, fig. 5,*a*)‡. Labrum typically rounded or bullate above the palps (Text-fig. 5,*e*). Terminal segments of both rami of cirrus II armed with a bunch of stoutly built, lanceolate and serrated spines among the pinnate setae ..... (4)

2. (2*a*). Sutures between shell plates with interlocking teeth or interfolded laminae. (If shells very eroded these structures may sometimes be seen only internally.) Basis either membranous or with an outer calcareous rim round an inner membranous section.... (3)

2*a*. (2). Sutures between shell plates simple and not interlocking and only loosely articulated together. The lines marking the sutures between scuta and terga are straight, even in worn fully grown individuals and not shaped like the Greek letter psi as in most species of *Chthamalus*. Found in the highest intertidal zone. Shell much flattened and, if uneroded, often cinnamon-brown with four white ribs projecting into the orifice as teeth, from the tips of the side valves. Rostro-laterals and lateral plates often with internal pits or calluses. Basis always membranous ..... *C. withersi* Pilsbry, 1916.

3. (3*a*). Sutures between shell plates with zigzag interlocking joint owing to teeth. Paired, long slender, jointed caudal appendages present. Scutum and tergum separate and not ankylosed. Basis wholly membranous ..... *C. caudatus* Pilsbry, 1916.

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* Warning: exceptionally, large *C. withersi* may occasionally develop a fourth tooth on the mandible (see p. 43) but this fourth tooth is rarely doubled and there is generally no trace of comb-like arrangements of spines below it.

† *C. intertextus* stands in a somewhat anomalous position since it clearly has only three teeth on its mandible and has a peculiar semicircular labrum (like that of *C. caudatus*) which is not bullate. However, the terminal segments of cirrus II possess a few stout spines hidden among the pinnate ones (much less obvious than those of species with four-toothed mandibles within the genus). These spines (Text-fig. 1,*f*) are not of the regularly serrate pattern, resembling more the type of stout spine found in the genus *Chamaesipho*.

‡ Very juvenile specimens or individuals with damaged and regenerating mandibles of the *stellatus*-group may fail temporarily to show distinct comb-like sections in the lower part of their jaws and may exhibit a somewhat random arrangement of the spinelets (see *C. antennatus*, Text-fig. 4,*g*) reminiscent of the adult jaw in species with tridentate mandibles. Evidence from the examination of a number of specimens would make it appear that a developing or regenerating jaw of a typically " *stellatus*-pattern " passes through a kind of " *hembeli*-stage " of jaw development before reaching the comb-like arrangement of spinelets normally seen in adults below the fourth tooth. Generally in such cases, the doubled fourth tooth and lack of secondary toothing on teeth two and three are clues which help to key a specimen correctly.

3*a*. (3). Sutures formed by oblique interfolded laminae of radii and alae (when the shell is not eroded) and marked by prominent vertical lines of growth, giving a chevron-like appearance to the sutural areas of the shell (Text-fig. 3,*a*). When eroded, shell becomes a deep violet hue due to secondary calcification internally and sutures are marked by characteristically rounded wavy lines, as shown in Text-figure 3,*b* and *c*. Scutum becomes firmly ankylosed to its neighbouring tergum and basis often saucer-shaped with outer rim calcified and inner section membranous (seen in side view in Text-figure 3,*c*). Cirrus II and basal segments of cirrus III armed with stout, grapple-spines of unusual shape (Text-fig. 1*f*) ..... *C. intertextus* Darwin, 1854.

4. (1). With four teeth on mandible and sometimes even a small fifth tooth may be present. Between the group of spines forming the lower tip of the jaw and the fourth tooth is generally a fairly short comb-like section where the spinelets are of even size and length but are not fine and hair-like*. Terminal segments of cirrus II armed with very stout serrated spines with coarse side teeth ..... (5)

5. (5*a*). Inside of opercular valves not ruggedly sculptured and rarely pitted. Tergum broad near its basi-scutal corner and generally with two (or, at the most, two plus a partly developed third crest in larger individuals) for attachment of its depressor muscles. Scutum with a distinct, but shallow, depression for the attachment of the lateral depressor muscles, in which two low, incipient crests may be distinguished in full-grown individuals. Serrated stout spines of cirrus II with a double row of blunt, short, peg-like spines in which the two lowest are not separated from the rest by a distinct space (see Text-fig. 1,*h*) ..... *C. antennatus* Darwin, 1854.

5*a*. (5). Inside surface of opercular valves with more rugged sculpturing than in *C. antennatus* and mostly pitted deeply. Tergum narrowing towards its basi-scutal corner and folded along a line of deep pits along the axis drawn from the apex to the basi-scutal angle. Generally at least three crests for attachment of the tergal depressor muscle with larger and older individuals developing four crests. Scutum with a deep narrow pit for attachment of lateral depressor muscles and no sign of ridges or crests within this pit. Lanceolate spines of cirrus II stout and armed with a double row of stout pointed side spines, the bottom pair of which may be worn down to mere bumps, but which are separated from those above by a slight gap (Text-fig. 1,*i*) ..... *C. malayensis* Pilsbry, 1916.

Chthamalus intertextus Darwin, 1854

(Plate i, figure 1 ; Text-figures 1,*f* ; 3,*a-d*)

Chthamalus intertextus Darwin, 1854, illustrated ; Gruvel, 1912 ; Hoek, 1913 ; Pilsbry, 1916, 1927 ; Hiro, 1939, illustrated ; Utinomi, 1949, 1954 ; Tokioka, 1953 ; Newman, 1961, illustrated.

The possession of a unique collection of obvious shell peculiarities such as (1) a basis which is partly calcareous and partly membranous ; (2) the beautiful violet colour of the inside of the shell and the calcareous ring of the basis ; (3) the interlocking sutures between the parietes ; and (4) scuta and terga which tend to ankylose, so that only a trace of the original suture between each scutum and tergum remains (generally only towards the basal parts of the two valves) have contributed to the making of *Chthamalus intertextus* easy to determine. It has therefore not been confused in past accounts.

However, recent work by Newman (1961) has shown that Darwin's original description was incorrect in one important respect. Darwin stated that every full-grown specimen he investigated had the basal edge of the parietes " inflected rectangularly inwards, forming a smooth-edge ledge all round the basal membrane, which, in proportion to the width of this ledge, was by so much reduced in diameter ". Newman has found that the calcareous basal shelf inside the shell wall of *C. intertextus* was a product of secondary calcification of the basis, rather than, as Darwin believed, an inflected extension of the parietal walls. Newman also examined *C. hembeli* (Conrad) and *Chthamalus calcareobasis* Dora Henry (1957), which are most closely related to *C. intertextus* in both having calcareous bases, as well as other shell structures in common. In both these

* Had it been necessary to include *C. stellatus* and *C. challengeri* in this key, they would have been separated from other species at this point by possession of the following characters :— With four-toothed mandible, with a comb-like section between fourth tooth and spines of lower tip of the jaw broader than the corresponding structure in *C. malayensis* and *C. antennatus* and with much finer toothing—more hair-like than spine-like. Stout spines on terminal segment of cirrus II armed with double row of very fine spines (almost hair-like in structure)—never peg-like or spine-like, as in *C. malayensis* and *C. antennatus*.

species Newman pointed out that the limy base was also a product of secondary calcification which, in the case of *C. hembeli*, was also marked by the deposition internally of successive layers of shell material on top of the basis and the inner parietal wall, which obscured the interlocking junction of the parietes and basis and thus misled Darwin, and Henry who accepted Darwin's statement.

It is not intended here to go into detail of the anatomy, or of the slight variations which, no doubt, could be found in the present sample of *C. intertextus* from New Guinea, for the simple reason that the material available is considered to be too meagre to be representative of the world population of this species. Until collections of it are at least equivalent in their cover of the whole geographical area—as they have been in the other species discussed in this paper—it is sufficient merely to record additional facts which may help other workers on the group.

As has been the case in all other species described in this paper, the size of the specimens, in most cases, exceeds those seen by previous authors. Some of the facts about this sample are summarized in Table 3.

TABLE 3

Measurements of 10 Chthamalus intertextus *from Papua, New Guinea, taken in January,* 1964

Carino-rostral diameter, in mm.	Width of shell at right angles to the carino-rostral diameter, in mm.	Height, from lowest point of basis to highest on shell, in mm.	Breeding-conditions	Remarks
7·2*	9·4	3·0	eyed-nauplii present	
7·5	6·3*	3·2	no larvae	Colour : ash-grey to white externally with, in places, persistent yellow epidermis. Uneroded ; sutures interlocking
10·8	9·4*	3·2	eyed-nauplii present	Almost rectangular in shape Central membrane of basis oval and dark—black or navy-blue
11·6*	11·2	4·0	eyed-nauplii present	Membranous part of basis black
11·8	7·9*	3·0	eyed-nauplii present	Shape : almost rectangular ; membranous part of basis oval
12·5	11·5*	4·0	no larvae	
12·5	11·8	4·0	eyed-nauplii present	Calcareous basis + central membranous part, almost basin-shaped
12·5	12·0	4·0	eyed-nauplii present	Shell sculpturing : raised ribs or rows of white knobs—shell mauve when broken across, powdery—white on surface. Very worn
13·0*	11·5*	3·0	eyed-nauplii present	
14·0	9·0*	5·2	eyed-nauplii present	Basis an outer rim of bright mauve limy material and a central very dark membranous pit

* Growth restricted in some way, e.g. by crowding or by edaphic factors.

Again it becomes evident that the presence of developing nauplii inside the shell is by no means a proof that the barnacle concerned has attained its full size, as is so often assumed in earlier accounts. From Table 3 it may be seen that while the smallest barnacle was brooding nauplii, it was approximately only half as large as the largest one in the group measured.

For a full description of the shell and of the soft body the accounts of Darwin (1854, pp. 467–8, Plate 19, figs 1*a* and 1*b*) and of Hiro (1939, pp. 251–2, fig. 2) should be consulted, and for ecological and zoological information papers by Hiro (1939), Utinomi (1949 and 1954), and Tokioka (1953) will be found to contain valuable additional information.

Appearance of Shell

Most specimens examined were greatly eroded and showed scant evidence externally of the rather distinctive sculpturing on the shell, with which they began their lives. The shell plates of an uneroded individual were irregularly ribbed longitudinally and the whole shell was marked by numerous raised, horizontal lines-of-growth, as shown in Text-fig. 3*a*. The deep violet of the inner layer of the shell was visible only between these ribs where the yellowish epidermis had worn away and allowed erosion to begin. The interlocking of the sutures between adjacent plates begins as a most complex structure and, before erosion occurs, the radii are seen to consist of a series of laminae, paralleling the inner wall of the valve. These are " interleaved " rather than " interlocked ", with a series of similar laminae projecting in the opposite direction, outside and parallel to the inner wall forming the alae of the adjacent valve. All these projections carry numerous, obliquely-placed, fine lines of growth. When viewed *in situ* externally, they look like a series of chevrons. Usually only traces of the lines of growth and the ribs persist as longitudinal rows of white raised bosses on the worn, bright violet background of the inner layer of the parietes. After a certain amount of erosion, the sutures are simple and straight from the orifice outwards for a certain distance (all trace of the " chevrons " having disappeared), then each suture becomes wavy, with round interlocking projections and continues thus to the periphery of the shell (Text-fig. 3,*b* and *c*). These projections of the interlocking joints are too rounded to be called teeth. Internally the shell wall is coloured a deep violet and is much pitted.

Basis

The most outstanding feature of the shell of *C. intertextus* is the basis which is partly calcareous and partly membranous. Taken together, both these sections form a saucer-shaped structure, with the violet-coloured, calcareous section as an outer rim or flange and the dark membranous part occupying and filling over the central hole (see side view of whole shell in Text-fig. 3*c*). The width of the calcareous flange and, consequently, the sizes of the central hole vary. However, no specimen has been seen in which the central area was ever completely bridged over by limy structures.

Often the barnacle is found to be fastened over a small depression in the substratum and this applies, both in the softer rocks like calcarenite (so-called beach-rock) and in the much harder, dark volcanic rock of Hawaii (in a batch collected by Miss Isobel Bennett at Nanakula Beach, Honolulu, Oahu), or in material from the New Hebrides. The limitations placed on diametric growth in the three species *C. hembeli*, *C. calcareobasis* and *C. intertextus*, by secondary and internal calcification have been discussed by Newman (1961) and pose some very interesting questions as to the possible function of a " too-large " shell, of which the internal volume would appear to be progressively reduced, as the barnacle grows older. This is, in general, quite the reverse of what happens in the Family Balanidae. The suggestion is here made that its function may be concerned with reproduction for, when individuals are brooding nauplii,

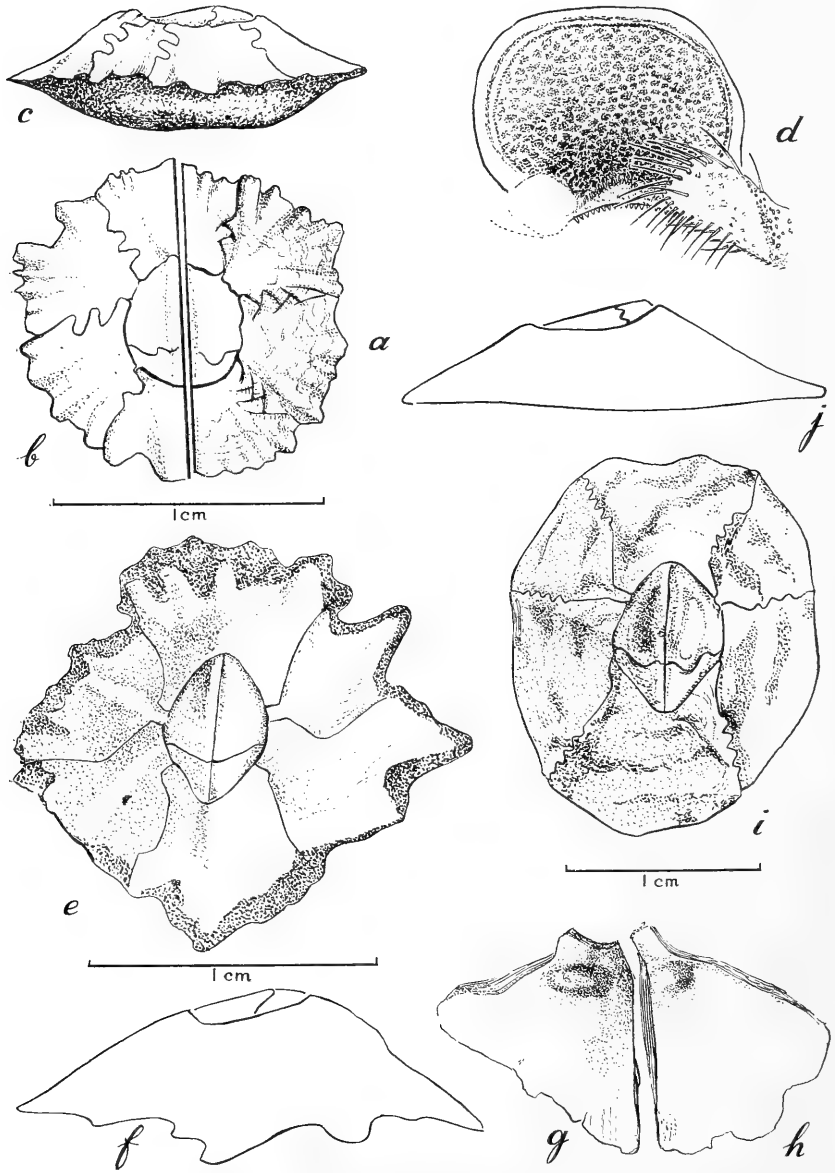

Fig. 3. Species of *Chthamalus* with flattened labrum and with mandibles generally with three major teeth. (*a-d*), *Ch. intertextus*, (*a-b*) half shells seen from above at different stages of shell erosion, (*a*) being moderately eroded and juvenile with distinctly interlocking and overlapping sutures with " chevron " appearance, (*b*) a moderately eroded older specimen with " chevrons " worn away ; secondary calcification has produced a deeply violet coloured shell and sutures with rounded interlocking processes ; (*c*) side-view with calcareous basal ring of basis depending below shell ; (*d*) labrum (front view) with right palp removed to show pocket, funnel-like, semi-circular protrusion, channelled towards the toothed groove leading to the mouth ; (*e-h*) *Ch. withersi*, (*e*) shell from above, (*f*) side-view of shell in silhouette, (*g*) rostro-lateral and (*h*) lateral shell plates seen from inside, showing pocket-like outpushings of shell (occasionally they may be secondarily calcified and be represented by a callus) ; (*i-j*) *Ch. caudatus*, (*i*) shell from above with toothed sutures and (*j*) shell in side-view silhouette.

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the space round the soft body is completely filled up by developing young. The secondary sealing-off of the shell may in some way reduce evaporation or help to retain moisture for brooding young.

Scutum and Tergum

Erosion of these shell plates leads to the loss of all trace of lines of growth on the external surfaces of the opercular valves. Their most distinctive feature, however, is that secondary calcification leads to the fusion of each scutum with its tergum and the loss of any clearly defined line of articulation between them, in adult specimens. In younger individuals (carino-rostral diameter of 9·0 mm.) there may be no trace of the former suture in the apical parts of the valves, while a trace may remain nearer to their basal margins. It is, however, generally impossible to separate the scutum from the tergum without breaking the valves at some point, other than the old suture. Internally they show little definite structure, except that areas of shell where muscles attach are generally paler in colour than the remaining areas of deep violet. This is specially noticeable in the case of the four crests for attachment of the tergal depressor muscles and for the scar for the adductor muscles of the scuta. The inner side of the tergum is generally considerably darker than the scutum owing to greater secondary calcification. Both valves show internal pitting. While the scuta and terga are firmly interlocked in *C. calcareobasis* and *C. hembeli*, they are never ankylosed, as in the present species.

Soft Body

If the calcareous flange of the basis is well-developed, the soft body may be completely obscured from below until the basis is broken away. In younger individuals, where secondary calcification is only just beginning, the soft body lies exposed and is seen, in material newly preserved in alcohol, to have a pale hyaline blue colour, with occasional darker blue areas, e.g. both the rami of cirri I and II and especially the inner surfaces of the pedicels of the remaining cirral pairs. The tergo-scutal flaps are a navy blue with lighter brown margins. The membrane lining the shell is black or navy blue, as is the membranous part of the basis. The outer ends of the trophi are a pale brown, in contrast to the general pale blue of the rest of the body, and to the bluish semicircular funnel-like process on the labrum, above the groove.

There is no *caudal appendage* and the *penis*, which is of moderate length, is pale brown proximally, fading out to white towards its tip. It shows a ringed structure. The eyed-nauplii are cream-coloured. It should be remembered that these colours refer to recently preserved material, as the author has not handled live material.

Trophi

Viewed from in front, the *labrum* carries a distinctive, semicircular projection, curved round to form a funnel or scoop rather than a rounded and bullate structure. The anterior surface of the labrum, above the palps, is mottled by dark punctate markings giving it an appearance similar to that seen in certain beach-worn specimens of brain corals. It may be blue or bluish-brown and is well furnished with muscles (internally). The actual groove of the labrum carries a row of peg-like teeth with a fringe of hairs above and is a wide, shallow "⌒"-shaped structure. The *palps* are carried adpressed in slight depressions below the "funnel" which is seen to be channelled towards the groove of the labrum, leading into the mouth (Text-fig. 3*d*). The palps are as described by Darwin, and the *mandible* is similar to Hiro's illustration (1939, fig. 2A), with three major teeth above, and a coarsely toothed lower angle. Teeth 2 and 3 carry secondary teeth along their upper margins. *Maxilla I* varies only slightly from Hiro's (1939) fig. 2B. In the New Guinea

material, there is clearly a pair of smaller spines between the notch and the two much larger ones above. *Maxilla II* is swollen, carries numerous long bristles, but the distinct notch is free from bristles.

Cirri

The first two pairs of cirri are much shorter and more bristly than the remaining four pairs, and have both rami dark blue, although their pedicels are generally light coloured. In several individuals the posterior ramus in each of cirri I and II had been damaged and the regenerating rami were only approximately 1/3 of the length of the normal anterior ones. However, this was exceptional. Normally *cirri I* and *II* have their rami subequal, with cirrus II slightly longer than I. The anterior ramus in both these cirri was slightly longer and broader than the posterior one, in spite of the fact that they normally contained the same number of segments—varying between 5 and 7 (or even more, in very large individuals). Marked inequality in the numbers of segments between the anterior and posterior rami of any one cirrus is generally indicative of recent damage and regeneration. Both cirrus I and II bear longish, pinnate setae anteriorly on their distal segments. There are generally many more of these pinnate bristles on the anterior than on the posterior ramus. In addition, the terminal segment and some of the more distal segments of the anterior ramus of cirrus II carry bunches of short stout, forwardly-directed grapple-like spines with paired lateral hooks, round the bases of the longer, fine pinnate ones. They resemble the short stout spines seen in *Chamaesipho columna* or, more especially, those of *Chamaesipho brunnea* which were first illustrated by Moore (1944, Plate 46). They are very numerous on the most distal four or five segments of the anterior ramus and their numbers fall off towards the sixth or seventh segment, below the tip. Their structure is shown in Text-fig. 1*f*, and from circumstantial evidence their function is believed to be to hold and concentrate the food particles, after they have been sieved out of the water by the bunches of pinnate spines. *Cirri III–VI* are of structure normal to the group except for the three or four basal segments of cirrus III, which are furnished with grapple spines similar to those on cirrus II. Their rami are sub-equal in length and numbers of segments and the more central segments of most rami carry four pairs of long spines anteriorly with an occasional exceptional one with five pairs. In this last case the fifth pair is generally very short and visible only under high magnification.

The batch of *C. intertextus* from Papua, New Guinea, collected by Miss Judy Bryan, had obviously been taken after a period of feeding and in many specimens the cirri were clogged with food particles which were arranged in such a manner as to suggest that the pinnate spines, acting together, function much as gill-rakers do in fish, and the grapple-like spines, at their " roots ", hold and concentrate the food.

Habitat

Specimens examined in the British Museum (Natural History) were labelled " Philippines—ex Museum Cuming " and presumably this batch is the Type material for Darwin's species. Some of them were growing on a piece of coral-boulder or calcarenite and were aggregated so closely together that they were a little reminiscent of the honeycomb-like aggregations of *Chamaesipho columna*, to be described below. However, the shells of these crowded individuals did not appear, from inspection, to have coalesced as happens in similarly crowded *C. columna*.

The specimens from Papua, New Guinea, were growing on intertidal rocks, near mean tide level (fide Miss J. Bryan, who collected the first batch of specimens in this area).

Hiro (1939, p. 252) records *C. intertextus* as growing on " the under sides of rocks, together with *Octomeris brunnea* " in Formosa. Utinomi (formerly

Hiro) in his 1954 account of the cirripedes of the Tokara Islands, and Tokioka (1953) give additional ecological information about its occurrence in the mid-tidal zone (along with the pulmonate, *Siphonaria subatra* Pilsbry) where it is one of the zone-indicators, in the area of shore, below the littorinid zone and above the *Ostrea* zone.

Distribution

Australasia: Examples of *C. intertextus*, taken in this zoogeographical area, are from Idlers' Bay near Port Moresby in Papua, New Guinea, and were collected by Miss Judy Bryan. A later batch from Mr. W. Filewood confirmed that they are plentiful among the boulders there. It has not yet been taken along the northern shores of the Australian continent.

World Occurrence: *Chthamalus intertextus* is recorded from the Philippines Archipelago—(the type locality of Darwin, 1854); in the Bay of Kankamaraan on the south coast of Kangean Island, in Indonesia (N. of Java). This latter was considered a doubtful record by Hoek (1913), for it was allegedly " dredged in 22 m., from a muddy bottom ", by the Siboga Expedition. This is indeed very unlikely, because *intertextus* is an intertidal species. It is considered that there is little doubt that Hoek's identification is correct and that the general locality where it was taken is correct. However, the data about the dredging is doubtful. Other records are as follows:—Diamond Head by Pilsbry (1916, 1927), and several other localities on Oahu Island, Hawaii, recorded in collections of various museums of the world; at Kaiko, Taiwan (Formosa), by Hiro (1939); at Genka and Benoki, W. coast of Okinawa-zima, in the Ryukyu Islands by Utinomi (1954), and at Kapingamarangi Atoll, S. of the Caroline Islands, by Newman (1961). A batch, showing weathering half-way between the uneroded form (with chevron-like sutures) and extremely worn individuals in which much secondary calcification has occurred, was taken by Dr. Lane at Lolowai, Oba Island, New Hebrides, on volcanic rock. One of these is illustrated in Plate i, fig. 1. The present author has also had a single, dried shell from Fiji Islands sent to her, but the exact locality within the Fiji Islands is unknown. Gruvel (1912) has also recorded this species from several islands in the Tuamotu Group. It will thus be appreciated that *C. intertextus* ranges eastwards across the Pacific from the Philippines and Indonesian Islands to Hawaii, through the Melanesian and Micronesian Islands.

Chthamalus caudatus Pilsbry, 1916

(Plate ii, figure 4 (habitat); Text-figures 1,*e* and 3,*i-j*)

Chthamalus caudatus Pilsbry, 1916, figured; Nilsson-Cantell, 1921, figured, 1930, 1932; Hiro, 1937, figured; Endean, Kenny and Stephenson, 1956; Stephenson, Endean and Bennett, 1958; Zevina and Tarasov, 1963, figured.

Chthamalus sp. Withers, 1932.

Ecological surveys of Queensland shores revealed the widespread occurrence of *Chthamalus caudatus* along the eastern Queensland coast whereas before, it was only recorded in Australian Museum collections at Brampton Island (off Mackay) and Hayman Island. The results of these surveys, published in 1956 (Endean *et al.*) were the first literature records of *C. caudatus* as part of the Australian fauna. Later it was also found during the resurvey of Low Isles by W. Stephenson, Endean and Bennett (1958). Its somewhat atypical occurrence at Low Isles may be explained by the presence on that reef of a stand of *Rhizophora* and *Bruguiera* mangroves, for it is only on the roots and trunks of these trees that *C. caudatus* finds a suitable substrate, within the limits of its vertical range, where there is adequate shade.

Although *C. caudatus* has been adequately described and figured by Pilsbry (1916), Nilsson-Cantell (1921) and Hiro (1937), it seems desirable to append

a short description of Australian material, since they may grow to one and one-half times the size of previously recorded specimens and slight differences in structure appear with age.

Appearance and Shell Structure

In spite of a superficial resemblance in shape and colour to eroded specimens of *Chthamalus withersi* or to *Chthamalus malayensis*, *C. caudatus* is readily distinguishable by the possession of (1) zigzagged sutures between the shell plates (distal to the sheath area of the shell) and (2) a pair of caudal appendages. If the toothed sutures are not easily seen externally, they can usually be seen internally. The caudal appendages are disclosed by dissecting the soft parts away from the shell and looking between the bases of the pedicels of the cirri VI and it may be necessary to use fine needles to separate them. They are quite long.

The colour of the shell is generally a light ash grey, with wavy ledges of yellow lamina, or darker lines showing between the successive layers of the shell plates in eroded individuals (see Text-fig. 3*i*). The outer rim of the shell, however, is often a dark horny-brown and similar in colour to the shells of moderately eroded *C. withersi*. As the wavy toothed sutures may sometimes be visible only internally, it is possible to make a mistake in identification of *Chthamalus* from the high intertidal zone. The rhomboidal orifice is comparatively large; the shell is generally oval in outline or may sometimes tend towards a rectangular shape, and this is reflected in the table of measurements (Table 4), in which the carino-rostral diameter always slightly exceeds the breadth of the shell. The flattened low conical shape is reflected in the height measurements. These were taken at the carinal end since this valve is generally a little higher than the rostrum (Text-fig. 3*j*).

TABLE 4

Dimensions of Australian Chthamalus caudatus

Locality	Carino-rostral diameter in mm.	Breadth of shell in mm.	Height in mm.
Point Vernon, South Queensland	12·0	10·5	2·5
,,	10·5	8·5	2·4
,,	12·1	11·5	2·2
Curtis Island, Q'ld.	15·0	10·0	2·4
,,	13·3	13·0	2·5
Low Isles, Queensland	13·1	12·0	2·9
,,	15·0	12·0*	3·3
Cockatoo Island, Yampi Sound, W.A.	6·0	5·5	2·0
,,	6·5	5·1	2·0

* Growth laterally distorted by crowding.

In larger-sized barnacles, the outer margins of the shell plates often form a broad flange-like area round the central cavity which rarely extends beyond the immediate area, roofed by the opercular plates. On the lower surface of this flanged area, the edges of the alae may thicken and grow downwards towards the basis forming wavy, butress-like structures running from the lower edge of the sheath to the circumference of the shell. Similar structures in *C. depressus* (Poli) have been described by Utinomi (1959, p. 393).

Internally the shell colour is either a dark purplish-grey or light brown, while the soft body is light coloured with the cirri greyish. There are patches of dark pigment round the bases of the spines on each segment. Developing larvae are a creamy yellow. The sheath passes insensibly into the lower part of the parietes. The basis is dark, often black, and completely membranous.

The shell plates are fairly smooth externally and show little trace of ribs or folds even near their outer margins. There is also little trace of radii externally but the alae of the carina and rostrum are especially well developed. The carina was taller than the rostrum in all specimens measured.

Opercular Valves

There is considerably more sculpturing in the opercular valves of well-grown Australian *C. caudatus* than is shown in Pilsbry (1916, Plate 73, figs 1–1*a*). In an uneroded barnacle, lines of growth are prominent on both the scuta and terga and the layers of yellow lamina alternate with the layers of calcareous matter.

The *scutum* has a longitudinal fold from the apex to the basal margin externally and the tergum may have pits shaped like inverted " V "s near their apices, for the reception of the tip of the scuta. However, most specimens are too greatly eroded to show these structures. Instead, the well-marked articular ridges and furrows between the scuta and terga are clearly to be seen and a central, wide groove appears between the two scuta formed by the inflected occludent margins. The darker coloured, underlying layers of the scuta and terga may show through where the ash-grey shell matter has been eroded.

Internally the scutum is often yellow centrally, with a dark purplish margin bordering the valve and there may be some pitting. The incurved basi-scutal margin forms a small pit for attachment of the lateral depressor muscles. The pit for the adductor muscle is clearly defined but has little suggestion of a ridge below it.

The *tergum* is generally darker internally than the scutum and is wider above the articular furrow. There are a variable number of rather irregular crests (five or more) for the attachment of the tergal depressor muscles and they project quite noticeably below the basal margin. Internally a deep, narrow groove runs longitudinally down the centre of the tergum but does not extend right to the apex, though in larger barnacles it may reach the basi-scutal angle. In a *C. caudatus* with a carino-rostral diameter of 6·5 mm. a groove is beginning to develop, whereas in one with diameter 12·1, it is a marked feature of the shell. The articular furrow is well developed.

Soft Body

The most interesting feature of *C. caudatus* is the pair of long, slender caudal appendages, a feature not recorded in any other species in the genus.

Trophi

The *labrum*, when viewed from in front, has a distinctive, flattened, semi-circular process above the palps, somewhat similar to that in *C. intertextus*. The anterior surface of the groove of the labrum carries numerous triangular denticles along its whole length and there are numerous fine hairs, especially in a central area above the denticles. The semi-circular funnel-like projection is well provided with muscles. *Palps.*—The long bristles of the upper anterior corners of the two palps overlap slightly centrally. The palps are clavate and are as illustrated by Nilsson-Cantell (1921, Text-fig. 57*a*) but the Australian specimens tend to have many more bristles than are shown in his illustration. The *mandible* has three main teeth without secondary side-teeth on them and a pectinated lower angle in which the second spine from the lower angle is longest and the 8 or so spines above it are nearly equal and similar in size to the lowest one. There is little or no variation from Pilsbry's illustration (1916, fig. 92*c*). *Maxilla I* has two distinct notches anteriorly so that the spines are divided into three groups. Its shape and the arrangement of the spines are closely similar in Australian specimens to Pilsbry's drawing (1916, fig. 92*b*). The only difference seen in the Australian material is the presence of three pairs

of shorter spines situated immediately below the two large upper spines above the upper notch ; and the presence of a series of fine hairs along its lower border. *Maxilla II* has a wide notch, free of spines, and is very similar in shape to that depicted by Nilsson-Cantell (1921, Text-fig. 57*b*) except that larger Australian specimens tend to have more long bristles along the straightish lower border (Nilsson-Cantell's figure is reversed and shows the lower border, above). Viewed from in front, before dissection, *C. caudatus* has a pronounced " beard " hanging from the two maxillae II.

Cirri

In *cirrus I* the rami were unequal, the anterior one being longer and stouter than the posterior one (segmental numbers of the order of 8 and 6 segments respectively were found or, in a small specimen of 6·5 mm. diameter, from Yampi Sound, Western Australia, 7 and 5). The more distal segments had pinnate spines in addition to ordinary setae. The shape of *cirrus II* apparently changes with increase in size. A small Yampi Sound specimen had the anterior ramus slightly longer and certainly stouter than the posterior one, as in cirrus I, although the numbers of segments in the two rami were almost equal, e.g. 7 or 8 anteriorly and 8 posteriorly. In a larger individual the posterior ramus was longer and slightly narrower than the anterior one and this was reflected in the segmental count of 8 (anterior) and 11 (posterior). A still larger specimen showed a tendency for the posterior ramus to grow even longer. Again, there are some finely pinnate long spines on some segments of the anterior ramus (Text-fig. 1*e*) but no trace was found of the short stout pectinate spines of the type found in some other species in the genus. *Cirrus III* had sub-equal rami and frequently equal numbers of segments, ranging from 13 to 18, in the material examined. Segments of both rami were found to carry 3 or 4 pairs of longer spines—often 3 pairs on the anterior one and 4 on the posterior but this was not invariable. *Cirri IV*, *V* and *VI* each had sub-equal rami and the numbers of segments of the anterior and posterior rami were nearly always equal, except where there was evidence of damage and regeneration. There were generally 4 pairs of spines on each segment of the anterior ramus and sometimes 5 pairs on the segments of the posterior ramus of the same cirrus. The two smaller pairs of spines are only seen under high magnifications.

The *penis* was moderately long (longer than cirrus VI even when slightly contracted). It had a ringed appearance which was more pronounced when it was greatly contracted. Distally it was not ringed and carried scattered hairs along its length, with two tufts of fine hairs at its tip.

The *caudal appendage* is generally long, thin, and at least half as long as cirrus VI or slightly more. At the junction between segments a series of fine and, in some cases, long hairs ring the segments. Each segment generally has a central, dark cross-marking on it. In a small specimen of 6·5 mm. carino-rostral diameter there were 17 or 18 segments in its caudal appendages, whereas one with the diameter of 12·0 mm. had 22 or 23 segments. Pilsbry's type specimen (U.S. National Museum 48087) is intermediate both in size and number of segments in its caudal appendage, so that it would appear that the number of segments in the caudal appendage increases proportionately with shell growth.

Habitat

The occurrence of *C. caudatus*, within its geographical range, depends on the presence of adequately shaded areas in the upper intertidal zone. Its vertical range in Queensland is from mean high water (occasionally it may occur higher where conditions are particularly favourable for its settlement) down to approximately mean low water level. Its range thus overlaps those of *Chthamalus withersi* and *Chthamalus malayensis* but these species can grow fully exposed on the rocks whereas *C. caudatus* tends to be cryptic in habit.

Distribution

Australian : Along the eastern coast of Queensland where suitable habitat conditions prevail, from Point Vernon (near Great Sandy Island) in the south, northwards along the mainland coast and on the high islands inside the Great Barrier Reef to Port Douglas in the north. Collecting ends at this point on the Queensland coast and it is likely that *C. caudatus* occurs right up the rocky coast and round into Torres Strait. It also is recorded in the north of Western Australia at Yampi Sound, on Cockatoo Island. No organized barnacle collecting has been done east of this point towards Cape York. The absence of records for this species in this area at present is therefore of little significance. Withers (1932) recorded a species of *Chthamalus* as a sub-fossil in beach rock from Magnetic Island, Queensland. It was found on examination to be *C. caudatus*.

Extra-Australian Records : A few sporadic records of *C. caudatus* occur in most areas of the Indo-Malayan Archipelago as follows :—Catabalonga, Samar Island in the Philippines (Pilsbry, 1916) ; West coast of Sumatra and at Pisang Island (opposite Maccluer Gulf) in West Irian (botn records by Nilsson-Cantell 1921 and 1930 respectively) ; the South China Sea (Zevina and Tarasov, 1963) ; and Arakabyu Island in the Palao Islands (Hiro, 1937).

Chthamalus withersi Pilsbry, 1916

(Plate ii, figures 1, 2, 5 ; Text-figures 1,*d* and 3,*e–h*).

Chthamalus withersi Pilsbry, 1916, figured ; Nilsson-Cantell, 1921, figured, 1930, 1932, 1938 ; Broch, 1931, listed only ; Hiro, 1937, figured ; Kolosváry, 1941 ; Endean, Kenny and Stephenson, 1956 ; Endean, Stephenson and Kenny, 1956 ; Zevina and Tarasov, 1963, figured ; Southward, 1964.

? *Chthamalus rhizophorae* de Oliveira, 1940, figured, 1941, figured.

Having examined the Type of specimens of Pilbry's *Chthamalus withersi* (U.S. National Museum Number 48088 which included a Holotype and a series of paratypes), it is obvious that his original (1916) description was based on juvenile specimens. Now that a large series of *C. withersi* from Australia, and the islands to the north of it, have been examined, it is necessary to emend his description to include characters not usually evident in the barnacles until the full adult size is reached. Some hint of the changes seen in larger specimens was given by Nilsson-Cantell (1921, p. 296) who examined a specimen with a carino-rostral diameter of 13·0 mm., whereas Pilsbry's largest had measured 9·5 mm. in diameter. The collections examined by the author have, in addition to the many small specimens with size ranges similar to those handled by Pilsbry, many barnacles of large size, ranging in carino-rostral diameter from 10·0 mm. to 21·0 mm. The largest specimens were collected by the Dutch Snellius Expedition of 1929–30 on mangroves, at various points in the Celebes and other nearby islands.

The largest Australian *C. withersi* seen so far also occur on mangroves, in the Cairns district, Queensland. Here specimens of up to 16·5 mm. carino-rostral diameter were taken by the author and careful searching would no doubt, have revealed even larger specimens in the area.

Many details of occurrence, population size, interspecific reaction to a second *Chthamalus* species (*C. malayensis*), and its environmental preferences in Queensland are described in the two papers recording the ecological surveys of Endean *et al.* (1956). It is extremely common on the upper parts of wharf and bridge piling and on the roots and lower trunks of the red mangrove, *Rhizophora*, in Queensland as may be seen in Plate ii, fig. 1, 2, 5.

When the structures of full-grown *C. withersi*, newly recorded below, are taken into account, the Brazilian species *Chthamalus rhizophorae* de Oliveira (1940 and 1941) is found to resemble it extremely closely. The South American

species also occurs on mangroves and has, so far, only been recorded in the vicinity of Rio de Janeiro, a port. The possibility of its having been transported by shipping from the Indo-Malayan area cannot altogether be ruled out, especially as *C. withersi* may be regarded, in Queensland at least, as a fouling species on wharf piles and therefore capable of being transferred to, and transported by, shipping.

The author has unfortunately not been able to examine de Oliveira's type material, lodged in the Instituto Oswaldo Cruz, but has examined specimens from Cananeia (Brazil, near latitude 25° S.), identified as *C. rhizophorae* by Dora P. Henry, in the collections of the U.S. National Museum, Washington D.C. (Number 101193). A large example of these, with a carino-rostral diameter of 20 mm., was so similar in shell structure to the largest *C. withersi* in the present Australian series, that it is suggested that *C. rhizophorae* de Oliveira may have to be synonymized with *C. withersi* Pilsbry. The soft body parts were not, however, available for dissection. In the absence till now in literature of a description of fully-grown *C. withersi*, de Oliveira's erection of a new species for his South American material was logical and it will remain to be seen if the new African species of Stubbings (the description of which is said by Southward to be in press) is indeed new or whether it is in fact *C. rhizophorae* or *C. withersi*.

Pilsbry's description, with additions by Nilsson-Cantell (1921), is adequate for the general run of *C. withersi* material collected on coastal rocks and wharf piles on the east coast of northern Queensland and at Darwin, Northern Territory (no organized barnacle collecting has been done between these two areas), but their accounts are inadequate for specimens which have reached full maturity (carino-rostral diameter 15·0 mm. upwards). Transitional stages during growth show gradual development of the structures present in fully adult barnacles, so that any lingering doubts as to the inclusion of the largest specimens in *C. withersi* Pilsbry are dispelled.

Emended description of C. withersi *Pilsbry*, 1916

Table 5 sets out a series of shell measurements of *C. withersi* of varying sizes, ranging from 10·0 mm. to 21·0 mm. carino-rostral diameter.

It is clear from this table that Pilsbry's material was far from full grown. It should also be mentioned, that evidence of breeding is by no means a criterion of full maturity in this species.

Appearance and Shell Structure

Chthamalus withersi has a much flattened conical shape; the basis is generally sub-circular and wavy in outline, as shown in Text-fig. 3,*e*,*f*. The carino-rostral diameter is in general slightly greater than the width of the shell. The shell tends also to be slightly narrower towards its scutal end, when growth has been unrestricted. The general colour may vary from cinnamon brown (uneroded or juveniles) to ash grey in adults.

In *C. withersi*, growing on mangroves, the outer layer of bark may appear to " ride up " over the shell rim, as though the growing shell were ploughing into it. However, in full-grown specimens this effect is rarely seen and the barnacle appears to be attached, in the normal way, on top of the bark.

The shell tends to be slightly higher towards the rostral end, but this is not invariable. The smooth shell plates are articulated very loosely, even when the shell is more than 12 mm. in diameter, and this applies to the opercular valves also which, when eroded, never display the capital psi (Ψ)-shaped articulation pattern seen in so many other species of *Chthamalus*. This is rather unusual in a genus in which the scuta and terga are so often interlocked strongly together. Worn shells show a comparatively straight line of articulation between the scuta and terga.

Older *C. withersi* may show low, poorly developed regular folds or ribs, while juveniles show broad wavy folds, often visible only towards the outer dark rim where growth is active and the shell is not yet eroded. Radii on the shell plates cannot be seen externally, but in larger shells the alae of the carinal and lateral valves are markedly developed.

The orifice is moderately large in full-grown specimens and almost diamond-shaped. In medium-sized and smaller individuals it tends to be rhomboidal in outline, with the scutal angle somewhat rounded. Often 4 or 2 small projecting white teeth occur where the summits of the lateral and rostrolateral valves project slightly into the orifice. Internally these tooth-areas are white, as opposed to the usual purple-grey or brown colour of the rest of the interior of the shell. Sometimes the whole inner shell is white but even in these the tooth-section is still distinguishable from the rest. The teeth usually mark

TABLE 5

Shell measurements of C. withersi

Locality	Carino-rostral diameter in mm.	Width of shell at right angles to carino-rostral in mm.	Height of shell at the rostrum in mm.
Halfmoon B., near Cairns, Queensland, Australia	10·0	8·0	2·1
,,	15·1	14·0	4·5
,,	16·0	15·0	3·6
,,	16·5	16·3	5·4
Darwin, Northern Territory, Australia	11·0	10·0	1·5
,,	11·0	10·0	3·0
,,	14·0	12·0	3·9
Mamudja, Celebes, Indonesia	15·4	13·6	3·5
,,	16·0	14·9	4·9
,,	17·0 (This diameter " distorted " by crowding)	18·4	5·0
,,	19·9	16·0	5·0
,,	21·0	19·0	5·0

the summits of light-coloured stripes on the lateral and rostrolateral plates. These four light stripes show best in uneroded, cinnamon-coloured individuals but, while rarely evident in large eroded, grey-coloured specimens, the four white tooth-patches still generally show internally.

Pilsbry (1916, Plate 73, fig. 2*e*) describes and figures the internal surface of a rostrolateral compartment showing a sunken oval pit or callus below the white summit of the valve. Such are indeed common in *C. withersi*, occurring even in juveniles. As growth proceeds, however, a second and even more distinct pit may appear on each lateral valve also (see Text-fig. 3,*g*,*h*). Sometimes the largest individuals show pits only on the laterals, those of the rostrolaterals tending to be filled up, at maturity. This seems most marked when the sideways growth of the rostrolateral valves is restricted. Perhaps these pits are associated with breeding in some way, by providing additional room for brooding developing nauplii.

Scutum and Tergum

In Australian specimens up to 10 mm. in carino-rostral diameter, the opercular valves have few outstanding characters. There are, however, generally considerably more structures than shown in the illustrations of

Pilsbry (1916, Plate 73, figs. 2*a*–2*d*) and Hiro (1937, fig. 4*h*, *i*). There is an oval pit for attachment of the adductor muscles, shallow but quite discernible; and a small, outwardly-curved surface with an extremely shallow pit on it, near the basitergal corner of the scutum, where part of the lateral depressor muscle is attached. The scutum becomes quite thick and strong in mature individuals. The occludent margin always seems to be thickened and rolled inwards, as shown by Pilsbry. In no specimen, however mature, was the articular ridge or furrow ever developed to form anything more than a shallow wavy fold and trough where it articulates with the tergum. It does not interlock strongly like the pieces of a jigsaw puzzle, as happens in most other species of *Chthamalus*. The articular ridge and furrow of *C. withersi* is more pronounced in juveniles than in mature specimens which is unusual. In some uneroded specimens there may be a light stripe on the tergum, parallel with the scutal margin. The tergum is distinctive among species of *Chthamalus* found in Australia in that it is nearly triangular, with the scutal and basal margins nearly equal and both much longer than the carinal one. The basal margin is slightly sinuous in well-grown individuals and, although there is a slightly convex curve towards the basiscutal corner, it cannot be regarded as a spur. The interior of the valve in adults is white and grey or purplish-grey and is generally somewhat fretted and pitted, parallel to the margins. Along the scutal and carinal border the inturned edges tend to become thickened and to grow almost at right angles to the main plane of the valve. This is especially true for the scutal margin, with the result that the tergum has a deep V-shaped furrow along its length. The number of crests for the attachment of the depressor muscles is amazingly constant throughout the size range, being four, unless the valve has been damaged. Externally, if uneroded, simple lines of growth may be seen on both scutum and tergum and, in juveniles, traces of a hairy outer lamina may persist.

Soft Body

As in many chthamalids the animal body is very much smaller than the shell-size would suggest. The tergo-scutal flaps are brown, but most of the soft body is a pale creamy brown except for the following darkened areas :— the outer sides of cirri I and II, the pedicels of cirri III to VI which are darkened on their inner sides. The proximal part of the penis and a ring round the mouth opening are also darker, and patches of dark pigment occur on the segments of the rami of cirri III to VI round the bases of the spines. The mouth-ring is made up of a broad, darkened band along the arched groove of the labrum and the outer ends of the trophi—especially the tips of the second maxilla which form the lower arc of the circle. However, the colour fades fairly rapidly in mounted specimens. One specimen from Mamudju, Celebes, taken in August 1929 by the Dutch Snellius Expedition, had large developing embryos which were bright yellow. The basis is wholly membranous.

Trophi

The *labrum* is in general somewhat flattened anteriorly and semi-circular shaped above the palps, not truly bullate but not as distinctly channelled towards the shallow U-shaped groove above the mouth, as in *C. intertextus*. This groove is bridged across by a straight, clear chitinous structure which carries at its centre a row of 28 or so peg-like teeth. Neither Pilsbry's nor Nilsson-Cantell's illustrations show the structure of the labrum as it appears in specimens examined from various Australian localities or from the Celebes, Indonesia. It would appear that Pilsbry's drawing (1916, fig. 91D) was made from below, so that the normal U-shaped groove above the teeth and the flattened front of the upper part of the labrum were obscured, while Nilsson-Cantell's (1921, Text-fig. 51*a*) fails to show the straight surface from which the teeth arise. Australian specimens also show several triangular denticles on either side of

the peg-like teeth, in well-grown specimens, but their size and number seem to depend on the size of the barnacle. In a medium-sized specimen from Mamudju, Celebes, up to six denticles occurred beside, and at a higher level than, the central peg-like ones. There is also a fringe of hairs above the teeth, which are seen even in smaller specimens. The palps are basically the same as shown in Nilsson-Cantell's drawing (1921, Text-fig. 51*b*) except that the lower anterior corner is generally slightly more rounded and there are considerably more bristles on it. Their arrangement is, however, correctly depicted by him, with longest bristles on the lower anterior part getting progressively shorter towards the upper border and along the upper margin. *Mandible.*—There is variation in the number of major teeth on the mandible, from 3 to 4 being the usual range, though the latter number is encountered only in very large specimens and then only occasionally. The most frequent count for the large teeth is 3, as stated by Pilsbry. However, several specimens from the Celebes and Northern Queensland had 4 teeth. In one individual from Mamudju in the Celebes, with an estimated carino-rostral diameter of 20–21 mm. (shell damaged slightly), the mandibles had 3 large teeth on one side and 4 on the other. In the latter, the 4th large tooth had obviously been derived by the enlargement of the uppermost denticle of the pectinated lower angle. A smaller individual, from Darwin, Australia, was found to have mandibles with 2 and 3 large teeth on the right and left sides, respectively. It would appear from this evidence, that the numbers of large teeth on the mandible is not definitive in *C. withersi* until the animal is fully grown. However, the majority of specimens of this species will be found to have 3 large teeth on the mandible. *Maxilla I* has its spines most distinctly divided into 3 groups by two well-marked notches. In the upper group two large, strong spines are followed below by two pairs of small spines, above a U-shaped notch. The central group of medium-sized spines comprises 6–8 pairs, arising from the edge of the jaw which is usually fairly straight in this section of maxilla I—not curved as in the lobes above and below it. Below them is generally a V-shaped notch. The lower, protuberant corner of maxilla I carries from 5 to 6 pairs of small spines, comparable in size with those situated just above the upper notch. This structure is substantially the same as was described and figured by Pilsbry (1916, fig. 91*c*) and the only character noted in the present material, not figured by him, is the distinct fringe of hairs near the outer tip of the lower margin. *Maxilla II* has not been figured and Nilsson-Cantell's description (1921, p. 296) does not mention the large number of bristles present on the anterior or free border above and below the wide, shallow notch. There is also a dense patch of rather long bristles arising low down on the outer side of the organ.

Cirri

The first two cirri are short and darker in colour than the remainder. Cirrus I has its rami strongly incurved towards the mid-line, so that its effective sweeping action is almost at right angles to that of Cirri III–VI. Several of the more distal segments and the terminal segments of both *Cirri I* and *II* carry numerous pinnate setae, the structure of which is shown in Text-fig. 1*d*. They are especially numerous and clumped along the inner sides of the rami where their felted mass forms an efficient straining organ for food catching. In many of the preserved specimens, almost every fine side-hair on the pinnate spines had a particle entangled with it, so as to give the spines a knobbed, rather than a plumose, appearance. It was at first thought that *C. withersi* possessed spines intermediate in structure between pinnate and the lanceolate spines seen in *C. challengeri* or *C. antennatus*. However, in individuals free from entangled food particles, they were found to be merely normal pinnate spines, the combined effect of which was to serve a function similar to that of gill-rakers in fish. In cirrus I the anterior ramus is longer by at least two

of its segments and considerably stouter than the posterior one. The number of segments in younger individuals is generally less than in older ones, with 7 in the anterior and 6 in the posterior ramus while fully-grown specimens tend to have 8 or 9 segments in both rami. Often segmental numbers vary from right to left side in the same animal, so that too much importance should not be attached to them diagnostically. *Cirrus II* is similar in general structure to *I*, with the anterior ramus slightly longer than the posterior one, but only a little wider. The numbers of segments in the two rami tend towards equality in full-grown specimens, while in younger ones the anterior ramus may contain one segment more than the posterior one, e.g. 7 to 8 segments in the anterior and 6 to 7 in the posterior one. A large specimen from Mamudju, Celebes, had 9 segments on the left anterior ramus and 8 on the right, while both posterior rami contained 8 segments. Several individuals had 8 segments in both rami and this seems to be the full adult number, where no regeneration has occurred. *Cirri III–VI* are similar in structure, long and curled but *III* is somewhat shorter than the remaining three pairs. Their rami are subequal both in length and in the number of component segments of any one pair. Anteriorly each cirral segment has a dark, pigmented area round the bases of the three pairs of large spines arising there. Careful search, over a series of specimens of varying sizes, failed to find any individual with more or less than three pairs of large spines on the more central segments of the rami. However, Nilsson-Cantell's record of occasional cases of 4 pairs of spines (1921, p. 296) cannot be disregarded, in view of the variation from 3 to 4 teeth on the mandibles seen in present specimens. The *penis* is moderately long, dark proximally and ringed, with scattered fine hairs along its distal section. There are small tufts of hairs above and below the opening, on its tip. There is no *caudal appendage.*

The discovery, in well-grown *C. withersi*, of occasional specimens in which there are 4 major teeth on the mandible raises the question whether this species should still be associated with the *hembeli*-complex of species of genus *Chthamalus*, all of which have 3 major teeth on their mandibles. However, a review of other features of *C. withersi*, and other species associated with the *hembeli* group, shows that it has the characteristic pectinated lower angle to its mandible, with the largest denticle at, or near, the tip ; there is no trace of the comb-like groups of spines as seen in the species belonging to the *stellatus*-complex ; it mostly has only 3 major teeth on the upper part of the mandible (only occasionally 4) ; the distal segments of cirrus II have no stout, toothed lanceolate spines. Instead there are numerous fine, pinnate spines on both cirrus I and II. The balance is thus heavily in favour of retaining *withersi* in the *hembeli* group, though it shows certain characteristics that place it in a somewhat intermediate position between these major sub-groups of the genus.

Habitat

Chthamalus withersi grows attached to intertidal rocks, wharf piles and Red Mangroves in the highest intertidal area in tropical eastern Australia (Plate ii, figs 1, 2, 5). On rocks exposed to full sunlight, it tends to survive only in crevices or areas of slight shade ; however, in the shaded areas of wharf piles and on mangrove trees it reaches not only its largest size but also its greatest density of population (see Plate ii, figs 2, 5). In Australia its vertical range is from a little below the high water mark of spring tides down to the level of high water neap tides or even mean sea level (Endean, Kenny and Stephenson, 1956). It is tolerant to considerable fluctuations in the salinity and conditions of considerable turbidity in the seawater.

Distribution

Australian : Along the east coast of Queensland from Hervey Bay (near Great Sandy Island) in the south, northwards right up the Queensland mainland

coast (as opposed to the Great Barrier Reef itself) to Cooktown. It also occurs at Mandorah, near Darwin, Northern Territory. Between these two last localities no systematic barnacle collecting has yet been done but its presence there is likely. On the other hand, the absence of records of *C. withersi* from Yampi Sound in Western Australia, westward to Carnarvon and thence to Shark Bay, is probably significant, since collections have been made along this coast, at the author's request, by trained collectors who were specially looking for it and who found its niche on the mangroves occupied by another species of *Chthamalus*, namely *C. malayensis*.

World Occurrence: The locality of the Type is "from a reef opposite Cebu Philippine Islands", Pilsbry (1916). It has also been recorded at Tjillatjap, Java; Billiton, two new records from the Celebes area came from collections made by the Dutch Snellius Expedition, 1929, from Maratoea (N.E. Borneo) and Mamudju (Celebes) in Indonesia. It also occurs at Pisang Island (opposite Maccluer Gulf in W. New Guinea); Baie van Dampelas, west coast of Celebes; Chandipur, E. Pakistan; Bombay (in a collection sent to the author for identification by Y. M. Bhatt of Bombay University), Thana (near Bombay), Balasore, Orissa and Port Canningall in India; Elphinstone Island and Port Maria, Mergui Archipelago. Other than the specimens from Bombay, the other records above occur in the writings of Nilsson-Cantell (1921, 1930, 1938). Additional records are Mandarai Pier, Kororu Island, in the Palao Islands (Hiro, 1937); the South China Sea (Zevina and Tarasov, 1963) and the following records are taken from museum collections :—on bark of mangroves, near Old Panama; taken during the Pinchot Expedition of 1929 and identified by H. A. Pilsbry. This identification was confirmed by the author, in 1963, at the Academy of Natural Sciences, Philadelphia, Penn., U.S.A. (This record near the Panama Canal suggests a possible route of introduction of *C. rhizophorae* de Oliveira ? = *C. withersi* to Brazil.) Further records are from Kei Islands, Arafura Sea; and as *Chthamalus rhizophorae* de Oliveira, by Dora P. Henry at Cananeia, Brazil (in U.S. National Museum, No. 101193, U.S. National Museum, Washington, D.C.).

It is thus the most widely ranging of species in the genus *Chthamalus*, occurring in Australia.

Chthamalus antennatus Darwin, 1854

(Plate i, fig. 4, Plate ii, fig. 7 (ringed specimen) and Text-figs 1,*h*; 4,*a-g*)

Chthamalus antennatus Darwin, 1854, illustrated; Weltner, 1897; Gruvel, 1905, illustrated; Broch, 1922, illustrated; Pope, 1945, illustrated; Dakin, Bennett and Pope, 1948, 1952; Bennett and Pope, 1953, 1960; Endean, Kenny and Stephenson, 1956; Womersley and Edmonds, 1958, illustrated; Wisely and Blick, 1964.

Chthamalus antennatus was originally described by Darwin (1954, with the shell illustrated in Plate XVIII, fig. 2, and Cirrus III on Plate XXIX, fig. 3—*nec* "fig. 2" as given on page 460 of his text); by Nilsson-Cantell (1921, 1926, both illustrated); Broch (1922, illustrated) and by Pope (1945, illustrated). Ecological and distributional data are available in the following accounts; Dakin, Bennett and Pope (1948, 1952), Bennett and Pope (1953, 1960), Endean, Kenny and Stephenson (1956), and Womersley and Edmonds (1958) and information on the breeding period has recently been published by Wisely and Blick (1964).

Careful investigations of collections housed in a number of European Museums has shown that the following records of *C. antennatus* are based on misidentifications :—in Chile (Gruvel, 1905); at Amanu Is. in the Tuamotu Group (Gruvel, 1912); at Santander, Spain (Gruvel, 1920) and at Broome in north Western Australia (Broch, 1916).

Obvious misidentifications of Indomalayan and Pacific species of *Chthamalus* are fairly common in literature prior to Pilsbry's 1916 Bulletin. Early records

of *C. antennatus* in Chile, Patagonia, Spain and the Tuamotus Group are due to misidentifications. Some characters which, in the keys given by previous authors, would appear to be unique to certain species often are not so, and may occur in several species, e.g. the long outer ramus on cirrus III occurs, for instance, in *C. antennatus* and *C. cirratus* (Chile and Peru). Again, juveniles or young of *C. antennatus* and *C. malayensis* and other species with 4-toothed mandibles often appear superficially very alike, so that records of *C. stellatus*, *C. malayensis* and even *C. challengeri* have often been confused with the present species. In view of this, and of current interest in the genus *Chthamalus* and the forthcoming regrouping of species by Zullo, some further anatomical details are given, since this endemic Australian species is little known abroad.

Description

Chthamalus antennatus is one of the more heavily built and larger species in the genus, although much smaller than either *C. hembeli* and *C. calcareobasis*. Whilst the basal area of *C. antennatus* may be no greater than that of several other Australian species in the genus its walls rise fairly steeply, practically from the circumference, and its shape is that of a truncated cone. There is no tendency to develop a flattened flange round a centrally raised area, as seen in large *C. caudatus* or *C. withersi*. This accounts for its more massive appearance and the larger soft body within the shell.

Table 6 gives the measurements of 20 well-grown specimens, taken from localities noted for exposure to heavy wave action. Crowding is seen to cause exaggerated upward growth so that a tubular shell is formed, with the summits of the rostro-laterals tending to form small " teeth " projecting into the orifice. If growth is unrestricted the shell tends to have its length and width sub-equal, and erosion of the tops of the shell valves may result in the formation of highly polished areas resembling ivory. Inside, the shell is generally smooth, flesh pink in colour and rarely pitted. The shell plates are very strongly articulated by overlapping radii and alae which are not toothed but which may show distinct lines of growth.

Darwin's original account is so detailed and accurate that little need be added except to clarify the characters needed to determine species within the *stellatus*-complex. Text-figures 1,*h* and 4,*a-g* illustrate the more important features distinguishing *C. antennatus* from its nearer relatives.

Maximum sized specimens in the present series exceed the largest, so far described, by 3·2 mm. in the carino-rostral diameter. However, there seems to be no further modification of features described by Darwin in these larger animals. However, some comment is called for on the fact that, while Pilsbry (1916, p. 296) placed *C. antennatus* in the group, later characterized as the *hembeli*-group by Nilsson-Cantell (1921), the latter author and Broch (1922, p. 306) both placed it correctly in the *stellatus*-complex of genus *Chthamalus*. Examination of large series has shown that most individuals have the mandible similar to the illustration in Broch (1922, fig. 51*a*)—a typically *stellatus* pattern of mandible. However, several large individuals in tubular shaped shells or ones where the lower tip of the mandible had been damaged and was in process of regenerating had mandibles in which the lower angle was coarsely pectinated and had no clearly defined, comb-like section between the lower tip of the jaw and the lowest major teeth. They were thus somewhat intermediate in structure between a typical *hembeli* and a typical *stellatus* mandible. They have been commented on by Darwin in his original description. Other shell and body characters, however, definitely align *C. antennatus* with the *stellatus* group of species, even in those which have atypical lower tips to the mandible.

Opercular Valves

Darwin's dismissal of the opercular valves as being " hardly distinguishable from those of *C. stellatus* " has encouraged certain of the misidentifications,

such as that of Broch (1916, p. 14). Broch's specimens were examined at the Stockholm Naturhistoriska Riksmuseet (Registered No. 278) and found to be juveniles of *C. malayensis*.

The first illustration of opercular valves was published by Nilsson-Cantell (1926, Text-fig. 3) and shows few definite characters, apart from the two crests on the tergum for the attachment of the depressor muscles. Text-fig. 4,*d* and *e*, shows the opercular valves of a well-grown individual. The scutum is smooth internally and but little sculptured in comparison with *C. malayensis*, but it shows two incipient crests within the depression for attachment of the lateral

TABLE 6

Measurements of 20 *well-grown* C. antennatus *from very exposed habitats*

Locality	Carino-rostral diameter in mm.	Width at right angles to carino-rostral diam. in mm.	Height at tallest part of shell in mm.	Remarks
Harbord, Sydney, New South Wales. 19.xi.1964	9·5	9·5	3·5	" Normal " shape not restricted by crowding
	11·0	11·0	4·9	
	11·6	12·3	3·5	
	12·8	14·0	3·5	
	13·5	11·2	3·6	
	15·0	15·2	5·0	Crowded ; tall
	15·0	15·0	5·9	
	16·0	17·4	5·3	Normal shape
	16·0	18·0	5·5	
	18·5	16·0	5·0	
Eucla, Great Australian Bight, Western Australia	8·4	7·4	5·3	On a limpet shell
	10·0	10·0	9·0	Tall, tubular form owing to crowding. Tendency to have toothed orifice
	10·5	9·3	10·5	
	12·0	11·5	7·0	Distorted. Average height for species should be nearer 4·5–5·0 mm. for shells of this size.
	13·0	9·6	6·5	
Cape Forestier, S.E. Tasmania	11·0	10·5	4·5	Normal shape
	12·0	12·0	6·0	
	15·5	15·0	6·7	
	16·0	16·1	5·7	
	18·8	19·0	9·5	Grown in restricted space. Tall form

depressor muscles. The broad tergum has generally two crests for attachment of its depressor muscles. Although more than 300 specimens have been examined from areas throughout its geographical range, none has been seen with three complete crests—two is the normal complement or at the most (and only occasionally) two crests plus a small rudimentary " half-crest " may be found. Other species in the *stellatus*-complex generally have four or more crests on the tergum or, on rare occasions, three crests plus a rudimentary " half-crest ".

Soft Body

The soft body is larger than in other Australian species of *Chthamalus*.

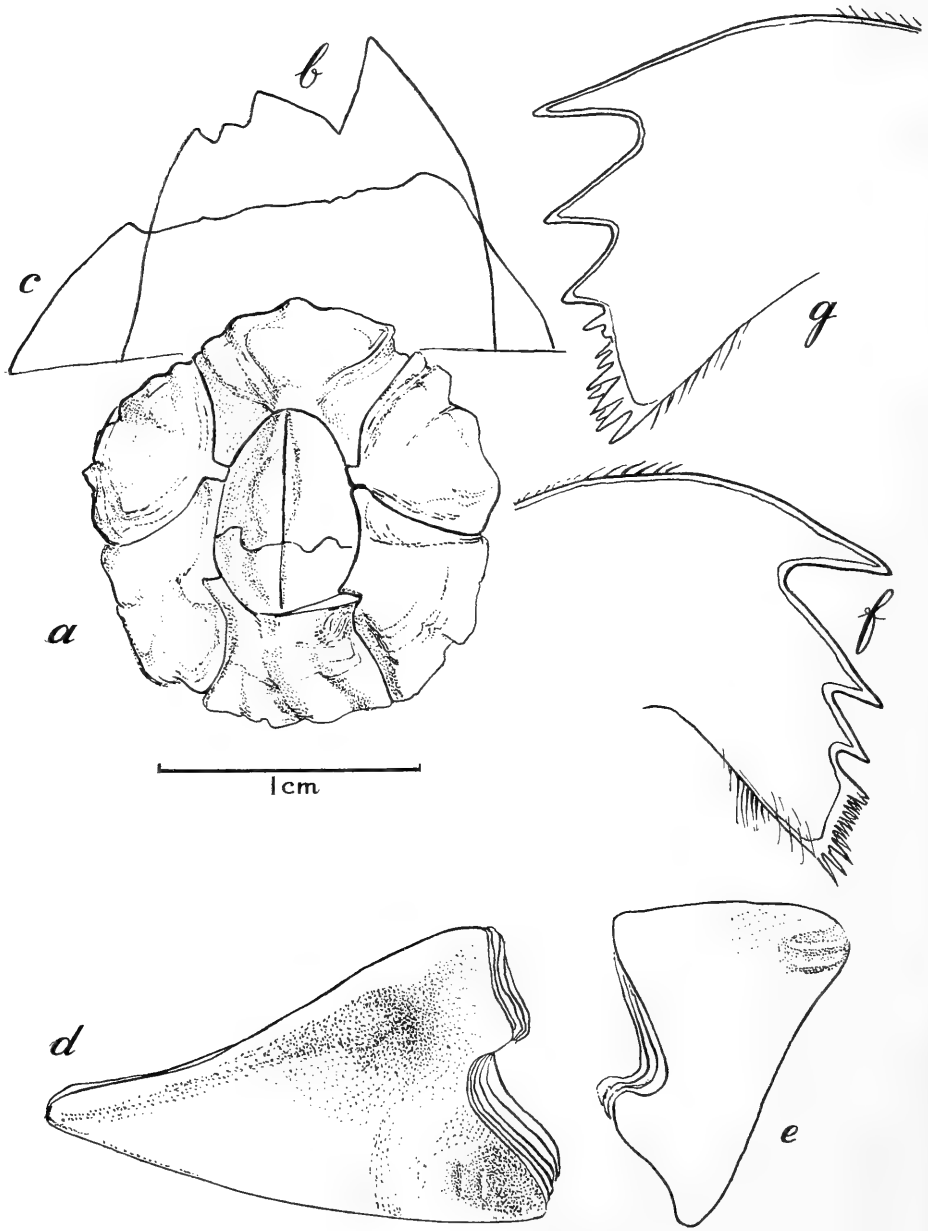

Fig. 4. *Chthamalus antennatus*. (*a*) Whole shell of a large and moderately eroded individual ; (*b-c*) side views in silhouette of (*b*) " tall " form resulting from crowding during growth and (*c*) more " normal " form ; (*d*) scutum, interior view, showing comparative featurelessness of valve except for two incipient crests within the well-marked depression for attachment of the lateral depressor muscles ; (*e*) tergum, interior view, with two prominent crests for depressor muscles ; (*f*) a normally shaped mandible, with a short comb-like section composed of coarse spinelets in its lower section ; (*g*) regenerating mandible after damage to lower tip (the pair of (*f*) but drawn to a slightly larger scale), showing the coarsely pectinate (*hembeli*-stage) through which the *stellatus*-type of mandible passes after damage and repair.

F. J. Beeman del.

Colour

The basis is dark and wholly membranous ; the tergo-scutal flaps are dark black with a white rim round the opening. There is another light rim round the membrane at its point of junction with the lower end of the sheath and the basal margins of the opercular valves. The prosoma is light and greyish but cirrus I and most of II and parts of the pedicels of the remaining four cirral pairs are dark bluish-grey (fading into grey, after long preservation). The penis is, by contrast, white with a darkened proximal part, where narrow, raised dark rings occur. There are the usual dark areas round the bases of the spines on each segment of the rami of cirri III–VI. In material freshly preserved in 70% alcohol, the front of " the face " is a dark blue colour, because the pigment seems to be concentrated round the bases of the bristles which arise from the free surface of the trophi. There is a most distinctive, arched, blue loop above the apex of the notch of the labrum.

Trophi

The *labrum* is typically bullate with a wide inverted V-shaped groove and five moderately large, triangular denticles on either side of a central haired section at the apex of the groove. There are also hairs above the teeth. The rows of teeth are not continuous in all individuals from side to side, as shown in the dorsal view by Nilsson-Cantell (1921, Text-fig. 53*a*). The *palps* are almost rectangular in shape except for the median lower border which is slightly rounded. The upper and median borders and outer tip carry longish hairs—shorter along the upper border and becoming progressively longer towards the lower, median edge of the organ. The *mandible* is variable and appears in two main shapes. The commoner one has three large main teeth above, followed by a fourth smaller, generally double tooth (Text-fig. 4*f*). Below this is a comb-like section in which, however, the teeth of the " comb " are somewhat coarser than those of *C. stellatus* as shown in fig. 84 of Pilsbry (1916). Below this again are generally four long, spine-like teeth, forming the lower angle of the jaw. This is essentially a *stellatus*-pattern of jaw. Some large specimens, taken in areas subjected to maximum exposure to wave action, frequently show damaged mandibles in course of regeneration, in which there is a different pattern in the lower tip of the jaw—this variation was described by Darwin (1854, p. 460). They have three upper teeth, the fourth (often incipiently doubled) is almost indistinguishable as shown in Text-fig. 4,*g*, but it is definitely present. Below it is a coarsely pectinated section, with other spines showing at random between and behind the coarser spines—there is no " comb-like " section. Sometimes mandibles of the right and left sides may vary and while the left one may have a *stellatus*-pattern for its lower tip, the right may have a " *hembeli* " one. However, in the individuals with somewhat *hembeli*-like jaws the small, fourth double tooth can generally be seen, thus enabling the real affinities of *C. antennatus* within the genus *Chthamalus* to be recognized. The *first maxilla* has its spines separated into three groups by a well-marked upper notch and a less obvious lower notch, situated just above the bunch of small, bristle-like spines forming the lower corner of the organ. The upper notch is shaped like the letter " U " on its side, with a rounded bottom and there are no spines arising from its side-walls or within the notch. There are two or three very large spines at the upper corner of the jaw and generally two smaller pairs just above the notch. The central section carries, between notches, a varying number (7–9) of medium-sized spines while the nine or so bristle-like spines below the second notch form a brush. The upper and lower borders of maxilla I carry a few hairs. *Maxilla II* is stouter basally than is shown in Nilsson-Cantell's illustration (1921, Text-fig. 53), the anterior notch is distinct, rounded and free from bristles, and the spines along the lower margin are longest.

Cirri

Cirri I and II are slightly unequal but both are considerably shorter than the remaining pairs, *Cirrus I* generally having six segments in both rami in adults and each carrying a few long, pinnate bristles on its terminal segment. *Cirrus II* has generally five segments in the anterior ramus and six in the posterior one. Its pedicel is produced anteriorly into an oval-shaped outgrowth, fringed with fine bristles. Both terminal segments of the rami carry very stout, lanceolate spines furnished with a double row of stout peg-like serrations. There are four (or five) of these denticulate spines on the anterior ramus and even more on the posterior one. Their structure is distinctive among the closely related species in the *stellatus*-complex and therefore diagnostic (Text-fig. 1,*h*). The illustration of them in Broch (1922, fig. 51*c*) is not sufficiently detailed to disclose the finer structures which have now been found to be important. Cirrus III was adequately and ably described by Darwin (1854, pp. 460–1) who made it very clear that the character of a very long, often tightly coiled, outer ramus was by no means universally present in all individuals. However, most subsequent authors, ignoring his warning, have placed undue emphasis upon it as a diagnostic feature for the species. An investigation was undertaken to determine the frequency of occurrence of the long outer ramus of cirrus III and to look for other characters which might be used to diagnose *C. antennatus*.

A total of more than 150 individuals in samples of 20 (except for one locality in Southern Tasmania where only 10 were available), representing five localities spread throughout the range of *C. antennatus* on the eastern Australian coast, was dissected. All degrees of exposure to wave action were represented in the localities chosen, ranging from sheltered oceanic (as at Balmoral, Sydney) to very exposed (as at Harbord, also near Sydney). The only clear result of this investigation was that in no case did 100% of individuals in any locality possess the long outer ramus on cirrus III whereas in one quarter of the samples, 100% did not have it, both rami being short and subequal in length. In several batches only 15% of the barnacles possessed the long ramus. No clear-cut correlation could be found between the presence or absence of the long cirrus and the age-groups of the barnacles or of any specific seasonal or environmental factors. There was some indication, however, that increased predation by the molluscs *Dicathais orbita* and *Morula marginalba* was taking place in the late summer when local *C. antennatus* contained developing nauplii. In late January, 1957, up to 70% of the population at Pearl Beach in Broken Bay, N.S.W., had long outer rami on cirrus III and 80% were brooding developing larvae. Samples taken in the same area, three weeks later, had none and from 20–35% still contained developing nauplii. The predators were very active in the area. The evidence is inconclusive and proper experiments would be required to find out whether the long outer rami were lost naturally after a moult or as a result of misadventure, either during release of larvae or by the action of predators. The barnacle population contained a range of sizes of shell, presumably of different ages, and all had lost the long outer ramus. Here is a nice field investigation waiting for some student's attention. Wisely and Blick (1964) have established that the main liberation of nauplii in *C. antennatus* occurs in Sydney specimens in late spring and continues intermittently until May, so that an investigation of predation over this period might be fruitful.

After injury, regeneration leads to the formation of subequal rami on cirrus III but what happens at the next moult is unknown. Does the outer ramus tend towards the antenniform stage once more, and lengthen during subsequent moults? This is possible because many large-sized individuals do have long outer cirri, and it is felt unlikely that so fragile an organ could escape damage throughout all the moults and other vicissitudes in the life of a species living in such exposed conditions.

Cirri IV–VI are normally shaped, for the genus, and have subequal rami. In cirrus IV most of the segments towards the middle of the rami have four pairs of anterior spines ; cirrus V has some segments with four spines but the majority generally have three pairs of spines, on both rami ; but cirrus VI almost invariably carries three pairs of spines on each of its segments.

Habitat

Chthamalus antennatus flourishes under conditions of maximum exposure to high seas and to periods of long exposure to air and sunlight. The level of shore rocks, where it lives, may be exposed to air for as much as 98% of the time though in the warmest part of its range (S. Queensland) the author has noted a tendency to settle in somewhat shaded areas on the rocks. In the central coastal area of New South Wales, in localities exposed constantly to rougher seas, it may be attached to rocks up to the level of extreme high water mark of spring tides or in favourable localities, even in the splash zone above it, on the side walls of regular drainage channels or areas where spray is constantly blown.

Coastal surveys showed that the vertical range of *C. antennatus* had its upper limit considerably lowered in Victoria and Tasmania, where air and sea temperatures are somewhat lower than they are in the rest of its geographical range (Bennett and Pope, 1953). In fact, from Cape Otway westwards for 200 miles in Victoria and at Maatsuyker Island, off SW. Tasmania where prevailing winds, especially in summer, cause exceptionally cool air temperatures to prevail during the greater part of the year, there are breaks in its horizontal geographical range where it is virtually, if not quite, absent (Bennett and Pope, 1953, 1960 ; Womersley and Edmonds, 1958).

Distribution

Australian : This species ranges from Bustard Head (S. of Gladstone) in Queensland southwards on the fully exposed, oceanic coasts of southern Queensland, through New South Wales, Victoria and Tasmania and thence westward along the coast of South Australia in the Great Australian Bight into Western Australia, at least as far as Eucla and a little beyond. It was not found farther to the west, at Cheyne Beach or in the Albany area of Western Australia.

Specimens from Broome, Western Australia, named by Broch (1916) were examined in Sweden and proved to be juveniles of *C. malayensis*.

World Occurrence : It is believed that all records of *C. antennatus* from areas other than in southern Australia—e.g. those of Gruvel (various dates and countries)—are wrongly identified and even the records of an unknown species of *Chthamalus* at Whangerei and Poor Knights Islands in New Zealand, on the east coast of the Northland Peninsula, by Cranwell and Moore (1938) were later found by Moore (1944) to be juveniles of her new species, *Chamaesipho brunnea*, which goes through a six-valved stage during its development. There is no reliable record of this species outside Australian localities.

Chthamalus malayensis Pilsbry, 1916

(Plate ii, figs. 3, 6, 7 ; Text-figs 1,*i* ; 5,*a-g*)

See Utinomi (1954) for earlier bibliography and add the following :—

Chthamalus malayensis : Kolosváry, 1941 (part only of the material under this name is true *C. malayensis*) ; Utinomi, 1949 (important distribution table), 1954 ; Endean, Kenny and Stephenson, 1956 ; Endean, Stephenson and Kenny, 1956 ; Stephenson, Endean and Bennett, 1958 ; Stubbings, 1961 ; Karande and Palekar, 1963, illustrated ; Zevina and Tarasov, 1963, illustrated ; Southward, 1964.

C. antennatus : Gruvel, 1912 ; Broch, 1916, illustrated.

C. moro Pilsbry : See synonymy in Utinomi, 1954, but add Broch, 1922, illustrated ; Utinomi, 1949.

C. challengeri : Nilsson-Cantell, 1921 (part only of *C. challengeri*), 1938.

C. challengeri f. *krakatauensis* : Broch, 1931, illustrated.

C. stellatus : Darwin, 1854 (part only, including at least specimens from Philippine Islands) ; Hoek, 1913, illustrated ; Kruger, 1914 (recorded as *C. stellatus* var. *communis* Darw.) ; Pilsbry, 1916 (? material from Port Cuyo in the Philippines which should be *malayensis* ?) ; Nilsson-Cantell, 1921, 1934, 1938 ; Stubbings, 1936 ; Daniel, 1956.

In the comments made on the genus some of the difficulties experienced in attaching the correct name to the Australian material belonging to this species were given and a glance through the list of authors in the above synonymy and in the synonymy in Utinomi's paper (1954) will show clearly the confusion that has arisen over the identity of *Chthamalus malayensis* in written accounts of European systematists. Several workers have allotted slightly differing batches of *C. malayensis* to 2, 3, or even, in the cases of Broch and Nilsson-Cantell, to no less than 4 different species. If one plots on a map of the South China Sea and the Indomalayan island chain, the distributions attributed in literature to *C. malayensis* (with its synonym *C. moro*), and those of *C. stellatus* and *C. challengeri*, the result is chaotic. It is as though a giant hand had shaken out a mixture of species at random like pepper out of a pepper pot, and they had landed anywhere throughout the area. There is no pattern in the distributions, and common sense appears to have been forgotten in the process. Colder water species have been recorded at the equator and tropic species in the cool temperate seas.

No doubt this confusion has been in part due to the comparatively late recognition of *C. malayensis* (1916) as a separate species, and in part to its almost protean ability to acquire differing shapes and weathering under slightly differing ecological conditions, coupled with the fact that many of the earlier workers looked no deeper than shell structure and a few obvious characters of the soft parts to determine their species.

The present review has covered the examination of large collections taken along some 7,000 miles of the Australian coastline—from Great Sandy Island in southern Queensland, northwards to Cape York and thence to several scattered areas along the northern coastline (e.g. Groote Eylandt, Darwin and Yampi Sound) into Western Australia, but from Port Hedland frequent sampling points were possible, westwards and southwards to Garden Island, off Fremantle in southern Western Australia. In addition material from New Caledonia, New Guinea, Indonesia and India has also been dissected. This probably constitutes the largest sample of *C. malayensis* yet worked and after this experience, and having examined Pilsbry's types and struggled through the tangled jungle of literature dealing with the species, it is the author's considered advice to future systematists, attempting to revise the genus *Chthamalus*, not to waste time in trying to straighten out the errors of earlier writers. Although this has been done in the present instance, and the source (or sources) of error in each case listed in the above synonymy has been traced, it is felt that this review is not the correct place in which to document these data. Rather should future reviewers obtain reasonably large samples of each species belonging to the *stellatus*-complex, from relevant localities and reexamine them for himself in order to list the characters belonging to each of the species that have been confused with *C. malayensis*. Only in this way will a clear picture be obtained of their true relationships. A special warning is also necessary about several misleading errors in Pilsbry's original description of the soft parts of *C. malayensis*. The shell parts of this species are clearly designated as type material in the United States National Museum, in Washington, D.C., United States of America (Registered No. 48084) but are dissociated from any soft body material. The author was informed that the late H. A. Pilsbry had retained his micro-

slide material and that it might be found in the Department of Mollusks of the Philadelphia Academy of Natural Sciences, where Pilsbry formerly worked. With the help of Dr. Tucker Abbott, in Philadelphia, Pilsbry's microslides were traced in his former Department and a set, obviously associated with work recorded in Bulletin 93 of U.S. National Museum (1916), was located and examined for possible evidence. These microslides had originally been mounted in glycerine jelly but were unringed and had deteriorated badly. In fact it is doubtful if any measure could be found to restore them to a state in which they could be usefully examined. They were *not* designated as part of the type material, however, and, in any case, no trace could be found of any microslide labelled "*C. malayensis*". As *C. malayensis* can fortunately be distinguished by its shell parts alone with certainty, if necessary, by an expert it has been possible to learn that there are serious incongruities if not errors, in Pilbry's original description and illustration of the soft animal parts of this species. These errors have proved to be particularly misleading and are, no doubt, the *fons et origo* of all subsequent confusion over this species—a confusion that has been quite unnecessary since *C. malayensis* is, as Utinomi (1954) and other subsequent authors have clearly been able to recognize, a valid species well defined and demarcated from its most closely related species, *C. antennatus*, and should never have been confused with the more distantly related *C. stellatus* and *C. challengeri*. Use of Table 2 (above) should help future workers using collections already named in northern European Museums to rename the specimens that have been incorrectly determined. In actual practice, except for fringe areas of zoogeographical overlap, it should be almost possible to determine closely related species of the *stellatus*-complex on zoogeographical areas alone.

The errors specially noted in Pilsbry's original account occur both in the written material and in his fig. 90A (1916, pp. 310–312, since *C. moro* = *C. malayensis*). The illustrations both for *C. malayensis* and *C. moro* on his Plate 72 are, however, correct. The following characters of *C. malayensis*, as described by Pilsbry, are not correct:—(*a*) Cirrus II which, contrary to his statement, does possess stout spines which are large-toothed and have a characteristic shape, whereas any of the *C. challengeri*, dissected by the author, do not have similar spines (Pilsbry's 1916 drawing of *C. challengeri*, fig. 87C, is therefore incorrect and much more like *C. malayensis*); (*b*) in the mandible the lowest tip of the adult jaw generally has only two slightly larger teeth, not three as stated; (*c*) the maxilla is not as illustrated (Pilsbry, 1916, fig. 90A) but has a clearly defined, upper U-shaped notch devoid of spinelets, above which there are two very stout, large spines (*nec* 3 as he states) with three slightly smaller ones below them followed by the clear notch; (*d*) Cirrus VI may have four pairs of spines on each segment in one ramus and/or three or four on the other.

Under these circumstances it would seem best to redescribe *C. malayensis* in some detail and to refer to more recent and reliable descriptions and illustrations. However, before embarking on this it should be stated that the author has compared the types of Pilsbry's two species *C. malayensis* and *C. moro* (held in the collection of the U.S. National Museum, Washington, D.C., in the U.S.A.) and there is no doubt at all that Utinomi's (1954) action in synonymizing these two species is correct. In the Australian collections of *C. malayensis*, the smooth-shelled, generally quickly-grown, taller shell of the "*moro*" kind occurs side by side with those with ribbed shells and smooth walls and the flatter shape which is associated with the name *C. challengeri* Hoek forma *krakatauensis* Broch (first used by Broch (1931) for specimens from Krakatau Island). Broch's illustrations show that his specimens from Krakatau Island were indeed *C. malayensis*, and this was confirmed when Broch's "Type sett and lectotypes" were examined in the Zoological Museum of the University in Copenhagen, Denmark; Utinomi's decision (1954, p. 18) in synonymizing *malayensis* and *C. challengeri* f. *krakatauensis* Hoek is thus also confirmed.

Appearance and Shell Structure

Many Australian specimens of *C. malayensis* on the rocky substrate (Plate ii, fig. 6) have the shape of the specimens described by Broch (1931, as a form of *C. challengeri*) and observation has shown that they are comparatively young or half-grown specimens, even though they may be breeding. Further growth and erosion lead to a loss of the distinct ribs with projecting processes round the circumference of the shell and only traces of the ribs remain, near the circumference of the shell as seen in Plate ii, fig. 7 (the specimens not ringed in the photograph) which shows fully grown somewhat eroded specimens from Western Australia. The largest barnacle in this illustration is a specimen of *C. antennatus*, from eastern Australia, deliberately placed on the timber among the *C. malayensis* to emphasize the differences in shell ribbing, size, and general facies, of the two species at a similar stage of their growth—differences which are obvious to the eye, but hard to record in written descriptions. As juveniles, while their shells are still thin and fragile, *C. malayensis* and *C. antennatus* are similar externally and this accounts for Gruvel's (1912) and Broch's (1916) mis-identifications of material from, respectively, Amanu Island, Tuamotu Group and from Broome in north Western Australia.

It is interesting to follow the progress of Hiro–Utinomi's ability to recognize *C. malayensis* in its many forms, as his ecological experiences of it increased over the years and the size of the population sample he handled grew greater, for my own experience has paralleled his, in almost every respect. One sees how, by placing too much reliance on the accounts and illustrations of earlier writers, one could believe that anything from three to five distinct species were present, but later found that they belonged to one highly variable species, able to grow attached to rocks, or to mangroves (in areas where *C. withersi* was not present, to compete for lebensraum), or to molluscs and other barnacles and how in each of these situations the shape of the shell differs greatly in appearance. Three of the more common variants of shell sculpturing are shown in Text-fig. 5,*a–d*, but there are still other frequently recurring patterns of shell erosion not depicted. The final stage is reached when senescent barnacles, with carino-rostral diameters of 14 mm. or more, show a somewhat rectangular shape with only faint traces of ribs, often marked merely by a linear series of black pits with dark corium showing through and with raised shell bumps round them, the last remnants of the original ribs. The opercular valves are so worn as almost to be characterless externally except for the deeply sinuous sutures marking the interlocking of the scuta and terga. This last shell type is particularly common on mangroves or on the rocky shore between Carnarvon and Broome, in the northern part of Western Australia, whereas in Queensland *C. malayensis* rarely attains such dimensions and the shell form that is most favoured in this environment (chiefly on intertidal rocks) is the more stellate, smoother form shown in Plate ii, figure 6, or in Text-fig. 5,*b*, which shows a half-shell in which the ribs appear only near the circumference.

However, in spite of these varying shell shapes, internal structures are constant and a detailed description of these will be given. Special stress will be laid on diagnostic characters, for there is no complete recent description, since Utinomi's important paper (1954, pp. 18–21), which did much to clarify the nomenclatural muddle but did not redescribe the species. Plate ii, figs 3, 6 and 7 and Text-fig. 5 have been chosen to illustrate the appearance of Australian specimens. The only widely differing form, not shown in the present work, is the smoother rather juvenile-shaped kind usually found in localities with less water movement—the prototype of Pilsbry's original *C. moro* and now recognized as a synonym of *C. malayensis*. It is illustrated (as *C. moro*) by Hiro (1937, fig. 4,*a–c*). As may be seen in his figure, it has the rather featureless opercular valves, typical of juvenile *Chthamalus*. In particular only three of the usual four crests for attachment of the tergal depressor muscles have been developed on the tergum. Examination of a series of barnacles

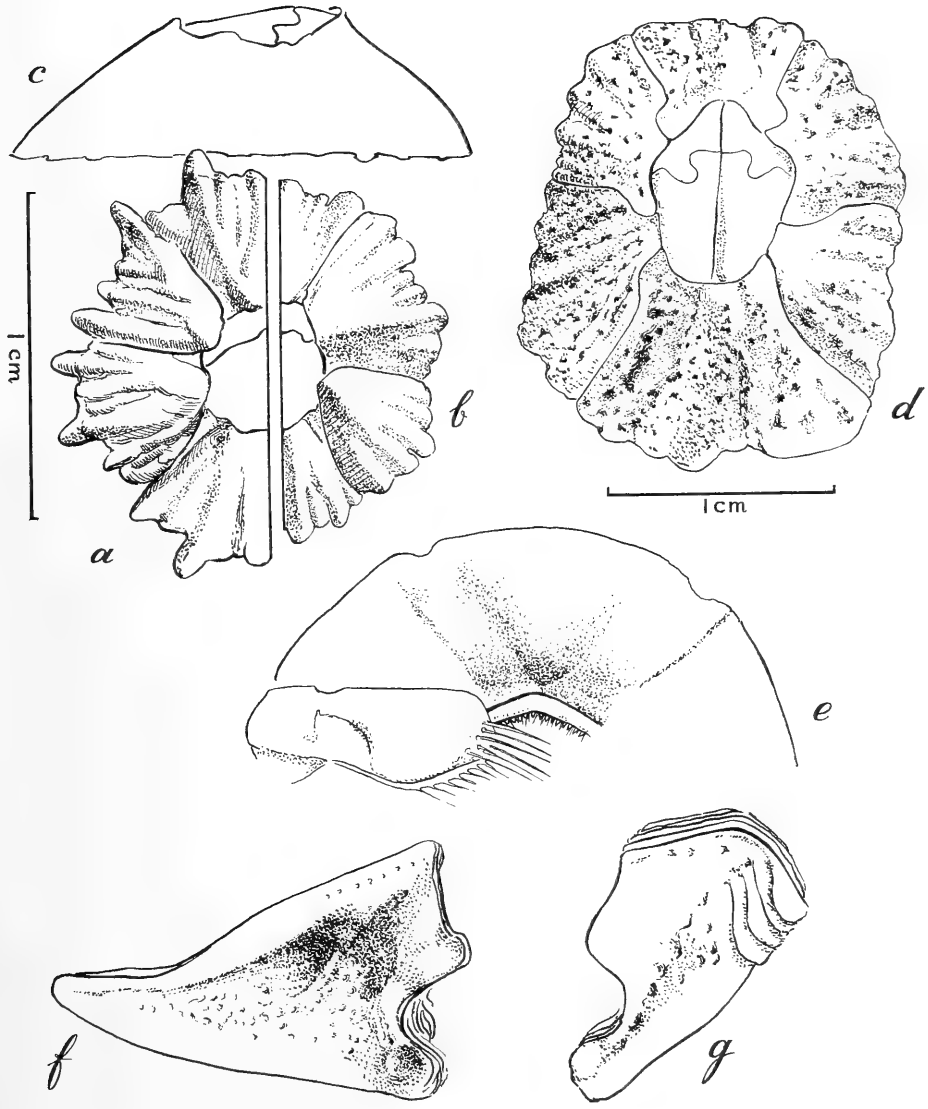

Fig. 5. *Chthamalus malayensis*. (*a-d*) varied shapes, and sculpturing of shell plates. (*a*) half shell of a young and uneroded individual growing on rock (typical of the ribbed form designated by Broch as *C. challengeri* forma *krakataueusis*) ; (*b*) half-shell of a slightly older and more weathered individual, but far from mature, showing no pitting of the shell externally (typical of majority of specimens occurring on rock in Queensland intertidal zone) ; (*c*) side view (silhouette) of a typical *C. malayensis* ; (*d*) fully mature, much eroded specimen grown on a mangrove from the north of Western Australia, much pitting showing externally ; (*e*) labrum of typically swollen or bullate pattern, with left palp removed to show teeth and hairs along the groove above the mouth ; (*f*) scutum, interior view showing rugged sculpturing, pitting (as opposed to smoother interior of *C. antennatus*) of general surface and the deep clearly defined pit for the insertion of the lateral depressor muscle ; (*g*) tergum, interior view, showing four crests for depressor muscles attachment, and the prominent central row of pits about which the valve is bent at an obtuse angle.

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of increasing size would, however, have shown that, as they grow, first three, then three plus a sort of " half crest " would be found, then four, and sometimes even five full crests might occasionally be seen. However, four crests is the more usual number in mature specimens. It should be remembered that this species can also breed long before it reaches full size, so that the presence of developing larvae in the mantle cavity does not necessarily mean that one is dealing with a full-grown *C. malayensis*.

However, it is interesting to note that the characteristically deep pit on the scutum for the attachment of its lateral depressor muscles is already well in evidence in the " *moro* " form and at an early growth stage, and the small ledge, below the attachment of the adductor muscle of the scutum, is almost non-existent. Correspondingly-sized and -aged *C. challengeri* are generally already showing a well-raised ridge, below the pit for the adductor muscle, in any material that has been worked by the author. This included " co-type " material (juveniles) kindly made available by Dr. J. P. Harding of the British Museum (Natural History) of London.

The effect of special factors in the tropical environment on the shells of intertidal barnacles would seem to be profound but, in the absence of experimental work, we cannot even guess whether it is just the extraordinarily hot temperatures and consequent high rate of evaporation, or whether some unknown factor like more intense ultra-violet radiation or the effects of heavy monsoonal rains, and so on, are operating. Whatever the controlling factor or factors may be, it seems to be connected, if not primarily at least secondarily, with the intensity of the sunlight, for the appearance of two batches of *C. malayensis* settled simultaneously in the same area (the one in shade and the other in full sunlight) are often so different as to look like two different species i.e. the ones grown in shade resemble the *moro* kind of shell. Another special feature of tropical shores is the presence, at least along the northern coast of Western Australia, of mangrove trees in the higher intertidal zone, which are not necessarily associated all year round with the soft mud of coastal rivers and much turbidity in the sea. It is along this part of the Australian coastline that *C. malayensis* has, as it were, taken to the trees and developed the larger rectangular-shelled individuals with carino-rostral diameters of 15·0 mm. or more. Only traces of the numerous narrow original ribs remain near the outer margin, and their shells are deeply pitted internally. Often the pits open externally on the shell plates, at the end of one of the bosses marking the last remnant of the ribs (Text-fig. 5*d*). The sutures between the shell plates are simple and untoothed but are more firmly articulated together than they are in *C. withersi*.

Uneroded *C. malayensis* are generally ash grey and have 4–6 ribs per plate —narrower than the ribs or folds in correspondingly aged *C. antennatus* or *C. challengeri*. There may be a tendency for the ribs of *C. malayensis* to bifurcate towards the circumference of the shell so that the width of the ribs remains constant, but their number per shell plate increases gradually as they age. The basis of the shell is wholly membranous. Internally the colour of the shell is a dark grey and it is generally considerably pitted.

Measurements of 10 individuals collected at Onslow in Western Australia are given in Table 7. This sample showed considerable size variation and differing shell weathering as set out in the last column. They were collected by Mrs. L. Marsh, on 29/9/1959 and none contained developing larvae. A batch taken towards the end of December 1964, however, from Cockatoo Island, Yampi Sound in Western Australia (collected by N. Hoffman) had their mantle cavities filled with well-developed, eyed-nauplii, almost ready for release.

These measurements of a truly tropical sample of *C. malayensis* indicate its shape and generally low-growing habit. Only rarely will intense crowding cause it to assume a more tubulo-conical form. In localities favourable to *C. malayensis*, i.e. where there is some degree of water movement and slightly

less turbidity than usually occurs in many tropical seas, it may colonize the rocks just as thickly as *Chamaesipho columna* does in the temperate zone, and may appear as a broad whitish band along the rocky shore, just above or mingled with the band of the tropical oyster, *Crassostrea amasa* (Iredale). Such an area is illustrated in Plate ii, fig. 3 and was on an offshore rock stack at Yorkey's Knob, near Cairns in Queensland.

Opercular Valves

Reference has been made above to the variability in form and structure of the opercular valves in shell with differing external appearance, but no reference has been made to their more constant characters which can be used to diagnose *C. malayensis*. Variability of form in these plates is well shown in Utinomi's drawings (1954, fig. 2,*a-h*) but constant characters can be recognized in them too. Again it is best to ignore previous descriptions except Utinomi's.

TABLE 7

Measurements of 10 C. malayensis *from Onslow, Western Australia*, 29.ix.1959

Carino-rostral diameter in mm.	Width in mm.	Height in mm. (at highest point)	Remarks
7·2	8·2*	3·6*	Uneroded—pale grey, ribbed Tergo-scutal flaps jet black
8·5	8·5	2·5	Small, uneroded, ribbed form
11·8*	11·0	5·0*	Very eroded
12·5	9·6	4·5	Shaped like *C. antennatus* due to crowding. Very eroded
13·9	11·9	6·5*	Very eroded
14·5	12·0	4·5	Very eroded
14·6	13·5	4·3	Rectangular in shape and very eroded
15·0	13·4	4·3	Very eroded
16·2	11·6*	5·0	Rectangular in shape, growth crowded. Very worn. Rows of black bosses, along former rib-line
17·0	17·1	6·4	Basis dark (black) wholly membranous and undamaged

* Distorted due to crowding.

The scutum always has a deep pit near its basi-tergal corner, directed upwardly towards the apex, and this forms the point of attachment for the lateral depressor muscle. It is deeper and more pronounced than the pits in related species like *C. antennatus* and *C. challengeri* and there is no trace within it of small crests for attachment of the muscles, as seen in *C. challengeri*. In *C. antennatus* the corresponding lateral depressor pit is only moderately developed and traces of raised crests may be seen within the pit, making this species intermediate in structure in this respect between *challengeri* and *malayensis*.

The scutum of *C. malayensis*, while lacking the very prominent and well-marked ridge, seen in *C. challengeri*, below the scar of attachment for the lateral depressor muscle, nearly always has a small ledge, especially in well-grown shells, below and towards its tergal side. The differences in this structure, and the opercular valves in general, may be appreciated by comparing two sets of illustrations by Fujio Hiro of *C. challengeri* in his 1932 paper (Text-fig. 1,*a–d*) and *C. malayensis* in his 1939 work (Fig. 1,*b–c*). To these need only be added the statement that Australian specimens of *malayensis* behave similarly to the populations described by Utinomi (1954, pp. 18–21), remembering while reading Utinomi's account, that Nilsson-Cantell was confused over the systematics of this species and that Pilsbry had failed to note the coarsely built,

pectinated spines associated with cirrus II in *C. malayensis*, so that Utinomi's comment and comparisons with the descriptions of these authors should be disregarded.

The *tergum* of *C. malayensis* (Text-fig. 5,*g*) in older individuals is generally broad towards its apex but narrower towards its basi-scutal corner than in the corresponding valves of *C. antennatus*. It is folded about an axis running from its apex to the basi-scutal tip and this fold is often emphasized internally by a line of very distinct pits which sometimes merge to form a narrow furrow. The inner surface is much pitted in older barnacles and there are generally four more or less parallel crests for attachment of the tergal depressor muscles (occasionally $3\frac{1}{2}$ in juveniles or $4\frac{1}{2}$ to 5 crests in very old individuals). This contrasts sharply with the most closely related species in Australia, *C. antennatus*, in which there are only two crests for tergal depressors, or at the most two plus a partially developed third crest, in very old individuals.

Soft Body

Colour :—In newly preserved material (in 70% alc.) the prosoma is a light creamy colour and the cirri are correspondingly light but with more of a pale grey tone. Cirri I and II have rami a dark, somewhat purplish-grey, and pedicels a lighter shade of the same general tone. Other cirri have darkened patches on the inner sides of their pedicels and concentrations of dark pigment round the bases of the large anterior paired spines on each segment of the rami. The proximal part of the penis is also dark, the rest of it being startlingly white, by contrast. It is very long, and tapers gradually to a fine tip. Developing eyed-nauplii were pinkish-white. There is no dark ring of pigment round the mouth, as in some other chthamalids ; instead, only the blades of the palps and the outer tips of the mandibles and of maxilla II were slightly darker than the rest of the head region. There is no caudal appendage.

Trophi

The *labrum* is of the " normal " bullate shape, i.e. bulging smoothly, above the area where the spatulate tips of the palps lie recessed in grooves and closely adpressed to the labrum. Their lower borders are almost parallel to those of the notch of the labrum which is broadly " Λ "-shaped. There is a slight thickening of the walls of the V and a flattening at the peak of the groove, the side walls of which carry a row of broadly triangular teeth with a row of close-growing hairs above them. Frequently food particles and debris are entangled between the teeth and the hairs and they have to be brushed away before the structure of the notch can be seen. The lower borders of the palps carry a fringe of long bristles which depend over the mouth opening. These are longest medially. The *mandible* is essentially of the four-toothed, *stellatus* pattern, in which the 4th tooth is smaller and is frequently doubled. Below the 4th teeth, however vestigial they may be, there is generally an appreciable change in the style of the dentition or spinulation except in the case of damaged and regenerating jaws which will be described below. From this point downward to the two large spike-shaped spines arming the lowest tip of the jaw, the spines are generally placed parallel to one another like the teeth in a comb and are of smaller size ; however, they are not fine and hair-like as in *C. stellatus* and *C. challengeri*. Great variation has, however, been seen in this lower part to the jaw and even, as between right and left sides of the one individual and this can usually manifestly be traced to regeneration on the part of one mandible. Often the nature of the injury can still be seen. As juveniles, or during regeneration or in certain individuals, the lower tip of the mandible is reminiscent of the *hembeli* jaw pattern, i.e. there is no comb-like section below the 4th tooth or, alternatively, it is so drastically reduced as to be virtually absent, being replaced by a few moderately-sized spines arranged as in the coarsely pectinated part of *C. hembeli*. This condition is

shown (for *C. moro*) by Broch (1922, fig. 52*a*). Only with maturity and in the absence of damage and regeneration does the " normal " jaw shape develop. It is as though juveniles and regenerating *C. malayensis* (like *C. antennatus*) have to pass through a *hembeli*-stage during the development of their much toothed and highly complex mandibles. *Maxilla I* is also somewhat variable as regards the finer details of shape and the exact arrangement of the spines. In addition the angle from which it is viewed can make a difference to the appearance of the largest spines above the notch (from one angle there appear to be three very large spines, whereas from another angle only two of the largest size may be seen). As a rule there are three of slightly smaller size below and partly between them. Hiro's illustration (1939, p. 251, fig. 1E) gives an excellent picture of the shape of the mandible in the majority of specimens examined from Australian localities. An interesting feature is the presence of a well-marked upper notch, shaped like the letter U, lying on its side. The walls of this notch are devoid of spines and only the tips of a fine hair or two (from the side wall of the mandible) may project behind or in front of it. Such hairs have no basal connection with the notch itself. This contrasts with the structure of the maxilla of *C. stellatus* and *C. challengeri* in which the notch is much more obscure, more V-shaped and has several spines with their bases originating along the upper borders of the notch indentation. They may even obscure any view of the notch itself. The differences between *C. malayensis* and for example *C. stellatus* (s. str.) may be appreciated by comparing Hiro's figure of *malayensis*, referred to above, with his own later illustration of *C. stellatus* (Utinomi, 1959, fig. 5*b*) made after an intensive review of Mediterranean specimens in which he established the nature of the differences between *C. stellatus* (*s.s.*) and the rediscovered species *C. depressus* (Poli).

It is virtually useless to refer to published figures and descriptions of the mandible of *C. malayensis* in earlier works than that of Hiro (1939) unless one knows the details of the nomenclatural confusion in each of the papers concerned. It is believed, for instance, that Pilbry's original description (fig. 90*a*) is an illustration of the mandible of *C. challengeri* or *C. stellatus*. It is certainly unlike that of a true *malayensis* and, as has already been outlined above, his account of the soft parts in this species cannot be checked against microslide mounts since this species alone seems to be missing from the batch used in the preparation of his great 1916 monograph. *Maxilla II* is of the usual bi-lobed pattern with a wide, rounded notch free from bristles. Above this notch is a row of stiffish, larger bristles (more spine- than hair-like) arranged like the teeth of a comb and sticking out more or less at right angles from the wall. Below the notch the bristles are thickly clumped and hair-like, being shorter near the notch and increasing gradually in length round the lower tip of maxilla II. Long hairs occur not only on the lower border but up the outer sides of each of these organs towards the rear, giving a bearded and be-whiskered effect like a man with both a " goatee-beard and mutton-chop whiskers ". Seen from in front, the " face " is very hirsute. From above, each of the second maxillae is triangular in outline, with the base broad proximally. The two maxillae II seem to be more closely adpressed to one another than is usually the case in the genus and together they form a most effective lower lip, broader than the average. The mandibles and maxillae I, on the other hand, are comparatively smaller than those seen in the 3-toothed species of the genus.

Cirri

The first two pairs of cirri are much shorter than succeeding ones and exceedingly setose. They are approximately equal in length and in each the anterior ramus is slightly stouter and a little longer than its posterior fellow. Typically *cirrus I* has the number of segments as follows :—anterior ramus eight and the posterior one seven. The numbers of segments may, however, vary slightly in the population, but is of that order. Both rami of cirrus I

are heavily setose and the bunches of bristles, on segments, towards the centre of the rami, form a felted mass of pinnate-type setae. These apparently act together to strain food particles from the water. They had frequently to be brushed clear of detritus and small plankton in order to see their structure. There are also present, jointed, larger pinnate setae on the terminal segments of both rami of cirrus I. Towards the posterior, inner margin of the anterior ramus, six or so of the basal segments carry numerous peg-like, short stout spines, the apparent function of which is to project into the fringe of setae round the opposing posterior ramus, thereby locking the two together and forming a broader and more rigid scoop-like structure of the rami which act together and increase its efficiency as a feeding organ. Even the segments of the pedicels of *C. malayensis* are more heavily fringed than those of *C. antennatus* and some of these setae are of the pinnate type. The posterior ramus of cirrus I lacks the stout peg-like spines posteriorly. In *Cirrus II* the segmental counts are respectively eight and six (or of that order) for anterior and posterior rami. The stouter anterior ramus carries setae and spines of four main types, namely (1) stout, lanceolate, toothed spines; (2) pinnate, hair-like bristles; (3) ordinary straight spines; and (4) posteriorly placed peg-like spines on several basal segments. Of these, the lanceolate spines merit special attention, since their structure can be used in diagnosing the species. Each of these lanceolate spines is armed by a double row of coarse, pointed spikes, the lowest of which are separated from those above by a diastema-like gap. In some species there is a trace of a joint in the spine at this point, and the lower teeth-like projections are associated with the top of the " basal " section as opposed to the distal or " blade " part of the lanceolate spine. In large individuals with very eroded shells (of the type depicted in Text-fig. 5,*d*) the lowest spines may be reduced (by wear or erosion) to mere bumps, whereas in younger specimens they are generally spine-like. The double row of serrated spines above the gap may also be worn but are always coarser in build than corresponding structures in either *C. stellatus* or *C. challengeri*. They are generally, however, more pointed and not quite so coarse and peg-like as those of *C. antennatus*. This last species lacks the two lower spines below the diastema gap. It is hard to reconcile Pilsbry's statement about cirrus II in the original description (1916, p. 311) with what occurs in the material examined. His statement, " The spines of the terminal segments are as described and figured for *C. stellatus* ", is unfortunate when there is so marked a difference in the coarseness of the serrations in the two species. If he merely meant that serrated spines were present on cirrus II, as opposed to the absence of such spines (as in the species *C. withersi* and *C. caudatus*), his remarks are understandable but it is felt that much of the confusion in identifications of *Chthamalus* barnacles from the Indomalayan Peninsula stems from this statement and one can fully understand Nilsson-Cantell's feeling (1921, p. 276) that he could not really distinguish Pilsbry's *C. malayensis* from other closely related species. In fact Nilsson-Cantell (1921) omitted it from his key to the species of *Chthamalus* and from this time onwards appears to have been unable to recognize the species correctly, referring it sometimes to *C. challengeri* but mostly to *C. stellatus*. Moreover, his redescription of *C. challengeri* in his 1921 monograph (pp. 279–281) obviously includes both *C. malayensis* and *C. challengeri*, and still further adds to the confusion. He specifically mentions the differences in the structures of the lanceolate spines of cirrus II in specimens from Java [= *C. malayensis*] in which the serrated side teeth are " kraftig " whereas in Japanese [= *C. challengeri*] specimens they are " schwacher " (see Table 2). The number of stout spines in each terminal segment of the rami of cirrus II varies slightly from barnacle to barnacle, but they are of the order of from six to nine. They also occur in segments below the terminal ones, in varying numbers, among the bunches of pinnate spines, but one has to explore several planes of focus, under high magnification, before all may be viewed and counted.

When a large sample of *C. malayensis* in varying age groups and from varying localities is dissected, stout spines may be found varying in coarseness and structure from a coarse pinnate-type, through a number of stages, where the " blade " part distal to the joint of the spines appears to have shortened and thickened while its side hairs have correspondingly thickened and become blunter, till they become tooth-like. The basic structural relationship between the stout, lanceolate spines and the longer more delicate spines thus becomes obvious, especially so where damage to the tip of cirrus II has led to regeneration of the organ. It apparently takes some time and perhaps several moults before the stout spines return to their normal, pre-damage shape. This again may lead to confusion in specific determination unless one is experienced in the group and underlines the necessity for examination of larger series of specimens when determining species.

Considerable magnification and controlled lighting may be necessary to disclose the presence of pinnate setae, but they are generally long and fine, and occur in bunches, anteriorly on the segments, tending to form matted clumps. They occur thus, from near the basal segment of each ramus to the segment just below the tip, and are more thickly clustered on the anterior than on the posterior ramus. Short stout, curved spines are again found along the posterior border of the anterior ramus, opposite to the nearest border of the posterior ramus, where they may be seen to interlock into spaces between the bases of its setae. However, they occur only in pairs—generally one pair per segment (not scattered in a random clump as they did on cirrus I) on the lowest three or four segments. The lowest segment may sometimes carry two pairs of spines. While not quite as setose as cirrus I, the second cirrus of *C. malayensis* is nevertheless a very efficient food-sieving organ. Cirri III–VI are similar in structure to one another and of the ordinary pattern for posterior cirri, sub-equal in the length and in the numbers of segments of the anterior and posterior rami. Each segment, apart from a few basal ones has four pairs of anterior spines of which the longest is the upper one and the shortest lowest. The lowest pair have their bases placed close together and sometimes are both broken off so that the segment may appear to have three spine pairs. However, the site of the missing fourth pair can generally be seen. The *penis* is longer than cirrus VI in most specimens and is closely annulated. There is no *caudal appendage.*

Habitat and certain aspects of ecology

When not restricted, by competition for settlement space (with *C. withersi* from above and with the oyster *Crassostrea amasa*, below), *Chthamalus malayensis* occupies a wide band on the open rock faces in Queensland and may be found throughout the upper half of the tidal range of spring tides and even into the splash zone in areas noted for constant choppy or rough seas, though this is rather exceptional in Queensland. Populations of *C. malayensis* are generally most dense between mean high water and the low water level of neap tides. The occurrence of this species on the mainland coast of Queensland and the effects of environmental factors on its distribution have been discussed by Endean, Kenny and Stephenson (1956). It has also been the subject of a more detailed autecological study by post-graduate student, Miss Judy Bryan (University College of Townsville, Queensland), and the author has read drafts of her thesis. The results of her work remain, as yet, unpublished and are therefore unavailable. However, with due acknowledgement to Miss Bryan a few of the most relevant facts are quoted here where they supply actual figures for tidal heights, ranges and percentages of exposure for the approximations noted in the present author's field observations: Within a spring tidal range of 12 feet 10 inches, *C. malayensis* may occur throughout the upper half of the range and even beyond it into the splash zone, if such a zone exists. It is densest between the levels 8–11 feet above zero tide mark

and the largest individuals occur most frequently towards the upper part of its range. Populations tend to be most dense on near vertical rock faces (in Queensland). Plate ii, fig. 3 shows an area where the numbers of *C. malayensis* per unit area rival the most dense barnacle populations seen on temperate Australian shores. The width of rock in the photograph was approximately 35 cm. Such dense populations can, however, only be found in tropical Australia, where the right substrate occurs within the barnacle's tidal range and where conditions of turbidity and salinity are suitable. One feels that the " paucity " of populations of barnacles in the tropics, often mentioned by other authors, is attributable, more often than not, to the lack of suitable substrates lying within the tidal range of the species which form dense aggregations such as *C. malayensis* and *C. withersi*, rather than to a lack of barnacle larvae which seek to populate the shores. Miss Bryan noted that when the vertical range of *C. malayensis* was related to the graph of theoretical exposure to air, some individuals might be exposed for up to 90% of the time and the minimum exposure was of the order of 30%. Air temperatures in Queensland can range to 35° C and even more, for short periods. Breeding was most actively carried out in the warmer part of the year, larval settlement occurring mostly from November, through the eight succeeding months to June, with the period of densest larval settlement in November through to February. Although Miss Bryan's work covers the effects of predators and experimental investigations of physical factors in the environment, it would be premature to disclose her findings here.

According to field notes and observations supplied to the author by Mrs. Loisette Marsh with her collections from the northern part of Western Australia, *C. malayensis* behaves somewhat differently there from what it does in Queensland, for it occurs not only in the usual manner on rocks (between the 14 and 20 feet levels where the tidal range is 33 feet) but also invades the mangroves and settles on their trunks and prop roots and on wharf piles. This habitat is occupied in Queensland, as a rule, by the species *C. withersi* which can tolerate the turbidity and lowered salinities normally associated with the mangroves there. However, *C. withersi* has not been recorded westward of Darwin (Northern Territory). Some of these northern *C. malayensis*, taken from the mangroves, attain relatively enormous sizes (see Table 7) but it has not been possible, from the notes supplied by collectors and in the complete absence of chemical and physical data of the environment from this area, even to hazard a guess as to why *withersi* is absent and its place on mangroves has been taken by *malayensis*. It is hoped to investigate the area personally later, meanwhile only the facts, as known, can be set down. The shells of many of the Western Australian *C. malayensis* differ in appearance from those common in Queensland, as may be appreciated by comparing Text-fig. 5,*b*,*d* (*d* being a well-grown individual from Onslow, W.A.). It is also a matter of interest that at the extreme southern end of its range in Western Australia (Garden Island, off Fremantle), *C. malayensis* reassumes the shell shape and appearance seen in individuals taken in central Queensland, i.e. it is smoother shelled and regularly ribbed, as shown in Plate ii, fig. 7. In *C. malayensis*, more than in any other species, one can appreciate the profound changes caused in the cirripede shell by varying factors of the environment. In the relatively high humidities that obtain, desiccation seems to pose less of a threat to life than perhaps some other effects of the environment, such as sunlight or the opportunity to catch food. The higher a barnacle grows on the shore in the tropics, the less it seems to be troubled by predacious molluscs and its distribution seems to be controlled mainly by physico-chemical factors.

Distribution

Australian: This species is the most widely distributed *Chthamalus* on mainland Australia, for it ranges from Hervey Bay (approximately 25° 30′ S).

in S.E. Queensland, northwards to Torres Strait and thence westward along the northern tropical coast right round to Shark Bay in Western Australia. From there southwards, sporadic records occur down to the vicinity of Garden Island (off Fremantle) but it is rare in this last locality. *Chthamalus malayensis* also occurs in Papua, New Guinea (taken by Judy Bryan), but little systematic collecting for barnacles has been carried out round this vast island, and absence of records of it there from areas other than Papua, is not significant, for the present.

World Occurrence: Owing to the tremendous confusion of *C. malayensis*, by a number of previous authors, with *C. stellatus*, *C. challengeri* and *C. antennatus* no detailed listing of localties will be given from earlier literature. It will be necessary to resurvey all previous collections to be certain of their identifications. This applies to most specimens in European and some American Museums. However, in principle, it may be taken that *C. malayensis* ranges throughout the Indomalayan region as follows: From the Persian Gulf (Stubbings, 1961) along the coasts of India and Pakistan, Malaya, and the South China Sea (Zevina and Tarasov, 1963) to Formosa (Hiro, 1939). Hiro points out that its ecological equivalent in Japan's more temperate seas is *C. challengeri*, whereas in temperate Australia it is replaced by *C. antennatus* and *Chamaesipho columna* in the south-east. It also ranges widely in Indonesia, the Philippines, Palao Islands, and several Islands in the Arafura Sea. To these literature records the following new ones should be added: Kambang Island, near Timor (taken by the Dutch Snellius Expedition of 1929 on 26–28th November, on mangroves); New Caledonia in the following areas where it was collected by the author: Reef north of Heinghène (E. Coast) 13/7/1960, on intertidal rocks and on rocks and mangroves at Baie des Citrons and at Ricaudy in July 1960 (both in the vicinity of Noumea); at Carlisle Bay, Santa Cruz Island, Santa Cruz Group (29/7/1926, collected E. Troughton and A. Livingstone), and Suva, Fiji, on mangroves in Kumbuna Creek (Station 24, Te Vega Expedition, 26/8/1963, collected by Isobel Bennett). It thus ranges widely in tropical waters.

Genus Chamaesipho Darwin, 1854

Chamaesipho columna (Spengler) Darwin, 1854, Type species of genus; Gruvel, 1905; Moore, 1944.

C. scutelliformis Zevina and Tarasov, 1963.

Lepas columna Spengler, 1790.

Type species for Darwin's genus *Chamaesipho* was *Lepas columna* Spengler (1790). Allegedly it came from a Tahitian locality (Otaheite). With it, in genus *Chamaesipho*, Darwin associated a new species, *C. scutelliformis*, which he believed was "probably from the seas of China". Zevina and Tarasov (1963) recently confirmed the occurrence of *scutelliformis* in the South China Sea and Gruvel (1905) extended its range to the Indian Ocean. P. H. Fischer (1884) recorded it in the New Caledonian Archipelago where, however, recent collecting by the author has failed to find it.

In his 1854 monograph Darwin assigned Australian and New Zealand specimens of *Chamaesipho* to Spengler's species *C. columna*, but did so with considerable reluctance, since the original description was very incomplete. This matter will, however, be discussed fully when the species is described below.

Only one species has been added since the two listed by Darwin, namely *C. brunnea* from New Zealand, described by Lucy Moore in 1944, the type locality being Lyall Bay, near Wellington. Previous New Zealand authors had confused *C. brunnea* with, and included it in their accounts of, *C. columna*. Miss Moore's paper clears up the earlier confusion between these two species and defines their geographical ranges in New Zealand. She has shown that *C. columna* occurs throughout New Zealand, whereas *C. brunnea* is limited to

warmer waters of the North Island and the north-eastern segment of the South Island. The present survey shows that its range does not extend to Australia.

Although there are only two species in Australia and New Zealand, the genus *Chamaesipho* figures most prominently in the intertidal zone, because of its dense populations (e.g. in the case of *C. columna* up to 3,000 per square foot of rock) in New South Wales, frequently forming a light-coloured frieze along the rocks, as seen in Plate 7, fig. 1 of Dakin, Bennett and Pope (1948).

The Australian species of *Chamaesipho* is adapted to withstand a fair degree of desiccation since it lives above mean sea-level where it is often subjected to long periods of hot sunshine and drying winds. The fusing of the four shell plates into a tubular shell wall may possibly be a survival factor by cutting down evaporation. Only the one species, *C. columna*, occurs in Australia.

Key to the species of Chamaesipho

1. (2). Four-valved (at least in adult stage), depressed Chthamalids of small size (five mm. carino-rostral diameter) with the rostrum much smaller than the other three shell plates. The upper part of the sutures adjacent to the rostrum persist when their lower sections grow together and become obliterated. Compartments other than the rostrum pierced by a series of four oval apertures—one in each lateral and two in the carina. These extend as shelly tubes to the base of the barnacle. Tergum with a wide, blunt, centrally placed spur and without pits between the attachment crests for the depressor muscles. Orifice relatively small ..... *C. scutelliformis* Darwin
2. (1). Four-valved Chthamalids when adult, though juveniles commence with six, with large rostral valves and no orifices in any valves. All traces of sutures between the parietes generally obliterated at an early stage of growth. Shell often tubular and tall, with the orifice proportionately larger than in *C. scutelliformis*, and often only slightly smaller than the basis. Tergum with little trace of a spur and with pits between the ridges for the attachment of the depressor muscles ..... (3 or 4)
3. (4). Carino-rostral diameter of adult shell generally no more than six mm., and in tall, tubular specimens the height may be more than three times the diameter. Soft body with navy blue coloration, even after preservation. Tergum with four to six deep pits between the crests for the depressor muscles. There is a small but distinct adductor ridge on the scutum. Mandible with four to five teeth of which third and fourth may be doubled. Grapple-like spines on the anterior ramus of cirrus II with only one or two (and occasionally three) pairs of side " teeth " or hooks (see Text-fig. 1,*g*) ..... *C. columna* (Spengler)
4. (3). Shell of adult generally larger than in foregoing species. Carino-rostral diameter up to 24 mm. and height up to 19 mm. The greater width of the shell proportionately to the height, and the thicker parietes make it easy to distinguish from *C. columna*. Soft body light and dark brown in colour. Scutum has almost no trace of an adductor ridge. The tergum has no adductor ridge and no spur. Crests for the depressor muscles about seven in number with pits between them. Cirrus II with grapple-like spines with three or more pairs of hooked side teeth ..... *C. brunnea* Moore.

Chamaesipho columna (Spengler), 1790

(Plate i, figure 5 ; Text-figure 1,*g*)

Lepas columna Spengler, 1790.

Chamaesipho columna Darwin, 1854 ; Gruvel, 1905 ; Broch, 1922 ; Nilsson-Cantell, 1926 ; Moore, 1944 ; Pope, 1945 ; Dakin, Bennett and Pope, 1948, 1952 ; Bennett and Pope, 1953, 1960 ; Womersley and Edmonds, 1958 ; Wisely and Blick, 1964.

The species *Lepas columna* was first erected by Spengler in 1790 for specimens which had probably been collected during one of Cook's Expeditions. Apparently, however, this material was incomplete, for Spengler did not refer either to the characteristic structures of the opercular valves or to the features of the soft body parts. The locality quoted was " Otaheite ".

In his monograph (1854), Darwin placed Australian and New Zealand specimens of *Chamaesipho* in Spengler's species, *L. columna*, but did so with some reluctance because, although Spengler's original description fitted his material in all but one of the few characters described, namely size, Spengler's account was not sufficiently detailed for Darwin to be sure that Australasian specimens belonged to the same species.

The dimensions given by Spengler for his *Lepas columna* were: height 26·5 mm. and breadth 17·0 mm. The largest Australian specimen in the present series has the following measurements: height 19 mm. and diameter 6·0 mm., which are considerably less than Spengler's figures. It is by no means certain that they represent the largest specimens in Australia but it is unlikely that any would ever be found as large as those of Spengler. On this count alone Darwin's use of Spengler's specific name for Australasian material must come into question.

In discussing New Zealand *Chamaesipho*, Lucy B. Moore (1944, p. 317) also expressed doubts about the advisability of using the name *C. columna* (Spengler) for the commoner New Zealand species of the genus *Chamaesipho*. She stated " It seems highly likely that our barnacle is not *L. columna* in Spengler's sense ". However, she continues to use the *C. columna* (sensu Darwin) for New Zealand and Australian material, since this name is so widely current in Australasia. It has been thought worth while in the present review to re-examine the position, and to attempt to clarify the situation.

Identification of Australasian Chamaesipho *with* L. columna *Spengler*

In the first place, it is not likely that a species of *Chamaesipho* from a tropical locality such as Tahiti (given as the type locality) would be identical with one from the southern shores of Australia and temperate New Zealand, especially when it is known that *C. columna* (sensu Darwin) is strictly limited in its Australian distribution to the temperate region reaching the northern, warmer end of its range some 400 miles south of the Tropic of Capricorn.

Although one or two isolated specimens of *C. columna* have been collected by the author at Lord Howe Island, on intertidal rocks, the species has failed to establish itself there. The two specimens found were stunted and atypical in shape, being more like *C. scutelliformis* in basal outline than regularly-shaped Australian *C. columna*. The seas around Lord Howe Island (lat. 32° S.) are warm enough to allow limited development of patches of reef corals and, at the time of collection, the author attributed *C. columna*'s failure to become established as being due to its inability to survive in the warmer sea temperatures there.

Tahiti lies well to the north of the Tropic of Capricorn and has a tropical molluscan shore fauna (fide Dr. H. Rehder in a personal communication to the author). The Australian species is favoured by the cooler conditions obtaining on the shores of southern New South Wales and Victoria judging by its size and density. In southern Tasmania, however, conditions may in farthest south be too cold for the development of large communities. On the grounds of sea temperatures alone the present author would agree with Moore that a New Zealand and Australian species of *Chamaesipho* is unlikely to be identical with one from the tropics. There is, however, the possibility that the locality quoted by Spengler for his *L. columna* may have been incorrectly recorded by the collector or have been confused during the long voyage to Europe. A similar case of a presumably transposed locality occurs in a mollusc described by Spengler (fide Dr. D. F. McMichael, Curator of Molluscs, the Australian Museum). A species of *Austrocochlea* which was collected by Cook's party, almost certainly at Kurnell, New South Wales, had been attributed to a wrong country. This mollusc material passed to Humphrey in England and thence to Spengler. It was finally described by Chemnitz (1781, Conchylien Cabinet (Martini), 5: 230, Plate 185, figs. 1850, 1851). It was stated there, to have come from New Zealand where no such shell occurs.

In the absence of the Type material, which the author was unable to locate in European Museums, it is only possible to re-examine available facts, and to take into account any recent findings and see if further light can be cast on the problem. The biggest objection to the acceptance of Spengler's

specific name for Australasian material has been the disparity in the size of the specimens described by Spengler and that of Australasian *Chamaesipho*. It is, however, believed that there is a possible explanation for this which will be set out below.

A re-examination of Spengler's description, as translated from the original Danish by Dr. T. Gislén (quoted in Moore, 1944, p. 316–7), reveals a statement (probably the one that convinced Darwin that he could use Spengler's name for Australian material): " A beautiful Patella . . . . is exteriorly completely covered by small cylinder-shaped Lepades, like those I have just described. They stand as small columns close to each other, and resemble a honeycomb because of their white angular openings. These also are from Otaheite ".

As limpets are absent from certain tropical islands, the author consulted Dr. Harald A. Rehder (Curator, Division of Mollusks, U.S. National Museum, Washington, D.C.) who has recently carried out extensive field work on Tahitian shores. He stated that limpets, of the genus *Cellana* (formerly known as *Patella*) are found in Tahiti as well as on Pitcairn Island but, he said, he had never seen any of them covered by barnacles of any kind. This statement is considered significant since, in his letter, Dr. Rehder said " Last year (1963) I covered fairly carefully the entire coastline of Tahiti " and as he was working on molluscs especially, it is felt he would have seen *C. columna* on limpets at least, even if he had not noticed them on the rocky reefs.

Several other scientists, at the author's request, have searched for *C. columna* on the shores of Tahiti but have also failed to find it. One is thus led to the supposition that it does not occur there today and probably never did. Spengler's material, judging from the date of publication, is probably material taken during one of Captain Cook's voyages, during which both Tahiti and New Zealand were visited and the suggestion is made that an error has occurred in giving the locality of the barnacles. Had it been " New Zealand " and not " Tahiti " everything in the original description would be explicable. A mistake, such as is suggested, is fairly likely, as both countries were inhabited by Polynesians and any place names obtained from the indigenous peoples would sound similar. Confusion between the two would be easy if labelling was inadequate at the time of collecting and cases of wrong localities have already been shown to have occurred in other specimens handled by Spengler from Cook's Expeditions.

Supporting New Zealand as the original locality for Spengler's *L. columna* are the following facts :—

(1) Spengler described limpets with their shells covered with closely packed *C. columna*, as being also from Tahiti. Such an association of barnacles and limpets is common in New Zealand (and Australia) but (fide Dr. Rehder) is not found in Tahiti.

(2) *Chamaesipho columna* has not been recorded in Tahiti since Spengler's original record. It is, however, one of the commonest intertidal animals in New Zealand, occurring in the honeycomb-like aggregation described.

(3) Only in recent years has Lucy Moore shown that not one, but two, species of *Chamaesipho* occur on New Zealand shores. Till that time both species were included in *C. columna* but an ecologist (Oliver, 1923, p. 535) had noted that barnacles from the upper part of the *Chamaesipho* range were of considerably larger size. It was this larger type that proved to be *C. brunnea* Moore.

It is suggested that herein may lie the explanation for the apparently impossibly large size given by Spengler for his species *L. columna*, which no subsequent worker has been able to equal in specimens from Australasia. If Spengler's original sample were New Zealand in origin, he may have been examining a mixed batch of *C. brunnea* Moore and *C. columna* (sensu Darwin). The large measurements quoted, may have applied to a specimen of *C. brunnea*,

which is much more likely to approximate to Spengler's dimensions than *C. columna*. Later workers in New Zealand failed to recognize the second species in the *Chamaesipho* zone until 1944, so it is quite likely that Spengler could also have made a similar mistake, especially if the material he had was eroded and had the opercular valves and soft parts missing, as apparently it had. The acceptance of a New Zealand origin for Spengler's *L. columna* would make his original description much more credible but would still leave doubts as to which of the two New Zealand species should carry the specific name *columna*. Many of the shell characters given are equally applicable to both the species from New Zealand but, of the few remaining characters, the following apply better to the smaller more ubiquitous New Zealand species of *Chamaesipho*: (1) the description of the orifice; (2) the barnacles' habit of growing in honeycomb-like aggregations; (3) the orifice is more nearly equal in size to the basal opening of the shell and sometimes is larger. Spengler described the opening of the shell thus, " It is wide and much larger than the lowest part of the shell "; and finally (4) its habit of forming a honeycomb-like covering on the shell of a limpet. *Chamaesipho brunnea* is of a size too large to crowd enough specimens on to a limpet shell to produce a honeycomb appearance; moreover Moore (1944) does not record it on limpets. The only one of Spengler's characters that would better fit *C. brunnea* rather than the smaller species is that of size.

The majority of Spengler's characters therefore apply to the smaller Australasian species and it is felt by the present author that the specific name *C. columna* should rightly be restricted to it. This would fortunately fit in with Darwin's (1854) use of *C. columna* for the small Australian and New Zealand barnacles, of which he gave an excellent augmented description, and Miss Moore's use of the names *C. columna* and *C. brunnea* for the two New Zealand species would be valid. The use of *C. columna* (sensu Darwin and Moore) is and has been in wide use in Australia and New Zealand for approximately 100 years. It is therefore desirable to continue this usage if it can possibly be done without infringing the International Code. It is hoped, at a later date, to take the necessary steps and, after due enquiries, to establish neotypes for the species and set the current use of name on a proper basis.

Description of Australian C. columna

Darwin supplemented the original description of *C. columna* by adding considerably detailed accounts of the opercular valves and soft parts as well as the shell plates, and Broch (1922) and Nilsson-Cantell (1926) have added further details. A more detailed description of New Zealand material was given by Moore in order to differentiate between *C. columna* and *C. brunnea*, and there is little need to add to her account. Shell characters and ecological data for Australia are described and illustrated in Pope (1945); Dakin *et al.* (1948); Bennett and Pope (1953, 1960); and Womersley and Edmonds (1958). A few comments on similarities or differences between Australian and New Zealand specimens will be given.

Shell

In shape and appearance of the shell and orifice, Australian *C. columna* are comparable with the New Zealand ones but the dimensions of the largest Australian specimen from a collection made at Cape Bridgewater in Western Victoria are slightly larger than measurements quoted by Moore, namely, height 19 mm. and width 6 mm. The surface of the parietes is only occasionally pitted in Australian specimens and there is little trace of regular ribbing on the shell; however, the lower edge of the shell may have a crimped, wavy outline in crowded specimens. As in New Zealand, juvenile specimens may show six shell valves but these are soon reduced to four and all trace of sutures between them may subsequently be lost.

The plates of the shell may be thicker in the low-growing individuals forming part of a " honeycomb " or in solitary specimens, but in crowded, tall specimens the walls are generally thin and brittle. The sheath is comparatively short and lined by a dark membrane and has a series of darker slightly-raised rings, marking the successive positions of attachment of the opercular membrane during growth. The term " rifled " (used in Gislén's translation of the original description) implying a spiral marking on the sheath is not strictly correct, at least in Australian material. The lower margin of the sheath does not depend freely into the shell cavity. The structure of the opercular valves is distinctive among Australian Chthamalidae especially in the case of the tergum, owing to the presence of the 4–6 deep pits which, with their separating crests, form the attachment for the depressor muscles and occupy about half the length of the basal margin. The illustrations of these valves by Moore (1944, Plate 46, left column, *a*) and Darwin (1854, Plate 19, fig. 3,*b*,*c*) should be consulted, rather than those of Nilsson-Cantell (1926, Text-fig. 4,*h*,*i*) which show the tergum with crests without associated pits for the attachment of the depressor muscles. In several Australian specimens there was a slight demarcation of a spur from the margin of the tergum. In most, however, the spur and the basi-scutal corner of the valve are one and the same.

Soft Body

The structures of the soft body have been adequately described by Moore and only slight variations from New Zealand material are found in the Australian population. *Colour*: The colour is navy blue in general but the free margins of the scuto-tergal folds may be a horny brown colour. The cirri and the proximal part of the penis are also navy blue but the prosoma and thoracic region are lighter in colour.

Trophi: The *labrum* is bullate with a wide, V-shaped groove, the anterior border of which is fringed by numerous crowded hairs, especially towards the peak of the V. Moore reports five denticles on the labrum, and in the present examples there are also five but they are asymmetrically placed, with one denticle placed on one arm of the V and four on the other. Nilsson-Cantell (1926, Text-fig. 4*a*) shows a considerably larger number of denticles. The *mandible* has four, or sometimes five, teeth of which teeth three and four may be doubled. The fifth tooth, when present, is centrally placed in the pectinated lower section of the jaw as shown in Nilsson-Cantell (1926, Text-fig. 4*c*). This pectinated area of the jaw has regular, fine teeth except where a fifth tooth is present and where the strong tooth-like spine or spines form the lower angle of the mandible. There is no secondary side-toothing on the main teeth and the structure of the whole organ is strongly reminiscent of the jaw pattern found in the *stellatus* subgroup of genus *Chthamalus*. The first *Maxilla* is as described by Moore (1944). The two large upper spines are followed below by 3–5 pairs of small spines in the " notch ". A second small notch delineates, below, a central, fairly straight cutting edge which may carry up to seven pairs of larger spines, second in size only to the topmost ones. The lower rounded point of the maxilla I has 6–7 pairs of finer spines. The upper and lower margins are haired. *Maxilla II* in the present sample differs in shape from Text-fig. 4*e* in Nilsson-Cantell (1926) in that its free tip is generally more pointed and projects further than the rest of the cutting edge. The notch is distinct and without spines, although there are numerous spines above and below it. The spines on the anterior border are in general longer than shown by Nilsson-Cantell.

Cirri

Cirri I and II are distinctly shorter than Cirri IV–VI, while cirrus III is intermediate in size and structure between the other two groups. *Cirrus I* has the anterior ramus longer by several segments than the posterior one and

is stouter towards its base. Both rami carry numerous fine spines, bunched anteriorly, many of which are pinnate. In addition, peculiar grapple-like, stout short spines also occur on the central segments, as described by Moore (1944). *Cirrus II* generally has its anterior ramus shorter by at least three to four segments (or even more) and is stouter than the posterior one which may be similar in general build or longer and more filiform, as noted by Darwin, Broch (1922) and Moore. Many had cirrus II with both rami similar in build (except that the anterior one is longer and carries considerably more setation) but one or two had the posterior ramus longer and with the more distal segments similar in structure and setation to the rami of the more posterior cirri but in these, the three or four basal segments carried bunches of pinnate setae plus crowded groups of grapple-like spines of the type shown in Text-fig. 1,*g*. The anterior ramus of cirrus II carries dense bunches of spines (both pinnate and ordinary) anteriorly, together with numerous grapple spines on the more distal segments. They are specially abundant round the bases of segments 4–6. These grapple-like spines are obviously similar in origin to the stout lanceolate spines seen in certain species of the genus *Chthamalus* and in fact are closely similar in build to those of *Chthamalus intertextus*. In all the grapple spines the paired recurved side spines are less numerous than the serrations in the lanceolate spines of other Chthamalids. In Australian material grapple spines vary both in the number of segments on which they occur and also in the number found on each segment. They appear to serve as grapples to hold food particles. *Cirrus III* generally has sub-equal rami and otherwise is as described by Moore, possessing both the plumose spines and the hooked, three- or five-pointed grapple spines described for cirrus II. The latter occur on the basal segments amidst the thick tuft of spines. No specimen with antennae-form posterior rami have been seen in the present batch. Each segment of cirrus III towards the centre of the ramus carries five pairs of long normal spines. *Cirri IV* to *VI* are normal in structure and nearly equal in size ; moreover, the paired rami are sub-equal. Each segment is bullate and bears four pairs, sometimes five pairs, of stout spines of which the distal pair is longest and size decreases towards the proximal part of the segment.

The *penis* is stout, ringed and even in a somewhat contracted state is longer than cirrus VI. It tapers rapidly towards its tip which has scattered hairs along it. There are two tufts of moderately long hairs at the very tip. There is no *caudal appendage*. In the Sydney area of New South Wales, Wisely and Blick (1964) record *C. columna* breeding in winter and early spring.

Habitat

Chamaesipho columna shows a preference for attaching to a rocky substrate on exposed coasts in Australia and its range does not extend far inshore, in inlets or harbours. Moore records it " very occasionally " on wood, but none have yet been recorded on this substrate in Australia. It grows in the upper half of the intertidal zone approximately up to the mean or the lower high water levels of spring tides. The upper level of its distribution depends tremendously on the amount of wave action in the area. Its range extends downshore to a varying degree, according to environmental conditions and whether it meets competition for attachment from other species. In New South Wales its vertical range is apparently limited below, by competition with the two surf barnacles, *Catophragmus polymerus* and *Tetraclita rosea* for, in areas of western Victoria where lower sea and air temperatures exclude the surf barnacle, *Catophragmus polymerus*, *C. columna* ranges further down the shore to the short algal turf near low water of neap tides (Bennett and Pope, 1953, p. 117).

Geographical Distribution

Australian : *Chamaesipho columna* occurs on the temperate shores of Australia from the region of Cape Byron in northern N.S.W., southwards to

Victoria and Tasmania, where it occurs on all exposed coasts and, finally, it ranges westward along the southern coast of the continent to Point Sinclair (in the eastern half of the Great Australian Bight) where it is recorded by Womersley and Edmonds (1958, Plates 1, 2). It has also been taken on one occasion at Lord Howe Island in the Tasman Sea but had failed to establish itself here.

World Occurrence: Moore has recorded *C. columna* on all the shores of both the North and South Islands of New Zealand and in the Kermadecs. The validity of the record of this species by Spengler for Tahiti (Otaheite) has been challenged above and, until it is confirmed, it is believed that it should be disregarded.

Discussion

The collections studied for the present review contained individuals in each species of markedly greater size than any previously described. As the specific distinctions in many species of Chthamalids become increasingly clear in fully grown material, the descriptions have been modified, where necessary. It is felt that the recording of details of anatomy for each species will be of special interest to workers presently engaged in a phylogenetic review of the family. The importance of basing specific identifications on as many characters as reasonably can be used, cannot be overstressed because of the undoubtedly close relationships evident between species from widely separated zoogeographical regions as well as those from adjacent localities. The differences between species are realities but are often very difficult to define, and are best shown in such details as the structure of the serrated spines of cirri I and II or the fine differences to be seen in the pinnate spines (see Text-fig. 1,*b–e*) which are less likely to vary than the more evident shell characters generally used.

While the general patterns of the trophi of most chthamalids are basically alike, the fine differences between species can often best be appreciated by viewing the barnacle's "face" from the front, before beginning dissections of the mouth parts. The shapes of the "beard" and "side whiskers" are often quite characteristic and some species are notably more bristly than others. *Catophragmus polymerus*, for instance, is extremely well provided with setae round its mouth parts. There is often also a characteristic colour pattern round the mouth.

The degree to which the rami of cirri I and II are curved in over the mouth is also characteristic in certain species and the type of teeth and general arrangement of the teeth and hairs above the groove of the labrum can also be of specific importance. However, the necessity of focusing the microscope through several planes should be remembered, as there may be teeth on two separate levels and hair on yet another. The very distinct triangular teeth of *Chthamalus withersi*, lying on either side of the peg-like teeth, seem to have been overlooked previously because of failure to explore the different levels of the groove of the labrum.

In existing keys to species of the genus *Chthamalus*, stress has been laid on the structure of the mandible as a means of subdividing this somewhat unwieldy genus into sub-groups. The present study has shown, however, that the dividing line between those species with the so-called tridentate or *hembeli* jaw and those with the quadridentate or *stellatus* kind of mandible is sometimes a rather hazy one, especially if one is dealing with juveniles or individuals which are regenerating jaws after damage (by no means a rare occurrence). It is considered that some other characters might be preferable to use for the primary separation of *Chthamalus* into sub-groups. For example, the presence or absence of calcareous layers in the basis, even if it is a product of secondary calcification, might result in more natural subgroups since it would bring together *Chthamalus hembeli* (Conrad), *C. intertextus* and *C. calcareobasis* Henry which have been shown by Newman (1961) to have many

shell structures in common that differ rather markedly from remaining species in the genus, and this might be borne out by comparisons of the morphology of their soft bodies which were, unfortunately, not available in the present instance for examination.

Another interesting character which may be obscured, unless special care is taken during the making of microslides of the labrum, is seen in species like *Chthamalus intertextus* and *C. caudatus*, as contrasted with species like *C. malayensis* and *C. antennatus* which have the normal rounded or bullate labrum, characteristic of the family. It is the semicircular, rather funnel-like structure on the front of the labrum above the palps, best seen when the " face " of the barnacle is examined before dissection. The muscles which can regulate it and cause it to assume the funnelled shape which leads towards the mouth, can be seen in cleared preparations, and in *C. intertextus* the whole of this peculiar structure, with its pitted surface (like a brain coral in appearance), seems to function as a hopper to channel the food particles (swept towards it by the incurved cirri I and II and by the palps) towards the mouth.

Other species of *Chthamalus* may also possess the peculiar type of labrum described above, for one author remarks, without being specific, that the semicircular extension on the labrum of *C. caudatus* is seen in several other species of *Chthamalus*. If it is of more widespread occurrence, it might prove to be a significant character for differentiating subgroups within the genus since, so far as Australian material is concerned, it is associated with species included by Nilsson-Cantell (1921) in his so-called *hembeli* group.

Living, as they do, in the upper half of the intertidal zone the actual times available to the various species of shore chthamalids for feeding is limited to their periods of immersion. This ranges from a mere 2% of the time at the highest levels to a maximum of approximately 30% of the time for mid-tide species. That the Chthamalidae have managed to flourish in such conditions is a clear indication of the efficient food-capturing adaptations that have been evolved within the group. It was therefore of interest to find that only two broad patterns of food-capturing have apparently been evolved and that they can be correlated with the degree and force of water movements experienced by the barnacles during feeding. The two groups of species showed morphological difference in their mouth parts and cirri which are considered to be of an adaptive nature.

Some of the adaptations enabling chthamalid barnacles to catch sufficient food appear from circumstantial evidence to be very effective. Attention was first drawn to this matter during the preparation of microslide mounts. Many cirri and mouthparts were entangled with food particles and debris and much patient brushing and picking clean of serrated spines was necessary to reveal the underlying structures. It was noticed that there were two fairly well defined patterns of distribution of the particles and one could be associated with the requirements of feeding on the high shore for very short periods under relatively calm conditions, and the other could be associated with the need to capture and hold food in turbulent waters—turbulence due either to surf or to choppy seas, or to the currents caused by strong tidal ebb and flow. These last are greatest in the mid-tidal zone.

In *Octomeris brunnea*, *Chthamalus caudatus* and *C. withersi* food particles were found fairly evenly distributed and entangled in the setation of the cirri and mouth parts and were not aggregated markedly into bolus-like clumps. The exception was *O. brunnea*, where a slight tendency was noticed for particles to be caught and amassed in the bunches of pinnate setae towards the base of the anterior ramus of cirrus III. However, these aggregations of food were not as large as those seen in species to be mentioned below.

Feeding in these high shore, tropic species is apparently carried out in a hurried and indiscriminate way by the sweeping of all particles forwards

towards the labrum. In those species with the semicircular processes above the palps the food can be quickly diverted towards the mouth and even the possession of a flat-fronted labrum, rather than a bullate one, would have adaptive advantages for feeding. There is no evidence of a tendency to " pick over " the food particles. It is perhaps significant that among the Australian species of *Chthamalus* those with the most highly developed semicircular funnels on their labra (*C. caudatus* and *C. intertextus*) tend to be hypobiotic in habit. Is this adaptation of the labrum connected in some way with their need to feed in an " upside down " position? However, this would have to be verified experimentally.

In the turbid and briefly slack water conditions obtaining on the high shore during normal conditions of high tide in tropical seas, there is no lack of suspended detritus or other particles, as may be verified by standing on this part of the shore when the tide is at its highest or by looking at the deposits of organic matter left at high tide mark on beaches. One can well imagine the effectiveness of making a series of quick, sweeping dips with very setose cirri in this concentration of food particles and the brushing of them quickly towards the mouth, as outlined above. In the swifter flowing water movements of the mid-tide zone or under the action of surf, the retention of fine detritus would be almost impossible owing to the flushing action of the water. Here other feeding mechanisms designed to entangle and hold larger food particles as well as detritus have been developed.

In *Catophragmus polymerus*, *Chamaesipho columna*, *Chthamalus antennatus*, *C. intertextus* and *C. malayensis*, in addition to the particles of food distributed randomly among the pinnate setae, there were compact, rounded clumps of food, entangled and held by the serrated spines and these aggregations were most difficult to dislodge by brushing. The spines often had to be picked clean by means of fine needles in order to show their structure. The fact that these serrated or grapple spines are situated opposite the level of mouth and within reach of the jaws is also considered significant. Small planktonic organisms and detritus were detected in the food clumps on the spines. It would appear that particles sieved and " dip-netted " from the water by the tufts of pinnate setae are gradually passed downwards on the ramus and accumulated and held by the stout serrated spines till they form small rounded masses. Such an accumulation could later be picked or brushed off by the toothed and setose mandibles or other mouth organs and passed into the mouth. Indeed, several such balls of food matter were discovered between the jaws of individuals which had been feeding just prior to preservation. In such species where food is picked over and transferred to the mouth by the trophi from the anterior cirri, a bullate labrum would be no disadvantage.

Serrated spines or grapple-spines occur in *Catophragmus*, *Chamaesipho* and *Chthamalus antennatus* which live on surf beaten rocks and also in *Chthamalus malayensis* and *C. intertextus*, the two species which live on those parts of the tropical intertidal zone most exposed to water movements. While the wave action they experience is not comparable with that consistently endured by the three southern Australian species mentioned, it is nevertheless the maximum experienced within the Australian tropics and the one most consistently subjected to strong ebb and flow of tidal currents.

No ecological information was supplied with the New Guinea material of *Chthamalus intertextus*, except that it occurred with *C. malayensis* in the mid tide zone. Hiro (1939) records the species also with *Octomeris brunnea* " on the underside of boulders " at Taiwan, so the peculiar combination of feeding adaptations it possesses may be a reflection of its special needs for feeding both in an inverted position and in waters showing a considerable degree of movement.

If serrated spines and extra setation are indeed effective adaptations for feeding in turbulent seas, one would expect to find most adaptive structures of this kind in the surf barnacle, *Catophragmus polymerus*, since of all Australian

intertidal chthamalids it is subjected to roughest seas for the longest periods and, conversely, one would expect to find fewest of them in *Chthamalus withersi* since it occurs in areas subjected to least water turbulence.

This is indeed so, for *Catophragmus* (Text-fig. 1,*a*, *b*) not only has cirri and mouth parts that are extremely setose, with many setae of the feathery pinnate type, but it also carries numerous stout barbed spines on the distal segments of the rami of cirrus II; the groove of the labrum, above the mouth carries both hairs and teeth. In addition, each of the segments of the rami III–VI carries a small thick tuft of shorter bristles situated centrally between the rows of paired longer spines. These short bunches of spines serve to trap and hold food particles (Text-fig. 2,*a*). Such bunches of short spines also occur in stalked barnacles in the genus *Mitella*, but they are not found generally in any other species of the family Chthamalidae in Australia. Darwin (1854) mentions that in *Catophragmus imbricatus* the intermediate spines on each segment of cirri III to VI are fewer in number than in *Catophragmus polymerus*. By contrast *O. brunnea* (generally considered as a closely related genus) has tufts of short intermediate spines on only a few of the basal segments of the anterior ramus of cirrus III and not on every segment of cirri III–VI. Their limited occurrence in *Octomeris brunnea* can perhaps be linked with the fact that such structures are unnecessary for food capture in calmer tropical seas. In fact they might be a hindrance to the quick propulsion of fine food particles towards the mouth.

In *Chthamalus withersi* the front of the labrum above the palps is somewhat flattened, but in no specimen among those dissected did any individual show signs that the labrum could assume the funnel-like shape seen in *C. caudatus* and *C. intertextus*. The smaller central teeth and wide shallow groove of the labrum could be adaptations allowing free movement of minute food particles into the mouth. As organs to strain the particles from the water and propel them towards the mouth, the unspecialized but very setose cirri I and II are very effective and the incurving of their rami would be an added advantage for the quick and effective gathering and swallowing of food in a short time. Short, serrated spines are completely lacking in *C. withersi* which would appear, therefore, to be unable to hold aggregations of food or catch and imprison active plankton of slightly larger size.

Intermediate between *Catophragmus* and *Chthamalus withersi* in the adaptations developed for holding and concentrating food particles are *Chamaesipho columna*, *Chthamalus antennatus*, *C. malayensis* and *C. intertextus*. All have either short spines with serrations or grapple-like spines on their second cirri, as well as the tufts of pinnate setae. In addition *C. intertextus* and *Chamaesipho columna* have grapple-spines on a few basal segments of the anterior ramus of cirrus III, directly opposite the mouth, though in neither of these species are there tufts of spines on all the other cirral segments. *Chthamalus malayensis* has extra stout spines posteriorly on certain of the basal segments of the anterior ramus of cirri I and II, which are thought to act as devices locking together the two rami much as hamuli may lock together the wings of certain insects. In this way a wide and more rigid structure could result for dipping food particles from the water. Such stout posterior spines occur only on the anterior rami and are often found interlocked with the fringe of setae of the posterior ramus but, as with the other structures mentioned as possible feeding adaptations, much experimental work and detailed study of corresponding organs in other barnacles is necessary before their effectiveness or otherwise as adaptations for feeding in the rigorous environment of the upper half of the intertidal zone can be truly evaluated.

The different combinations of adaptive feeding structures found, for instance, in each of the four tropical species in the genus *Chthamalus* in Australia point to the fact that each of the species may indeed be feeding in a slightly different way or on a slightly differing diet, and hence be occupying a different

ecological niche, even when, as has occasionally happened, three of them have been collected within a circumscribed area of a few square centimetres. An intensive study of the group Chthamalidae could do much to clarify some of our ideas about intertidal niches and related problems.

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EXPLANATION OF PLATES I AND II

Plate I. Five Species of Australian Chthamalidae. 1, *Chthamalus intertextus* growing on basalt. Traces of interlocking laminae (like lines of growth) appear adjacent to the wavy suture, to the left of the lowest shell plate. 2, *Catophragmus polymerus*. 3, Well-grown and heavily eroded *Octomeris brunnea* (originally described as *O. intermedia* but proved to be adult of species in fig. 6). *Left* (from below). showing central hole in basis, and *right* from above. 4, Fully grown *Chthamalus antennatus* from Sydney. Note light enamel-like apices on certain plates of shells (3 top left barnacles). Accompanying littorinid is *Melarapha unifasciata*. 5, A group of *Chamaesipho columna* with accompanying littorinid molluscs. 6, Juvenile *Octomeris brunnea* (not to same scale as those in view 3) with narrow ribs and well-defined interlocking sutures.

Plate II. Some Tropical *Chthamalus* spp. and their habitats. 1, Roots of the Red Mangrove, *Rhizophora*, provide a suitable substrate for *Chthamalus* barnacles. A stream near Cairns, Queensland. 2, Closer view of the root system of *Rhizophora*, showing *Chthamalus withersi* generally on the lower side of the roots. 3, Dense populations of *Chthamalus malayensis* in a favourable habit, tropical Queensland (see text). 4, Typical habitat for *O. brunnea* and *Chthamalus caudatus* in shaded sides or under the overhang of tumbled boulders, on the higher areas of tropical shores. These two barnacles are not visible on the rocks normally, and are generally overlooked. 5, Pier of road bridge over a coastal creek in central coastal Queensland, showing dense barnacle populations in upper intertidal zone. From the pointing finger upwards, *Chthamalus withersi* covers the surface, while below this a species of *Balanus* replaces it entirely. 6, The smooth, ribbed form, common in juvenile *Chthamalus malayensis* or in Queensland specimens generally. 7, Eroded adult *Chthamalus malayensis* from Western Australia wharf timber. A single *Chthamalus antennatus* from Sydney has been placed alongside (in the white circle) for comparison in size and sculpturing.

CHROMOSOME NUMBERS IN SOME AUSTRALIAN LEAFHOPPERS (HOMOPTERA AUCHENORRHYNCHA)

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With an Appendix by J. W. Evans, Australian Museum, describing a new genus and species of Eurymelidae

(Plate iii)

[Read 31st March, 1965]

Synopsis

Chromosome numbers are recorded for twenty-seven species of Eurymelidae, thirty species of Cicadellidae and eight other species of Homoptera Auchenorrhyncha. A study of meiosis reveals bivalent co-orientation at Anaphase I in the Auchenorrhyncha while a consideration of chromosome numbers suggests several trends related to the phylogeny of the Cicadellidae. Having diffuse centromeres (or polycentric chromosomes), chromosome number may be a more variable character in leafhoppers than in other groups.

Introduction

The Australian flora has for some time been subject to cytological investigation (for review see Smith-White, 1959), while the fauna, in particular, insects, has suffered neglect in this respect. The incomplete taxonomy of most insect groups and the unavailability of keys, continue to make such studies difficult.

Australian leafhoppers, however, constitute a welcome exception for, although keys are not yet available, the group has been studied extensively by Dr. J. W. Evans and the identification of specimens has become practicable.

In the present work an attempt has been made to examine representatives of all distinctive groups but efforts were especially concentrated on collecting a representative sample of the only family of leafhoppers endemic to Australia, the Eurymelidae.

Interest has been added to the problem because leafhoppers belong to the Hemiptera, the only known order of insects whose chromosomes lack localized centromeres (Hughes-Schrader & Ris, 1941 ; White, 1954). It was hoped the study might reveal the phylogenetic significance of chromosome number and its variation in groups where the restrictions imposed by localized centromeres are not present.

Methods

Material for cytological examination (usually the whole insect) was fixed in ethanol-acetic acid (3 : 1) for 24 hours and then washed and stored in absolute alcohol at −10° C. Storage under these conditions did not result in any detectable deterioration of the material. Some specimens were fixed and stored in chloroform : alcohol : acetic acid solution (4 : 3 : 1). This was equally satisfactory, except that some difficulty was encountered in spreading the cells after several months of storage.

Spermatogonial squashes were made in aceto-orcein. Although both meiotic and mitotic cells were examined where possible, the bulk of the chromosome determinations were made on meiotic cells of 1st and 2nd division.

TABLE 1

List of Chromosome Numbers

Family and Species	Haploid Chromosome No.	Locality*
CICADELLOIDEA		
1. EURYMELIDAE		
EURYMELINAE		
Eurymela		
fenestrata Le Pelletier & Serville	10+X	3, 4, 5, 8, 10, 13, 14, 16, 19, 20, 22, 53
distincta Signoret	10+X	23, 24
erythrocnemos Burmeister	10+X	25
Eurymeloides		
pulchra Signoret	10+X	4, 8, 26, 27, 28
bicinctus Erichson	10+X	29, 32
punctata Signoret	10+X	40, 41
perpusilla (Walker)	10+X	47
Eurymelops bicolor (Burmeister)	10+X	5, 19, 41, 42
Paureurymela parva Evans	10+X	25
Pauroeurymela amplicinta (Walker)	10+X	39
Eurymelita terminalis (Walker)	10+X	43, 44, 45
Aloeurymela gearyi Evans†	9+X	43, 46
Eurymelessa moruyana Evans	10+X	47
Eurymelella tonnoiri Evans	10+X	18
POGONOSCOPINAE		
Pogonoscopus myrmex China	10+X	31
IPOINAE		
Ipoella		
fidelis Evans	10+X	4, 34, 43, 46, 5, 41
sp. (novo) (62.11.200)	10+X	5
sp. (novo) (62.4.33)	10+X	13
Ipoides		
hackeri Evans	10+X	43
honiala (Kirkaldy)	10+X	48
Anipo		
pallescens Evans	10+X	5, 13
brunneus Evans	10+X	27, 28
Katipo		
rubrivenosa (Kirkaldy)	10+X	5, 6, 39
signoreti Evans	10+X	47
Anacornutipo lignosa (Walker)	10+X	19, 20, 43, 46
Opio multistrigia (Walker)	6+X	5
2. CICADELLIDAE		
ULOPINAE		
Taslopa montana Evans	9+X	1, 33
	8+XY	38
Cephalelus		
minutus Evans	10+X	3, 11, 17
sp. (64.2.35.2)	10+X	38
JASSINAE		
Batrachomorphus sp. (64.1.34.4)	9+X	34
APHRODINAE		
Euacanthella palustris Evans	9+X	15
TARTESSINAE		
Tartessus		
flavipes Spanberg	13+X	18
fulvus (Walker)	12+X	1, 30, 33, 36, 38, 48, 49, 55
sp. (62.4.69)	13+X	44
AUSTROAGALLOIDINAE		
Austroagalloides brunnea Evans	11+X	29

* See end of Table 1 for key to localities.
† See Appendix.

TABLE 1—*Continued*

List of Chromosome Numbers

Family and Species	Haploid Chromosome No.	Locality*
LEDRINAE		
Thymbrini		
Rhotidoides dongarrensis Evans ..	10+X	30
Rhotidoides sp. (64.9.30.2) ..	10+X	30
Putoniessa sp. (64.4.33.3) ..	10+X	33
Stenocotini		
sp. (64.9.30.5)	10+X	30
CICADELLINAE		
Cicadella angustata (Evans) ..	8+X	1
IDIOCERINAE		
Idiocerus sp. (63.4.17.4)	8+X	17
HECALINAE		
Paradorydium brighami Kirkaldy	10+X	34
TYPHLOCYBINAE		
Erythroneura sp. (63.4.15.6) ..	9+X	15
Typhlocyba sp. (63.3.4.2)	9+X	4
sp. (64.3.38.4)	8+XY	38
DELTOCEPHALINAE		
Deltocephalus		
longuinquus (Kirkaldy)	4+X	17
	3+X	17
taedius (Kirkaldy)	5+X	35, 15, 37
sp. (64.1.34.2)	4+X	34
sp. (64.3.18.4)	5+X	18
sp. (64.3.1.14)	5+X	1, 3, 38
sp. (64.3.15.5)	6+X	15
sp. (64.3.15.1)	5+X	15, 35
Phrynophyes kirkaldyi Evans ..	9+X	3
Aconurominus flavidiventris (Stål) ..	7+X	17
Balclutha sp. (64.1.34.5)	7+X	34
Nesoclutha obscura Evans	8+X	17
3. MEMBRACIDAE		
Sextius virescens Fairmaire	10+X	5, 48, 50, 51, 54
Eufairmairia fraternus Distant ..	10+X	19, 49
Other AUCHENORRHYNCHA		
CERCOPOIDEA		
Philagra parva Donovan	7+X	5, 48
CICADOIDEA		
Cyclochila australasiae Donovan ..	9+X	5
FULGOROIDEA		
FLATIDAE		
Siphanta sp.	13+X	5
EURYBRACHIDAE		
Dardus erebus Distant	13+X	51, 52
FULGOROIDEA sp. (64.9.30.6)	13+XY	30
COLEORRHYNCHA		
PELORIDIIDAE		
Hemiodoecellus fidelis (Evans)	2N=22, 23 in males	2

* See end of Table 1 for key to localities.

Key to Localities

1. Collin's Bonnet, T.; 2. Shoobridge Bend, Mt. Wellington, T.; 3. Mt. Nelson, T.; 4. Sandy Bay, T.; 5. Rookwood, N.S.W.; 6. Spring Hill, T.; 7. Hollow Tree, T.; 8. Homebush, N.S.W.; 9. Huon River, Franklin, T.; 10. Parramatta, N.S.W.; 11. Geeveston, T.; 12. Arve River, Hartz, T.; 13. Roseville, N.S.W.; 14. Como. N.S.W.; 15. Springs, Mt. Wellington, T.; 16. Blakehurst, N.S.W.; 17. Bruni Island, T.; 18. Lake St. Clair, T.; 19. Wellington, N.S.W.; 20. Coonabarabran, N.S.W.; 22. Sale, Vic.; 23. Murrurundi, N.S.W.;

24. Lucas Heights, N.S.W. ; 25. Barjarg, Vic. ; 26. Bankstown, N.S.W. ; 27. Windsor, N.S.W. ; 28. Dubbo, N.S.W. ; 29. St. Ives, N.S.W. ; 30. King's Park, W.A. ; 31. Red Hill, W.A. ; 32. Mt. Colah, N.S.W. ; 33. Adamsfield, T. ; 34. Deniliquin, N.S.W. ; 35. Cradle Mt., T. ; 36. Huon Valley, T. ; 37. Huonville, T. ; 38. Plateau, Mt. Wellington, T. ; 39. Warrah, N.S.W. ; 40. Regents Park, N.S.W. ; 41. Chester Hill, N.S.W. ; 42. Canberra, A.C.T. ; 43. Bourke, N.S.W. ; 44. Nyngan, N.S.W. ; 45. West Wyalong, N.S.W. ; 46. Walgett, N.S.W. ; 47. Grampians, Vic. ; 48. Glenmorgan, Qld. ; 49. Gunnedah, N.S.W. ; 50. Trangie, N.S.W. ; 51. Westmar, Qld. ; 52. Toowoomba, Qld. ; 53. Launceston, T. ; 54. Bendigo, Vic. ; 55. Cobar, N.S.W.

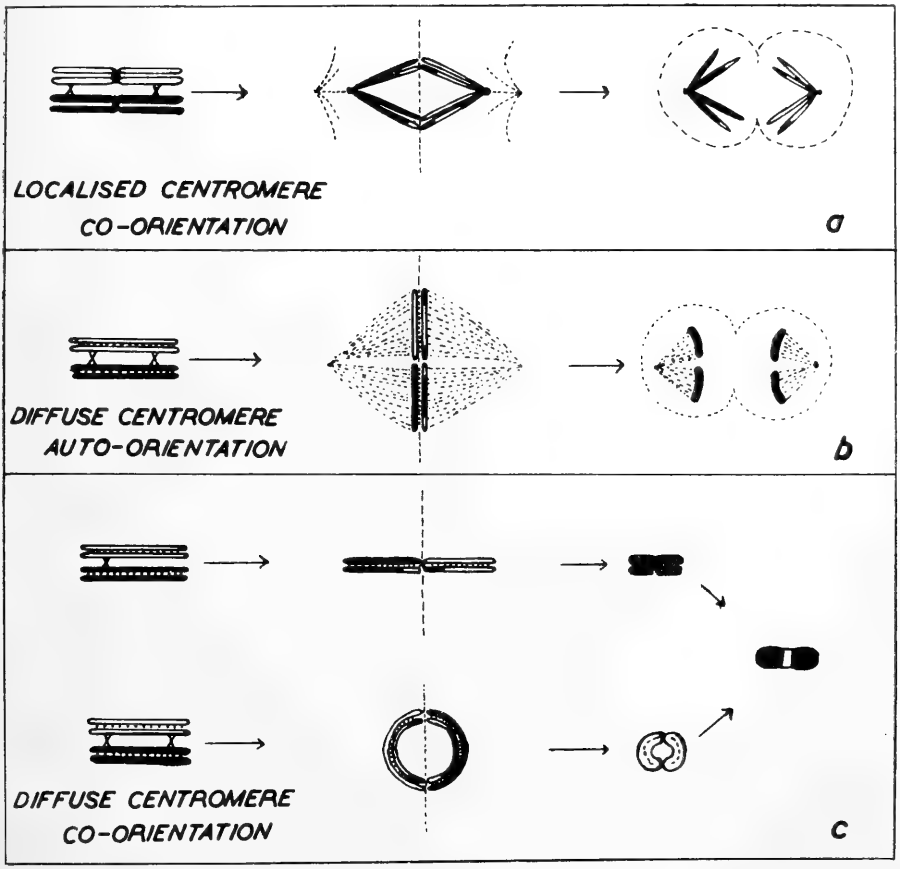

Fig. 1. Diagrammatic representation of bivalent behaviour at first division of meiosis : (*a*), when the centromeres are localized as occurs in most organisms ; (*b*), in Aphids and Coccids and the plant genus, *Luzula* ; (*c*), in Auchenorrhyncha and Psyllidae indicating the two ways of forming the metaphase bivalent which result in co-orientation. (*c*) was interpreted from meiotic cells of *Eurymela fenestrata*.

Characteristics of Meiosis

During meiosis and mitosis in Homoptera the spindle attaches along the entire length of the chromosome, producing characteristic configurations at metaphase and anaphase (Fig. 1, *b*, *c*, and Plate iii). In aphids and coccids (Fig. 1, *b*) the homologues of each bivalent orient independently on the metaphase plate (auto-orientation) resulting in post-reduction (Ris, 1942, 1945 ; Brown, 1954 ; Hughes-Schrader, 1948). In Psyllids (Whitten, unpublished) and in the Auchenorrhyncha the bivalents orient in the normal manner (co-orientation) resulting in pre-reduction (White, 1954 ; Halkka, 1960*a*). Rhoades (1961) questions the occurrence of co-orientation in the Auchenorrhyncha and suggests careful observation may reveal that the diffuse centromere is always associated

with auto-orientation. Unequivocal evidence has been found to show this is not the case.

In *Deltocephalus longuinquus* (Cicadellidae), males normally possess four bivalents plus an X chromosome. However, one individual was found with three bivalents plus an X while another had two bivalents, a trivalent and an X (see Fig. 2 and Plate iii, *h*). Since all the other species of *Deltocephalus* so far examined have four or more bivalents (see Table 1) it is suggested that a fusion has taken place between two chromosomes in *D. longuinquus* and the population is polymorphic for this fusion.

An analysis of anaphase I and metaphase II cells from the heterozygous individual indicated that the fused chromosomes go to one pole while the two single chromosomes are drawn to the opposite pole. This outcome is not possible if auto-orientation were operating. A careful analysis of chiasma terminalization and bivalent orientation in *Eurymela fenestrata* confirms this finding (Fig. 1, *c* and Plate iii, *b*, *c*, *d*).

The phylogenetic significance of co-orientation in the Auchenorrhyncha and the Psyllidae will be discussed elsewhere.

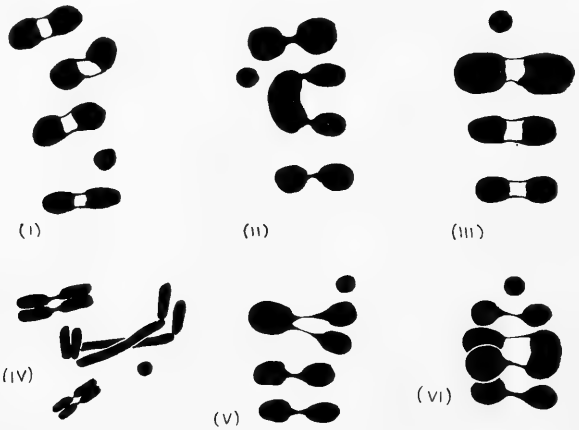

Fig. 2. (i-iii), Different karyotypes in the one population of *Deltocephalus longuinquus*. In (ii) there is heterozygosity for a chromosomal fusion, while in (iii) there is homozygosity for the fusion ; (iv), diakinesis in the heterozygous individual ; (v), (vi), early anaphase showing co-orientation.

Discussion of Chromosome Numbers

1. Eurymelidae

The Eurymelidae comprise approximately one hundred species. Although the twenty-seven species examined constitute only a small sample of the family, they are representative, including nine of eleven genera of the Eurymelinae, six of the fourteen genera of the Ipoinae, and one of the genera of the Pogonoscopinae.

With two exceptions, chromosome numbers are constant in the family, and it may be argued that the haploid number of 10 autosomes and an X chromosome is basic and primitive in the family and the two deviant species, viz. *Aloeurymela gearyi* (9+X) and *Opio multistrigia* (6+X) are derived forms.

It is interesting to note that the monotypic genus *Opio* is distinctive morphologically and ecologically from the remaining genera and it is probable that *Casuarina* has served as its food plant for a considerable period while most representatives of the Eurymelidae are associated with *Eucalyptus* (Evans, 1959, and personal communication).

The low chromosome number in *Opio* probably indicates a reduction in recombination index, and, in consequence, an increased genetic stability. The

stability of its environment (i.e. of its host, *Casuarina*) may well have offered the conditions favouring such a reduction in recombination index. A comparison of karyotypes (Fig. 3, *a*, *b*) suggests the reduction was accomplished by four independent fusions involving two chromosomes to give two large and four small bivalents at metaphase 1. A simple fusion would explain the karyotype of *A. gearyi* although it is not obvious which chromosomes may have been involved (Fig. 3, *b*, *c*).

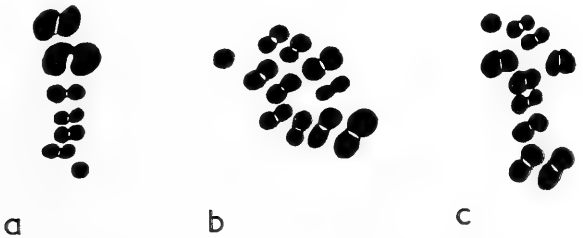

Fig. 3. Karyotype of (*a*) *Opio multistrigia* showing six bivalents and an X chromosome ; (*b*) *Eurymela fenestrata*, with ten bivalents and an X chromosome ; (*c*) *Aloeurymela gearyi*, with nine bivalents and an X chromosome.

2. Cicadellidae

The Cicadellidae comprise approximately ten thousand species and, of these, some two hundred have been examined cytologically (Halkka, 1959, 1960*b*). Consequently it is both difficult and dangerous to draw conclusions from the present data. Nevertheless several trends can be recognized.

Some primitive cicadellids (e.g. some Ulopinae) feed on moss and reeds (Evans, 1947) : those groups represented in Australia which are of later evolutionary development are predominantly arboreal (e.g. Jassinae, Tartessinae, Austroagalloidinae) while, according to Evans, " those leafhoppers of most recent development feed on grasses and herbaceous plants though not limited to these plants ". This advanced group (e.g. the Deltocephalinae) are adapted to a broad range of environmental conditions and consequently are more widely distributed than the more primitive cicadellids which tend to be relict in their distribution.

Halkka (1959) had noted that the chromosome numbers of the Deltocephalinae are more varied than those of the " primitive " groups. This variability is understandable in the light of the morphological and zoogeographical evidence. He has further noted that the chromosome numbers are lower in the Deltocephalinae and has concluded that recent evolution has been associated with a reduction in chromosome numbers. In fact, this finding forms the basis for most of his phylogenetic considerations.

The present results (Table 1) support Halkka's hypothesis. The Deltocephalinae have a lower mean chromosome number and their range (3+X to 9+X) is larger than other groups. *Opio multistrigia* and *A. gearyi* in the Eurymelidae, as previously mentioned, are further examples of derived forms with reduced chromosome numbers.

The reduction in chromosome number is undoubtedly due to fusion of chromosomes. Either the fusion of the X chromosome to an autosome giving a Neo-XY sex mechanism, or simply the fusion of two autosomes, is possible. Halkka (1959) cites several examples of sex chromosome-autosome fusion while *Taslopa montana* (Table 1) provides another. An example of autosome fusion is found in *D. longuinquus* where, of eight individuals examined, six were 4+X, one was 3+X and one a " hybrid " (Fig. 2).

Variation of chromosome number within the same population of a species with localized centromeres should normally lead to the elimination of one or other type or else lead to the establishment of two distinct races because of the increased

incidence of meiotic non-disjunction. Species with diffuse centromeres would not encounter this difficulty when different chromosome numbers are present. White (1957*a*, 1957*b*) has shown the occurrence of individuals heterozygous for a broken/fused chromosome is extremely rare in the grasshopper *Moraba scurra* even though the two races, which have different chromosome numbers, are contiguous for many miles. Selection must be relatively strong against such individuals although it would appear non-disjunction may not be responsible for the reduced fitness in this case. White (1956) cites several other instances (e.g. the mantid *Ameles heldreichi*, the grasshopper *Trimerotropis sparsa*, and the mollusc *Purpura lapillus*) where broken/fused heterozygotes occur in natural populations, but these examples must be rather exceptional.

Thus it may well be that, having diffuse centromeres, chromosome number in leafhoppers is a more adaptable character than it is in other organisms and hence is more subject to variation associated with environmental requirements. Nevertheless it is still of some significance in phylogenetic considerations. An examination of a large sample of the remaining 9,800 or more species will no doubt shed light on the problem.

Summary

1. Chromosome counts have been recorded for 64 species of Homoptera Auchenorrhyncha.

2. An examination of meiosis in the group reveals that the bivalents are co-orientated. In particular the behaviour of chromosomes heterozygous for a fusion supports this conclusion.

3. 10+X is suggested as the base number for the Eurymelidae.

4. The evidence presented supports Halkka's thesis that the more advanced leafhoppers have lower chromosome numbers and that the numbers are more varied in these groups.

5. The presence of diffuse centromeres renders chromosome number more adaptable as a character for selection.

Acknowledgements

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I am indebted to Dr. W. D. Jackson and Professor S. Smith-White for reading the draft manuscript and offering invaluable advice.

In particular I wish to thank Dr. J. W. Evans for identifying the material and for his continued interest and helpful criticism in reading the draft manuscript.

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Explanation of Plate iii

(*a*) Bouquet stage of meiosis in *Eurymela fenestrata* (Eurymelidae) ; (*b*, *c*) Two consecutive stages of diakinesis in *E. fenestrata* ; (*d*) Metaphase I in same ; (*e*) Diakinesis in *Deltocephalus taedius* ; (*f*) Metaphase II in same ; (*g*) Diakinesis in *Aconurominus flavidiventris* (Stål) (Cicadellidae) ; (*h*) Diakinesis in *Deltocephalus longuinquus* showing trivalent.

APPENDIX

In response to a request from Mr. Max Whitten, a new genus and species of Eurymelidae are described below.

A NEW GENUS AND SPECIES OF EURYMELIDAE
(Homoptera, Cicadelloidea)

J. W. Evans
Australian Museum

Eurymelinae

Aloeurymela, gen. nov.

On the face of the head the labium terminates between the middle coxae and the anterior margin of the ante-clypeus is depressed below the rest of the sclerite. The crown of the head is only slightly wider against the eyes than in the centre. The tegmen has a well developed appendix. The hind tibiae have one spur and a few additional small spines. The male genitalia have oval sub-genital plates bearing terminal hook-like styles arising from the ventral margins.

Type species.—*Aloeurymela gearyi*, sp. nov.

In coloration and general appearance *Aloeurymela* resembles genera comprised in the Ipoinae rather than those in the Eurymelinae. It is included in the last-named subfamily because of the characters furnished by the male genitalia, in particular the presence of a well developed ventral accessory clasping process associated with the sub-genital plates.

Aloeurymela gearyi, sp. nov.
(Fig. 4)

Length, ♂, ♀ 4·8 mm. General appearance long and narrow, sometimes with a characteristic diamond-shaped marking on the folded tegmina. Face of head pale apricot, or dark brown, mottled with yellow ; lora and maxillary plates pale brown. Crown and pronotum pale or dark brown, or black, mottled with pale brown or greyish-white. Scutellum concolorous with the pronotum

but a darker shade. Tegmen basally concolorous with the head and thorax with two irregular transverse whitish fasciae, which may be confluent in the costal area. Male genitalia as in Fig. 4 (the aedeagus may have an additional spine to the one shown in the figure).

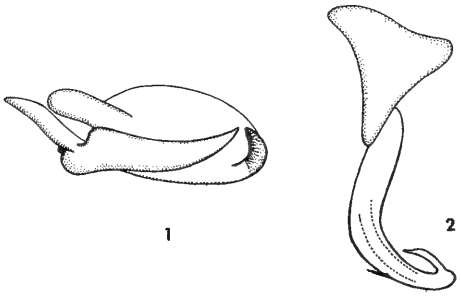

Fig. 4. *Aloeurymela gearyi*. 1, subgenital plate and paramere; 2, aedeagus.

Holotype ♂ and *Allotype* ♀ from Cunnamulla, Queensland (coll. N. Geary, 11/41) in the Australian Museum.

Known distribution elsewhere.—Perth (Western Australia); Gilruth, Moolooka (Queensland); Walgett (New South Wales).

THE DISTRIBUTION OF THE NOTONECTIDAE (HEMIPTERA) IN SOUTH-EASTERN AUSTRALIA

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[Read 28th April, 1965]

Synopsis

The distribution and relative abundance of species of Notonectidae found in south-east Australia are discussed. Fourteen species occur in this region, eleven in the genus *Anisops*, two in the genus *Enithares* and one in the genus *Paranisops*.

Introduction

The Notonectidae (" back swimmers ") are common in freshwater habitats of Australia, such as rivers, creeks, pools and waterholes. Several authors have discussed the taxonomy of the species found in Australia, including Kirkaldy (1897, 1904) and Hungerford (1934, 1940). Hale published several papers on the Notonectidae (1923, 1924, 1925). He described all the known Australian species, several of which were new, and established the genus *Paranisops*. Brooks (1951) revised the genus *Anisops* on a world basis and described twelve new species from Australia. He solved many taxonomic problems associated with this genus.

There are eight genera in the Notonectidae, five of which have been recorded from Australia. Australian species of *Nychia* and *Notonecta* have been described by Hale (1925) and Kirkaldy (1897), but they were not encountered during the course of this study. *Anisops*, *Enithares*, and *Paranisops* are the only genera known to occur in south-eastern Australia.

The distribution of the Australian Notonectidae is not well known and this paper describes the known distribution of species found in south-eastern Australia.

Materials and Methods

This study is based on specimens collected from more than 120 localities by the author and colleagues, during 1962 and 1963. The collection has since been deposited in the Macleay Museum, University of Sydney. The area visited includes most of New South Wales and Victoria, with some localities in the eastern part of South Australia, and Brisbane, Queensland. The Notonectid collections of the Australian and South Australian Museums were inspected but were not examined in detail.

Most specimens were preserved in 70% alcohol although representatives of each species were pinned. The technique adopted for the examination of the male foreleg of *Anisops* was that described by Brooks (1951). After removal from the insect the organs were cleared in 5% caustic potash solution and dehydrated in alcohol. Except where otherwise stated, specimens from the various localities mentioned in the text were collected by the author.

Genus Anisops

Anisops is the dominant Notonectid genus in Australia and the following twenty-two species have been recorded from this continent :

A. barrenensis Brooks *	*A. malkini* Brooks *
A. calcaratus Hale †	*A. nasuta* Fieber *
A. canaliculata Brooks † *	*A. nodulata* Brooks *
A. deanei Brooks †	*A. occipitalis* Breddin *
A. doris Kirkaldy †	*A. ocularis* Hale *
A. elstoni Brooks †	*A. paracrinita* Brooks *
A. endymion Kirkaldy	*A. semita* Brooks *
A. evansi Brooks ‡	*A. stali* Kirkaldy †
A. gratus Hale †	*A. tasmaniaensis* Brooks ‡
A. hackeri Brooks †	*A. thienemanni* Lundblad †
A. hyperion Kirkaldy †	*A. windi* Brooks *

* North Australian species
† South-east Australian species
‡ Tasmanian species

Many of these species have been collected only in the far north, in the Cape York and Darwin areas. Ten of them were collected in the south-east of the continent during the present study, as well as *A. tahitiensis* which has not previously been recorded from Australia.

Only the males of the genus have reliable diagnostic characters. They can be distinguished from the females by the single tarsal segment of the foreleg and the lateral prongs on the third segment of the rostrum. A key to the genus *Anisops* was presented in Brooks' (1951) paper, but as this includes almost eighty species it was felt that a simplified key of the local species would be of some value.

Key to males of south-east Australian Anisops

1.		Small species, less than 5 mm. in length 2
		Larger species, greater than 5 mm. in length 3
2.	(1)	Facial tubercle * with a median groove, without median depression of pronotum ..... *A. canaliculata*
		Facial tubercle without median groove, with median depression of pronotum *A. elstoni*
3.	(1)	Greatest width of head slightly greater than width of pronotum ..... *A. doris*
		Greatest width of head less than width of pronotum 4
4.	(3)	Large species greater than 8 mm. in length 5
		Medium-sized species less than 8 mm. in length 6
5.	(4)	Vertex † extends beyond eyes into a cephalic horn, without spur on tibia of foreleg ..... *A. stali*
		Vertex not extended beyond eyes, with spur on tibia of foreleg ..... *A. calcaratus*
6.	(4)	Dorsal surface of pronotum with a median depression ..... *A. gratus*
		Dorsal surface of pronotum without median depression 7
7.	(6)	Facial tubercle raised into a median carina ..... *A. tahitiensis*
		Facial tubercle not raised into a median carina 8
8.	(7)	Front femur broad ; dorsal and ventral margins almost parallel for basal three-fourths of its length ..... *A. thienemanni*
		Dorsal and ventral margins of front femur not parallel 9
9.	(8)	Apex of third rostral segment wider than base of fourth segment ..... *A. deanei*
		Apex of third rostral segment equal to base of fourth segment 10
10.	(9)	Anterior tarsus with a median row of five setae ..... *A. hyperion*
		Anterior tarsus with more than five setae in two rows ..... *A. hackeri*

* Facial Tubercle : The modified region of the space between the eyes, immediately above the labrum.

† Vertex : The anterior dorsal margin of the space between the eyes.

Anisops thienemanni Lundblad
(Fig. 1*a*)

This is the most common and widespread species in south-east Australia and is most abundant on the western plains of New South Wales. It also occurs on the slopes and tablelands of the Great Dividing Range but is rare on the east coast, having been collected from only two localities in that area (Morwell and Narooma).

Localities :—New South Wales : Hartley, 5/8/62 ; Narooma, 30/12/62 ; Goulburn, 26/12/62 ; Lake Bathurst (W. Williams), Jan. 1962 ; Canberra, A.C.T., 26/12/62 and 20/1/63 ; Gunning, 20/8/62 ; Taralga, 4/8/62 ; Cooma, 26/12/62 ; Thredbo, Crackenback River, 28/12/62 ; Glanmire, 11/8/62 ; Koorawatha, 16/1/63 ; Wellington, 28/8/62 ; Forbes, 26/4/62 ; Young, 16/1/63 ; Brungenbrong, 19/1/63 ; Gulargambone (J. Anderson), 26/12/62 ; Coonabarabran (J. Bishop), 28/6/62 ; Warren (P. Bailey), 30/6/62 and (J. Bishop), 12/8/62 ; Wagga Wagga, 16/1/63 ; Yerong Creek, 16/1/63 ; West Wyalong, 25/4/62 ;

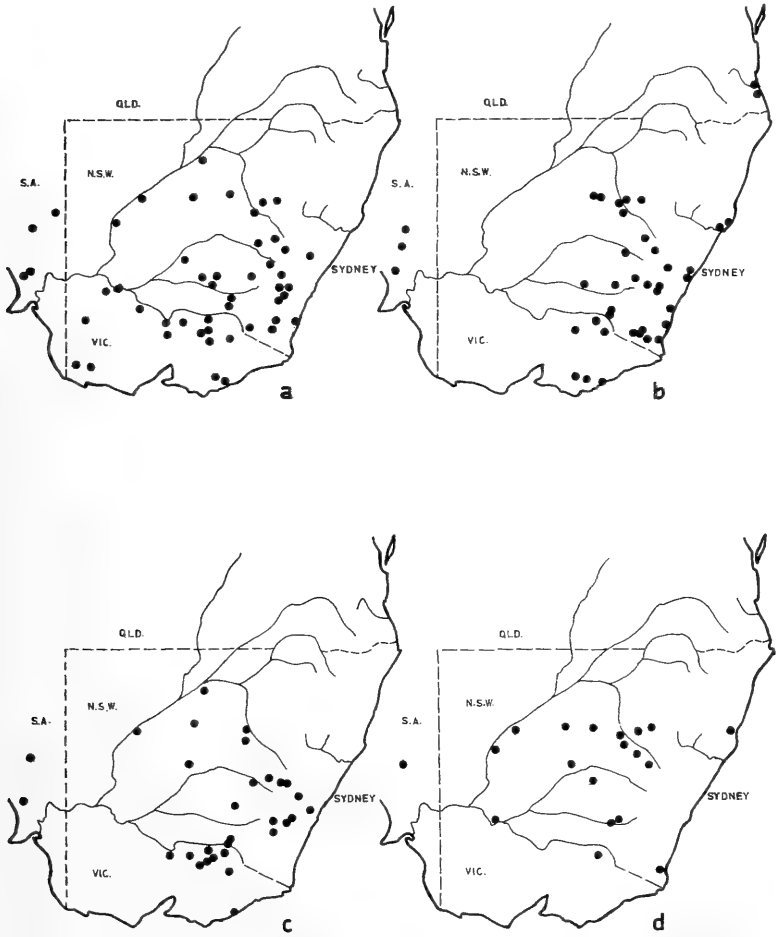

Fig. 1. Distribution of *a, A. thienemanni ; b, A. deanei ; c, A. hyperion ; d, A. stali.*

Leeton, 23/4/62 ; Yenda, 22/4/62 ; Lake Cargelligo (J. Bishop), June, 1962 ; Cobar, 27/8/62 ; Nyngan, 1/7/62 ; Bourke (J. Bishop), 5/7/62 ; Wilcannia, Caltigena Tank, 27/8/62 ; Menindee, 26/8/62 ; Euston, 22/8/62. Victoria : Sale, 18/1/63 ; Morwell, 18/1/63 ; Nareil, 19/1/63 ; Benambra, 19/1/63 ; Mt. Hotham (W. Williams), Jan. 1962 ; Violet Town, 16/1/63 ; Winton, 16/1/63 ; Wungnhu, 21/8/62 ; Echuca, 21/8/62 ; Lake Cooper (W. Williams), Jan. 1962 ; Nyah, 22/8/62 ; Hattah Lakes (W. Williams), 27/8/62 ; Lake Hindmarsh (W. Williams), Jan. 1962 ; Casterton (W. Williams), 19/8/61 ; Hamilton (W. Williams), Jan. 1962. South Australia : Mingary, 28/8/62 ; Oodla Wirra, 25/8/62 ; Truo, 23/8/62 ; Sheoak Log, 23/8/62.

Anisops deanei Brooks
(Fig. 1*b*)

A common species, particularly on the coast. It is often found on the slopes and tablelands but rarely occurs on the inland plains.

Localities :—New South Wales : Bulahdelah, 22/8/62 ; Raymond Terrace, 22/8/62 ; Marsden Park, 24/6/62 ; Waterfall, 5/5/62 ; Narooma, 30/12/62 ; Bemboka, 29/12/62 ; Milton, 30/12/62 ; Nimmitabel, 29/12/62 ; Kanangra Walls, 20/1/63 ; Goulburn, 26/12/62 ; Collector, 20/1/63 ; Gunning, 20/8/62 ; Cooma, 26/12/62 ; Berridale, 19/1/63 ; Jindabyne, Saw Pit Creek, 27/12/62 ; Glanmire, 11/8/62 ; Wellington, 28/8/62 ; Cootamundra, 16/1/63 ; Forbes, 26/4/62 ; Gulargambone (J. Anderson), 24/4/62 ; Gilgandra, Castlereagh River (J. Bishop), 29/6/62 ; Trangie, 27/8/62 ; Warren (P. Bailey), 30/6/62 ; Young, 16/1/63 ; Yerong Creek, 16/1/63 ; Mullengandra, 20/8/62 ; Nyngan, 1/7/62 ; Hermidale, 27/8/62 ; Leeton, 23/4/62. Victoria : Bairnsdale, 18/1/63 ; Nareil, 19/1/63 ; Chiltern, 16/1/63 ; Morwell, 18/1/63 ; Heyfield (W. Williams), 25/11/62 ; Violet Town, 16/1/63. South Australia : Oodla Wirra, 25/8/62 ; Burra, 25/8/62 ; Sheoak Log, 23/8/62. Queensland : Brisbane, 27/5/62 ; Petrie, 31/5/62.

Anisops hyperion Kirkaldy
(Fig. 1*c*)

The distribution of *A. hyperion* is similar to that of *A. thienemanni*. It is rare on the coast but common on the slopes and ranges and also occurs on the western plains, though not as frequently as the latter species.

Localities :—New South Wales : Mittagong, 3/8/62 and 20/8/62 ; Kanangra Walls, 20/1/63 ; Goulburn, 26/12/62 ; Gunning, 20/8/62 ; Collector, 20/1/63 ; Canberra, A.C.T., 20/1/63 ; Glanmire, 11/8/62 ; Bathurst, 28/8/62 ; Manildra (J. Bishop), June 1962 ; Forbes, 26/4/62 ; Trangie, 27/8/62 ; Warren (J. Bishop), 12/8/62 ; West Wyalong, 25/4/62 ; Yerong Creek, 16/1/62 ; Mullengandra, 20/8/62 ; Bourke (J. Bishop), 5/7/62 ; Cobar, 27/8/62 ; Mount Hope (J. Bishop), June, 1962 ; Wilcannia, 27/8/62. Victoria : Bairnsdale, 18/1/63 ; Benambra, 19/1/63 ; Chiltern, 16/1/63 ; Violet Town, 16/1/63 ; Winton, 16/1/63 ; Glenrowan, 16/1/63 ; Yarrawonga, 21/8/62 ; Wungnhu, 21/8/62 ; Echuca, 21/8/62. South Australia : Oodla Wirra, 25/8/62 ; Sheoak Log, 23/8/62.

Anisops stali Kirkaldy
(Fig. 1*d*)

A. stali is most common on the inland plains of New South Wales and similar areas of the surrounding States. It has been collected near the coast (Wingham and Bemboka) and on the western slopes of the Dividing Range. Altitude may be a factor affecting the distribution of this species as it has not been found in the higher areas of this region.

Localities :—New South Wales : Wingham, Jan., 1962 ; Bemboka, 29/12/62 ; Cudgegong River (J. Bishop), 5/11/62 ; Cootamundra, 16/1/63 ; Junee, 16/1/63 ; Gulargambone (J. Anderson), 24/4/62 ; Wellington, 28/8/62 ; Coonabarabran (J. Bishop), 28/6/62 ; Trangie, 27/8/62 ; Warren (P. Bailey), 30/6/62 and (J. Bishop), 12/8/62 ; Lake Cargelligo (J. Bishop), June, 1962 ; Hermidale, 27/8/62 ; Mount Hope (J. Bishop), June, 1962 ; Cobar, 27/8/62 ; Wilcannia, 26/8/62 ; Menindee, 26/8/62 ; Euston, 22/8/62. Victoria : Chiltern, 16/1/63. South Australia : Oodla Wirra, 25/8/62.

Anisops calcaratus Hale
(Fig. 2*a*)

This species is uncommon and is found mostly in the arid inland areas. It appears to have a distribution similar to *A. stali*.

Localities :—New South Wales : Canberra, A.C.T., 20/1/63 ; Manildra (J. Bishop), June, 1962 ; Wellington, 28/8/62 ; Coonabarabran (J. Bishop),

28/6/62 ; Cootamundra, 16/1/63 ; Junee, 16/1/63 ; Trangie, 27/8/62 ; Hermidale, 27/8/62 ; Cobar, 27/8/62 ; Menindee, 26/8/62. VICTORIA : Bairnsdale, 18/1/63 ; Chiltern, 16/1/63. SOUTH AUSTRALIA : Oodla Wirra, 25/8/62.

ANISOPS ELSTONI Brooks
(Fig. 2*b*)

This is a comparatively rare species. It has been collected from several localities near Sydney but does not occur far inland. (The most westerly collection was made at Narrandera, N.S.W.)

Localities :—NEW SOUTH WALES : Badgery's Creek, 7/8/62 ; Marsden Park, 1/7/62 ; Raymond Terrace, 22/8/62 ; Narooma, 30/12/62 ; Valley Heights, 5/8/62 ; Mittagong, 3/8/62 ; Narrandera, 25/4/62. VICTORIA : Benambra, 19/1/63 ; Winton, 16/1/63.

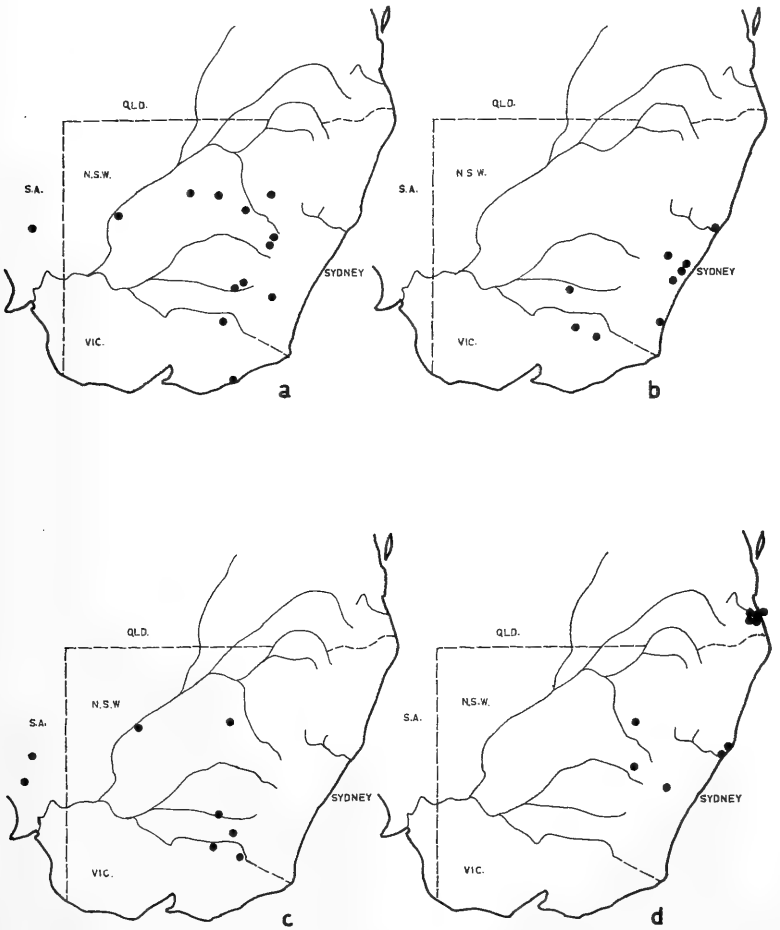

Fig. 2. Distribution of *a*, *A. calcaratus* ; *b*, *A. elstoni* ; *c*, *A. gratus* ; *d*, *A. hackeri*.

ANISOPS GRATUS Hale
(Fig. 2*c*)

This uncommon species occurs throughout the inland plains. It has not been collected on the coast or tablelands.

Localities :—NEW SOUTH WALES : Yerong Creek, 16/1/63 ; Leeton, 23/4/62 ; Nyngan, 1/7/62 ; Wilcannia, 26/8/62. VICTORIA : Nareil, 19/1/63 ; Yarrawonga, 21/8/62. SOUTH AUSTRALIA : Oodla Wirra, 25/8/62 ; Burra, 25/8/62.

Anisops hackeri Brooks
(Fig. 2*d*)

This species is uncommon in south-eastern Australia but it is the dominant Notonectid of the Brisbane area. Its distribution seems confined mainly to the north-east of the region.

Localities :—New South Wales : Bulahdelah, 22/8/62 ; Raymond Terrace, 22/8/62 ; Kanangra Walls, 20/1/63 ; Forbes, 26/4/62 ; Gulargambone (J. Anderson), 24/4/62. Queensland : East Ithaca Creek, Brisbane, 24/5/62 ; Upper Brookfield, Brisbane, 30/5/62 ; Toowong Creek, Brisbane, 26/5/62 ; Ferny Grove, 27/5/62 ; Petrie, 31/5/62.

Anisops doris Kirkaldy
(Fig. 3*a*)

This is a rare species with distribution similar to *A. hackeri*. It is common in Hawkesbury Sandstone creeks in the Sydney area where it is often found in association with *P. inconstans*.

Localities :—New South Wales : Booral, 22/8/62 ; Waterfall, 5/5/62 ; Appin, March, 1962 ; Picton Lakes, 7/10/62 ; Manilla (J. Bishop), 25/6/62 ; Cudgegong, 5/11/62 ; Warren (P. Bailey), 30/6/62. Queensland : Upper Brookfield, Brisbane, 30/5/62.

Anisops canaliculata Brooks
(Fig. 3*a*)

The type locality of this species is Barron River, North Queensland. It has only been collected by the author at Petrie, Queensland, and may be a " northern " species whose distribution extends as far south as this locality.

Localities :—Queensland : Petrie, 31/5/62.

Anisops tahitiensis Lundblad
(Fig. 3*a*)

This species has been found in New Guinea, the New Hebrides and the Solomon Islands (Brooks, 1951 ; Lansbury, 1963) but has not previously been recorded from Australia. It is common in the Brisbane area and probably occurs in other localities in Queensland and northern New South Wales.

Localities :—Queensland : East Ithaca Creek, Brisbane, 24/5/62 ; Toowong Creek, Brisbane, 26/5/62 ; Ferny Grove, 27/5/62 .

Genus Enithares

More than 40 species in this genus are distributed through Africa and southern Asia (Hungerford, 1956). Two species have been recorded from this country, both of which occur in south-eastern Australia.

Key to Australian Enithares

1. Vertex not extended markedly beyond the eyes in both sexes, narrow ridge of ventral abdominal keel, males without spur on anterior trochanter ..... *E. bergrothi*
2. (1) Vertex extended markedly beyond eyes in both sexes, broad ridge of ventral abdominal keel, males with spur on anterior trochanter ..... *E. hackeri*

Enithares bergrothi Montandon
(Fig. 3*b*)

This is a common species with a distribution similar to *A. deanei*. It is found on the east coast as well as the tablelands and slopes but is rare on the western plains.

Localities :—New South Wales : Raymond Terrace, 22/8/62 ; Waterfall, 5/5/62 ; Valley Heights, 5/8/62 ; Manilla, 25/6/62 ; Richlands, 4/8/62 ; Taralga, 4/8/62 ; Canberra, A.C.T., 20/1/63 ; Glanmire, 11/8/62 ; Cudgegong, 5/11/62 ;

Cowra, 16/1/63 ; Gulargambone (J. Anderson), 24/4/62 ; Mullengandra, 20/8/62 ; Wagga Wagga, 16/1/63. VICTORIA : Tambo River (W. Williams), 23/2/62 ; Morwell, 18/1/63 ; Chiltern, 16/1/63 ; Winton, 16/1/63 ; Wangaratta, 16/1/63 ; Dalyston (W. Williams), 2/9/62 ; Tallarook, 17/1/63 ; Kul Kyne (W. Williams), 27/8/61. SOUTH AUSTRALIA : Sheoak Log, 23/8/62. QUEENSLAND : East Ithaca Creek, Brisbane, 24/5/62 ; Toowong Creek, Brisbane, 26/5/62.

ENITHARES HACKERI Hungerford
(Fig. 3*b*)

This species is rare in south-eastern Australia and was only collected in three localities during this study. The type locality is Brisbane, Queensland.

Localities :—NEW SOUTH WALES : Manilla, 25/6/62 ; Leeton, 23/4/62. VICTORIA : Wangaratta, 16/1/63.

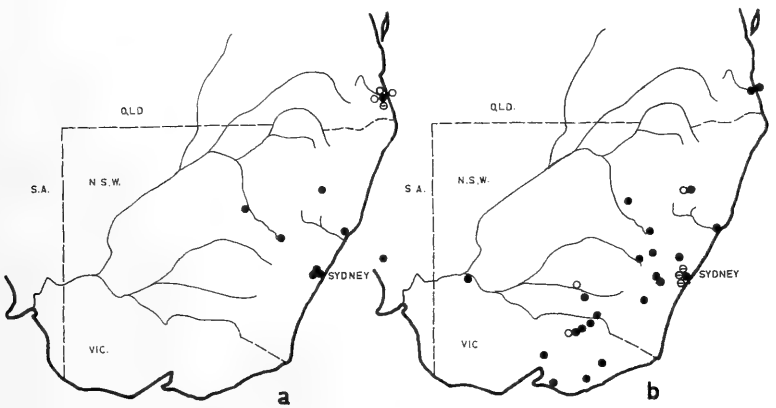

Fig. 3. Distribution of *a*, ● *A. doris*, ○ *A. tahitiensis*, ⊙ *A. canaliculata* ; *b*, ● *E. bergrothi*, ○ *E. hackeri*, ⊙ *P. inconstans*.

Genus PARANISOPS

This genus was established by Hale (1924) from specimens obtained at Epping, N.S.W. There is only one known species, *P. inconstans*, which is of special interest as it occurs in two distinct morphological forms. There is a black winged variety as well as a pale form which lacks functional hindwings. This species has only been found near Sydney (type locality) and Brisbane (Hungerford, 1934). Only the pale form, which is quite common in Hawkesbury Sandstone creeks around Sydney, was collected during this study.

PARANISOPS INCONSTANS Hale
(Fig. 3*b*)

Localities :—NEW SOUTH WALES : Waterfall, 5/5/62 ; Appin, March, 1962 ; Heathcote, March, 1962.

DISCUSSION

Most species of Notonectidae found in south-eastern Australia are more common within restricted areas of this region. Several species (*A. thienemanni*, *A. hyperion*, *A. stali*, *A. calcaratus* and *A. gratus*) are more prevalent on the inland plains and the slopes of the Great Dividing Range. Others (*A. deanei*, *A. elstoni*, *A. hackeri*, *A. doris* and *E. bergrothi*) have more easterly distributions and are usually found near the coast. *A. hackeri* and *A. doris* seem confined to the north-east.

Suitable aquatic habitats in inland areas usually consist of man-made dams and waterholes which are often isolated and many miles apart. The species found in these areas may have better dispersal powers than the " coastal "

species and thus be better adapted to invade an arid environment where habitats are widely separated. The other species may be limited to the coast and ranges where the heavier rainfall ensures an adequate supply of freshwater habitats.

Several species are often found together in the same locality. This is particularly so in western areas, where the scarcity of habitats may be responsible for this gregariousness.

There are several species of *Anisops* with type localities in North Queensland. *A. canaliculata* is the only one of these which has been found outside this area and is probably a " northern " species whose distribution range extends farther south than the others.

P. inconstans commonly occurs in Hawkesbury Sandstone creeks and seems rigidly restricted to this habitat as it has not been found elsewhere in the region. This limited distribution may be explained by the predominance of the pale form which is incapable of flight.

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THE HISTOLOGY AND ANATOMY OF THE REPRODUCTIVE SYSTEM OF THE LITTORAL GASTROPOD *BEMBICIUM NANUM* (LAMARCK) (FAM. LITTORINIDAE)

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[Read 28th April, 1965.]

Synopsis

In *Bembicium nanum* the sexes are separate and easily distinguishable ; the female by the yellow ovipositor, the male by the conspicuous penis.

The histology and anatomy of the male reproductive system of *B. nanum*, apart from the shape of the penis, the absence of penial glands, the compact nature of the testis and the germinal epithelium of the testis, are similar in general to other littorinids. However, in the female reproductive system, greater differences are found ; the renal oviduct is lined by a phagocytic syncytium, the receptaculum seminis is modified for storage, nourishment and phagocytosis of sperm, and the bursa copulatrix functions only as an organ for reception of spermatozoa.

Time of spawning appears to be independent of the time of year and different for each individual. Egg masses are slightly more numerous in the spring and summer months. Large seasonal differences in the size of the reproductive system and extensive resorption of gametes do not occur. In *B. nanum* resorption of spermatozoa is restricted to the vesicula seminalis of the male system and to the receptaculum seminis of the female system. Slight resorption of ova appears to occur in the renal oviduct of the female reproductive system of *B. nanum*. This limitation of phagocytosis of gametes in *B. nanum*, in comparison with North Sea littorinids, may be related to the milder climatic variations in the Sydney coastal areas.

INTRODUCTION

Little is known of reproduction and development in Australian littorinids (Anderson, 1960). Apart from a brief and rather inaccurate description by Kesteven (1902) and a brief reference by Anderson (1958) in a taxonomic survey of the genus *Bembicium*, no details of the reproductive system of *B. nanum* have yet been described. In the following work, the anatomy and histology of the reproductive system of *B. nanum* are described. Differences from North Sea littorinids are noted and related to continuous breeding throughout the year in *B. nanum*.

METHODS

Males and females of *B. nanum* were collected at intervals during 1961 and 1962 on the rock platforms of the ocean coast near Sydney. Animals, removed from their shells and relaxed in fresh water, were dissected under a binocular microscope. For histological studies, Smith's formol-bichromate, 5% formol saline and Baker's formaldehyde calcium were found to be the most suitable fixatives. To prevent hardening, material was taken to 95% alcohol, transferred to 1% celloidin in methyl benzoate, followed by benzene, then embedded in paraffin (M.P. 56°C). Sections were cut at 8μ and stained in Ehrlich's haematoxylin and eosin or Heidenhain's azan stain.

RESULTS

Male Reproductive System

As in all male prosobranchs, the testis (Fig. 1) in *B. nanum* lies in the visceral spire over the digestive gland, its tubules being grouped around the visceral arterial system (Anderson, 1958). The wall of each tubule is a flattened germinal epithelium. Within this lies a dense layer of spermatocytes, then a layer of spermatids, while mature spermatozoa (Fig. 2) and nurse cells (Fig. 3) with finely vacuolated cytoplasm and attached spermatids and spermatozoa occupy the lumen.

The small tubules unite and open into the coiled vesicula seminalis which runs along the axial surface of the spire and opens anteriorly into the vas deferens (Fig. 1).

The vesicula seminalis is about 200μ in diameter and is lined by cuboidal, vacuolated epithelial cells (Fig. 4). Spermatozoa are found in the vacuoles together with nurse cells, penetrating the epithelium, and in an unorientated mass in the lumen.

Fig. 1. Male reproductive system of *B. nanum*. The mantle cavity has been opened dorsally and the kidney has been folded to the right.

The vas deferens (Fig. 5) is short, about 100μ in diameter, lined by a ciliated cuboidal epithelium and surrounded by a thin layer of circular muscle, followed by a layer of connective tissue. It passes into the connective tissue under the kidney and continues as the prostate gland on the right side of the mantle cavity.

The prostrate gland looks like a complete duct in dissected specimens (Fig. 1), but is composed of an attached right and freely-hanging left lobe, separated ventrally so that the lumen of the gland opens into the mantle cavity. Each lobe has a deep ciliated sperm groove on its inner edge (Fig. 8).

Anteriorly, the prostate becomes a closed tube, the free edges of the two lobes fusing in the ventral midline.

The columnar epithelium lining the lobes of the prostate gland has two types of cells, gland cells and supporting cells (Fig. 6). Each gland cell has a basal nucleus, a single nucleolus and granular cytoplasm containing numerous eosinophil granules, especially in the narrower distal parts of the cell. The supporting cells, regularly placed between the gland cells, are expanded distally and compressed to thin cytoplasmic strands proximally. The free surfaces of the cells are densely ciliated, the cilia being longest on the edges of the sperm groove and in the groove itself. Many mucous cells are found in the epithelium

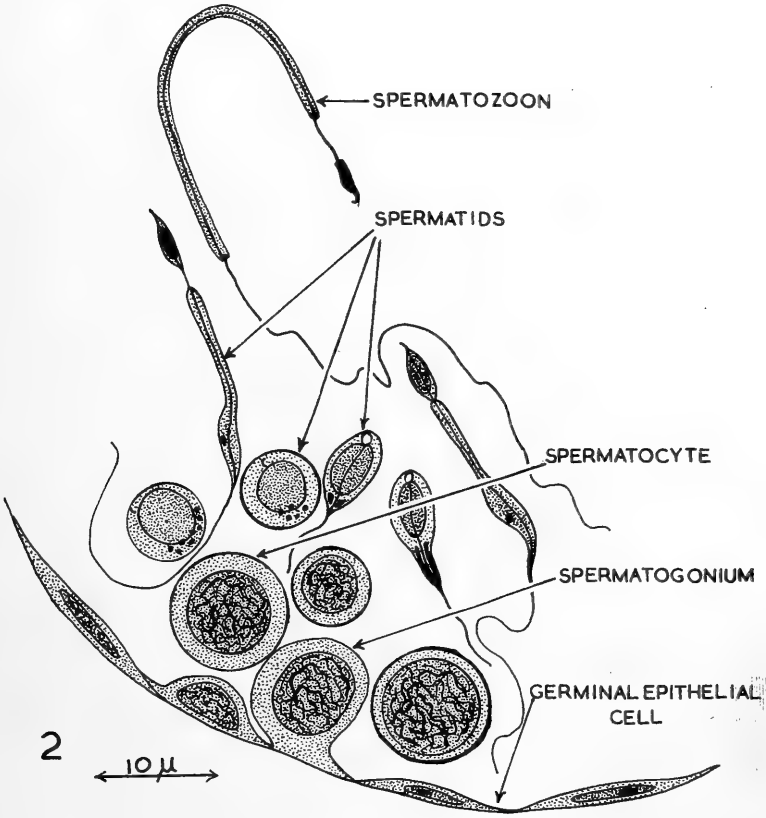


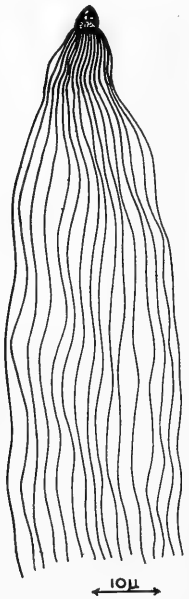
Fig. 2. *B. nanum*. T.S. through the wall of a testicular tubule.

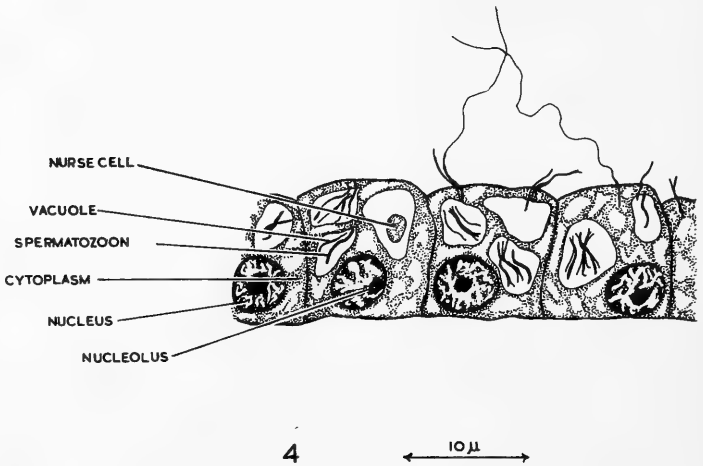
of the edge of the left lobe (Fig. 7). No muscles appear under the prostate epithelium, but circular and longitudinal muscles are found under the mantle epithelium on the outer edge of the left lobe.

At the mouth of the mantle cavity, the prostate gland continues as the anterior vas deferens (Fig. 1), a narrow duct 75μ in diameter, lined by ciliated cuboidal epithelium and surrounded by a muscle sheath composed of circular, longitudinal and transverse muscle (Fig. 9). The anterior vas deferens passes along the foot to the right of the buccal mass, in a ridge of dense connective tissue and opens anteriorly into the penis.

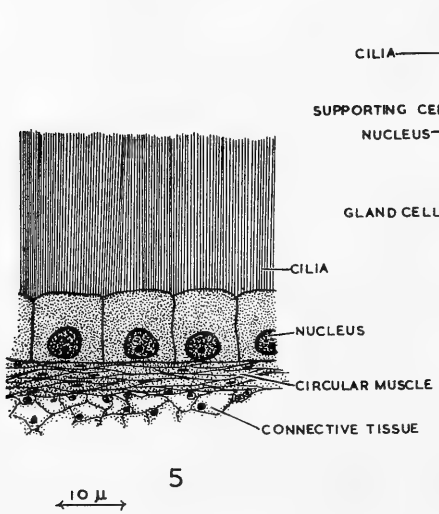
The penis (Fig. 1), a conical projection slightly dorso-ventrally flattened, is covered by a ciliated columnar epithelium. Underlying the latter is a thin layer of circular muscle, then layers of dorso-ventral and oblique muscles, while longitudinal muscles run through the connective tissue

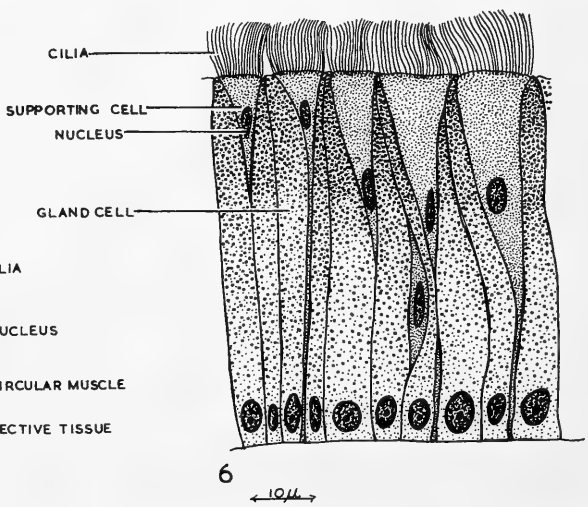
internally. The connective tissue has numerous blood spaces and the penial nerve lies in a ventral position. The penial duct, which runs through the penis dorsally, is 200μ in diameter and is lined by ciliated columnar cells, 75μ high (Fig. 10). A thin coat of circular, longitudinal and transverse muscles lies immediately external to this epithelium.





Figs 3, 4. *B. nanum*. 3, Nurse cell with attached spermatozoa ; 4, T.S. through the wall of the vesicula seminalis.





Figs 5, 6. *B. nanum*. 5, T.S. through the wall of the vas deferens ; 6, T.S. through the wall of the prostate gland.

Female Reproductive System

Like the testis, the ovary (Fig. 11) lies over the digestive gland and its tubules are grouped around the visceral arterial system, this arrangement being seen in young specimens only (Anderson, 1958). The wall of each tubule is a flattened germinal epithelium, with developing oocytes projecting into

the lumen of the tubule and mature oocytes lying in the lumen (Fig. 12). The ovarian tubules open into a single duct, the renal oviduct (Fig. 11), which runs through the connective tissue under the kidney.

The wall of the renal oviduct is composed of a syncytial epithelium with scattered oval nuclei, each with a single nucleolus, and an external sheath of circular muscle. Large vacuoles, 10μ in diameter, filled with large, yolky, eosinophil granules, also occur in the epithelium cytoplasm (Fig. 15). Anteriorly, the renal oviduct dilates, then narrows and opens into the pallial oviduct or "uterus" (Fig. 11). In its narrower region the renal oviduct has a typical ciliated cuboidal epithelium.

Immediately behind the opening of the renal oviduct into the pallial oviduct is the opening of the receptaculum seminis (Fig. 11). This is a short blind duct lying in the mantle cavity between the renal oviduct and pallial oviduct, in which it is embedded anteriorly. Posteriorly, the receptaculum

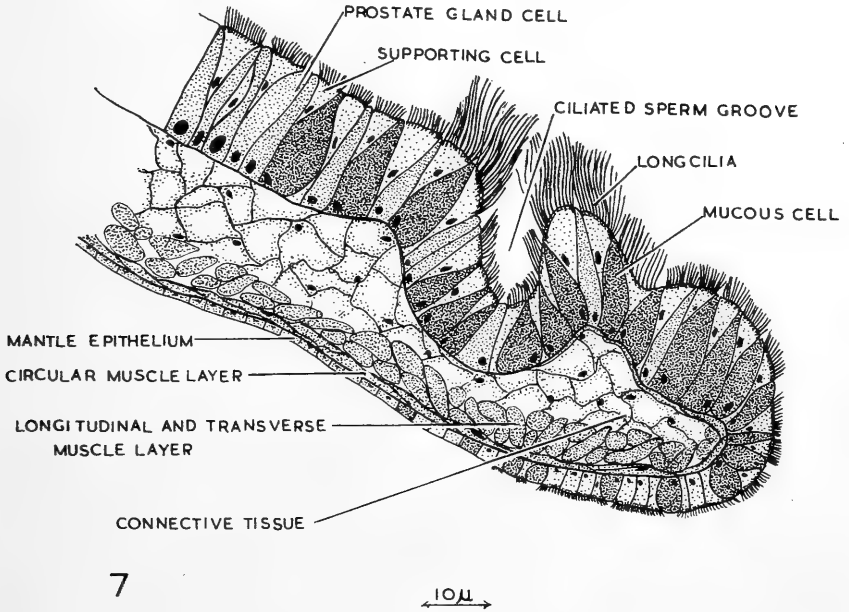


Fig. 7. *B. nanum.* T.S. through the left lobe of the prostate gland.

seminis ends in a bulb, 300 μ in diameter, lined by unciliated, cuboidal epithelial cells and filled with unorientated spermatozoa (Fig. 17). Anteriorly, it is laterally compressed, with diameters of about 300μ and 150μ (Fig. 13). In this anterior portion, its ventral epithelium, which lines a deep groove, is a syncytium with large oval nuclei. Numerous spermatozoa are found with their heads embedded in the syncytium (Fig. 16). Dorsally, the epithelium is columnar and is composed of three cell types : mucous cells, cells containing granules and spermatozoa, and ciliated supporting cells (Fig. 14). The mucous cells each have a granular cytoplasm staining evenly with haematoxylin and a basal nucleus containing a single nucleolus. The cells containing granules and spermatozoa, presumably phagocytically digesting the latter, also have a basal nucleus containing a single nucleolus, but their cytoplasmic granules stain strongly with eosin. Neither of these cell types is ciliated. The supporting cells, between them, are expanded distally and bear cilia about 10μ high. A circular muscle sheath, 10μ thick, surrounds the receptaculum seminis.

The pallial oviduct has, running ventrally along its length, a channel with densely ciliated cuboidal epithelium, 5μ high (Fig. 18). Its lateral and dorsal

walls, on the other hand, are enlarged to form a posterior albumen gland and an anterior jelly gland. The two glands lie to the right of the rectum on the dorso-lateral wall of the mantle cavity and can be seen through the thin mantle tissue (Fig. 11). The albumen gland (Fig. 19) is a large mass of much folded epithelium, the lumen between the epithelial folds connecting with the ventral

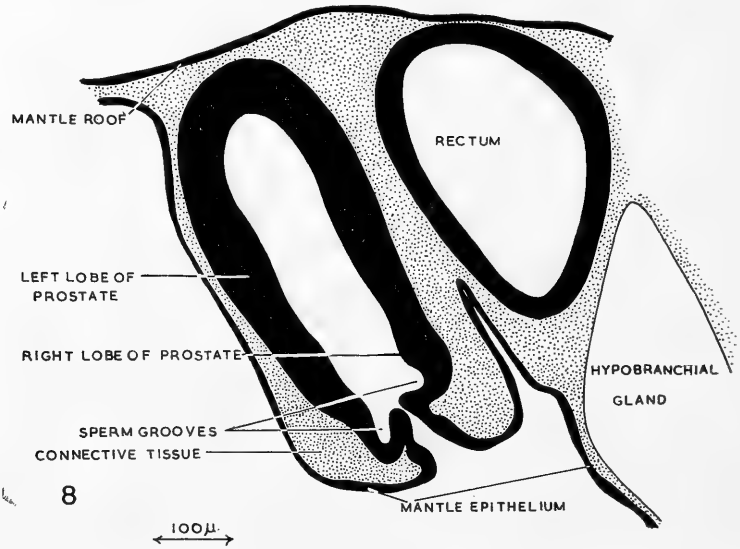
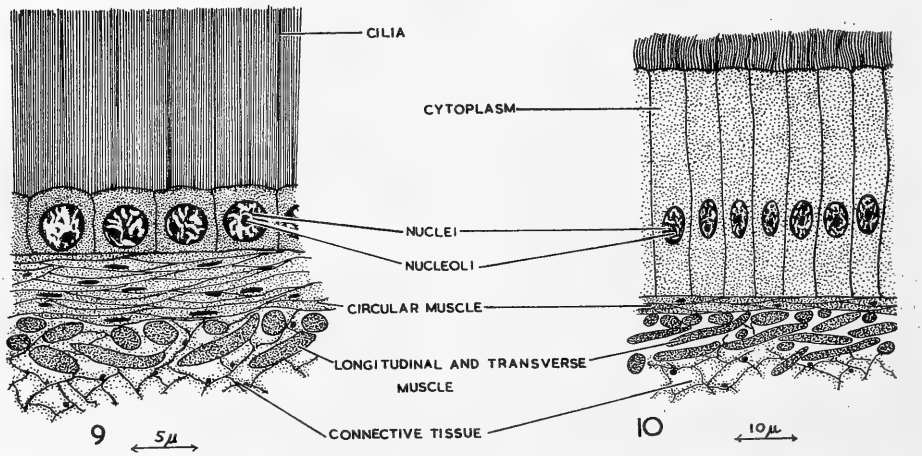


Fig. 8. *B. nanum.* Diagrammatic T.S. through the roof of the mantle cavity showing the relative positions of the prostate gland, rectum and hypobranchial gland.



Figs 9, 10. *B. nanum.* 9, T.S. through the wall of the anterior vas deferens; 10, T.S. through the wall of the penial sperm duct.

channel of the oviduct. Both glandular and supporting cells occur in the epithelium. The densely ciliated supporting cells are each expanded distally and are connected to the basement membrane by thin cytoplasmic connections and have a spindle-shaped, densely staining nucleus at the base of the distal expansion. The albumen gland cells are filled with secretion droplets staining heavily with haematoxylin, these droplets being more numerous in the distal parts of the cells. The nucleus of each cell is oval, basal and has a single

nucleolus. The epithelium of the albumen gland is covered externally by a coat of circular muscle, 5μ thick.

The jelly gland (Fig. 11) is composed of the two thickened, folded, lateral walls of the pallial oviduct, with the lumen between them opening into the ventral channel of the pallial oviduct. The gland cells (Fig. 20) are filled with

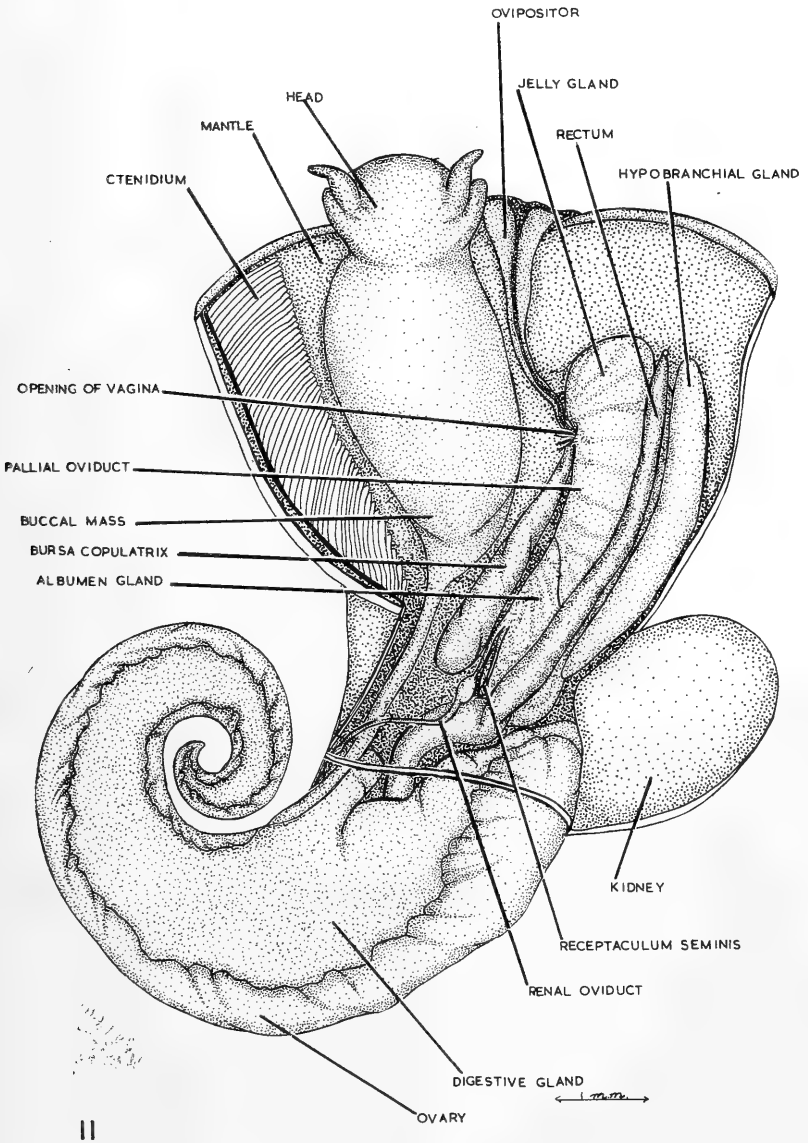


Fig. 11. Female reproductive system of *B. nanum*. The mantle cavity has been opened dorsally and the kidney has been folded to the right.

secretion droplets which stain heavily with haematoxylin. The supporting cells are similar to those of the albumen gland.

Opening anteriorly into the ventral channel of the pallial oviduct is the bursa copulatrix, a large blind duct, 300μ in diameter, which lies to the right of the oviduct in the mantle cavity (Fig. 11). Its ciliated columnar epithelium (Fig. 22) is thrown into folds of varying size (Fig. 21), which are supported by

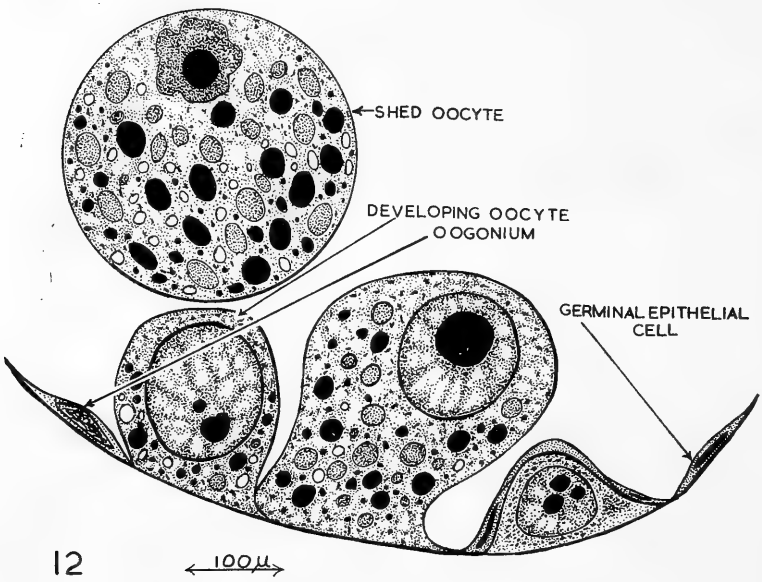
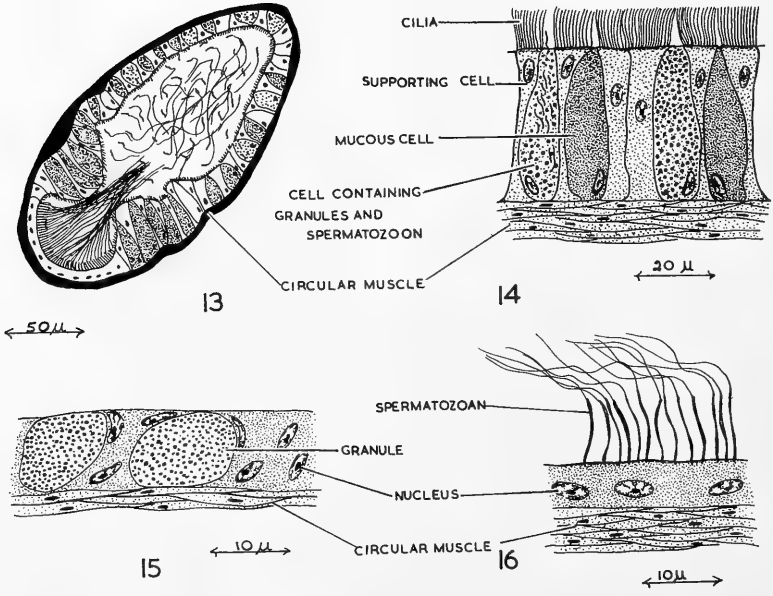


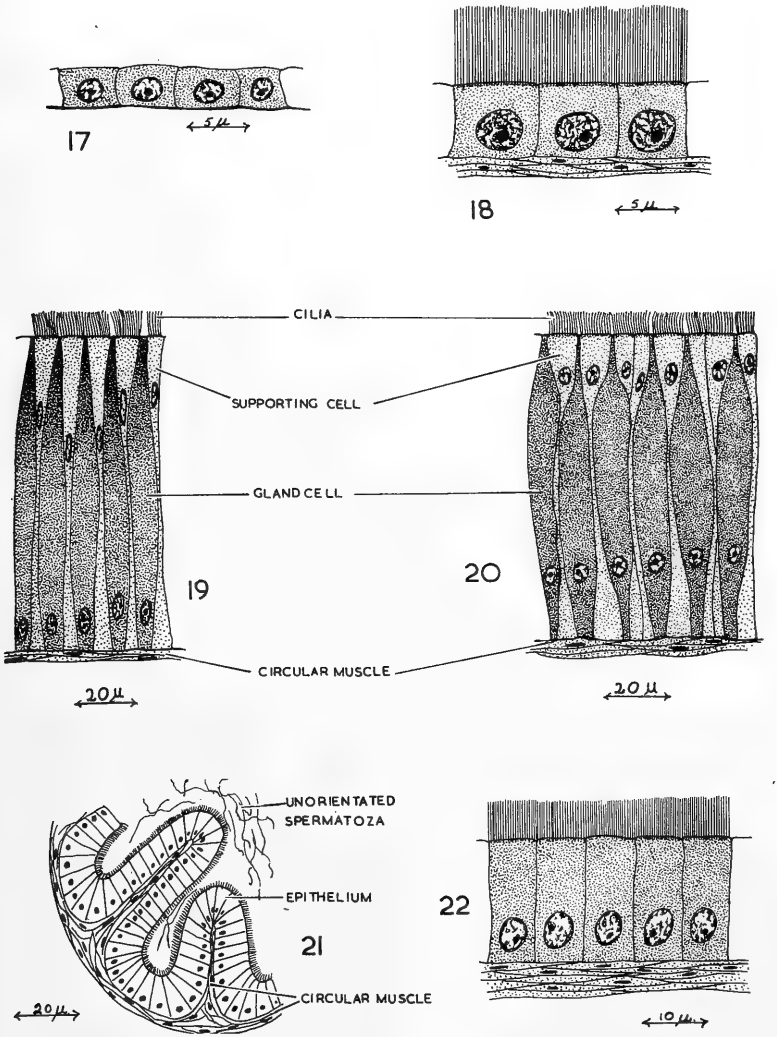
Fig. 12. T.S. through the wall of an ovarian tubule of *B. nanum*.



Figs 13–16. *B. nanum*. 13, T.S. through the receptaculum seminis ; 14, T.S. through the dorsal epithelium of the receptaculum seminis ; 15, T.S. through the wall of the renal oviduct ; 16, T.S. through the ventral syncytium of the receptaculum seminis.

extensions of muscle from a surrounding muscular sheath. Unorientated spermatozoa are found in the lumen of the bursa copulatrix.

At the mouth of the mantle cavity the bursa and oviduct unite as a short vagina (Fig. 11). From this, a ciliated groove runs between two lobes on the foot, to the right of the buccal mass and head. These lobes comprise the



Figs 17–22. *B. nanum*. 17, T.S. through the wall of the posterior bulb of the receptaculum seminis ; 18, T.S. through the wall of the ventral channel of the pallial oviduct ; 19, T.S. through the wall of the albumen gland ; 20, T.S. through the wall of the jelly gland ; 21, diagrammatic T.S. through the wall of the bursa copulatrix ; 22, T.S. through the wall of the bursa copulatrix.

ovipositor. Each lobe has a ciliated epithelium, 50μ high, in which many mucous cells are found. The epithelium at the edge of the groove is similar, but about 20μ high. Beneath the epithelium of the ovipositor is a ridge of circular and transverse muscle.

Numerous large, granule-filled cells were recorded in the tissues of the reproductive system of *Littorina rudis* by Linke (1933), who supposed them

to be amoebocytes of excretory function. Similar cells were seen in the tissues of *B. nanum*, especially in the epithelium of the albumen gland, jelly gland, ventral channel of the pallial oviduct and bursa copulatrix.

Discussion

Male Reproductive System

The histology and anatomy of the reproductive system of *B. nanum* are similar in general to those of *Littorina littorea*, *L. obtusa*, *L. rudis* and *Cremnoconchus syhadrensis*, described by Linke (1933, 1935). Anderson (1958), however, has already noted the following differences between the male reproductive systems in *Littorina* and *Bembicium*: the shape of the penis, the absence of penial glands and the compact nature of the testis, which lies over the digestive gland in *Bembicium*. Anderson's results are confirmed here and further differences have also been noted. The germinal epithelium in the testis of *B. nanum* is a flattened epithelium, not the syncytium described by Linke in other littorinids. Linke also described seasonal phagocytosis of spermatozoa in the testes of littorinids. No seasonal phagocytosis of spermatozoa was observed in the testis of *B. nanum*.

As in *L. littorea*, *L. obtusa*, and *L. rudis* (Linke, 1933) and in *Ocinebra erinacea*, *Nucella lapillus*, *Nassarius reticulatus* and *Buccinium undatum* (Fretter, 1941), phagocytosis of spermatozoa and degenerating nurse cells occurs in the vesicula seminalis of *B. nanum*. The muscular vas deferens apparently acts as a sphincter, regulating flow of spermatozoa from the vesicula seminalis into the prostate.

Kesteven (1902), who briefly described the male reproductive system of *B. nanum*, made no reference to the prostate, referring to it as a closed vas deferens. In fact, the prostate is open and glandular. Spermatozoa move along the ciliated groove of the prostate gland and receive the prostate secretion before moving into the closed penial sperm duct.

Female Reproductive System

Kesteven's (1902) description of the anatomy of the female reproductive system of *B. nanum* contained a number of errors, namely, his attribution of reduction in overall size of the system to non-breeding periods, his description of the " uterus " and his omission of the receptaculum seminis and bursa copulatrix.

As in *L. obtusa* and *L. rudis* (Pelseneer, 1911 ; Linke, 1933), sexual ripeness is independent of the time of year and is different for each individual in *B. nanum*. Absence of seasonal phagocytosis of eggs in the ovary of *B. nanum* (cf. other littorinids, Linke, 1933) may possibly be due to the milder climatic variations in the Sydney coastal area, as compared with those in the North Sea coastal areas. Kesteven (1902) noted a marked overall reduction in the size of the female reproductive system, especially in the ovary, but no such reduction was noted in this examination of *B. nanum*. His diagram of the female system appears to be of an immature specimen and his observations on size reduction were probably due to either immaturity or examinarion of parasitized specimens.

No phagocytosis of eggs occurs in the renal oviduct of other littorinids (Linke, 1933), but Fretter (1941) described it in the ingesting gland of other prosobranchs. While no ingesting gland is found in *B. nanum*, phagocytosis of eggs appears to occur in the renal oviduct.

Using the methods outlined above, the difficulties encountered by Linke in the histological examination of the " uterine " glands in the pallial oviduct were overcome. Using these techniques, it was possible to identify the anterior jelly gland and the posterior albumen gland in the pallial oviduct of *B. nanum*. A similar arrangement of glands was found in the pallial oviduct of *B. auratum* by Anderson (1958), but she gave no details of histological structure. The

enlarged " uterus " recorded by Kesteven in *B. nanum* is in fact these glands of the pallial oviduct. The muscular supporting bands he described are not muscular tissue, but folds of glandular material (Fig. 11). The glands are surrounded by a very thin coat of muscular tissue. During secretion of the albumen gland in *Littorina*, Linke described extrusion of the upper parts of the gland cells into the lumen of the gland. Presumably, this was a fixation artifact as no such extrusions are found in the albumen gland of *B. nanum*. The structure of the jelly gland is similar to that described by Linke (1933) in *L. obtusa* and *L. littorina*.

Kesteven (1902) made no reference to the receptaculum seminis and bursa copulatrix in *B. nanum*. The position of the receptaculum seminis and bursa copulatrix is similar to that recorded by Anderson (1958) in *B. auratum*. In *Littorina* Linke (1933) described a receptaculum seminis lined by a syncytial epithelium, in which sperms are embedded. The receptaculum of *B. nanum* differs from that of *Littorina* in a number of ways : in *B. nanum* the receptaculum swells to form a bulb lined by cuboidal epithelium and filled with unorientated spermatozoa ; the anterior part is lined ventrally by a syncytium in which spermatozoa are embedded, and dorsally by an epithelium composed of mucous and ciliated supporting cells, and cells containing granules and spermatozoa. The latter cells are presumably phagocytic. No similar receptaculum seminis has been described in other prosobranchs.

Unlike the bursa copulatrix of *Littorina*, which is lined by a syncytium and contains orientated spermatozoa (Linke, 1933), the bursa copulatrix of *B. nanum* is lined by a ciliated columnar epithelium, contains unorientated spermatozoa, and functions only as a receptor organ for spermatozoa.

Acknowledgements

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THE REPRODUCTION AND EARLY LIFE HISTORIES OF THE GASTROPODS *NOTOACMAEA PETTERDI* (TEN.-WOODS), *CHIAZACMAEA FLAMMEA* (QUOY AND GAIMARD) AND *PATELLOIDA ALTICOSTATA* (ANGAS) (FAM. ACMAEIDAE)

D. T. Anderson
University of Sydney

[Read 28th April, 1965.]

Synopsis

Notoacmaea petterdi, with an externally fertilized egg 150μ in diameter, develops into a planktonic lecithotrophic trochophore in 16 hours, remains planktonic for 30 hours, during which it transforms into a simple veliger, then settles, alternating crawling with intermittent swimming, during a period of eight days. Feeding does not begin until settlement is permanent, by which time metamorphosis is well advanced. Development in *Chiazacmaea flammea*, with a 130μ egg, and *Patelloida alticostata*, with a 150μ egg, follows a similar course, but in *C. flammea* permanent swimming is maintained for 60 hours and permanent settlement attained after four more days, while in *P. alticostata* swimming for 60 hours is followed by settlement over three more days. The form and dimensions of the eggs and larvae in these three species resemble those of *Acmaea testudinalis*, but associated with a more prolonged subsistence on yolk, *C. flammea*, *P. alticostata* and especially *N. petterdi* have a more extended swimming-distributive phase than *A. testudinalis*.

Introduction

Although several species of acmaeid limpet are commonly represented along the New South Wales coast (Dakin, 1953), their reproduction and early life histories have not been investigated (Anderson, 1960). Little is known of larval development in the Acmaeidae, the only comprehensive description being that of Kessel (1964) for *Acmaea testudinalis*. The present study of *Notoacmaea petterdi*, *Chiazacmaea flammea* and *Patelloida alticostata* shows that their larval development differs from that of *A. testudinalis* in a number of interesting ways.

Materials and Methods

For *N. petterdi*, which inhabits upper littoral vertical rock faces exposed to the ocean surf, animals collected from the rock platform at Harbord, N.S.W., in July and August 1964 and in January 1965 were found to contain ripe gametes at both periods, suggesting that breeding occurs throughout the year. For *Chiazacmaea flammea*, which lives in association with oysters intertidally in estuarine waters, animals collected from the shores of Middle Harbour, N.S.W., in August 1964 and January 1965 also contained ripe gametes at both times, similarly indicating a prolonged breeding season. For *Patelloida alticostata*, which lives at very low levels on intertidal coastal rock platforms, animals containing ripe gametes were obtained from Long Reef, N.S.W., in January 1965, but have not yet been examined at other times of the year.

Larvae of each species were obtained by artificial fertilization, after releasing eggs and sperm by dissection of the adults. Eggs were divided into batches of about 100 and allowed to stand in 300 ml. of filtered sea-water for 30 minutes before adding a few drops of sperm suspension. Swimming trochophores resulting from successful fertilization were transferred by means of a pipette to Petri dishes of filtered sea-water, a similar transfer to fresh sea-water being effected each day until permanent settlement had occurred. All cultures were maintained at 20°C.

Results

Notoacmaea petterdi

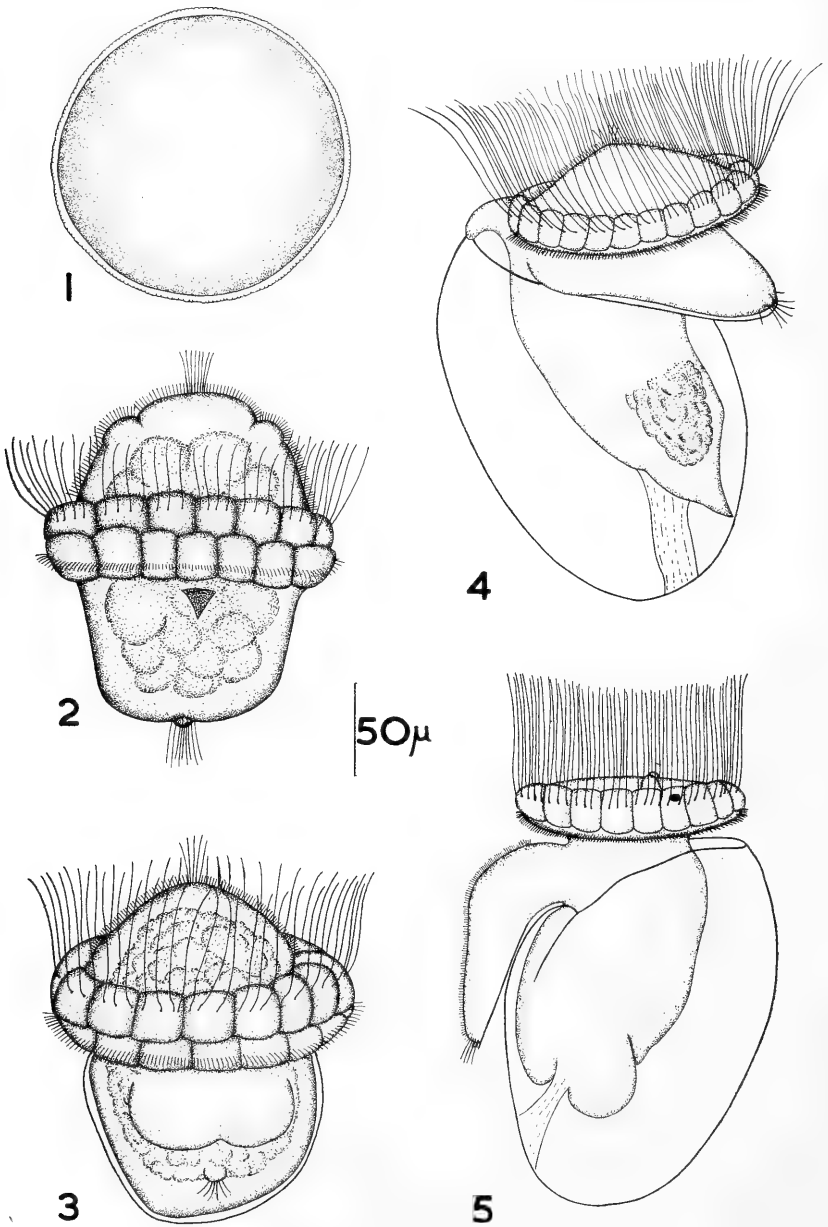
The mature oocytes of *N. petterdi* (Fig. 1) are pink in colour, uniformly yolky and opaque, covered by a thin egg membrane and, after immersion in sea-water for 30 minutes, spherical, with a diameter of 150μ. Sea-water immersion also causes a thin layer of colourless jelly to swell up on the surface of the egg, but there is no indication of adhesion between eggs, suggesting that they float freely in the water following natural spawning. Sixteen hours after fertilization, free-swimming yolky trochophores (Fig. 2) are found swimming near the water surface by means of a prototroch of long coarse cilia. The action of the prototroch is intermittent, the larva either swimming at random in short darting bursts or drifting with the prototroch folded forwards. The prototrochal ciliary beat has a clockwise metachronal rhythm but the larva itself does not rotate while swimming. Behind the prototrochal ring is a ring of short vibrating cilia, while anteriorly and posteriorly lie apical and terminal tufts of stationary cilia, held extended while the larva is in motion. The episphere with its paired antero-lateral protuberances is also covered by short, slowly waving cilia. Due to the internal mass of yolky macromeres, the trochophore retains the pink coloration of the egg, but its outer parts are colourless.

At about 19 hours, the foot rudiment begins to grow out ventrally behind the prototroch and during the next five hours the trochophore develops into a simple early veliger (Fig. 3). The prototroch shows little change of form, but its action becomes more vigorous and continuous, so that long periods of steady swimming in a semi-upright position near the water surface are interspersed with short resting periods during which the larva gradually sinks through the water. No unidirectional response to light is observed at this or any other stage of development. The episphere in the early veliger is already reduced in size, and has lost its paired protuberances, although its apical tuft and general ciliation are retained. The hyposphere, in contrast, is enlarged and elaborated, with a conspicuous, bilobed, ventral foot rudiment and a globular, colourless, dorsal shell. Due to dorsal enlargement of the hyposphere, the original terminal tuft of cilia is pushed postero-ventrally and now sprouts from a small protuberance behind the foot. The interior of the veliger is still occupied by a pinkish mass of yolky macromeres.

During the second day of development, the veliger continues to swim in an upright position near the water surface, with the velar cilia maintaining their clockwise metachronal beat, rising through the water, then sinking again at intervals when the velar cilia come to rest. At the same time, the veliger (Fig. 4) increases greatly in size and shows numerous structural changes. In the velum, the velar cilia grow longer and retain their vigorous activity, but the velar cells become much smaller, indicating the onset of a gradual metamorphosis. The episphere, although retaining its ciliation, also becomes smaller, being much flatter at the end of the second day than at the beginning. The foot, in contrast, increases in size as a triangular wedge incorporating the terminal tuft and its protuberance at the apex, and secretes an operculum on its posterior face. The colourless larval shell is greatly enlarged, with the visceral mass, attached posteriorly to the shell by paired columella muscles, occupying only part of it, the remainder being occupied by the mantle cavity. Torsion occurs during the second day, so that the mantle cavity becomes dorsal in position, but neither withdrawal into the shell nor muscular movements of the animal are observed during this time. The main mass of yolk is now concentrated in the visceral mass, but the remainder of the tissues are also semi-opaque and not obviously differentiated.

Further progress in development and metamorphosis during the third day (Fig. 5) is accompanied by a change in behaviour. From continuous swimming, the behaviour of the larva alters to long periods of sedentary attach-

ment to the bottom interspersed with brief slow swimming excursions upwards through the water. Even agitation of the dish in which the larvae are maintained fails to alter this pattern. The larval shell grows no larger, but the velum becomes slightly smaller and its cilia begin to shrink. The episphere



Figs 1–5. *Notoacmaea petterdi*. 1, Mature oocyte; 2, trochophore, 16 hr., ventral view; 3, veliger, 24 hr., ventral view; 4, veliger, 41 hr., ventrolateral view; 5, veliger, 65 hr., lateral view.

becomes flattened and shows the onset of differentiation of the eyes as a pair of dark brown dorso-lateral pigment spots and tentacles as a pair of blunt, short protuberances ventral and median to the eyespots. The head and visceral mass retain the pinkish-brown opacity indicative of continued lecithotrophy,

but the beginnings of differentiation of the gut can be discerned in the visceral mass and the columella muscles become contractile, producing complete withdrawal into the shell in response to stimulation. The foot also becomes highly muscular and mobile, elongates slightly in a posterior direction, and develops a layer of short, continuously-beating cilia over its ventral surface. Slow creeping in an exploratory manner over the substratum on the ciliated sole of the foot begins towards the end of the third day, but the larva is unstable in the creeping position and frequently tips over to one side or the other. Spasmodic beating of the velar cilia during creeping appears to assist in maintaining balance while the foot is in this rudimentary condition.

During the fourth day, although brief swimming excursions continue, metamorphosis becomes more evident and the capacity for strong attachment and creeping in a straight line on the foot is enhanced (Fig. 6). The velum continues to shrink, its cilia becoming finer and shorter, while the tentacles elongate and become highly mobile. The ciliated foot is also greatly elongated antero-posteriorly, while in the visceral mass, although some yolk remains, the coil of the intestine leading to the anus becomes conspicuous. Crawling on the foot occurs in the typical snail manner, the shell being held upright and the tentacles extended forwards, outwards and downwards, rhythmically tapping the substratum in front of the animal. In contrast to their activity during the earlier phase of more unstable crawling, the velar cilia now remain at rest, partly covered by the shell, as the animal creeps along. While attached by the sole of the foot, however, the animal cannot withdraw fully into the shell, part of the foot remaining uncovered when columella muscle contraction occurs and the shell is clamped down on the body. Full withdrawal is possible only if the foot becomes detached from the substratum.

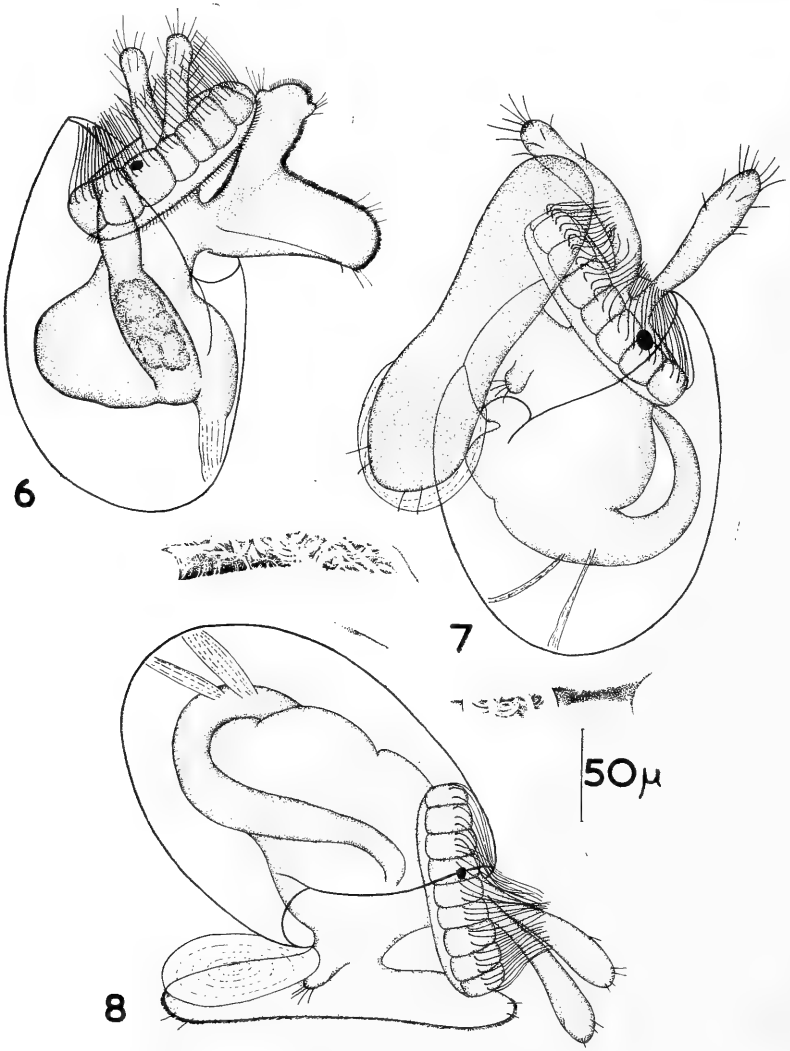
During the fifth day, the same type of crawling behaviour is pursued more vigorously, with the tentacles and the anterior end of the foot pushing out from side to side in what appears to be an exploratory manner, and with frequent changes of direction. At the same time, internal differentiation proceeds rapidly in the visceral mass, the coiled gut becoming more obvious, and the tentacles grow longer and the eyespots larger. A general increase in muscular activity is also evident during this time. The velum, however, does not appear to undergo further reduction.

Progressively, development in the same direction continues during the next four days, growth of the foot and tentacles being accompanied by further differentiation of the visceral mass (Fig. 7). The velum reduces in size only very slowly during this time, although its cilia become finer and shorter and the swimming excursions made become more and more infrequent and more and more feeble. On the last of these days, further addition to the margin of the shell begins, giving it the circular marginal outline of an incipient adult shell, and following this, on the tenth day, the capacity for swimming is lost. The animal (Fig. 8) crawls actively on its foot, and if dislodged, immediately reattaches. The gut is by now very well developed and although feeding has not yet begun, it is obvious that it must soon do so. Development was not followed beyond this point.

Chiazacmaea flammea

The mature oocytes of *C. flammea* (Fig. 9) are brown in colour, uniformly yolky and opaque, covered by a thin egg membrane and, after immersion in sea-water for 30 minutes, spherical, with a diameter of 130μ. A layer of colourless jelly covering the egg swells to a thickness of about 10μ, but there is no evidence of adhesion between eggs. Like those of *N. petterdi*, they probably float singly and demersally after natural spawning. Fourteen hours after fertilization, free swimming trochophores (Fig. 10) are found near the water surface, swimming by a metachronal clockwise beating of the long thick cilia of the prototroch, short curving bursts being interspersed with periods of rest.

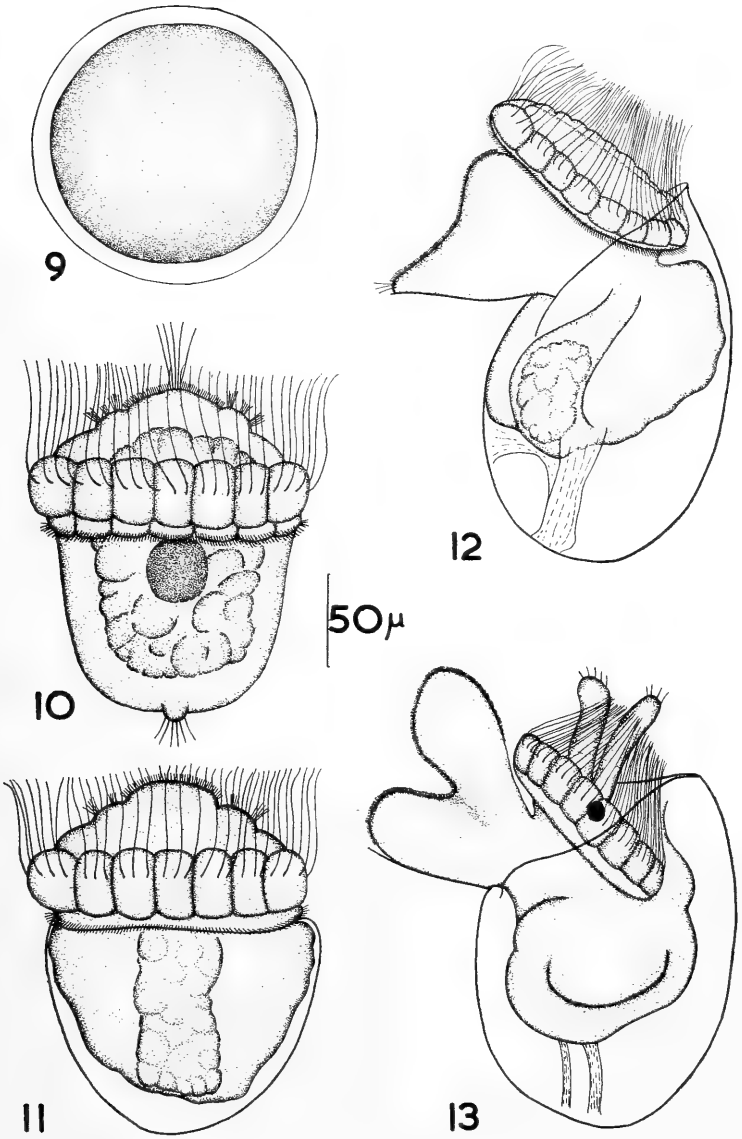
The brown coloration of the egg is retained in the yolky interior of the trochophore, occupied by macromeres. On the conical episphere, in addition to a general motionless ciliation and paired antero-lateral protuberances, is an apical tuft of long cilia, normally held stiffly upright during swimming but also showing slow bending and waving movements. The hyposphere is unciliated save for a terminal tuft of long motionless cilia borne on a small postero-ventral protuberance. In all general respects the trochophore of *C. flammea* is similar to that of *N. petterdi*.



Figs 6–8. *Notoacmaea petterdi*. 6, Early metamorphosis, 90 hr., lateral view ; 7, continuing metamorphosis, 6½ days, ventral view ; 8, first permanently settled stage, 10 days, lateral view.

Development proceeds rapidly. Within the next five hours (Fig. 11), the hyposphere enlarges dorsally, the globular larval shell is secreted, and a small simple foot rudiment grows out mid-ventrally behind the prototroch. The latter undergoes little change, but swimming in a semi-upright position becomes more or less continuous, with periods of slow swimming interspersed with short faster curving bursts. The episphere shows no change other than loss of the apical tuft.

During the remainder of the first and throughout the second day (Fig. 12), steady swimming near the water surface continues as the veliger becomes progressively elaborated. In spite of this, the prototroch undergoes reduction in size during this time, although its cilia remain long and active. The episphere becomes flattened and unciliated, while behind the prototroch, the foot rudiment



Figs 9–13. *Chiazacmaea flammea*. 9, Mature oocyte ; 10, trochophore, 14 hr., ventral view ; 11, veliger, 19 hr., dorsal view ; 12, veliger, 44 hr., lateral view ; 13, early metamorphosis, 4½ days, lateral view.

enlarges, growing posteriorly, secretes an operculum, and becomes ciliated over its ventral surface. The larval shell is greatly enlarged and the visceral mass undergoes torsion and begins to show differentiation of the gut. Some muscular activity also becomes evident in the foot and visceral mass, but withdrawal into the shell does not occur. In swimming, the velum is projected antero-dorsally, with the visceral mass and shell suspended below it, and the

beating of the velar cilia draws the animal along in a vertical position with the foot trailing. The visceral mass is still opaque, due to the presence of brownish yolk reserves.

Steady swimming and progressive development continue during the third day, the visceral mass becoming more differentiated and the foot longer and more muscular. During the fourth day (Fig. 13), paired dark brown eyespots are developed dorso-laterally on the episphere, while ventral and median to them paired tentacles grow out. At the same time, the velum begins to shrink and swimming becomes interspersed with periods during which the larva settles and crawls very slowly and feebly on its foot, with the shell held upright. Gradually over the next three days, with little further change in appearance, the capacity for swimming is lost and crawling greatly improved. The mode of crawling is similar to that of *N. petterdi* at the corresponding stage. By this time, most of the yolk reserves have been utilized but there is no evidence that feeding begins before settlement has become permanent. Development was not followed beyond this point.

Patelloida alticostata

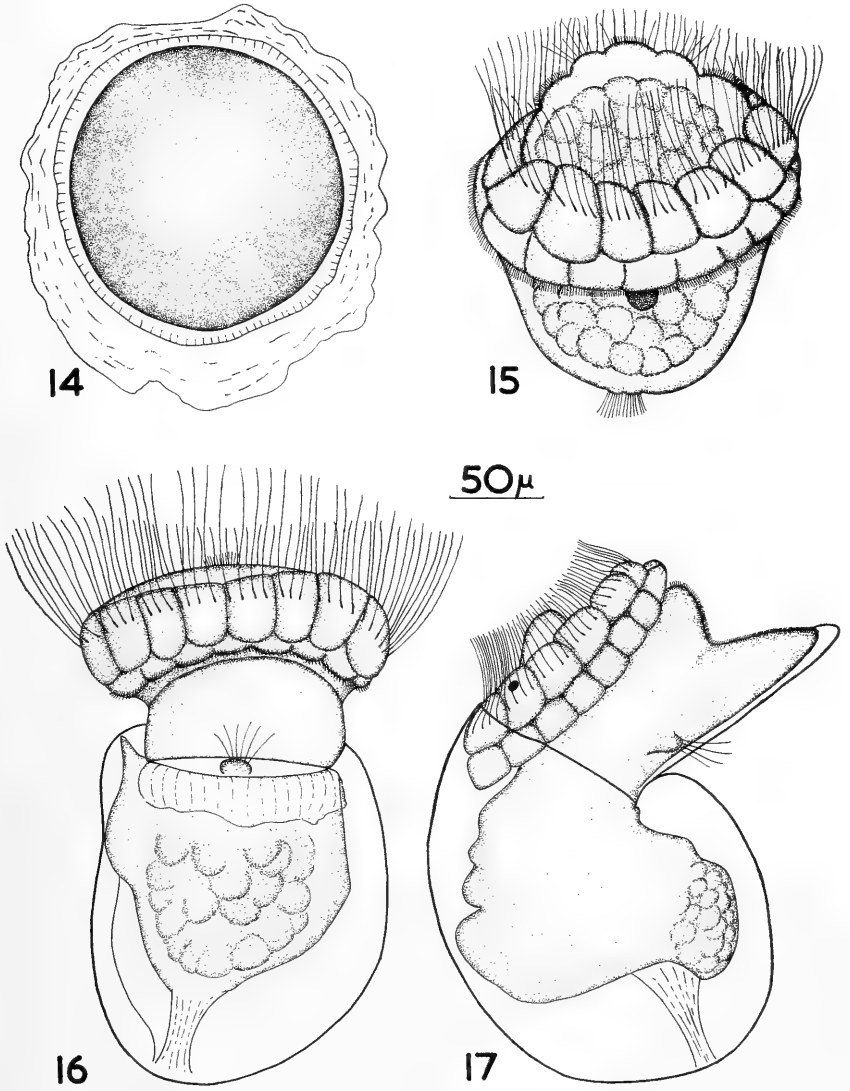
The mature oocytes of *P. alticostata* (Fig. 14) are yellow in colour, uniformly yolky and opaque, covered by a thin egg membrane and, after immersion for 30 minutes in sea-water, spherical, with a diameter of 150μ. Sea-water immersion also causes a double layer of colourless jelly to swell up around the egg, a uniform, dense, inner layer being covered by a less dense, irregular, outer layer. Some tendency to adhesion is observed between eggs, and it is possible that in natural spawning the eggs adhere temporarily as a gelatinous egg mass until hatching and escape of the trochophores occurs.

Trochophores (Fig. 15) are found swimming actively near the surface of the water 18 hours after fertilization. They are semi-opaque, filled internally with a mass of yellow yolky macromeres, and differ from the trochophores of *N. petterdi* and *C. flammea* in a number of ways. The prototroch is more protuberant, with a large number of much finer cilia and, although these beat in clockwise metachronal rhythm in the usual way, the swimming of the trochophore is a slow continuous straight line progression, without the darting, curving movements characteristic of the other species. The conical episphere is finely ciliated, with low paired antero-lateral protuberances bearing long cilia, and with little development of an apical tuft. The hyposphere bears the usual terminal tuft of fine cilia.

During the second day of development (Fig. 16), the prototroch enlarges slightly as a velum, its cilia become more powerful and steady swimming near the water surface continues. At the same time, the episphere flattens and loses much of its ciliation, while the hyposphere enlarges and differentiates as a dorsal visceral mass secreting a globular shell and a ventral foot rudiment secreting a posterior operculum. The visceral mass is still very yolky. Torsion occurs towards the end of the second day.

During the third day of development (Fig. 17), steady swimming in a semi-upright position continues, but the velum begins to shrink. The episphere also becomes more flattened and develops a pair of brown eyespots. Little change occurs in the foot rudiment other than development of a fine ventral ciliation, but the larval shell becomes further enlarged and the visceral mass further differentiated, showing retention of yellow yolk reserves mainly ventrally. Muscular movements in general are not conspicuous in the larva at this stage, and, although complete withdrawal into the shell is possible, accompanied by sinking through the water, there is no attachment or creeping on the substratum. The early phases of metamorphosis, however, proceed rapidly during the fourth day, with further reduction of the velum, outgrowth of paired tentacles on the head, elongation of the foot, and further differentiation of the organs of the visceral mass. Muscularity is greatly increased, and by the

end of the fourth day crawling predominates over swimming. After two further days, although the reduced velum is still retained, the crawling habit has become permanent and the young animal is closely similar to the young of *N. petterdi* illustrated in Figure 8. Feeding does not begin until settlement is complete.



Figs 14–17. *Patelloida alticostata.* 14, Mature oocyte ; 15, trochophore, 18 hr., anteroventral view ; 16, veliger, 42 hr., ventral view ; 17, veliger just entering metamorphosis, 66 hr., lateral view.

Discussion

In *N. petterdi* and *C. flammea*, eggs are probably spawned singly into the water, as in *Acmaea virginea* and *Acmaea fragilis* (Boutan, 1898 ; Willcox, 1898, 1900), since they show no tendency to adhere after artificial release. In *P. alticostata*, in contrast, released eggs adhere temporarily by their outer jelly coats, and it is possible that in natural spawning they aggregate as a transient egg mass, as in *Acmaea testudinalis* (Kessel, 1964).

For *Acmaea testudinalis*, Kessel (1964) has shown that at 12°C, the 140μ egg hatches as a free-swimming trochophore in 10–13 hours. It remains lecithotrophic for about 50 hours, attaining during this period a well developed pretorsional veliger stage with a circular monotrochal velum. Planktotrophy then begins, torsion occurs and the veliger remains planktotrophic, with further development of the shell, foot and visceral mass, for about 25 hours. Towards the end of this period, eyes and tentacle rudiments begin to differentiate in the head and swimming begins to alternate with periods of crawling on the now well developed foot. Permanent settlement, with crawling and feeding, is established within 15 hours (i.e., by the time the larva is four days old) but metamorphosis, with loss of the velum and operculum, further elaboration of the head and foot and onset of secretion of the adult shell, does not become obvious until 11 days after settlement.

Development in *N. petterdi*, *C. flammea* and *P. alticostata*, while generally similar in the three species, differs from that of *Acmaea testudinalis* in a number of ways. Although egg dimensions, mode of spawning and fertilization, and early hatching as a lecithotrophic free-swimming trochophore are shared in common, and planktonic life is equally brief (about 30 hours in *N. petterdi* and 60 hours in *C. flammea* and *P. alticostata* at 20°C, compared with about 75 hours in *Acmaea testudinalis* at 12°C), lecithotrophy is maintained throughout planktonic life. Development of the eyes and tentacles and onset of velar shrinkage are more precocious than in the planktotrophic larva of *A. testudinalis*. At the same time, the transition to permanent settlement, preceding the onset of feeding, occurs more slowly, taking three days in *P. alticostata*, four days in *C. flammea* and eight days in *N. petterdi*, and is accompanied by gradual metamorphosis and functional differentiation of the organs of the visceral mass.

Thus *N. petterdi*, *C. flammea* and *P. alticostata* are adapted to a more economical utilization of yolk reserves than *Acmaea testudinalis*. The biochemical basis of this difference is obscure, but if we regard the planktotrophic development of *A. testudinalis* as primitive, it is a difference which appears to offer certain advantages. In the absence of velar elaboration, planktotrophic life in *A. testudinalis* is necessarily brief and rapid permanent settlement is essential to the transition from planktonic to bottom feeding, even though the onset of metamorphosis is delayed for several days. In *C. flammea*, *P. alticostata* and especially *N. petterdi*, with similar larval dimensions and a similar simple velum, permanent planktonic life is equally brief, but planktonic feeding is obviated and the delayed onset of bottom feeding is associated with intermittent swimming excursions during the several days before secretion of the adult shell begins. Thus development is more direct but the distributive planktonic phase is more prolonged. From such a mode of development it is but a short step to the ovoviviparity and birth as a crawling juvenile described for the Arctic *Acmaea rubella* by Thorson (1935).

Acknowledgements

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MALARIA IN THE D'ENTRECASTEAUX ISLANDS, PAPUA, WITH PARTICULAR REFERENCE TO *ANOPHELES FARAUTI* LAVERAN

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[Read 28th April, 1965]

INTRODUCTION

The observations set out below were made during the years 1956–59, as part of the investigations into the status of malaria in the indigenous population of the D'Entrecasteaux Islands, carried out jointly with the Medical Officer, at the direction of the Department of Public Health.

Detailed studies were made to obtain understanding of the pre-operational norm, necessary for appraisal of any noticeable events which may occur after vector control is begun. Previous observations of other workers on the behaviour of *A. farauti* are related to observed events in the D'Entrecasteaux Islands.

About 40,000 anophelines were taken resting or biting outdoors, indoors and in window traps in more than 50 hamlets and several European stations. Extensive larval collections were also made. The majority of the collections were from coastal hamlets. Attention was also paid to garden houses and to mountain hamlets. The inland anophelines taken on Fergusson Island occurred at a height of about 400 feet above sea level. An anopheline species distribution list for the D'Entrecasteaux Islands has been published (Spencer and Spencer, 1960).

GENERAL DESCRIPTION

The D'Entrecasteaux Islands lie roughly 60 miles to the north and north-east of Milne Bay, and have an extended coastline totalling nearly 100 miles in length, a submerged mountain range with three main islands. The highest mountain peak rises to over 8,000 feet. The coastal strip varies in width. In many places it is characterized by swamps and lagoons of varying size. Steep mountain drainage results in bars and deltas at the mouths of streams.

The population of 30,000 indigenes is scattered in small hamlets, often of about ten houses only. Many of the hamlets are coastal; the mountain dwellers frequently visit the coast and may have fishing shacks. The majority of houses are on stilts. The roofs are usually of overlapping sago leaf, the walls of parallel upright sago stems, and the floors of palm slats. Most activities are carried on outside the house. The village people may retire about 9 p.m., or may sit outside until late in the night, especially on moonlight nights. They do not become accustomed to the bites of anophelines which worry them a great deal. Mosquito nets are not commonly used.

Recruiting from these islands, as a work force for other areas, has been heavy. The period spent away is about 18 months at a time. There are also trading movements to and from the " mainland " (the island of New Guinea) and the other islands. Important features of the social organization here are the small size and physical separation of the hamlets, the restricted number of people inhabiting them, and their placing relative to anopheline breeding grounds.

The coastal hamlets and fishing shacks are built near small mountain streams with their attendant backwaters and lagoons. Separate garden houses are a feature of some groups (often distant from the hamlet house), and these may be built without walls. Hamlet houses in some places may lack walls. In some places the yam harvest is stored in a separate room or on an overhead platform within the house.

Annual rainfall has varied from 59″ to 149″. The average is probably about 100″. The northern end of Goodenough Island has a well-marked wet and dry season, with rain particularly concentrated in the months December to March. Elsewhere in the D'Entrecasteaux Group rain falls throughout the year, with no particular pattern, except a possibility of lower and higher rainfall cycles extending over periods of three or more years. The average maximum and minimum monthly temperatures vary between about 70° and 90° F, the range being between 62° and 95° F. Relative humidity averages vary from 74 per cent to 88 per cent, with 57 per cent as the lowest figure.

Observations in Unsprayed Areas

Anophelines were collected resting or biting, outdoors and indoors, and in window traps, in more than 50 hamlets and several European stations, of the three main islands of the D'Entrecasteaux Group. Extensive larval collections were also made. The majority of the collections were from coastal hamlets. Attention was also paid to garden houses and to mountain hamlets.

Standard techniques were used before and after spraying. Mosquitoes collected by sucking-tube were transferred to small mosquito-net cages tied by tapes to rigid frames attached to a plywood base. These cages were wrapped in moistened cottonwool and carried in a calico bag. Fed mosquitoes survived very well in them. Where hourly time-groups were required, as for man-biting catches throughout the night, 12 such cages were used.

We measured the incidence of association of the vector species with man by means of man-biting catches, as described by Pampana (1963). We standardized our technique on a 12-hour catch, 6 p.m. to 6 a.m., during the course of these investigations. Two collectors alternated throughout the night. They were dressed in shorts and shirts, and each caught from his own legs for a three-hour period before resting. These men were skilled and reliable. Initially they used mouth sucking tubes, later the battery-operated suction devices which made the collecting both much easier and more efficient. Wherever possible, the collectors sat among, or near, the village people at their normal activities.

Outdoor biting

Over one series of pre-spraying catches covering a 14-month period, a total number of 76 outdoor biting catches was recorded. These catches were made at varied localities on the perimeter of the three large islands of the D'Entrecasteaux Group. Within this series were two series of repeated catches carried out at Uiaupolo hamlet (nine catches), and Bwalalea hamlet (20 catches), these two hamlets being considered typical coastal hamlets reasonably representative of many others.

Indoor biting

Over 11 months of the pre-spray period, a total series of 31 indoor biting catches was made. A few comparative catches were made initially outdoors and indoors on the same night.

Night house-resting

The pre-spraying resting pattern, or position within and on the house relative to time, was investigated in (*a*) a number of different hamlets, and

(*b*) in the same hamlet, by all-night catches and limited-period catches (10 p.m.–2 a.m.) from all parts of the house.

1. For resting position, state of feeding, and a gross time-distribution (before and after midnight, etc.), the results from the different hamlets were combined.

2. For the hourly resting time-pattern, collections were made from the same three houses over three successive nights, making a total of nine house/nights. A number of collectors maintained as nearly as possible a continuous collection from all parts of the house on each night. Disturbance would probably contribute to lowered numbers of resting mosquitoes.

Pre-spraying window-trap studies

Window traps were fixed to " window " apertures on ordinary hamlet houses. A continuous series was carried out in the hamlet of Bwalalea. The results were averaged.

Dissections were carried out on time-group samples of the window-trapped mosquitoes, to form the basis for an estimation of the movements of nulliparous and parous individuals. The ovarioles were examined in saline to determine if they were nulliparous or parous, to arrive at a value for " p ", and to attempt age estimations for individual mosquitoes.

Pre-spraying sporozoite rate

The full series of dissections embraces three " anopheline ecological units ", the hamlets of Bwalalea and Uiaupolo, and the hamlet of Mapamoiwa together with Mapamoiwa station. These units lie in a line along the north-western coastal strip of Fergusson Island, separated by intervening bush, but the interlinking human traffic means that from the point of view of infection risk these three areas must be combined: together they may be regarded as reasonably representative of the island group. The anophelines dissected included those caught biting in hamlets and in garden houses, resting in houses by day and by night, and resting outdoors by day. The window-trap series was from Bwalalea hamlet only.

Human blood index

To establish the pre-spraying human blood index, blood meal smears from outdoor resting mosquitoes were taken according to standard procedures recommended by WHO, and precipitin testing was carried out by the Lister Institute (England).

Anopheles Species Recorded

A. farauti—widespread, abundant, and the major vector.

A. punctulatus—also widespread, with distinct fluctuations of population: of more limited and more localized importance than *A. farauti*, but contributes to the transmission of malaria in these islands.

A. koliensis—adults found in very low numbers in a few places.

A. subpictus—widespread, and at times abundant: importance as a possible vector not known. Showed a decided tendency to attack man and to rest within houses.

A. annulipes—adults rarely taken, larvae sometimes numerous; apparently little affinity for human blood.

A. bancrofti—larvae taken in a few places: no adults taken: adults were collected on Goodenough Island during the war.

A. longirostris—both adults and larvae taken in low numbers from a few places.

The *A. punctulatus* complex needs further taxonomic investigation. We found a number of specimens, from several localities, of *A. punctulatus* with

irregular black scaling on the apical pale part of the proboscis, sometimes extensive. These specimens resemble Woodhill's suggested hybrids between *A. punctulatus* and *A. farauti*. The geographical distribution of species recorded during the pre-spray survey is shown in Figure 1, Spencer and Spencer, 1960.

In a total of 6591 anophelines taken biting out of doors throughout the night, from 83 catches spread over two years, the species composition was as follows: *A. punctulatus* (2·5 per cent), *A. farauti* (94·6 per cent), *A. subpictus* (2·7 per cent), *A. koliensis* (seven specimens only), *A. longirostris* (two specimens only).

In a smaller series of indoor biting catches throughout the night, less widely spread, *A. farauti* formed 97·7 per cent of the total of 1926 anophelines taken from 31 catches spread over two years, with a few *A. punctulatus* and *A. subpictus* and one specimen of *A. annulipes*.

In night house-resting catches with a total of 1668 anophelines from 49 houses, *A. farauti* again dominated (92·8 per cent) with *A. punctulatus* (0·3 per cent) and *A. subpictus* (6·9 per cent). These catches included a period when *A. subpictus* numbers rose due to a prolonged dry spell. Surprisingly, two adult *A. subpictus* were taken resting at night in houses about 400 feet above sea level and well inland.

A. farauti is thus by far the dominant anopheline of the D'Entrecasteaux Islands, as it is also of all the outer islands to the north, east and south-east —the perimeter of the Milne Bay District—and beyond.

With suitable rainfall, localized population explosions of *A. punctulatus*, limited in time, have been observed in the D'Entrecasteaux Islands. Although this species may appear to be absent from an area, colonization of transient surface pools can be rapid. It is widely distributed throughout the D'Entrecasteaux Islands, normally occurring in small numbers.

Behaviour of Adult Mosquitoes

Interrelationship of human and anopheline ecology

It is important to have a clear idea of the normal dispersion and behaviour of anopheline populations in relation to areas inhabited, or not inhabited, by human beings, and of the normal manner and rate of build-up of anopheline populations under favourable conditions.

In the D'Entrecasteaux Islands there are large gaps between clusters of human population, of forest, kunai grass and secondary growth, with a low density of indigenous mammalian fauna. The distance between individual hamlets, or hamlet groups, may be greater than the expected range of flight of anophelines, with consequent isolation of the populations. The coincidence of highly suitable breeding places, and a concentration of suitable hosts, is likely to result in a convergence of anopheline activity within the hamlet area and around its edge. Outside the hamlet areas—and the tracks radiating from them where interference with bush, and night movements of people, offer a suitable coincidence of hosts and breeding opportunity—it is less likely that large concentrations of anophelines can occur.

Under the circumstances outlined above, *A. farauti* populations can build up closely dependent upon individual human communities and their domestic animals. The anopheline populations can be expected to become less dense as the distance from the hamlet becomes greater, unless the hamlets are situated close together with overlapping anopheline populations. The closer the spacing of the hamlets, the looser the association of any individual *A. farauti* with a particular hamlet.

Observations show high adult and larval densities in and around hamlet areas (the " domestic " populations) allied usually with low densities in garden and bush areas (the " wild " population). Residual spraying should cause

reductions in anopheline density in hamlet areas, and the effects of spraying should extend some distance into the perimeter areas.

Hamlets represent the more permanent human communities. Temporary human communities are also formed, to engage in fishing, gardening, making of sago, or other extra-hamlet activities. If such a temporary community remains in one area long enough and conditions are suitable, it will cause the formation about itself of a concentration of breeding from the base level "wild" anopheline population. Such places are usually not protected by the insecticide umbrella. A residual focus of infected mosquitoes here may survive the comings and goings of different family groups, and infect the later comers.

Outdoor and indoor biting in hamlet areas, biting in garden houses, and day-time biting

The data discussed in the next two sub-sections throw light on the normal patterns of biting and the mosquitoes' basic relationship to man. They also suggest the degree of contact with the insecticide that the mosquitoes are likely to have.

The peak period of attack for *A. punctulatus* was 12 midnight to 3 a.m. For *A. subpictus* there was abrupt rise after 9 p.m., but no noticeable peak period.

The results of outdoor and indoor human bait catches, relating to *A. farauti* alone, are shown in Table 1. The calculated average value of the outdoor biting incidence is 62·0 bites per man per night, and of the indoor biting incidence is 65·2 bites per man per night. The mean value is 63·6 bites per

TABLE 1

A. farauti: *Night-biting catches and indoor-resting catches*
Results arranged to show hourly fractions of biting cycle
(Pre-spray catches in various localities)

Time	Outdoor biting June 1957–Aug. '58 (catches = 58)		Indoor biting Oct. 1957–Aug. '58 (catches = 25)		Night indoor resting May 1959 (catches = 9)	
	Number taken	Percentage of total	Number taken	Percentage of total	Number taken	Percentage of total
6–7 p.m.	135	3·8	77	4·7	71	5·7
7–8 p.m.	213	5·9	86	5·3	78	6·3
8–9 p.m.	289	8·0	105	6·4	134	10·8
9–10 p.m.	389	10·8	151	9·3	122	9·8
10–11 p.m.	418	11·6	164	10·1	157	12·6
11 p.m.–12 midnight	431	12·0	231	14·2	187	15·1
12 midnight–1 a.m.	395	11·0	187	11·5	144	11·6
1–2 a.m.	392	10·9	160	9·8	120	9·7
2–3 a.m.	291	8·1	132	8·1	92	7·4
3–4 a.m.	269	7·5	133	8·2	70	5·6
4–5 a.m.	236	6·6	112	6·9	43	3·5
5–6 a.m.	133	3·7	90	5·5	24	1·9
Total	3.591		1.628		1.242	

man per night. A reasonable average figure, relating to the whole island group, and to all seasons, is 65 bites per man per night. This figure represents an assessed over-all risk for a large area in which malaria is endemic, and in which there is constant movement and interchange of the people.

The incidence of attack in night outdoor biting by *A. farauti* tended to increase to a plateau lasting from about 9 p.m. to 2 a.m., followed by a fairly steady decline (Table 1). There is no real peak of attack. Pre-midnight attack is slightly greater than post-midnight attack, approximately 53 per cent : 47 per cent for a total of 4600 *A. farauti*.

It is suggested that sample outdoor leg biting catches of *A. farauti* can be made for any convenient hours of the night, and the total density per man per night calculated from the percentages shown in Table 1. Alternatively, the catcher may sit outside while the village people do, then move inside when they go into their dwelling for the night. The nature of the dwelling allows free entry and exit to the mosquitoes. In effect, as shown below, mosquitoes associated with inhabited areas follow the movements of the people. *A. farauti* adults, after biting outdoors, will rest on objects near their hosts—stones, tree buttresses, grass, etc., and have been seen fully engorged in large numbers.

From Table 1 it will be seen that the indoor attack builds up more slowly than the outdoor attack, there is an intensification of biting after midnight, and a fall in activity after about 1 a.m. Pre-midnight and post-midnight attacks are the same, 50 per cent : 50 per cent.

A small series of night biting catches in garden houses was carried out to determine whether there is a bush population which will attack under those circumstances. The attack rate was low ; nevertheless in the relatively remote and isolated garden house, attack does occur. Garden houses and other temporary shacks are occupied for varying periods of time by varying numbers of people. These structures often lack walls.

Day-time biting by *A. farauti* has been noted in a number of different places—Solomon Islands, Australia, New Hebrides, Trobriand Islands (see Black, 1955). We did not experience day-time attack in the D'Entrecasteaux Islands.

Night resting in and on houses, entry and exit, age composition and longevity

House-resting catches were continuous throughout the night and were from all parts of the house, including eaves, stumps, and under the floor. With continuous collection, the resting rate largely reflects arrival and entry rate (Table 1).

High house-resting densities tend to precede high indoor-biting incidence, although the peak period of resting is at the time of heaviest indoor biting. Pre-midnight resting is, however, at a higher density than post-midnight resting (60 per cent : 40 per cent). This ratio was observed in all parts of the house except the cross beams.

About 60 per cent of anophelines taken resting on houses at night were taken from inside the houses (verandas are included). The favoured resting position, 60 per cent of total resting indoors, is on the walls below the level of three feet. Unfortunately this is the region from which most insecticide is rubbed off by people sitting on the floor and leaning against the walls. Female anophelines also rest on such objects as yams stored inside the house. Examination of distribution throughout the night shows no especially favoured time for resting underneath the house, but there is a concentration on the eaves and inside the roof between 10 p.m. and midnight, and on the inside walls between 11 p.m. and 1 a.m. The fall in resting density between 9 p.m. and 10 p.m. (Table 1) is most marked in those resting on the walls, and is probably due to the movements of people inside the house as they settle down for the night.

As would be expected, the numbers of resting and biting anophelines varied greatly in individual houses, with the type of construction, relative distance from the breeding places, number of people and domestic animals associated with the house, and presence of a domestic fire. Apparently a fire affected the anophelines by lowering the humidity in its vicinity rather than by the smoke produced.

Under the conditions of maximum disturbance caused by continuous all-night collecting from all parts of the house, only 26·5 per cent of those taken during the night were either partially or fully fed. With intermittent collecting, the proportion of fed females rose to an over-all 61·2 per cent of the total catches. Also, the proportion of empty females decreased throughout the night, from 50·5 per cent of the total in the first quarter of the night to only 18·8 per cent

TABLE 2

A. farauti: *Pre-spray catches in outlet window traps on houses, Bwalalea, July–August 1959 (Two series, maximum of four traps in each)*

Time	All-night trap catches (traps removed every hour) (12 catches)			All-night trap catches (traps removed every three hours) (38 catches)	
	Number taken	Percentage per hour	Percentage per 3 hours	Number taken	Percentage per 3 hours
6–7 p.m.	63	7·3			
7–8 p.m.	26	3·0			
8–9 p.m.	38	4·4	14·7	456	16·4
9–10 p.m.	33	3·8			
10–11 p.m.	47	5·5			
11–12 midnight	29	3·4	12·7	491	17·7
12–1 a.m.	65	7·6			
1–2 a.m.	51	5·9			
2–3 a.m.	90	10·5	24·0	581	20·9
3–4 a.m.	61	7·1			
4–5 a.m.	116	13·5			
5–6 a.m.	239	27·9	48·5	1,246	44·9
Total	858			2,774	

in the last quarter. These results indicate resting before and after feeding, and also suggest that females entering early in the night may rest longer before feeding than those entering later in the night. Metselaar (1957) records unfed anophelines in West Irian resting up to 110 minutes. A noticeable number of fed resting females had apparently not taken a full blood meal. (The percentage of partially-fed females may be on the high side because of disturbance due to the collectors.)

Selection of the host may be at random. As well as cats and roosting fowls, pigs and dogs may be available. However, pigs are not numerous in most villages. The results of precipitin tests on night-resting *A. farauti* in one village without pigs showed a human blood index of 0·69 and a dog blood index of 0·31. In another village the human blood index of night-resting *A. farauti* was 0·97 (Spencer, 1962).

Window-trap studies of exit from houses (Table 2) show that 66 per cent of the total exit takes place after midnight. The exit rate jumps after midnight, with a sharp climax between 5 a.m. and 6 a.m. Although these window-trap studies were on open hamlet houses, with a multiplicity of possible exits, the results parallel closely those from the carefully controlled trap hut experiments in Hollandia carried out by Van Thiel and Metselaar (1954).

Most females entering houses to feed leave again the same night, and usually few adults can be found resting in houses by day, even where night populations are heavy. Metselaar (1957) found in West Irian that 12·3 per cent of 1607 anophelines remained in the trap hut the day following entry. Few adults appear to remain within the house for the whole period of the gonotrophic cycle, as 94 per cent of *A. farauti* females found by day within houses were recently fed. Day-time house-resting anophelines were usually found low on the walls in the room most used by the occupants. Black (1955) has discussed previous records of day-time house-resting *A. farauti*. We did not find males resting in houses during the day, although an occasional male has been found inside a house or a window trap at night.

TABLE 3

A. farauti: *Age-grading of parous females entering outlet traps before and after midnight*

Number of dilatations	Number in each age-group		
	Entering trap 6–12 p.m.	Entering trap 12–6 a.m.	Total
1	14	27	41
2	24	18	42
3	11	8	19
4	1	6	7
5	1	0	1
>5	2	1	3

About 10 per cent of females entering houses leave again without feeding. Dissections show that these unfed females may be nulliparous or parous. The majority of females taken in window traps are fully fed, but partially-fed females (both nulliparous and parous of different ages) occur (Table 3). The dusk exodus (6–7 p.m.) is likely to include those females which have rested in houses during the day. Females remaining indoors to mature their eggs likewise include both nulliparous and parous specimens.

Dissections from window-trap catches show that only 34·7 per cent of the nulliparous mosquitoes leave the house by midnight. Among parous ones nearly 50 per cent of the total catch has already left the house by midnight, and with a falling rate of arrival and accelerating rate of departure after midnight, the stay of the parous mosquitoes (and consequently their contact with the insecticide) may be generally shorter than that of the nulliparous mosquitoes. It is possible that bursts of females which have just laid eggs arrive to swell the numbers in houses between 9 p.m. and midnight.

Daily variations in the proportion parous in window-trap catches were also recorded for a period of two months (Table 4). The relative abundance of nulliparous *A. farauti* tended to vary with the density of population, as would be expected. During breeding flushes, nulliparous and young parous females predominated; as the over-all density fell, the proportion of older females increased.

Supposing a two-day gonotrophic cycle for the majority of *A. farauti* under observed conditions, "p" can be derived by taking the square root

of the proportion parous.[1] Three derivations were made from window-trapped mosquitoes: (1) for one population cycle, covering one full rise and fall in numbers; (2) for a period of steady population; (3) for the whole period of observations (two months). The value of "p" was 0·85 in each case, and this is therefore considered a reasonable pre-operational figure for *A. farauti*, although it is derived from a selected sample (window-trapped females only).

Day-time resting out of doors

Both males and females can be found resting among the secondary growth at the edges of the hamlet clearing, scattered in damp and sheltered situations. It is likely that both males and females move out from the breeding grounds after emergence. We did not find resting females in any numbers on the edges of breeding places, in day-time searches, unless these were situated near a collection of native dwellings.

TABLE 4

A. farauti: *Pre-spray weekly variations in numbers trapped and proportion parous in window-trap catches, in relation to rainfall*

Period	Number caught/ trap/night	Proportion parous (and No. dissected)	Rainfall (inches)
14–17 July	36	0·70 (67)	0·85
19–20 July	101	0·41 (29)	0·55
21–31 July	17	0·81 (117)	—
1– 5 August	9	0·76 (55)	—
8–14 August	20	0·71 (173)	—
16–19 August	17	0·86 (95)	—
25–29 August	10	0·52 (89)	4·78
1– 3 September	24	0·85 (104)	11·92
Mean proportion parous		0·734 (729)	

In a series of 848 *A. farauti* taken outdoors by day around the edges of a native hamlet clearing (on Fergusson Island), 292 were males. In the females, 36 per cent were gravid, 56 per cent were fed but not fully gravid, and 8 per cent unfed. The proportion gravid is much higher than in females resting in houses during the day-time (one per cent) or taken in window traps (two per cent).

Oviposition and gonotrophic cycle

Fully gravid females probably leave their day-time resting place about dusk to lay their eggs. The flaccid and distended appearance of the ovaries in *A. farauti* females dissected immediately after they were caught attempting to bite suggests that females return immediately after oviposition to feed again.

The gonotrophic cycle for the majority of parous coastal *A. farauti* is almost certainly two days. Partially-fed females may need a longer period to complete the cycle. The possibility must be considered that the gonotrophic cycle may not be regularly completed in two days when the opportunities available to the female to lay eggs are restricted. It appears probable that the nulliparous period extends over five days. Dissections of females made within 12–15 hours of their entering window traps indicated that the time taken to reach stage III of ovary development might be shorter for parous females than for nulliparous.

SPOROZOITE RATES

The monthly sporozoite rate of *A. farauti*, in a series of 6049 dissections extending over two and a half years, varied between zero and about 1·6 per cent (Table 5). The over-all sporozoite rate from all catches was 0·63 per

[1] According to Davidson (1954, *Nature*, 174: 792 and 1955, *Ann. trop. Med. Parasit.*, 49: 24), this interpretation is valid only if the sample dissected is limited to females caught when the ovaries are in stage III of development.

cent. This is probably too low, and a more representative estimate would be one per cent in an average year. There was some indication that infected anophelines are particularly likely to occur in June–July. In 1958, within the monthly fluctuations there appeared high proportions of infected anophelines in different localities at the same time, e.g. in February at the hamlet of Uiaupolo and at Mapamoiwa station, in March at the hamlet of Bwalalea and at Mapamoiwa station.

TABLE 5

Sporozoite rates in A. farauti *and* A. punctulatus *in pre-spray periods*

Quarterly period	*A. farauti*		*A. punctulatus*	
	No. dissected	% positive	No. dissected	% positive
1956/IV[a]	18	0·0	145	0
1957/I	123	0·8	43	0
1957/II	360	0·28	41	0
1957/III	383	0·52	5	0
1957/IV	183	0·0	12	0
1958/I	564	1·4	2	0
1958/II	482	1·6	4	(1/4)
1958/III[b]	210	0·95	0	–
1958/IV	0	–	0	–
1959/I[c]	647	0·77	0	–
1959/II	3,079	0·36	1	0
Total	6,049	0·63	253	0·4

[a] November and December only. [b] July and August only. [c] February and March only.

Among 18 sporozoite-positive *A. farauti* found in the period February to July 1958, the rates of positivity were eight positive (in 154 dissected) caught biting in hamlets, five positive (in 48 dissected) caught resting indoors, and five positive (in 92 dissected) caught resting out of doors.

Between March and July 1959, in a total of 774 dissections of *A. farauti* taken resting on houses at night, the sporozoite rate was 0·9 per cent. In the same period, in a total of 2733 dissections from window traps in the same hamlet area, the sporozoite rate was 0·29 per cent. The difference suggests that the catches from the window traps contain a higher proportion of nulliparous and young parous females than the night-resting catches. In 253 salivary gland dissections of *A. punctulatus*, one positive specimen occurred. This was in a night-biting catch (Table 5).

POST-OPERATIONAL OBSERVATIONS

Reduction in anopheline densities on Goodenough Island

Spraying began on Goodenough Island with DDT in November, 1958. The second spray round using dieldrin was on schedule six months later. The third spray round, also using dieldrin, was apparently delayed until it was four months overdue.

Since spraying began, a marked and persistent reduction in anopheline density throughout the inhabited parts of the island has occurred.* Both adults and larvae are relatively scarce. This can be taken as the effect of spraying under the existing ecological conditions, superimposed upon natural fluctuations due to climatic factors.

In April 1959, about four and a half months after the first spray round of DDT, the total number of *A. farauti* taken resting on the walls of houses between 10 p.m. and 2 a.m. had been reduced (in four villages) from an average of 25 per house in 1957 to an average of 0·5 per house, and *A. subpictus* was

* Written at the end of 1960.

not found at all. The night-resting searches were extended to a total coverage of 21 villages around Goodenough Island. Of 187 houses searched, only 31 had anophelines resting on the walls between the hours of 10 p.m. and 2 a.m. The total number of anophelines taken from the 21 villages was 135 *A. farauti*, three *A. punctulatus* and two *A. subpictus*. This indicated a marked reduction in anopheline density. In most of the positive houses, the total number resting on the walls during the four hours of observation was less than five in each house. Only a minority of positive houses were new, or had new walls. In some of them the spraying was patchy.

The above observations were followed up in June 1959 by an all-night biting catch in 11 villages where similar catches in 1958 had yielded averages of 93 *A. farauti* and 16 *A. subpictus* per man per night (Table 6). Seven observations now gave a negative result, and the over-all average biting

TABLE 6

Results of man-biting all-night catches in hamlets of Goodenough Island, surveyed in two successive years

A. Average biting density in seven hamlets surveyed twice before spraying

Year	Mosquitoes per man per night	
	A. farauti	*A. subpictus*
1957	174	1
1958	82	12

B. Average biting density in eleven hamlets surveyed once before and once after DDT-spraying

Year	Mosquitoes per man per night	
	A. farauti	*A. subpictus*
1958	93	16
1959[a]	9	0

[a] Seven of the 11 hamlets gave a negative result —*see* text.

densities were nine *A. farauti* and no *A. subpictus*. In the four positive villages above the average catches, per man per night, were 24 *A. farauti* and no *A. subpictus*, compared with 1958 averages in these four villages of 87 *A. farauti* and 22 *A. subpictus*.

One year later, in June–July 1960, immediately following the third spray round (dieldrin), an experienced collector reported a marked scarcity both of larval and of adult anophelines. Small numbers of mature *A. farauti* larvae were found in five places. A total of five adult *A. farauti* for the whole island was taken in a " leaking " mosquito net. Limited biting catches from 10 p.m. onwards showed correspondingly small numbers of adult *A. farauti*, the only species taken.

Since the start of spraying, *A. farauti* occurred in such small numbers and with such a very scattered distribution, as to discriminate against any study of post-operational behaviour patterns.

Reduction of anopheline densities on Fergusson Island

Spraying began on Fergusson Island in March 1959 with dieldrin. A " check " area was retained during the first spray round where pre-operational entomological observations were continued until June 1959. The second spray

round was carried out on schedule in September of 1959, and dieldrin was used again. On this round the former " check " area was included. The third spray round on Fergusson Island had not begun at the time of the anopheline survey.

This survey of Fergusson Island during July and August 1960 investigated larval numbers and distribution, and a " leaking " mosquito net was used for a rough estimation of adult numbers, as on Goodenough Island.

From this survey an over-all reduction in anopheline densities was evident on Fergusson Island also. It seems that adult anophelines, while reduced in number and distribution over the whole of Fergusson Island, remain most apparent in the former " check " area, where catches of up to 39 anophelines in one night were recorded from the " leaking " mosquito net. The total number of adult anophelines from 20 villages sampled in this way—including some villages which previously had dense anopheline populations and heavy biting rates—was 177 *A. farauti*, 13 *A. punctulatus*, and five *A. subpictus*. Of the total of 177 *A. farauti* more than half came from within the former " check " area.

Mature *A. farauti* larvae were taken from 14 places on the island's perimeter, only three of these within the former " check " area. Mature larvae were more apparent, both in numbers and in distribution, than on Goodenough Island. Two *A. punctulatus* larvae were found outside the former " check " area. No larvae were recovered well inland, although *A. farauti* adults occurred in noticeable numbers in one mountain village.

Discussion

The age composition of the hamlet or " domestic " populations of *A. farauti* is variable, depending upon the rate of emergence of new individuals and the rate of dying off of all age-groups. The nulliparity ratio tends to reflect the numerical trend shown by trap catches and expected from rainfall distribution: it is by itself a useful comparative measure of events. The estimated mortality rate is 15 per cent per day. The oldest individuals seen to date were estimated to be three weeks old.

The pre-operational data form a basis for deriving the following entomological indices. Macdonald's (1957) symbols are used:

(1) " m " (anopheline density in relation to man) for coastal hamlets and all seasons, is equal to the man-biting rate (ma) divided by the man-biting habit (a), viz. $\frac{65 \text{ (bites per man per night)}}{0{\cdot}375 \text{ (estimated man-biting habit)}} = 173$;

(2) " a " (man-biting habit) = blood preference $\times$ gonotrophic cycle $= 0{\cdot}75 \times 0{\cdot}5 = 0{\cdot}375$;

(3) " s " (sporozoite rate, or proportion with sporozoites in their glands) $= 0{\cdot}01$;

(4) " p " (probability of survival through one day, estimated as the square root of proportion parous) $= 0{\cdot}85$.

From the epidemiological viewpoint, attention should be focused on two problems, (a) transmission within villages, and (b) transmission outside villages. These twin problems may be overlapping, or quite separate, according to the distances involved and the degrees of interference with natural ecology, between the village areas and the areas of temporary habitation outside the village. We may have to think in terms of separate ecological units, or overlapping or continuous ones.

For example, if a sago marsh suitable for anopheline breeding, temporarily but regularly inhabited by members of one village group, lies within flight range of the village, transmission within that village overlaps with transmission outside that village and in the sago marsh area.

On the other hand, if the gardening area lies some miles away from any village and is separated from all villages by virgin forest, transmission of malaria by an anopheline population established in relation to the gardening area will in all probability be quite separate from transmission within the villages depending upon those gardens.

A third situation is that in which villages sited in a swampy coastal area, where there are abundant breeding places to produce a dense anopheline population, may be well separated from each other, but joined into a continuous ecological unit by an abundant wild mammalian fauna (such as pigs and wallabies) which sustains a dense anopheline population between the villages.

Each of the three situations presents difficulties in control, and one or other of them will be present in all parts of this Territory. The best theoretical chance of good control of transmission within the villages occurs when the villages are isolated units set in clearings in virgin forest. Both *A. farauti* and *A. punctulatus* are evidently very susceptible to residual insecticides in settled village areas. The marked reduction in adult numbers which occurs after spraying is evidence of this.

These factors must all be taken into account when evaluating the sequence of events which follow upon spraying. They are also relevant in determining where we should concentrate our attention. It may be that control of transmission by residual spraying can never be adequate because we cannot fully protect the people by this means alone during their extra-village activities.

Acknowledgements

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A NOTE ON BLOOD PREFERENCES OF *ANOPHELES FARAUTI*

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[Read 28th April, 1965]

A total of 702 blood meals from *A. farauti* females collected on Fergusson Island, New Britain, and Nissan Island, were sent to the Lister Institute, London, under arrangement with the World Health Organization. The results of precipitin tests on these are set out and discussed.

The aim was to establish a definite figure for the " human blood index "[1] in the villages of the D'Entrecasteaux Islands in the Territory of Papua and New Guinea.

Copies of this paper were distributed by the World Health Organization as a paper in the WHO/Mal series of documents (WHO/Mal/337, 1962), a series which does not constitute formal publication.

Unfortunately, after the paper was accepted for publication in the PROCEEDINGS, it appeared in the *Papua-New Guinea Medical Journal*, vol. 7, no. 1, dated December 1964. It is therefore unnecessary to reprint it here.

ED.

[1] " Human blood index " is suggested by the World Health Organization (1959) as a better term for the closeness of relationship of vector to man than " anthropophilic index ", and is defined as the proportion of freshly fed *Anopheles* giving a positive precipitin reaction for human blood.

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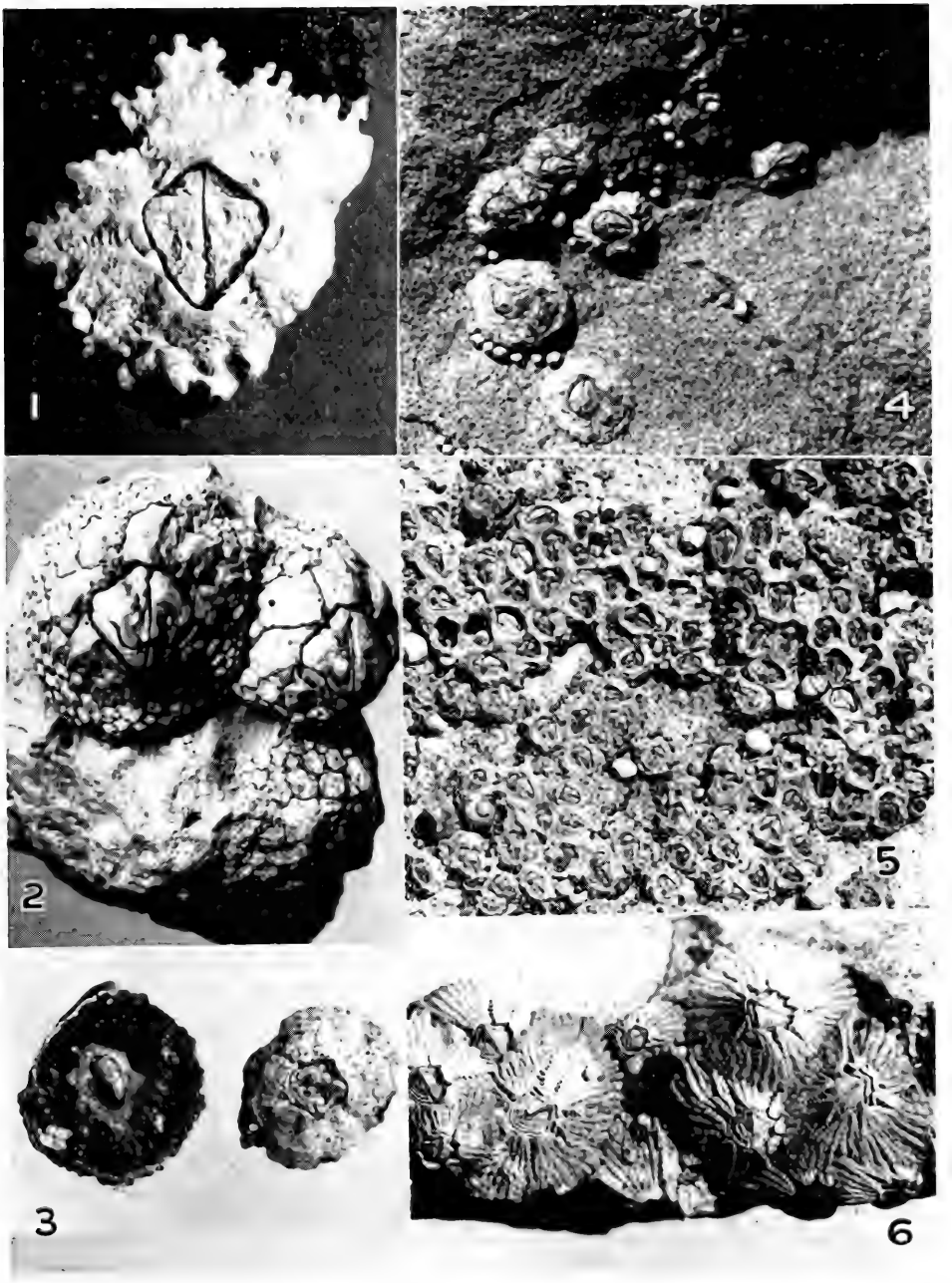
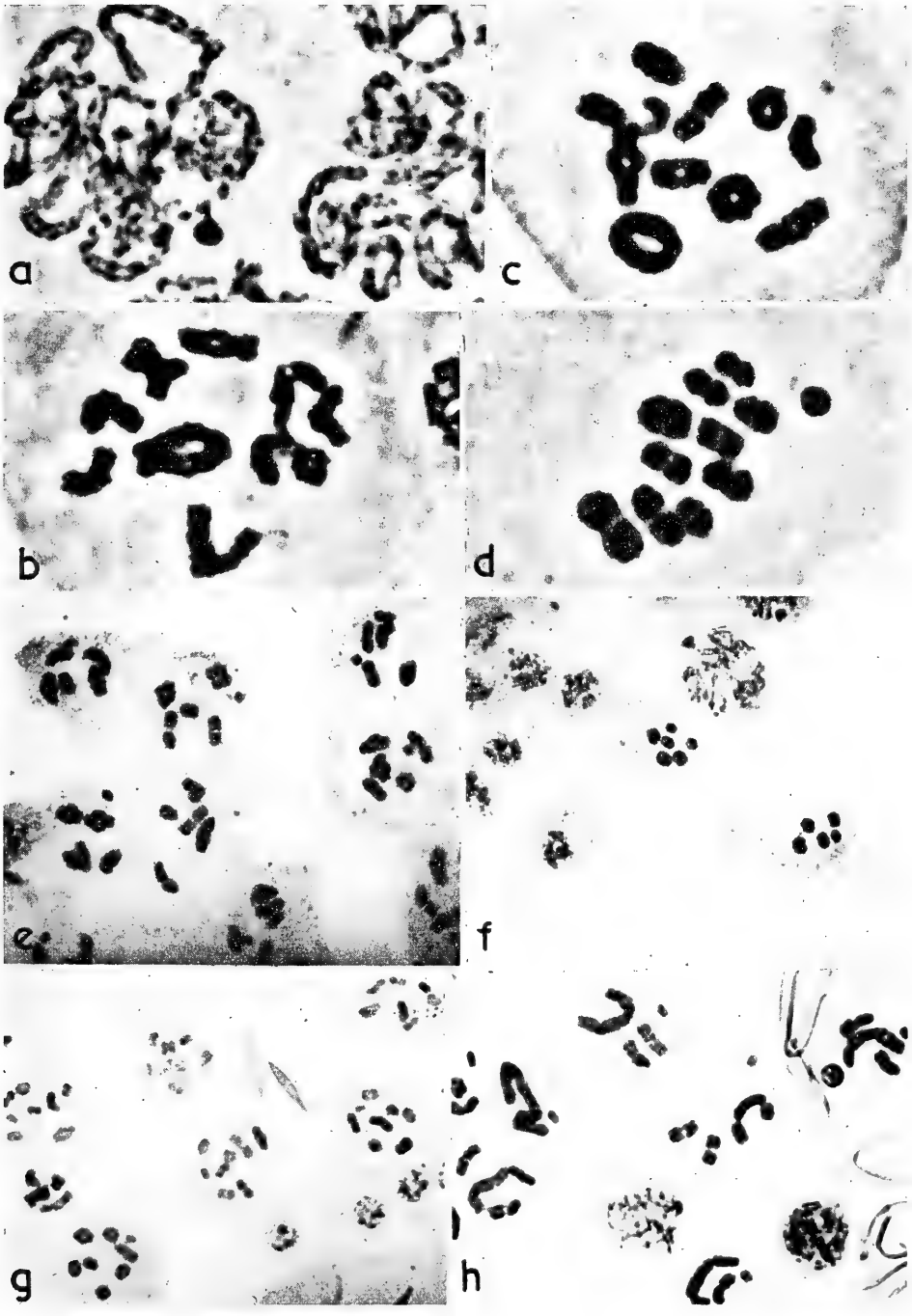


Five species of Australian Chthamalidae.

Some tropical *Chthamalus* spp. and their habitats.



Chromosome numbers in some Australian leafhoppers.

STUDIES ON THE INHERITANCE OF RUST RESISTANCE IN OATS

III. GENETIC DIVERSITY IN THE VARIETIES LANDHAFER, SANTA FE, MUTICA UKRAINE, TRISPERNIA AND VICTORIA FOR CROWN RUST RESISTANCE

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[Read 30th June, 1965]

Synopsis

Segregation in the F_2 and F_3 generations for rust reaction was studied in certain crosses between members of the group of crown rust resistant varieties comprising Landhafer, Santa Fe, Trispernia, Mutica Ukraine (Ukraine) and Victoria, all resistant to the prevalent Australian races, to assess their genetic diversity with regard to genotypes for resistance. Behaviour in the seedling stage to several races as well as adult plant field reaction was studied. The two factor pairs in Landhafer conditioning adult plant resistance, one of which conferred seedling resistance in addition, were independent of the factors in the varieties Santa Fe, Trispernia and Victoria. The seedling reaction type of Landhafer was epistatic over those of Trispernia and Victoria. The factor for both seedling as well as adult plant resistance in Santa Fe was independent of the factors in Victoria and epistatic to them. Certain modifying gene(s), however, resulted in the expression of a reaction type similar to that characteristic of Victoria by suppressing the Santa Fe gene. The Santa Fe factor was considered allelic with the factors for seedling resistance in the varieties Ukraine and Trispernia, no susceptible segregates occurring within the limits of the population size studied. The factors were not considered identical, however, since Trispernia exhibited a higher reaction type and the allele in Ukraine conditioned resistance to fewer races than that in Santa Fe. The reaction type of Santa Fe was dominant over that of Trispernia in tests with four races, but with race 203 the Santa Fe gene was inhibited by the action of a pair of complementary factors, one contributed by each variety. The three factor pairs in Ukraine, two acting in complementary fashion, involved in adult plant resistance were independent of the Santa Fe gene. Indirect evidence indicated that the factors responsible for seedling resistance in Santa Fe and Victoria were genetically independent. The independence of the factors conditioning adult plant resistance in Landhafer and Ukraine and likewise the independence of the Ukraine and Victoria adult plant factors could not, however, be established in the absence of studies on the appropriate crosses.

Introduction

In a previous paper (Upadhyaya and Baker, 1962*b*) the mode of inheritance in the resistant varieties Landhafer, Santa Fe, Mutica Ukraine, Trispernia and Victoria was reported in the seedling and adult plant stages to certain of the most prevalent field races of crown rust (*Puccinia coronata avenae* Erikss.) in Australia. The relative merits of these varieties in their role in breeding for resistance depend, in addition to the mode of inheritance they exhibit, largely on their diversity with regard to their genotypes for resistance. Information on this latter aspect was obtained from intervarietal crosses between them and is currently presented to show whether the genes which they possess are identical, allelic, or distinct and non-allelic to Australian races.

It also has been pointed out previously that such knowledge is vital to an understanding of the basis and significance of information revealed by physiologic race surveys since these varieties, together with the variety Bond, of which the inheritance will be subsequently reported, form the nucleus of the varieties in the current set used for such surveys.

Literature Review

Results of crosses of the varieties under study with susceptible varieties were reported by Upadhyaya and Baker (1960, 1962*b*). Seedling resistance to various Australian crown rust races was conditioned by a single factor pair

in each of the varieties Landhafer, Santa Fe, Mutica Ukraine (Ukraine) and Trispernia, and by four factors, $\underline{Vc_a\ Vc_b}$ (linked complementary) and $\underline{IVc_2\ Vc_2}$ (linked) in the variety Victoria. For adult plant resistance the variety Landhafer possessed an additional recessive factor and Victoria two additional factors $\bar{V}c_1$ and $\bar{V}c_3$. $\underline{IVc_2\ Vc_2}$ were also operative in the adult stage but not $\underline{Vc_a\ Vc_b}$. $\bar{V}c_1$ was linked with $\underline{Vc_a\ Vc_b}$. The factors for seedling resistance in Sant Fe and Trispernia, but not Ukraine, also conditioned adult plant resistance. The adult plant resistance of Ukraine was conditioned by three dominant factors, two acting in complementary fashion.

Several investigators have presented results of studies on crosses between certain or all of the resistant varieties currently being reported. Litzenberger (1949) and Simons and Murphy (1954) found that the factors for resistance in Landhafer and Santa Fe were independent. Finkner (1954) reported that the resistance of Landhafer was genetically independent of those of Santa Fe, Trispernia and Victoria; the factors involved in Ukraine and Victoria were also considered independent. Simons and Murphy (1954) noted complicated inheritance in certain crosses between these varieties. Landhafer × Trispernia gave transgressive segregation with plants more resistant than either parent. A cross between Santa Fe and Trispernia did not indicate allelism between the genes in these varieties.

However, some of the factors found in certain varieties were considered by various investigators to be allelic with, but different from, those in other of the varieties. Finkner (1954) proposed genotypes thus: Ukraine MMUU, Santa Fe $M_1M_1U_1U_1$ (or M_1M_1) and Trispernia M_2M_2 and/or two other factors. Both factors in Ukraine were dominant over those with which they were allelic in Santa Fe; similarly M_1 was dominant to M_2. Finkner, Atkins and Murphy (1955) reported that one (M_1) of the two linked genes in Santa Fe was allelic with the single gene M in Ukraine, and recessive to it.

With race 57 of the pathogen, and representing the single genes found to condition resistance in Landhafer and Victoria as L and V respectively, Finkner (1954) concluded that the allelic and non-allelic relationships with regard to dominance or epistasis were in the following order: M or $U > M_1$ or U_1 or $L > V > M_2$. The immune reaction of Ukraine was dominant or epistatic to that in the other varieties.

Materials and Methods

F_1, F_2 and F_3 generations were studied for crown rust reactions in crosses between the five varieties under study. The following crosses were not included because either the cross was not made or the F_1s failed to set seed due to adverse environmental conditions: Ukraine × Landhafer, Ukraine × Trispernia, Ukraine × Victoria and Trispernia × Victoria.

Crown rust races employed for testing were 203, 226, 237, 237–4, 259 and 286. These are described by Baker and Upadhyaya (1955) and were built up from field isolates.

The experimental procedures were set out by Upadhyaya and Baker (1960).

Experimental Results

F_1 reaction types

The reaction types in the F_1 of the various crosses in the seedling and also the adult plant stages, together with those of the parents to different specific races as well as field inoculum, are presented in Table 1.

Genes conditioning resistance in certain of these varieties will be suggested below to be allelic. In these cases the F_1 behaviour was an indication of the dominance relationship. In cases of non-allelism the degree and type of epistasis manifest was evident from the F_1 behaviour. From the data in Table 1 in

TABLE 1

Reaction types in the seedling stage and reactions in the adult plant stage of the parents and F_1s in certain oat crosses to specific races or field inoculum of Crown Rust

Parental Varieties or Cross.	Reaction types in seedling stage, Race 203	237	237–4	226	259	286	Reactions in adult plant stage, Race 203	237	237–4	226	259	Field inoculum.
Landhafer and Santa Fe[1]	; — 1 =	; — 1 =	; — 1 =	; — 1 =	; — 1 =	4	I	I	I	I	I	I
Ukraine[1]	4	; — 1 =	; — ; =	4	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	R	R	I	S	I(98%)
Landhafer × Santa Fe	; — 1	;	;	;	; — 1	—	I	I	I	I	I	I
Landhafer × Trispernia	—	—	—	—	1	—	—	—	—	—	—	R
Landhafer × Victoria	; — 1	1cn	1cn	;	1 — 1+	1n — 2–n	—	R	—	I	R—MS	R
Santa Fe × Ukraine	—	;	; , 1 =[1]	—	;	—	R	R	R	R	R	—
Santa Fe × Trispernia[1]	—	—	—	3–c	2	—	—	—	—	—	—	I
Santa Fe × Victoria	—	—	—	—	1+, 2++	1n — 2–n	—	—	—	—	—	I

[1] Reactions observed at temperatures above 80°F.

I = Immune, R = Resistant, MR = Moderately resistant, MS = Moderately susceptible, S = Susceptible.

TABLE 2

F_2 seedling segregation for reaction type in crosses involving the oat variety Landhafer to certain races of Crown Rust to which both parents were resistant

Cross.	Race used	F_2 Reaction types				Total		Expected ratio	P value
		; (R)	1 (SR)	2– (In)	3–4 (S)				
Santa Fe × Landhafer	226[1]	119	69	1	18 (12·9)	207		11R : 4SR : 1S 15(R+SR) : 1S	<0·01 0·2–0·1
	203	122	18	1	13 (9·6)	154		11R : 4SR : 1S 15(R+SR) : 1S	0·2–0·1 0·3–0·2
	237–4[1]	190	102	1	28 (20·1)	321		11R : 4SR : 1S 15(R+SR) : 1S	<0·001 0·1–0·05
	259	255	92	5	29 (23·9)	381		11R : 4SR : 1S 15(R+SR) : 1S	0·7–0·5 0·7–0·5
	Total	686	289		88 (66·4)	1063		15(R+SR) : 1S	0·02–0·01
		; (R)	1+(SR)	(2–3c) (In)	3–4(S)				
Landhafer × Trispernia	259[2]	101	188	58	27 (23·4)	374	Total	4R : 9SR : 2In : 1S	0·1–0·05
		; (R)	1+(SR)	1n(SR)	2–n (In)	(3–4) S			
Victoria × Landhafer	203	73 (174·8)	102	37 (41·9)	7	15 (16·3)	234	75(R+SR)[4] : 18(SR+In)[5] : 7S	0·95–0·9
	226	96 (99·0)	9	18 (23·8)	1	8 (9·2)	132		0·5–0·3
	237[2]	43 (111·0)	64	26 (26·6)	3	12 (10·4)	148		0·8–0·7
	Total	387 (384·8)		91 (92·3)		35 (35·9)	513		0·99–0·95
	237–4[3]	— (35·8)	32	101 (97·2)		10 (10·0)	143	25(R+SR)[4] : 68(R+SR)[5] : 7S	0·8–0·7

[1] Identical plants tested first to race 237–4 and then to race 226.
[2] Reaction types corrected from F_3 behaviour.
[3] Reaction types recorded at temperatures of about 80°F.
[4] R and SR reactions due to homozygosity or heterozygosity of Landhafer genotype.
[5] R and SR reactions due to homozygosity or heterozygosity of Victoria genotype.
(Expected values in brackets).
R = Resistant, SR = Semi-resistant, In = Intermediate, S = Susceptible.

certain cases the lower reaction type (higher resistance) was either completely dominant or epistatic or the F_1 reaction type was intermediate between the parental types. In tests against races 259 and 286, Victoria being susceptible to the former and Landhafer and Santa Fe susceptible to the latter race, the F_1s of crosses of Victoria with Landhafer and Santa Fe showed intermediate reaction types. In other cases F_1 reaction types slightly or distinctly less resistant than either parent were observed. This occurred in the crosses Landhafer × Santa Fe, Santa Fe × Ukraine and Santa Fe × Trispernia tested with certain races.

F_2 segregation

(i) Seedling tests

The results of studies at the seedling stage on F_2 populations of crosses tested with one or several different races to which both parents were resistant are presented in Tables 2 and 3. Table 2 pertains to crosses involving the variety Landhafer.

In the cross Santa Fe × Landhafer the presence of approximately one susceptible plant in 16 in all tests suggested that the single factor pairs for resistance in both these varieties revealed in their crosses with susceptible varieties were genetically independent. Thus 7/16 of the population were expected to be resistant similar to the parents giving a " ; " to " 1= " reaction type, and one-quarter semi-resistant resulting from the heterozygous effect of each incompletely dominant gene singly. Doubly heterozygous plants on this hypothesis would comprise one quarter of the F_2 population and their reaction type might be expected to be resistant corresponding to that shown by the F_1 seedlings which varied from " ; " to " 1—1n " according to particular tests. However, when tested to this predicted 11 resistant : four semi-resistant : one susceptible seedling ratio in the F_2 generation it was obvious that in two out of the four cases the number of semi-resistant plants was considerably in excess of that calculated, indicating that some of the doubly heterozygous class had a higher reaction than that predicted, due probably either to environmental effects or to the segregation and action of modifying genetic factors.

In this cross also, whilst individual tests showed good agreement with the predicted 15 (resistant + semi-resistant) : one susceptible F_2 seedling, there was a small, though not statistically significant, excess number of susceptible plants in all cases and, due to this, the total of all tests did not show a good fit to a dihybrid 15 : 1 ratio, the P value being 0·02—0·01. It is difficult to explain this result since, if any linkage were envisaged between the genes in Landhafer and Santa Fe, they would be expected to be present in the repulsion phase, resulting in a deficiency rather than an excess of susceptible plants. In this cross a few F_2 seedlings of an intermediate (" 2— ") reaction type were observed and for statistical tests these were grouped with the semi-resistant class.

In F_2 segregates of the cross Landhafer × Trispernia, the factor pair in Trispernia, in the absence of that in Landhafer, in the heterozygous condition was expected to show an intermediate reaction type varying from " 2 " to " 3c " from the behaviour of Trispernia in crosses with susceptible varieties ; only those seedlings homozygous for the Landhafer factor pair were expected to give a resistant (" ; ") reaction type. Thus the expected F_2 ratio was four resistant : nine semi-resistant : two intermediate : one susceptible plant. The deviations were not significant at the five per cent level. However, by grouping the two middle classes and comparing with a four resistant : 11 intermediate : one susceptible plant ratio, a better fit was obtained statistically, the P value being 0·5—0·3 compared with 0·1—0·05.

Since in the cross Landhafer × Victoria the F_1 behaviour showed epistasis or partial epistasis of the Landhafer reaction type, according to the particular race employed, three-quarters of the F_2 seedlings in this cross were expected

to show the homozygous or heterozygous reaction type of the Landhafer gene similar to that in its crosses with susceptible varieties. One-quarter would therefore be expected to show a "; " to "1= " reaction type and one-half a "1 " reaction type or one approximating this at normal temperatures (below 75° F). The remaining 25 per cent was expected to show segregation for the Victoria type crown rust resistance in the ratio of 71·9 per cent resistant ("1n " to "2 " reaction types) : 28·1 per cent susceptible (Upadhyaya and Baker, 1960). Due to the presence of the large number of segregating factors involved in the cross, the distinction between the "; 1= " and "; 1 " reaction types was not clear cut and the two classes were combined for statistical calculations. Hence the expected F_2 ratio in this cross was 75 per cent "; " to "1 " reaction types (due to Landhafer), 18 per cent "1n " to "2 " (due to Victoria), and seven per cent susceptible. Results with three races separately and the combined total agreed well with this hypothesis. The tests involving race 237–4 were conducted at temperatures between 75° and 85° F. At these temperatures it was observed previously that the Landhafer factor alone in the heterozygous condition gave plants of an intermediate ("2 " to "3—c ") reaction type. In this instance the expected ratio was 25 per cent resistant ("; " to "1 " reaction types) : 68 per cent intermediate ("2— " to "3c " reaction types) : seven per cent fully susceptible, and the observed results agreed satisfactorily with this hypothesis.

In the cross Santa Fe × Ukraine 570 and 147 seedlings respectively were tested to races 237–4 and 237 and no susceptible segregates were observed, indicating that the single factor pairs in each case were allelomorphic or closely linked. Although to races to which both were resistant the reaction type was very similar in both varieties, the factors were not identical since that in Ukraine conditioned resistance to fewer races. It has been shown previously that the resistance of Santa Fe to a large number of races to which it is resistant is due to the same factor pair (Upadhyaya and Baker, 1962*b*).

Results involving F_2 seedling segregation in crosses of Santa Fe with Trispernia and Victoria are presented in Table 3. In the total F_2 population of 840 seedlings involving tests with four races, no susceptible segregates were observed in the cross Santa Fe × Trispernia. In tests involving race 259, 13 plants were noted with a slightly higher reaction type than Trispernia but this may have been due to segregation of modifying genes or to high temperature effects on reaction type. The absence of susceptible segregates in F_2 indicated that the factors in Santa Fe and Trispernia were allelic or closely linked. The genes were considered to be distinct in view of the consistently higher reaction type of Trispernia. Hence the single factor pairs in each of the three varieties Santa Fe, Ukraine and Trispernia conditioning seedling resistance were considered to constitute an allelic series.

Since F_1 seedlings in the cross Santa Fe × Victoria were tested only with races 259 and 286, to neither of which were both parents resistant, no evidence was available on epistastis of reaction types. However, following the observations on a Victoria × Landhafer cross where the Victoria reaction type with characteristic necrosis was hypostatic, the hypothesis of 25 per cent Santa Fe reaction types, 50 per cent intermediate between Santa Fe and Victoria (resistant reaction types with no necrosis), 18 per cent Victoria reaction types (resistant with necrosis) and seven per cent susceptible segregates in F_2 was adopted. On this hypothesis only in tests involving race 237–4 was a good statistical fit obtained. In the other two tests the number of Santa Fe types was too few and the Victoria reaction types in excess of that expected. A satisfactory statistical fit was obtained in these cases only when the resistant classes of reactions were grouped and the hypothesis of 93 resistant : seven susceptible F_2 plants adopted. This suggested that the Santa Fe reaction type was not completely epistatic to that in Victoria or that segregating modifying genes from one or both parents were operative.

TABLE 3

F_2 seedling segregation for Crown Rust reaction type in crosses involving the oat variety Santa Fe with the varieties Trispernia and Victoria, to races to which both parents were resistant

Cross.	Race used	F_2 Reaction types					Total	Expected ratio	P value
		;	1 = , 1	1+ , 2–	2	3–4			
Santa Fe × Trispernia ..	226[2]	175	—	50 (56·3)	—	—	225	3(;) : 1(1+ , 2–)	0·5–0·3
	230[2]	65	—	22 (21·8)	—	—	87	do.	0·99–0·95
	237–4[1]	36	—	84 (90·0)	—	—	120	1(;) : 3(other reaction types)	0·3–0·2
	259[3]	147	129	119	13	—	408	do.	<0·001
		(102·0)		(306·0)					
		;	1 = , 1	1n	2–n	3–4			
Santa Fe × Victoria ..	203	100	230	145	13	31 (36·3)	519	(*a*) 25(;) : 50(1 = , 1) : 18(1n & 2–n) : 7(3–4) (*b*) 93(R) : 7(S)	<0·001 0·5–0·3
	226[2]	112	24	56	15	17 (15·7)	224	(*a*) 75(; & 1 = , 1) : 18(1n & 2–n) : 7(3–4) (*b*) 93(R) : 7(S)	<0·001 0·8–0·7
	237–4	20 (27·0)	64 (54·0)	16 (19·4)	—	8 (7·6)	108	(*a*) 25(;) : 50(1 = , 1) : 18(1n & 2–n) : 7(3–4) (*b*) 93(R) : 7(S)	0·3–0·2 0·9–0·8

[1] Plants with ' ; ' reaction types only separated out.
[2] Reactions recorded in temperature controlled room (65 ± 2°F).
[3] Reactions read at normal temperatures in glasshouse.
(Expected values in brackets.)
R = Resistant (reaction type 2 or lower), S = Susceptible.

(ii) Adult plant tests

Results of F_2 segregation in the adult plant stage under field conditions are presented in Table 4.

It was shown in a previous paper (Upadhyaya and Baker, 1962*b*) from data on the cross Burke × Landhafer that, under field conditions, Landhafer possessed an additional factor (recessive in action) for crown rust resistance operative in the adult plant stage only. With the operation of three independent factor pairs conditioning adult plant resistance (one recessive in action) in crosses involving Landhafer with Santa Fe or Trispernia, a ratio of 61 resistant : three susceptible plants was expected for F_2 field segregation. In the cross Santa Fe × Ukraine the expected ratio was 249 resistant : seven susceptible with four factors involved (three from Ukraine, two acting in dominant complementary

TABLE 4

F_2 segregation for adult plant field reaction to Crown Rust in certain crosses involving the resistant oat varieties Landhafer and Santa Fe with other resistant varieties

Cross	Adult plant field reactions				Total	Expected ratio	P value
	I	R	MR	MS–S			
Santa Fe × Landhafer ..	343	96	10	23 (22·1)	472	61 : 3	0·9–0·8
Landhafer × Trispernia ..	184	50	19	16 (11·7)	249	61 : 3	0·3–0·2
Victoria × Landhafer ..	201	3	—	2 (2·3)	206	98·88 : 1·12	0·9–0·8
Santa Fe × Victoria	207	9	28	14 (15·4)	258	94·05 : 5·95	0·8–0·7
Santa Fe × Ukraine	56	6	5	2 (1·5)	69	249 : 7	0·7–0·5
Santa Fe × Trispernia[1] ..	– 453 –			0	453	all R	—

[1] No separate classification for the different types of resistance carried out (Expected values in brackets.)

I = Immune, R = Resistant, MR = Moderately resistant, MS = Moderately susceptible, S = Susceptible.

fashion and one from Santa Fe). No susceptible segregates were expected in F_2 in the cross Santa Fe × Ukraine since the same factors conditioned both seedling and adult plant resistances in each case and the seedling resistances were previously indicated to be allelic (or closely linked). The segregations in crosses involving the variety Victoria were based upon the presence of four factor pairs in this variety, Vc_2Vc_2 and IVc_2IVc_2 linked with ten per cent recombination, and two independent factor pairs, $V\bar{c}_1V\bar{c}_1$ and $V\bar{c}_3V\bar{c}_3$ giving in crosses with susceptible varieties 5·95 per cent susceptible adult plants (Upadhyaya and Baker, 1960). With the two factors for adult plant resistance contributed by Landhafer the percentage of susceptible F_2 plants would be expected to be 1·12 in the cross Victoria × Landhafer.

In all the above cases in F_2 adult plant segregation good agreement statistically between observed and expected results was observed on the basis of these hypotheses presented. In the cross Santa Fe × Victoria the percentage of susceptible plants would be expected to be 1·49 with the four factors from Victoria and one from Santa Fe. Hence in the 258 plants tested, approximately four susceptible plants would have been expected. This deviates markedly

from the 14 observed. The results in the cases of this cross were best explained on the operation of only one of the two factors (Vc_1 or Vc_3) conditioning adult plant resistance in Victoria, on which basis 15·4 susceptible plants would have been expected.

These results confirmed the operation of the following factors conditioning adult plant resistance to crown rust: Two factors in Landhafer (one recessive in inheritance).—One factor each in Santa Fe and Trispernia, the factors being allelic and identical with those conferring seedling resistance.—Three factors in Ukraine, two acting in complementary dominant fashion.—One factor in Victoria linked with a dominant inhibitor gene and one or two additional adult plant factors according to the particular cross involved.

F_3 segregation

Seedling tests of F_3 progenies from seedling classified F_2 plants were conducted by taking representative samples from the major F_2 reaction categories. The expected F_3 behaviour in the various crosses was as follows:

Cross	F_3 behaviour		
	Resistant	Segregating	Susceptible
Santa Fe × Landhafer	7	8	1
Landhafer × Trispernia	7	8	1
Santa Fe × Trispernia	All resistant		
Santa Fe × Ukraine	All resistant		
Victoria × Landhafer Victoria × Santa Fe	40·4%	52·6%	7·0%

These expectancies could be further categorized and subdivided in certain cases thus:

Landhafer × Trispernia

Resistant 7, comprising four homozygous for the partially epistatic Landhafer resistance ("1=" reaction type) denoted by Ld, one homozygous for Trispernia resistance ("1+" reaction type) denoted by Tr, and two segregating for Landhafer and Trispernia reaction types (denoted by Ld : Tr), the hypostatic Trispernia gene appearing due to the heterozygous state of the Landhafer gene in this particular genotype.

Segregating 8, comprising four segregating for the Landhafer reaction type (preponderant), Trispernia reaction type and susceptible plants, two segregating for Landhafer reaction type and susceptibility, the designation Ld (Tr) : S being used to represent both categories, and two segregating for Trispernia reaction type and susceptibility (designated Tr : S).

Santa Fe × Trispernia

All resistant, comprising one homozygous for the Santa Fe resistance (";" to "1=" reaction type), two segregating for the Santa Fe and Trispernia resistances ("1+" reaction type), designated as S.F. : Tr, and one homozygous for Trispernia resistance.

Victoria × Landhafer

Resistant 40·4 per cent, comprising 25·0 per cent homozygous for the epistatic Landhafer resistance (denoted by Ld), 10·3 per cent segregating for the Landhafer and Victoria reaction types (symbolized as Ld : Vc), and 5·1 per cent homozygous for the Victoria resistance (denoted by Vc).

Segregating 52·6 per cent, comprising 39·8 per cent segregating for Landhafer resistance and susceptibility, or Landhafer and Victoria resistances and susceptibility (designated as Ld (Vc) : S), and 12·8 per cent segregating for Victoria reaction type and susceptibility (denoted as Vc : S).

Susceptible 7·0 per cent, comprising those segregating for susceptibility and a low proportion of Victoria type resistant plants (symbolized as S : Vc) and those lines homozygous susceptible (denoted as S).

Victoria × Santa Fe

Similar categories to those in the Victoria × Landhafer cross.

In the cross Santa Fe × Ukraine no segregation was noted in tests involving a mixture of races 237 and 237–4. Table 5 presents the F_3 data relevant to Santa Fe in crosses with Landhafer and Trispernia and shows good agreement between observed and expected results.

TABLE 5

Seedling behaviour of F_3 lines in crosses involving the resistant oat variety Santa Fe with the resistant varieties Landhafer and Trispernia tested with Race 203 of Crown Rust

Cross	F_3 Behaviour			Total	P value
	Res.	Seg.	Sus.		
Santa Fe × Landhafer	105 (110·3) Homo.S.F.	131 (126·0) Seg.S.F. : Tr.	16 (15·8)[1] Homo.Tr.	252	0·9–0·8
Santa Fe × Trispernia	28 (26·8)	51 (53·5)	28 (26·8)[2]	107	0·9–0·8

[1] = Expected ratio 7 : 8 : 1 resp.
[2] = Expected ratio 1 : 2 : 1 resp.
Res. = Resistant, Seg. = Segregating, Sus. = Susceptible. Homo. S.F. = Homozygous for Santa Fe reaction type (;). Seg. S.F. : Tr. = Segregating for Santa Fe reaction type (;) and Trispernia reaction type (1+). Homo. Tr. = Homozygous for Trispernia reaction type (1+).
(Expected values in brackets).

Data involving the three other crosses studied, Landhafer × Trispernia and Victoria in its crosses with Landhafer and Santa Fe, are presented in Table 6. Comparison of expected and observed results within the previously indicated subclasses of two of the three F_3 categories, viz. homozygous resistant and segregating, in these crosses are included in this table. There was good statistical agreement between observed and expected results, except in the cross Santa Fe × Victoria where the agreement was satisfactory only when the major classes (resistant, segregating and susceptible) were considered but not further subdivided.

When the F_2 classification for reaction types was based on F_3 breeding behaviour in the three crosses, 75 per cent would be expected to be Landhafer or Santa Fe types, 18·75 per cent Trispernia or 18 per cent Victoria types, and the remainder susceptible. From F_3 data the appropriate factors were separated as follows where the observed and expected numbers (in brackets) are compared :

	Ld. or S.F. types	Tr. or Vc. types	Susceptible
Landhafer × Trispernia	135(136·5)	34(34·2)	13(11·3)
Victoria × Landhafer	63(62·3)	15(14·8)	5(5·8)
Santa Fe × Victoria	293(320·0)	104(76·2)	29(29·8)

TABLE 6

Seedling behaviour of F_3 lines in the crosses Landhafer × Trispernia, Victoria × Landhafer and Santa Fe × Victoria tested with races to which both parents were resistant

F_3 behaviour	Cross studied											
	Landhafer × Trispernia Race 226				Victoria × Landhafer Race 203				Santa Fe × Victoria Races 226 and 237			
	Exp. ratio	Reaction type(s)	Obs.	Exp.	Exp. ratio	Reaction type(s)	Obs.	Exp.	Exp. ratio	Reaction type(s)	Obs.	Exp.
Resistant	4	Ld.(1 =)	48	45·5	25·0	Ld.(1 =)	25	20·8	25·0	S.F.(1 =)	78	106·5
	2	Seg. Ld.(1 =) & Tr.(1+)	21	22·8	10·3	Seg. Ld.(1 =) & Vc.(1n)	11	8·6	10·3	Seg. S.F.(1 =) & Vc.(1n)	54	43·9
	1	Tr.(1+)	8	11·4	5·1	Vc.(1n)	4	4·2	5·1	Vc.(1n)	37	21·7
Segregating ..	6	Seg. Ld.(1 =), Tr.[1] (1+) & S(4)	66	68·3	39·8	Seg. Ld.(1 =), Vc.[1] (1n) & S(4)	27	33·0	39·8	Seg. S.F.(1 =), Vc.[1] (1n) & S(4)	161	169·6
	2	Seg. Tr.(1+) & S(4)	26	22·8	12·8	Seg. Vc.(1n) & S(4)	11	10·6	12·8	Seg. S.F.(1 =) & S(4)	67	54·5
Susceptible ..	1	S(4)	13	11·4	7·0	S(4)	5	5·8	7·0	S(4)	29	29·8
Total	16		182	182·2	100·0		83	83·0	100·0		426	426·0
				$\chi^2 = 2·04$ P = 0·9–0·8				$\chi^2 = 2·81$ P = 0·8–0·7				$\chi^2 = 23·99$ P < ·001 major classes (Res., Seg., Sus.) $\chi^2 = 0·15$ P = 0·95–0·9

[1] These reaction types would be expected to be absent in certain lines.
Ld. = Homozygous for Landhafer reaction type (1 =); Tr. = Homozygous for Trispernia reaction type (1+); Vc. = Homozygous for Victoria reaction type (1n); S.F. = Homozygous for Santa Fe reaction type (1 =); S = Homozygous susceptible reaction type (4). Res. = Resistant, Seg. = Segregating, Sus. = Susceptible.

The observed frequencies in the first two crosses showed no significant deviations from those expected. In the cross Santa Fe × Victoria, however, it was clear that an excessively large number of lines showed the Victoria reaction type on the hypothesis adopted. Reference has already been made to similar conclusions based on F_2 data. Unfortunately, as previously indicated, no studies of F_1 reaction type where epistasis could be directly assessed were carried out in this cross in tests involving races to which both parents were resistant. The greater number of F_2 plants and of F_3 lines showing the Santa Fe type of resistance suggested the epistatic behaviour of the Santa Fe reaction type over that of Victoria. The general observation in all crosses in general, that the lower reaction type was epistatic, supports this hypothesis. Certain genotypes, however, involving the variety Victoria, seemed to have inhibited the action of the Santa Fe gene. Such behaviour was evident in studies on correlated tests of identical F_3 lines involving race 226 (to which both parents were resistant) and race 286 (to which only Victoria was resistant). The data are included in Table 12.

Relationship of seedling reaction types to different races and to adult plant field reactions

(i) F_2 seedling vs. F_2 seedling

This correlation was studied only in the cross Landhafer × Santa Fe, where 321 F_2 plants were first classified for primary leaf reaction type to race 237 and the leaves subsequently cut off and of these 207 were then inoculated at the secondary leaf stage with race 226. Perfect correlation of reaction types was observed in this test.

(ii) F_2 seedling vs. F_2 adult plant

This association was studied in all crosses except Victoria × Landhafer. Classified seedlings were transplanted and tested in the field for subsequent adult plant behaviour. The resistant class was expected to maintain its resistance at the adult plant stage in Landhafer crosses but, due to the operation of an additional factor conditioning adult plant resistance in this variety, the seedling susceptible class was expected to produce some resistant adult plants. In the cross Santa Fe × Landhafer, 86 seedlings tested maintained their resistance; in the cross Landhafer × Trispernia only one plant giving an intermediate type of reaction for the heterozygous condition of the Trispernia gene gave a susceptible field reaction, the other 193 seedlings maintaining their resistance as adult plants. In the susceptible class one plant out of nine in the former cross and five out of thirteen in the latter cross remained fully susceptible, the segregation thereby conforming within approved statistical limits to the expected 3 resistant : 1 susceptible ratio. These resistant adult plants, in both cases from the susceptible seedling group, varied in reaction type, one being immune, six resistant, and one moderately resistant in the cross Santa Fe × Landhafer, the corresponding figures in the cross Landhafer × Trispernia being three, four and one, thus showing that the factor conditioning only adult plant resistance in Landhafer was incompletely dominant in inheritance.

Since the single factor pairs conditioning seedling as well as adult plant resistance in both Santa Fe and Trispernia were previously shown to be allelic (or closely linked) in the seedling stage, no susceptible F_2 adult plant segregates were expected in the cross between these two varieties; none were observed among 192 plants tested.

In tests involving race 226 (to which Ukraine was susceptible) seedling resistant F_2 plants in the cross Santa Fe × Ukraine were expected to remain resistant as adult plants due to the influence of the Santa Fe gene, and susceptible seedlings were expected to show a 57 resistant : 7 susceptible adult plant segregation due to the action of the three factors (two acting in complementary

fashion) conditioning adult plant resistance in Ukraine. In the cross Victoria × Santa Fe in tests involving races to which both parents were resistant, seedlings possessing the Santa Fe reaction type (" ; " to " 1= ") were expected to remain resistant as adult plants. The group of seedlings possessing the Victoria reaction type (" 1n ") and those susceptible were expected to show some susceptible and resistant adult plants respectively. Previously cited F_2 data indicated that in this cross only one factor conditioning solely adult plant resistance in Victoria was operative. This factor, when linked with two complementary factors for seedling resistance, was expected to show the following relationship between seedling and adult plant behaviour in F_2:

Adult plant reactions	Seedling reaction types		
	Santa Fe type	Victoria type	Susceptible
Immune—Moderately resistant	100%	66·9%	9·5%
Moderately susceptible —Susceptible ..	—	5·0%	18·6%

Data relating to crosses of Santa Fe with Ukraine and Victoria are presented in Table 7. In all cases good statistical fits to the expected results were clearly obtained and confirmed the operation of three factors in Ukraine and one major factor in Victoria for adult plant resistance.

TABLE 7

Relationship between seedling reaction types and adult plant reactions to Crown Rust of F_2 plants in crosses of the oat variety Santa Fe with the varieties Ukraine and Victoria

Adult plant reactions	Seedling reaction types (Race 226)[1]							
	Santa Fe × Ukraine			Santa Fe × Victoria				
	;	1=, 1	3–4	;	1=, 1	1n	2–n	3–4
Immune	59	7	—	34	15	27	—	1
Resistant	5	3	3	—	—	2	—	3
Mod. Res.	3	2	11	—	—	—	11	—
Total	67	12	14	34	15	29	11	4
			(12·7)			(35·5)		(5·0)
Mod. Sus. and Susceptible	—	—	1	—	—	—	1	8
			(2·3)			(2·6)		(9·9)
P value			0·7–0·5[2]				0·7–0·5	

[1] Seedling reaction types corrected from F_3 behaviour.
[2] Yates' correction factor applied for small numbers.
Mod. Res. = Moderately resistant, Mod. Sus. = Moderately susceptible.
(Expected values in brackets.)

(iii) F_2 seedling vs. F_3 seedling

The F_3 behaviour of representative samples from each F_2 class of reaction type was studied in all crosses except Santa Fe × Ukraine. In certain cases the particular race to which the F_2 was tested was used in a mixture with certain other races for F_3 tests. In other cases, a mixture not involving the particular race used in F_2 was utilized, whilst in one test an identical strain

(race 226) was used in tests for both generations. The data pertinent to these studies are set out in Table 8 and were designed to study the postulated breeding behaviour of F_2 genotypes based on reaction types and to investigate if the same factors were operative against all races.

In the cross Santa Fe × Landhafer one plant each from the highly resistant class ("; " reaction type) and moderately resistant class ("2— " reaction type) of F_2 segregates gave susceptible progenies. The latter plant would have been expected to be heterozygous on reaction type and hence segregate in F_3. Classification as homozygous susceptible may have been erroneous, due to the chance absence of a resistant plant, but this would be highly improbable statistically in the sample of approximately 25 plants tested in each F_3 line. One moderately resistant F_2 plant ("2-- " reaction type) also gave a homozygous susceptible line, but this could occur statistically at a relatively nigh probability level as pointed out by Upadhyaya and Baker (1962*a*). Except for these instances, the first of which was almost certainly due to an error in classification, labelling or transplanting, all other plants from the different F_2 reaction classes behaved as expected, indicating correlated inheritance to all races with which they were tested, since no mixed reaction types were observed on the same leaf by the use of inoculum comprising a mixture of races.

In the cross Santa Fe × Trispernia there was also good agreement between observed and expected results. The operation of certain modifying genes was indicated, however, since from the "1 " reaction type in F_2, 12 plants gave homozygous nighly resistant progenies similar to Santa Fe ("; " to "1= " reaction type). In the F_2 classification also certain seedlings had shown reaction types higher than Trispernia; the progenies of these plants showed reaction types similar to Trispernia at normal temperatures of about 75°F, except for one plant which showed segregation for the Santa Fe and Trispernia reaction types.

In the cross Victoria × Landhafer also good agreement between the F_2 reactions to race 237 and F_3 behaviour to a mixture of races 226, 237 and 237–4 was shown. Only four lines—one homozygous resistant for the Victoria reaction type and three segregating for Victoria type resistance and susceptibility —were observed from F_2 plants in the "1— " to "1 " reaction type category intermediate between that of Landhafer and Victoria and expected to segregate for the Landhafer reaction type and susceptibility. This discrepancy may have been due to difficulty in distinguishing the necrotic reaction type associated with the Victoria type of resistance on the basis of a single F_2 plant. Similarly, a small number of discrepancies were observed in the cross Landhafer × Trispernia. The difficulty in distinguishing a "2 " reaction type with the associated "green island " from a "3 " type with the pustule surrounded by chlorosis resulted in three plants assigned to the former class giving homozygous susceptible progenies and two to the latter class producing segregating progenies. Apart from these instances it was clear that the same factors in the two varieties conditioned resistance to the four races 226, 237, 237–4 and 259.

In the cross Santa Fe × Victoria, F_2 plants classified for reaction type to race 203 were tested for their progeny reactions against races 226 and 237 separately. Reactions in F_3 were corrected, taking into account behaviour to both races since small numbers of seedlings were tested to each race separately. For example, if an F_3 line was apparently homozygous resistant to one race in the small sample tested, but segregating to the other, its behaviour was indicated as segregating. In another test, F_2 and F_3 reaction types were noted when both were tested against the same race—race 226. Agreement between observed and expected results was not completely satisfactory in this cross and discrepancies existed in certain instances. From among the 85 F_2 plants classified as possessing the Santa Fe reaction type ("; "), three were found to

TABLE 8

F_3 behaviour of F_2 plants classified for seedling reaction type to Crown Rust in crosses involving the resistant oat varieties Landhafer and Santa Fe

F_2 Reaction types of various crosses to different races		F_3 reactions to race(s)						Total
		226, 237, 237–4 and 259						
Race 259		Res.	Seg.	Sus.				
Santa Fe × Landhafer	;	35	18	1				54
	1	1	23	—				24
	2–	—	3	1				4
	3–4	—	—	7				7
		226, 237, 237–4 and 259						
		S.F.[1]	S.F. : Tr.[2]	Tr.				
Santa Fe × Trispernia	;	13	12	—				25
	1	12	36	2				50
	2–	—	6	20				26
	2	—	1	5				6
		Ld.	Ld. : Tr.	Tr.	Ld.(Tr.) : S.	Tr.: S.	S.	
Landhafer × Trispernia	;	46	13	—	11	—	—	70
	1–2=	1	7	1	46	1	—	56
	2–	—	4	2	6	3	—	15
	2	—	—	2	3	21	3	29
	3–4	—	—	—	—	2	12	14
		226, 237 and 237–4						
Race 237		Ld.	Ld. : Vc.	Vc.	Ld.(Vc.) : S.	Vc. : S.	S.	
Victoria × Landhafer	;	3	1	—	3	—	—	7
	1– –1	—	1	1	8	3	—	13
	1n – 2–n	—	—	4	—	4	—	8
	3n	—	—	—	—	3	—	3
	3–4	—	—	—	—	—	7(2 S. : Vc.)	7
		226 and 237						
Race 203		S.F.	S.F. : Vc.	Vc.	S.F.(Vc.):S.	Vc.:S.	S.	
Santa Fe × Victoria	;	32	10	1	2	1	—	46
	1	11	7	2	43	—	—	63
	1+, 3–c	—	—	—	15	2	—	17
	1n, 2–n	—	6	19	19	26	—	70
	2n, 3n	—	—	1	2	8	—	11
	3–4	—	—	—	—	1	16(8 S.Vc.)	17
Race 226			226					
	;	11	9	2	14	2	1	39
	1	—	2	—	13	—	—	15
	1n– 2–n	—	—	5	—	20	—	25
	2n– 3n	—	—	2	1	4	1	8
	3–4	—	—	—	—	1	10(3 S. : Vc.)	11

Reaction types indicated as follows :—S.F. = Homozygous ; – 1 = ; Tr. = Homozygous 1+ ; Ld. = Homozygous ; – 1 = ; Vc. = Homozygous 1n ; S. = Homozygous 3-4 reaction types ; S.F. : Tr., etc. = segregating for S.F. and Tr. reaction types etc. ; Ld. (Tr.) : S., etc. = segregating for Ld. reaction type and susceptibility or Ld. and Tr. reaction types and susceptibility, etc. ; S. : Vc. = segregating for Vc. reaction type and susceptibility with preponderance of susceptible plants ; Res. = Homozygous resistant ; Seg. = Segregating ; Sus. = Homozygous susceptible.

be homozygous for the Victoria reaction type (" 1n "), three segregated for this reaction type and susceptibility, and one was homozygous for susceptibility. Of 78 plants classified as showing a " 1 " reaction type, intermediate between Santa Fe and Victoria, two were homozygous for the Victoria type of resistance, whilst two segregated for the Victoria reaction type. A total of 28 plants from

TABLE 9

F_3 seedling behaviour to certain Crown Rust races of F_2 plants classified for adult plant reaction in crosses involving the resistant oat varieties Landhafer and Santa Fe

Cross	F_2 Field reaction	F_3 Seedling behaviour or reaction type(s)						Total	P value
		Res.		Seg.		Sus.			
		Races 226, 237, 237–4 and 259							
Santa Fe × Landhafer	I	44		42		—		86	
	R	1		41		—		42	
	MR	—		7		3		10	
	MS–S	—		4		8		12	
		Races 226 and 226–2							
Santa Fe × Ukraine	I	14		26		7		47	
	R	1		3		2		6	
	MR	—		1		4		5	
	Total	15(14·8)		30(29·9)		13(13·3)		58	0·9–0·8
	MS–S	—		—		2(2·0)		2	—
		Race 226							
		S.F.	S.F.:Vc.	S.F.(Vc.):S.	V.c	Vc.:S.	S.		
Santa Fe × Victoria	I	13	11	27	5	4	—	60	
	R	1	—	5	1	1	1	9	
	MR	—	—	5	3	14	6[1]	28	
	MS–S	—	—	1	—	1	7[2]	9	
		Race 203							
		Ld.	Ld.:Vc.	Ld.(Vc.):S.	Vc.	Vc.:S.	S.		
Victoria × Landhafer	I	20	10	28	8	8	4	78	
	R	—	—	3	—	—	—	3	
	MS	—	—	—	—	—	2 (1 S. : Vc.)	2	

[1] Four lines segregating with preponderance of susceptible plants.
[2] Three lines segregating with preponderance of susceptible plants.
For interpretation of symbols S.F., etc., see Table 8.
(Expected values in brackets.)
I = Immune, R = Resistant, MR = Moderately resistant, MS = Moderately susceptible, S = Susceptible.

the 114 in the class showing the necrosis associated with the Victoria reaction type and classified as having " 1n ", " 2—n ", " 2n " or " 3n " reaction types showed segregation for the Santa Fe genotype, whilst one F_2 plant from the " 2n " to " 3n " reaction type category was homozygous susceptible. Most of these aberrant instances were those involving F_2 tests with race 203 and a closer association of reaction types between F_2 and F_3 seedlings was evident when race 226 was used in the F_2 generation.

The four plants under the F_2 " ; " reaction type category, producing susceptible progenies or segregating for Victoria type resistance and susceptibility, were almost certainly misclassifications. The discrepancies in other cases indicated that the F_2 classification was affected by modifying genetic factors or environmental variations. Further evidence for this was shown since 11 lines were homozygous resistant for the Santa Fe reaction type from F_2 plants classified as exhibiting a " 1 " or various intermediate reaction types. Later reported correlated F_3 studies involving different races produced unexpected results and, as indicated in Table 8, 28 F_2 plants out of 114 classified for the Victoria reaction type gave F_3 lines segregating for the Santa Fe factor as previously indicated.

(iv) F_2 adult plant vs. F_3 seedling

In this analysis the progenies of plants classified for adult plant reaction in the field were studied for seedling behaviour and the data are presented in Table 9.

This analysis involved tests on F_2 seedlings which had been initially classified for seedling reaction type and subsequent adult plant behaviour. In the cross Santa Fe × Landhafer three moderately resistant plants gave fully susceptible progenies. These presumably carried the recessive factor conditioning moderate resistance in the adult plant stage in Landhafer. Since these would be expected to comprise 3/64 of the population the number expected was 7·0. The probability of chance deviation was 0·2–0·1 for this result. Segregating progenies from the moderately resistant and moderately susceptible to susceptible classes of F_2 adult plants indicated that the single factor conditioning seedling as well as adult plant resistance in Santa Fe and/or Landhafer was incompletely dominant in the latter stage.

In the F_2 generation of the cross Santa Fe × Ukraine, the adult plant segregation conformed to a ratio of 249 resistant : 7 susceptible. Of these 249 resistant plants 64 were expected to produce homozygous resistant, 128 segregating and 57 homozygous susceptible lines. The progenies of the 58 resistant F_2 plants conformed to this hypothesis statistically, whilst two susceptible F_2 plants gave susceptible progenies as expected.

In the cross Santa Fe × Victoria, all the F_3 lines homozygous or heterozygous for the Santa Fe reaction type were expected to be derived from the resistant classes of F_2 plants. Of 63 lines of this type only one was derived from a susceptible plant and was probably an error in F_2 classification labelling. The expected ratio was one homozygous : 2 segregating progenies for this type of resistance. Twenty-five homozygous resistant lines were observed, giving a P value of 0·5—0·2 in the sample of 63. The remaining F_2 plants would depend for their resistance on the Victoria genes or would be susceptible. The expected behaviour of these classes in F_3 was as follows on the basis of the operation of one of the adult plant resistance factors in Victoria :

F_2 adult plant reaction	F_3 seedling behaviour (in percentages)		
	Resistant (Victoria type)	Segregating (Victoria type : susceptible)	Susceptible (including segregating with preponderance of susceptible plants)
Resistant	20·3	46·5	9·5 = 76·3
Susceptible	0·2	4·9	18·6 = 23·7
Total	20·5	51·4	28·1

Grouping together the field resistant F_2 groups (immune, resistant and moderately resistant) the observed and expected frequencies (in brackets) corresponding to the above table were as follows :

F_2 adult plant reaction	F_3 seedling behaviour		
	Resistant	Segregating	Susceptible
Resistant	9(8·7)	19(20·0)	7(4·1)
Susceptible	0(0·1)	1 (2·1)	7(8·0)

This indicated good agreement between observed and expected results.

In the cross Victoria × Landhafer, 206 F_2 plants were classified for adult plant reaction and the results are as previously set out and explained in relation to the data of Table 4. The progenies of the three resistant plants and 78 of the immune reaction class were tested. Of these 81 plants, four gave susceptible F_3 lines. From the behaviour of the Victoria genotype one-fourth of the resistant F_2 class was expected to produce susceptible F_3 lines, whilst F_3 behaviour due to the Landhafer genotype with a second factor acting solely at the adult plant stage was expected to give one-fifth of lines susceptible from the field resistant F_2 class. Hence, on combining the two genotypes one-twentieth of resistant F_2 adult plants were expected to give susceptible F_3 seedling progenies in a cross between the two varieties. The four such plants observed showed perfect agreement with the number expected.

Confirmation on the operation of the factor Vc_2 and its inhibitor was obtained since several lines in the two crosses involving Victoria showed segregation for the Victoria type of resistance with a preponderance of susceptible segregates. The behaviour of these subclasses has already been dealt with in the F_3 studies.

TABLE 10

Correlation of F_3 seedling behaviour to different races of Crown Rust in crosses involving the resistant oat variety Landhafer with certain other resistant varieties

Cross	F_3 behaviour to race	F_3 behaviour		
		Res.	Seg.	Sus. (incl. S. : Vc.)
	203	Race composite 226, 237, 237–4, 259		
Santa Fe × Landhafer	Res.	45	—	—
	Seg.	—	49	—
	Sus.	—	—	11
	226	Race composite 203, 237, 237–4, 259		
Landhafer × Trispernia	Res.	78	7	—
	Seg.	1	83	—
	Sus.	—	—	14
	203	Race composite 226, 237, 237–4		
Victoria × Landhafer	Res.	48	1	—
	Seg.	—	61	—
	Sus.(incl. S. : Vc.)	—	1	16[1]

[1] One line segregated S. : Vc. (Susceptible and Victoria reaction type plants, with susceptible types preponderant) in both tests, two segregated S. : Vc. to race composite only and one segregated S. : Vc. to race 203 only.

Seg. = Segregating, Res. = Resistant, Sus. = Susceptible

S. : Vc = Segregating for susceptible reaction type and Victoria reaction type, with preponderance of the former.

(v) F_2 seedling vs. F_3 seedling

The relationship of F_3 reactions in crosses involving Landhafer and Santa Fe are presented in Tables 10, 11 and 12. The same seedlings were tested with one race on the primary leaf and then either with a mixture of races or a second race on the secondary leaves. From Table 10 which involves data

TABLE 11

Correlation of seedling behaviour of F_3 lines to Crown Rust Race 203 and a composite of Races 226, 237, 237–4 and 259 in a cross between the resistant oat varieties Santa Fe and Trispernia

F_3 reactions to Race 203	F_3 behaviour to composite of Races		
	S.F.	S.F. : Tr.	Tr.
S.F.	11(10·9)	2(0·0)	—
S.F. : Tr.	13 (12·5)	40 (48·8)	—
Tr. : S.F.[1]	1	4	—
Tr.	— (1·6)	6(3·3)	26
χ^2 values	1·04, P = 0·7–0·5 ; 2·01, P = 0·5–0·3		

[1] Tr. : S.F. = Segregating for 1+ and ; −1 = reaction types, with the former preponderant. For interpretation of symbols S.F., etc. see Table 8.
(Expected values in brackets.)

TABLE 12

Correlation of seedling behaviour of F_3 lines to Crown Rust Race 226 and Races 237, 259 and 286 respectively in a cross between the oat varieties Santa Fe and Victoria

	F_3 behaviour to Race	F_3 behaviour to Race 226						Total
		Res.		Seg.		Sus.		
237	Res.	59		6		—		65
	Seg.	8		69		—		77
	Sus.	—		1		22		23
		S.F.[1]	S.F. : Vc.	Vc.	S.F.(Vc.) : S.	Vc. : S.	S.(incl. S. : Vc.)	
259	Res. (S.F.)	11	—	—	—	—	—	11
	Seg.	—	8	—	24	—	1	33
	Sus.	—	—	6	—	21	4	31
286	Res. (Vc.)	8	11	21	—	—	—	40
		(17·6)		(22·0)				
	Seg.	19	5	1	41	24	—	90
		(29·3)		(0·0)	(41·4)	(25·0)		
	Sus.[2]	15	5	—	23	1	—	44
		(16·1)		(0·0)	(22·6)	(0·0)		
	χ^2 values P = 0·5–0·3	2·08		—	0·011 0·95–0·9	—	—	

[1] For interpretation of symbols S.F., etc. see Table 8.
[2] Eight lines showed S. : Vc. behaviour.
(Expected values in brackets.)
Res. = Homozygous resistant, Seg. = Segregating, Sus. = Homozygous susceptible.

relating to Landhafer crosses in such tests it was clear that there was complete agreement in reaction types in the cross Landhafer × Santa Fe. Discrepancies in the cross Landhafer × Trispernia were almost certainly due to delayed germination of some seeds in tests involving race 203. Reactions to race 203 and to the mixture of races 226, 237 and 237–4 were correlated in the cross

Victoria × Landhafer, except for two lines which were found to be segregating to the mixture of races but which were resistant and susceptible respectively to race 203. These discrepancies were probably due to errors in classification and the data indicated that the same factors conditioning seedling resistance were responsible for resistance to all the races to which both parents were resistant.

In the cross Santa Fe × Trispernia, F_3 lines were first tested to race 203 and then to a mixture of races. From the reactions presented in Table 11, 14 lines which segregated when tested with race 203 were fully resistant to the mixture of races. Similarly six lines which were homozygous for the Trispernia reaction type to race 203, gave segregating reactions to the race mixture.

Again, certain lines showed a preponderance of Trispernia reaction type plants over Santa Fe types in tests with race 203. These facts indicated the operation of certain modifying factors, which inhibited the expression of the Santa Fé gene. On the assumption of a pair of such complementary factors the expected behaviour of the F_2 Santa Fe reaction class to the mixture of races was seven homozygous lines homozygous for the Santa Fe reaction type, 8 segregating for Santa Fe and Trispernia reaction types, and one homozygous for the Trispernia reaction type. All Trispernia reaction type F_2 plants were expected to produce lines homozygous for such reaction type. The deviations were not statistically significant on this hypothesis. Minor modifications were observed in tests against the mixture of races both in F_2 and F_3 studies, since some plants in the homozygous Santa Fe lines showed " 1= " and " ; " reaction types on the same leaf.

In the cross Santa Fe × Victoria, 426 F_3 lines were tested against race 226. On the secondary leaves of 75 lines reactions to race 259, to which Victoria was susceptible, were recorded ; similarly, on 174 lines reactions to race 286, to which Santa Fe was susceptible, were noted. In another test 155 lines were tested against race 237. Relationship of the reaction types in the three cases is shown in Table 12.

In tests involving races 226 and 237, to which both Santa Fe and Victoria were resistant, certain lines were resistant to one race but segregated to the other. Delayed germination, whereby certain plants escaped infection, may have been responsible for this difference. There was a general agreement in the behaviour to the two races indicating the operation for the same factors for resistance in each case except for one line which gave a segregating reaction against race 226 but a susceptible reaction to race 237, and this discrepancy was probably an error in classification. The general agreement in the reactions indicated the operation of the same factors in each variety against the two races.

In tests involving race 259 it was expected that lines homozygous for the Santa Fe reaction type would remain resistant, those segregating for the Santa Fe reaction type would segregate, whilst those of the Victoria type or susceptible to race 226 would be susceptible to race 259. There was almost complete agreement with this hypothesis except for one line, an obvious misclassification error, which was susceptible to race 226 but segregated in tests involving race 259.

In tests against race 286, from data included in Table 12, eight lines from the homozygous Santa Fe reaction type class to race 226 were homozygous resistant for the Victoria reaction type, thus clearly indicating the epistatic behaviour of the Santa Fe reaction type in this cross. On this basis the expected frequencies in the homozygous Santa Fe reaction type F_3 lines to race 226 were 20·5 per cent homozygous for the Victoria reaction type, 51·4 per cent of lines segregating for the Victoria reaction type, and 28·1 per cent of lines susceptible in tests involving race 286. All F_3 progenies showing segregation for the Santa Fe and Victoria reaction types (designated as S.F. : Vc.) in tests involving race 226 were expected to be homozygous for the Victoria reaction type (designated

as Vc.) when race 286 was inoculated onto identical seedlings. From Table 12 it was obvious that the class S.F. : Vc. did not behave as expected, nor did the homozygous Santa Fe (S.F.) category, where there was an excess of susceptible lines. However, when the two classes S.F. and S.F. : Vc. were combined, good statistical agreement was obtained. Therefore the 10·3 per cent S.F. : Vc. class, giving only the Victoria reaction type, was added to the 20·5 per cent of the S.F. category to race 226 expected to behave similarly. The satisfactory agreement resulting from this procedure indicated the action of some modifying gene(s) which resulted in the expression of a reaction type resembling that characteristic of Victoria in certain lines in the S.F. : Vc. category to race 226, despite the absence of the genetic factors conditioning the Victoria type of resistance. This was also apparent since five lines susceptible to race 286 were obtained from the S.F. : Vc. class to race 226. In the other reaction classes to race 226, results from tests involving race 286 showed good agreement between observed and expected figures except for two lines, one in the Victoria reaction class and one in the category segregating for the Victoria type of resistance.

In the cross Victoria × Landnafer 114 lines were tested to both race 259 and race 286, Victoria being susceptible to the former and Landhafer to the latter race. When observed and expected results were compared on the basis of independent segregation, the chi-square value was 3·76 for four d.f., giving a P value between 0·5 and 0·3, indicating that the factors for resistance in the two varieties were independent.

Discussion and Conclusions

Segregation studies in crosses between certain members of the group of varieties comprising Landhafer, Santa Fe, Trispernia, Ukraine and Victoria, all resistant to the prevalent Australian races of crown rust, established certain facts which substantiated previous findings but provided additional information.

Firstly, the two factors in Landhafer conditioning adult plant resistance, one of which conferred seedling resistance as well, were independent of the factors in the varieties Santa Fe, Trispernia and Victoria. Indirect evidence indicated that the factors were also independent of that responsible for seedling resistance in the variety Ukraine. The reaction type of Landhafer was epistatic over those of Trispernia and Victoria.

The factor for seedling as well as adult plant resistance in Santa Fe was independent of the factors in the variety Victoria and epistatic to them. Some modifying gene(s), however, resulted in the expression of a reaction type similar to that characteristic of Victoria by suppressing the Santa Fe gene. The Santa Fe factor was allelic with the factors for seedling resistance in the varieties Ukraine and Trispernia. The factors in the three varieties were not identical, since the gene in Santa Fe conditioned resistance to a larger number of races than did the allele in Ukraine. The allele in Trispernia exhibited a higher reaction type than that in Santa Fe or Ukraine. The resistance of Santa Fe was dominant over that of Trispernia in tests against races 226, 237, 237-4 and 250 but with race 203 the Santa Fe gene was inhibited by the action of a pair of complementary factors, one contributed by each variety, which resulted in the expression of the Trispernia reaction type in the F_1 between the two varieties.

The cross between Santa Fe and Ukraine also revealed the independence of the factors for adult plant resistance in the variety Ukraine from the alleles for seedling resistance. Since the factors in the three varieties Santa Fe, Trispernia and Ukraine conditioning seedling resistance were allelic, even though segregation was not studied in crosses of Ukraine with Trispernia and Victoria, nor in the cross Trispernia × Victoria, it could be assumed from the evidence of other crosses that the factors responsible for seedling resistance in Santa Fe (as well as Trispernia and Ukraine) and Victoria were genetically independent.

The independence of the factors conditioning adult plant resistance in Landhafer and Ukraine, and the independence in turn of the Ukraine and Victoria adult plant factors, could not, however, be established in the absence of studies on the appropriate crosses.

The concept of allelism of the factors conditioning seedling resistance in the varieties indicated is proposed, although, as indicated by Luig, McWhirter and Baker (1958) with higher plants where segregating population sizes are restricted compared with microorganisms, it is technically difficult to establish closer linkage of less than a few crossover units. However, as reviewed, the hypothesis of allelism has been proposed by various North American workers, and is accepted until evidence is advanced to refute it. In this connection the fact that race 286, described by Baker and Upadhyaya (1955), and first found in low proportions on adult plants of the variety Trispernia, proved susceptible on seedlings of Trispernia, Santa Fe and Ukraine as well as Landhafer, is of interest.

F_2 seedling segregation was studied in crosses of Santa Fe with Landhafer, Ukraine and Trispernia and in the cross Landhafer × Trispernia against race 286, to which all four varieties were susceptible. No complementary gene action between these varieties was indicated since no F_2 seedling gave a resistant reaction. This also excluded the possibility of the operation of any inhibitor against this race.

These results confirmed certain conclusions proposed by Litzenberger (1949), Finkner (1954), Finkner *et al.* (1953) and Simons and Murphy (1955). More factors were, however, identified in the present instance because a larger number of races were employed in the seedling stage analyses and studies were were also made on adult plant segregation in the field.

In conformity with the symbols used in describing the factors found in Victoria (Upadhyaya and Baker, 1958), the genes for resistance revealed in the current studies are designated thus :

Landhafer—Ld_1—for adult plant resistance and seedling resistance to races 203, 226, 226–2, 230, 237, 237–4 and 259 ; —$\bar{Ld}_2$—responsible for adult plant resistance only.

Santa Fe—Sf_1—conferring adult plant resistance and seedling resistance to the same races as Ld_1 ; —Tr_a—complementary to a factor (Tr_b) in Trispernia, complementary gene action resulting in the expression of the Trispernia reaction type and inhibition of the action of Sf_1 against race 203.

Mutica Ukraine—Sf_1'—responsible for seedling resistance to races 237 and 237–4 and allelic to Sf_1 ; —$\bar{Mu}_1$—conferring adult plant resistance ; —$\bar{Mu}_a$ and $\bar{Mu}_b$—complementaty genes for adult plant resistance.

Trispernia—Sf_1''—allelic with Ld_1 but exhibiting a higher reaction type ; —Tr_b—complementary to Tr_a.

In the case of non-allelic genes the lower reaction type was consistently epistatic in the seedling stage.

Additional genes were revealed in certain of these varieties in crosses with Bond and will be reported in a subsequent paper.

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THE OCCURRENCE AND COMPOSITION OF MANNA IN EUCALYPTUS AND ANGOPHORA

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Synopsis

Manna, an exudate from the injured leaves and branches of certain eucalypts and angophoras, has a different composition from the sap. The mode of occurrence, composition and the methods of analysis employed are given. An hypothesis is advanced that the manna is the result of the action of the enzymes of the saliva of insects on the sugars present in the phloem sap.

INTRODUCTION

The secretion of manna by certain eucalypts was noted early in the 19th century. Virey (1832) described it in a paper to the *Journal de Pharmacie* and Mudie mentioned it in a report on *E. mannifera* in 1834. In 1843 Johnston examined this manna and distinguished it from the manna of commerce. The principal sugar in eucalyptus manna he called melitose (now called raffinose) whereas commercial manna consists mainly of mannitol. A saccharine exudation from *E. punctata* was examined by Smith (1897) who identified the sugar with raffinose. He observed that the manna exuded from a wound in the tree was caused by the larva of a wood-borer. It was noted that where the puncture had not entirely penetrated the bark, the exudation was white and attracted ants, but where the puncture had penetrated right through the bark and had entered the wood, a mixture of manna and kino exuded and was not taken by ants. Smith found that the manna consisted of raffinose and a small amount of reducing sugar, that it was exuded from the tree as a syrupy liquid and crystallized on evaporation. No further reference to eucalyptus manna has been found except a statement in several books that *E. viminalis* secretes a sugary substance called manna.

In the present paper the term " manna " will be confined to the saccharine secretion from the trees themselves. It excludes the sugary secretion from aphids, scale, lerps and other insects. These have been called manna by some writers, e.g. Penfold and Willis (1961), but are entirely different in composition from the manna discussed in this paper.

MODE OF OCCURRENCE AND COMPOSITION

Manna has been observed not only on the wood of *E. punctata* and on the leaves of *E. viminalis* and *E. mannifera* as mentioned above, but the writer has collected it also from the wood of *E. maculata* and from the leaves of *E. punctata*, *E. maculata*, *E. citriodora*, *E. tereticornis*, *Angophora floribunda* and *A. costata*.

On leaves and twigs it occurs as white nodules of interlaced acicular crystals, the nodules varying in diameter from 1·5 to 4 mm. and weighing about 0·005 to 0·03 grammes. Occasionally larger nodules occur but, after growing to a certain size, most of the nodules appear to be dislodged by the motion of the leaves in the wind or they are dissolved by dew or rain. The largest nodule found on a leaf was the size of a pea and weighed 0·07 gramme. The secretion from the trunk or a large branch of a tree may weigh several grammes, but it generally consists of a number of smaller nodules or tears.

The manna occurs only on the site of a wound inflicted by an insect. In more than 600 attempts to obtain manna by wounds artificially inflicted by punching holes in leaves, scarifying twigs, cutting leaves in half, drilling a hole in the trunk or cutting a blaze in the tree, not one resulted in the generation of manna. On the other hand, leaves partly eaten by an insect or timber infested with a borer will frequently produce manna from the wound. The secretion of manna does not take place immediately a leaf is injured. Several hours or even days may elapse before exudation commences. In the case of a leaf the manna always occurs at the severed end of a vein (Fig. 1). On a terminal shoot the nodule of manna conforms to the shape of the phloem sheath of the shoot and sometimes invests the truncated end of the shoot. The manna is secreted from the vein of a leaf at the rate of 0·001 to 0·0025 gramme per day. There is evidence that in some cases the rate of growth of a nodule varies,

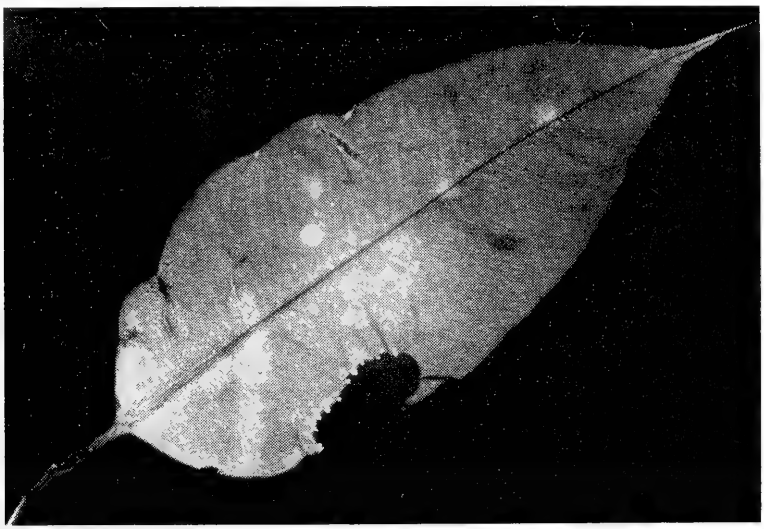

Fig. 1. Leaf of *E. maculata* showing nodules of manna on end of veins.

the nodule being alternately large and small in diameter. When a nodule is removed from a leaf, the wound often continues to " bleed " and form another nodule. As the manna exudes from the wound it crystallizes below that already formed. The nodules thus increase by accretion from below and, not like a stalactite, by having the newer material deposited on the distal end. The manna is secreted from the leaves and young twigs as a liquid but appears to crystallize immediately. No free liquid has been observed in the nodules on the leaves. The secretion from the trunk and large branches of a tree, however, often remains liquid for some time and may run down the trunk several centimetres before it crystallizes.

The secretion of manna takes place throughout the year but appears to be most abundant in the spring and early summer, when the growth of new leaves is most rapid. Also, it has been noticed that the nodules occur more frequently on the side of the tree facing the sun. The rate of formation of manna thus appears to be related to the rate of flow of the sap.

The analysis of several specimens of manna from the leaves and twigs of angophoras and eucalypts has shown that it is not just dried sap which has exuded from the wound. The comparison of paper chromatograms of the sugars of manna and of the juice expressed from an uninjured leaf of the same age as that from which the manna was taken, shows a marked qualitative and

quantitative difference in composition. The approximate proportions of the various sugars present in the manna and the corresponding leaves are shown in Table 1.

Actually, in most cases of injury to a leaf or to a branch the wound does not " bleed ". Only about one of every hundred injured leaves will secrete manna. It appears that some special environment or condition is needed to permit the formation of manna. It is postulated that this condition is the secretion of an enzyme by the insect, possibly in the saliva, which hydrolyses the pectins and hemicelluloses of the cells forming, *inter alia*, galactose and/or galactose phosphate which, under the influence of another galactosidase or glycosidase, synthesizes raffinose from sucrose, melibiose from glucose and, in some cases, stachyose from raffinose present in the phloem fluid. It may be suggested that the causative agent is not the saliva of the insect but a micro-organism introduced indirectly into the wound. That this is improbable is supported by the observation of Fisher (1945) that inoculation of cuts on *Myoporum platycarpum* with three micro-organisms most abundant in its manna did not cause manna formation.

TABLE 1

Comparison of the approximate proportions of sugars in the manna with those of the leaf-sap of E. maculata, E. punctata *and* A. costata

Sugar	*E. maculata*		*E. punctata*		*A. costata*	
	Manna	Leaf	Manna	Leaf	Manna	Leaf
Stachyose	0	0	2	0	10	0
Raffinose	80	5	80	10	65	10
Melibiose	10	0	0	0	0	0
Sucrose	6	85	10	80	20	70
Glucose and Fructose ..	4	10	8	10	5	20

The presence of galactose in the tissue surrounding the injury to leaves has been detected, but no galactose has been found in the uninjured part of the leaf. That this process of synthesis of raffinose is possible is supported by another investigation (not yet complete) in which the sap of the stems of *E. maculata* is ingested by a scale insect, *Eriococcus coriaceus* (Mask.). The secretion of this insect consists of a mixture of some five or six galactosides varying in complexity from di- to penta-saccharides. In this case the cell sap has actually passed through the alimentary tract of the insect as distinct from the manna which is formed in the plant substance itself. It is suggested that some similar enzyme is involved in both cases. It is relevant to this investigation to note that Lechevallier (1962) obtained an α-galactosidase from germinating barley with which she converted sucrose into raffinose.

Since the concentration of sugars in the phloem sap is not constant, being dependent on the rate of photosynthesis, translocation, metabolic transformations and other processes, so the composition of manna varies. In the leaf, which is relatively rich in sucrose and poor in glucose, the manna consists largely of raffinose and contains little or no melibiose. The phloem sap of the trunk and larger branches, on the other hand, contains a much higher proportion of glucose and consequently the manna is richer in melibiose. This sugar is about 20 times as soluble in water as raffinose and hence the exudate from the trunk and larger branches takes longer to crystallize and is more fluid than that of the leaves. This accounts for its habit of often running down the trunk or branch several centimetres before it crystallizes.

The results of the analyses of specimens of manna from different sources are shown in Table 2. It will be seen that they vary slightly from sample to sample but in general they consist of about 60% sugars, 16% water (mainly

water of crystallization), and a small amount of ash. The remaining 20% has been shown to contain pectin and uronic acids. The manna has a pH of 5·3 and an acid number of 3·75 to 5·1

It should be noted that mannitol, a major constituent of the manna of *Myoporum platycarpum* (Hatt and Hillis, 1947), has not been found in any specimen of eucalyptus or angophora manna so far examined.

The individual sugars and their relative proportions in each specimen of manna were determined by paper chromatography. The identity of the sugars was deduced by comparison of their spots on the chromatogram with those of authentic specimens of the respective sugars when subjected to certain tests. These tests included their $R_{glucose}$ values, the characteristic colours given with various spray reagents, the preparation and examination of the osazones (of those sugars which yielded them) and, in the case of tri- and tetra-saccharides, by identification of the products of hydrolysis with acid and with invertase.

TABLE 2

The composition of specimens of manna from different sources

	E. maculata Leaf	*E. punctata* Leaf	*E. punctata* Trunk
Loss on drying	16·6	14·4	17·04
Ash	3·6	1·3	1·6
P_2O_5	0·66	Trace	Trace
Total sugars (as glucose)	58·8	66·0	61·17
Reducing sugars (as glucose)	4·3	4·2	18·72
	79·0	81·7	79·81

It is not always possible to determine which insect inflicted a particular wound from which manna exudes. The secretion of manna does not take place immediately an insect attacks the plant, so that frequently the insect causing the wound has gone before exudation commences. However, some of the less mobile insects have been observed on the site of the manna secretion. For example, the blister on a leaf caused by the leaf-miner *Philactophaga eucalypti* (Frogg.) has been found with a number of nodules of manna attached to the margin inside the blister. The larva of the leaf case-moth *Hyalarcta hubneri* (Wwd) and of the saw-fly *Perga dorsalis* (Leach) have both been identified as causing the secretion of manna. A wound in the trunk of *E. punctata* from which manna was flowing was caused by the larva of a beetle (not identified).

The majority of the specimens of manna, both eucalypt and angophora, came from the leaves of suckers growing around the stumps of trees that had been felled. Only rarely do specimens occur on mature trees. The most abundant source of leaf manna is *E. maculata*, followed by *E. mannifera* and *E. punctata*. Only very few specimens have been taken from the leaves of *E. citriodora*, *E. tereticornis* and the two angophoras. None of the other eucalypts in this district has yielded any specimens. The most productive source of manna from the trunk and large branches is *E. punctata*.

EXPERIMENTAL

The sugars present in the manna were identified by paper chromatography and the results confirmed by other tests such as the examination of the osazones and the products of hydrolysis by acid and by invertase. In the chromatographic examination, Whatman's no. 1 paper was used. The descending solvent method was found to give the best results, using as developing solvents A, butanol-acetone-water 3 : 4 : 1 and, when a two dimensional chromatogram was required, solvent B, butanol : ethyl acetate : acetic acid : water 5 : 4 : 2 : 2.

As reference sugars, stachyose, raffinose, sucrose and glucose were mainly used, but other standard sugars were used on occasions. Table 3 shows the $R_{glucose}$ values of the sugars for solvents A and B at 25°.

After about 20 hours' development in the tank the papers were dried at 105° and treated by the method of Bailey and Bourne (1960). The components of the manna were identified not only by their $R_{glu.}$ value but also by the characteristic colours given by the spray. The presence of the fructofuranose group in the molecule was detected by spraying with naphthoresorcinol : HCl : acetone 1 : 2 : 200. The group was indicated by the development of a reddish-orange colour on heating.

TABLE 3

$R_{glucose}$ values of sugars at 25° for solvents A and B

Sugar	Solvent A	Solvent B
Stachyose	0·06	0·058
Raffinose	0·24	0·18
Melibiose	0·33	0·26
Sucrose	0·66	0·56
Galactose	0·86	0·90
Glucose	1·00	1·00
Fructose	1·15	1·29

The oligo-saccharides were further identified by hydrolysis with 0·2N HCl and also with invertase. Hydrolysis by HCl was carried out at 70° for one hour and hydrolysis by invertase at 35° for 24 hours.

The determination of the relative proportions of stachyose to raffinose, of raffinose to sucrose, etc., was made by comparing the area and intensity of colour of the stains on a chromatogram with those of a number of standard solutions of sugars of known concentration.

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AUSTRALIAN LARVAL CARABIDAE OF THE SUBFAMILIES HARPALINAE, LICININAE, ODACANTHINAE AND PENTAGONICINAE (COLEOPTERA)

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C.S.I.R.O., Canberra

[Read 30th June, 1965]

Synopsis

Larvae of the following Carabidae are described and figured for the first time: *Cenogmus castelnaui* Csiki (Harpalinae); *Lestignathus cursor* Erichs. and *Dicrochile brevicollis* Chaud. (both Licininae); *Eudalia macleayi* Bates (Odacanthinae); and *Scopodes simplex* Blackb. (Pentagonicinae). The subfamily Pentagonicinae and all five of the genera were previously unknown in the larval state.

This is the second of a projected series of papers (for the first, see Moore (1964)) dealing with Australian carabid larvae, a group about which singularly little information has ever appeared in print. The ultimate aim of the series, namely, the recognition and description of all the principal genera, is likely to prove a long-term project, in view of the size of the fauna and of the difficulties associated with the collection of adequate larval material in an essentially arid environment. However, the piecemeal description of isolated genera, as they become available, serves the very important immediate purpose of adding to our knowledge of world carabid larvae as a whole, and so providing a better perspective for developing the general classification admirably pioneered by van Emden (1942). Thus, on the basis of even the present very limited material, it has been possible to add three subfamilies and nine genera to the tally of those already positively identified in the larval stage. Addition of the few important subfamilies remaining as yet unknown (some of which will undoubtedly fall to the lot of Australian coleopterists) would place the taxonomy of larval Carabidae on a sound basis and allow it to play its full part in the understanding of carabid evolution as a whole.

Subfamily Harpalinae

Cenogmus castelnaui Csiki (*rotundicollis* Cast.)

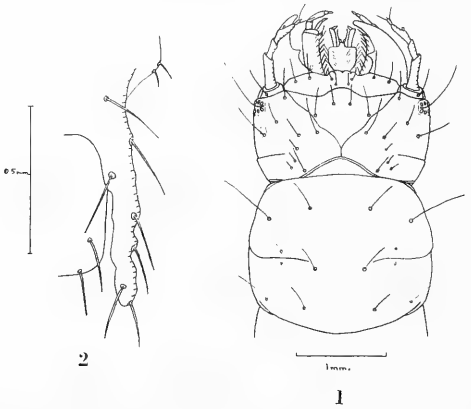
(Figs 1–2)

Mostly pale, whitish; head light brown, the tips of the mandibles darker.

Head rather large, very transverse, moderately sclerotized; frontal piece triangular, almost reaching hind-margin; epicranial suture very short; ventral suture obliterated anteriorly; nasale truncate, not prominent, lightly cuspidate; neck weak but with strong cervical keels; ocelli present, six on each side; postocular furrows feeble; mandible short and stout, with a basal penicillus; retinaculum small; antenna slender, shorter than the mandible, four-segmented; maxilla setose; inner lobe present as a stout tubercle, fused with the stipes, unisetose before apex; maxillary palp three-segmented, the palpiger distinct; labium quadrate, palp two-segmented; ligula small, bisetose, the setae situated on small tubercles. *Pronotum* slightly transverse, lightly sclerotized, slightly broader than head; legs short and stout, with two subequal terminal claws. *Abdomen* with tergites lightly sclerotized, unmargined at sides; pleurites and ventrites membranous; cerci fixed, very short, unsegmented but with setiferous nodes; pygopodium stout, slightly shorter than the cerci.

Length (including cerci): L_2, 10 mm.; L_3, 12–13·5 mm. Head-width: L_2, 1·7 mm.; L_3, 2·0 mm.

Described from one L_2 and three L_3, Koojan, W.A., 16.viii.61 (L. E. Koch), taken from soil, in association with many adults. Although the adults were not reared individually, they appeared in numbers in laboratory trays of Koojan pasture material, where the larvae in question were the only coleopteron previously observed. The identification therefore seems secure.



Figs 1–2. *Cenogmus castelnaui* Csiki, third instar larva (L_3). 1, Fore parts. 2, Right cercus and pygopodium, right side.

In their systematic characters, *Cenogmus* larvae agree well with the general description given by van Emden (1942, p. 39) for larval Harpalini (=Harpalinae in the sense of the present paper) and they appear to come close to the South American genus *Anisotarsus* Chaud. Important characters linking the two genera include the fusion of the inner lobe to the stipes, the small retinaculum and the weakly marked postocular furrows. The main point of difference that can be made out concerns the abdominal praeterga which, in *Anisotarsus*, are defined by a transverse furrow (van Emden, *loc. cit.*), but in *Cenogmus*, are not differentiated from the corresponding terga.

Subfamily Licininae

Lestignathus cursor Erichs.

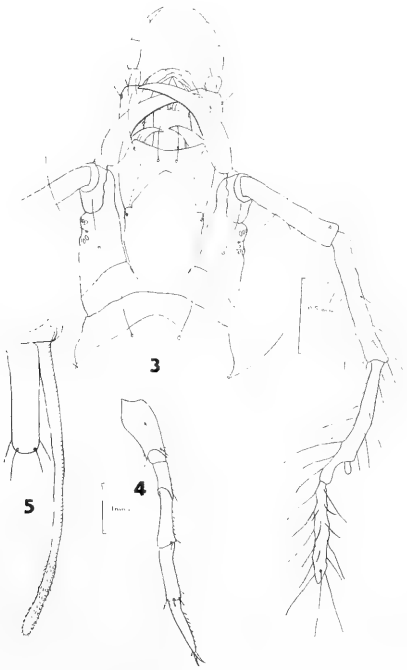
(Figs 3–5)

Very slender larvae, with exceptionally long appendages. Sclerites dark brown; intersegmental membranes and underside mostly pale.

Head small, elongate, strongly sclerotized; frontal piece reaching hind-margin; ventral suture forked anteriorly; nasale emarginate, unarmed; neck weakly marked; cervical keels weak; ocelli present, six on each side; mandible slender, the terebrum finely and irregularly dentate; retinaculum long, falcate; antenna very long and slender, all four segments elongate; vesicle well-marked; maxilla setose; inner lobe a well-marked tubercle, with a stout apical seta; maxillary palp three-segmented; palpiger distinct; labium elongate, the palp stout, two-segmented; ligula minute, bisetose. *Pronotum* elongate, conical, tapering anteriorly to width of head, strongly sclerotized; legs long and slender, with two subequal terminal claws. *Abdomen* with tergites strongly sclerotized, margined anteriorly and laterally; cerci long and slender, smooth, unsegmented and unarmed but pubescent towards apex, not articulating with the ninth segment, but each attached to a separate sclerite; pygopodium slender, tubular, about one-third the length of the cerci.

Length (including cerci): L_3, 20–23 mm. Head-width: L_3, 1·0–1·1 mm.

Described from two L_3, Tasmania: Waratah and Mount Field, 21–26.i.61 (B. P. Moore), taken in wet forest litter. The Waratah specimen occurred in company with numerous adults of *Lestignathus cursor* Erichs. (length, 13–16 mm.) and *L. foveatus* Sl. (length, 7–8 mm.), but only the former species was noted at Mount Field. In view of the size of the larvae and of their obvious licinine affinities, *Lestignathus cursor* and four species of *Dicrochile* (*quadraticollis* Cast., *goryi* Guér., *brevicollis* Chaud. and *minutus* Cast.) would appear to be the only candidate species on the Tasmanian list. However, larval *Dicrochile brevicollis* have since been identified from mainland material (see below) and they prove so distinct from the Tasmanian larvae as to leave no doubt that the latter belong to the large species of *Lestignathus*.



Figs 3–5. *Lestignathus cursor* Erichs., third instar larva (L_3). 3, Head. 4, Right hind leg. 5, Right cercus and pygopodium.

Dicrochile brevicollis Chaud.

(Figs 6–7)

Upperside largely shining black, except head, which is mostly red; ventrites brown, intersegmental membranes pale, whitish.

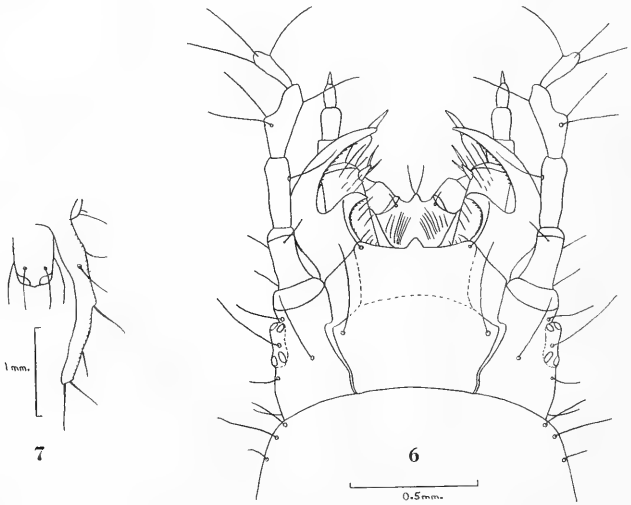
Head small, quadrate, lightly sclerotized; frontal piece reaching hind-margin on a wide front; ventral suture forked anteriorly; nasale a single triangular projection; no obvious neck; no cervical keels; ocelli present, six on each side; mandible strongly curved, denticulate; retinaculum large, falcate, denticulate; basal penicillus present; antenna slender, four-segmented, longer than the mandible; vesicle minute; maxilla setose; inner lobe well marked, with two stout, subapical setae; maxillary palp three-segmented; palpiger distinct; labium trapezoidal; ligula small, bisetose; labial palp stout, two-segmented. *Pronotum* trapezoidal, widest near base, closely adapted to head, strongly sclerotized; legs rather short, strongly spinose, with two subequal terminal claws. *Abdomen* with tergites and pleurites strongly and completely

sclerotized, the tergites margined anteriorly and laterally ; ventrites moderately sclerotized ; cerci short, fixed and unsegmented but with setiferous nodes ; pygopodium short and stout.

Length (including cerci) : L_2, 11–12 mm. Head-width : L_2, 1·0–1·1 mm.

Described from two L_2, East Queanbeyan, N.S.W., 13.i.65 (B. P. Moore), taken from under stones in a dried-up river course, and in company with numerous adult *D. brevicollis*. *Dicrochile* is the only genus of Licininae, with adults of sufficient size, that would be expected to frequent such a habitat.

Larvae of *Lestignathus* and *Dicrochile* differ so widely in general habitus as to suggest that the two genera belong to separate phyletic lines. Such a conclusion is in agreement with the latest arrangement of adult Licininae (Ball,



Figs 6–7. *Dicrochile brevicollis* Chaud., second instar larva (L_2). 6, Head. 7, Right cercus and pygopodium.

1959), where, according to its special mandibular characters, *Dicrochile* is placed in an isolated group. Nevertheless, both genera agree well with the general diagnosis for larval Licininae given by van Emden (1942) and they both show an important subfamily character not mentioned by that author, namely, the pronounced anterior forking of the cranial ventral suture. Jeannel (1942) first drew attention to this distinction from other subfamilies (where the ventral suture is almost always a simple groove) and he looked upon it as involving the formation of a true gula. However, Hinton (1963), who refers to the central segment as the ventral apotome, has shown that it is not homologous with the gula of the adult : the enclosing sutures merely represent lines of weakness associated with ecdysis.

Subfamily Odacanthinae

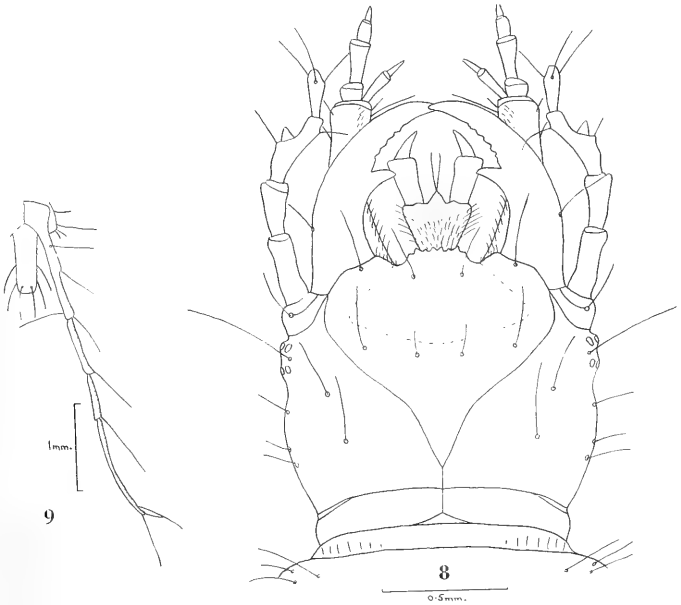
Eudalia macleayi Bates

(Figs 8–9)

Sclerites dark brown ; head light brownish-testaceous ; underside mostly pale, whitish.

Head of average size, quadrate, moderately sclerotized ; frontal piece broadly triangular, not reaching hind-margin ; epicranial suture well marked ; egg-bursters a row of spinules inside the frontal suture on each side ; nasale and adnasalia rather prominent, together forming an irregularly octodentate lobe ; neck strongly marked ; cervical keels present ; ocelli present, six on each side ; mandible rather long, slender, the terebrum serrate ; retinaculum strong,

smooth ; basal penicillus present ; antenna four-segmented, as long as mandible ; vesicle large ; maxilla setose ; inner lobe replaced by a stout seta ; maxillary palp three-segmented ; palpiger large ; labium trapezoidal ; ligula triangular, bisetose ; labial palp slender, two-segmented. *Pronotum* transverse, broader than head ; apex and base of equal width ; sides regularly curved ; legs rather long, spinose, with two subequal terminal claws. *Abdomen* with tergites and pleurites moderately sclerotized, the latter rather prominent ; tergites margined anteriorly but scarcely so at sides ; cerci long and slender, with setiferous nodes, fixed at base but with three articulations ; pygopodium short, tubular.



Figs 8–9. *Eudalia macleayi* Bates, third instar larva (L_3). 8, Head. 9, Right cercus and pygopodium.

Length (including cerci) : L_1, 5·0–5·5 mm. ; L_3, 12–14 mm. Head-width : L_1, 0·47–0·54 mm. ; L_3, 1·2 mm.

Described from two L_1 and eight L_3, Murrumbidgee River, A.C.T., x.60, xi.61 (B. P. Moore), taken amongst gravel at the water's edge, and in company with numerous adults. *Eudalia macleayi* is the only known Odacanthine from this habitat.

The larvae run smoothly to Colliurini (=Odacanthinae), genus *Colliuris* in van Emden's (1942) key and in the absence of material of this northern genus, it is impossible to make out suitable separation characters. However, the evident close agreement in structural characters, between two such geographically isolated genera, serves to support the general system of classification proposed.

Subfamily Pentagonicinae

Scopodes simplex Blackb.

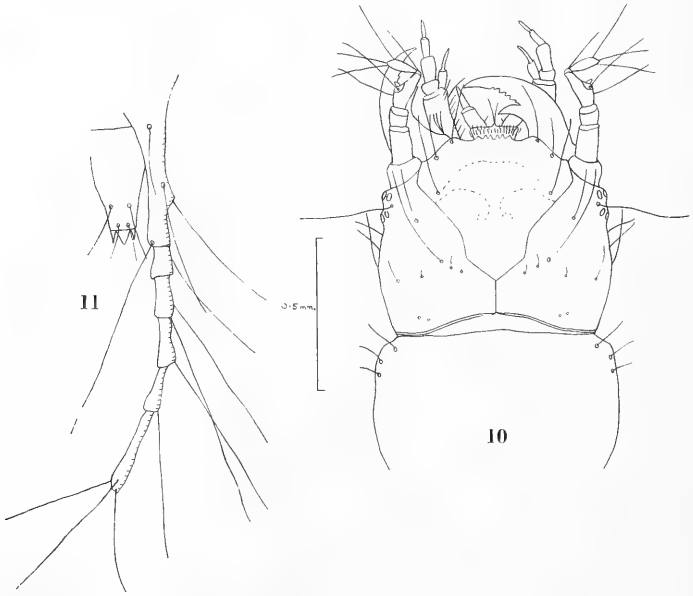
(Figs 10–11)

Upperside mostly dark chestnut-brown ; underside straw-coloured.

Head of average size, quadrate, strongly sclerotized ; frontal piece large, not reaching hind-margin ; epicranial suture distinct ; ventral suture simple ; nasale, with adnasalia, sexdentate ; neck not apparent ; no cervical keels ; ocelli present, six on each side ; mandible rather slender, the terebrum with

fine, rather blunt teeth ; retinaculum strong, smooth ; basal penicillus present ; antenna four-segmented, about as long as mandible ; vesicle well marked ; maxilla weakly setose ; inner lobe replaced by a fine seta ; maxillary palp slender, three-segmented ; palpiger distinct ; labium small, trapezoidal ; labial palp slender, two-segmented ; ligula small, bisetose. *Pronotum* subrectangular, transverse, strongly sclerotized ; legs short, spinose, with two subequal terminal claws. *Abdomen* with tergites strongly sclerotized, unmargined ; cerci slender, moderately long, fixed, but with five articulations and numerous very long setae ; pygopodium short, conical.

Length (including cerci) : L_3, 5·8–6·2 mm. Head-width : L_3, 0·66–0·70 mm.



Figs 10–11. *Scopodes simplex* Blackb., third instar larva (L_3). 10, Fore parts. 11, Right cercus and pygopodium.

Described from eight L_3 and the exuviae from which a pharate adult was bred, Mount Kosciusko (6,000 feet), N.S.W., 26.ii.62, 27.i.65 (B. P. Moore), taken in the open, in company with numerous adults. The bred individual failed to free itself completely from the pupal membranes but its characters are sufficiently developed for positive identification.

This is apparently the first larval Pentagonicine to be recognized and described ; its characters suggest a rather close relationship with the Odacanthinae although, in the adult stage, the two subfamilies are usually placed far apart, largely on account of the state of the anterior coxal cavities (uniperforate in Odacanthinae, biperforate in Pentagonicinae, *teste* Sloane, 1923 ; Jeannel, 1948). However, the value of this character may need to be re-assessed.

According to present data, larvae of the two subfamilies may be separated thus :—

Neck well marked ; cerci with three articulations—ODACANTHINAE (*Eudalia, Odacantha*).
Neck not apparent ; cerci with five articulations—PENTAGONICINAE (*Scopodes*).

Acknowledgement

The author is grateful to Mr. L. E. Koch, Curator of Insects in the Western Australian Museum, for providing material of *Cenogmus castelnaui*, of the Harpalinae—a subfamily where reliably identified larvae are seldom to be obtained.

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SOME LAELAPID MITES OF SYNDACTYLOUS MARSUPIALS

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[Read 30th June 1965]

Synopsis

Australolaelaps greeni, n. sp., is described from the peculiarly Tasmanian *Bettongia cuniculus* (Potoroinae, Macropodidae), and *Haemolaelaps calypso*, n. sp., from *Petaurus breviceps* (Phalangerinae, Phalangeridae), which occurs throughout eastern Australia and New Guinea. The comparative anatomy of the species of *Trichosurolaelaps* and *Australolaelaps* is tabulated, all being parasites of recent syndactylous marsupials in the Australian zoogeographical region. Both genera are recognized as valid. The former comprises two species-groups, one from peramelids and one from phalangerids and *Hypsiprymnodon*, the sole member of an aberrant macropodid subfamily with traces of its scansorial ancestry. The latter comprises parasites of the remaining macropodid subfamilies (Potoroinae and Macropodinae).

Among the mite parasites of the peculiarly Australian syndactylous marsupials is a small group of laelapids with heavily armed coxae and edentate chelicerae. Through the courtesy of Mr. J. H. Calaby, Division of Wildlife Research, C.S.I.R.O., Canberra, I recently received a new species of this, perhaps the most characteristic of all the Australian laelapid groups. As there has been some uncertainty about the natural grouping of these mites, the description of the new species (genus *Australolaelaps*) seems worthwhile. The opportunity is also taken to tabulate the comparative anatomy of all ten species involved, and to suggest a natural classification based both on morphology and ecology.

A new species of the *ulysses* species-group, genus *Haemolaelaps* Berlese, is also described.

AUSTRALOLAELAPS GREENI, n. sp.

(Figs 1–6)

Diagnosis: Within the genus *Australolaelaps*, *A. greeni*, possessing an immense hook on coxa II and elongate peritremes, is much closer morphologically to the new combination *A. validipes* (Domrow)* than to *A. mitchelli* Womersley. This is confirmed by ecological data. *A. greeni* and *A. validipes* parasitize potoroines, while all known hosts of *A. mitchelli* are macropodines. From Table 1 below, the two species from rat-kangaroos may be separated, in both sexes, by the number of setae on the dorsal shield and, in the female, by the number of usurped ventral setae on the genitoventral shield.

* The original assignment of this species to *Echinonyssus* Hirst (1925) was based solely on coxa II, but it now seems that the hook on this segment has evolved separately in the two groups. It should also be pointed out that *Hirstionyssus* da Fonseca (1948) is a synonym of *Echinonyssus*, whose type species (*E. nasutus* Hirst, a common parasite of Malaysian primates—or insectivores according to some authorities—of the genus *Tupaia*, Tupaiidae) is only one step removed (hook on coxa II stronger, vertex extended) from *E. callosciuri* and other species with incipient hooks on coxa II recently described from Eurasian rodents and insectivores (see Willmann, 1952; Delfinado, 1960; Bregetova and Grokhovskaya, 1961; and Wang, 1962). *Echinonyssus* has not crossed Wallace's line to the east—*E. musculi* (Johnston), a cosmopolitan parasite of the introduced house mouse, is, however, now present in Australia (Domrow, 1961, 1963)—and, apart from zoogeographical considerations, may be separated (i) from *Trichosurolaelaps* by the absence of (*a*) an armed tritosternal base, and/or (*b*) usurped ventral setae on the genital shield, and (ii) from *Australolaelaps* by the absence of (*a*) usurped ventrals in the female, and (*b*) modifications to femur and tarsus II in the male.

Types: Holotype female, allotype male, 13 paratype females, four paratype males and two morphotype deutonymphs from the Tasmanian rat-kangaroo, *Bettongia cuniculus* (Ogilby) (Potoroinae, Macropodidae, Marsupialia), Green's Beach, Tasmania, 6.iv.1964, R. H. Green *leg.* The holotype, allotype and one pair of paratypes have been lodged in the Australian National Insect Collection, C.S.I.R.O., Canberra.

Female: Idiosomal length in mounted, only slightly compressed specimens always within circumscribed limits 440–473, av. 454 μ. Dorsal shield textureless, about twice as long as wide, slightly concave vertically and midlaterally, semicircular in posterior quarter. Margin, though somewhat eroded, distinct vertically and laterally, leaving some setae from shield series free in adjacent cuticle. Shield with 33 pairs of setae, those on posterolateral margins somewhat stronger, and one subterminal pair minute; also with few paired pores in anterior half. Dorsal marginal cuticle with six to eight pairs of setae with rather stronger shafts than those on shield. Stigmata dorsolaterally located, with short peritremes showing two parallel series of net-like markings; peritremal shields extending forward from tip of peritremes, with eight-shaped sclerotization evident on focussing more deeply.

Venter. Sternal shield extensive, but textureless, broadly arched and very weakly defined anteriorly; posterior margin not identified. Six sternal setae and four spot-like sternal pores present. Metasternal complex represented only by obsolescent shieldlets and adjacent setae. Genital shield broad, truncate posteriorly, textureless except for two weak areolations (muscle insertions); marginal strip less heavily sclerotized than disc of shield; with two genital setae, two pores and four usurped ventral setae. Genital operculum strongly rayed, encroaching broadly onto sternal area; supported by two weakly sclerotized apodemes between coxae IV. Anal shield large, twice as long as wide, of all body shields the most heavily sclerotized; minutely granulate discally and heavily sclerotized laterally, with weak longitudinal striae; cribrum present. Anus set well forward, with adanal setae slightly behind its centre; postanal seta centrally placed, slightly weaker than adanals. Only merest indications of metapodal shields. Ventral body cuticle with about ten pairs of setae, of which some posterolateral pairs are decidedly stronger than remainder.

Legs. Coxal setal formula 2.1.2.1, anterior seta on coxa II obliterated by hypertrophy of process on anterodorsal margin, which forms immense, ventrally directed hook, with minute striate ridges basally. Formulae for remaining segments: trochanters 6.5.5.5; femora 13.11.6.6; genua 13.11.9.9; tibiae 13.10.8.10; tarsi –.16.16.16 (this parallels Till's 1963 formulae for *Androlaelaps* Berlese, including *Haemolaelaps* Berlese, except for genu IV, which in *A. greeni* has one fewer setae). Coxa I with rather sharp, backwardly directed process on anterobasal angle; I-IV with somewhat blunter excrescence on posterior aspect. Anteroventral margin of coxa IV spinulose. Femora I and II with basally directed setigerous spur dorsally; femur IV with somewhat similar, but asetose, elevation. All tarsi rather irregular in outline, especially on posterior face. All leg setae slenderly tapering, two or three on posterior aspect of tarsi II and III being somewhat expanded and hyaline basally. Tarsus I with dorsodistal sensory zone, including one distinctly bent rod. Pulvilli I with shorter stalk and weaker claws than II-IV.

Gnathosomal and inner posterior hypostomal setae subequal, much stronger than outer posterior and anterior hypostomals. Labial cornicles ill-defined. Deutosternum with about five denticulations mostly in double file. Tritosternum with very weakly barbed base and laciniae. Palpi with five free segments; setal formula (trochanter to genu) 2.4.6; tibia probably with 11 setae, including two dorsodistal rods; tarsus with bifurcate claw and several setae, one of which is quite long. Chelicerae with basal segment short, and distal segment slenderly tapering; digits elongate, weak and edentate; corona absent.

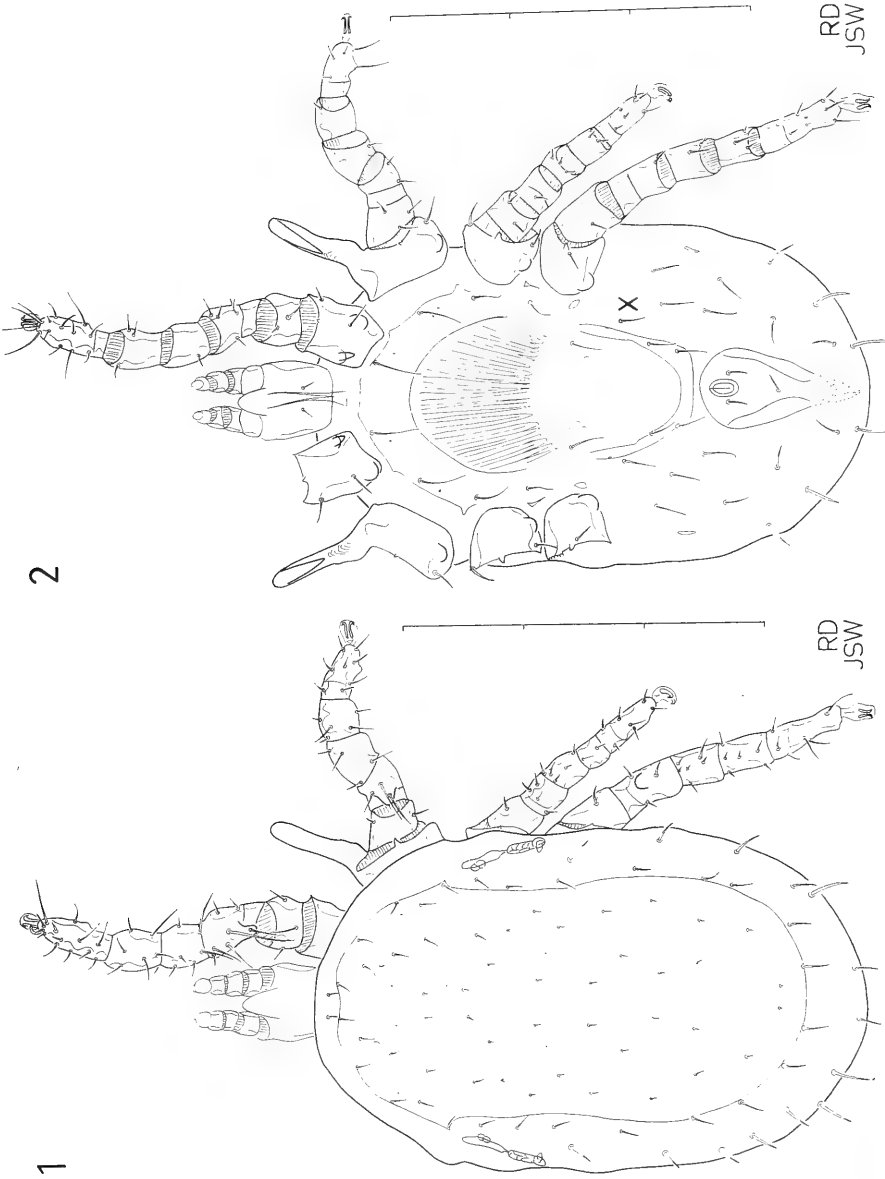


Fig. 1. *Australolaelaps greeni*, n. sp.—Dorsum ♀. (Each division on the scales equals 100μ.)
Fig. 2. *Australolaelaps greeni*, n. sp.—Venter ♀.

Male: Idiosomal length more variable than in female; three specimens 418–429 and two 341 and 352 μ, all carefully mounted. Dorsal shield more evenly ovate than in female, slightly wider at humeral level; with all setae (33 pairs) set on shield and rather stronger than in female. Remainder of dorsum essentially as in female.

Venter. Sternogenitoventral shield produced anteriorly between coxae I, widest between coxae II and III and truncate behind coxae IV. Sternometasternal area with eight setae and four pores as in female. Genitoventral area with indications of more weakly sclerotized margins, two genital setae and six usurped ventral setae (i.e., pair of ventrals marked " X " near genitoventral shield of female actually taken onto shield in male). Genital aperture well in front of SI; internal duct elongate, leading back to between SII and III. Anal shield discrete, as in female. Ventral body cuticle with only six or seven pairs of subequal setae.

Legs larger in respect to idiosoma than in female. Coxal setal formula 2.2.2.1, coxa II with well developed pointed process on anterodorsal margin, but anterior seta normally developed. Coxa I with weak process and II and III with slight excrescence on posterior aspect. Coxa IV spinulose on anteroventral margin. Setigerous spurs on femora I and II incipient and femur IV unarmed above; femur II with strongly modified, flask-like seta on posteroventral aspect. Three distal segments of legs II each with one short seta posteroventrally with base strongly inflated. Tarsus II produced into strong spur ventrodistally, causing pulvillus to appear subterminal. Leg setation otherwise as in female, but somewhat stronger. Ambulacra as in female.

Gnathosoma essentially as in female, but chelicerae with movable digit coalesced with seemingly tubular spermatophore-carrier.

Deutonymph: Neither specimen is badly compressed. The smaller (idiosoma 412μ long) is, to judge from coxa II, prefemale; the larger (440μ) contains male so well developed that double setation hinders examination. Dorsally, including peritremes, as in male, with same 33 pairs of shield setae, although shield is even more reduced, at least in anterior half (see dotted line), than in female (seta marked " Y " is also off shield in premale).

Intercoxal shield elongate, with usual five pairs of setae. Anal shield as in adult.

Armature of coxae as in male, except for coxa II of prefemale, which bears both incipient hook and weak process on anterodorsal margin, but no anterior seta. Legs, apart from weakly developed setigerous spurs on femora I and II, unarmed and with setal formulae, including genu IV, as in adult. Sensory zone and ambulacra as in adult, but pulvilli I less sessile.

Gnathosoma, including chelicerae, as in female.

Notes: The syndactylous marsupials are confined entirely to the Australian zoogeographical region. They are absent from New Zealand (apart from the introduced *Trichosurus vulpecula*), but one genus, *Phalanger*, extends as far west as Sulawesi (Celebes). None have crossed Wallace's Line to the west (Darlington, 1957). Three distinct superfamilies are involved, the Dasyuroidea, Perameloidea and Phalangeroidea, but their phylogenetic relationships remain obscure (Simpson, 1945).

Two major dichotomies are in common use in marsupial classification. Using the condition of the incisor teeth, they may be divided into Polyprotodontia and Diprotodontia; using the condition of the second and third toes on the hind foot, they may be divided into the Didactyla and Syndactyla. However, as Simpson (1945) points out, " as might be expected of classifications based essentially on single characters, these are contradictory and unsatisfactory." Using the former, and confining ourselves to the Australian zoogeographical region, the Dasyuroidea and Perameloidea are polyprotodont,

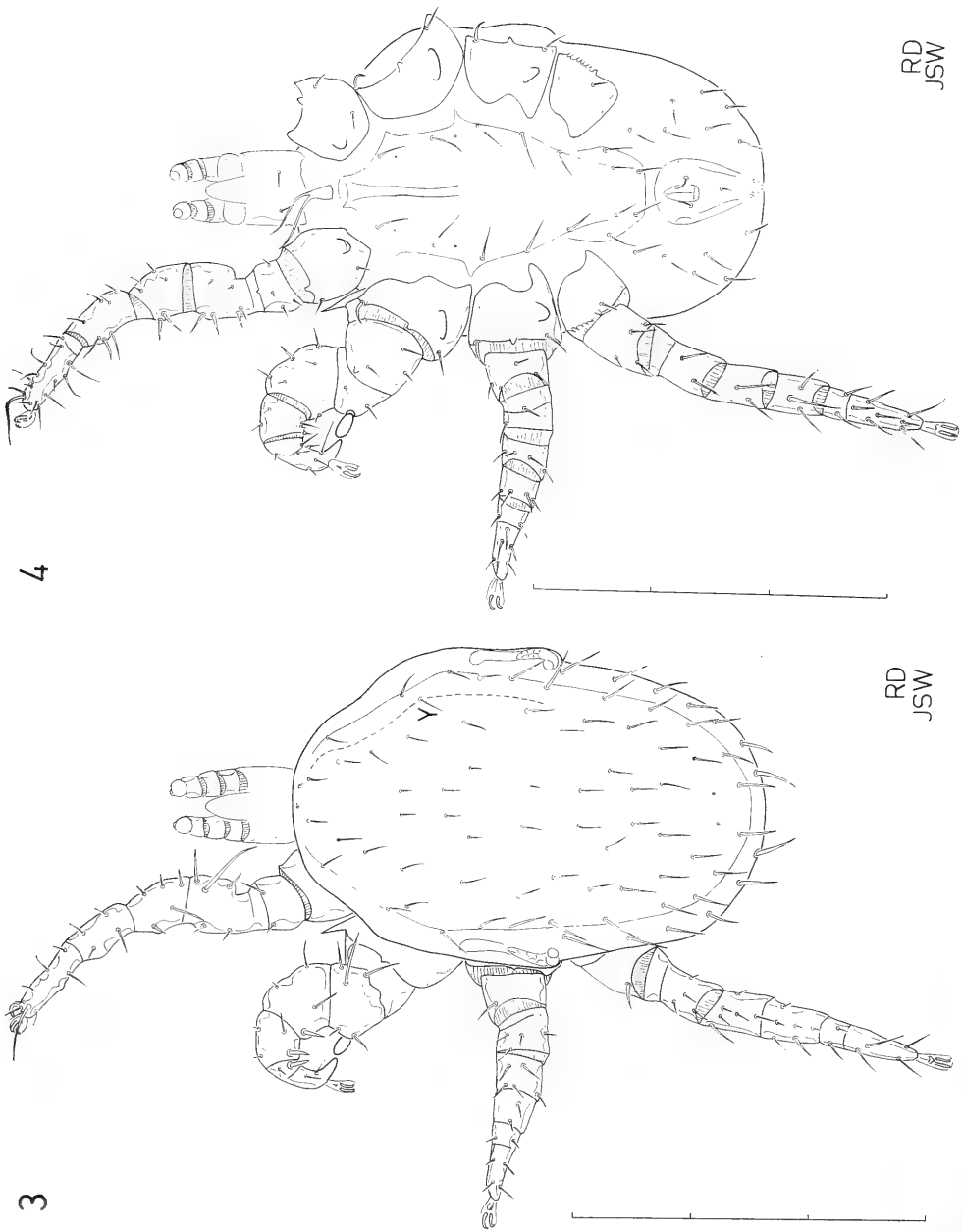


Fig. 3. *Australolaelaps greeni*, n. sp.—Dorsum ♂.
Fig. 4. *Australolaelaps greeni*, n. sp.—Venter ♂.

and the Phalangeroidea diprotodont; using the latter, the Dasyuroidea are didactylous, and the Perameloidea and Phalangeroidea syndactylous.

The problem is, therefore, should the perameloids, comprising the one (and only) syndactylous polyprotodont family Peramelidae, be associated with the dasyuroids on dentition, ignoring toe structure, or, vice versa, with the phalangeroids? The latter choice would seem to be indicated by the host-parasite relationships within the *emanuelae* species-group, genus *Trichosurolaelaps*, discussed below.*

A somewhat similar uncertainty surrounds the classification of the Phalangeroidea, which are all syndactylous diprotodonts, comprising the three families Phalangeridae, Macropodidae and the aberrant Phascolomidae (as only one mesostigmatic mite has been described from wombats, *Raillietia australis* Domrow (1961), this last family may be excluded from further discussion). The anatomy and phylogeny of the macropodids have been reviewed in detail by Tate (1948). They are usually considered to be descendants of remote ancestors of modern phalangerids, but it is difficult to indicate any one division of the latter that could have given rise to any of the macropodid subfamilies, all of which possess varied combinations of primitive and specialized characters. Excluding two extinct groups, the macropodids may be treated in the order Hypsiprymnodontinae, Potoroinae and Macropodinae.

The aberrant *Hypsiprymnodon*, its feet "already profoundly modified for leaping" and therefore macropodid in *habitus*, is, in fact, little removed in certain characters from the phalangerids—it "alone of all recent macropodid genera retains the big toe", and friction ridges, typical of scansorial animals, are still present on its feet (Tate, 1948). It is not unexpected, therefore, that the mite species peculiar to it is inseparable, even at species-group level, from the parasites of phalangerids, and forms, with them, the *crassipes* species-group, genus *Trichosurolaelaps*. The parasites of the remaining, and more typical macropodid subfamilies, confirm the generally sharp division between the phalangerids and macropodids—they form a distinct genus, *Australolaelaps*.

I am most grateful to Mr. Calaby for reviewing the preceding paragraphs of these notes, and for pointing out to me Ride's latest classification (1964) of the Marsupialia, which does not, however, affect my argument.

The species of mites may now themselves be reviewed. Four have been described from bandicoots (Peramelidae). These form a compact group, and all were originally assigned to *Trichosurolaelaps* Womersley (1956). The first was *T. emanuelae* Domrow (1958) from *Echymipera kalubu* in New Guinea, which was recognized on first examination as being a little atypical and was accordingly keyed out first, leaving the two species from phalangerids to a later couplet. It has since been recorded from N.G. bandicoots, including the type host on many occasions, by Domrow (1961) and Mitchell and Strandtmann (1964). The latter authors also described a further three species of

* To consider laelapid mites outside the scope of this paper, additional support for this choice is found in the host relationships of the *marsupialis* species-group, genus *Haemolaelaps* (see Womersley, 1958; Domrow, 1961, 1963). Of the four species whose hosts are known, two parasitize rat-kangaroos (Potoroinae, Phalangeroidea) and two bandicoots (Perameloidea).

I hasten, however, to add that there is also an argument for the former choice. Of the six species of *Mesolaelaps* Hirst, four are confined to peramelids and one is host-specific for dasyurids (the sixth includes both peramelids and dasyurids, but apparently not phalangeroids, amongst its numerous hosts). See Domrow (1958, 1962, 1963) and Wilson and Strandtmann (1963).

The wheel comes full circle when one considers the *ulysses* species-group, genus *Haemolaelaps* (see Domrow, 1964). Of the four species, one is confined to dasyurids, while the remaining three (including the new species described below from *Petaurus breviceps*) are parasites of phalangerids!

With many mite species undoubtedly still to be discovered when the rarer Australian mammals are examined for ectoparasites, this is clearly an approach which may prove profitable in future studies of marsupial phylogeny.

TABLE 1

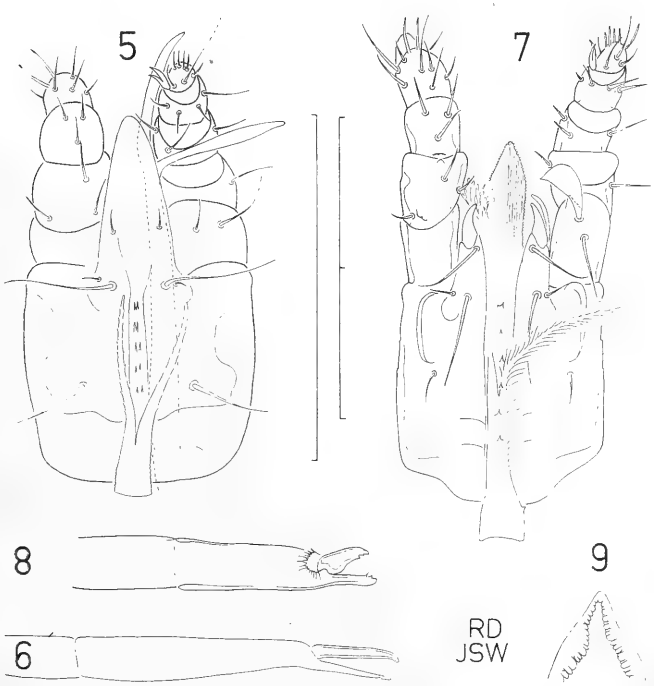
Comparative anatomy of species of Trichosurolaelaps *and* Australolaelaps

	Taxonomic character	Genus *Trichosurolaelaps*							Genus *Australolaelaps*		
		emanuelae species-group				*crassipes* species-group					
		emanuelae	*domrowi*	*whartoni*	*bakeri*	*crassipes*	*striata*	*harrisoni*	*validipes*	*greeni*	*mitchelli*
Dorsum	Setal pairs on shield[1] ♀/♂ ..	38/36	38/38	38/36	36/36	33/33	31/31	32/32	30/32	33/33	35/33
	Anterolateral shield setae sinuous ♂	+	+	+	(+)	—	—	—	—	—	—
	Gland under shield ♀	+	+	—	—	—	—	—	—	—	—
	Shield longitudinally striate ♂	—	—	—	—	+	+	+	—	—	—
	Posterolateral shield setae bladed ♂	—	—	—	—	+	+	+	—	—	—
	Peritremes[2] ♀/♂	L/L	L/L	L/L	L/L	L/S	L/S	L/S	S/S	S/S	O/O
Venter[3]	Usurped ventral setae ♀/♂ ..	2/4	2/4	2/4[8]	2/4	0/3	0/3	0/3	1/3	2/3	3/?3
	Holoventral shield[4] ♂	E	E	E	E	N	N	N	A	A	N
	Anal shield[5] ♀	B	B	B	B	L	N	N	L	L	L
	Metapodal shields[6] ♀	+	+	+	+	—	—	—	—	—	—
	Tritosternal spines[7] ♀/♂ ..	1/–	1/–	1/–	1/–	2/2	2/2	2/2	0/0	0/0	0/0
Leg II[9]	Anterodorsal coxal process ♀/♂	+/+	+/+	+/+	+/+	+/+	+/+	+/+	—/+	—/+	+/+
	Anterior coxal seta ♀/♂ ..	+/+	+/+	+/+	+/+	+/+	+/+	+/+	—/+	—/+	—/—
	Coxal hook ♀/♂	—/—	—/—	—/—	—/—	—/—	—/—	—/—	+/—	+/—	+/+[11]
	Enlarged femoral seta ♂ ..	—	—	—	—	—	—	—	+	+	+
	Distal tarsal spur ♂	—	—	—	—	—	—	—	+	+	+
Host (Marsupialia Syndactyla)		Pera-melidae	Pera-melidae	Pera-melidae	Pera-melidae	Phalang-eridae	Phalang-eridae[10]	Hypsiprymno-dontinae	Poto-roinae	Poto-roinae	Macro-podinae

1. The dorsal shield of the females, particularly in *Australolaelaps*, tends to be ill-defined, the marginal setae seemingly not borne on the shield at all. In freshly mounted material, however, these setae are seen to be set in the weakly sclerotized and textureless marginal strip of the shield and not in the adjacent striate cuticle. This effect is figured for *A. mitchelli* by Womersley (1956), and ten pairs of setae shown near the edge of the dorsal shield of *A. validipes* by Domrow (1955) actually belong to the shield series (the minute subterminal pair were also omitted in the original figure of the male of this species).
2. L = Long, S = Short, and O = Obsolescent.
3. The sternal shield is large and well-defined in all species of *Trichosurolaelaps*, but this shield, while extensive, is weakly defined, sometimes extremely so, in *Australolaelaps*.
4. E = Expanded and N = Not expanded behind coxae IV ; A = Anal shield discrete. I am grateful to the Director, S.A. Museum, Adelaide, for the loan of the allotype ♂ of *A. mitchelli*.
5. B = of Broad, L = of Long, and N = of Normal proportions.
6. Always distinct in the *emanuelae* species-group, and represented, at the most, by the merest indications in the other species.
7. Indications of a spine are evident in the males of one or two species of the *emanuelae* species-group.
8. Mitchell and Strandtmann (1964) figure five pairs, but the posteriormost pair is actually off the shield in the paratype in this Institute, confirming their statement in the text that four pairs are present.
9. Correlated differences also occur on other leg segments. Duplex setae are occasionally present, in either sex, in the *emanuelae* species-group. Pulvilli I are reduced and sessile in the males of the *crassipes* species-group. Setigerous spurs are present on femora I and II of the females, and, to a lesser extent, the males of *Australolaelaps* (indications of these may also be present in the *crassipes* species-group, but they are quite absent in the *emanuelae* species-group). A slight dorsal prominence is present on the dorsal aspect of femur IV in the females of both species from potoroines.
10. At least two of the three hosts involved also harbour *Haemolaelaps ulysses* Domrow (see Domrow, 1961, 1964).
11. In view of the extreme reduction of the peritremes and the more advanced host of this species, it is possibly better to consider the coxal hook as regressed rather than incipient. It is present in both sexes to the extent that, while it has eliminated the anterior seta, it does not hinder the development of the anterodorsal process.

Trichosurolaelaps from New Guinea as follows: *T. domrowi* and *T. whartoni*, both from *Peroryctes raffrayanus* (I am grateful to Dr. N. Wilson, B. P. Bishop Museum, Honolulu, for confirming that the host of the former species, originally listed as from a "marsupial skunk", was, in fact, a peramelid), and *T. bakeri* from a "bandicoot". No related species are yet known from the Australian mainland peramelid fauna which, apart from a single specimen of *Echymipera* (Tate, 1952), is not known to include the recorded host genera of *Trichosurolaelaps*.

The two closely related species from phalangerids mentioned in the previous paragraph are *T. crassipes* Womersley (1956), the type species, from *Trichosurus vulpecula* (Phalangerinae) in eastern Australia and also in New Zealand, where this possum has been introduced (Domrow, 1961; Mitchell and Strandtmann,



Figs 5–6. *Australolaelaps greeni*, n. sp.—5, Gnathosoma ♀ (ventral, with left palp dorsal); 6, Chelicera ♂.
Figs 7–9. *Haemolaelaps calypso*, n. sp.—7, Gnathosoma ♀ (ventral, with left palp dorsal); 8, Chelicera ♀; 9, Tectum ♀.

1964); and *T. striata* Domrow (1958) which was described from *Pseudocheirus laniginosus* (Phascolarctinae) in Queensland and subsequently recorded (Domrow, 1961, 1964) from *P. convolutor*, a species confined to Tasmania, and another phascolarctine, *Schoinobates volans*, in eastern Australia. Mitchell and Strandtmann (1964) note the occurrence of a species of *Trichosurolaelaps* on *Petaurus breviceps* (Phalangerinae) in New Guinea, but do not describe it for lack of material (this is *not* the species of *Haemolaelaps* described below).

Four species have been taken from macropodids. *Trichosurolaelaps harrisoni* Domrow (1961, 1962) (the use of the specific name *quadratus* in the second last line of p. 80 in the original description is a slip for which I apologize; it should read *harrisoni*, the name upon which I finally decided), was described from the musk rat-kangaroo, *Hypsiprymnodon moschatus*, which is restricted to north Queensland. As noted above, it clearly belongs with the parasites of phalangerids.

Two species are known from potoroine hosts (rat-kangaroos). *Australolaelaps validipes* was described from *Potorous tridactylus* in Queensland by Domrow (1955) who subsequently (1958, 1963) extended its range, on the same host, to New South Wales and Tasmania. A new species, extremely closely related to *A. validipes*, is described above from the peculiarly Tasmanian *Bettongia cuniculus*.

Womersley (1956) described *Australolaelaps mitchelli* from a small wallaby (*Protemnodon eugenii*, Macropodinae) in South Australia, and this species has since been recorded in Queensland from the larger *P. dorsalis*, and also from a pademelon, *Thylogale stigmatica*, another macropodine (Domrow, 1961, 1962). In addition to sharing several other characters, particularly on leg II of the male, *A. mitchelli* also shows the gross coxal modifications of the two parasites of potoroines in intermediate form. The three species are, I believe, congeneric.

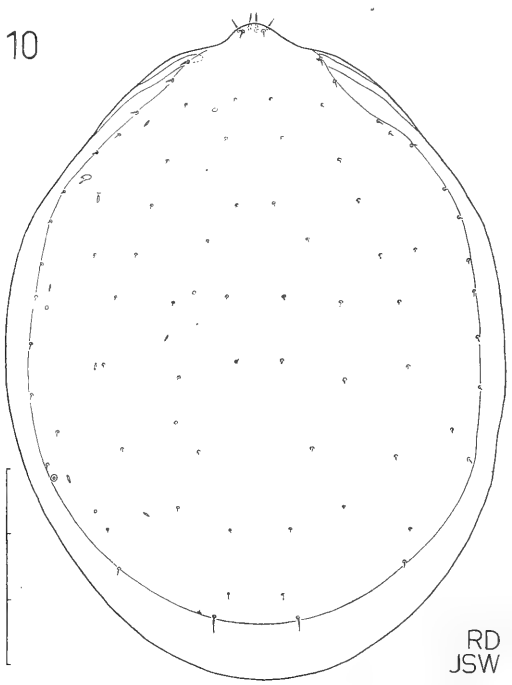


Fig. 10. *Haemolaelaps calypso*, n. sp.—Dorsum ♀.

The comparative external anatomy of these mites is set out in Table 1, which gives the characters of the dorsum, venter and leg II. The vertical division of the table into three sections is that indicated by morphological characters, and it will quickly be seen that this division is nicely correlated with host preferences.

I therefore accept both *Trichosurolaelaps* (with two species-groups, one from peramelids and one from phalangerids and *Hypsiprymnodon*, with *T. emanuelae* and *T. crassipes*, respectively, as *chefs de file*), and *Australolaelaps* (comprising the parasites of the remaining two macropodine subfamilies), as valid genera, distinct, as discussed above, from *Echinonyssus* (=*Hirstionyssus*).

Incidentally, this solution, natural on both morphological and ecological grounds, is also the one that does least violence—only one new combination is necessary—to the presently accepted classification, not that this is, in itself, a valid argument for the system I accept.

HAEMOLAELAPS CALYPSO, n. sp.

(Figs 7–11)

Diagnosis: In my key (1964) to the *ulysses* species-group, genus *Haemolaelaps*, *H. calypso*, a large species from a phalangerid showing the anterior seta on coxae II and III expanded and hyaline, and the anal shield only slightly wider than long, is nearest *H. ulysses* Domrow (1961). The two species are, however, abundantly distinct, *H. calypso* showing decidedly shorter setae on the dorsal shield, decidedly longer sternal and genital setae, a narrower genito-ventral shield and the differences in leg armature detailed in the description below.

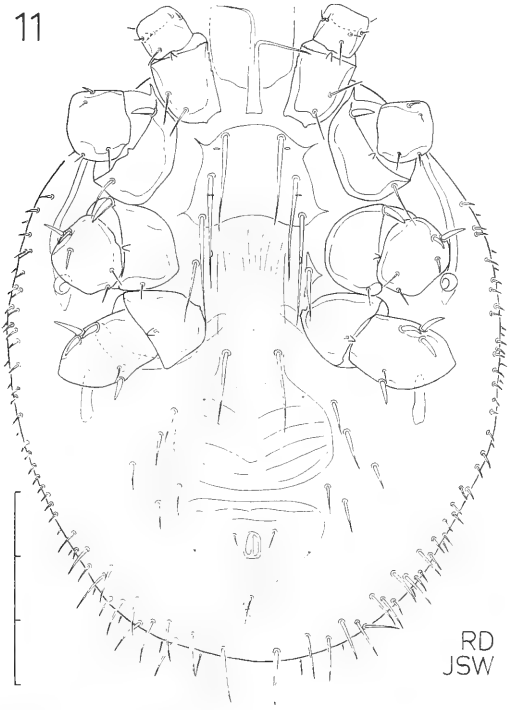


Fig. 11. *Haemolaelaps calypso*, n. sp.—Venter ♀.

Types: Holotype female and six paratype females from the sugar glider, *Petaurus breviceps* Waterhouse (Phalangerinae, Phalangeridae, Marsupialia), Bearii, north of Strathmerton, Vic., 20.vii.1964, R. M. Warneke *leg.* The holotype and one paratype have been lodged in the Australian National Insect Collection.

Female: Idiosoma a rounded oval, length within circumscribed limits 968–1012, av. 990 μ in six specimens, seventh slightly smaller, 935μ. Dorsum, apart from narrow marginal strip, entirely covered by single, rounded dorsal shield. Shield textureless except for few weak humeral striae ; bearing system of paired pores and 39 pairs of setae, which are extremely weak, except those at vertex, humeri and extreme posterior.

Sternal shield slightly wider than long, textureless. Anterior margin convex, posterior margin concave. Sternal setae strong, reaching well beyond insertions of subsequent pair. Two pairs of small transverse pores on shield. Metasternal shields weak, each bearing metasternal seta half as strong as sternals ; flanked internally by longitudinal pore. Genital shield only very slightly wider than anal shield ; operculum rayed ; traces of muscle insertions

present between two strong genital setae ; disc with chevron-like striae and two pores. Anal shield slightly wider than long, with one or two irregular striae anteriorly and two pores laterally. Anus centrally placed, with small adanal setae set near its anterior margin ; postanal seta slightly stronger, set immediately in front of distinct cribrum. Metapodal shields distinct, longitudinal and textureless. Peritremes extending forward almost to level of anterior margin of coxae I ; peritremal shields small, not extended posteriorly to fuse with exopodal shields IV. Ventral cuticle with five pairs of setae flanking shields ; margins with about 52 pairs of stiff setae.

Leg setation as follows : coxae 2.2.2.1 ; trochanters 6.5.5.5 ; femora 13.11.6.6 ; genua 13.11.9.9 ; tibiae 13.10.8.10 ; tarsi –.16.16.16 (excluding two terminal filaments). This compares exactly with the typical formulae given by Till (1963) for *Androlaelaps* Berlese *s.l.* (including *Haemolaelaps*), except that one seta less is present on genu IV (on checking *all* the species of the complex, the same is found to be true of *H. ulysses*, both in the holotype and an extensive series from *Schoinobates volans*, while *H. penelope* and *H. telemachus* are typical). Anterior seta on coxae II and III expanded and hyaline ; seta on coxa IV minute. Trochanters III and IV with three and four expanded hyaline setae respectively (against none in *H. ulysses*). Apically bifurcate setae present on femora only, formula 2.2.1.1. Remaining leg setation undistinguished. Ambulacra I only half as strong as II-IV, all with two claws.

Gnathosomal and outer posterior hypostomal setae subequal, considerably weaker than anterior and inner posterior hypostomals. Gnathobase with longitudinal hyaline flange anterolaterally ; deutosternum with about five denticles, mostly in single file. Tritosternum with laciniae strongly bipectinate. Labial cornicles quite well developed ; hypostomal processes, salivary stylets and epipharynx as figured. Tectum triangular, with marginal strip smooth and diaphanous, merging *via* dendritic line into denser central area as in other species of the complex. Chelicerae with movable digit bidentate ; fixed digit unidentate, with small pilus dentilis. Corona present. Palpal setal formula as detailed by Till (1963) for *Androlaelaps*, i.e. 2.5.6.14 (trochanter to tibia, including two dorsodistal tibial rods). One trochanteral seta hyaline and strongly foliate, obscuring small triangular outgrowth on ventrodistal margin of segment. Tarsus with few setae and rods in addition to bifid claw.

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Corrigendum

These Proceedings, vol. 89, part 1, page 161, line 11, *for* first " IV " *read* " III ".

COMPARATIVE STUDIES ON THE EXTERNAL ACOUSTIC MEATUS

I. THE MORPHOLOGY OF THE EXTERNAL EAR OF THE ECHIDNA (TACHYGLOSSUS ACULEATUS)

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(Plates iv-v)

[Read 30th June, 1965]

Synopsis

The study of the external ear of *Tachyglossus aculeatus* revealed that echidna has an intramuscular pinna which merges with the external acoustic meatus. The latter, a completely extracranial structure, consists of four chambers, each marked off by a sharp bend in the meatus. The morphological and functional significance of this arrangement is discussed.

INTRODUCTION

The marked specialization of the external ear of echidna (*Tachyglossus aculeatus*), combined with the conspicuous taxonomical position of the monotremes, makes the study of the acoustic passages of the echidna interesting, useful, and convenient as a starting point for broader investigations on the comparative histology of the external acoustic meatus.

The comparative histology of the external acoustic meatus is at present a virgin field. Concentration on the ear of the human and the dog prompted by clinical interests left us without morphological perspectives and without the basis for assessment of adaptations which can only be understood through comparative investigations. With this in mind, a variety of species were studied. The present paper is the first of a series of reports on the external acoustic meatus.

MATERIALS AND METHODS

The external acoustic passages of echidna were investigated by means of anatomical dissections and by study of unsaturated polyester resin casts.

THE MORPHOLOGY OF THE PINNA

The external opening of the acoustic meatus of the echidna is hidden completely by surrounding spines and hairs. Topographically, it is located close to the ventral margin of the region of the coat which bears spines and the distance between the anterior margin of hair and the opening of the external ear equals roughly the distance between the anterior end of the maxilla and the outer margins of the hair (Plate iv, fig. 1). However, the removal of skin makes the large opening leading into the spacious cavity visible (Plate iv, fig. 2). More complete dissection reveals that the cavity is in fact a pinna embedded in the skin and musculature. The pinna is orientated dorso-ventrally with its cartilaginous margin, bending medially to form a roughly triangular hiatus covered with the relatively short and dense hairs (Plate v, fig. 5). In the ventral portion of the pinna the lateral margins of the cartilage merge,

forming a large goblet-like structure. The median surface of the pinna is smooth and flat (Plate v, fig. 6). The pinneal cavity passes at once but at a right-angle into the external acoustic meatus.

The External Acoustic Meatus

The diameter of the external acoustic meatus is about a quarter of that of the pinneal cavity. The meatus itself is tortuous: at first (in the parapinneal portion) it runs anteriorly, then medially and finally turns dorsally to reach the base of the skull (Plate iv, fig. 4, and Plate v, fig. 6). The meatus is narrowest at its cranial end and widest in the proximity of the pinna (Plate v, fig. 7). On the internal surface of its wall the distinct crista is present (Plate iv, fig. 6). The cranial opening of the meatus is elongated (Plate v, fig. 8). The sharp angles between the various portions of the external acoustic passages divide the extracranial acoustic meatus and pinna into four (4) distinct chambers, the most external being formed by the pinna; this is elongated and contains hairs. The second chamber, directed anteriorly, is relatively spacious. The third and fourth are smaller in diameter and develop the internal cartilaginous crista. The wall of the meatus consists of cartilaginous "ribs" connected by a membrane.

Discussion

The external ears of all mammals and birds have the same general functions. To these belong: (1) expression; (2) temperature regulation; (3) protection of the middle and inner ear; (4) the isolation and localization of sound; and (5) the transmission of sound. These functions are modified from species to species. Nevertheless, they form a convenient reference frame for discussion and the assessment of adaptations and modifications within the particular auditory passages. Therefore, the conditions described above will be discussed in relation to these functions.

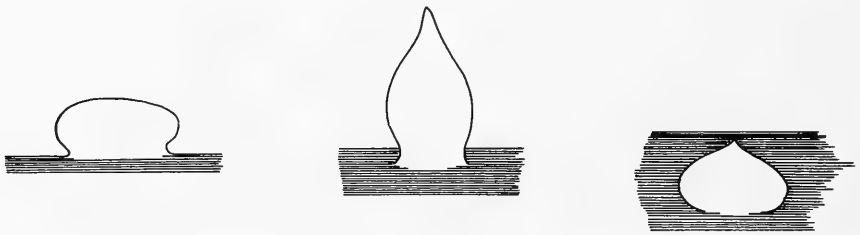
In most mammals the function of expression belongs wholly to the pinna, the muscular plate of the *platysma myoides* and to the facial nerve. The expressive ability of the pinna is governed by its size and the degree of its mobility. Animals of terrestrial habitat such as the horse, ox, and dog have large and freely mobile pinnae. Aquatic animals and those with subterranean or burrowing habits have a pinna of considerably reduced size, while primates of arboreal habit or descent have rather immobile ears. The musculature of the external ear develops from the *platysma myoides*, the cutaneous muscle of the second branchial arch, and the degree of mobility of adult external ears depends on the final connection of the pinna with this muscle. The human ear has lost most of its muscular connections, while the mobile and expressive ear of most terrestrial animals is connected with the platysma by special muscular strands—the auricular muscles. These muscles as well as the platysma are supplied by fibres from the facial nerve so that the expressive movements of the ears are stimulated by fibres from the same area of the central nervous system as those connected with the facial expression in man.

According to McKay (1894), in echidna the *panniculus carnosus* consists of three layers, and is innervated only by the cervical nerves, the auricular region being supplied by the second cervical nerve. However, Westling (1889) describes innervation of subcutaneous cervical muscles by both the facial and cervical nerves. Also Edgeworth (1935) pictures (after Schulman) the platysma in echidna together with *M. sphincter colli superficialis* in the area of the external acoustic meatus.

The intramuscular position of the pinna in echidna changed also the character of its movements: pinna is not moved by the muscle; instead, it is moved with the muscles. It is in fact a muscular cartilaginous insertion (*insertio cartilaginea*) comparable in a sense with the tendinous insertions in the

rectus system (Tucker, 1955). This insertion is large and isolated. The existence of different relations of pinna to the musculature (the echidna type being an extreme case) enables us to distinguish between the three types of pinna in mammals.

In relation to the platysma the mammalian pinna can acquire an *extra-platysmal* position, with no, or only negligible, connections with this muscle—e.g. *Homo* ; or a *supra-platysmal* position with only the deep portion of pinna connected with platysma and supplied by strong auricular muscles, e.g. Bovidae, Equidae. In echidna, we have the case of an intramuscular pinna connected with *panniculus carnosus*. The different types of relationship between the pinna and the musculature in mammals are shown diagramatically in Text-fig. 1. There is probably a relative lack of expression in echidna due to the factors mentioned above.



Text-fig. 1. Diagram showing the different types of relation between pinna and the muscles connected with it ; on the left side, extraplatysmal pinna, in the middle supraplatysmal pinna, and on the right side intramuscular pinna.

The attempts to explain the conditions in the echidna must develop into discussion of :

(*a*) Musculo-pinneal relations, such as invasion of pinna by the *panniculus carnosus* in echidna ; or of the acceptance of the above described relations as the primary condition and proceeding to the subsequent separation of pinna by the recession and differentiation of the cutaneous musculature in other mammals.

(*b*) Relating the intramuscular pinna to the way of life of *Tachyglossus*, especially to its defence technique which, at the same time, removes all surface protrusions and develops the powerful musculature for the erection of spines. Lack of sufficient differentiation in cortex, cranial nerves, platysma, and the connections between them cause a basic lack of suitable conditions for facial expression.

The pinna itself is characterized by :

a. The robustness of its cartilage ; *b*. Lack of morphological differentiation of its cartilage and of differentiation into separate cartilages ; *c*. The absence of any structure which can cause friction during the shift due to muscular contraction ; *d*. The fusion of the ventral margins of the cartilage resulting in the formation of the flask-like pinneal cavity ; and *e*. The presence of hair on the internal surface of the pinna.

The robustness of the cartilage and the thickness of its margins are probably related to the strong muscular insertions onto it ; lack of differentiation of separate cartilages may be related to the absence of independent and complicated movements. The absence of morphological differentiation of the cartilage itself is probably a result of the lack of the sound-dispersing function in the ear of echidna.

The smoothness of the median surface of the pinna and its flatness seem, however, to form a more general and therefore a more interesting feature. The median surface of the pinna is smooth in all types of ears, even in the extra- and supra-platysmal ears which can reduce friction by the lateral bending of

the pinna. It seems, therefore, that this smoothness of the median surface is phylogenetically a stable morphological feature, independent of the local forces and stresses.

The tubular shape of the pinna stresses again conditions indicated by its embedding in the musculature, and by the presence of hairs, that the external ear in echidna is not involved in the temperature regulative mechanism. The presence of the arterio-venous anastomoses in the echidna ear is nevertheless possible, and needs further investigation.

The most developed specialization in the echidna ear seems to be its protective adaptations; external hairs and spines guard the external opening of the meatus. All of these—hairs, spines, pinna and meatus—are connected with the cutaneous musculature. The entrance of foreign bodies can be next prevented by the dense hairs on the internal surface of the pinna. The narrowness and angularity of the meatus form another conspicuous protective mechanism: it can protect against the entrance of foreign bodies as well as against high intensity of sound.

In mammals the most common protective device against the high intensity of sound is the increase in the mobility of the pinna so that it can be turned away from the direction of intense sounds. Primates can achieve a similar effect by covering their ears with their hands, but aquatic mammals develop an especially long and angular meatus which serves the same purpose. In echidna, the external acoustic meatus is very long and very angular. It is also essentially an extracranial structure. Because of this extracranial position, passive mobility and frequent changes of plane, the mutual transmission of sound from bone to the meatus is negligible. The intramuscular pinna of the echidna has a poor ability to divert sounds into the meatus. This disability may be partially compensated by the diminishing diameter of each subsequent chamber. In a smaller chamber the same intensity of sound gives a stronger effect or, conversely, a fraction of the number of sound waves passed to a smaller chamber will give the same acoustic effect.

The functional significance of the crista (Plate v, fig. 6) could not be assessed adequately on the material at my disposal.

The external ear of echidna was pictured without description by Westling (1889) and mentioned by Winge (1941). It was also studied in more detail by Ruge (1898) who considered pinna in echidna to be a derivative of the hyoid bone. He found a ramification of the hyoid bone merging with the tympanic cartilaginous ring, which is closely connected with the external acoustic meatus, the latter merging with the pinna. However, the same author found the above connections less pronounced in *Ornithorhynchus*, and intended to prove his point through a series of comparative embryological investigations which, however, to my knowledge were never published. Both the descriptions of Ruge (1898) and Winge (1941) differ from our findings. According to Ruge (1898) the oval pinna is perforated by the canal, and has a transverse process. Winge (1941) did not account for the geniculate structure of the external acoustic meatus. In our material, the pinna was distinctly elongated, no canal or transverse process was observed, and the external acoustic meatus exhibited sharp bendings. The partially cartilaginous and partially membranous structure of the external acoustic meatus in echidna is noted by both previous authors, but not discussed, and its presence was confirmed in the present investigation.

Acknowledgements

I wish to express thanks to Mr. E. Hollywood for the photographs, and to Mrs. L. Endean for help with preparation of the manuscript. Thanks are also due to the Rural Credits Development Fund for financial assistance with the work.

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EXPLANATION OF PLATES IV–V

Plate iv

Fig. 1. *Tachyglossus aculeatus*. The topography of the ear. A notch indicates the position of the opening.
Fig. 2. *Tachyglossus aculeatus*. External ear, after removal of the skin.
Fig. 3. *Tachyglossus aculeatus*. The median view of the pinna, in relation to the musculature.
Fig. 4. *Tachyglossus aculeatus*. The resin cast of the external acoustic meatus, showing its bending, and relation to the pinna.

Plate v

Fig. 5. *Tachyglossus aculeatus*. Pinna and external acoustic meatus dissected away from the muscles (lateral view).
Fig. 6. *Tachyglossus aculeatus*. Morphology of the pinna and external acoustic meatus. Pinna completely dissected—note its flatness, close connection with the external acoustic meatus, and the presence of the cartilaginous crista inside the external acoustic meatus.
Fig. 7.—*Tachyglossus aculeatus*. The transverse portion of the external acoustic meatus.
Fig. 8. *Tachyglossus aculeatus*. Entrance of the external acoustic meatus into the skull.

THE DEVONIAN TETRACORAL *HAPLOTHECIA* AND NEW AUSTRALIAN PHACELLOPHYLLIDS

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(Plate vi)

[Read 28th July, 1965]

Synopsis

Research in progress on Australian Lower Devonian corals is exposing a gradation between the Cyathophyllidae and the Disphyllidae. It is therefore recommended that the Disphyllidae be demoted to subfamily rank within the Cyathophyllidae.

Haplothecia filata (Schlotheim), a disphyllinid from the Frasnian of Germany, is restudied and the genus *Haplothecia* upheld. Two phacellophyllids from New South Wales are also described: the first, *Bensonastraea praetor*, gen. et sp. nov., is from the Timor Limestone of probable Eifelian age, while the second, *Macgeea touti*, sp. nov., occurs in the Loomberah and uppermost Sulcor Limestones, both late Emsian or early Eifelian in age.

A new term, veprecula(e), is introduced for the type of spinose projections found on the sides of the septa in *Bensonastraea*.

Introduction

Preparation of systematic accounts of several Devonian tetracoral faunas in New South Wales has necessitated the undertaking of various ancillary investigations. One of these has been the restudy of the type specimen of the genus *Haplothecia*, and an evaluation of its relationship to highly carinate Australian species referred to *Phillipsastrea*.

The results of this study, together with the description of two new Australian species of a related family, form the subject of the present paper.

A New Morphological Term

The stability of morphological terms, which almost without exception characterizes current descriptions of tetracorals, stems mainly from Hill (1935, 1956). In these works carinae are defined as flanges, or flange-like elevations, on the sides of a septum formed by thickened trabeculae.

In *Bensonastraea*, a new genus described below, the septa bear small, but nevertheless prominent spinose projections which do not conform to the definition of carinae given above. As far as can be judged from the less than perfectly preserved available material, these are composed of fibrous skeletal material and appear to be prolongations of lateral trabeculae. If so, a very similar trabecular pattern has been figured by Różkowska (1953, text-fig. 6) in '*Synaptophyllum*' *soshkinae* (see McLaren, 1959, for a revision of *Synaptophyllum*. Różkowska's species possesses horseshoe dissepiments and is presumably a phacellophyllid).

It is here proposed that spinose projections of the type occurring on the septa of *Bensonastraea* be known as vepreculae, singular veprecula, from the latin meaning a small thorn. Vepreculae may be homologous with the synapticulae of scleractinian corals.

Systematic Description

Family CYATHOPHYLLIDAE Dana, 1846

According to the majority of recent classifications, the Cyathophyllidae are distinct from the Disphyllidae (= Phillipsastraeidae auct.). In reality, however, a basis for the recognition of the Cyathophyllidae has been possible only since Birenheide's (1963) redescription of *Cyathophyllum* and related genera. In view of this and other recent work (Philip, 1962 ; Pedder, 1966) on earlier Victorian faunas, the distinction between the families is much less clear. For example, among the fasciculate forms, species of *Tipheophyllum* such as *T. ops* and *T. cognatum* completely bridge the gap between the Cyathophyllidae and Disphyllidae, and among the massive forms this gap is bridged by species such as *Hexagonaria approximans*. It is therefore proposed that the Disphyllidae be relegated to subfamily rank within the Cyathophyllidae.

Subfamily Disphyllinae Hill, 1939

Haplothecia filata (Schlotheim)

(Text-figs 1, 2, 4, 7)

1820. *Madreporites filatus* Schlotheim (*partim*), p. 359, var. α only.
1885. *Haplothecia filata* Schloth. sp. Frech, pp. 68, 69, Pl. 4, figs 7, 7*a*.
1951. *Phillipsastraea filata* (Schloth.), Soshkina, pp. 98–100, text-fig. 36, Pl. 18, figs 1*a*, *b*.
1952. *Phillipsastraea filata* (Schlotheim), Soshkina, p. 101, Pl. 42, figs 141.
1956. *Haplothecia filata* (Schloth.), Hill, p. 280, figs 191. 1*a*, *b*.

Type series.—Frech (1885, p. 68) states that Schlotheim's specimens included *Phillipsastrea hennahi* as well as a specimen from the Lias of Würtemberg. The specimen figured by Frech is technically a lectotype and is now in the Institut für Paläontologie und Museum der Humboldt-Universität, Berlin, where it is registered Q. Kat. A. 138, p. 1530. Previous to the present investigation it consisted of two small pieces and four transverse sections, including the one figured by Frech. Frech's longitudinal section is now lost and as no other existed, the writer was permitted to prepare a new one.

The museum label indicates that the specimen was obtained from the Iberger Kalk, Winterberg bei Grund (Harz, Germany).

Description.—The corallum is cerioid with axes of adjacent corallites 5 to 8 mm. apart. Nothing of the exterior is preserved, but the disposition of the dissepiments suggests that there would have been a relatively wide calicular platform.

Neighbouring corallites throughout the corallum are separated by a wall, typically 2·5 to 3·5 mm. thick, composed of an apparently structureless light-coloured skeletal material divided by a dark axial plate.

Septa are not embedded in the wall. In the dissepimentarium they tend to be arranged in parallel groups so that some are almost parallel with the wall and a few are even contratingent with an adjacent septum ; the arrangement suggests a thamnasterioid origin. Septal counts range from 12 × 2 to 13 × 2 in the material studied by the writer ; however, Frech, who studied further specimens, gave the maximum as 15 × 2. Major septa may extend to the axis, but more commonly are just withdrawn from it ; the minor are either confined to the dissepimentarium, where they are scarcely differentiated from the major, or just project into the tabularium. Prominent yard-arm carinae are present in the dissepimentarium, but in the tabularium septa are smooth and thin. The carinae are so well developed that they may touch the wall where wall and septum are almost parallel. At the carinae, septa are trabeculate, whereas between them they are composed of an apparently structureless and lighter coloured material identical with that forming the wall. Frech's longitudinal section shows divergence of the trabeculae ; however, this is not

as marked as in normal phacellophyllids and in fact there is no divergence at all on one side of the newly prepared section. Calcite fibres spread upwards randomly from near the trabecular axis and are not grouped in discrete fascicles.

The dissepiments are mostly small and globose and are more or less horizontally disposed; towards the tabularium they steepen so that the transition to the tabularium is abrupt. Where septum and wall lie close together, dissepiments commonly occur between them.

In both longitudinal sections of the lectotype, the tabulae, which are considerably disrupted by septa, are closely spaced and generally flat.

Figs 1, 2. *Haplothecia filata* (Schlotheim), lectotype ×24. 1, Transverse section. 2, Longitudinal section. The stippling between carinae is diagrammatic and represents apparently structureless skeleton.

Remarks.—Frech (1885, p. 68) proposed the genus *Haplothecia* solely for this species. Subsequently the genus received little attention until reassessed by Lang and Smith (1935, pp. 549, 550), exactly 50 years later. Although Lang and Smith's conclusion that it is synonymous with *Phillipsastrea* has gained wide acceptance (Stumm, 1949, p. 35; Wang, 1950, p. 220; Soshkina, 1951, p. 98; Schouppé, 1958, p. 233; Soshkina and Dobrolyubova, in Orlov, 1962, p. 336), there is no indication that they examined topotypic material. Indeed both their description, which minimizes the differences between *Haplothecia filata* and *Phillipsastrea sensu stricto*, and their figures, which illustrate specimens that are not necessarily *Haplothecia*, suggest that they did not.

Thanks to Drs. Jaeger and Forbes it has been possible to compare the lectotype of *Haplothecia filata* with a topotypic specimen (Sedgwick Museum No. H43*c*, *d* from Barton Quarry, Devon) of *Phillipsastrea hennahi*, the type species of *Phillipsastrea*. The latter is thamnasterioid to subcerioid, has a phacellophyllid zone of trabecular divergence as well as a few horseshoe dissepiments and is, therefore, a phacellophyllid and not a disphyllinid.

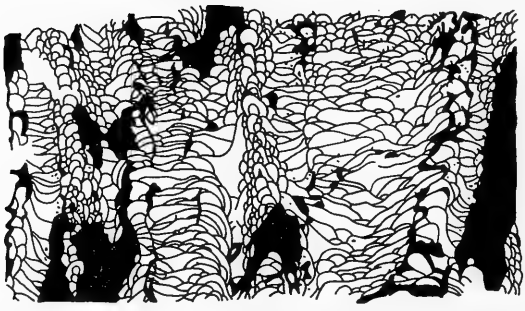
The allotment of *Haplothecia* to the Disphyllinidae must be regarded as provisional. The genus may have evolved from *Phillipsastrea* but, for the moment at least, the family Phacellophyllidae is reserved for corals having a normal phacellophyllid zone of trabecular divergence.

Family PHACELLOPHYLLIDAE Wedekind, 1921

Genus Bensonastraea nov.

Name derivation.—Patronym for W. N. Benson, pioneer geologist of the Great Serpentine Belt of New South Wales and Greek, ἀστρον = star, with traditional ending for coral genera.

Type species.—*Bensonastraea praetor*, sp. nov., see below.



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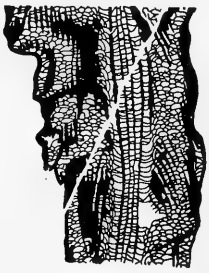

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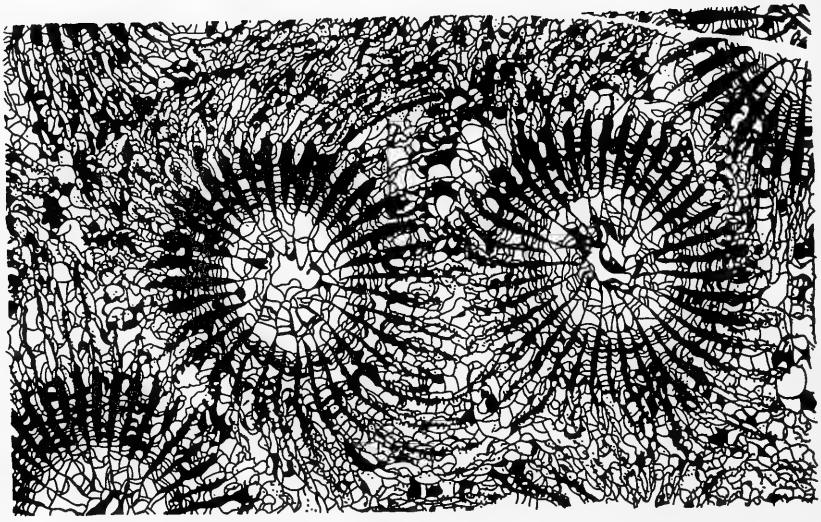

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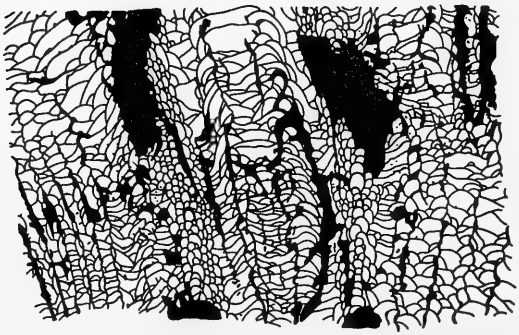

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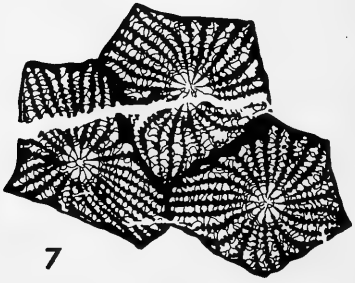

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Figs 3–7. 3, 5, 6, *Bensonastraea praetor*, gen. et sp. nov., holotype ×3. 4, 7, *Haplothecia filata* (Schlotheim), lectotype ×3.

Diagnosis.—Corallum thamnasterioid. Septa vepreculate. Trabeculae divergent exterior of the tabularium. Dissepimentarium and tabularium complex. Five zones present in dissepimentarium; from periphery inwards these are: broad zone of large and small, normal and lateral dissepiments; narrow zone of flat dissepiments; narrow zone of small outwardly-convex dissepiments; series of horseshoe dissepiments; and a narrow zone of inwardly-convex dissepiments. Tabularium divided into a narrow outer zone of flat tabellae; a periaxial zone of outwardly-convex tabellae; and a central region of more or less flat tabulae.

Remarks.—The new genus most obviously recalls *Keriophylloides* and *Billingsastraea*. Soshkina (1951, p. 102) erected *Keriophylloides* for *Keriophyllum astraeiforme* Soshkina (1936, pp. 62–64, figs 71, 72), an Eifelian species from the northern Urals, but subsequently, with Dobrolyubova as co-author (in Orlov, 1962, p. 336), merged the genus in *Billingsastraea* Grabau (1917, p. 957). The difficulties in recognizing *Billingsastraea* have been outlined previously by the present writer (1964*b*, p. 447); since then a further account of the genus has been given by Oliver (1964). Oliver's interpretation of *Billingsastraea* is similar to Ehlers and Stumm's (1953) and, if correct, *Keriophylloides* would be distinguished from it by its carinae which appear to be of the veprecular rather than the yard-arm type, its highly arched dissepiments giving rise to an exsert calicular rim, and by the dilation of its septa immediately exterior of the tabularium.

Bensonastraea is distinguished from both of these genera, and also from the polyonymous genus *Phillipsastrea* d'Orbigny (1849, p. 12), by its complex dissepimentarium. *Sulcorphyllum* Pedder (1964*a*, p. 366) and *Pseudoacervularia sensu* Różkowska (1953, p. 49) *non* Lang, Smith and Thomas (1940, p. 108) in some respects resemble the new genus, but are cerioid, have a different dissepimentarium, and lack vepreculae.

At the present time, only the type species is referred to *Bensonastraea* which may prove to be but a local offshoot from the central plexus of the Phacellophyllidae.

Bensonastraea praetor, gen. et sp. nov.

(Pl. vi, figs 1, 6, 7; text-figs 3, 5, 6)

Name derivation.—Latin, *praetor* = leader.

Type series.—Holotype, Geological Survey of New South Wales No. 3463, Timor Limestone (probably Eifelian), Portion 133, Parish of Lincoln, County Brisbane, N.S.W.; the collector is not recorded.

Diagnosis.—Large *Bensonastraea* with axes of adjacent corallites 12 to 23 mm. apart and tabularium normally 5 to 6 mm. in diameter. Septal count 17 × 2 to 21 × 2.

Description.—The corallum is thamnasterioid and apparently large; when first seen by the author, the holotype had already been cut and yet measured approximately 80 × 65 × 80 mm. Axes of adjacent adult corallites are separated by from 12 to 23 mm. and the tabularium is normally 5 to 6 mm. in diameter. No exterior surface is preserved.

There are 17 × 2 to 21 × 2 septa in adult corallites, although differentiation into two orders is evident only in the tabularium. Throughout most of the dissepimentarium septal arrangement is thamnasterioid with the peripheral ends of the septa being either confluent with, abutted against, or withdrawn from, a septum of an adjacent corallite; arrangement is radial in the tabularium. In the outer region of the dissepimentarium where vepreculae are abundant, the septa are thin and locally degenerate, being represented by vepreculae only. In the region of the horseshoe dissepiments, however, they are strongly dilated and are also asymmetrically (peripheral end blunter) fusiform in transverse

section ; vepreculae are fewer here and generally masked by thick sclerenchyme. In the tabularium septa are thin, straight or sinuous, and smooth ; the major commonly extend to within about 1 mm. of the axis, whereas the minor terminate close to the inner margin of the dissepimentarium. Trabeculae diverge in a zone opposite the horse-shoe dissepiments.

Five concentric zones may be distinguished in the dissepimentarium. The outermost of these is the broadest and consists of both large and small dissepiments ; lateral dissepiments are characteristic of this zone. The next zone is one of flat, sloping or sagging dissepiments. Inside these there is a narrow and, in places, discontinuous zone of small outwardly-convex dissepiments, typically up to three deep. Irregularly superposed horse-shoe dissepiments form the next zone ; these vary considerably in size and some are sigmoidal. The innermost zone consists of small inwardly-convex dissepiments, typically two to four deep.

The peripheral part of the tabularium is formed of flat tabellae, inside which there is a periaxial series of generally upwardly and outwardly convex plates. Flat, or only gently arched or sagging tabulae occupy the central region of the tabularium.

Macgeea touti, sp. nov.

(Pl. vi, figs 2–5, 8–11 ; text-figs 8–11)

? 1917. *Zaphrentis typlasmoides* Dun, p. 218. *Nomen nudum et oblitum.*
1918. *Zaphrentis* (?) sp. (sp. et subgen nov. ?) ; Dun in Benson, pp. 335, 375, 376, text-fig. 3, Pl. 34, fig. 1.
1922. *Zaphrentidae* (new genus) ; Benson, p. 143(60).

Name derivation.—Patronym for S. M. Tout who, according to Benson (1918, p. 322), " was the first to bring the Loomberah limestones under scientific notice ".

Type series.—Holotype and paratypes 1–4, University of New England Nos. F8851–8855 respectively, collected by the author from the Loomberah Limestone (late Emsian or early Eifelian) in Portion 58, Parish of Loomberah, County Parry, N.S.W. Paratypes 5, 6, University of New England Nos. F8856, 8857 respectively, collected by the author from the uppermost beds of the Sulcor Limestone (late Emsian or early Eifelian) at the northern end of the outcrop in Portion 249, Parish of Burdekin, County Inglis, N.S.W.

Diagnosis.—Solitary ceratoid to cylindrical tetracoral with a maximum known length and diameter 70 and 19 mm. respectively. Septa considerably dilated and commonly contiguous in a zone immediately exterior of the tabularium ; trabeculae divergent in this zone. Septal counts 18 × 2 to 24 × 2 at maturity. Dissepimentarium in two parts, an outer of predominantly flat plates and an inner of small and commonly masked horse-shoe dissepiments. Tabulae variable, mostly short and arched.

Description.—All available specimens are completely embedded in matrix ; from thin sections the corallum appears to be ceratoid in early stages and subcylindrical to cylindrical at maturity. Rejuvenescence occurred rarely. Specimens up to 70 mm. long and 19 mm. in diameter are known ; however, diameters in excess of 15 mm. are unusual.

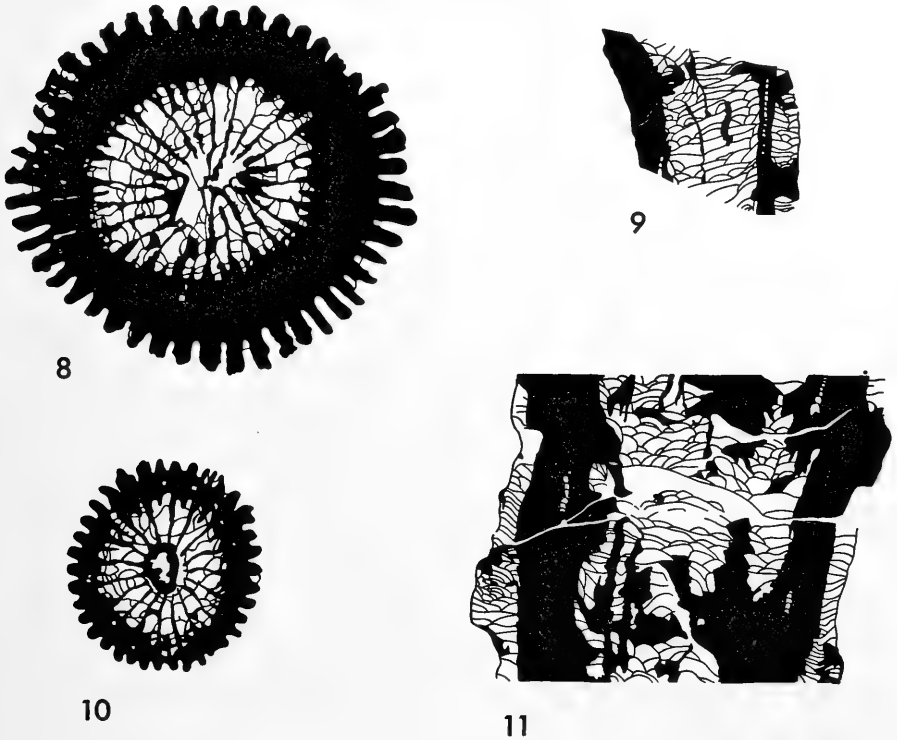
An epitheca is preserved in a minority of specimens ; where present it is between 0·15 and 0·25 mm. thick and consists of a thin dark axial plate and an inner lighter layer.

Arrangement of the septa is radial, or faintly pinnate about the presumed cardinal-counter plane. The major septa extend to near and in some cases beyond the axis, and may be rhopaloid or forked axially ; the minor just intrude the tabularium. Both orders of septa are considerably dilated in the dissepimentarium, appearing fusiform or wedge-shaped in transverse section, and are

commonly contiguous just exterior of the tabularium. In the tabularium they are irregularly bent and variably carinate. Septal counts vary from 18 × 2 to 24 × 2 in adult specimens.

Trabeculae diverge in the normal phacellophyllid manner. Fibre fascicles are prominent as dark regions in most sections, although individual fibres can not be discerned.

A series of flat or gently convex plates forms the outer region of the dissepimentarium ; this may be as much as 2 mm. wide, although it has been eroded from most specimens at the type localities. A collar of relatively small horse-shoe dissepiments constitutes the inner part of the dissepimentarium ;



Figs 8–11. *Macgeea touti*, sp. nov. ×3. 8, 11, holotype. 9, paratype 4. 10, paratype 2.

however, in many cases this is largely obscured by dilation of the septa. The horse-shoe dissepiments are normally superposed, but in some specimens from the Sulcor Limestone (e.g. paratype 6), short subsidiary strings of horse-shoe dissepiments branch from the main collar into the outer part of the dissepimentarium.

The tabularium, which is one-half to three-fifths the total width of the coral, is composed of numerous tabulae varying considerably in width and curvature ; locally these may be invested by sclerenchyme.

Remarks.—The relatively wide zone of flat dissepiments, the degree of dilation of the septa in the zone of trabecular divergence, and the low ratio between the number of septa and diameter, distinguish *Macgeea touti* from the majority of previously described species which are, of course, Givetian or Frasnian in age.

Macgeea (?) *murchisoni* (Penecke, 1894, pp. 595, 596, Pl. 7, figs 15–17) is probably the closest known species. It was originally proposed for a fragment

from the Emsian of the Carnic Alps and has subsequently been reported to be present in the Eifelian of both the type area (Heritsch, 1935, pp. 188, 189) and Armenia (Soshkina, 1952, p. 84, Pl. 18, fig. 65). Penecke's species differs from the new one in having more septa at a given diameter, and broader and more widely spaced tabulae. Specimens from the Emsian at Chalonnes (Le Maître, 1934, pp. 148, 149, Pl. 5, figs 3, 4) and from the Givetian at Ville De-d'Ardin (Le Maître, 1937, pp. 111–113, Pl. 7, figs 3–5, 11, 12 ; Pl. 8, fig. 7), which have been referred to *Thamnophyllum murchisoni*, are quite unrelated to *Macgeea touti*, as are the specimens, which have been compared with *T. murchisoni* (Firtion, 1957, p. 127, Pl. 5, figs 6, 7), from the Givetian of the Val de Bruche.

A number of species of *Pexiphyllum*, established by Walther (1928) on specimens from the Frasnian of Germany, resemble *Macgeea touti*. Apart from discrepancies in septal counts, septal dilation in these species is as prominent in the outer as in the inner region of the dissepimentarium, with the result that transverse sections of eroded specimens do not simulate cog-wheels, as those of *Macgeea touti* do.

In a footnote, Glinski (1961, p. 284) has claimed that *Macgeea* (Webster, 1889, p. 710) is a junior synonym of *Pterorrhiza* (Ehrenberg, 1834, p. 312). However, pending publication of figures of the interior of *Cyathophyllum marginatum* Goldfuss, the type species of *Pterorrhiza*, the present author prefers to retain the name *Macgeea* for species such as *M. touti*.

Acknowledgements

Assistance rendered by a number of geologists is gratefully acknowledged. Dr. E. O. Rayner and Mr. H. F. Whitworth of the New South Wales Department of Mines, sanctioned the loan of specimens from the Mining Museum, Sydney. Dr. J. W. Pickett, now also of the New South Wales Department of Mines, forwarded a description of the holotype of *Phillipsastrea hennahi*, while Mr. M. Mitchell, of the Geological Survey of Great Britain, provided photographs of the same specimen. Dr. C. L. Forbes arranged for loan of Barton Quarry corals from the Sedgwick Museum, Cambridge, and Dr. H. Jaeger, Humboldt Universität, Berlin, loaned part of the holotype of *Haplothecia filata* ; he also allowed a further section to be prepared from it.

Field-work, during which the type material of *Macgeea touti* was obtained, has been supported by University of New England's Research Grant No. 225.

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EXPLANATION OF PLATE VI

All figures $\times 2$

Figs 1, 6, 7. *Bensonastraea praetor*, gen. et sp. nov., holotype. Figs 2–5, 8–11. *Macgeea touti*, sp. nov. 2, 9, paratype 5; 3, 11, holotype; 4, paratype 2; 5, paratype 1; 8, paratype 6; 10, paratype 3.

SOME MITE PARASITES OF AUSTRALIAN BIRDS

ROBERT DOMROW
Queensland Institute of Medical Research, Brisbane

[Read 28th July, 1965]

Synopsis

Thirty-six species of mites from five families are listed from Australian birds.

LAELAPIDAE : New hosts are given for 13 species (*Ornithonyssus bursa, O. sylviarum, Pellonyssus reedi, Mesonyssus kakatuae, M. trichoglossi, M. belopolskii, M. melloi, M. geopeliae, Sternostoma cooremani, S. laniorum, S. thienponti, Ptilonyssus cractici* and *P. thymanzae*). Seven new records for Australia are listed : (*Sternostoma tracheacolum, Rhinonyssus himantopus, R. rhinolethrus, Larinyssus benoiti*—a genus also new to Australia, *Rallinyssus caudistigmus, Passeronyssus bradypteri* and *Ptilonyssus triscutatus*). Eight new species are described (*Sternostoma gliciphilae*, n. sp., from *Gliciphila indistincta*, Meliphagidae ; *S. zosteropus*, n. sp., from *Zosterops lateralis*, Zosteropidae ; *Ptilonyssus microecae*, n. sp., from *Microeca fascinans* and *Eopsaltria capito*, Muscicapidae ; *P. rhipidurae*, n. sp., from *Rhipidura fuliginosa*, Muscicapidae ; *P. dicaei*, n. sp., from *Dicaeum hirundinaceum*, Dicaeidae ; *P. gliciphilae*, n. sp., from *Gliciphila indistincta*, Meliphagidae ; *P. stomioperae*, n. sp., from *Stomiopera unicolor* and *Meliphaga flava*, Meliphagidae ; and *Hattena panopla*, n. sp., from *Gliciphila indistincta*, Meliphagidae.

SPELEOGNATHIDAE : *Speleognathopsis benoiti* and *Neoboydaia merops* are newly recorded from Australia.

CHEYLETIDAE : The genus *Neocheyletiella*, represented by *N. artami*, n. sp., from *Artamus cyanopterus* (Artamidae), is added to the Australian fauna.

TROMBICULIDAE : New records are provided for *Odontacarus australiensis, Leptotrombidium myzantha* and *Neoschoengastia posekanyi*. *Trombicula shiraii*, known only from the original series from Japan, is recorded from a migratory wader on the Great Barrier Reef.

TURBINOPTIDAE : The genus *Passerrhinoptes*, represented by *P. pomatostomi*, n. sp., from *Pomatostomus temporalis* (Timaliidae), is listed from Australia for the first time.

Recent accessions have included the most interesting variety of bird-parasitic mites detailed below. For further details on the Australian members of the families discussed, the reader is referred to Domrow (1964*a*, *b*, *c* ; 1965*c*) on laelapids ; Domrow (1965*a*) on speleognathids ; Womersley (1941) and Volgin (1964) on cheyletids ; Womersley (1952) on trombiculids ; and Domrow (1965*b*) on turbinoptids.

Messrs. D. P. Vernon and J. T. Woods, Queensland Museum, Brisbane, have checked many bird identifications, and Mr. J. H. Calaby, C.S.I.R.O., Canberra, provided some of the material. The collectors, acknowledged by their initials in the text, are, apart from myself, B. C. Allan, G. J. Barrow, J. Booth, I. D. Fanning, R. H. Green, H. I. McDonald, M. D. Murray, J. M. Paton, R. G. Rees, R. V. Southcott and J. S. Welch. I am most grateful to them all, and to Miss B. Nolan for typing the manuscript.

The holotypes and allotypes of new species have been deposited in the Australian National Insect Collection, C.S.I.R.O., Canberra ; paratypes, when available, have been lodged in the collections under the care of Drs. A. Fain (Prince Leopold Institute of Tropical Medicine, Antwerp), and R. W. Strandtmann (Texas Technological College, Lubbock), and myself.

Family LAELAPIDAE

ORNITHONYSSUS BURSA (Berlese)

Host records additional to those listed by Domrow (1963) are extremely heavy infestations with both females and protonymphs on two Australian black-shouldered kites, *Elanus notatus* Gould (Accipitridae, Falconiformes),

14.vi.1963, I.D.F. and R.G.R. (occasional specimens were taken on several other bird hosts with the same collection data, but as the risk of field contamination is high with such an active species, they have not been listed here); 1 protonymph from a fledgling laughing kookaburra, *Dacelo gigas* (Boddaert) (Alcedinidae, Coraciiformes), Brisbane, 17.xii.1964, R.G.R.; many females from around the vent of a pheasant coucal, *Centropus phasianinus* (Latham), Samford, 21.i.1964, R.G.R. and J.S.W., and 15♀♀ from a koel, *Eudynamys orientalis* (Linnaeus), Brisbane, 8.ii.1965, B.C.A. (both Cuculidae, Cuculiformes); also 7♀♀ from a starling, *Sturnus vulgaris* Linnaeus (Sturnidae, Passeriformes), Brisbane, 3.xii.1963, R.D. An interesting southerly record of this, the tropical fowl mite, is 2♀♀ biting children, Launceston, Tas., 7.i.1963, R.H.G.

Ornithonyssus sylviarum (Canestrini and Fanzago)

As all known Australian records of this species are from the far south-east of the continent (Womersley, 1956*a*; Domrow, 1963), the following record from Queensland is of interest: 1♀ from the welcome swallow, *Hirundo neoxena* Gould (Hirundinidae, Passeriformes), Brisbane, 3.xii.1963, R.D. The Australian *H. neoxena* is a migratory species, which departs for the northern parts of the continent in the autumn (Cayley, 1963). I have since seen 13♀♀ from nestlings of the blackbird, *Turdus merula* Linnaeus (Turdidae, Passeriformes) (introduced from Europe, and now common in S.E. Australia), Evendale, Tas., 5.i.1963, R.H.G. Also 1♀ from a golden whistler, *Pachycephala pectoralis* (Latham) (Pachycephalidae, Passeriformes), Esk, 14.vii.1965, R.D. and J.S.W.

Pellonyssus reedi (Zumpt and Patterson)

Five ♀♀ from the beautiful firetail, *Zonaeginthus bellus* (Latham) (Ploceidae, Passeriformes), Waitpinga, S.A., 31.xii.1963, J.M.P., comprise the second record of this species from Australia. See Womersley (1956*b*) and Till (1964). An additional synonym is *Steatonyssus stenosternus* Wang (1963). I am most grateful to Dr. F. Zumpt, South African Institute for Medical Research, Johannesburg, and the Director, South Australian Museum, Adelaide, for the gift or loan of material of this genus.

Mesonyssus kakatuae (Domrow)

One ♀ and 1♂ from the nares of a red-tailed black cockatoo, *Calyptorhynchus banksi* (Latham) (Psittacidae, Psittaciformes), Mitchell R., Gulf of Carpentaria, xi.1964, R.D., comprise a new host record. See Domrow (1964*a*) and Wilson (1964).

Mesonyssus trichoglossi (Domrow)

This species, previously recorded from several psittacids in Australia and New Guinea (Domrow, 1964*a*; Wilson, 1964), may now be recorded from a further Australian host: 2♀♀ from the nares of a little lorikeet, *Glossopsitta pusilla* (Shaw) (Psittacidae, Psittaciformes), Esk, 27.ii.1965, R.D. and J.S.W.

The specimens agree with the original description of the typical form, except that only twelve furled setae are present on the dorsum: four along midposterior margin of podosomal shield, one on shieldlet at each postero-lateral angle of podosomal shield, and three on each half of posterior dorsal shield (two on inner, and one on outer edge).

Mesonyssus belopolskii (Bregetova)

Six ♀♀, 10♂♂ and 2 nymphs from the nares of a pied heron, *Notophoyx picata* (Gould) (Ardeidae, Ciconiiformes), Mitchell River, xi.1964, R.D., comprise a new host record. See Domrow (1965*c*).

Mesonyssus melloi (de Castro)

Seven ♀♀, 4♂♂ and 1 nymph from the nares of two domestic pigeons, *Columba livia* Gmelin (Columbidae, Columbiformes), Brisbane, 2.xii.1964, R.D. and J.S.W., comprise a new host record for Australia. See Fain (1962*a*) and Domrow (1965*c*).

Mesonyssus geopeliae Fain

One ♂ from the nares of a peaceful dove, *Geopelia placida* Gould (Columbidae, Columbiformes), Mitchell R., xi.1964, R.D., comprises a new host record. See Fain (1964) and Domrow (1965*c*).

Sternostoma cooremani Fain

Two ♀♀ from the nares of a rainbow-bird, *Merops ornatus* Latham (Meropidae, Coraciiformes), Esk, 28.viii.1964, R.D. and J.S.W., comprise a new host record. Previous records, all from coraciiforms, are summarized by Domrow (1965*c*).

Sternostoma gliciphilae, n. sp.

(Figs 1–5)

Female.—A small, oval mite with idiosoma wider in anterior half, 440–473μ long. Podosomal shield with anterolateral margins ill-defined, but posterolateral margins distinct and virtually straight medially. Shield almost entirely covered by very sharply defined subhexagonal reticulation which is more heavily sclerotized than remainder of shield, giving the effect of honeycomb. Areas of muscle insertions nestle among this texture, and the shield further bears five pairs of minute setae both laterally and medially. Opisthosomal shield rectangular, with greater axis longitudinal; texture similar to that of podosomal shield; with about six minute setae. Dorsal cuticle otherwise unarmed except for two small, circular stigmata (without peritremes).

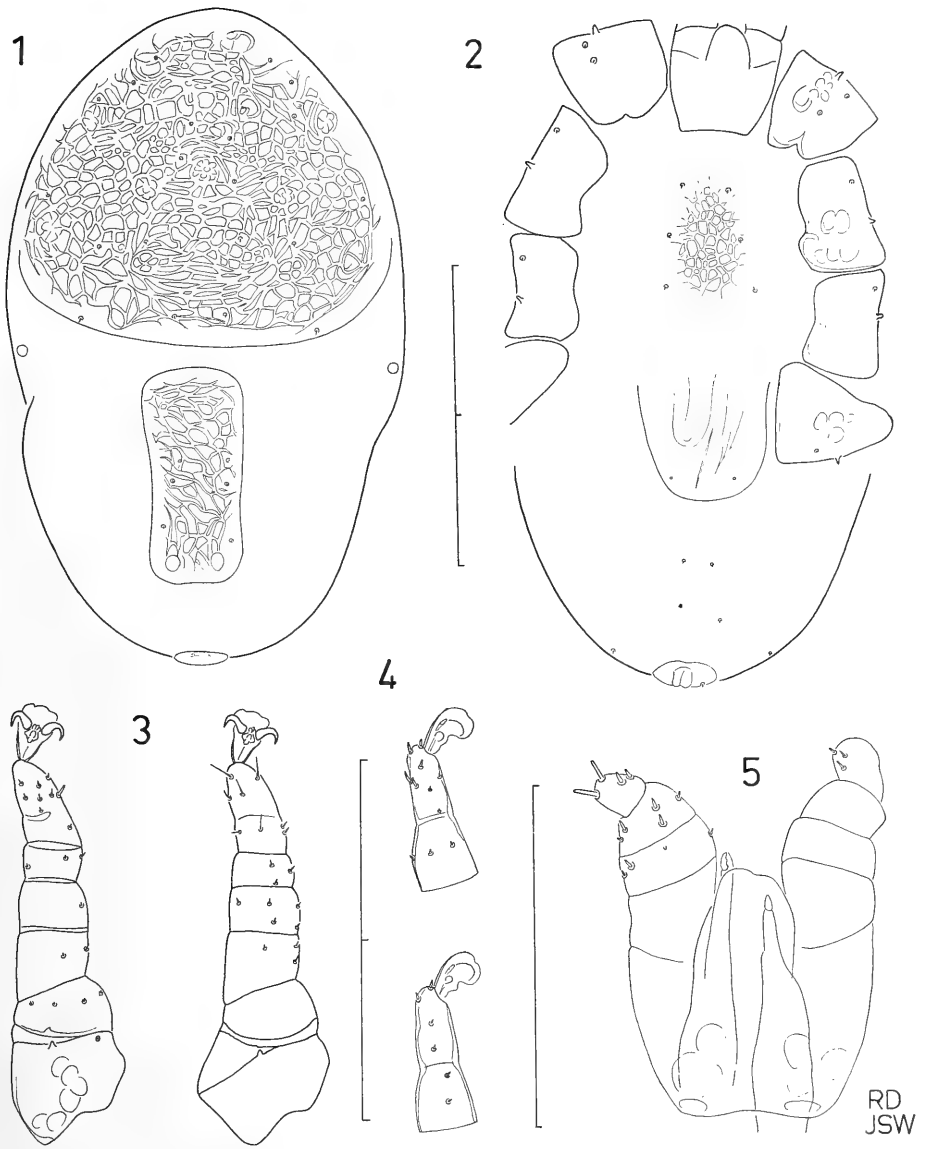
Sternal shield discally imitating texture of podosomal shield, but reticulation finer; encircled by six sternal setæ; margins evanescent. Genital shield short and broad, with nondescript texture and merest asetose traces of original genital setae. Anal shield terminal, typically with at least adanal setae and cribrum. Ventral cuticle typically with six minute setae arranged 4.2, but minor variations were noted as follows: (i) five setae rather than four in central group; and (ii) outer posterior pair of setae apparently lacking.

Coxal setal formula 2.1.1.1, with occasional asetose traces of posterior seta on coxae II and III (aberrations from the typical 2.2.2.1 of the Gamasina are apparently common in this genus, but they are of less than specific importance (see Fain, 1957; Fain and Bafort, 1963*b*; Furman, 1957; Hyland, 1962; Hyland and Clark, 1959; Hyland and Ford, 1961). Leg setation in general extremely weak, but few longer setae on tarsi II–IV. Tarsi I with several thicker setae dorsodistally. Claws I obsolescent; claws II–IV strongly curved, as is usual.

Gnathosomal and hypostomal setae apparently absent. Tritosternum absent. Palpi with four free segments, line of demarcation between tibia and tarsus indistinguishable. Palpal setation as figured. Chelicerae typical of genus.

Discussion.—*S. gliciphilae* is quite unlike other species of the genus in its peculiarly textured dorsal shield. It is, in addition, the only species known from a peculiarly Australian group of birds—only one species of the family Meliphagidae has crossed Wallace's Line to the west, see Leach [1958], whose classification is used in this paper.

Types.—Holotype female and two paratype females from the mucous membranes at the extreme posterior of the nares of a brown honeyeater, *Gliciphila indistincta* (Vigors and Horsfield) (Meliphagidae, Passeriformes), Esk, 16.i.1965, R.D. and J.S.W. Holotype NIC; paratypes RD.



Figs 1–5. *Sternostoma gliciphilae*, n. sp. Female.—1, Idiosoma (dorsal); 2, Idiosoma (ventral); 3, Leg III (ventral at left, dorsal at right); 4, Tarsus I (anterior above, posterior below); 5, Gnathosoma (ventral, with left palp dorsal). (Each division on the scales equals 100μ.)

Sternostoma laniorum Fain

Four ♀♀ from a crested bellbird, *Oreoica gutturalis* (Vigors and Horsfield) (Falcunculidae, Passeriformes), Mitchell, S.Q., 25.v.1964, I.D.F., and 1♀ from a rufous shrike-thrush, *Colluricincla megarhyncha* (Quoy and Gaimard) (Pachycephalidae, Passeriformes), mist-netted along the Innisfail-Palmerston Highway, 16.xii.1964, H.I.McD. and G.J.B., comprise new host records (other birds listed below from this latter locality were also netted, while almost all the others were shot). All specimens were taken from the nares, and the ventrodistal setae on tarsi II–IV are blunt in both series (see Fain, 1957, and Domrow,

1965*c*). Also 1♀ from a leaden flycatcher, *Myiagra rubecula* (Latham), a d 9♀♀ from a pale-yellow robin, *Eopsaltria capito* Gould (both Muscicapidae, Passeriformes), Innisfail, 3 and 4.viii.1965, R.D. and J.S.W.

Sternostoma thienponti Fain

One ♀ from the nares of a black butcher-bird (black phase), *Cracticus quoyi* (Lesson and Garnot) (Cracticidae, Passeriformes), Innisfail-Palmerston Highway, 11.xii.1964, H.I.McD. and G.J.B., comprises the second Australian record of this species, again from a cracticid (see Domrow, 1965*c*). Also 19♀♀ from a black butcher-bird (red phase), Innisfail, 1.vii.1965, G.J.B. and H.I.McD.

Sternostoma tracheacolum Lawrence

This widespread species may now be formally recorded from Australia (see Domrow, 1965*c*): 21♀♀ from the trachea of the Gouldian finch, *Poephila gouldae* (Gould) (Ploceidae, Passeriformes), Sydney, 19.x.1964, M.D.M. Previous records are summarized by Fain and Hyland (1962).

Sternostoma zosteropus, n. sp.

(Figs 6–12)

Female.—A small, oval mite with idiosoma shaped as in *S. gliciphilae*, n. sp., 402μ long in little deformed specimen figured, 495μ in second somewhat compressed specimen. Podosomal shield sharply arched anteriorly, sinuous laterally and posteriorly; surface heavily granulate except at extreme margins, marked by muscle insertions and bearing four pairs of setae both marginally and medially, in addition to two pairs of lateral pores. Opisthosomal shield subquadrate, of similar texture to podosomal shield. One specimen shows two stronger setae both anteriorly and posteriorly, as well as six smaller setae discally. The other shows two stronger setae posteriorly, two setae and perhaps four asetose indications of setae discally, while it is flanked anteriorly by an unpaired, stronger seta. Shield with pore in each posterolateral angle. Dorsal body cuticle with two distinct setae behind stigmata, which latter have no peritremes.

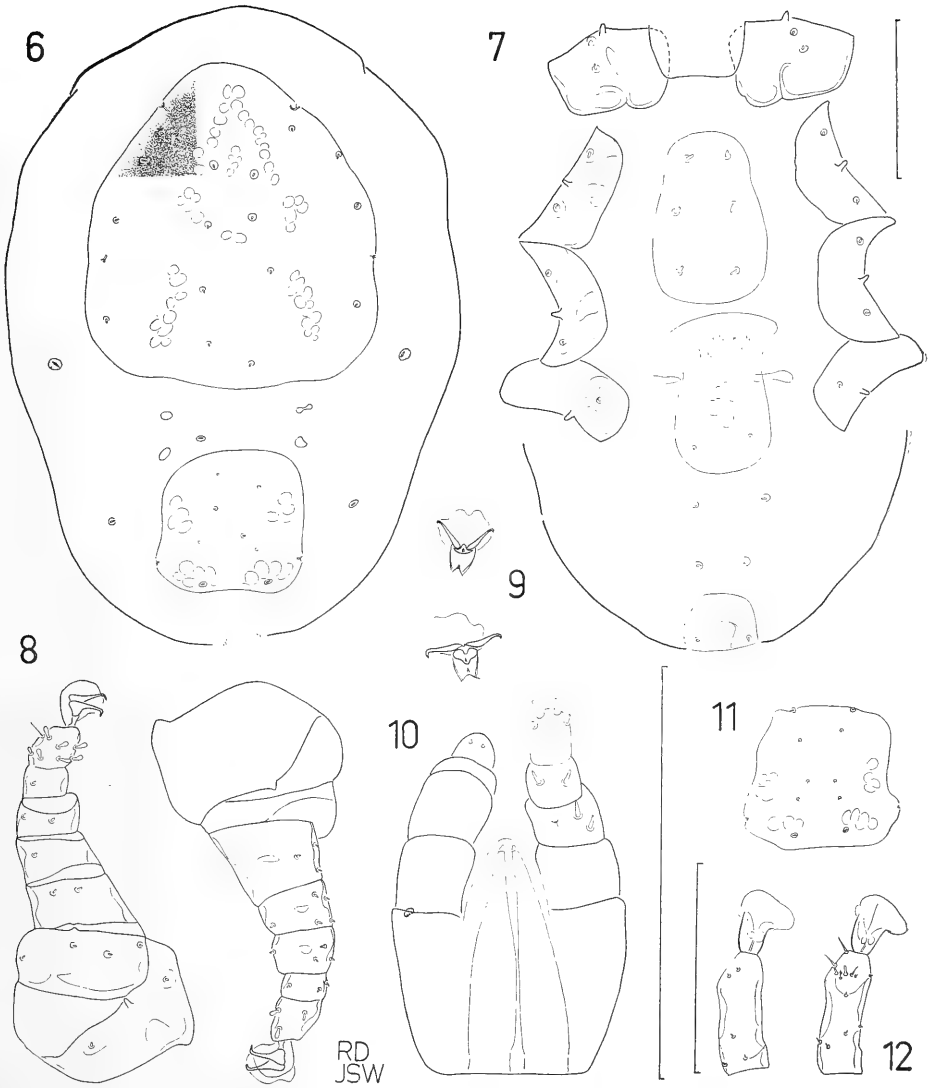
Sternal shield weakly granulate except for textureless, but rather well defined margins; bearing six blunt setae. Genital shield short and broad, weakly granulate, with muscle insertions and truncate, rayed operculum. Genital setae obsolescent. Anal shield terminal, with at least adanal setae and cribrum present. Ventral cuticle with four distinct setae.

Coxal setal formula 2.2.2.1, setae weak, as they are on all segments except tarsi. Tarsus I with sensory islet dorsodistally showing both longer setae and rodlets. Tarsi II–IV with setae arranged slightly differently from *S. gliciphilae*, showing the pattern typical of *Ptilonyssus*; all setae, except one, like elongate droplets. Claws I obsolescent; claws II–IV straight along most of their length, curved only distally.

Gnathosomal and hypostomal setae apparently absent. Tritosternum lacking. Palpi with four movable segments, the line of demarcation between tibia and tarsus virtually invisible; setation as figured. Chelicerae typical of genus.

Discussion.—*S. zosteropus* may be separated from all its described congeners by its peculiarly straight tarsal claws II–IV.

Types.—Holotype female and one paratype female from the nares of a grey-backed silvereye, *Zosterops lateralis* (Latham) (Zosteropidae, Passeriformes), mist-netted at Mt. Jukes, Mackay, vi.1964, R.D. and J.S.W. Holotype NIC; paratype RD.



Figs 6–12. *Sternostoma zosteropus*, n. sp. Female.—6, Idiosoma (dorsal); 7, Idiosoma (ventral); 8, Leg III (ventral at left, dorsal at right); 9, Ambulacrum III (two views); 10, Gnathosoma (ventral, with right palp dorsal); 11, Opisthosomal shield (variant); 12, Tarsus I (ventral at left, dorsal at right).

Rhinonyssus himantopus Strandtmann

This widespread parasite of waders may now be listed from Australia: 1♀ from a red-kneed dotterel, *Erythrogonys cinctus* Gould; and 2♀♀ and 3♂♂ from a masked plover, *Lobibyx miles* (Boddaert) (both Charadriidae, Charadriiformes), Mitchell R., xi.1964, R.D. All specimens were collected in the nares. The former series resembles Strandtmann's original (1951) specimens from *Himantopus* (Recurvirostridae, Charadriiformes), and the latter his later (1959) specimens from *Charadrius*. I am grateful to Dr. Strandtmann for the loan of specimens of this species, of which I have since seen 10♀♀, 4♂♂ and 1 nymph from black-fronted dotterels, *Charadrius melanops* Vieillot, Mitchell R., iv.1965, R.D., and 1♂ from a spur-winged plover, *Lobibyx novaehollandiae* (Stephens), Esk, 16.v.1965, I.D.F. and J.S.W.

Rhinonyssus rhinolethrus (Trouessart)

This widespread parasite of anseriforms may now be recorded from Australia: 2♀♀ from the nares of a whistling tree-duck, *Dendrocygna arcuata* (Horsfield) (Anatidae, Anseriformes), Mitchell R., xi.1964, R.D. It has also been recorded from the black duck, *Anas superciliosa* Gmelin, in New Guinea (Wilson, 1964), but I have as yet no such Australian record.

Larinyssus benoiti Fain

(Figs 13–21)

This genus and species may now be listed from Australia: 33♀♀, 9♂♂ and 2 nymphs from the nares of five Australian pratincoles, *Stiltia isabella* (Vieillot) (Glareolidae, Charadriiformes), Mitchell R., xi.1964, R.D. The only previous record is from *Galachrysia*, an African glareolid. Dr. Fain has kindly compared my illustrations with his specimens, and confirmed my identification.

Rallinyssus caudistigmus Strandtmann

This species, known only from American rallids (Strandtmann, 1948), may now be recorded from Australia: 6♀♀ and 1♂ from the nares of a dusky moorhen, *Gallinula tenebrosa* Gould (Rallidae, Gruiformes), Esk, 27.ii.1965, R.D. and J.S.W.

Passeronyssus bradypteri Fain

This species may now be listed from Australia: 4♀♀ from the nares of a rufous songlark, *Cinclorhamphus mathewsi* Iredale (Sylviidae, Passeriformes), Esk, 29.viii.1964, R.D. and J.S.W. The only previous record is from *Bradypterus*, an African sylviid (Fain, 1962*b*).

Ptilonyssus triscutatus (Vitzthum)

This parasite of European and African bee-eaters (see Fain, 1957) may now be recorded from Australia: 1♀ from the nares of a rainbow-bird, *Merops ornatus* Latham (Meropidae, Coraciiformes), Esk, 29.viii.1964, R.D. and J.S.W. The dorsum of femur III of this specimen shows an oblique row of three closely-set setae reminiscent of genu III in *Tyranninyssus* Brooks and Strandtmann (1960). See also Hyland (1961).

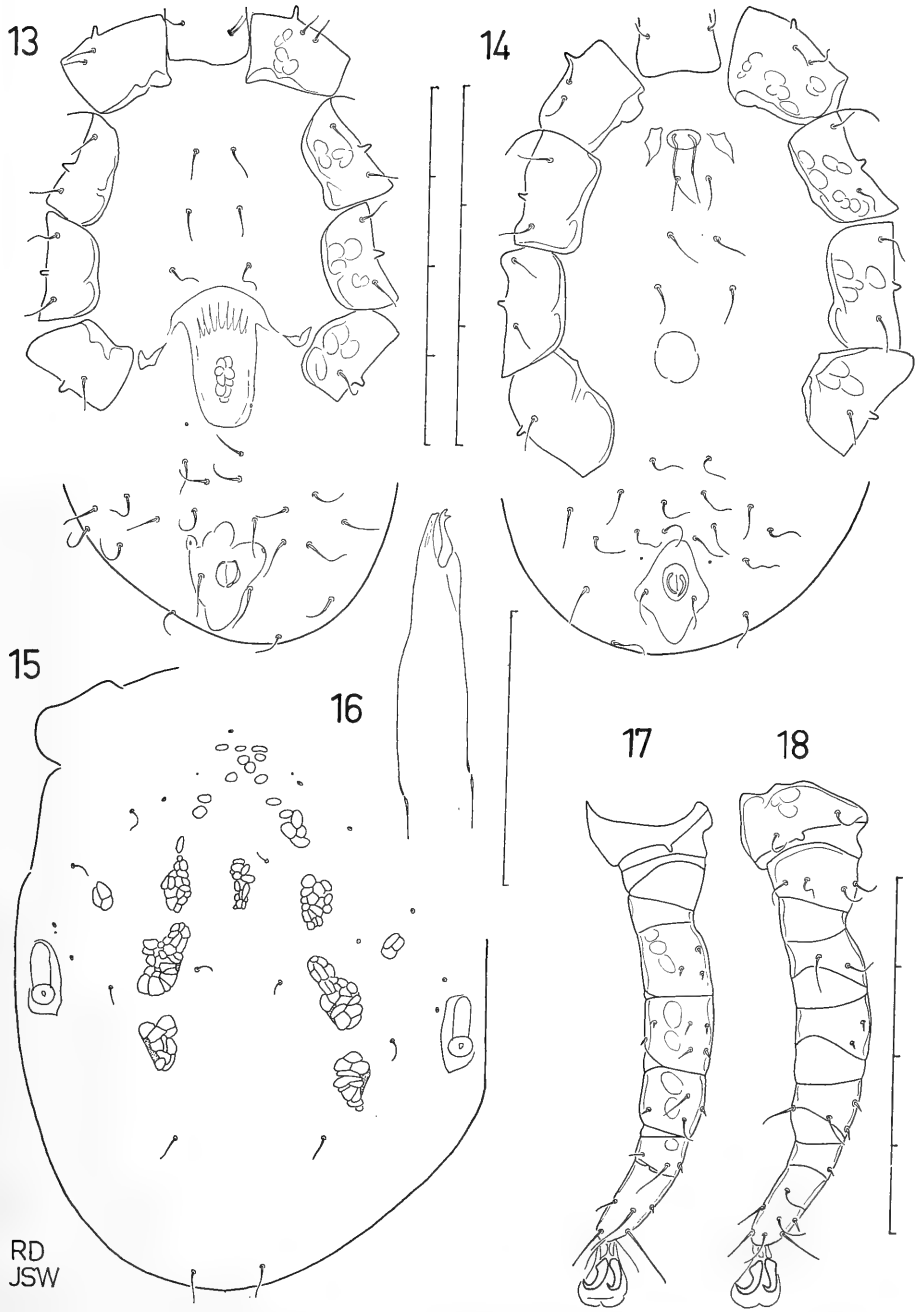
Ptilonyssus cractici Domrow

Seven ♀♀, 1 deutonymph and 1 protonymph from a black-backed butcher-bird, *Cracticus mentalis* Salvadori and d'Albertis (Cracticidae, Passeriformes), Chillagoe, 2.i.1965, G.J.B., comprise a new host record. See Domrow (1964*c*). I have since also seen 4♀♀ and 1 deutonymph from the nares of a white-winged triller, *Lalage tricolor* (Swainson) (Campephagidae, Passeriformes), Mitchell R., 7.iv.1965, R.D., which I assign to this species. They differ from paratypes only in showing the adanal setae set just behind the anus, and slight processes at the anterior edges of coxae II and the palpal trochanters (the former process is absent, and the latter incipient, in paratypes). Also 4♀♀ and 1 protonymph from a grey butcher-bird, *Cracticus torquatus* (Latham), Esk, 5.x.1965, R.D. and J.S.W. Finally, 1♀ from a laughing kookaburra, *Dacelo gigas* (Boddaert) (Alcedinidae, Coraciiformes), Esk, 14.vii.1965, R.D. and J.S.W. This seems an abnormal host, and it is recognized that "many records of stragglers are simply curiosities, though their publication should presumably not be suppressed" (Audy, 1956, *Bull. Raffles Mus., Singapore*, 28: 74).

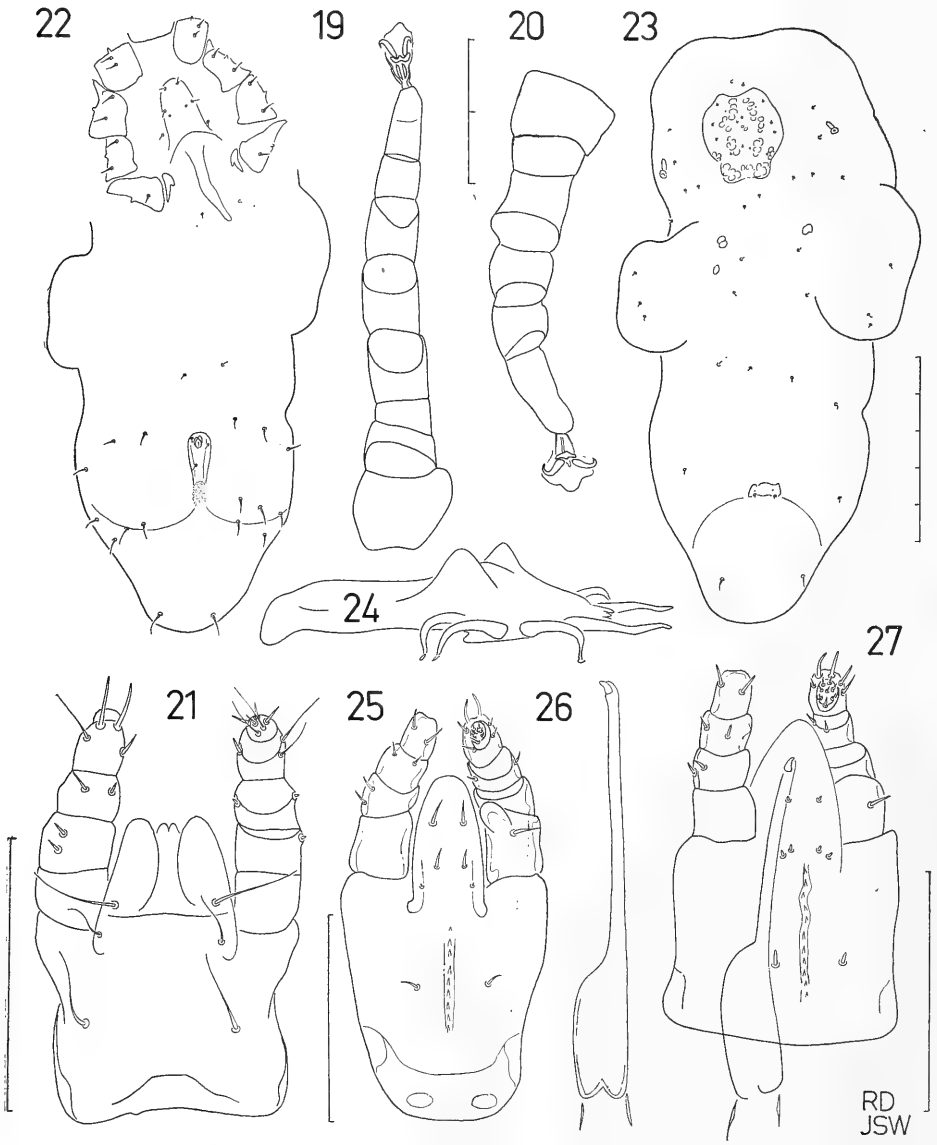
Ptilonyssus microecae, n. sp.

(Figs 25–26, 28–31)

Female.—An elongate mite with idiosoma about 850–880μ long in mounted, rather compressed specimens. Podosomal shield about one and a half times



Figs 13–18. *Larinyssus benoiti* Fain.—13, Idiosoma ♀ (ventral); 14, Idiosoma ♂ (ventral); 15, Idiosoma ♂ (dorsal); 16, Chelicera ♀ (lateral); 17, Leg III ♀ (dorsal); 18, Leg III ♀ (ventral).



Figs 19–21. *Larinyssus benoiti* Fain.—19, Leg IV ♀ (ventral); 20, Leg I ♀ (ventral); 21, Gnathosoma ♂ (ventral, with left palp dorsal).
Figs 22–24. *Ptilonyssus thymanzae* Domrow. Female.—22, Idiosoma (ventral, *M. chrysops*); 23, Idiosoma (dorsal, *M. chrysops*); 24, Whole mite ♀ (freehand, *M. notata*).
Figs 25–26. *Ptilonyssus microecae*, n. sp. Female.—25, Gnathosoma (ventral, with left palp dorsal, *Microeca*); 26, Chelicera (lateral, *Microeca*).
Fig. 27. *Ptilonyssus rhipidurae*, n. sp. Female.—Gnathosoma (ventral, with left palp dorsal).

as long as wide, and slightly wider in anterior half (223–228 × 154–161μ); with anterior and posterior margins nondescript and subequal, and lateral margins tending to convexity in anterior half. Shield not strongly outlined, very minutely granulate, with weakly marked muscle insertions and sixteen paired setae (in specimen figured, seta marked X is somewhat displaced to the front). Peritremalia and adjacent setae as in *P. rhipidurae*, n. sp. Middorsum with eight setae, of which midanterior pair is set between posterior of two pairs

of shieldlets. Hysterosoma with entire pygidial shield bearing traces of muscle insertions, at least one pore and two spinose pygidial setae ; surrounded by six setae arranged 4.2. All dorsal (and ventral) setae tapering to point somewhat stronger on posterior half of body.

Sternal shield elongate, very weakly defined and textureless, bearing two pores and six marginal setae. Genital shield shorter, somewhat flared posteriorly ; lateral margins not heavily sclerotized, bearing two genital setae ; disc denser, with granulations and muscle insertions ; operculum rayed. Anal shield almost twice as long as wide (125 × 74μ in holotype, 119 × 64μ in paratype), with anterior margin arched and lateral margins rather straight and sclerotized ; cribrum present. Anus set well forward, with adanal setae level with its anterior ; postanal seta present. Ventral cuticle with eight setae arranged 2.6 between genital and anal shields, and latter flanked by four additional setae.

Leg segments with setation as follows : coxae 2.2.2.1 ; trochanters 4.4.4.5 ; femora 9.7.4.5 ; genua 6.6.6.3 ; tibiae 7.7.6.6 (5 on one side of one specimen) ; tarsi –.15.15.15 (excluding two very fine terminal setae). Leg setae resembling those on coxae, slightly smaller dorsally ; two setae on dorsum of genu III set in enlarged alveoli ; two ventrodistal setae on tarsi II–IV slightly stronger. Tarsus I with dorsodistal sensory zone. Ambulacra I not greatly modified. Coxa II without process on anterodorsal margin.

Gnathosomal setae subequal to inner posterior hypostomals, slightly weaker than anterior hypostomals ; outer posterior hypostomals minute. Deutosternum with about nine denticles in single file. Chelicerae attenuate in distal two-thirds, with chelate portion occupying one-thirty-fifth of total length. Palpal setal formula 1.2.4.8 (including two dorsodistal tibial rods). Palpal trochanter distinctly salient on inner ventrodistal angle. Tarsus with about eight minute setae ; claw not detected. Tritosternum absent.

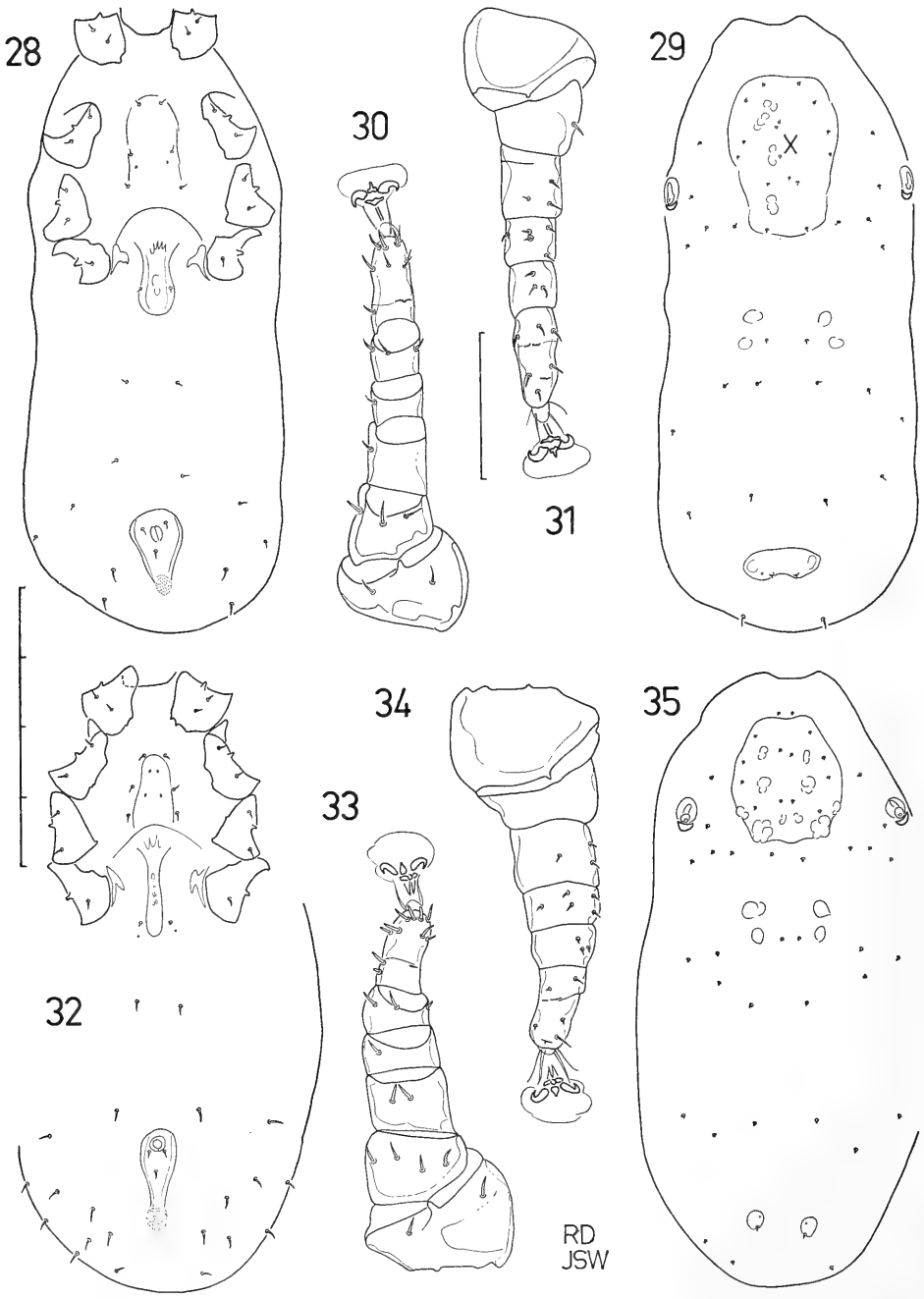
Discussion.—*P. microecae* recalls *P. motacillae* Fain, both possessing a saliency on the palpal trochanter, but the new species may be easily separated from Fain's by the shape and setation of the podosomal shield, the absence of a process on coxa II and (possibly) by the condition of the pygidial shield.

The few Malayan specimens from *Poliomyias mugimaki* (Temminck) (listed by McClure, 1963, as *Muscicapa mugimaki*) recorded by Fain and Nadchatram (1962) have the podosomal shield exactly as in *P. motacillae* and possess a process on coxa II. Further, at least in the specimen I have examined (through the courtesy of Dr. Fain), the pygidial shield is in a semidivided condition, being eroded midposteriorly. George (1961) has reported that the pygidial shield, while normally divided, may occasionally be entire in *P. echinatus* Berlese and Trouessart, while the opposite is true of two of thirteen females of *P. thymanzae* Domrow (1964*c*), *Myzantha melanocephala* (type host), Esk, 29.viii.1964, R.D. and J.S.W. I would tend to consider these Malayan specimens merely as variants of the widespread *P. motacillae*.

Types.—Two females were collected—one (holotype) from the nares of a jacky winter, *Microeca fascinans* (Latham), Esk, S.E.Q., 8.ii.1964, R.D., I.D.F. and J.S.W. ; and one (paratype) from a pale-yellow robin, *Eopsaltria capito* Gould, Mitchell River, xi.1964, R.D. Both hosts are muscicapids (Passeriformes). Holotype NIC ; paratype RD.

Ptilonyssus rhipidurae, n. sp.
(Figs 27, 32–35)

Female.—An elongate mite with idiosoma 693μ long in one unengorged and relatively uncompressed specimen, 781–869μ in replete specimens. Podosomal shield slightly longer than wide (172–178 × 143–156μ) ; anterior margin slightly concave, lateral margins convex and posterior margin weakly trilobed. Shield minutely granulate, with muscle insertions, including two posterolateral zones, weakly marked ; with twelve evenly arranged setae on



Figs 28–31. *Ptilonyssus microecae*, n. sp. Female.—28, Idiosoma (ventral, *Eopsaltria*); 29, Idiosoma (dorsal, *Eopsaltria*); 30, Leg III (ventral, *Microeca*); 31, Leg III (dorsal, *Microeca*).
Figs 32–35. *Ptilonyssus rhipidurae*, n. sp. Female.—32, Idiosoma (ventral); 33, Leg III (ventral); 34, Leg III (dorsal); 35, Idiosoma (dorsal).

shield, which is also preceded and followed by two setae. Five setae arranged 1.1.3 on each side between shield and peritremalia, which latter are as in *P. dicaei*, n. sp., but with poststigmatic shields present. Middorsum with band of ten setae, of which midanterior pair is between posterior of two pairs of shieldlets. Hysterosoma with row of six setae and two discrete, subcircular pygidial shields (each with pore and spinose seta, and flanked posterolaterally by one or two setae). All dorsal setae, except pygidials, minute rods ; setae on podosomal shield rather smaller than those on cuticle.

Sternal shield elongate, virtually textureless, but fairly well defined, bearing four pores and flanked by six setae. Genital shield narrow, with muscle insertions amidst longitudinal fluting ; operculum weakly rayed ; two genital setae and accompanying pores flank shield posterolaterally. Anal shield almost three times as long as wide (128–143 × 50–54μ), strongly arched anteriorly and slightly concave laterally ; lateral margins strongly sclerotized ; cribrum present, slightly expanded. Anus set well forward, preceding all three subequal anal setae. Ventral cuticle with six setae arranged 2.4 between genital and anal shields, and posterolaterally with 14 to 16 additional setae. Of setae on ventral cuticle and shields, only genitals are somewhat blunt, while remainder all taper to sharp point.

Leg segments with setation as follows : coxae 2.2.2.1 ; trochanters 4.4.4.5 ; femora 9.7.5.5 ; genua 6.6.6.3 ; tibiae 7.7.6.6 ; tarsi –.15.15.15 (excluding two extremely fine terminal setae). Setae on ventral face of segments (except on tarsi) tapering to point, resembling those on coxae; dorsal setae rather weaker. Some distal setae on tarsi II–IV somewhat bluntened. Tarsus I with dorsodistal sensory zone. Ambulacra I little modified. Coxa II with process on anterodorsal margin.

Gnathosomal setae twice as strong as posterior, and three times as strong as anterior hypostomals, all rather blunt. Deutosternum with about ten denticles in single file. Chelicerae attenuate in distal half, chelate portion occupying one-twenty-fifth of total length. Palpal setal formula 1.2.4.(7), two dorsodistal tibial rods included. Tarsus with about eight setae ; claw not detected. Tritosternum absent.

Discussion.—P. rhipidurae immediately calls to mind *P. macclurei* Fain, recorded from *Rhipidura albicollis* in Malaya and *R. leucophrys* in Australia (Fain, 1963*a* ; Domrow, 1964*c*). The two species may, however, be readily separated by the number of anal setae and the condition of the pygidial shield. Further, in *P. macclurei*, the setae of the idiosomal venter (coxae included) are stronger. (I might add that the merest traces of poststigmatic shields are present in *P. macclurei*, of which I have since taken two further series from *R. leucophrys* at Esk and Brisbane, 8 and 20.ii.1964, respectively.)

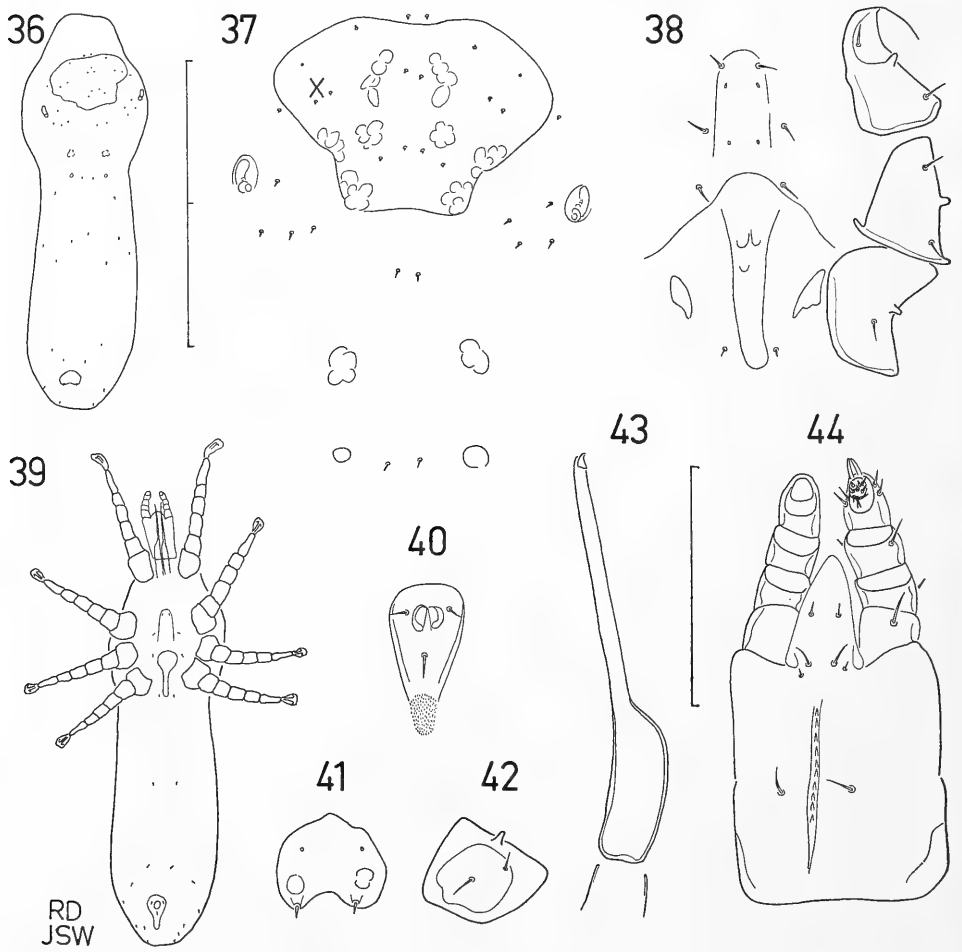
Types.—Four females were collected from the nares of a grey fantail, *Rhipidura fuliginosa* (Sparrman) (Muscicapidae, Passeriformes), Esk, 25.vii.1964, R.G.R. and J.S.W. Holotype NIC ; paratypes RD and AF.

Ptilonyssus dicaei, n. sp.

(Figs 36–44)

Female.—An elongate mite with idiosoma 960 and 1000μ long in two mounted, slightly compressed specimens. Podosomal shield one and a half times as wide as long (185 × 138 and 196 × 143μ) ; anteromedial margin slightly concave, anterolateral angles strongly convex ; posterior quarter of shield much narrower, with outline more irregular and slightly concave posteriorly. Shield with two pores and twelve setae, all paired (one of two setae marked " X " lacking on one side of one specimen) ; also two setae, both vertically and at anterolateral angles, set just off shield. Two closely-set setae immediately behind, and two groups of four setae between peritremalia and

posterolateral angles of shield. Middorsum with four shieldlets and eight setae arranged 2.6 in addition to two between posterior shieldlets. Pygidial shield convex anteriorly and concave posteriorly, with two pores and two spinose pygidial setae ; surrounding cuticle with eight setae arranged 4.4. Setae on podosomal shield weaker than remaining dorsal setae, perhaps slightly more spinose than figured. Both dorsal shields quite well defined, minutely granulate



Figs 36–44. *Ptilonyssus dicaei*, n. sp. Female.—36, Idiosoma (dorsal, freehand) ; 37, Podosomal shield, peritremalia and mid-dorsal shieldlets ; 38, Coxae II–IV, and sternal and genital shields ; 39, Whole mite (freehand, ventral) ; 40, Anal shield ; 41, Pygidial shield ; 42, Coxa I (ventral) ; 43, Chelicera (lateral) ; 44, Gnathosoma (ventral).

and with weak indications of muscle insertions. Each stigma provided with short peritreme, surrounded by very weak shieldlet. Poststigmatic shields absent.

Sternal shield elongate, weakly defined, virtually textureless and bearing SI and four pores ; SII and III free in cuticle. Genital shield narrow, not reaching beyond posterior margin of coxae IV ; granulate, with weakly rayed operculum and merest traces of muscle insertions ; flanked subposteriorly by two genital setae. Anal shield twice as long as wide (107 × 54μ in specimen with smaller podosomal shield), with anterior margin weakly defined and fairly straight ; lateral margins also straight, but more strongly sclerotized ; cribrum

present. Adanal setae near anterior of anus in specimen figured, but nearer posterior in second specimen. Postanal seta slightly stronger than adanals. Ventral cuticle with eight setae arranged 2.6 in front of, and six setae behind anus.

Leg segments with setation as follows : coxae 2.2.2.1 ; trochanters 4.4.4.3 ; femora 9.7.4.5 ; genua 6.6.5.4 ; tibiae 7.7.6.6 ; tarsi –.15.15.15 (excluding two extremely fine terminal setae closely associated with base of ambulacral stalk). Setae on ventral face of segments tapering, resembling those on coxae (two at apices of tarsi II–IV stronger) ; those on dorsum blunter and very much weaker. Tarsus I with dorsodistal sensory zone. Ambulacra I more slender than II–IV ; claws I slightly weaker than II–IV, little modified in shape. Coxa II without process on anterodorsal margin.

Gnathosomal setae slightly stronger than all three pairs of hypostomal setae, of which inner posteriors are longest and outer posteriors shortest. Deutosternum with about ten denticles in single file. Chelicerae attenuate in distal half, with chelate portion occupying one-thirtieth of total length. Palpal setal formula 1.2.4.8 (including two dorsodistal tibial rods). Tarsus with about eight minute setae ; claw seemingly present under oil-immersion, but extremely weak. Tritosternum absent.

Discussion.—The Old World and Australian nectar eaters, " a group of about 400 species entirely confined to the Old World and scarcely entering the north-temperate zone even there " (Darlington, 1957), comprise the four families Dicaeidae (flowerpeckers), Nectariniidae (sunbirds), Meliphagidae (honeyeaters) and Zosteropidae (silvereyes) (Mayr and Amadon, 1951). All four families are now known to be parasitized by an apparently closely related group of species of *Ptilonyssus* with the genital shield so narrowed that the genital setae, normally set on the shield itself, are left free in the adjacent cuticle.

Mayr and Amadon place the dicaeids next to the nectariniids, noting that their distributions are complementary, the former being Oriental-Australian and the latter African-Oriental, with only one species reaching Australia. One species of *Ptilonyssus*, *P. cinnyris* Zumpt and Till, has been described from African sunbirds, and may easily be separated from *P. dicaei* by having the podosomal shield decidedly longer than wide, with "a pair of conspicuous bristles on its posterior border ", and lacking the pygidial shield (*fide* Zumpt and Till, 1955 ; Fain, 1957). Dr. Zumpt has since kindly loaned me two paratype females of *P. cinnyris*, and, while they are much overcleared, they show, in addition to the two setae noted above, a pair of strong setae on each side between the podosomal shield and peritremalia. This recalls such species as *P. andropadi* Fain, *P. calamocichlae* Fain, *P. chlorocichlae* Fain, *P. ruandae* Fain, *P. prunellae* Fain and Bafort, *P. pittae* Domrow and *P. psophodae* Domrow (see Fain, 1957, 1963*a* ; Fain and Bafort, 1963*b* ; Domrow, 1964*b*).

Of the species of *Ptilonyssus* described from meliphagids, an essentially Australian family, *P. lymozemae* Domrow (1965*c*) shows a setal pattern on the podosomal shield most closely approaching that of *P. dicaei* (allowing for the minor movement of the vertical and extreme anterolateral pairs onto the shield proper). However, *P. lymozemae* shows obsolescent, divided pygidial shields in contradistinction to the fully-formed shield of *P. dicaei.*

P. ruandae Fain (1956*a*, 1957) is the only species of *Ptilonyssus* recorded from silvereyes, which are common in all three African, Oriental and Australian regions. This species, recorded both from Africa and Australia, shows a podosomal shield similar to that of *P. dicaei* in shape, with two anterolateral pores and an extremely similar setal pattern, both on and about the shield. Both species further possess entire pygidial shields and are, I believe, closely related. *P. ruandae*, however, has a more starkly cruciform podosomal shield, and exhibits several pairs of very strong dorsal setae quite absent in *P. dicaei.*

Types.—Three females were collected from the nares of a mistletoe-bird, *Dicaeum hirundinaceum* (Shaw) (Dicaeidae, Passeriformes), mist-netted in brushland at Mt. Jukes, near Mackay, N.Q., vi. 1964, R.D. and J.S.W. Holotype NIC; paratype RD. The third specimen, which was not taken into account in the above description, is in the care of Dr. Fain.

Ptilonyssus thymanzae Domrow
(Figs 22–24)

Three ♀♀ and 1 protonymph from two yellow-faced honeyeaters, *Meliphaga chrysops* (Latham), Samford, 18.i. and 8.v.1964, R.D., I.D.F. and J.S.W.; 1♀ from a Lewin honeyeater, *Meliphaga lewini* Swainson, Esk, 27.ii.1965, R.D. and J.S.W.; and 6♀♀ and 1 protonymph from a lesser Lewin honeyeater, *Meliphaga notata* (Gould), Innisfail-Palmerston Highway, 20.i.1965, H.I.McD. and G.J.B. (all Meliphagidae, Passeriformes), comprise new host records. All specimens have podosomal shields resembling that of the male sex figured by Domrow (1964*c*), while the females, especially of the first two series, are grossly engorged, with lobate body contours as in *P. meliphagae* Domrow, the anal and pygidial shields being just to the fore of the ventrally directed, posterior opisthosomal lobe (Figs 22–23). The midlateral dorsal lobes were seen to be erect and conical in life in the latter series (Fig. 24). The mouthparts of a female from *M. chrysops* are figured in Domrow (1965*c*). See also the above discussion on *P. microecae*, n. sp.

Ptilonyssus gliciphilae, n. sp.
(Figs 45–51)

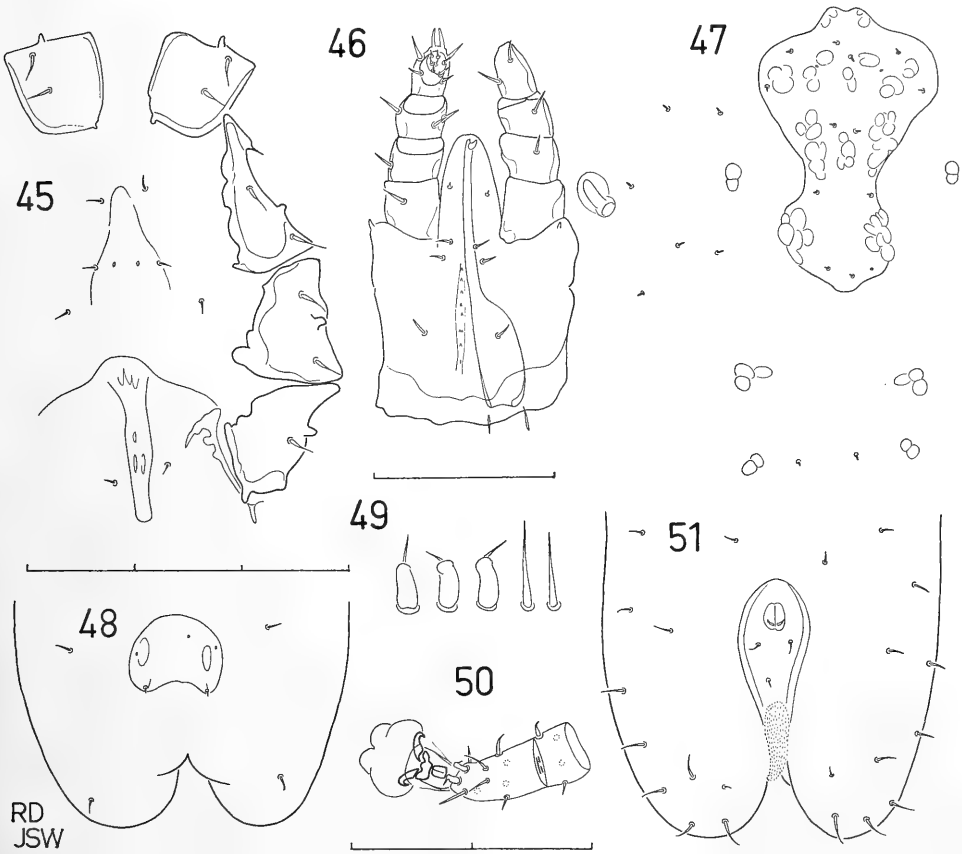
Female.—An elongate mite, but idiosomal length unavailable because of rupture during mounting procedure. Posterior margin of hysterosoma distinctly bilobed in one specimen. Podosomal shield one and a half times as long as wide (258 × 165μ); anteromedial margin "M"-shaped, anterolateral angles strongly convex; lateral margins concave, but shield expanding towards convex posterior margin. Shield with four pores and twelve setae, all paired (one posterior pore lacking on one side of one specimen); flanked midlaterally by two shieldlets. About six pairs of setae between shield and peritremalia, which latter are as in *P. dicaei*, n. sp. Middorsum with four shieldlets and 10 setae arranged 4.6 (not figured) in addition to two between posterior shieldlets. Pygidial shield much as in *P. dicaei*, both flanked and followed by one pair of setae. Both dorsal shields well defined, shagreened and marked by muscle insertions.

Sternal shield elongate, weakly defined, virtually textureless, and bearing SII and two pores; SI and III free in cuticle. Genital shield narrow, not reaching beyond posterior margins of coxae IV; with longitudinally arranged granulations, weakly rayed operculum and muscle insertions; flanked subposteriorly by two genital setae. Anal shield three times as long as wide (190 × 58μ), with anterior margin very strongly, and lateral margins only slightly convex; disc weakly granulate, but cuticle shagreened laterally; elongate cribrum present. Anal setae weak, particularly postanal; all behind anus. Two setae (not figured) on ventral cuticle between genital and anal shields, and latter shield surrounded by setae arranged 11.11 and 12.13, one of subposterior pairs being quite weak, cf. *P. myzanthae* Domrow, 1964*b*, also a parasite of meliphagids.

Leg segments with setation as follows: coxae 2.2.2.1; trochanters 4.4.4.5; femora 9.8.5.5; genua 6.7.7.5 (4 on one side of one specimen); tibiae 7.7.7.7; tarsi –.15.15.15 (excluding two extremely fine terminal setae closely associated with base of ambulacral stalk). Setae on ventral face of segments rather similar to those on coxae (two at apices of tarsi II–IV somewhat hypertrophied basally, with dorsally directed, filamentous apical portion at right angles to

shaft proper); those on dorsum considerably weaker, especially on legs I and II. Tarsus I with dorsodistal sensory zone. Ambulacra and claws much as in *P. dicaei*. Coxa II with strong process on anterodorsal margin.

Gnathosomal setae slightly stronger than subequal posterior hypostomals; anterior hypostomals extremely weak. Deutosternum with about eight minute denticles in single file. Chelicerae attenuate in distal half, with chelate portion occupying one-thirtieth of total length. Palpal setal formula 1.2.4.8 (including two dorsodistal tibial rods). Tarsus with about seven minute setae; claw not detected, even under oil-immersion. Tritosternum absent.



Figs 45–51. *Ptilonyssus gliciphilae*, n. sp. Female.—45, Coxae, sternal and genital shields; 46, Gnathosoma (ventral, with right palp dorsal); 47, Podosomal shield, peritremalia and mid-dorsal shieldlets; 48, Pygidium (dorsal); 49, Setae from tarsus IV (freehand); 50, Tarsus IV (ventral); 51, Pygidium (ventral).

Discussion.—Two other species of *Ptilonyssus* with accessory shieldlets flanking the podosomal shield are known from Australian meliphagids, *P. thymanzae* Domrow and *P. meliphagae* Domrow (1964*c*), but these have the podosomal shield, both in its shape and setation, quite different from that of *P. gliciphilae*. *P. gliciphilae* further differs (i) from *P. thymanzae* by the position of the adanal setae; and (ii) from *P. meliphagae* by the contours of the hysterosoma.

Types.—Two females were collected from the nares of brown honeyeaters, *Gliciphila indistincta* (Vigors and Horsfield) (Meliphagidae, Passeriformes), one

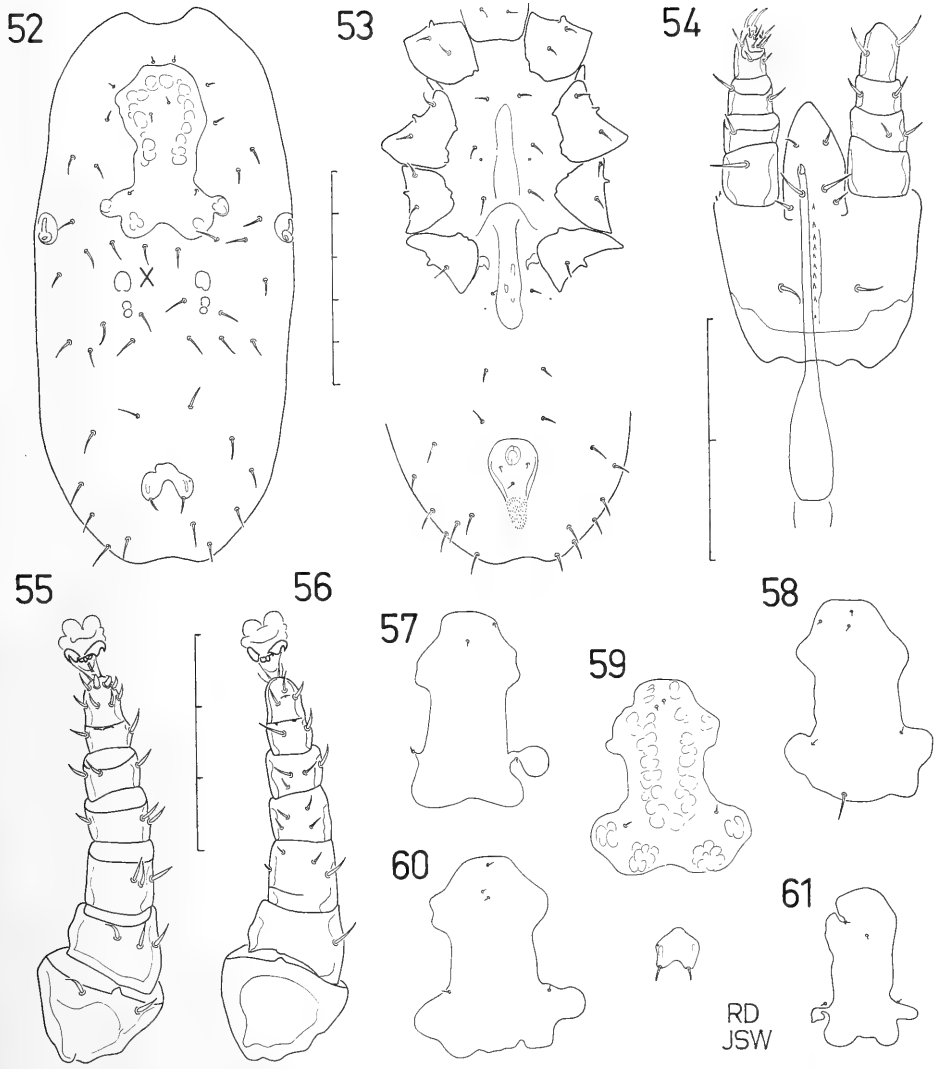
mist-netted in mangroves at Chelona, near Sarina, vi.1964; and one shot in flowering red bottle-brush (*Callistemon viminalis*), Esk, 15.x.1964, both R.D. and J.S.W. Holotype (the Chelona specimen) NIC; paratype RD.

Ptilonyssus stomioperae, n. sp.
(Figs 52–61)

Female.—An elongate mite with idiosoma 1,045–1,287μ long in four unengorged, relatively slightly compressed specimens (three from *Meliphaga*, one from *Stomiopera*), 1,386 and 1,529μ in two replete specimens from *Stomiopera*. Specimens from *Stomiopera* show a larger podosomal shield with antero- and posterolateral lobes well developed as in Figure 59. Three specimens show this format, the shield measuring 446–459 × 366–379μ. Two show the following aberrancies: one vertical seta on shield (Fig. 60) and one vertical and one body seta "X" on shield (Fig. 58). In both these specimens, the podosomal shield is longer (464μ), but wider (402μ) in the former and narrower (348μ) in the latter. A third aberrancy (Fig. 57) involves the loss of one posterolateral lobe, narrowing the shield to 459 × 324μ (measurements overall, as throughout this paper). Specimens from *Meliphaga* show the antero- and posterolateral lobes reduced, resulting in a smaller shield, typically 379–402 × 276–299μ in three specimens (Fig. 52). The fourth specimen is aberrant, with the shield even smaller (370 × 264μ), showing an increased insularity of the posterolateral lobes, leaving one shield seta marginal and the other free in the cuticle (Fig. 61). Shield well defined, distinctly shagreened and with muscle insertions particularly strongly marked in specimens from *Stomiopera*; bearing two usually closely-set setae anteriorly and two submarginal setae posterolaterally. Shield preceded by two vertical setae, flanked laterally by three pairs of setae and followed by two setae. Five additional setae arranged 1.1.3 present on each side between posterolateral lobes and peritremelia, which latter are contained in weakly sclerotized shieldlets. Middorsum with band of ten setae, of which midanterior pair is set between posterior of two pairs of shieldlets. Hysterosoma with about twelve setae surrounding pygidial shield, which is convex anteriorly and concave posteriorly, with muscle insertions and at least one pore laterally, and two pygidial setae posteriorly. In specimens from *Meliphaga* (Fig. 52), the shield is wider and somewhat irregular in outline; in specimens from *Stomiopera* (Fig. 59), it is narrower and more compact. All dorsal setae, including pygidials, particularly strong, except for verticals, those on, and one or two pairs flanking podosomal shield anterolaterally.

Sternal shield elongate, with extremely weak granulations and ill-defined margins; flanked by two pores and six setae. Genital shield narrow, distinctly granulate, with muscle insertions and rayed operculum; flanked subposteriorly by two setae and attendant pores. Anal shield slightly more than one and a half times as long as broad (219–233 × 120–125μ in three specimens from *Meliphaga* and two from *Stomiopera*; three other specimens from *Stomiopera* are 240–250 × 129–147μ); margins evenly rounded anterolaterally and fairly straight posterolaterally; cribrum present. Anus well forward, set in front of all three anal setae. Ventral cuticle with eight setae arranged 2.6 between genital and anal shields, which latter is flanked posterolaterally by an additional ten setae. Ventral setae also strong with exception of genitals and anals.

Leg segments with setation as follows: coxae 2.2.2.1; trochanters 4.4.4.5; genua 7.6.7.5; tibiae 7.7.7.7; tarsi –.15.15.15 (excluding two extremely fine terminal setae). Femora variable, 9.8.7 (6 on one side of one specimen) .6 in series from *Meliphaga*, and 9.8.8.6 (7 on one side of two specimens) in series from *Stomiopera*. Setae on ventral face of segments similar to those on coxae, but dorsal setae generally weaker. Two ventral setae at apices of tarsi II–IV with tips suddenly constricted and angulate, cf. *P. gliciphilae*, n. sp. Tarsus



Figs 52–61. *Ptilonyssus stomioperae*, n. sp. Female.—52, Idiosoma (dorsal); 53, Idiosoma (ventral); 54, Gnathosoma (ventral, with right palp dorsal); 55, Leg III (ventral); 56, Leg III (dorsal); 57–61, Podosomal shield (variants, 59 with inset of pygidial shield). (Figs 57–60 *Stomiopera*, remainder *Meliphaga*.)

I with dorsodistal sensory zone. Ambulacra I more slender than II–IV. Coxae II with process on anterodorsal margin.

Gnathosomal setae slightly smaller than inner posterior hypostomals; outer posterior and anterior hypostomals smaller still. Deutosternum with about ten denticles in single file. Chelicerae attenuate in distal two-thirds, chelate portion occupying one-thirty-fifth of total length. Palpal setal formula typically 1.3.4.8 (including two dorsodistal tibial rods), but may be one fewer setae on femur and/or genu. Tarsus with about six minute setae and weakly bifid claw. Tritosternum absent.

Discussion.—In showing the chelicerae suddenly attenuate distally and the pygidial shield entire and well developed, *P. stomioperae* is closest to *P. thymanzae* Domrow (1964*c*) among the species of *Ptilonyssus* parasitizing meli-

phagids, an essentially Australian group of passeriform birds. The former species, however, has the podosomal shield wider posteriorly, bearing only two pairs of setae, while this shield in the latter is wider anteriorly, and bears four to five pairs of setae. Further, the dorsal setation of *P. stomioperae* is decidedly heavier than that of *P. thymanzae*.

Types.—Ten females were collected from the nares of honeyeaters as follows: holotype and five paratypes from two white-gaped honeyeaters, *Stomiopera unicolor* (Gould), and four paratypes from a yellow honeyeater, *Meliphaga flava* (Gould), all mist-netted amidst flowering *Callistemon* in the bed of Magnificent Creek, Mitchell River, xi.1964, R.D. Holotype NIC; paratypes RD, AF and RWS.

Hattena panopla, n. sp.

(Figs 62–64)

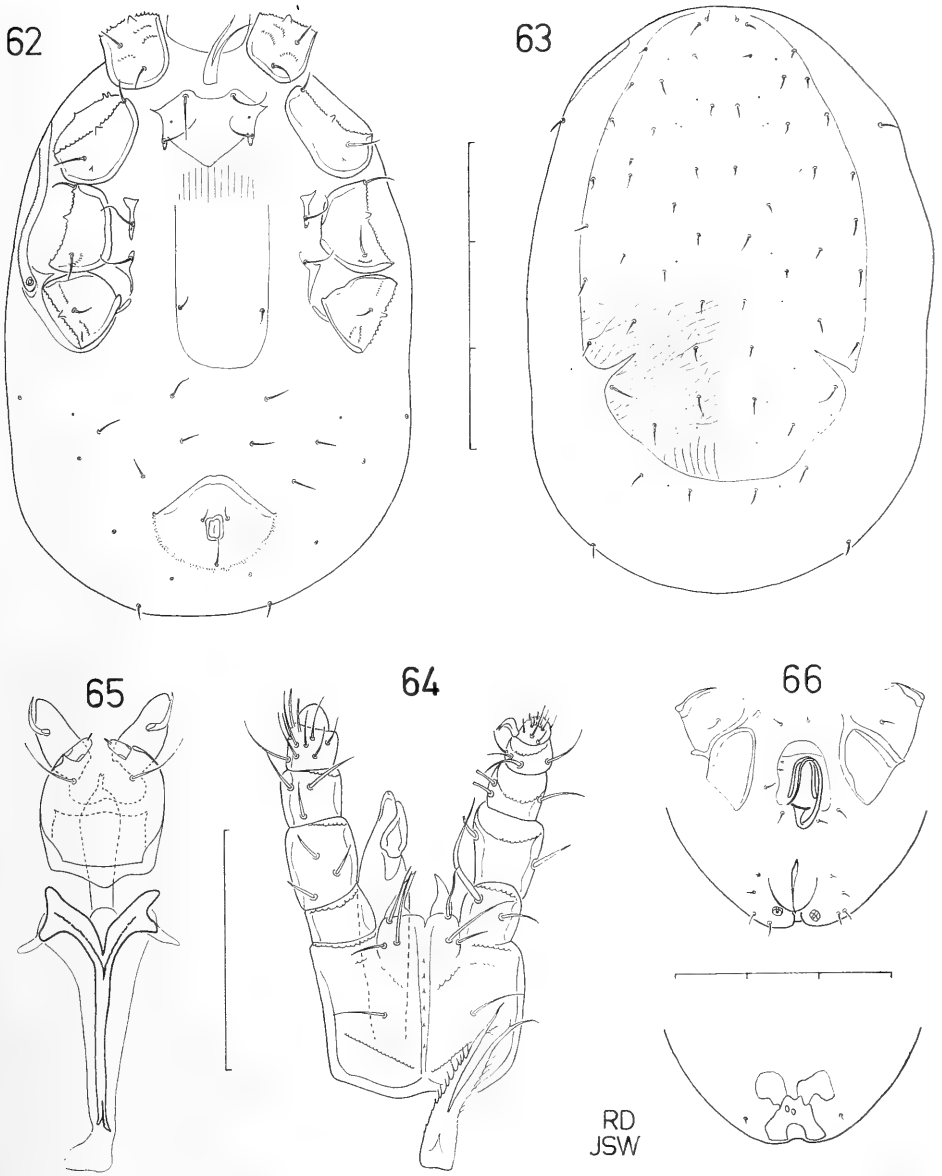
Female.—Idiosoma 547μ long in slightly compressed specimen. Dorsal shield reduced, marked by irregular, reticulate striae and lightly punctate. System of paired pores present on shield, together with 25 pairs of setae, of which four pairs are behind posterolateral incisions. Broad band of marginal cuticle with two setae humerally, two posteriorly and four in line closely following that of posterior margin of shield.

Sternal shield concave between SI, reduced and palely triangular behind SII, textureless. SI and accompanying pores on shield proper; SII and pores borne on minute posterolateral promontories. SIII and pores on shieldlets; metasternal setae on shieldlets. Genital shield unexpanded, barely reaching beyond posterior margins of coxae IV; bearing two setae and rayed operculum. Anal shield with anterior margin angularly convex and slightly denser than remainder of shield, whose surface is slightly reticulate. Posterior margin roundly convex, entirely occupied by narrow cribrum. Anus centrally placed, with adanal setae near its anterior margin, and weaker than postanal seta. Ventral cuticle with four pairs of setae preceding, and one pair following anal shield. Also with five pairs of distinct pores borne on small plaques. Peritremes extending forward to near level of posterior margin of coxae I, minutely crenulate at edges. Peritremal shields extended posteriorly to fuse with exopodal plates IV.

Coxae, some trochanters and gnathobase with rows of spinulose denticulations. Distal margins of leg and palpal segments similarly armed. All leg setae slenderly tapering, formulation as follows: coxae 2.2.2.1; trochanters 6.5.5.5; femora 12.10.7/6.6; genua 12.11.9.10; tibiae 12.10.8.10; tarsi –.16.16.16 (excluding two terminal filaments). This compares well with Till's (1963) formulae for *Androlaelaps* Berlese *s.l.* (including *Haemolaelaps* Berlese), except that one seta less is present on femora I and II and genu and tibia I. (The same formula occurs in *H. erosa* Domrow, where femur III is regularly 7.) Ambulacra all well developed, but claws obsolescent.

Gnathosomal and hypostomal setae subequal except for smaller outer posterior hypostomals. Deutosternum with six small denticles. Tritosternum small, but with two ciliated laciniae. Labial cornicles also small, sharply pointed. Palpal setal formula (trochanter to tibia) 2.5.6.14 (including two dorsodistal tibial rods), agreeing with that given by Till for *Androlaelaps*. Inner seta on palpal trochanter filamentous, and two on inner face of genu clavate. Tarsal claw two-tined. Chelicerae stout, with two strongly sclerotized digits, whose armature is not clear; corona absent.

Discussion.—As Baker and Yunker (1964) have recently reported blattisociine mites both in flowers and the nares of hummingbirds in America, it is of interest to note similar records from Australia. Members of this subfamily have been seen on the pollen-strewn beaks and bare facial skin of several noisy friar-birds, *Philemon corniculatus* (Latham) (Meliphagidae, Passeriformes), feeding in



Figs 62–64. *Hattena panopla*, n. sp. Female.—62, Idiosoma (ventral); 63, Idiosoma (dorsal); 64, Gnathosoma (ventral, with left palp dorsal).
Figs 65–66. *Passerrhinoptes pomatostomi*, n. sp. Male.—65, Gnathosoma and coxal apodemes I (ventral); 66, Hysterosoma (ventral above, dorsal below).

flowering *Eucalyptus* at Logan Village, S.E.Q., but these specimens are not now available for closer study. The opportunity has been taken, however, to describe a specimen from the nares of another honeyeater.

Using Evans' key (1957) (see also Chant, 1963), it is a little difficult to decide if this specimen is a blattisociine or a platyseiine, as the inner palpal trochanteral seta is filamentous, while the anterior hypostomals are not, etc. The former choice has been made, as, while the specimen little resembles the platyseiine genera figured by Evans and Hyatt (1960), it also shows the dorsal

shield laterally incised as in some blattisociine genera (Evans, 1958). However, in Evans' latter key, the new species will not run to either of the relevant genera, *Leioseius* Berlese or *Arctoseius* Sig Thor. Nor does it appear to belong to Baker and Yunker's two genera, *Rhinoseius* and *Tropicoseius*.

In some respects, particularly the erosion of the sternal shield and the shape of the anal shield, the new species appears congeneric with *Hattena erosa* Domrow (1963), described from an unidentified bird from Sabah (British North Borneo). In *H. erosa*, the dorsal shield (unincised) bears 21 pairs of setae and the sternal shield one pair; in *H. panopla*, the corresponding figures are 25 and two.

Types.—Holotype female from the nares of a brown honeyeater, *Gliciphila indistincta* (Vigors and Horsfield) (Meliphagidae, Passeriformes), Chelona, Sarina, vii.1964, G.B. Holotype NIC.

Family SPELEOGNATHIDAE

Speleognathopsis benoiti Fain

The following records (all adult specimens) are the first of this species from Australia: one from a black-fronted dotterel, *Charadrius melanops* Vieillot, Esk, 29.viii.1964, R.D. and J.S.W.; one from a red-kneed dotterel, *Erythrogonys cinctus* Gould, Mitchell River, xi.1964, R.D.; and ten from a masked plover, *Lobibyx miles* (Boddaert), Mitchell River, xi.1964, R.D. (all Charadriidae, Charadriiformes).

All three series show the seta on coxa II obsolescent (+), their coxal formulæ being, in turn, 2.+.1.1, 2.+.1.1 and 2.+.1.0. The first specimen agrees with the description of *S. charadricola* Fain (1964), except for the presence of (i) seta on coxa IV; and (ii) four setae (4B) rather than three (3B) on femur IV. The second specimen recalls *S. benoiti* Fain (1955, 1956*b*, 1963*b*), possessing five setae in the first postsensillary row and genital setae arranged 5.4, but differs from that species in having (i) only six setae (5B.1N) on femur I rather than 6B.1N; and (ii) three setae on femur IV rather than four. The third series agrees entirely with *S. charadricola*, but normally has four setae on femur IV rather than three (however, two show 4.3 and one even 3.3). Granting a considerable range of individual variation in this widespread and weakly sclerotized group of internal parasites, only one species need be involved, and I therefore consider *S. charadricola* a synonym of *S. benoiti*. This is further confirmed by a study of individual variation in the dorsal setal pattern of a series of 19 adults (one damaged specimen omitted) since collected in the nares of a single black-fronted dotterel (Mitchell River, 17.iv.1965, R.D.). The number of setae in the first postsensillary row was 4 three times, 5 seven times, 6 eight times and 7 once, the full formula for the lattermost specimen (2.7.4.3.2.5.2) showing three rows uneven.

Neoboydaia merops (Fain)

Four adults collected as follows are the first records of this species in Australia: rainbow-bird, *Merops ornatus* Latham (Meropidae, Coraciiformes), Esk, 29.viii.1964 and 27.ii.1965, R.D. and J.S.W.; and Innisfail-Palmerston Highway, i.1965, H.I.McD. and G.J.B. See Fain (1955, 1956*c*).

Family CHEYLETIDAE

Neocheyletiella artami, n. sp.

(Figs 67, 69)

Female.—An oval-bodied mite with idiosoma 366 and 410μ long in slightly compressed specimens. Dorsal shield evenly rounded, but very weakly defined anteriorly; narrower and irregular, but clearly demarcated posteriorly; virtually textureless and bearing two fine setae on extreme anterolateral margins. Dorsal

body cuticle with additional ten pairs of softly filamentous setae, all of which are minutely bipectinate, and two pairs of smooth adanal setae.

Ventral body cuticle with four sternal, two preanal and four adanal setae, all smooth. Valves of terminal genitoanal aperture each with four smooth setae.

Legs. Coxal apodemes I and II elongate, all discrete posteriorly; apodemes III and IV also discrete, but smaller. Coxal setal formula 2.1.1.1, all smooth. Remaining leg setation generally bipectinate (some pretarsals especially so), though shorter setae tend to be smooth, particularly ventrodistally. Trochanters 1.1.1.1, all ventral. All femora with one seta dorsally;

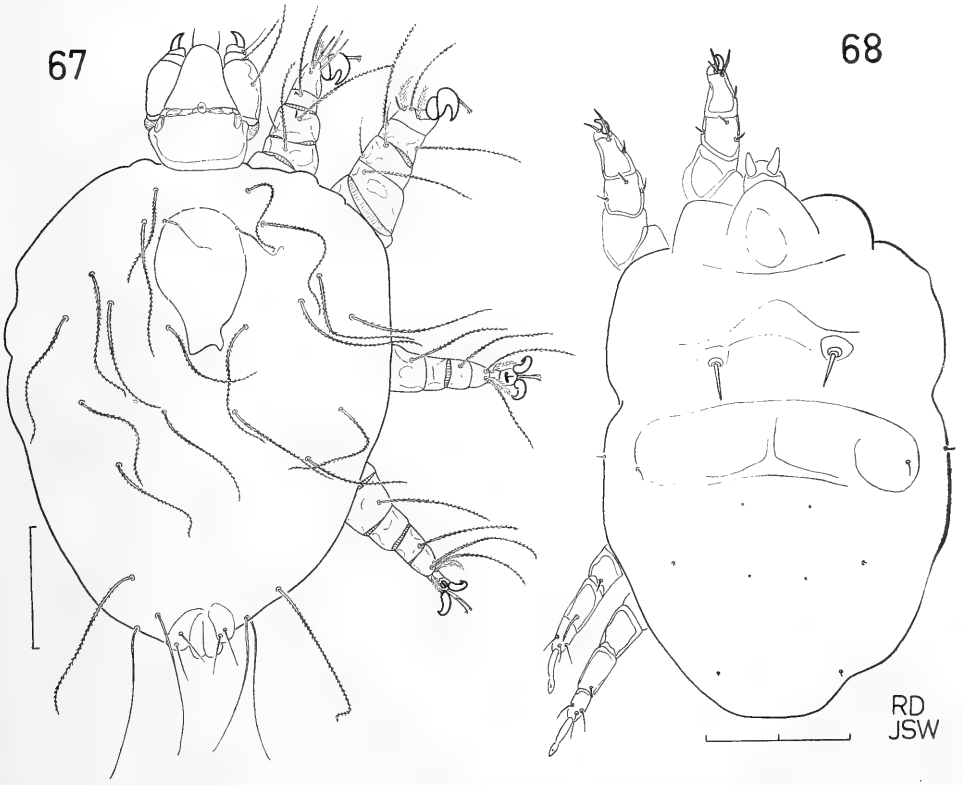


Fig. 67. *Neocheyletiella artami*, n. sp. Female.—Dorsum.
Fig. 68. *Passerrhinoptes pomatostomi*, n. sp. Female.—Dorsum.

I and II also with ventral seta. Genua I and II each with two setae dorsally; former also with dorsal rod; genu III with seta ventrally; genu IV asetose. Tibia I with one dorsal and three ventral setae; also with minute rod; tibia II with two setae both dorsally and ventrally; tibiae III and IV each with one seta dorsally and two ventrally. Tarsus I with five setae and five rods, four of latter borne on distinct dorsodistal saliency; tarsus II with seven setae and rod; tarsi III and IV with seven and six setae respectively, arranged as figured. Claws paired, strongly curved and somewhat swollen basally; attached to sclerotized basal apodemes. Pulvilli divided, with tips abruptly bent and minutely bifid.

Gnathosoma stout, with two setae ventrally on gnathobase and four on rostrum. Palpal trochanter obsolescent. Femur with one seta dorsally and two ventrally. Genu and tibia with seta both dorsally and ventrally. Tarsus

ill-defined, with about two setae and rod. All gnathosomal setae smooth except dorsal setae on palpal femur and genu. Chelicerae styliform, forming J with articulatory sclerites. Each arm of peritreme with five segments, sigmoid.

Discussion.—Of the species of *Neocheyletiella* Baker (1949) (less those forms with two dorsal shields removed in 1964 by Volgin to *Ornithocheyletia*), *N. artami* recalls *N. smallwoodae* Baker, but differs (as does *Ornithocheyla megaphallos*, *v. infra*), in having an additional pair of setae immediately behind the dorsal shield. Dr. R. L. Smiley, U.S. Department of Agriculture, Washington, has kindly compared my specimens with Dr. Baker's, and confirmed this difference.

Of the 19th century species listed by Baker (1949), only *Cheyletus macronycus* Mégnin (1878) seems near to *N. artami*. I am grateful to Dr. M. André, Paris, for the following information: "*Mégnin était Professeur à l'École Vétérinaire d'Alfort, près Paris. Sa collection est très probablement restée dans cette Institution mais, jusqu'ici, il n'a pas été possible de la retrouver. J'ignore si les échantillons sont provisoirement égarés ou bien s'ils ont disparu définitivement. En tout cas les exemplaires dont vous venez de me faire parvenir les illustrations sont certainement très voisins de* macronychus *et peut être appartiennent-ils à cette même espèce.*" Subsequent enquiries to Alfort have gone unanswered.

The genus *Ornithocheyla* was erected by Lawrence (1959), primarily on the male intromittent organ, for *O. megaphallos*, a parasite of a waxbill (Ploceidae, Passeriformes), for the loan of specimens of which I am most grateful to Dr. R. F. Lawrence, Natal Museum, Pietermaritzburg. *N. artami* is readily separated by its unisetose trochanter III, and the presence of a seta dorsally on tibia III and an additional seta on the ventral face of tarsus III. In addition, coxal apodemes I and II are free distally, the dorsal setae on femur and genu I are longer, and genuala I is internal to the adjacent seta.

Types.—Holotype female and paratype female from the dusky woodswallow, *Artamus cyanopterus* (Latham) (Artamidae, Passeriformes), Exeter, Tas., 9.iv.1964, R.H.G. Holotype NIC; paratype RD.

Family TROMBICULIDAE

Odontacarus australiensis (Hirst)

New host records for larvae of this species are: five from eyelids of one, and two from another Australian black-shouldered kite, *Elanus notatus* Gould (Accipitridae, Falconiformes), Dalby, 14.vi.1963, I.D.F. and R.G.R.; five from a nankeen kestrel, *Falco cenchroides* Vigors and Horsfield (Falconidae, Falconiformes), same data; nine from a grey-crowned babbler, *Pomatostomus temporalis* (Vigors and Horsfield) (Timaliidae, Passeriformes), Condamine, same data; three from a black-faced cuckoo-shrike, *Coracina novaehollandiae* (Gmelin) (Campephagidae, Passeriformes), Condamine, 6.vii.1963; 27 from a rufous whistler, *Pachycephala rufiventris* (Latham) (Pachycephalidae, Passeriformes), same data; and three from a noisy friar-bird, *Philemon corniculatus* (Latham) (Meliphagidae, Passeriformes), Logan Village, 16.vii.1963, R.D., I.D.F. and R.G.R. See Hirst (1925), Domrow (1956) and Brennan (1959). Also 1 larva from a Lewin honeyeater, *Meliphaga lewini* Swainson (Meliphagidae, Passeriformes), Innisfail, 2.viii.1965, R.D. and J.S.W.

Trombicula shiraii Sasa, Kano and Ogata

This species, previously known only from two larvae from the eastern golden plover, *Pluvialis dominica* (Müller) (Charadriidae, Charadriiformes) in Japan, may now be recorded from Australia as follows: 15 larvae from the bar-tailed godwit, *Limosa lapponica* (Linnaeus) (Scolopacidae, Charadriiformes), Heron Is., Great Barrier Reef, 8.i.1964, J.B. Japan and Australia are included in the range of both hosts. See Sasa *et al.* (1952) and Sasa and Jameson (1954).

LEPTOTROMBIDIUM MYZANTHA (Womersley)

Eleven larvae from a green-winged pigeon, *Chalcophaps chrysochlora* (Wagler) (Columbidae, Columbiformes), mist-netted at Mt. Jukes, Mackay, vi.1964, R.D. and J.S.W. ; and five larvae from a pale-yellow robin, *Eopsaltria capito* Gould (Muscicapidae, Passeriformes), Innisfail-Palmerston Highway, 11.ix.1964, H.I.McD., have been examined. See Gill *et al.* (1945), Womersley (1952), and Womersley and Audy (1957). The last authors say " the subgenus is not indicated in the original description of the larva on p. 71 ", but this is not true of either copy in this Institute. They further wonder if the " lousy jack " is the grey butcher-bird (*Cracticus torquatus*), but, in my experience, it is *Struthidea cinerea*, the apostle-bird (i.e. the first of the birds listed by Gill *et al.*), that goes commonly under this name in Queensland. The name stems from their frequent infestation with mites (presumably tropical fowl mites, which are popularly called " sparrow lice "), and has since been reported to me to be in use for two other Queensland birds, the grey-crowned babbler (*Pomatostomus temporalis*) and the introduced Indian myna (*Acridotheres tristis*). Of the several common names for *Struthidea* and *Pomatostomus*, " apostle-bird " and " happy family " are used interchangeably, while the former is also applied to the white-winged chough (*Corcorax melanorhamphus*). All three are gregarious (Cayley, 1963).

NEOSCHOENGASTIA POSEKANYI Wharton and Hardcastle

This widespread member of a bird-parasitic genus (Wharton and Hardcastle, 1946 ; Sasa and Jameson, 1954) has been once recorded from Australia (Derrick and Womersley, 1954), and the following material has since been noted : one larva (ACB635, formerly ACA1334), Wondecla, N.Q., 7.x.1943, R.V.S. ; and a very active colony of 12–15 reddish, newly-hatched larvae on top of burnt tree-stump, about 2′6″ from ground, Samford, 14.xi.1963, R.D. and I.D.F.

Dr. R. V. Southcott, Adelaide, has kindly made available his field notes on the first specimen. It was taken running over a book on an army field exercise in rainforest, and was recognized, at × 28, as a trombidiform larva. It was red in colour and reminded one of *Microsmaris* Hirst (Erythraeidae, see Southcott, 1961). Its eyes appeared 1 + 1 and between them were seen two dots. These dots were undoubtedly the expanded sensillae, which also appear quite dark in the Samford series, which was mounted directly from spirit into Hoyer's medium on the morning of capture. The eyes are rather 2 + 2, but they are borne on each side on a distinct ocular plate, and the posterior two are quite dwarfed by the convex corneae of the anterior pair.

Family TURBINOPTIDAE

PASSERRHINOPTES POMATOSTOMI, n. sp.

(Figs 65–66, 68, 70)

Female.—Idiosoma 750–770μ long in three mounted (but only slightly compressed) specimens, 836μ in fourth flattened specimen. Ovate, with five blunt extensions anterolaterally above gnathosoma and trochanters I and II (formermost bearing merest suggestion of dorsal shield) ; slightly constricted just in front of coxae III ; cuticle largely textureless, except for striations outlining evenly-arranged lobules middorsally, two of which each bear heavy seta with sclerotized insertion. Posterolateral margins with three pairs of setae (anterior pair much more evident than remainder) surrounding four pores. Pair of supracoxal III setae present.

Vulva transverse, flanked by six setae (anterior pair issuing from contiguous bases in one specimen) ; endogynium absent. Anus longitudinal ; adanal setae in four pairs. Details of unpaired internal duct near anus not clear.

Legs with five free segments, coxae incorporated into body wall. Apodemes I fused to form Y, with posterior arm twice as long as anteriors ; II sigmoid ;

III and IV contiguous and virtually complete. Coxal, trochanteral and femoral setal formulae 1.0.1.0, 1.1.1.0 and 1.1.0.0, respectively. Genua I and II with two basal setae and distal solenidion; genu III with solenidion; genu IV unarmed. All tibiae with seta (point of insertion variable) and dorsodistal solenidion (solenidia I–III three times as long as IV). Tarsi I and II much compacted, heavily sclerotized; with dark, curved claw issuing dorsally, together with two and one solenidia, respectively; each with about six minute setae ventrally. Tarsi III and IV normally formed, fully half as strong as corresponding tibiae, each with four slender setae (three dorsal and one ventral). It seems likely that the thickened (but pale and straight) structures set

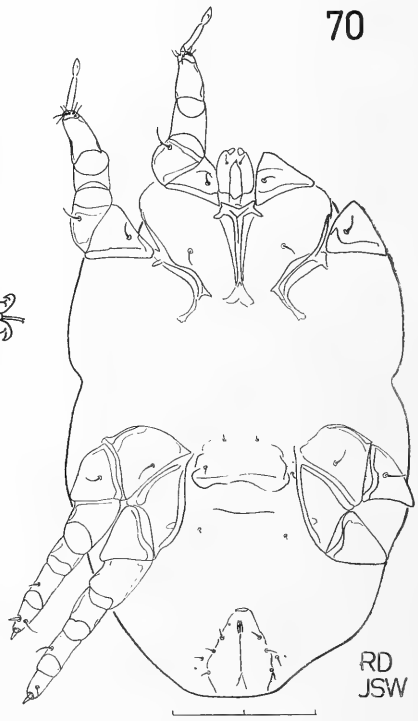


Fig. 69. *Neocheyletiella artami*, n. sp. Female.—Venter.
Fig. 70. *Passerrhinoptes pomatostomi*, n. sp. Female.—Venter.

terminally on the ventral aspect of tarsi III and IV are setae rather than claws. They are quite unlike claws I and II, and much resemble the thickened ventral seta on tarsus III. All ambulacra stalked and slightly expanded distally; I and II issue beneath claw, III and IV above terminal " spine ".

Gnathosoma as in male.

Male.—As in female unless otherwise stated. Idiosoma 660μ long. Hysterosoma with irregular X-shaped shield, whose posterior arms are the more heavily sclerotized; notched midposteriorly. Remnants of genital discs present. Penis support in reversed U; penis elongate, slenderly tapering throughout its single coil. Anal discs small, diameter 13μ. Gnathosoma minute, with two ventral setae. Palpi displaced ventrally, very weak, apparently with only one segment and at least one seta. Chelicerae set into biconcave dorsal emargination; shaft and fixed digit stout, movable finger very weak and slender.

Nymphs.—At least two free nymphal stages occur. One (apparently subadult) has idiosoma 750–760μ long, and is similar to female except for lack of vulva, ambulacra on all tarsi and fully-formed coxal apodemes III and IV. An earlier stage (640μ) is similar to subadult, but lacks all trochanteral, tibial IV and all but two genital setae.

Discussion.—Only one other species of *Passerrhinoptes* is known, *P. andropadi* Fain, which has been recorded from bulbuls (Pycnonotidae) in Africa and babblers (Timaliidae) in the Orient (see Fain, 1956*d*, 1960 ; Fain and Bafort, 1963*a* ; Fain and Nadchatram, 1962). Dr. Fain has kindly lent me paratypes of his species, as well as his Malayan specimen, and *P. pomatostomi*, while also a parasite of a babbler, is clearly separable in both sexes by (i) its two heavy dorsal setae ; and (ii) the proportions of the arms of the fused coxal apodemes I. Further, in the male, the adanal discs are decidedly larger, and the details of the opisthosomal shield differ.

Types.—Holotype female, allotype male, three paratype females and four morphotype nymphs from the nares of a grey-crowned babbler, *Pomatostomus temporalis* (Vigors and Horsfield) (Timaliidae, Passeriformes), Esk, 29.viii.1964, R.D. and J.S.W. Holotype and allotype NIC ; paratypes RD and AF.

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DEVELOPMENT OF THE EGGS AND EARLY LARVAE OF THE AUSTRALIAN SMELT, *RETROPINNA SEMONI* (WEBER)

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(Plates vii–ix)

[Read 28th July, 1965]

Synopsis

Retropinna semoni (Weber) is a small freshwater fish, occurring widely in eastern Australia. Its eggs, embryonic development, and early larvae are described.

Introduction

The Australian smelt, *Retropinna semoni* (Weber), has a wide distribution in eastern Australia, occurring throughout the great Murray-Darling River system and also in coastal streams (Munro, 1957). The species grows to a length of only 10 cm. and is unimportant either commercially or to the angler. However, in many areas it is extremely abundant and is preyed upon by several of the larger fishes utilized by man (Butcher, 1945 ; personal records).

The following account of the eggs, embryonic development, and early larvae of *R. semoni* is based on studies carried out at the Inland Fisheries Research Station, Narrandera, New South Wales. The studies were initiated following evidence of natural breeding in one of the experimental ponds at this Station.

Methods

Following the discovery of larval stages of *R. semoni* in an experimental pond on September 22, 1961, collections of adults in reproductive condition were made from the pond later the same day and also on September 23.

A first attempt to obtain fertilized eggs was made by adding milt to ova, apparently ripe but not strippable, removed from a female by dissection. No fertilization was achieved.

A second attempt proved successful. On this occasion the ova were readily stripped from a female, measuring 75 mm. total length, by applying slight pressure on the abdomen. Milt was expressed from a male, measuring 73 mm., in a similar manner, and placed onto the eggs held in a Petri dish. Water was immediately added to cover the eggs and the whole mixed by gentle shaking. Approximately 20 minutes later the eggs were washed with several changes of water and then transferred to a shallow enamel tray. This was immersed in a deeper tray, through which water was circulated. On the eighth day, when hatching appeared imminent, the water circulation was stopped to avoid loss of larvae in the overflow.

The temperature of the water flowing over the eggs was not controlled, but for the greater part of the hatching period fluctuated within the range 15.5 to 18.0°C. On two occasions, for periods of three to four hours, the temperature fell to about 13°C.

Measurements were made with an ocular micrometer. The photographs were taken using transmitted light.

Efforts were made to rear the larvae in glass and plastic containers in the laboratory. However, although various kinds of finely ground food were supplied, no feeding was observed and the longest that any larvae survived was 8 days.

The Eggs

The eggs when stripped are spherical, with an average diameter of 0.80 mm. Following fertilization they swell to an average diameter of 0.95 mm. They sink in fresh water and are strongly adhesive, becoming firmly stuck to the bottom of the hatching tray. The yolk is pale amber in colour. Initially it completely fills the egg, but quite a large perivitelline space is formed during the swelling of the thin capsule. One to several large and many small oil globules are present within the yolk.

Embryonic Development

The formation of the blastodisc commences almost immediately upon fertilization. Cytoplasm, which has hitherto invested the yolk in an invisible layer, slowly accumulates at the animal pole of the egg (Plate vii, fig. 1). When concentration of the cytoplasm is complete the formed blastodisc is of a lenticular shape, the surface of the yolk immediately opposite having flattened (Plate vii, fig. 2).

The first three or four cleavages occur within 3 hours following fertilization. These early cleavages, at least up to and including the fourth, take place regularly throughout the blastoderm, the blastomeres formed being fairly uniform in size (Plate vii, fig. 3). In a small number of eggs the cleavage rate was slower and in a few the cleavages were irregular, so that unequal blastomeres were formed. However, these eggs having retarded and/or obviously irregular development all died during the first two days. Subsequent mortalities until after hatching were few and development progressed more or less uniformly in all eggs.

Sixteen hours after fertilization the blastodermal cap has been formed. It is of a similar lenticular shape to that of the blastodisc but more opaque (Plate vii, fig. 4).

About 22 hours after fertilization the germ ring has reached approximately an equatorial position about the yolk. It is slightly thickened and appears to constrict the yolk sphere as it advances over it (Plate vii, fig. 5). The thickening of the germ ring is more pronounced on one side than the other, the thickened portion marking the posterior pole at which the embryonic shield develops.

The embryo is clearly evident and shows marked development at 41 hours. It extends approximately two-thirds the way around the yolk, and is noticeably thickened in the cephalic region. The thin blastodermal layer now almost fully encloses the yolk, except at the blastopore, situated just posteriorly to the tail end of the embryo, through which there is a slight bulging of the yolk.

About 47 hours after fertilization, the optic vesicles are easily discernible (Plate vii, fig. 6). The embryo is much thickened along its whole length, especially in the cephalic region, and dorsally protrudes markedly into the perivitelline space. Kupffer's vesicle, a small transparent sphere lying ventrally near the posterior end of the embryo, has appeared.

Considerable differentiation has occurred in the embryo by 66 hours after fertilization (Plate viii, figs 7, 8). The eyes are now very clear and the pupils have developed. The head is further enlarged and the lobes of the brain are apparent. Auditory capsules are present and more than 30 mesodermal somites are distinguishable. The embryo almost fully encircles the yolk, which is slightly constricted around the line of contact. To this point no pigmentation has been developed.

The embryo more than fully encircles the yolk at 95 hours, the tail slightly overlapping the head (Plate viii, fig. 9). The heart, which was not distinguished at 66 hours, is now easily seen. It is situated just under and posterior to the

eyes, and pulsates quite regularly. The first pigmentation has now appeared as series of melanophores on the sides of the body, along portion of the midline and to a lesser extent along the ventral edge. Otoliths have developed within the auditory capsules. The first movements, slight twitchings, of the embryo were observed at this stage.

At about 113 hours the embryo extends approximately one and a quarter times around the yolk, and the eyes are becoming quite heavily pigmented. Movements of the embryo are now more frequent, the posterior portion of the body being detached from the yolk and moving freely.

From this stage until hatching there is a continued increase in the length of the embryo, so that at 137 hours it encircles the yolk approximately one and a half times (Plate viii, fig. 10) and at 165 hours about two times (Plate viii, figs 11 and 12). There is a marked lateral expansion of the head, causing it to be roughly triangular in shape by 165 hours (Plate viii, fig. 12). The melanophores along the body increase in number, becoming more uniform and pronounced, and others develop at about 130 hours over the yolk sac. The dorsal and ventral fin-folds are clearly evident at about 130 hours.

Towards hatching the embryo moves almost incessantly, the tail twisting and switching from side to side and at intervals the whole embryo revolves completely within the egg capsule. The pectoral fins, now evident as transparent fan-like structures slightly posterior to the auditory capsules, become active and beat rapidly for increasing periods of time from about 210 hours onwards.

Hatching commenced at 216 hours after fertilization and all the larvae had emerged from the egg capsules by 225 hours.

The Larvae

The newly hatched larvae (Plate ix, figs 13 and 14) are extremely elongate in form, the average total length being 4.61 mm. The head is inflected downwards and is anteriorly rounded, so that the eyes appear ventrally placed. The mouth is present as a small opening situated below the eyes, but is probably non-functional for the first day or so after hatching. The auditory capsules are comparatively large and protrude prominently from the sides of the head. A small mass of yolk contained in an elongate, ovoid sac is still present at hatching. A single oil globule is present within the anterior end of the yolk sac. The hind portion of the alimentary canal is clearly evident as a long, straight tube and the anal opening is situated two-thirds the way along the body. Both the dorsal and ventral fin-folds are fairly uniform in height throughout and are continuous with the caudal fin-fold, which is slightly more expanded and lobate.

On hatching, the larvae congregated near the surface and sides of the hatching tray. For most of the time they remained fairly passive, normally orientated horizontally with dorsal side uppermost, but occasionally, particularly if disturbed, swimming actively with apparently well directed movements.

One day after hatching, the yolk sac and contained oil globule are both much reduced in size (Plate ix, fig. 15). The head has now pivoted forwards and upwards, so that the mouth is situated more anteriorly and the eyes lie slightly more dorsally than in the newly hatched larva. The straightening of the head contributes to a relatively large increase in length, so that the average total length attains 5.25 mm.

After two days the yolk has been almost completely absorbed and the oil globule has disappeared (Plate ix, fig. 16). Up to this time there is evidence of continued differentiation in the larvae, particularly in the head region. The jaws are now well developed, the auditory capsules further enlarged, and the pectoral fins larger, stronger and much easier to see. Compared with the increase in length over the first day, that during the second is small, the average total length of the two-day larvae being 5.29 mm.

Following the complete utilization of the yolk on the third day, development of the larvae almost ceased and there was evidence of emaciation. This was undoubtedly due to unsuitability of food provided. A slight increase in length occurred to the fifth day, the average total length of larvae then surviving being 5.51 mm. No further growth was recorded and the single eight-day larva measured only 5.30 mm., the shrinkage possibly being due to a natural consolidating of tissues, but more probably to the larva having to resort to its own body substance for nourishment.

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EXPLANATION OF PLATES VII–IX

Plate vii

Fig. 1. Egg 17 min. after fertilization. Incomplete blastodisc.—Fig. 2. Egg 1 hr. after fertilization. Complete blastodisc.—Fig. 3. Egg 3 hr. after fertilization. Sixteen cells.—Fig. 4. Egg 16 hr. after fertilization. Blastodermal cap.—Fig. 5. Egg 22 hr. after fertilization. Germ ring at equatorial position.—Fig. 6. Egg 47 hr. after fertilization. Blastopore closed, embryo protruding into perivitelline space, and optic vesicles evident.

Plate viii

Figs 7, 8. Egg 66 hr. after fertilization. Brain lobes, pupils of eyes, auditory capsules, and somites distinct.—Fig. 9. Egg 95 hr. after fertilization. Embryo completely encircling yolk, first pigmentation on body.—Fig. 10. Egg 137 hr. after fertilization. Embryo encircling yolk approx $1\frac{1}{2}$ times, eyes heavily pigmented, melanophores over yolk sac.—Figs 11, 12. Egg 165 hr. after fertilization. Very advanced embryo, encircling yolk approx. 2 times.

Plate ix

Figs 13, 14. Newly hatched larva. Average length 4·61 mm.—Fig. 15. One day old larva. Average length 5·25 mm.—Fig. 16. Two days old larva. Average length 5·29 mm.

THE FIRST ZOEA OF THE SOLDIER CRAB *MICTYRIS LONGICARPUS* (GRAPSOIDEA : MICTYRIDAE)

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(*Communicated by Dr. E. J. Reye*)

[Read 28th July 1965]

Synopsis

The first zoea of *Mictyris longicarpus* is described and figured.

M. longicarpus Latreille, 1806, is one of the most characteristic elements of the estuarine sand flat fauna on the eastern Australian coast. No information on its larval development is available.

METHODS

Ovigerous female *M. longicarpus* were collected from Moreton Bay, southern Queensland, and kept in aerated filtered seawater containing 200,000 i.u. of penicillin per litre. All experiments were carried out at 25°C but the photoperiod was not controlled. Usually seawater was changed daily, occasionally after two days.

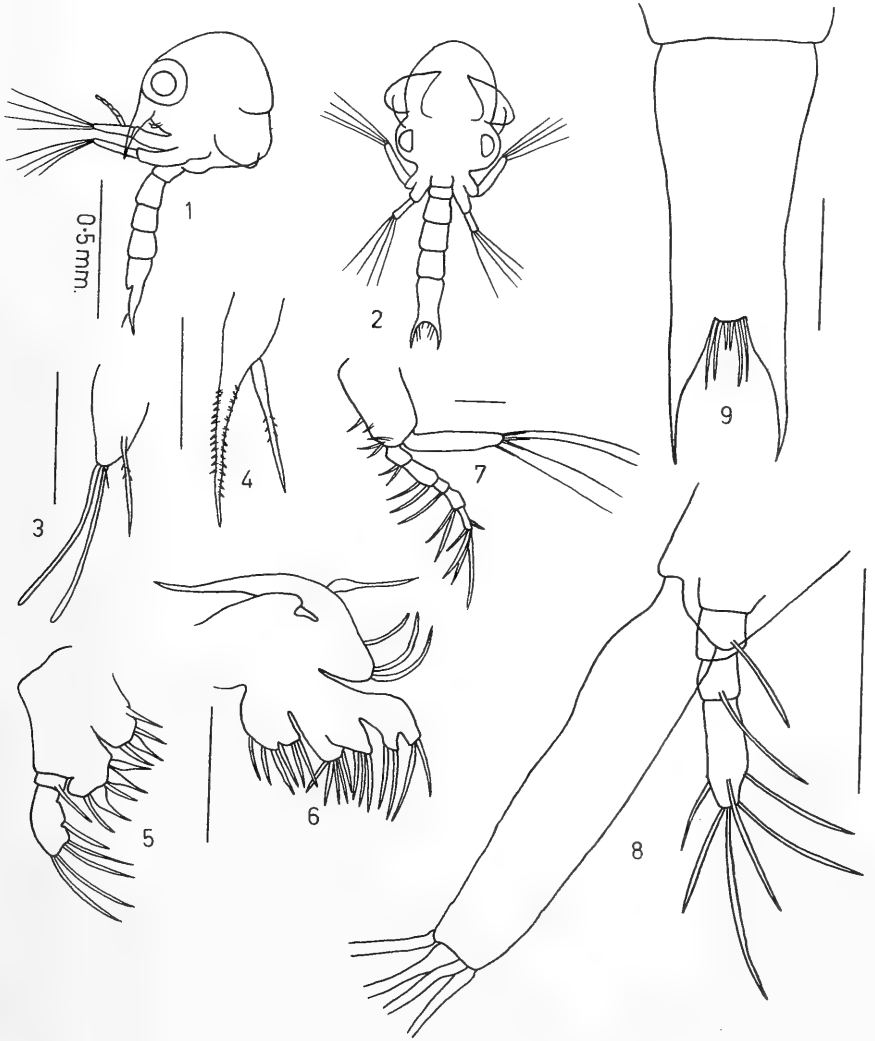
When hatching was imminent each female was confined to a separate container, at first an aquarium, later a finger bowl. By this method, many " prezoeae " were obtained but all remained sluggishly on the bottom of the container. The eggs of one female hatched successfully. She was observed to flex and relax her abdomen rhythmically, sweeping the pleopods outwards and inwards with the same rhythm. Thus the hatching larvae were swept out and away from the rest of the egg mass. All the eggs this female was carrying hatched within a period of ten minutes, and all were first zoeae. They swam actively and continuously and aggregated in that part of the finger bowl where maximum illumination prevailed.

Because of the limited success obtained with the method described above, egg masses were removed from females prior to hatching. Groups of from 100 to 500 eggs were dissected under the microscope and were placed in a compartmented perspex container with a water depth of 2.5 cm. The compartments were of two sizes, having surface areas of approximately 20 and 40 cm^2. The maximum number of eggs per square cm. of water surface was 25. A shaking machine vibrating through a very small amplitude at 120 times per minute housed the container, which was covered with a lid of the same transparent perspex. Successful hatching was obtained repeatedly under these conditions and eggs were maintained for up to eight days prior to the hatching of healthy zoeae.

After hatching, the zoeae were divided into groups of from 10 to 200 per compartment. Any sluggish or dead larvae were removed when the seawater was changed. *Artemia* nauplii were added to the compartments but were not eaten by the zoeae. *Melarapha scabra* trochophores were similarly rejected. Zoeae survived for twelve days, eventually dying of starvation.

Description of the First Zoea

The first zoea of *M. longicarpus* is illustrated in Figures 1–9. The cephalothorax bears a rostral spine only. The dorsal and the lateral spines are absent. Extensive flanges are present on the lateral and postero-lateral margins of the carapace. There are five abdominal segments and the telson, all of which have chromatophores. There is a secondary chromatophore on the first maxilliped but none on the second.



Figs 1–9. 1, Lateral view of *M. longicarpus* first zoea. 2, Posterior view. 3, Antennule. 4, Antenna. 5, Maxillule. 6, Maxilla. 7, First maxilliped. 8, Endopodite of second maxilliped. The four setae of the exopodite have been truncated. 9, Telson.
The scale lines for Figs 3–9 are 0·1 mm.

The antennule (Figure 3) has two terminal aesthetes and a terminal seta about one-fifth the length of the aesthetes. A subterminal spine is also present. The antenna (Figure 4) has a tapered protopodite which bears two rows of short spines. The exopodite bears a long spine somewhat swollen proximally. This antenna is of the B_1 type of Aikawa (1933, p. 126). The mandible was not examined. The endopodite of the maxillule (Figure 5) has four terminal setae,

one subterminal seta, and one seta projecting from the basal segment. There are five spines on the basal endite and the coxal endite has four spines.

The unsegmented endopodite of the maxilla (Figure 6) has two terminal setae and two subterminal setae. There are eight spines on the basal endite and six on the coxal endite. From the distal margin of the scaphthognathite four soft bristles project. The first maxilliped (Figure 7) has four swimming setae on the exopodite. The setation of the five-segmented endopodite is 5–2–1–2–2 (beginning with the distal segment). The second maxilliped (Figure 8) likewise has four swimming setae on the exopodite, while the setation of the three-segmented endopodite is 6–1–1. The telson (Figure 9) is of the B type according to Aikawa's classification (1929, p. 23). There is a dorsal spine on each prong of the fork. Inside the fork, there are three pairs of spines on a median lobe, the outer two pairs being about twice as long as the inner pair.

Discussion

Starvation inhibits moulting, and the failure to rear the larvae through the first moult was due evidently to the unsuitability as food of the nauplii and trochophores provided.

Features of greatest importance in the classification of brachyuran first zoeae are the nature of the second antenna and telson (Lebour, 1928 ; Aikawa, 1937). Other significant characters are the presence or absence of carapacial spines, and the setation of the maxillae and maxillipeds. *Mictyris longicarpus* first zoea resembles the first zoeae of *Macrophthalmus* in the nature of the second antenna and telson (Aikawa, 1937, p. 152, 153). Table 1 compares the setation of the mouthparts in *Mictyris longicarpus* and *Macrophthalmus* (Aikawa, 1929, p. 28, 31).

Table 1

Setation of Mouthparts

Species	Mx. I	Mx. II	Mxpd. I	Mxpd. II
Mictyris longicarpus	5–1	2–2(4)	5–2–1–2–2	6–1–1
Macrophthalmus spp.	5–1	2–2(4)	6–3–1–2–2	6–1–1

Further, *Macrophthalmus* first zoeae lack lateral carapacial spines as does the first zoea of *Mictyris longicarpus*. Despite the very close resemblance between *Mictyris longicarpus* first zoea and those of *Macrophthalmus*, the former can be distinguished readily by its lack of a dorsal carapacial spine.

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PLANT PARASITIC NEMATODES IN FRUIT TREE NURSERIES OF NEW SOUTH WALES

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(*Communicated by Dr. C. D. Blake*)

[Read 28th July, 1965]

Synopsis

Soil samples taken from under 11 kinds of fruit trees in 20 nurseries and from a few bearing orchards in New South Wales, were examined for plant parasitic nematodes. Spiral nematodes (*Helicotylenchus* spp.) were present in all areas and associated with all root stocks examined. Root lesion nematodes (*Pratylenchus* spp.) were also widely distributed. Stubby root nematodes (*Trichodorus* spp.) were more prevalent in Gosford than in other districts and were associated with *Citrus* spp. The citrus nematode (*Tylenchulus semipenetrans* Cobb) was found in one quarter of the samples examined from citrus at Gosford and Sydney, in one sample of fallow soil and in a young orange planting in the Murrumbidgee Irrigation Areas (M.I.A.) established from plants imported from Gosford. Stylet nematodes (*Tylenchorhynchus* spp.) were found only in the M.I.A., and dagger nematodes (*Xiphinema* spp.) were found infrequently in the Gosford, Sydney and M.I.A. districts. The citrus, root lesion and stubby root nematodes were present sufficiently often to pose a threat to new orchards planted with stocks from infested nurseries.

Introduction

A few samples of soil taken from a nursery near Gosford, New South Wales (N.S.W.), by the author in 1957 yielded many nematodes known to be parasitic on the roots of plants. Such nematodes were found also in samples of soil taken from areas then growing either native bush or grasses and from cultivated areas devoted to forage, fruit and vegetable crops. These collections were studied by Drs. M. W. Allen and R. C. Colbran at the University of California, U.S.A., who confirmed the author's identifications. Included in these collections were 15 species in nine genera known, or thought to be plant parasites. Either larvae or insignificant numbers of adults of four other genera known to contain plant parasites were found. Table 1 lists the nematodes and the plants with which they were associated.

The presence of the genera *Meloidogyne*, *Pratylenchus*, *Radopholus* and *Tylenchulus* species, which live within roots, and of *Helicotylenchus* and *Rotylenchus* spp., which are not always removed when roots are washed, raised the question whether these nematodes are introduced to new orchard areas with nursery stock.

Methods

Samples of soil and small roots were taken to a depth of six to eight inches after the top one to two inches of soil had been removed. Most samples, each of about 500 ml., were treated separately, but a few from two or more sites along a nursery row were bulked before treatment. Nurseries near Gosford, Sydney, Bathurst, Orange, Griffith, Leeton and Yanco were sampled. In addition, five young orchards and three " virgin " or long fallow areas were sampled. About 300 samples were collected between October 1 and December 11, 1964.

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TABLE 1

Plant parasitic nematodes in soil samples collected in New South Wales in 1957

Nematode	Plants with which associated
Criconema sp.	orange
Criconemoides mutabile Taylor	maize on old grassland
Criconemoides xenoplax Raski	peach, cowpea
Criconemoides sp.	*Casuarina* sp.
Helicotylenchus multicinctus Cobb	Kikuyu grass, peach, *Eucalyptus pilularis*
Helicotylenchus nannus (Steiner) Andrassy	banana, *Casuarina* sp., *Cynodon* sp., *Datura* sp., grape, nectarine, orange, pineapple, strawberry
Hemicycliophora sp.	banana, maize, *Eucalyptus maculata, E. pilularis*
Heterodera sp.	*Casuarina* sp.
Meloidogyne javanica (Treub) Chitwood	Kikuyu grass
Meloidogyne sp.	banana, strawberry
Paratylenchus sp.	asparagus, maize, orange, peach, tobacco
Pratylenchus minyus Sher and Allen	tomato
Pratylenchus thornei Sher and Allen	cauliflower
Pratylenchus sp.	lucerne
Radopholus similis (Cobb) Thorne	banana, Kikuyu grass, pineapple
Rotylenchus brachyurus Steiner	grape
Rotylenchus robustus (de Man) Filipjev	*Eucalyptus* sp. and mixed grasses
Rotylenchus sp.	mixed grasses
Trichodorus minor Colbran	asparagus, banana, Bermuda grass, *Casuarina palulosa*, *Datura* sp., grape, nectarine, orange, pineapple, strawberry
Trichodorus porosus Allen	*Casuarina* sp., *Eucalyptus* sp., nectarine, peach
Trichodorus sp.	peach, pineapple, *Eucalyptus* sp.
Tylenchulus semipenetrans Cobb	orange (on sour lemon stock)
Tylenchorhynchus brevidens Allen	lucerne
Tylenchorhynchus latus Allen	cauliflower
Tylenchorhynchus sp.	strawberry

Nematodes were extracted from 250 ml. of soil by either an elutriator (Seinhorst, 1956) or a flotation method (Jenkins, 1964). These methods yielded comparable results and were used interchangeably. The nematodes were killed by heating in a water bath to 125°F and preserved in 4% formalin. For all observations reported the nematodes were recovered from the soil samples within 10 days of being collected.

RESULTS

Tables 2 and 3 show marked differences in the distribution of nematodes between nurseries. Some nurseries grew citrus, others predominantly stone or pome fruits, while others grew all of these. Thus, it is difficult to separate the effects of host and location on nematode infestation. Some species appear to be widely distributed and others more restricted both as to district and host. The species, in so far as they could be determined, the plants with which they were associated, and the districts in which they were found are summarized.

Criconemoides teres Raski was found in a sample of " virgin " soil near Gosford and in apple, peach and orange (*Poncirus trifoliata* stocks) nursery rows near Sydney. *Criconemoides* sp. larvae also were found in the Gosford and M.I.A. districts associated with *P. trifoliata* stocks and in a plum seedling planting near Sydney.

Helicotylenchus nannus (Golden) Perry was associated with *P. trifoliata* stocks, grapefruit, orange, pear and plum plantings and in " virgin " soil in the Gosford district, and with all these plants as well as apple, lemon, walnut and in fallow soil near Sydney. In the Bathurst-Orange district it was found in plantings of apple and peach seedlings. *H. multicinctus* (Cobb) Golden was found near Gosford in a planting of *P. trifoliata* seedlings and, near Sydney,

TABLE 2

Distribution of principal genera of plant parasitic nematodes in fruit tree nurseries of New South Wales

Nursery plant and District	Number of Samples Infested								Number of samples examined
	Criconemoides	*Helicotylenchus*	*Paratylenchus*	*Pratylenchus*	*Trichodorus*	*Tylenchorhynchus*	*Tylenchulus*	*Xiphinema*	
Apple									
Sydney	2	14	—	4	1	—	—	2	15
Bathurst–Orange	—	8	—	5	—	—	—	—	26
M.I.A.*	—	8	4	12	—	4	—	1	14
Apricot									
Sydney	—	6	1	—	—	—	—	—	6
M.I.A.	—	5	2	5	1	8	—	1	12
Cherry									
Sydney	—	3	4	1	—	—	—	—	4
Bathurst–Orange	—	1	—	—	—	—	—	—	2
Citrus									
Gosford	1	29	2	6	33	—	8	—	42
Sydney	4	45	1	4	4	—	14	4	49
M.I.A.	2	2	1	3	2	1	—	1	6
Grape									
M.I.A.	—	2	—	2	1	—	—	2	8
Mulberry									
Sydney	—	2	—	1	—	—	—	—	2
Nectarine									
Sydney	—	2	—	—	—	—	—	—	2
M.I.A.	—	2	—	3	1	—	—	—	3
Peach									
Sydney	4	14	—	1	—	—	—	2	14
Bathurst–Orange	—	6	—	3	—	—	—	—	8
M.I.A.	—	2	5	7	—	5	—	—	20
Pear									
Gosford	—	2	—	1	2	—	—	—	2
Sydney	—	6	—	—	—	—	—	—	7
Bathurst–Orange	—	2	—	1	—	—	—	—	6
M.I.A.	—	—	—	2	1	—	—	—	2
Plum									
Gosford	—	2	—	1	2	—	—	—	14
Sydney	1	10	—	3	—	—	—	—	13
Walnut									
Sydney	—	2	—	1	—	—	—	—	2
M.I.A.	—	1	—	2	—	2	—	1	2

* Murrumbidgee Irrigation Areas

TABLE 3

Principal genera of plant parasitic nematodes in soils from bearing orchards and "virgin" or fallow areas

Source	*Criconemoides*	*Helicotylenchus*	*Paratylenchus*	*Pratylenchus*	*Trichodorus*	*Tylenchorhynchus*	*Tylenchulus*	*Xiphinema*	Number of samples examined
Apple									
Sydney	—	6	—	6	—	—	—	1	6
Bathurst–Orange	—	1	—	—	—	—	—	—	3
Orange									
Gosford	—	2	—	2	2	—	2	—	2
M.I.A.*	1	2	4	10	10	—	2	7	17
"Virgin" soil or fallow									
Gosford	1	4	—	—	—	—	—	—	4
Sydney	—	7	—	1	—	—	1	—	7
M.I.A.	—	1	—	2	—	—	—	1	2

* Murrumbidgee Irrigation Areas

in plantings of peach and plum. In addition, *Helicotylenchus* sp. larvae were found in a planting of walnut at Sydney, plantings of apple and pear near Bathurst, in lemon, nectarine and peach plantings and in fallow soil in the M.I.A. *Helicotylenchus* spp., therefore, were found more frequently and associated with a larger number of plants in the Gosford and Sydney districts than in the M.I.A.

Paratylenchus nanus Cobb was found only in the M.I.A. and was associated with apple, apricot, peach and *P. trifoliata* stocks. A few specimens of *Paratylenchus* sp. were found near Gosford associated with citrange stocks, near Sydney with lemon and cherry, and in the M.I.A. with apricot.

The genus *Pratylenchus* was represented by many species and was widely distributed. *P. coffeae* (Zimmerman) Goodey was associated with apple and peach near Bathurst, with apricot in the M.I.A., and with apple, cherry and mulberry near Sydney. *P. minyus* Sher and Allen was associated with plum at Gosford, apple, lemon, peach and plum near Sydney, with apple at Bathurst, and with apple, apricot, grape, lemon, nectarine, peach, pear, *P. trifoliata* stocks and walnut in the M.I.A. *P. penetrans* (Cobb) Chitwood and Oteifa was seen only in a collection from apple in the M.I.A. *P. zeae* Graham was associated with apple, cherry, lemon and *P. trifoliata* stocks and in fallow land near Sydney, and with peach and pear in the Bathurst-Orange district. Specimens of *Pratylenchus* which could not be further identified were found associated with lemon, *P. trifoliata* and orange stocks at Gosford, with apple, apricot and cherry at Sydney, and with apple, apricot and peach in the M.I.A.

Trichodorus minor Colbran was found associated with apple and lemon near Gosford and with apricot, peach, pear and *P. trifoliata* in the M.I.A. *T. porosus* Allen was associated at Gosford with citrange, lemon, orange, *P. trifoliata* and pear stocks, near Sydney with lemon and orange, and in the M.I.A. with apricot, grape, orange and *P. trifoliata*. *T. teres* Hooper was associated with citrus at Gosford. Specimens of *Trichodorus*, the species of which could not be determined, were found at Gosford in grapefruit and plum plantings, at Sydney in fallow soil, and in the M.I.A. in plantings of lemon and orange.

Specimens of *Tylenchorhynchus* which appeared to be *T. brevidens* Allen were associated with apple, apricot, grape, peach and walnut in the M.I.A. and in the same area *Tylenchorhynchus* sp. was found in a planting of *P. trifoliata* stocks.

Larvae of *Tylenchulus semipenetrans* Cobb were found in large numbers in soil from nursery rows of citrange, lemon and orange seedlings and from an orange grove near Gosford, in soil from rows of lemon, orange and *P. trifoliata* as well as a fallow area near Sydney, and from three young orange plantings on stocks of rough lemon, orange and *P. trifoliata* near Yanco in the M.I.A. The young trees in the latter plantings were said to have been grown from seed at Gosford.

Xiphinema americanum Cobb was found in small numbers in soil from rows of apple and peach stocks near Sydney and from grape, *P. trifoliata* and walnut in the M.I.A. *Xiphinema* spp. were found also in soil from apple and *P. trifoliata* rows near Sydney, and from apple, apricot and grape in the M.I.A.

A few specimens of larvae or lone adults of *Belonolaimus* (Sydney: plum), *Hemicycliophora* (Gosford: "virgin" soil), *Hoplolaimus* (Sydney: pear), *Longidorus* (Sydney: apple, peach and pear), *Meloidogyne* (Sydney: peach and fallow), *Rotylenchus* (Gosford: *P. trifoliata*; Sydney: peach and fallow) and *Tylenchus* (Sydney: peach; M.I.A.: apple and peach) were found. These are considered incidental.

Discussion

The failure to find a nematode species in a few samples does not necessarily indicate that it is not present in the area or that the plant in question is not a host. However, its absence or rare occurrence in one area or crop as opposed to another can be taken to indicate that it probably does not exist there in serious numbers because it has not been introduced, has been introduced only recently, or the plants in the area are not suitable hosts for its rapid reproduction. Proper interpretation of the observations presented here requires knowledge of the host range and the pathogenicity of the nematodes on the various crop plants. Such information is at present lacking. Many of the nurseries are infested with weeds which may be better hosts than the crop plant. Thus, numbers of nematodes per soil sample may not be meaningful unless the nematode in question is known to be pathogenic on the crop plant. Finally, the determination of species sometimes is questionable because authentic slides for comparison were unavailable.

Relatively few nematodes were found in samples from the Bathurst-Orange district. This district had been unusually wet for several weeks before the samples were collected. Some sites had been flooded and all were nearly saturated with water when sampled. Thus, the results from this district may not be valid.

The genus *Helicotylenchus* was ubiquitous, occurring in more than half of the samples and in 12 of the 13 samples from "virgin" or long fallow soils examined. Golden (1956) showed that *R. buxophilus* was pathogenic on boxwood, but the significance of this genus in this study is unknown. On pineapple in Hawaii special nematodes appear to cause limited injury, but they are so widespread that control measures in the nursery alone would not be justified.

The genus *Pratylenchus* (root lesion nematodes) is also widespread. One or more species were found in all four districts and associated with all crops sampled. *P. minyus* Sher and Allen was found also in fallowed soil in the M.I.A. Colbran (1953) showed that *P. coffeae* causes serious injury to apples in Queensland, while Seinhorst and Sauer (1956) found *P. scribneri* and *P. vulnus* attacking grapes in Victoria. Because this genus is pathogenic and widespread, it poses a threat to new orchard plantings and warrants control measures being considered.

Species of the genus *Trichodorus* (stubby root nematodes) which were found in three-quarters of the samples from citrus nurseries in the Gosford district, in fewer nurseries in the Sydney and M.I.A. districts, but again associated with citrus. Stubby roots symptoms in citrus were seen frequently in this study. The genus contains known parasitic species and an attempt should be made to prevent its spread to new citrus planting.

The citrus nematode (*Tylenchulus semipenetrans* Cobb) has been recognized as a pathogen in citrus and grapes in Australia for some time (Seinhorst and Sauer, 1956 ; Sauer, 1962). In this study it was found in nurseries in the Gosford and Sydney districts, in an orange orchard near Gosford, and in the M.I.A. The trees with which it was associated in the M.I.A. were raised at Gosford. It was not associated with other crops, but was recovered from a fallow soil at the border of a nursery near Sydney. It is a serious pest in citrus and poses a threat to the yield from any planting made with infected nursery stock. It can be controlled in orchards but at a very much greater expense per tree than in the nursery. Every effort should be made to eliminate this nematode from nursery stock.

Xiphinema species (dagger nematodes) found infrequently in the Sydney and M.I.A. districts are of interest because the genus contains vectors of plant viruses. These nematodes and *Longidorus* spp. merit study, but do not appear to be a threat at present.

Other nematodes, *Belonolaimus*, *Criconemoides*, *Paratylenchus*, *Tylenchorhynchus* and *Tylenchus* were encountered infrequently and are not likely to be carried in nursery stocks.

A successful control measure for one of the more serious nematode pests in nurseries, such as the citrus nematode, is likely to control other nematodes at the same time. Studies of chemical treatment of the soil, treatment of lifted root stocks, with either a nematicide or heat or both, before sale, should be pursued vigorously.

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DIURNAL VARIATION IN THE RELEASE OF POLLEN BY *PLANTAGO LANCEOLATA* L.

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(*Communicated by Dr. D. Walker*)

[Read 28th July, 1965]

Synopsis

An air sampler was used to record the pollen release of *Plantago lanceolata*. The pollen catch indicates a tendency for pollen release to reach a major morning peak which is followed by a secondary peak two to four hours later. Observations were also made on anther exertion. Some of the observations indicate two main periods of anther exertion during the day.

Introduction

Percival (1955) has observed anther dehiscence for *Plantago lanceolata* at hourly intervals. She records that anthers are presented from 0400 to 1700 hr., with a period of peak presentation from 0700 to 1000 hr. Anthesis can take place when the relative humidity is 100% and is suppressed at temperatures below 10°C (Percival, 1955). Hyde and Williams (1946) also observed that flowering is suppressed below 10°C and that flowering may be profuse at high humidity (80% or more) although dehiscence may then be delayed. Hyde and Williams, who made observations of the impact and gravity catch on slides exposed in a stand of *Plantago lanceolata*, noted that the catch rose steeply between 0600 and 0800 hr. or 0800 and 1000 hr., slides were changed at two-hourly intervals, and then fell more or less steeply (Hyde and Williams, 1946).

A simple air sampler was devised for the detection of pollen release by *Epacris paludosa*. The effectiveness of the sampler was checked with *Plantago lanceolata* which is known to be anemophilous. Pollen grains were collected in quantity. It appeared from a single observation that the daily distribution of pollen released by *Plantago lanceolata* has two peaks, the first major peak being followed by a minor peak after a lapse of three hours. A series of observations was made with the air sampler to investigate this diurnal variation. Another set of observations was made on anther exertion.

Air Sampler

A tube 1′3″ long and $1\frac{3}{4}$″ in diameter was constructed of Bristol board. A slot was cut at the mid point of the long axis for the insertion of a microscope slide. The tube was attached to a "Pifco vacette" vacuum cleaner by a plasticene collar, the tube and cleaner being held in laboratory clamps.

The mouth of the tube was adjusted vertically to be at the point midway between the highest and lowest heads on the plant under observation and 9″ from the nearest flowering head. The sampler was operated for periods of three-quarters of an hour. The slides were changed at the end of each running period and the cleaner switched off for a quarter of an hour to prevent overheating. The slides were smeared with silicone fluid (AK2000) and were inserted in the tube with the adhesive surface towards the open end.

A cover slip ($1\frac{1}{2}$″ × $\frac{7}{8}$″) was placed on each slide after its removal from the tube. The cover slip was sealed with clear nail lacquer and the excess

silicone fluid removed. The slides were than traversed four times under a microscope at a total magnification of × 100 at intervals of five mm. The mean number of grains observed per traverse was calculated for each slide.

The efficiency of the sampler is not known, but is probably low (cf. Gregory, 1961). The observed pollen catch should be taken as a relative rather than an absolute record. Even though Gregory (1961) has pointed out that the performance of an air sampler should be explored experimentally before use, the assumption has been made that the mean number of grains observed per traverse is directly proportional to the amount of pollen released by the plant during the exposure of the slide.

Observations of Pollen Release

Pollen release was recorded with the air sampler on five occasions (Table 1). On four occasions the observations were made on a second floor balcony of the H. C. Coombs Building, the Australian National University. At this time the extensive stands of *Plantago lanceolata* on disturbed ground in the vicinity of the H. C. Coombs Building had finished flowering, and a control run of the sampler established only a negligible background of atmospheric pollen. The balcony faces to the east and is shaded from direct sunlight, except between 0700 and 1000 hr. On 9.2.65 observations were made on a plant growing in a garden some three miles to the north of the H. C. Coombs Building.

Table 1

Duration of observations of pollen release, and the number of heads on the observed plants

Date	Duration of observations	Number of flowering heads	Number of immature heads	Number of mature heads
21·1·65	0615–1800	25	16	—
9·2·65	0500–1545	15	17	22
11·2·65	0515–1700	20	11	8
19·2·65	0500–1645	19	2	1
20·2·65	0500–2400	19	2	1
21·2·65	0000–2400	19	2	1
22·2·65	0000–0445	19	2	1

The plants used at the H. C. Coombs Building were lifted from the same garden the previous evening, placed in 6″ earthernware flower pots and watered copiously. On 21.1.65 and 11.2.65 the plant was watered at 0600 hr., but not thereafter. On 19, 20, 21 and 22.2.65 a drip watering system was set up and the plant watered continuously.

With the exception of the plant used on 21.1.65, all plants at the H. C. Coombs Building were shaded from direct sunlight between 0700 and 1000 hr.

Observations of air temperature, humidity (when a whirling hygrometer was available) and cloud cover were made at hourly intervals during the running of the air sampler. On 9, 19, 20 and 21.2.65 air movement was also recorded.

Temperature and humidity were recorded on the balcony at the H. C. Coombs Building five feet from the plant. In the garden, temperature and humidity were recorded at a shaded station 25 yards away from the plant and six feet above it.

Air movement was recorded on 19, 20 and 21.2.65 in arbitrary units by a sensitive anemometer (C. F. Casella and Co., London, catalogue number 684A) adjacent to the plant. To prevent illumination of the plant no observations of air movement were made during the hours of darkness on 20, 21 and 22.2.65. Air movement was recorded in the garden adjacent to the plant

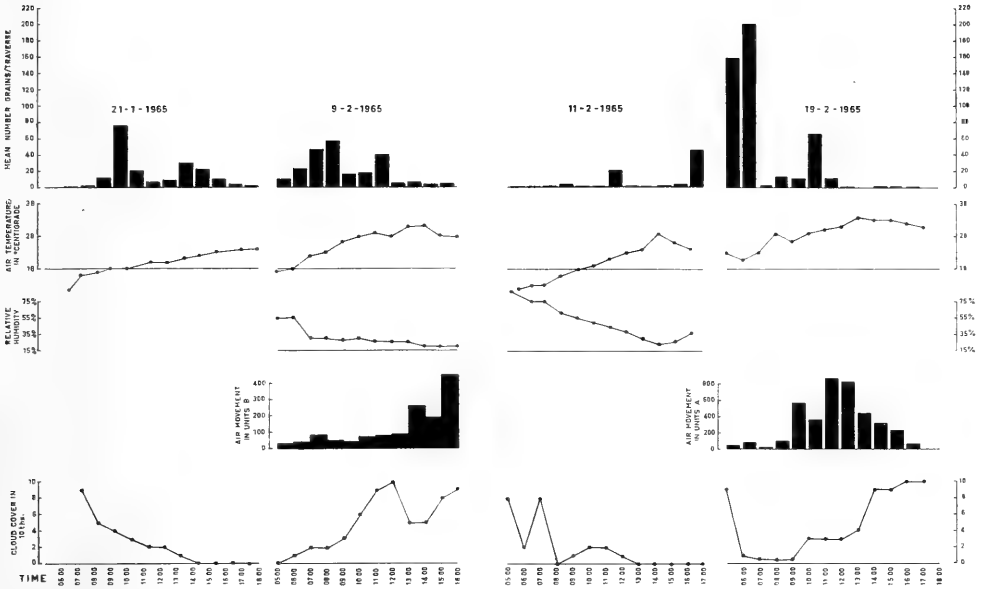

Fig. 1. Record of pollen catch from *Plantago lanceolata*.

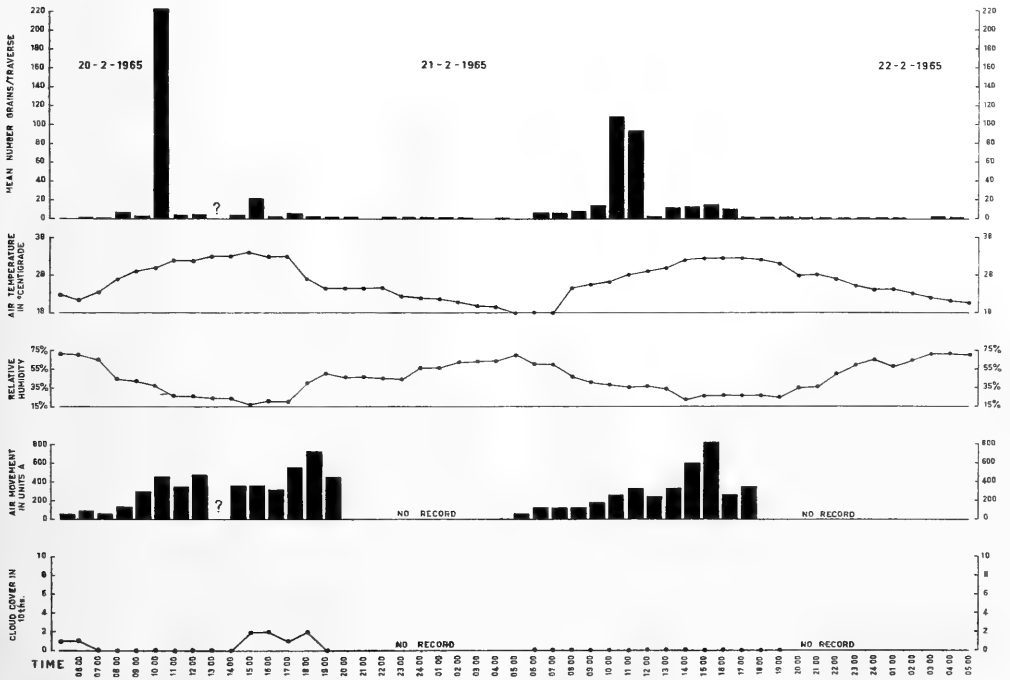

Fig. 2. Record of pollen catch from *Plantago lanceolata*.

with a cup counter anemometer (R. W. Munro, London, Mark II), the recorded units of which represent hundredths of a mile.

On three occasions, 21.1.65, 9.2.65 and 19.2.65 (Figure 1) the pollen catch reached a morning peak, declined and then reached a second peak two to three hours later. On 11.2.65 (Figure 1) no significant peak was observed until 1115 to 1200 hr. when pollen release appears to have been slight ; a second more pronounced peak was recorded four hours later, between 1615 and 1700 hr.

Observations were made continuously from 0500 hr. on 20.2.65 until 0445 hr. on 22.2.65 (Figure 2). The plant under observation was that used on 19.2.65. The " Pifco vacette " vacuum cleaner ceased to function at

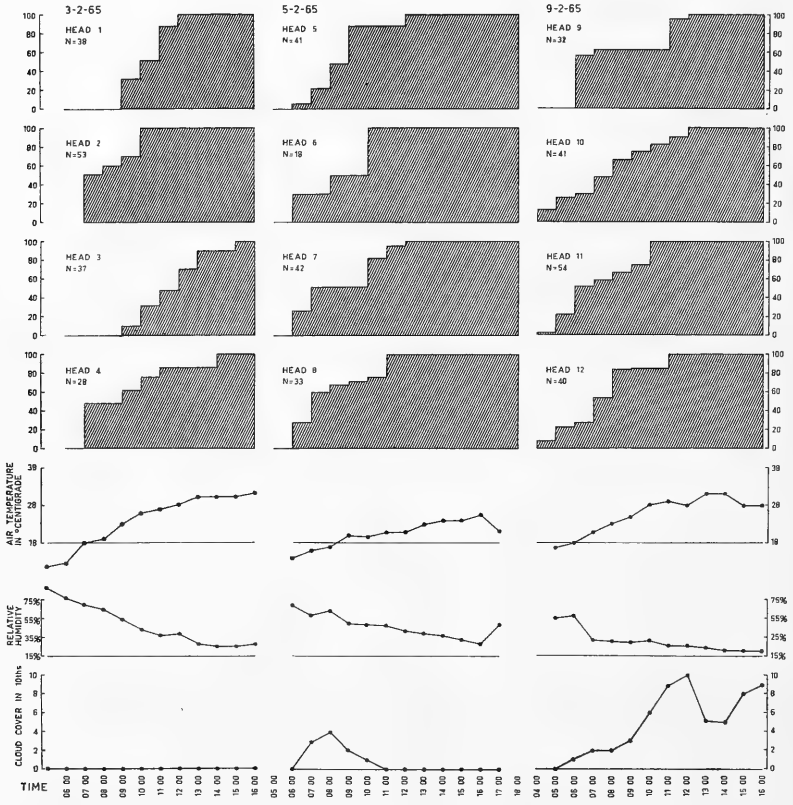

Fig. 3. Record of anther exertion by *Plantago lanceolata*.

1300 hr. on 20.2.65 and was replaced by a Hoover cleaner. On 20.2.65 there was a marked peak in pollen catch between 1000 and 1045 hr. This was followed by a secondary peak between 1500 and 1545 hr. but the change of vacuum cleaner makes it difficult to assess the importance of the second peak. On 21.2.65 (Figure 2) there was a peak period of pollen release between 1000 and 1145 hr. ; no subsequent peak was observed.

Observations of Anther Exertion

A series of observations was made on flowering heads of *Plantago lanceolata* in the garden. The heads were examined at hourly intervals and the number of anthers that had been fully exerted since the previous observation counted. Exerted anthers were marked with a 1% aqueous solution of safranine with

the addition of two parts per 100 of soap solution. The stain was applied with a hypodermic needle.

On each occasion four heads were observed (Figure 3). On 3.2.65 each head was on a separate plant, on 5.2.65 on a single plant, and on 9.2.65 again on different plants.

Once anthesis commenced on heads 1, 3, 5, 10, 11 and 12 it appeared to proceed at a fairly constant rate until complete for the day. On heads 2, 4, 6, 7, 8 and 9 anthesis tended to occur in two bursts, the second following the first after a period of two to five hours.

In order to observe any influence of the sun's position on anther exertion, each head was scored in four quadrants orientated SE–NE, NE–NW, NW–SW, and SW–SE. The numbers of anthers exerted in each quadrant during three periods are given in Table 2. On 3.2.65 there was a tendency for more anthers to be exerted in the quadrant facing the sun than in the others. This was not apparent on the other occasions.

Table 2

Numbers of anthers exerted in four quadrants

Date	Time	Quadrants			
		SE–NE	NE–NW	NW–SW	SW–SE
3.2.65	0800–1000	24	19	16	19
	1000–1300	4	24	16	19
	1300–1700	—	—	10	5
5.2.65	0800–1000	30	23	24	28
	1000–1300	14	1	8	6
	1300–1700	—	—	—	—
9.2.65	0800–1000	38	37	31	33
	1000–1300	6	4	—	18
	1300–1700	—	—	—	—

Discussion

The pollen catch at Canberra falls mainly within the limits noted by Percival for anther dehiscence (Canberra Time is Eastern Standard Time). On no occasion did the air temperature fall below 10°C. The late summer of 1965 was a particularly dry period with marked diurnal fluctuations in temperature and humidity and with mainly clear skies.

On the six days when pollen release was observed the first peak occurred between 0600–0700 hr. and 1100–1200 hr. (Table 3). With the exception of 21.2.65, the major peak was followed by a second peak (Table 4). The time intervals between the two peaks vary from two to four hours (Table 5).

Table 3

Time of day, relative humidity and air temperature for first peak pollen catch

Date	Time	Relative Humidity	Air Temperature °C
21.1.65	0900–1000	—	18
9.2.65	0800–0900	30	24
11.2.65	1100–1200	40	22
19.2.65	0600–0700	—	22
20.2.65	1000–1100	30	31
21.2.65	1000–1100	37	27

TABLE 4

Time of day, relative humidity and air temperature for second peak pollen catch

Date	Time	Relative Humidity	Air Temperature °C
21.2.65	1300–1400	—	21
9.2.65	1100–1200	25	28
11.2.65	1600–1700	37	24
19.2.65	1000–1100	—	30
20.2.65	1500–1600	20	33

Neither air movement nor cloud cover appears to influence pollen catch directly.

Hyde and Williams (1946) did not comment on two peak periods of pollen release in *Plantago lanceolata*. However, their impact and gravity catches record fluctuations in the pollen released from a large number of plants in a stand, rather than from a single plant. Even so, their record (Hyde and Williams, 1946) shows multiple peaks for impact catch on two out of nine days. Hyde and Williams (1945) have noted that two grasses, *Festuca rubra* and *Holcus lanatus*, as a rule flower slightly in the morning and more profusely in the afternoon and that this is reflected in the pollen catch on gravity and impact slides by a minor morning peak followed later in the afternoon by a major peak.

The record of anther exertion is ambiguous ; it is possible that the staining technique may have interfered. Nevertheless anthesis tended to take place in two bursts on six of the 12 observed heads (cf. *Centaurea nigra*: Percival

TABLE 5

Duration of interval between first and second peaks

Date	Interval between first and second peak in hours
21.1.65	3
9.2.65	2
11.2.65	4
19.2.65	3
20.2.65	4

1950). There is some indication that the position of the sun influences the course of anther exertion in *Plantago lanceolata* (cf. *Papaver orientale* : Percival, 1950).

On 5.2.65 and 9.2.65 anthesis had begun at or before 0600 hr. On 3.2.65 the flowering heads were saturated by a heavy dew. The plants were growing along the foot of a garden fence which shaded them from the early morning sun. However, it was noted that sunlight fell on heads 2 and 4 between 0700 and 0800 hr. through cracks in the fence ; anther exertion began at this time. Heads 1 and 3 were in the shade of the fence until 0900 hr., when anthesis began.

CONCLUSIONS

Pollen release in *Plantago lanceolata* may reach two peaks during the day but there is some variation in this behaviour. The data are not sufficiently detailed to allow the detection of causal factors.

Speculations can be made about the nature of the circumstances which lead to diurnal variation in pollen release. If it is supposed that anthers are exerted at regular intervals during the day and that early morning conditions

are unfavourable to pollen release, then a relatively large release of pollen is to be expected when the inhibition is removed. Thereafter pollen release should fall to a constant rate. However, the frequently observed double peak of pollen release and the less certain parallel behaviour in anther exertion do not support this hypothesis. It would seem more likely that the first main peak represents the attainment of favourable conditions for pollen release and that the magnitude of this peak reflects the accumulation of exerted anthers in which dehiscence has not, or has only partly, taken place. The second peak would then reflect the second burst of flowering, although it appears to be a more common phenomenon than the observation of anther exertion would substantiate.

Acknowledgements

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THE VERTEBRATE FAUNA OF " GILRUTH PLAINS ", SOUTH-WEST QUEENSLAND

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(*Communicated by Dr. Mervyn Griffiths*)

[Read 28th July 1965]

Introduction

This paper presents a list of the vertebrates identified on a defined area in the semi-arid zone of south-west Queensland. Despite the apparently harsh temperature and rainfall conditions, more than 200 species were observed during a three-year period.

In addition, an attempt has been made to give some indication of the density and seasonal distribution of the birds and mammals.

Environment

" Gilruth Plains " is situated near Cunnamulla, latitude 28° S (approximately), longitude 146° (approximately). It is a 40,000 acre C.S.I.R.O. field station concerned with research into wool production. The climate is semi-arid with a 15–inch mean annual rainfall.

We consider that " Gilruth Pains " should give a representative picture of the fauna of this zone because :

(i) The vegetation is diverse and contains examples of most associations typical of this semi-arid region. " Gilruth Plains " is primarily a mosaic of mulga-box (*Acacia aneura–Eucalyptus populnea*), gidgee-buddah (*Acacia cambagei–Eremophila mitchelli*), ironbark-spinifex (*Eucalyptus melanophloia–Triodia* spp.) and Mitchell grass (*Astrebla* spp.) with small areas of coolibah (*Eucalyptus microtheca*), pine (*Callitris columellaris*), and swamp.

(ii) Seasonal conditions during the period of observations represented the normal climatic pattern with a range from severe drought to lush pasture conditions. Permanent surface water was always available in bore drains and small dams while large areas of temporary swamp formed after heavy rain.

Method of Recording

The following list of vertebrates was compiled during the period October 1960 to October 1963.

While the authors did devote some time to searching specifically for vertebrate fauna, especially for birds and mammals, a large number of the species were either observed when the authors were engaged in other field work or collected by members of the staff of " Gilruth Plains ".

The fish species were identified by Mr. G. P. Whitley of The Australian Museum. Species of Amphibia and Reptilia for which there are housed specimens (marked H on list) were identified by Mr. H. G. Cogger of The Australian Museum. The location of housed specimens is shown on the list thus : Hg, Specimen(s) housed at Gilruth Plains ; Hm, Specimen(s) housed at The Australian Museum.

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The Australian Reed-Warbler (*Acrocephalus australis*) and Gould's Wattled Bat (*Chalinolobus gouldii*) were identified by Mr. Warren Hitchcock and Mr. John Calaby respectively, of C.S.I.R.O. Division of Wildlife Research, Canberra. The remaining frog and reptile species were authoritatively determined, although housed specimens of these species are not available.

All other species of birds and mammals were identified by one or both of the authors. The 9th Edition of "An Australian Bird Book" by J. A. Leach was used as a reference for bird identification.

Where possible, each bird or mammal species is placed in one of four broad density classes depending on how often an observer is likely to see it.

The classes are defined as follows: A, At least once per day; B, Once per 10 days; C, Once per 100 days; D, Once per 1000 days.

Additional symbols used were: M, Species is migratory and is thus present for only part of each year. The density class of an M species refers only to part of the year; S, When the presence of species appears to be governed by seasonal conditions; E, Exotic species.

Fish

Madigania unicolor (Native Grunter) Hg
Gambusia affinis (Mosquito Fish) E Hg
Carassius auratus (Goldfish) E Hg

Frogs

Cyclorana australis Hmg
C. alboguttatus
C. platycephalus Hm
C. cultripes Hm
Notaden bennetti Hmg
Limnodynastes fletcheri Hmg
Hyla rubella Hmg
H. caerulea Hm
Uperoleia marmorata Hg

Tortoise

Chelodina longicollis (Long-necked Tortoise)

Snakes

Pseudechis australis (Mulga Snake) Hmg
Demansia nuchalis—carinata group. (Brown Snake) Hmg
Denisonia suta (Whip Snake) Hm
Brachyurophis australis (Australian Coral Snake) Hg

Lizards

Geckonidae

Diplodactylus tessellatus (Variegated Gecko) Hmg
D. strophurus
D. williamsi Hmg
Lucasius damaeus (Bearded Gecko)
Nephrurus laevis (Smooth Knob-tailed Gecko) Hg
Heteronota binoei (Bynoe's Gecko) Hmg
Rhynchoedura ornata (Beaked Gecko) Hm
Gehyra variegata (Dtella) Hmg
Oedura marmorata (Velvet Gecko) Hg

Agamidae

Amphibolurus barbatus (Jew Lizard) Hmg
A. muricatus (Tree Dragon) Hmg

Scincidae

Tiliqua scincoides (Blue Tongue) Hg
Trachysaurus rugosus (Shingle-back) Hg
Egernia striolata (Arboreal Skink) Hmg
Ablepharus boutonii Hmg
A. lineo-ocellatus Hm
A. timidus Hmg
Sphenomorphus lesueurii (Lesueur's Skink) Hmg
Rhondona punctatovittatum Hmg

Pygopodidae

Lialis burtonii (Common Snake Lizard) Hmg
Pygopus nigriceps

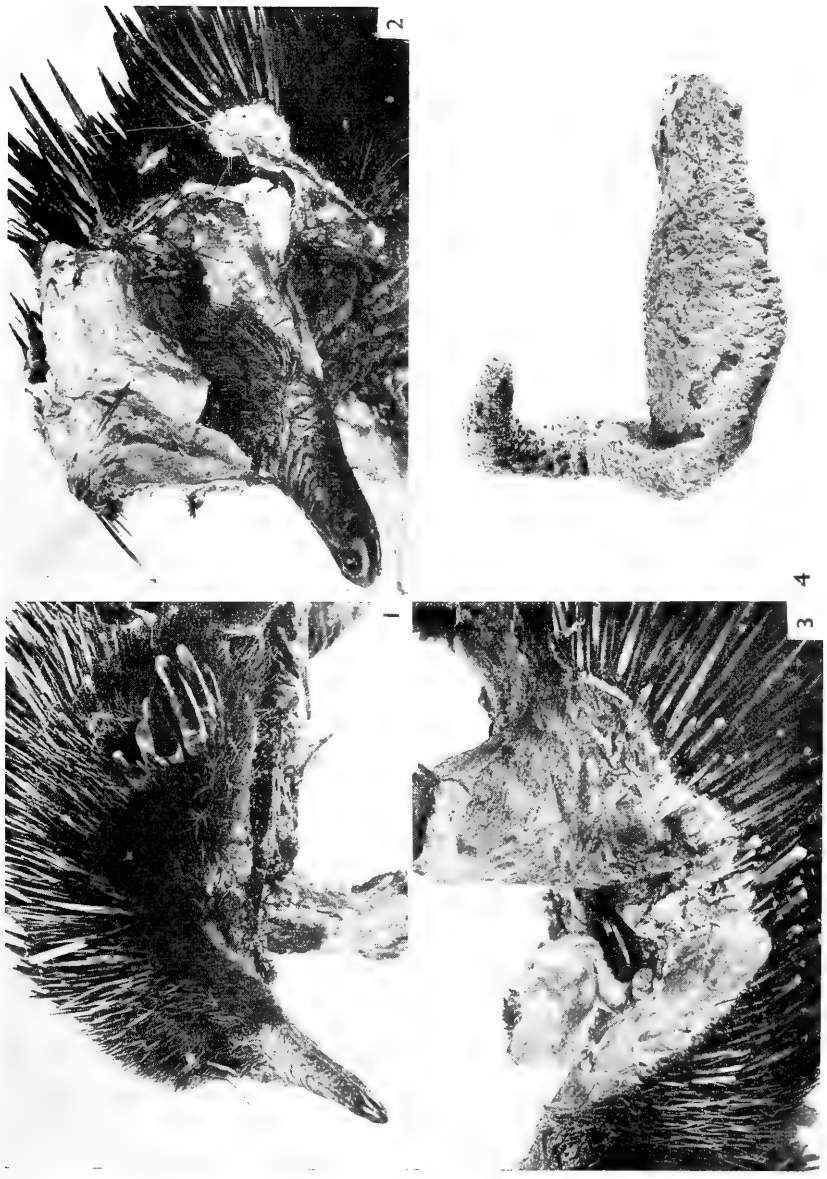
Varanidae

Varanus gouldii (Gould's Goanna) Hg
V. tristis (Black Goanna) Hg

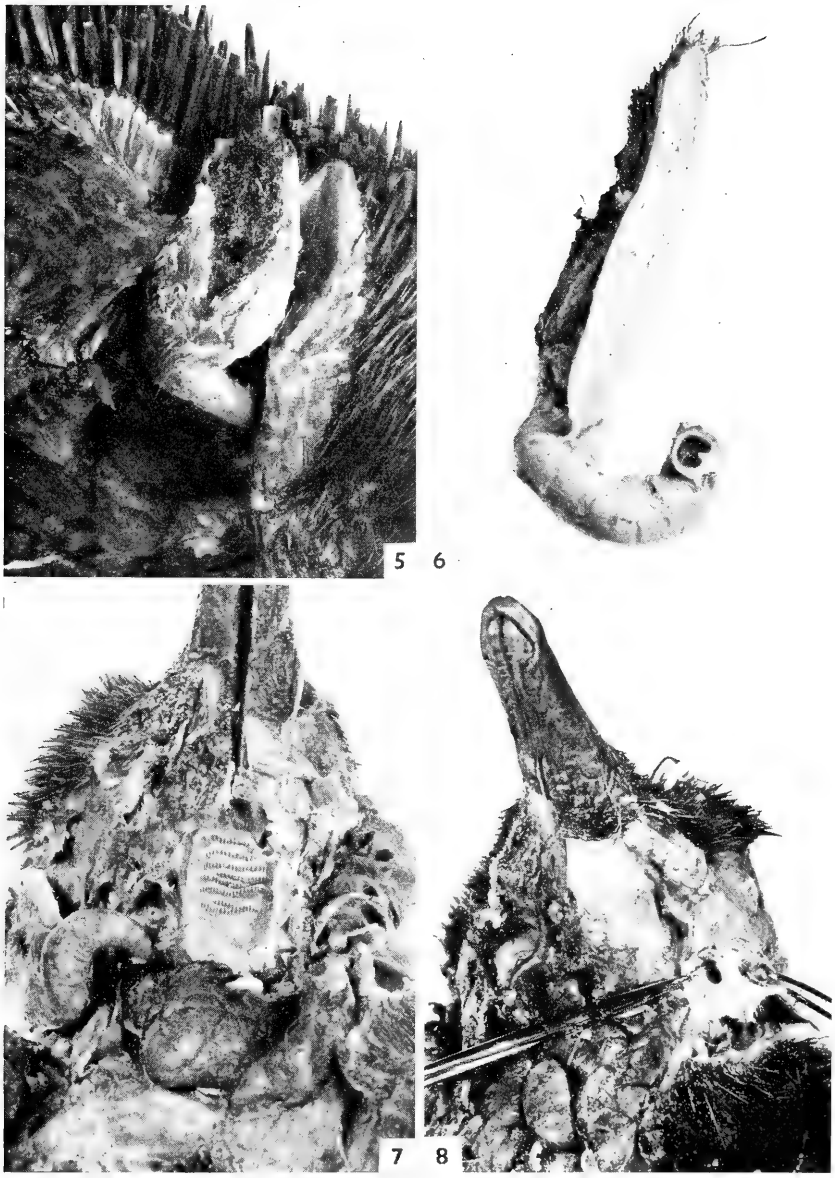
Birds

Dromaius novae-hollandiae (Emu) A
Podiceps poliocephalus (Hoary-headed Grebe) CS
P. ruficollis (Little Grebe) BS
Pelecanus conspicillatus (Pelican) CS
Phalacrocorax carbo (Black Cormorant) CS
P. melanoleucos (Little Pied Cormorant) CS
P. sulcirostris (Little Black Cormorant) CS
Ardea novae-hollandiae (White-faced Heron) A
A. pacifica (White-necked Heron) A
Egretta alba (White Egret) DS
E. garzetta (Little Egret) DS
Threskiornis molucca (White Ibis) CS
T. spinicollis (Straw-necked Ibis) BS
Plegadis falcinellus (Glossy Ibis) DS
Platalea flavipes (Yellow-billed Spoonbill) BS
P. regia (Royal Spoonbill) CS
Cygnus atratus (Black Swan) CS
Chenonetta jubata (Maned Goose) B
Anas gibberifrons (Grey Teal) A
A. rhynchotis (Blue-winged Shoveler) DS
A. superciliosa (Black Duck) BS
Malacorhynchus membranaceus (Pink-eared Duck) B

Aythya australis (White-eyed Duck) CS
Circus assimilis (Spotted Harrier) C
Accipiter cirrocephalus (Collared Sparrow-Hawk) B
Hieraaetus morphnoides (Little Eagle) C
Aquila audax (Wedge-tailed Eagle) A
Haliastur sphenurus (Whistling Eagle) A
Milvus migrans (Fork-tailed Kite) A
Elanus notatus (Black-shouldered Kite) D
Falco berigora (Brown Hawk) B
F. cenchroides (Nankeen Kestrel) A
F. longipennis (Little Falcon) B
Coturnix pectoralis (Stubble-Quail) BS
Turnix velox (Little Quail) AS
Grus rubicundus (Brolga) B
Tribonyx ventralis (Black-tailed Water-Hen) CS
Fulica atra (Coot) DS
Eupodotis australis (Bustard) C
Lobibyx novae-hollandiae (Spur-winged Plover) A
Zonifer tricolor (Banded Plover) BS
Charadrius melanops (Black-fronted Dotterel) A
Erythrogonys cinctus (Red-kneed Dotterel) CS
Erolia acuminata (Sharp-tailed Sandpiper) D
Rostratula benghalensis (Australian Painted Snipe) DS
Himantopus leucocephalus (White-headed Stilt) A
Recurvirostra novae-hollandiae (Red-necked Avocet) CS
Stiltia isabella (Australian Pratincole) C
Burhinus magnirostris (Southern Stone-Curlew) C
Larus novae-hollandiae (Silver Gull) DS
Chlidonias hybrida (Marsh Tern) CS
Geopelia cuneata (Diamond Dove) A
G. placida (Peaceful Dove) A
Phaps chalcoptera (Forest Bronzewing) A
Histriophaps histrionica (Flock Pigeon) D
Ocyphaps lophotes (Crested Pigeon) A
Kakatoe galerita (White Cockatoo) D
K. leadbeateri (Pink Cockatoo) A
K. roseicapilla (Galah) A
Leptolophus hollandicus (Quarrion) A
Aprosmictus erythropterus (Red-winged Parrot) A
Barnardius barnardi (Ring-neck Parrot) A
Psephotus haematogaster (Blue Bonnet) A
P. varius (Mulga Parrot) A
Melopsittacus undulatus (Budgerygah) A
Cuculus pallidus (Pallid Cuckoo) A
Chalcites basalis (Horsfield Bronze-Cuckoo) C
Cacomantis pyrrhophanus (Fan-tailed Cuckoo) D
Scythrops novae-hollandiae (Channel-billed Cuckoo) C
Tyto alba (Barn Owl) C
Ninox novae-seelandiae (Boobook) B
Eurostopodus guttatus (Spotted Nightjar) B
Aegotheles cristata (Crested Owlet-Nightjar) B
Podargus strigoides (Tawny Frogmouth) B
Eurystomus orientalis (Dollar-Bird) D
Apus pacificus (Fork-tailed Swift) C
Dacelo gigas (Laughing Kookaburra) A
Halcyon pyrrhopygius (Red-backed Kingfisher) A
H. sanctus (Sacred Kingfisher) B
Merops ornatus (Rainbow-Bird) AM
Mirafra javanica (Horsfield Bushlark) B
Hirundo neoxena (Welcome Swallow) C
Hylochelidon ariel (Fairy Martin) A
H. nigricans (Tree Martin) A
Pteropodocys maxima (Ground Cuckoo-Shrike) A
Coracina novae-hollandiae (Black-faced Cuckoo-Shrike) A
C. robusta (Little Cuckoo-Shrike) B
Lalage sueurii (White-winged Triller) A
Rhipidura fuliginosa (Grey Fantail) AM
R. leucophrys (Willie Wagtail) A
Seisura inquieta (Restless Flycatcher) A
Microeca fascinans (Jacky Winter) A
Petroica goodenovii (Red-capped Robin) A
P. cucullata (Hooded Robin) A
Acrocephalus australis (Australian Reed-Warbler) D
Pachycephala rufiventris (Rufous Whistler) A
Colluricincla harmonica (Grey Shrike-Thrush) A
Oreoica gutturalis (Crested Bellbird) A
Pomatostomus temporalis (Grey-crowned Babbler) A
Epthianura aurifrons (Orange Chat) CS
E. tricolor (Crimson Chat) BS
Gerygone fusca (Fuscous Warbler) A
Smicrornis brevirostris (Brown Weebill) A
Acanthiza chrysorrhoa (Yellow-tailed Thornbill) A
A. nana (Little Thornbill) B
A. uropygialis (Chestnut-tailed Thornbill) A
Aphelocephala leucopsis (Eastern Whiteface) A
Malurus assimilis (Purple-backed Wren) A
M. leuconotus (White-winged Wren) A
M. melanotus (Black-backed Wren) C
Cinclorhamphus cruralis (Brown Songlark) A
C. mathewsi (Rufous Songlark) B
Anthus australis (Pipit) A
Artamus cinereus (Black-faced Wood-Swallow) A
A. leucorhynchus (White-breasted Wood-Swallow) BS
A. minor (Little Wood-Swallow) CS
A. personatus (Masked Wood-Swallow) CS
A. superciliosus (White-browed Wood-Swallow) AS
Climacteris affinis (White-browed Tree-Creeper) C
C. picumnus (Brown Tree-Creeper) A
Neositta chrysoptera (Orange-winged Sittella) B
Dicaeum hirundinaceum (Mistletoe-Bird) A
Pardalotus substriatus (Red-tipped Pardalote) A
P. rubricatus (Red-browed Pardalote) C
Melithreptus brevirostris (Brown-headed Honeyeater) B
Meliphaga penicillata (White-plumed Honeyeater) A
M. virescens (Singing Honeyeater) A
Myzomela nigra (Black Honeyeater) CS
Plectorhyncha lanceolata (Striped Honeyeater) A
Grantiella picta (Painted Honeyeater) DS
Gliciphila indistincta (Brown Honeyeater) A
Myzantha flavigula (White-rumped Miner) A



Tachyglossus aculeatus.



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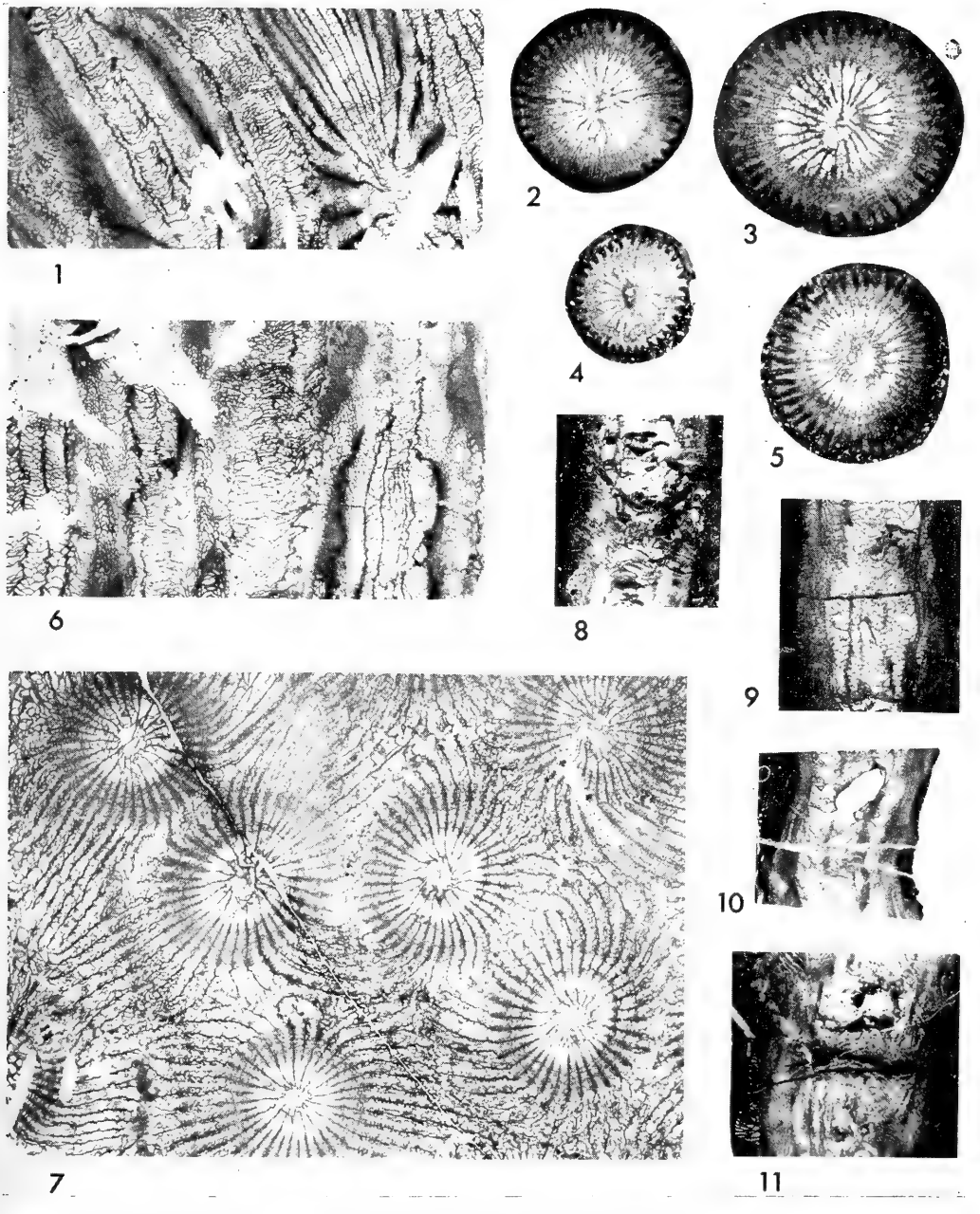
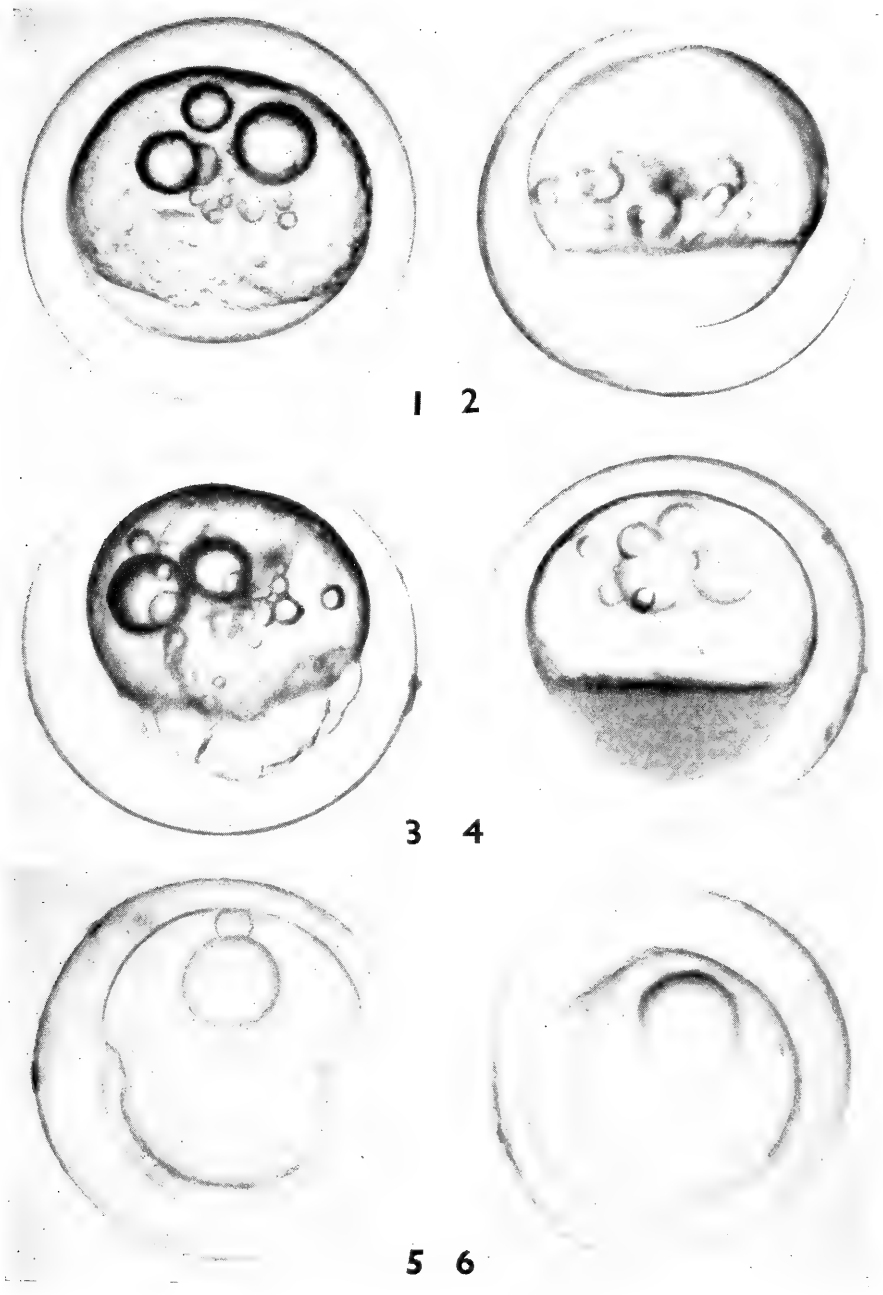
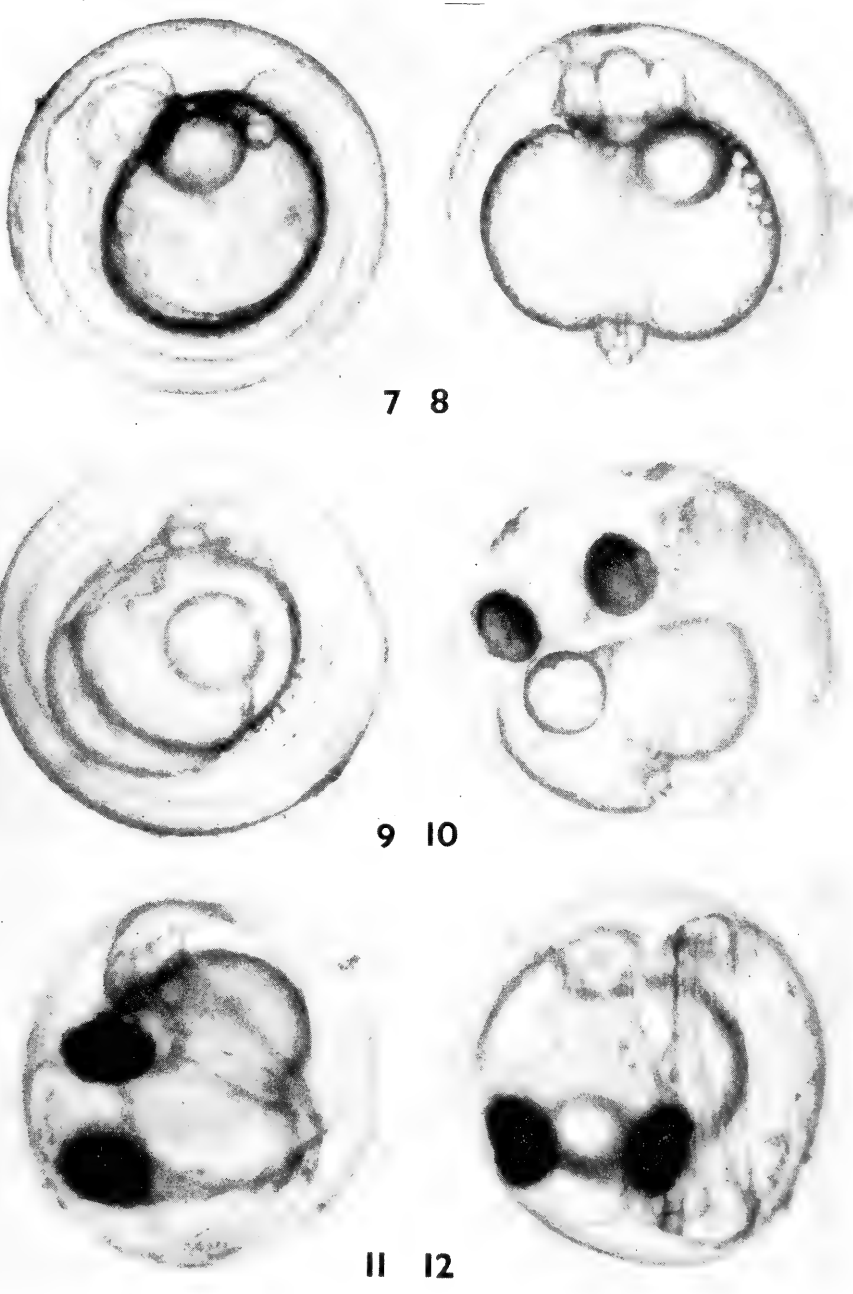


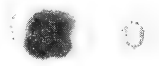
1, 6, 7. *Bensonastraea praetor*, 2–5, 8–11. *Macgeea touti*.



Development of egg of *Retropinna semoni* (Weber).



Development of egg of *Retropinna semoni* (Weber).



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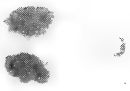

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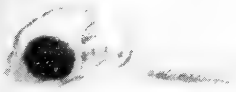

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Larvae of *Retropinna semoni* (Weber).

Acanthagenys rufogularis (Spiny-cheeked Honeyeater) A
Entomyzon cyanotis (Blue-faced Honeyeater) A
Philemon citreogularis (Little Friar-Bird) BS
P. corniculatus (Noisy Friar-bird) AS
Passer domesticus (House Sparrow) DE
Zonaeginthus guttatus (Diamond-Firetail) D
Taeniopygia castanotis (Zebra Finch) A
Steganopleura bichenovii (Banded Finch) A
Oriolus sagittatus (Olive-backed Oriole) B
Corvus bennetti (Little Crow) B
C. cecilae (Crow) C
C. coronoides (Raven) A
Cracticus nigrogularis (Pied Butcher-bird) A
C. torquatus (Grey Butcher-bird) A
Gymnorhina tibicen (Black-backed Magpie) A
Corcorax melanorhamphus (White-winged Chough) B
Struthidea cinerea (Apostle-bird) A
Grallina cyanoleuca (Magpie-Lark) A
Chlamydera maculata (Spotted Bower-bird) A

Mammals

Tachyglossus aculeatus (Echidna) C
Macropus rufus (Red Kangaroo) A
M. robustus (Wallaroo) D
M. canguru (Grey Kangaroo) A
Sminthopsis macrura-crassicaudata group (Fat-tailed Marsupial Mouse) C
Chalinolobus gouldii (Gould's Wattled Bat)
Vulpes vulpes (Fox) AE
Felis catus (Cat) AE
Mus musculus (Mouse) BE
Capra hircus (Goat) CE
Sus scrofa (Pig) CE
Orytolagus cuniculus (Rabbit) AE

Addendum

The following animals were seen on " Gilruth Plains " but were not identified with sufficient confidence to justify placing them on the main list. They should not be quoted as locality records until their presence has been confirmed.

Acanthophis antarcticus (Death-Adder)
Falco peregrinus (Peregrine Falcon)
Acanthiza lineata (Striated Thornbill)
Pomatostomus ruficeps (Chestnut-crowned Babbler)
Phascogale tapoatafa (Brush-tailed Phascogale
Trichosurus vulpecula (Brush-tailed Possum)
Chalinolobus morio (Chocolate Wattled Bat)

Discussion

The vertebrate fauna of this relatively small area consists of at least three fish, nine frogs, one tortoise, four snakes, 23 lizards, 151 birds and 12 mammals, giving a total of more than 200 species. It is apparent that this climatic zone is in no sense inimical to vertebrates. It would be of great interest to compare the size of this fauna with that of an area of comparable size in the arid or temperate zone, but we know of no similar surveys in these regions.

Acknowledgements

The authors are indebted to Messrs. G. P. Whitley and H. G. Cogger of The Australian Museum, Sydney, and Messrs. W. Hitchcock and J. Callaby of C.S.I.R.O. Division of Wildlife Research, Canberra, for identifying specimens, to Mr. C. H. S. Dolling, Officer in Charge, " Gilruth Plains ", for his continuous encouragement of the work, and to Mr. M. Schrader of Cunnamulla for critical reading of the manuscript.

FURTHER OBSERVATIONS ON THE LIFE HISTORIES OF LITTORAL GASTROPODS IN NEW SOUTH WALES

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(Plate x)

[Read 29th September, 1965]

Synopsis

The spawn and early development are described for: (1) *Xenogalea labiata* (Perry) (Cassididae), in which several females appear to contribute capsules, each containing numerous small eggs, to a large common egg mass; (2) *Bedeva hanleyi* (Angas) (Muricidae), which lays dome-shaped capsules in which many eggs are consumed as nurse eggs and only a few embryos hatch as well developed crawling juveniles; (3) *Morula marginalba* (Blainville) (Thaididae), which lays bluntly rounded capsules containing numerous eggs hatching as planktotrophic veligers; (4) *Nassarius* (*Alectrion*) *particeps* (Hedley) (Nassariidae), which lays numerous stalked triangular capsules each containing a single egg developing to a crawling stage before hatching; (5) *Siphonaria denticulata* Quoy and Gaimard (Siphonariidae), which lays gelatinous egg strings containing numerous eggs hatching as planktotrophic veligers.

Each species is briefly discussed in relation to other species of its family, and a summary is given of development in N.S.W. littoral prosobranchs.

Introduction

A number of authors have recently described the spawn and early development of Australian littoral gastropods (H. Anderson, 1958; D. T. Anderson, 1959, 1960, 1961, 1962, 1965; MacIntyre, 1961; Murray, 1962*a*, 1962*b*, 1963, 1964). The present paper reports further observations on this subject for the mesogastropod *Xenogalea labiata* (Perry) (Cassididae), the neogastropods *Bedeva hanleyi* (Angas) (Muricidae), *Morula marginalba* (Blainville) (Thaididae) and *Nassarius particeps* (Hedley) (Nassariidae), and the pulmonate limpet *Siphonaria denticulata* Quoy and Gaimard (Siphonariidae). Of these species, the spawn and development of *X. labiata*, *M. marginalba* and *N. particeps* have not hitherto been described. The egg capsules of *B. hanleyi* were figured by Hedley (1916) and Roughley (1925) and the egg strings of *S. denticulata* by Dakin (1953; Plate 55), but development of the eggs of these species has not been investigated.

Materials and Methods

Materials for the studies described in this paper have been gained from several sources. The egg mass of *X. labiata* was collected by Miss I. Bennett of the School of Biological Sciences, University of Sydney, from a sub-littoral rock face at Fairlight, N.S.W., in November, 1963. It was preserved shortly after collection, and observations have been made only on the egg mass itself and on the single developmental stage which it contains. The egg mass of *N. particeps* was also collected by Miss I. Bennett, at Long Reef, N.S.W., in October, 1962. This mass was maintained in aerated seawater in the laboratory and a number of observations made on the development of the embryos.

Capsules identified as those of *B. hanleyi* by comparison with the descriptions given by Hedley (1916) and Roughley (1925) were collected on numerous occasions during the winter months of 1962 and 1963 on the undersurfaces of loose rocks in tidal pools at Bradley's Head, on the north shore of Port Jackson. Their absence from this locality during the remainder of the year indicates

that the species is a winter breeder. These capsules were also maintained in aerated seawater in the laboratory, and observations made on the development of the embryos.

Morula marginalba was taken spawning on the underside of mid-littoral rocks at Long Reef, N.S.W., in January, 1963. The egg capsules were collected, maintained in aerated seawater in the laboratory and studied at intervals until the embryos hatched. Repeated searching at this and other localities where *Morula* is common has failed to provide further capsules, so that the general breeding habits are not yet clear. The ovaries of females, however, do not contain ripe eggs during the winter months.

Observations made at frequent intervals in the spring and summer of 1961/62 and 1962/63 at Harbord, N.S.W., and Long Reef, N.S.W., showed that *Siphonaria denticulata* breeds at least from September to March in these localities. Numerous egg masses were found attached to rock surfaces in the habitat of the adults, and animals were frequently seen in the act of spawning. Masses collected on various occasions were maintained in aerated seawater in the laboratory and studied at intervals until the embryos hatched.

Drawings of spawn, embryos and larvae investigated were made with the aid of a camera lucida. The photograph of Plate x was taken by the Department of Illustration, University of Sydney.

Results

Xenogalea labiata

The spawn of *X. labiata* (Plate x) is a large, irregular, sponge-like mass consisting of several thousand egg capsules. The entire mass, when collected, had dimensions of about 30 cm., and observations made at the time of spawning suggest that it is the common product of several females spawning together. When fresh, the mass was pinkish-orange in colour, the colour being imparted by the eggs contained in the capsules.

The capsules themselves are colourless and translucent and are cemented together as shown in Figure 1. Each capsule is roughly rectangular in shape, about 2·5 mm. long and 1·5 mm. broad, with a thin irregular base plate attached to the capsules below it in the mass. The capsule contains a colourless albumen in which float several hundred eggs, each about 160 μ in diameter, filled with pale orange yolk. All the eggs in the capsule develop simultaneously, proceeding through a yolk-filled gastrula stage (Fig. 2). Development beyond this stage was not observed.

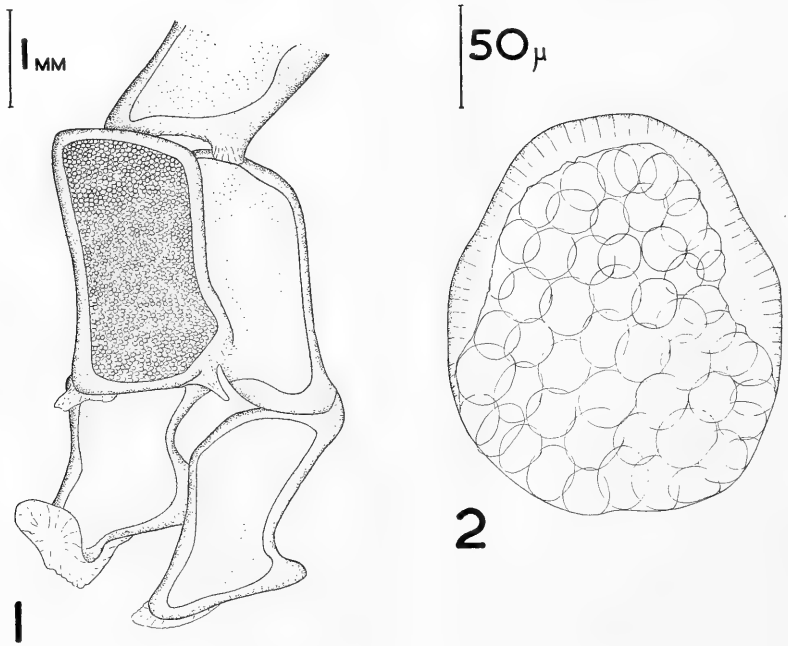
Bedeva hanleyi

The spawn of *B. hanleyi* consists of a group of about 10–20 separately attached, dome-shaped capsules, each about 3 mm. in diameter, whitish in colour and semi-transparent, with a transparent oval apical membrane (Fig. 3). Inside the capsule lie between 50 and 70 eggs, floating in a colourless albumen. A horny transparent base plate completes the capsule structure.

The eggs are opaque white, very yolky, and ovoid in shape, with a long diameter of 250 μ. Only about 15 eggs develop in each capsule, the remainder serving as nurse eggs for the developing embryos. A yolky early veliger stage, with an inconspicuous velum, simple colourless shell, small foot, and large, yolky visceral mass develops in about 4 days and begins to move slowly through the jelly in the capsule. Within a further 4 days, enlargement of the velum occurs, accompanied by elongation and ciliation of the foot and outgrowth of a convex, ciliated oral hood. The stomodaeum also becomes well developed, preliminary to the onset of the ingestion of nurse eggs. Further development during the next 7 days results in broadening of the velum and slight subdivision into 4 velar lobes, formation of black eyespots on either side of the oral hood, and the beginning of spiral coiling of the shell (Fig. 4). As the velar lobes

enlarge, each becomes wrapped around a nurse egg which rests against its concave posterior face. This, however, appears to be a simple consequence of the crowded conditions within the capsule and not a factor in nurse egg absorption.

Direct feeding on the nurse eggs now begins and is completed in about 5 days, during which the veligers retain a large active velum and glide rapidly through the albumen of the capsule. Some growth occurs during this phase, but the major part of the ingested yolk becomes stored in the visceral mass. Subsequent growth at the expense of the stored yolk proceeds at a slightly variable rate in different embryos in the capsule for a further 11 days. Gradual velar resorption is accompanied by elaboration of the head, foot and visceral mass and growth of the coiled shell, which becomes brown-pigmented (Fig. 5).



Figs 1–2. *Xenogalea labiata*. 1, egg capsules; 2, gastrula stage.

The fully developed juveniles, about $4\frac{1}{2}$ weeks old, escape in rapid succession from the capsule through an aperture formed by breakdown of the apical membrane. The newly hatched, crawling juvenile (Fig. 6) has a shell length of about 900 μ.

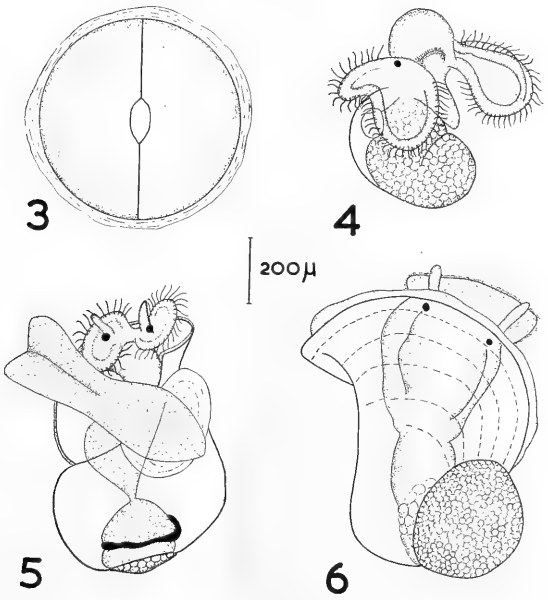
Morula marginalba

The spawn of *M. marginalba* consists of groups of about 20 low, rounded capsules. Each capsule (Fig. 7) has a tough, translucent wall, normally whitish in colour but sometimes tinged with purple, with a transparent thin oval area in the middle of one side through which hatching later occurs. The capsule is attached to the rock by an irregular, transparent, horny base plate and is filled with a colourless albumen in which float between 100 and 200 spherical, yellow, yolky eggs 220 μ in diameter.

The eggs in the capsule develop simultaneously, passing through a yolky trochophore stage to an early veliger stage (Fig. 8) within 2 days of oviposition. In the early veliger, the velum is still rudimentary, but a ciliated oral hood and stomodaeum are well developed, the foot rudiment is conspicuous and the yolky visceral mass is covered dorsally by a simple transparent shell.

During the next 3 days, the veliger becomes well developed (Fig. 9) and begins to move actively through the capsule albumen by means of its velar cilia. Torsion occurs and the shell enlarges and begins to develop a spiral form. The foot elongates, becomes ciliated, develops paired statocysts and secretes an operculum. The velar lobes expand and develop paired brown eyespots. The visceral mass remains yolky and undifferentiated, however, and no withdrawal of the head and foot into the shell is observed.

During the ensuing week, the veliger enlarges further and becomes highly active and much more differentiated (Fig. 10). The oral hood is reduced in size, but the velar lobes become larger and brown-pigmented around their margins. At the base of the right lobe, a tentacle grows out, tipped with a fan of stiff cilia. The foot also enlarges and becomes brown-pigmented on its ventral face. Further growth and coiling of the shell is accompanied by the



Figs 3–6. *Bedeva hanleyi*. 3, egg capsule; 4, 15-day veliger; 5, 25-day veliger; 6, newly hatched juvenile.

formation of numerous yellowish spots on the shell surface, together with the deposition of brown pigment at the umbo and around the margin (Fig. 11). The visceral mass develops a pulsating larval heart and a coiled gut in which the stomach is black-pigmented and contains yolk particles rotated by ciliary action. The yellowish yolk is now confined to the apex of the visceral mass.

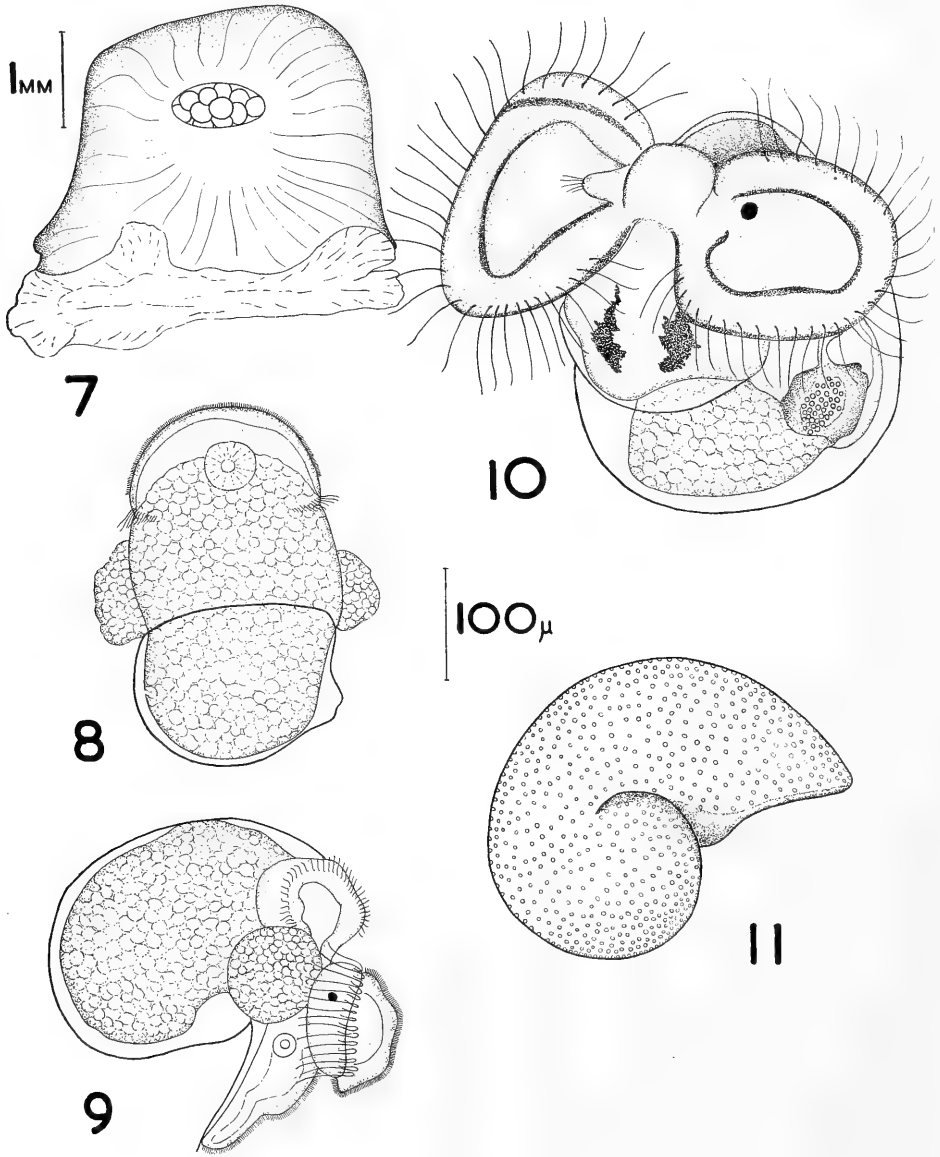
Due to the increased pigmentation of the developing veligers, egg capsules 12 or more days old are brown in colour, in contrast to the yellowish colour of fresher capsules.

Between 12 and 18 days after oviposition, little further change is observed in the veligers in the capsule, apart from a gradual reduction in the amount of yolk in the visceral mass. The veligers continue to swim actively in the capsule jelly, however, and at about 18 days the thin window in the side of the capsule breaks down and the veligers escape to a free swimming existence. Their development after hatching was not followed.

Nassarius particeps

The egg mass of *N. particeps* used in the present investigations was taken at the time of oviposition. Two females were associated with it, and both

proved to have numerous ripe oocytes in their ovaries. Whether both were contributing capsules to the egg mass could not be decided with certainty, but the extent of the mass suggested possible cooperative spawning. The mass consisted of several hundred small, stalked, triangular capsules attached by



Figs 7–11. *Morula marginalba*. 7, egg capsule ; 8, 2-day veliger ; 9, 5-day veliger ; 10, 12-day veliger ; 11, shell of 12-day veliger.

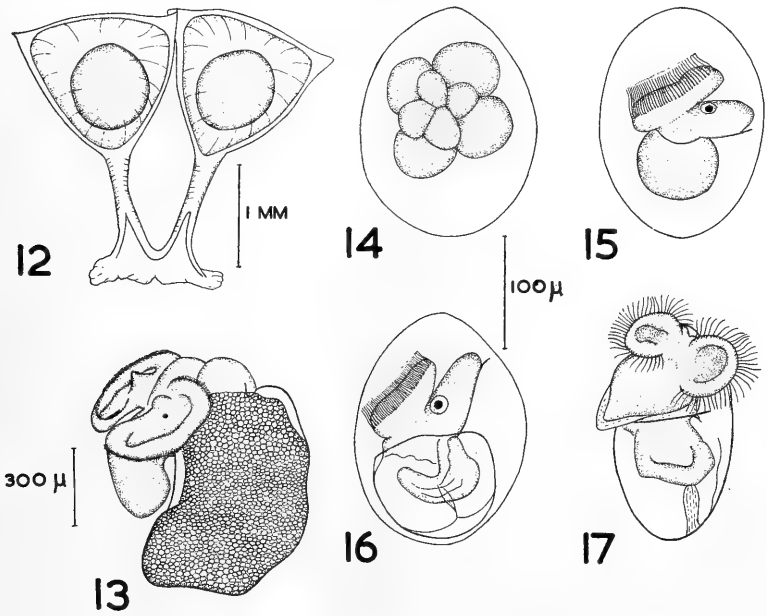
confluent base plates as a single layer directly to the under surface of a rock in the lower littoral, and covered an area of many square cms.

Each egg capsule of *N. particeps* (Fig. 12) is about 2·5 mm. in height colourless and translucent, and filled with a colourless albumen in which floats a single large, yellowish, spherical egg about 700 μ in diameter. In spite of the size of the egg, cleavage is total and the first two divisions are only slightly

unequal. Development proceeds through a highly modified veliger phase in which the velar lobes, although ciliated, remain relatively small and produce only slow rotation of the embryo inside the capsule. Development of the head, foot and shell are well advanced after 7 days (Fig. 13), although the large visceral mass is still yolk-filled and little differentiated. By 12 days, reduction of the velum is in progress and the yolk reserves are beginning to lessen. Development was not followed beyond this point but there seems little doubt that *N. particeps* hatches as a crawling juvenile, probably about 1 mm. in length.

Siphonaria denticulata

The egg mass of *S. denticulata* is an irregular, gelatinous, spiral coil about 5 cm. long, creamy-white in colour and firmly glued to the rock surface in the habitat of the adults. The jelly is colourless and the numerous closely-packed



Figs 12–13. *Nassarius particeps*. 12, egg capsule ; 13, 7-day veliger.
Figs 14–17. *Siphonaria denticulata*. 14, embryo after 3rd cleavage, from animal pole ; 15, 3-day veliger ; 16, 5-day veliger ; 17, newly hatched veliger.

eggs embedded in it are whitish and translucent. Each egg is about 100 µ in diameter and is enclosed in an ovoid, transparent egg capsule about 200 µ long and 160 µ broad.

The eggs cleave in a typical spiral manner, the first two divisions being equal, the third unequal (Fig. 14). Blastula and gastrula phases are passed through in 24 hours and a simple yolky trochophore is completed 48 hours after oviposition. During the third day of development, the operculate foot, bilobed velum and globular shell of an early veliger develop (Fig. 15). Growth and internal differentiation now set in and the veliger begins to rotate vigorously within its capsule. The ciliated gut becomes conspicuous as the yolk reserves are finally resorbed (Fig. 16) and hatching of the veligers as actively swimming planktotrophic larvae (Fig. 17) occurs on the sixth day after oviposition.

Hatched veligers fed on the diatom *Nannochloris* continued to swim and grow for a further 4 days, becoming more differentiated internally and developing a slight spiral twist to the shell. Laboratory culture beyond this stage was not achieved.

Discussion

Xenogalea labiata

Very little is known of spawning in cassidid mesogastropods. The only two previous descriptions of egg capsules appear to be those of Erlanger (1893) for *Cassidaria echinophora* and Lo Bianco (1899) for *C. echinophora* and *Cassis sulcata*. These brief notes suggest that the egg mass of *X. labiata* is typical for the family, but it is not yet known whether the apparent cooperative spawning of *X. labiata* is a characteristic of cassidids.

Embryonic and larval development in the Cassididae remain to be described, but the number and dimensions of the eggs of *X. labiata* suggest that this species hatches as a pelagic planktotrophic veliger. In contrast, it appears from the work of Erlanger (1893) and Lo Bianco (1899) that the eggs of *Cassidaria echinophora* are larger (280 μ in diameter) and that only a few develop, the remainder serving as nurse eggs, to hatch at an advanced stage, probably as crawling juveniles.

Bedeva hanleyi

The present work confirms the descriptions given by Hedley (1916) and Roughley (1925) of the egg capsules of *B. hanleyi* and also shows that development includes feeding on nurse eggs and ends in hatching from the capsule as a crawling juvenile. Hatching at the crawling stage is characteristic of Muricidae (Anderson, 1960 ; MacKenzie, 1961 ; Murray, 1963, 1964) and, as pointed out by Thorson (1946), dome-shaped capsules of the type laid by *B. hanleyi* have been described for several species of *Trophon*, the genus to which *B. hanleyi* is alternatively referred. Feeding on nurse eggs has not previously been recorded in this genus, but is well known for other muricids (e.g. species of *Murex*, *Neptunea*, *Nucella* : Lebour, 1937 ; Ankel, 1937, 1938 ; Thorson, 1935, 1946 ; Natarajan, 1957 ; Golikov, 1961) and may yet be found in other species of *Trophon* or *Bedeva*.

Morula marginalba

Spawning and development in Thaididae have been described for a number of species of *Thais* (e.g. Burkenroad, 1931 ; Chari, 1950 ; Butler, 1953 ; Natarajan, 1957), all of which produce egg capsules of the general type exemplified by *M. marginalba*, though the shape of the capsule and the position of the hatching membrane vary in different species. Dakin (1953) has also figured massed capsules of the same general type for *Dicathais orbita*. Only one previous reference has been made to the egg mass of a species of *Morula*, however, that of Ostergaard (1950) for *M.* (= *Drupa*) *dumosa* and the gelatinous egg mass described is so aberrant for the family that it seems likely to be a misidentification.

The mode of development of the numerous encapsulated eggs in *M. marginalba*, and the form of the pelagic planktotrophic veligers at hatching, are closely similar to those of several species of *Thais* (e.g. *T. haemastoma* : Burkenroad, 1931 ; Franc, 1948 ; Butler, 1953 ; *T. bufo* : Natarajan, 1957 ; *T. javanica* : Natarajan, 1957 ; *T.* species B, *T.* species C : Natarajan, 1957). The genus *Thais*, however, also includes species with larger eggs which hatch at a later stage of development and are only briefly pelagic (e.g. *T. tissoti* : Natarajan, 1957) and species which develop directly to hatching as crawling juveniles (e.g. *T. emarginata* : Dehnel, 1955). It cannot be assumed, therefore, that the mode of development in *M. marginalba* is characteristic of all species of *Morula*.

Nassarius particeps

In several species of *Nassarius*, the females spawn bottle-shaped capsules containing numerous small eggs which hatch as pelagic planktotrophic veligers

(Lebour, 1937 ; Thorson, 1946 ; Natarajan, 1957 ; Scheltema, 1961, 1962). A similar mode of spawning and development is also described by Amio (1957) for *Tritia festivus*. In a number of Indo-Pacific nassariids, however, the spawn comprises numerous small triangular capsules with confluent base plates, each containing a single egg. It is to this group that *N. particeps* belongs. In *N. costata* and *N. thersites*, the capsules are stalkless, the eggs are relatively small (200 μ and 250 μ in diameter respectively), and hatching occurs as pelagic veligers which probably adopt a planktotrophic existence (Natarajan, 1957). In *N. liviscens*, the capsules have short stalks, the eggs are larger (320 μ in diameter), and development is more direct, with hatching occurring as a veliger in which the velum is relatively small and the visceral mass large and yolky. Development and metamorphosis to a crawling juvenile are completed in this species during a brief pelagic lecithotrophic phase (Amio, 1957). In *N. suturalis* the capsules have long stalks, the eggs are large (probably about 400 μ in diameter), and development appears to be direct, with hatching occurring as a crawling juvenile (Risbec, 1935). *N. particeps*, with its long-stalked capsules and very large eggs, shows the most extreme adaptation to direct development yet known for nassariids with this type of spawn.

Siphonaria denticulata

The egg mass and development of *S. denticulata*, hatching as a small planktotrophic veliger, are similar to those of several species of intertidal siphonariid limpet (Morton, 1955 ; Knox, 1955 ; Voss, 1959). In *Kerguelenella stewartiana* and *Siphonaria kurracheensis* the egg capsules contain a greater volume of albumen and the embryos hatch as crawling juveniles in a more typical pulmonate manner (Thorson, 1940 ; Knox, 1955), but *K. stewartiana* is a sub-Antarctic littoral species from Stewart Island and *S. kurracheensis* is a semiterrestrial species occurring in the Persian Gulf.

Conclusions

Studies of prosobranch reproduction in the northern hemisphere have shown that planktonic larvae are of common occurrence among temperate species (Thorson, 1946, 1950). Along the New South Wales coast, many more species need to be studied before any corresponding generalization can be made for the 52 species of littoral prosobranch listed by Dakin (1953) as common to this vicinity. At the same time, the species whose development has been recorded are now sufficient in number to warrant grouping into the developmental types distinguished by Thorson (1946, 1950), as follows :—

(*a*) Viviparous species—none yet described.

(*b*) Species with a non-pelagic development—5. *Bembicium melanostoma* (Littorinidae), *Glossaulax aulacoglossa* (Naticidae), *Cymatilesta spengleri* (Cymatidae), *Bedeva hanleyi* (Muricidae), *Nassarius particeps* (Nassariidae) (Anderson, 1959, this paper ; H. Anderson, 1958 ; Murray 1962*b*, 1964).

(*c*) Species with a very short pelagic life (a few hours to a few days)—5. *Cellana tramoserica* (Patellidae), *Notoacmaea petterdi*, *Patelloida alticostata*, *Chiazacmaea flammea* (Acmaeidae), *Melanerita melanotragus* (Neritidae) (Anderson, 1962, 1965).

(*d*) Species with a long pelagic, planktotrophic veliger life—11. *Bembicium nanum*, *Bembicium auratum*, *Melaraphe unifasciata*, *Nodilittorina pyramidalis* (Littorinidae), *Velacumantus australis* (Potamididae), *Conuber conicum*, *Conuber strangei* (= *sordida*), *Conuber melastoma* (Naticidae), *Cypraea caput-serpentis* (Cypraeidae), *Xenogalea labiata* (Cassididae), *Morula marginalba* (Thaididae) (Anderson, 1961, 1962, this paper ; MacIntyre, 1961 ; Murray, 1962*b*, 1964 ; Ostergaard, 1950).

Thus 11 out of 21 species whose developmental type is known almost certainly have a long planktonic larval life, a proportion which accords with

expectations based on northern hemisphere studies. Further investigation, however, may yet alter this picture, since of the remaining 31 common species, many are archaeogastropods, unlikely to have a long planktonic life, and several others belong to families for which non-pelagic development is characteristic.

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EXPLANATION OF PLATE X

The animal and part of the egg mass of *Xenogalea labiata*.

OBSERVATIONS ON THE FINE STRUCTURE OF THE MERISTEM OF ROOT NODULES FROM SOME ANNUAL LEGUMES

P. J. Dart* and F. V. Mercer†

(Plates xi-xxv)

[Read 29th September, 1965]

Synopsis

The fine structure of the meristematic zone of the root nodules of subterranean clover, barrel medic and purple vetch was examined with thin sections of $KMnO_4$ and OsO_4 fixed tissue. The nodule meristematic cell has basically the same ultra-structure as other types of meristematic cells, as described in the literature. The differentiation of the cells produced by the meristem to form the cells invaded by the rhizobia is also described. The fine structure of the nodule husk cells is compared with those of the nodule meristem.

Introduction

The root nodules of subterranean clover and barrel medic and purple vetch are formed by the differentiation of cells produced by an apical meristem. The cells which differentiate basally in relation to the zone of cell division form the region of the nodule which becomes filled with bacteroids, while cells differentiating terminally and laterally form the husk or nodule cortex, and in this region further differentiation forms the vascular system of the nodule. Development of cells in the bacteroid zone of the nodule has been described (Dart and Mercer, 1963*a*, 1963*b* ; 1964).

Materials and Methods

Plants of subterranean clover (*Trifolium subterraneum* L. var. Clare) inoculated with the effective *Rhizobium trifolii* str. TAI, and barrel medic (*Medicago tribuloides* Desr. str. 173) inoculated with the *Rhizobium meliloti* strain SU277.1, an effective strain, or SU237, were grown in sand culture in a greenhouse. This latter strain forms nodules which are red for only 3–5 days. A description of these nodule types has been given previously (Dart and Pate, 1959). Nodules from *Vicia atropurpurea* Desf. (purple vetch) formed by the effective *Rhizobium* strain SU331 were also examined. For the effective strains, slices of 1–4 week old nodules were examined ; but for the SU237 strain, slices were taken from nodules both before they became pigmented and during the pigmented phase. The nodule slices were fixed in $KMnO_4$ or OsO_4, stained in uranium acetate, and embedded in araldite. Thin sections were examined in a Siemens Elmiskop I or II.

Full details of techniques have been described previously (Dart and Mercer, 1963).

Observations and Discussion

The low power electron micrographs (Pls xi ; xii, *a* ; xiii) show the general fine structural features of the nodule meristematic cells. There is a relatively large nucleus usually containing one nucleolus, mitochondria, proplastids, Golgi bodies, endoplasmic reticulum occasionally connected with the nuclear membrane, a ground cytoplasm with many ribosome-like particles, and occasionally " spherosomes " and unidentified vesicular organelles. As can

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be seen, the basic structure is similar to the ultrastructure of other types of meristematic cells (e.g. root apex Whaley *et alii*, 1960 ; Falk, 1962 ; and stem apex Buvat, 1958). This confirms the suggestion made from light microscope observations that " the meristematic cell of the nodule corresponds to a meristematic cell of any growing region " (Fred, Baldwin and McCoy, 1932). Intercellular spaces are not usually present in the meristem, but develop as the cells differentiate (Pl. xi).

Mitochondria

In $KMnO_4$ fixation, the mitochondria are mostly spherical to ellipsoid in shape, and have the usual structure with cristae arising from the inner limiting membrane and a homogeneous matrix between the cristae. Mitochondria from meristematic and newly differentiated cells usually contain a prominent ' vacuole ' in this matrix, superficially similar to the *Rhizobium* nucleoid, and it is tempting to associate this region with mitochondrial deoxyribonucleic acid (e.g. see Nass and Nass, 1963 ; Nass *et alii*, 1965 ; Bell and Mühlethaler, 1964 ; Gibor and Granick, 1964). Occasionally some mitochondria have figure-of-eight shapes, a narrow constriction separating the two lobes—suggesting division by constriction (Pl. xiv, *b* ; Pl. xxiii, *a*). Similar origins for new mitochondria have been proposed by other workers (e.g. Whaley *et alii*, 1960). No large promitochondrion bodies which segment to form mitochondria (Bal and De, 1961 ; Manton, 1962 ; Vesk, Mercer and Possingham, 1965) were found in the nodule meristem. Mitochondria in the differentiated uninvaded cells usually are smaller with fewer cristae than those of the meristem.

Proplastids

These organelles are prominent features of the nodule meristematic cell, and are scattered through the cytoplasm. They are usually bounded by two membranes which enclose a poorly developed internal membrane system and a matrix or stroma. The limiting membrane generally stains more deeply in $KMnO_4$ fixation than any of the other cell membranes. The internal membranes are formed by invagination of the inner limiting-membrane (Pl. xvii, *c* ; Pl. xviii, *a-c*) or from a " prolamellar body ".

In leaf tissue a prolamellar body has been implicated in the formation of the internal plastid membranes (e.g. Mühlethaler and Frey-Wyssling, 1959). In the nodule plastids the ' bodies ' are much smaller and the membrane bounded compartments less organized than those found in leaf tissue (Pl. xviii, *a-c*).

In the proplastids of the nodule, small ($\simeq$ 60 Å diameter), electron-dense granules are found. These are distributed through the stroma of the proplastids before, and at the beginning of, starch formation (Pl. xvi, *a* ; Pl. xviii, *e*) but in young plastids with small starch grains they may be arranged in groups (Pl. xv, *b* ; Pl. xvii, *a*, *b*). The particles resemble the phytoferritin described by Hyde *et alii* (1963) as occurring in young bean and pea plant plastids. Bergersen (1963) has also observed small electron-dense granules in soybean nodule plastids. The particles are much more readily resolved in OsO_4 fixation (Pl. xv, *b* ; Pl. xvi, *a*) for in $KMnO_4$ fixation the electron-density of the plastid stroma tends to mask the granules. In older plastids with large starch grains the particles can occasionally be found. The particles are sometimes organized into a tight array from which tubular (?) profiles appear to originate (Pl. xvii, *a*, *b*). Similar ' tubules ' often run between the normal, internal plastid membranes and the inner limiting membrane of the plastid (Pl. xvii, *a*, *d*, *e* ; Pls xix ; xx ; xxi *b*) but are much less electron dense than the normal plastid membranes. Often there are several of these profiles running roughly parallel to each other, superficially resembling a mitochondrion in outline, although the tubule diameter is much smaller than the profile of a mitochondrion crista in cross section. Serial sections show that the tubules, with the enclosing dense-staining plastid membranes are often organized into a separate, oval-

shaped " compartment " at the edge of the plastid. The membrane bounding the " compartment " in the plastid stroma is not continuous in all sections with the plastid limiting membrane which forms the rest of the " compartment " boundary. The " compartment " would appear to be formed by an invagination and folding back of the inner-limiting membrane of the plastid (Pls xix ; xx).

The proplastids in the differentiating cells adjacent to the meristem often have bud-like protrusions (Pls xiv, *c* ; xv, *d* ; xviii, *e*), usually with several membranes running across the " bud ".

The nodule proplastids appear to arise in two related ways—by segmentation of a large membrane bounded body (Pl. xiv, *a*, *b*) and by constriction division of an existing proplastid (Pls xiii ; xxiv, *b*). A similar situation has been described by Vesk, Mercer and Possingham (1965) for the proplastids of leaves of *Zea mays*. Plastids in the nodule meristematic cells rarely contain starch and have few internal membranes, but synthesis and development of these accompanies cell enlargement and vacuolation (Pls xi, *a* ; xii, *b*).

In the bacteroid-filled cells plastids become elongated and filled with elongate starch grains (Dart and Mercer, 1963*a*, 1964) while in the adjacent noninvaded cells the plastids are oval-shaped, and contain three or four large roughly circular, starch grains, but much more plastid stroma remains than in the plastids of the invaded cells (Pl. xvii, *c*).

As with the mitochondria, proplastids in the nodule meristem often contain, in the stroma, small electron empty ' vacuoles ' crossed by very fine fibrils (Pl. xiv, *a*). The similarity between these areas and the bacterial nucleoid has been remarked on by others (e.g. Ris and Plaut, 1962), the implication being that these are the deoxyribonucleic acid-containing regions in the plastid (see Gibor and Granick, 1964 ; Gunning, 1965).

Golgi Bodies

Several Golgi bodies are usually present in each thin section of the meristematic cell and each consists of a varying number of flattened discs. Occasionally in $KMnO_4$ fixation, the membrane bounding each disc can be resolved into a unit membrane (Robertson, 1960). Often the rims of the discs are enlarged into vesicular structures which form a sequence ranging from a slightly inflated periphery to large sacs, some of which apparently bud off to form small single membrane bounded vesicles in the cytoplasm, as described for other cells (Whaley *et alii*, 1960, 1964). As in other plant cells (e.g. Whaley and Mollenhauer, 1963), these Golgi vesicles appear to be associated with cell plate and primary wall formation.

Ground Cytoplasm

In $KMnO_4$ fixation the ground substance is a homogeneous granular matrix, while in OsO_4 fixation electron-dense, 120–150 Å diameter ribosome-like particles are found, dispersed through the cytoplasm and associated with the endoplasmic reticulum (Pls xii, *a* ; xiii ; xv, *a* ; xvi, *a*). Surface views of the reticulum (Pl. xiii) show the ribosomes may be organized in a spiral or a linear array with some 8–12 ribosomes per unit (polyribosome ?). The relative concentration of ribosomes in the cytoplasm decreases as the cells differentiate and vacuolation begins. A marked increase in ribosome numbers (mostly free in the cytoplasm) occurs following infection thread invasion and subsequent release and dispersal of the *Rhizobium* cells through the host cytoplasm. The endoplasmic reticulum system is rather sparse in the meristematic cells and is mostly plate-like and generally granular. The amount of endoplasmic reticulum appears to be even less in differentiating cells (Pl. xii, *b*) before *Rhizobium* invasion. Small spherosome-like bodies (see Frey-Wyssling *et alii*, 1963 ; Drawert and Mix, 1962) are sometimes found in the nodule meristematic cells but are more frequently seen in the differentiating cells. These bodies

have an electron-dense granular composition, and are surrounded by a dense staining membrane. Sometimes an electron-empty region is found in the centre of these bodies (Pl. xviii, *e*). Similar bodies have been found in maize and rye root meristem cells (Whaley *et alii*, 1960 ; Fabergé and Lewis, 1962). Occasionally other unidentified inclusions resembling a sack of tiny vesicles are found (Pl. xxii) in both $KMnO_4$ and OsO_4 fixation, as well as small vesicles with a single membrane enclosing a homogeneous ground substance (Pl. xxii, *a*). The former are closely associated with the endoplasmic reticulum and similar bodies are found next to the cell wall enclosed by the plasma membrane (Pl. xxii, *b*, *d*). This suggests that the bodies may be involved in transport of materials from the endoplasmic reticulum to the cell wall. Jensen (1963) has recently reported that similar bodies in cotton synergids are specialized endoplasmic reticulum vesicles. Occasionally membrane profiles of what is presumably endoplasmic reticulum contain a dense inclusion (Pl. xxii, *a*).

Nucleus

The interphase nucleus occupies a major proportion of the volume of the nodule meristematic cell. In $KMnO_4$ fixation the nucleus is clearly bounded by two unit membranes that are usually closely appressed to each other and OsO_4 fixation shows that the outer membrane is studded with ribosomes. Nuclear pores and larger gaps are occasionally present and there are often several connections between the nuclear envelope and endoplasmic reticulum (Pl. xi).

In early interphase cells, gaps much wider than the normal nuclear pore are often present in the nuclear envelope. Similar large gaps occur in newly invaded, differentiated nodule cells. In both these cell types ribosome synthesis is active at this stage as well as the synthesis of new cytoplasmic proteins. Woodard *et alii* (1961) have shown that in pea root meristem cells there is a rapid synthesis of ribonucleic acid in early interphase. The large gaps in the nuclear envelope would permit rapid transfer of ribosomes to the cytoplasm if in fact ribonucleic acid and protein are organized into ribosomes in the nucleolus (see Bonner and Huang, 1962). Little structure is observable in the interphase nucleoplasm with $KMnO_4$ fixation but occasionally denser granulation, presumably corresponding to chromatin material, can be seen, while the nucleolus appears as a more electron-dense area usually circular in outline. In OsO_4 fixation followed by uranyl acetate staining considerable structure can be seen in the nucleus. Several areas of dense staining materials with an overall granular appearance are present. These dense, presumably euchromatin areas have an irregular outline and are bounded by an electron-lucent nucleoplasm containing dispersed fibrillar material (Pls xii, *a* ; xv, *a*).

The nucleolus is clearly defined in OsO_4 fixation with uranium acetate post staining. It is basically more electron-dense than the surrounding nucleoplasm and chromatin. Occasionally the nucleolus is haloed by an area free of electron-dense material (Pl. xii, *a*) but, as Lafontaine (1958) observed, there are often places where chromatin and nucleolus merge together (Pl. xv, *a*). The nucleolus itself contains tightly packed 130–150 Å diameter granules. The nucleolus often has a relatively electron-lucent core and in the granular cortex there often appears to be filamentous material $\cong$ 100 Å wide.

Cell Plate Formation in the Meristem

Following cell division the nuclear membrane often has large gaps near the region of cell plate formation. The new cell plate begins as a collection of vesicular material lined by endoplasmic reticulum and phragmosomes, between the two telophase nuclei. Vesicle coalescence, and consolidation of the electron-lucent material within the new vesicle aggregates, mark the beginning of wall synthesis which continues centripetally (Pl. xi, *b*). In the initial stages of new wall synthesis there are several intercellular endoplasmic

reticulum connections. The pattern of cell division parallels closely that outlined by Porter and Caulfield (1958) and Porter and Machado (1960) for onion root-tip cells, and Whaley *et alii* (1960) for maize root meristematic cells. Towards the end of cell plate formation, evenly dispersed electron-dense material is deposited at the centre of the new wall. As in cell plate formation this zone (middle lamella ?) then consolidates and expands centripetally.

Differentiation of the nodule meristematic cell

After division has ceased the newly-formed cells undergo differentiation to form the husk and bacteria-filled zone of the nodule. The continuous differentiation of the cells and the continuous infection of the differentiated cells maintain a zone, generally three cells wide, between the meristem and the zone of infection.

Vacuolation of the cytoplasm is the first change, associated with differentiation of the nodule cells. Various theories have been proposed for the origin of vacuoles in plant cells, and in electron micrographs of the nodule meristem, profiles of vacuoles can be found which are consistent with most of these views. The most usual " method " of vacuole formation observed in the nodule cells was that described by Mühlethaler (1958) where a phase difference becomes apparent in the cytoplasm (Pl. xxiii, *a*) and as this region expands a tonoplast is synthesized *de novo* at the interface in several parts before joining to form the tonoplast observed around fully-developed vacuoles. Buvat (1957, 1958, 1960) and Poux (1962*a* and *b*) proposed that vacuoles are initiated by expansion of the two membranes of the endoplasmic reticulum. Membrane profiles consistent with this can be found in differentiating nodule cells (Pls xxii, *a* ; xxiii, *c*) but these may well be plasmolysis figures of vacuoles rather than stages in vacuole formation. Small vesicles are sometimes found associated with the plasmalemma suggesting that pinocytosis might be occurring. Weiling (1961) has suggested that subsequent expansion of pinocytotic vesicles forms a vacuole. In some meristematic cells there are small irregular-shaped, membrane-bounded bodies with phase differences characteristic of vacuoles (Pl. xi). These are presumably the " pro-vacuoles " that Whaley *et alii* (1962) and Leech *et alii* (1963) suggest are transformed into true vacuoles. Marinos (1963) claims that the tonoplast in barley shoots is derived from a swelling of the outer Golgi body cisterna but no profiles suggestive of this have been found in the nodule meristem.

The vacuoles in the nodule usually contain a sparsely distributed, electron-dense material. Occasionally dense granular bodies are found in the vacuole and sometimes sharply defined differences in electron-density (phase difference?) exist within the vacuole.

The tonoplast is not always preserved after $KMnO_4$ fixation, but better preservation is obtained with OsO_4 fixation. The tonoplast can be resolved into a unit membrane structure (as defined by Robertson, 1960) with a dark-light-dark profile of overall dimension 90–100 Å. Occasionally after OsO_4 fixation electron-dense material adheres to the vacuole side of the tonoplast.

Some of the cells which differentiate adjacent to the meristem remain uninvaded by *Rhizobium* cells. A proportion of these uninvaded cells, which usually have a thin layer of peripheral cytoplasm intact, degenerate just before adjacent cells become infected. This involves a loss of the cytoplasmic matrix and disorganization of the usual organelles, leaving the plasmalemma and most of the tonoplast intact. In these cells the membranes are readily resolved (Pl. xvi, *b*)—possibly due to a lack of background cytoplasm obscuring the structure, but could also conceivably be due to a change in the membrane structure itself, induced during the cell degeneration. Occasionally small electron-dense lines cross between the two dense lines of the tonoplast membrane giving the membrane a banded appearance similar to the ' globular ' structure observed in mitochondrial and some cytoplasmic membranes by Sjöstrand

(1963). These 'degenerate' uninvaded cells are thought to be a defence mechanism response of the host cell to restrict invasion by *Rhizobium*. Alternatively, these non-living cells may be functioning as vascular or conducting tissue as has been postulated for degenerate cells in pea cotyledon tissue (Bain and Mercer, 1965).

In meristematic cells, but more frequently in the differentiated, recently invaded cells, the plasmalemma often invaginates, enclosing a system of tightly coiled membrane-bounded tubules and vesicles (Pl. xxi, *b*). These structures resemble the lomasomes observed in fungi (Girbardt, 1961 ; Moore and McAlear, 1961 ; Peyton and Bowen, 1963). Invaginations of the plasmalemma are also found, with only a few membrane-bounded vesicles between the plasmalemma and the cell wall similar to the structures observed by Grun (1963) in *Solanum* root meristem cells and by us in barrel medic and subterranean clover root meristem cells (Dart and Mercer, unpublished observations). In some cells a single membrane fragment is sometimes found immediately outside the plasmalemma in the cell wall material (Pl. xvi, *b*) and occasionally membranous elements are found deeper in the wall layers (Pl. xxi, *b*). These membrane fragments may be remains from the deposition of material during cell wall thickening (Wardrop, 1964). An incorporation of small, single membrane-bounded vesicles, with the vesicle membrane fusing with the plasma membrane, also appears to be involved in wall development (Pl. xxii, *b*). In other places the vesicles themselves appear to be incorporated in the wall (Pl. xvi, *b*).

Plasmodesmata are frequently observed between meristematic cells, becoming less so as the cell differentiates with associated cell wall growth. Some of these plasmodesmata are branched (Pl. xviii, *e*) and in some the plasmalemma is observed to evaginate and line the structure so that the plasmalemmas of adjacent cells are contiguous. Some plasmodesmata-like structures which penetrate the cell wall are completely bounded in the wall by a membrane-like structure. These might also be Frey-Wysslings " wall papillae " (1962). Only an outer dense zone with an adjacent electron-empty zone can be resolved, presumably because the inner dense line of the membrane (assuming it is a unit membrane) merges with the electron-dense material enclosed by the " membrane " (Pl. xxi, *a*).

Nodule Husk Cells

Quite a distinct difference is apparent between the cells of the nodule meristem and the large, vacuolated, " protective " cells that enclose the nodule. The husk cells have a very large central vacuole, and a thin layer of cytoplasm containing a few small mitochondria with few cristae, Golgi bodies and segments of endoplasmic reticulum (Pls xxiv ; xxv). Plastids are few in number and large in size. Starch formation increases with distance from the meristem. The vacuoles usually contain more stainable material than the vacuoles of cells about to be invaded by infection threads (compare Pl. xxv and Pl. xii, *b*).

The nucleus lies in the thin layer of cytoplasm adjacent to the cell wall and often has a wrinkled appearance (Pl. xxv, *c*). Plasmodesmata connections between the husk cells are prevalent—and usually occur in groups (Pl. xxv), possibly corresponding to apit field. Some of the husk cells lose their cytoplasmic contents, leaving a granular material attached to the cell wall in places.

Conclusion

There are no basic differences in fine structure between the nodule meristems of subterranean clover, barrel medic or purple vetch. It can be seen that the ultrastructure of the meristematic cell is very similar to the basic ultrastructure of the root meristematic cell. It seems that meristems have a similar subcellular organization and pattern of activity whether they are " normal " structures or whether they arise as a response to invasion by *Rhizobium*.

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Explanation of Plates xi–xxv

Plate xi.

a. Panorama of the meristematic zone of a barrel medic nodule (SU237). Vacuole formation and cell enlargement has commenced in some cells. The single arrow points to a ' provacuolar body ' in a meristematic cell which appears to have a ' tail ' of endoplasmic reticulum. The double arrow points to an ' unknown body ' which is bounded by a single membrane. n—nucleus, v—vacuole. $KMnO_4$ fixation. ×11,000.

b. Cell plate formation in a meristematic cell of a barrel medic nodule (SU237). Endoplasmic reticulum and small vesicles (Golgi vesicles ?) are closely associated with the new wall. The Golgi bodies (g) appear to be budding off small vesicles. The double arrow points to a major discontinuity in the wall. The small mitochondria have prominent ' vacuoles ' (e.g. arrow). p—phragmosome (?). $KMnO_4$ fixation. ×35,000.

Plate xii.

a. Meristematic cell of a 7-day-old barrel medic nodule (SU237). The nucleus contains sparsely distributed fibrillar material but around the dense nucleolus (Nu) there is a ' halo ' virtually free of fibrils. In the ground cytoplasm there are free ribosomes and some ribosomes attached to endoplasmic reticulum. The proplastids (p) have shrunk during preparation. OsO_4 fixation. ×12,500.

b. Panorama showing the vacuolating cells adjacent to the meristem in a barrel medic nodule (SU237). Most of the plastids contain starch grains. A few sparsely distributed, plate-like endoplasmic profiles are present. $KMnO_4$ fixation. ×11,000.

Plate xiii.

Portion of a meristematic cell from a barrel medic nodule (SU237) showing the distribution of ribosome-like particles, endoplasmic reticulum, Golgi bodies and mitochondria. Surface views of the endoplasmic reticulum show the ribosomes often grouped (polyribosomes ?) into whorled, rosette arrangements (e.g. arrows). The free ribosomes are also grouped in units (e.g. circles). The plastid (p) at the bottom of the figure appears to be dividing by constriction. The inset shows some of the ribosome-like particles in more detail : some of them are attached to endoplasmic reticulum. OsO_4 fixation. $\times 20{,}000$. Inset $\times 40{,}000$.

Plate xiv.

a. Large proplastid bodies in a newly-invaded cell. One appears to be dividing by constriction (arrow). The proplastids contain small electron empty regions (e.g. double arrow) containing fine fibrils which are reminiscent of a bacterial nucleoid (n). $\times 35{,}000$.

b. Irregularly-shaped proplastids are apparently segmenting (see double arrow) in a non-invaded meristematic cell. One of the mitochondria has a figure-of-eight profile suggestive of division by constriction (single arrow). w—cell wall. $KMnO_4$ fixation, barrel medic nodules (SU237). $\times 20{,}000$.

c. Shows a small ' bud ' on a plastid from a barrel medic nodule (SU277.1). $\times 40{,}000$.

Plate xv.

a. Interphase nucleus and part of the cytoplasm of a differentiating cell adjacent to the meristem of a barrel medic nodule (SU277.1). The nucleus contains a prominent nucleolus (nu) and several smaller more diffuse electron dense areas (c—presumably euchromatin). OsO_4 fixation. $\times 20{,}000$.

b. Plastid from a vacuolated, non-invaded cell of a subterranean clover nodule fixed in OsO_4. The plastid contains a large, central starch grain and several closely packed arrays of phytoferritin-like particles (e.g. arrow). In the adjacent cytoplasm several ribosome-like particles (r) are present, along with a Golgi body (g). $\times 50{,}000$.

Plate xvi.

a. Plastids from a meristematic cell of a subterranean clover nodule fixed in OsO_4. The plastids contain numerous phytoferritin-like particles and several larger, osmiophilic bodies (o). Ribosome-like particles (r) are mostly free in the cytoplasm. $\times 60{,}000$.

b. Degenerate non-invaded cell in a barrel medic nodule (SU277.1). The tonoplast (t) and plasmalemma (pl) are resolved into a dense-light-dense profile. An invagination of the plasmalemma (arrow) contains several circular membrane profiles apparently embedded in the cell wall and possibly the remains of vesicular packages of material incorporated in the wall. The double arrow indicates another membrane profile running parallel to the plasmalemma and between it and the cell wall. $KMnO_4$ fixation. $\times 70{,}000$.

Plate xvii.

a. Proplastid filled with phytoferritin-like particles. These are aggregated in one portion of the plastid (single arrow). The double arrow points to three small tubular elements attached to the limiting plastid membrane. $\times 60{,}000$.

b. Another aggregation of the small, electron-dense, particles with some fine tubules running between the aggregation and the plastid limiting membrane. $\times 35{,}000$.

c. Plastid from a non-invaded cell. The plastid containing four large starch grains and two areas where an internal plastid membrane is joined to the limiting membrane by fine tubules (arrows). In Fig. *d* another plastid has been sectioned closer to the edge and shows several of the tubules running between internal plastid membranes and the limiting membrane. 7*a*–*d* $KMnO_4$ fixation, barrel medic nodules (SU277.1). 7*c* and *d*. $\times 40{,}000$.

Plate xviii.

a. and *b*. are serial sections of a plastid from a vacuolating barrel medic (SU237) nodule cell. An array of small membrane-bounded compartments in the plastid stroma resembles a ' prolamellar body '. In Fig. *c* a similar body (arrow) can be seen with a well-developed internal plastid membrane attached. The double arrow indicates the junction of an internal plastid membrane with the peripheral membrane. The internal membrane changes from a plate-like form to a tubule at the junction.

d. Shows a ' bud ' on a plastid from a barrel medic (SU277.1) nodule (division by constriction ?). Small, electron-dense, phytoferritin-like particles are present in the plastid stroma.

e. Shows a large proplastid from a vacuolated non-invaded nodule cell. The plastid stroma contains numerous phytoferritin-like particles and the ' bud ' on the right contains numerous circular profiles—apparently small, membrane-bounded tubules cut in cross section. A branched plasmodesmata is shown in more detail in the inset. The plasmalemmas of adjacent cells are contiguous and line the plasmodesmata. s—spherosome-like body. $\times 50{,}000$. Inset $\times 130{,}000$. Figs *a–d* $\times 40{,}000$. $KMnO_4$ fixation, barrel medic nodules. (*d*—SU277.1 ; *a*, *b*, *c*, *e*, *f*—SU237).

Plates xix–xx.

Plates xix and xx are serial sections (in sequence) of parts of two plastids from a recently invaded cell in a purple vetch nodule.

Plate xix, *f* is oriented about 90° to Plate xix, figs *a–e*. The figures illustrate an arrangement (arrows) of small tubules and plastid membranes. Plate xx, *i* is the same section as Plate xx, *f* showing the location of the tubules within the plastid. Adjacent mitochondria (m) show that the membranes of the plastid inclusion have a different appearance from the mitochondria cristae (e.g. arrow). $KMnO_4$ fixation. Pl. xix, *a–h*, Pl. xx, *a–h* $\times 40{,}000$; Pl. xx, *i* $\times 20{,}000$.

Plate xxi.

a. Shows numerous plasmodesmata-like fragments in the cell wall of an uninvaded, vacuolated cell of a subterranean clover nodule. One of the fragments (arrow) is apparently completely bounded by a membrane—presumably the plasmalemma. $KMnO_4$ fixation. $\times 60{,}000$.

b. Recently-invaded cell in a barrel medic nodule (SU237). The plasmalemma invaginates to enclose a lomasome-like body (l) containing a tightly coiled system of membranes. Membrane envelope synthesis is almost completed around an adjacent *Rhizobium* cell. The inset shows the lomasome-like body at higher magnification. $KMnO_4$ fixation. $\times 40{,}000$. Inset $\times 100{,}000$.

c. Portion of three differentiating cells adjacent to the meristem. Narrow tubular elements are present in the cell wall adjacent in the middle lamella region and adjacent to a small intercellular space. The arrow indicates where a cristae of a mitochondrion has been sectioned tangentially showing the circular plate-like profile of the cristae. The endoplasmic reticulum is closely associated with the cell wall (double arrow). Barrel medic nodule. $KMnO_4$ fixation. $\times 60{,}000$.

Plate xxii

a. Newly invaded cell and two adjacent uninvaded cells in a barrel medic nodule (SU237) with their intercellular space filled with an electron-dense material. The double arrow points to a profile which could be interpreted as the origin of a vacuole by expansion of endoplasmic reticulum. The single arrow points to bodies containing small vesicles and at (i) a similar body appears to be fused to the cell wall. A dense body (c) is apparently enclosed by endoplasmic reticulum. Another unidentified inclusion is present (b), and it consists of a single enclosing membrane and a homogeneous matrix. A similar body is indicated by the double arrow in Fig. *a*. Yet another unidentified organelle (u) is present in this cell. $KMnO_4$ fixation. $\times 40{,}000$.

b. In *b* two of the bodies containing small vesicles (arrows) lie close to the cell wall and at (i) one has fused with the wall. The double arrow indicates a small bulge of the cell wall partly bordered by similar material to that enclosed by the arrowed bodies suggesting that this may be a later stage of incorporation of wall material to that at (i). Three similar bodies are adjacent to the cell wall (i) in Fig. *d*. In Fig. *b* endoplasmic reticulum profiles and small single-membrane-bounded vesicles are present close to the wall in much greater ' concentration ' than in the rest of the cytoplasm suggesting that they also may have a role in cell wall development.

c. Portion of a meristematic cell from a barrel medic nodule showing the unidentified bodies (ub) with the single limiting membrane enclosing a number of small vesicles. Similar bodies can also be found after OsO_4 fixation. g—Golgi cisternae. *a–d*, $KMnO_4$ fixation. *b* $\times 25{,}000$; *c* $\times 40{,}000$; *d* $\times 50{,}000$.

Plate xxiii.

a. A ' phase difference ' (v) is apparent in the cytoplasm of a cell from a barrel medic nodule meristem (SU237). It is suggested that this is the first stage in vacuole formation. The arrow indicates a mitochondrion with a figure-of-eight profile suggestive of division by constriction. $\times 30{,}000$.

b. A cytoplasmic bridle crosses the vacuole of a differentiating cell in a barrel medic nodule (SU237). The bridle contains a mitochondrion and some endoplasmic reticulum (er). $KMnO_4$ fixation. $\times 20{,}000$.

c. Profile of a vacuole (v) in a subterranean clover nodule with a constricted region where the tonoplast resembles an endoplasmic reticulum profile. The arrow points to other membrane-bounded elements which may be vacuole or expanded endoplasmic reticulum. $KMnO_4$ fixation. $\times 25{,}000$.

Plate xxiv.

a. Young husk cells from a barrel medic nodule (SU237) showing that they contain a similar complement of organelles to the uninvaded, vacuolated cells basal to the meristem. The plastids are relatively large and mitochondria small. The cell wall in places has conspicuous blebs (arrows) which may be the site of incorporation of new wall material. At the top left of the figure an oblique cut through the wall shows several plasmodesmata in cross section (e.g. circle). $KMnO_4$ fixation. $\times 10{,}000$.

b. Plastid from a barrel medic nodule (SU277.1), uninvaded cell, with two small starch grains and two narrow constrictions suggestive of division. $KMnO_4$ fixation. $\times 40{,}000$.

Plate xxv.

a. The cell wall between two husk cells is crossed by several large plasmodesmata. In an adjacent cell (d) the vacuole has collapsed and the cell is degenerating. The arrow points to a coiled membrane fragment. Subterranean clover nodule. $\times 12{,}800$.

b. Shows the thin layer of cytoplasm in some husk cells from a barrel medic nodule (SU237). The cell walls are crossed by several plasmodesmata. $KMnO_4$ fixation. $\times 10{,}000$.

c. Cortex region of a barrel medic nodule (SU237), showing the nucleus (n) and several mitochondria closely appressed to the cell wall. Plasmodesmata are conspicuously grouped in the cell wall. $\times 12{,}800$.

CERIOID STRINGOPHYLLIDAE (TETRACORALLA) FROM DEVONIAN STRATA IN THE MUDGEE DISTRICT, NEW SOUTH WALES

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(Plate xxvi)

[Read 29th September, 1965]

Synopsis

Melrosia rosae, gen. et sp. nov. and *Melasmaphyllum mullamuddiensis*, gen. et sp. nov. are described from near Mudgee. This is the first record of cerioid members of the Stringophyllidae and the relationships and stratigraphic significance of the occurrences are discussed.

Stratigraphic Introduction

Study of the previously poorly-known Devonian tetracoral faunas of an area near Mudgee, New South Wales, has revealed that two cerioid species belonging to the Stringophyllidae are developed at two different stratigraphic horizons. From their respective associated faunas it appears that the occurrence of *Melasmaphyllum* gen. nov. is stratigraphically lower than that of *Melrosia* gen. nov.

Melasmaphyllum is known, as yet, only from its type locality within the Sutchers Creek Formation[1], the youngest Devonian beds in the Queens Pinch area which is located about 12 miles south-east of Mudgee. Other tetracorals identified from this formation include *Pachyphyllum* auct., *Dendrostella*, *Dohmophyllum*, *Tryplasma* and *Pseudamplexus*, and brachiopods found in shales interbedded with the limestones of the formation include ? *Dolerorthis*, *Phragmophora* s.s., *Leptostrophia* and *Adolfia*. *Tryplasma* and *Pseudamplexus* were thought by Hill (1957, p. 43 and p. 49) to be absent from beds younger than Emsian ; also, Williams (1953, p. 40) considered *Leptostrophia* to be absent from beds younger than Lower Devonian, and *Dolerorthis* is not yet recorded from rocks younger than early Devonian (Boucot, 1960 ; Philip, 1962). On the other hand *Pachyphyllum*, *Dendrostella*, *Dohmophyllum*, *Phragmophora* and, to a lesser degree, *Adolfia* are suggestive of a Middle Devonian age by comparison with known extra-Australian stratigraphical ranges. The age of the assemblage is thus uncertain.

Comparisons of the fauna from the Sutchers Creek Formation with faunas described from elsewhere in Eastern Australia are rather inconclusive. The tetracoral assemblage is very similar to that from the Sulcor Limestone in the presence of *Tipheophyllum*, *Xystriphyllum*, *Phillipsastraea* s.l., *Trapezophyllum* and *Pseudamplexus* (Hill, 1942*b*). It could be suggested on the basis of Brown's (1942) correlation of the Sulcor and Loomberah Limestones and Pedder's (1964, p. 437) " Eifelian or Givetian " age for the Loomberah that the Sutchers Creek Formation is Middle Devonian. The faunas from the Buchan district (Hill, 1950 ; Talent, 1956) have no obvious similarities with faunas of the Sutchers Creek Formation although the latter appears to be younger than the fauna from the Kilgower Member of the Wentworth Group described by Talent (1963) as Emsian.

[1] The new stratigraphic names introduced herein will be formally defined and fully described in a future publication.

Melrosia is known at present from only the type locality where it is plentiful in limestones exposed in the core of an anticline near " Melrose " homestead, about five miles east-south-east of Mudgee. These limestones are correlated with well-bedded limestones of the Mount Frome Limestone[1] on the south-west slopes of Mount Frome to the north of " Melrose ". The presence of *Endophyllum*, stringophyllids and *Pachyphyllum* auct. at " Melrose " and Mount Frome suggests a Middle Devonian age by comparison with overseas ranges.

All type material has been deposited at the Department of Geology and Geophysics, University of Sydney (S.U.G.D.). No prefix is given for the numbers of fossil specimens housed there, but in explanations to text-figures the letter W precedes numbers referring to thin sections upon which figures are based. Grid references refer to the Dubbo 1 : 250,000 topographic sheet.

The author wishes to acknowledge all assistance given during this work, especially from Professor Dorothy Hill who drew attention to the similarities between *Melasmaphyllum* and *Xiphelasma*, and from Professor Hill and Dr. B. D. Webby who criticized the manuscript.

Systematic Palaeontology

Phylum COELENTERATA
Class ANTHOZOA
Order TETRACORALLA
Family STRINGOPHYLLIDAE Wedekind, 1922.

This family is distinguished principally by lonsdaleoid dissepiments,[2] concave or flat tabular floors, and septa consisting of stout, contiguous or separate, monacanthine trabeculae. The only compound forms previously described have been fasciculate species for the reception of which Birenheide (1962) erected *Stringophyllum* (*Sociophyllum*), which Pedder (1964, p. 444) considered to be a distinct genus. Solitary species have been placed in a number of genera of which only *Stringophyllum* Wedekind, 1922, and *Neospongophyllum* Wedekind, 1922, were recognized by Engel and Schouppé (1958) and Birenheide (1962), the latter considering *Neospongophyllum* a subgenus of the type genus ; the two forms are principally distinguished by the prominent lonsdaleoid dissepimentarium in *Neospongophyllum*. *Vollbrechtophyllum* Taylor, 1951 (pro *Schizophyllum* Wedekind, 1925, non Verhoeff, 1896) was held by Taylor to be distinct from *Stringophyllum* in having peripherally discontinuous major septa. Any such attempts to differentiate a third group in addition to *Stringophyllum* and *Neospongophyllum* must be regarded with suspicion until specific variation of these taxa is adequately documented. *Loipophyllum* Wedekind, 1925, and *Vollbrechtophyllum* were treated as junior synonyms of *Neospongophyllum* by Engel and Schouppé (op. cit.).

Some of the species assigned to *Grypophyllum* Wedekind, 1922, including the type species, can be likened to *Stringophyllum* in that their minor septa are often short, aborted or even discontinuous (Middleton, 1959, p. 143 et seq.). It is quite possible that when lineages of species become evident some of these species at present placed in *Grypophyllum* will prove to be genetically related to *Stringophyllum* and some to *Acanthophyllum* Dybowski, 1873 ; Birenheide (1961, p. 128) has already suggested the latter, and Engel and Schouppé (1958) were so impressed by the similarities between *Grypophyllum* and *Stringophyllum* that they considered them as type genera of subfamilies

[2] McLaren (*in* McLaren and Norris, 1964, p. 5) advocated the use of the term " wandblasen " to replace the term " lonsdaleoid dissepiments ". There does not seem to be any fundamental difference in the mode of secretion of lonsdaleoid dissepiments and post-septal dissepiments, as McLaren suggests. Therefore the only advantage of McLaren's usage is the ease of distinction between dissepiments preceding both major and minor septa and those preceding only the minor septa. The change in terminology is no more explanatory of the sequence of structural elements than the system recommended by Hill (1935) and has not been adopted herein.

of the Stringophyllidae. The tabulae developed in *Stringophyllum* indicate a close relationship with *Acanthophyllum*, whereas the flat or weakly concave tabulae often seen in *Neospongophyllum* and *Sociophyllum* suggest a different origin, possibly from a *Spongophyllum*-like ancestor. *Melrosia* appears to be closely related to *Xystriphyllum* Hill, 1939, possibly most closely to *X. dunstani* (Etheridge, 1911) which commonly has lonsdaleoid dissepiments. *Melasmaphyllum* is similar to *Spongophyllum* Edwards and Haime, 1851, but possesses axially discrete trabeculae; among possible ancestors of *Melasmaphyllum* are many of the species ascribed to *Spongophyllum*, as well as *Neomphyma pseudofritschi* Soshkina.

Hill (1957, p. 43) lists as " the earliest *Stringophyllum*, *S. carnicum* (Charlesworth, 1914) ", from probably lower Devonian strata in the Carnic Alps. Wang (1948, p. 18, and 1950, p. 215), Engel and Schouppé (1958, p. 96) and Spassky (1964, table 16, p. 104) also considered that stringophyllids appeared in the Lower Devonian. The only apparent evidence given by Wang and Engel and Schouppé concerns Australia, so this age determination was probably based on misconstrued estimates of the age of the Moore Creek Limestone (Hill, 1942*b*) and some of the North Queensland limestones (Hill, 1942*a*); Hill considered these probably Middle Devonian. So there appears to be little evidence to suggest that stringophyllids first appeared in the Lower Devonian.

The only report of cerioid Stringophyllidae appears doubtful; Smith (1945, p. 55) likened a Canadian cerioid form to *Spongophyllum semiseptatum*; but the Canadian form is probably not a stringophyllid, as Birenheide (1962*b*, p. 65) has remarked. Other comparable cerioid tetracorals include *Spongophyllum*, *Donia* Soshkina, 1951, and *Endophyllum abditum* Edwards and Haime, 1851; all possess peripherally discontinuous septa but none exhibits discrete trabeculae in the axial region. Apart from the axially discontinuous septa, *Melasmaphyllum* and *Melrosia* are identical with *Spongophyllum* and *Xystriphyllum* respectively. *Donia* was considered by Soshkina (1951) and Pedder (1964) to be a disphyllid and this opinion seems justified by the nature and arrangement of the dissepiments as well as the septal structure. *E. abditum* is quite distinct in having domed tabular floors. *Kozlowiaphyllum* Rhukin, 1938 (see Soshkina, 1962, p. 335) is a Silurian cerioid form possibly related to *Spongophyllum*; further information is needed to clarify this genus. The apparent nature of the septa of *Australophyllum praeclarum* Crickmay (1962, p. 6, Pl. II, figs 4–5) suggests that it may well belong in the Stringophyllidae, despite the fact that the septa are not discontinuous axially; this form may be close to *Melasmaphyllum*.

Genus Melrosia, novum

Type Species: *Melrosia rosae*, sp. nov.

Diagnosis: Cerioid tetracorals with septa consisting of monacanthine trabeculae which may be discrete axially. Major septa long; minor septa are almost completely suppressed. Lonsdaleoid dissepiments weakly developed peripherally. Tabular floors concave, often with an axial depression in the close-set tabulae.

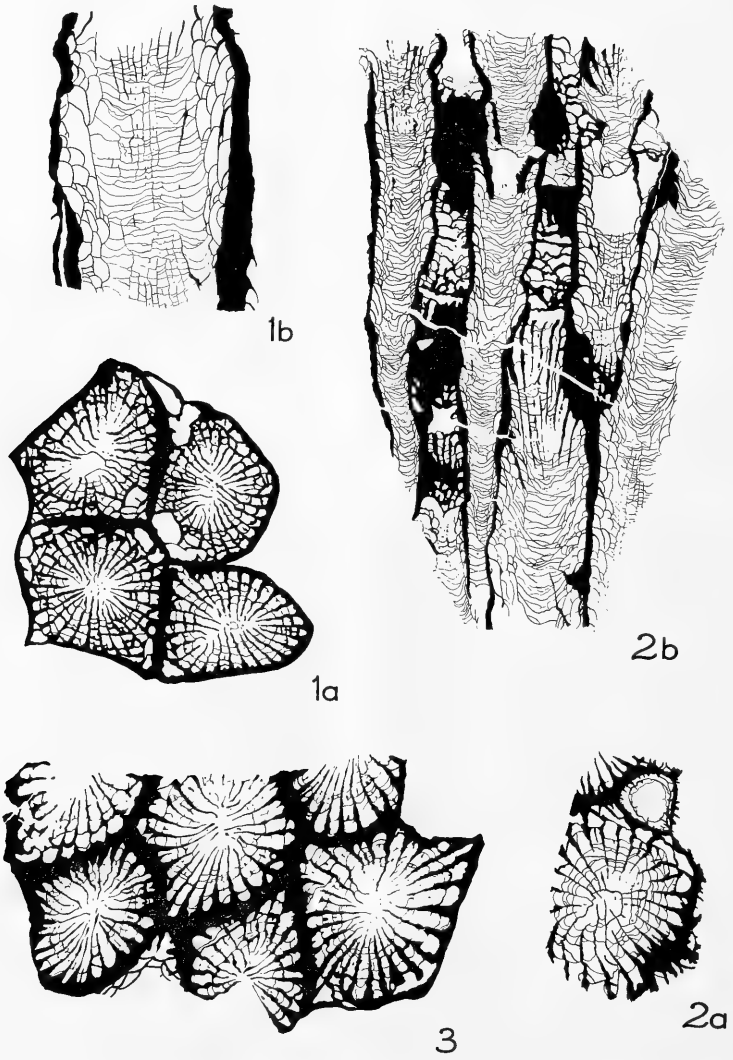
Remarks: This genus, at present monospecific, differs from *Melasmaphyllum*, gen. nov., in general septal, dissepimental and tabular features. Apart from the cerioid habit it is very close to the normal *Stringophyllum* style in having long, axially discontinuous septa with characteristic bilateral symmetry about the plane containing the cardinal and counter septa.

Derivation of Names: The genus takes its name of feminine gender from the property " Melrose ", on which it occurs; the species is named for my wife whose encouragement has been invaluable.

MELROSIA ROSAE, sp. nov.

Pl. xxvi, fig. 1 ; Text-figs 1–3

Diagnosis : *Melrosia* with 25 to 29 major septa at an average diameter of 9 mm. ; two to five rows of steeply inclined dissepiments are present, the outer ones often being lonsdaleoid ; tabularium from one-half to three-fifths of corallite diameter.



Text-figs 1–3. *Melrosia rosae*, gen. et sp. nov. ; 1*a*. Transverse section of holotype 21104, W1128, ×2·4. 1*b*. Longitudinal section of one corallite from holotype 21104, W1129, ×2·4. 2*a*. Transverse section of paratype 21105, showing lateral bud, W1121, ×2·4. 2*b*. Longitudinal section of paratype 21105, W1122, ×1·6. 3. Transverse calical section of paratype 21106, W1147, ×2·4.

Description : Coralla are apparently hemispheroidal, and growth form cerioid ; corallites are generally irregularly hexagonal and up to 11 mm. in diagonal diameter. Mode of increase is uncertain, but apparently peripheral ; buds mature gradually, having an early stage where dissepiments are few and septa short (Text-fig. 2*a*).

From 26 to 31, but generally about 28, major septa extend almost to the axis, where they are occasionally represented by isolated monacanths ; minor septa extend to about half their length, and are seldom continuous, generally appearing as crests on the dissepiments or more rarely as discrete monacanths. Peripherally major septa are strongly dilated, forming a stereozone about 0·5 mm. thick ; dilation is much less in minor septa, but lessens in both orders towards the axis and is weak in the tabularium. Bilateral symmetry is moderately developed about the plane containing the two short protosepta (Pl. xxvi, fig. 1). Trabeculae are moderately inclined both peripherally, diverging slightly towards the axis, and are about 0·2 mm. in diameter.

Dissepiments occur as two to five rows of steeply inclined, flattened plates, a few of which function as lonsdaleoid dissepiments (first order " wandblasen ") ; commonly some act as bases (second order " wandblasen ") of minor septa which appear as stout, isolated trabeculae between the much more continuous major septa.

Tabulae may be complete or incomplete ; tabular floors may be regularly and moderately concave or may form broad, gently axially-inclined rims with a broad, deep axial depression ; tabularium occupies from one-half to three-fifths of corallite diameter with steeply- or gently-inclined peripheral areas abutting sharply on, or conforming broadly with slope of, dissepiments.

Remarks : The discontinuous nature of the septa indicates that the affinities of this species are with *Stringophyllum* rather than *Xystriphyllum*.

The species *Xystriphyllum dunstani* and *Spongophyllum cyathophylloides* Etheridge, 1911 (see Hill, 1939) from Clermont, Queensland, may well be phylogenetically connected with this species although neither possesses axially discontinuous septa.

Material : Holotype, 21104 (W1128–9), Pl. xxvi, fig. 1, Text-figs 1*a–b* ; paratype, 21105 (W1121–2), Text-figs 2*a–b* ; paratype, 21106 (W1147–8), Text-fig. 3 ; Other material : 21107 (W464–5) ; 21108 (W1149–50) ; 21109 (W1140) ; 21110 (W469–70) ; 21111 (W460–1) ; 21112–21117, 21118 (W466–7) and 21119 (W462–3).

Type Locality : S.U.G.D. locality number Mu/IV/60, grid reference 26279658 ; immediately north of quarry, north-west of " Melrose " homestead ; in portion 54, parish of Bumberra, county of Philip.

Typical Formation : Mount Frome Limestone.

Genus Melasmaphyllum, novum

Type Species : Melasmaphyllum mullamuddiensis, sp. nov.

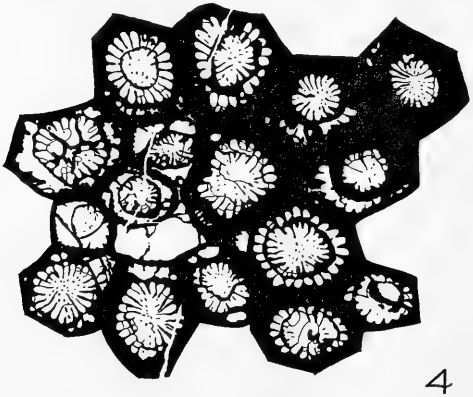
Diagnosis : Cerioid tetracorals with very large, prominent lonsdaleoid dissepiments. Septa consist of monacanthine trabeculae which are often separated axially ; minor septa mostly limited to short ridges just emerging from septal stereozone. Tabulae generally flat, rarely concave.

Remarks : This genus is distinct from *Melrosia*, gen. nov., and can in some respects be considered a cerioid counterpart of *Neospongophyllum*. It appears at present to be monospecific.

Xiphelasma Smith and Lang, 1931, is rather similar to *Melasmaphyllum* ; Hill (1956*a*, F312) treated *Xiphelasma* as a junior subjective synonym of *Storthygophyllum* Weissermel, 1894, which is " like *Tryplasma* but cerioid and with a narrow zone of dissepiments " (Hill, loc. cit.). *Storthygophyllum* (= *Xiphelasma*) differs from *Melasmaphyllum* in possessing rhabdacanthine trabeculae as well as in detailed nature of septa, tabulae and dissepiments.

Two Russian species assigned to *Neomphyma* Soshkina, 1937, are similar to *Melasmaphyllum* ; the Gedinnian *N. pseudofritschi* Soshkina (1962, p. 335, Pl. 19, fig. 1) and the Ludlovian *N. rosiformis* Zheltonogova (1961, p. 81, Pl.

S20, figs 3*a–b*) are structurally similar to *Melasmaphyllum*, as is *Spongophyllum originalis* Kraevskaya (1955, p. 214, Pl. 41, figs 3*a–b*) but all three differ from *Melasmaphyllum* in not possessing discrete trabeculae axially. The same applies to some cerioid members of *Spongophyllum* with large lonsdaleoid dissepiments. *Melasmaphyllum* may be genetically related to these species.



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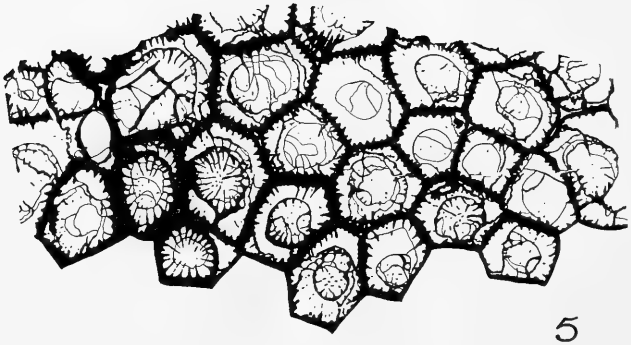

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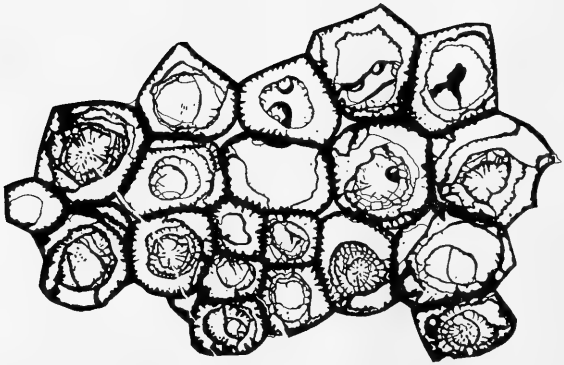

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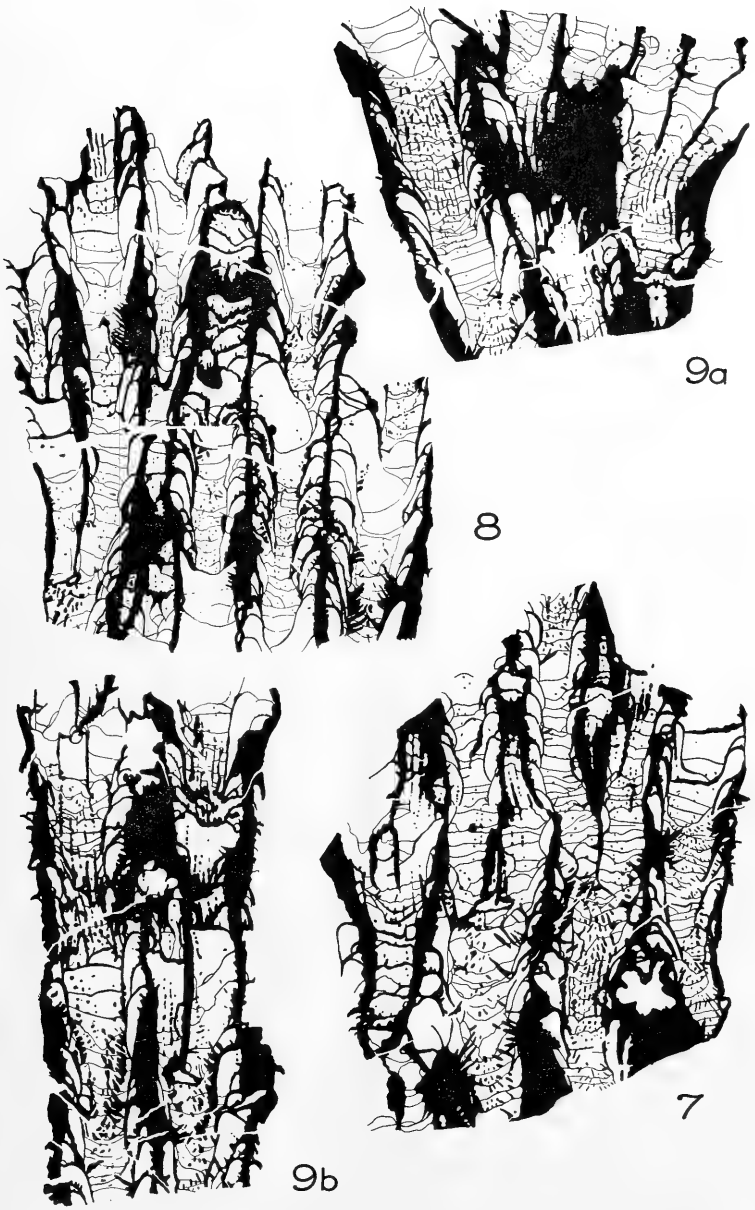
Text-figs 4–6. *Melasmaphyllum mullamuddiensis*, gen. et sp. nov. Transverse sections of holotype, 21103, all ×2·4. 4. Proximal part of corallum, W999. 5. Median part of corallum, W869. 6. Distal part of corallum, W1179.

Derivation of Name: The name of the genus is partly based on the Greek word (neuter gender) for "black spot"; the species is named after nearby Mullamuddy Creek.



Text-figs 7–9. *Melasmaphyllum mullamuddiensis*, gen. et sp. nov. Longitudinal sections of holotype, 21103, illustrating in places mode of increase. All ×2·4. 7. Proximal part of corallum, W1000. 8. Distal part of corallum, W870. 9*a*, *b*. Distal part of corallum, W836.

Melasmaphyllum mullamuddiensis, sp. nov.

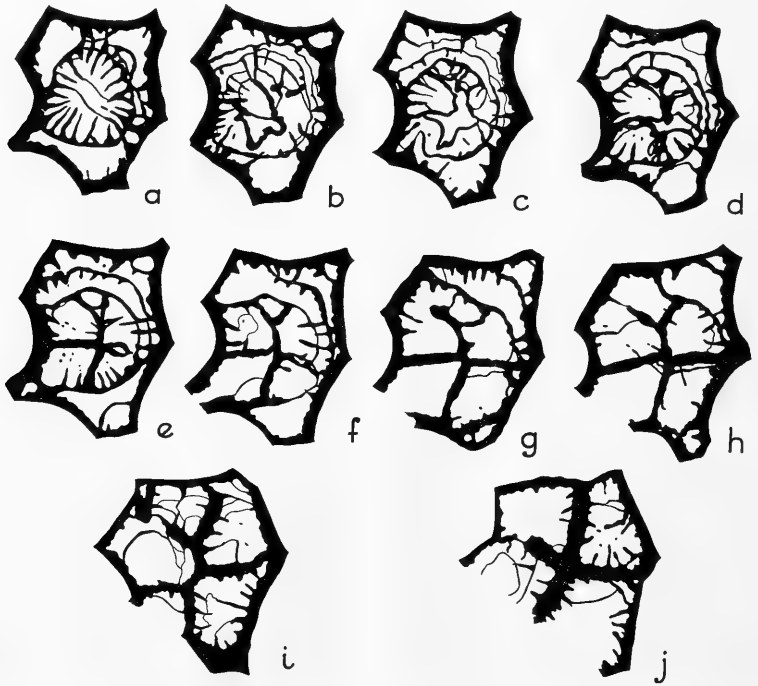
Pl. xxvi, fig. 2 ; Text-figs 4–10

Diagnosis : *Melasmaphyllum* with from 19 to 24 major septa strongly dilated peripherally and generally discontinuous axially and with an average corallite diameter of about 6 mm. ; major septa long, occasionally with weak bilateral symmetry ; minor septa represented by only short trabecular crests. Lonsdaleoid dissepiments long and wide, generally in one row. Tabulae complete and distant, flat or weakly concave. Up to six daughter corallites

parricidally produced by axial increase ; peripheral increase rare. Tabularium from one-third to three-fifths of corallite diameter.

Description : Corallum hemispheroidal and apparently originally reached 30 cm. in diameter. Corallites are mostly polygonal ; in distal parts of corallum there may be irregular subtriangular spaces between walls where three corallites approach each other, and more rarely with narrow spaces between weakly curved walls ; maximum diagonal diameter is about 8 mm., average diameter in longitudinal section is 5 to 6 mm. ; corallites have four to seven sides, generally five or six walls which are mostly straight.

From 19 to 24 major septa are sometimes wholly developed but generally are strongly interrupted peripherally by lonsdaleoid dissepiments and where developed axially are represented only by large monacanths. Minor septa are



Text-fig. 10. *Melasmaphyllum mullamuddiensis*, gen. et sp. nov. Serial transverse sections of 21103B/8, illustrating budding, ×4. Distance of sections above *a.* measured in millimetres : *b.* 0·8 ; *c.* 1·1 ; *d.* 1·3 ; *e.* 1·7 ; *f.* 2·3 ; *g.* 3·2 ; *h.* 3·9 ; *i.* 5·6 ; *j.* 7·5. Where the limits of drawings are regular, this represents epitheca.

very strongly suppressed and may be completely absent ; peripherally they are sometimes distinct as low ridges between larger major septa, and where developed elsewhere are seen only as isolated monacanthine crests on dissepiments. Septa are mostly straight and dilated peripherally to form a thick stereozone up to 0·5 mm. thick, but on the average coat a thin epitheca to a thickness of 0·2 mm. Bilateral symmetry is weakly developed ; cardinal septum not distinct. Despite poor preservation monacanthine trabeculae about 0·3 mm. in diameter can be seen diverging within the plane of a septum so as to be separated along the axial edge ; peripherally the inclination of trabeculae is generally at about 45° to a horizontal plane, but occasionally subhorizontal ; towards the axis they may be almost vertical.

In mature corallites, the tabularium varies in width from one-third to three-fifths of the total diameter. Tabulae are generally complete, and are

mostly flat or may be occasionally weakly convex, weakly concave, or delicately scalloped ; from 16 to 22 irregularly to regularly spaced tabulae are spaced in a length of 10 mm. Usually there is one series of long, steeply-inclined lonsdaleoid dissepiments which may extend about half-way around the corallite and up to one-third of the maximum diameter.

Increase is almost invariably axial and parricidal, only one possible instance of peripheral increase having been observed (Text-fig. 5). No interruption is seen in the vertical continuity of tabular structures as daughters are not produced high on calical walls, above the space formerly occupied by the parent polyp. In increase a complex thickening develops on a tabula and eventually extends by means of furcation to the periphery, producing up to six daughters which attain adult characteristics in a length of about 6 mm. ; this outward spread may be irregular with the axial plate and one or more septa being fused while the plate is still only a thickening or may proceed more or less symmetrically (Text-fig. 10). This undulating tabular thickening is at first a simple non-planar sheath but eventually it extends distally along ridges in its surface. Apparently from the proximal edges of the apices of ridges in this thickening a thin median plate analogous to normal epitheca develops and persists distally throughout all daughters.

Remarks : The validity of the erection of a new taxon on a single specimen may well be queried. The monotype consists of a large colony, probably of several hundred corallites exhibiting no more than a reasonable amount of phenotypic variation. Despite the absence of further material, which thorough collecting has failed to yield, there is no reason to consider this colony a pathological variant or an end member of a variable species ; in the associated fauna of compound tetracorals none of the species of *Hexagonaria*, *Phillipsastraea* s.l., *Pachyphyllum* s.l., *Trapezophyllum*, and *Xystriphyllum* can be considered similar to *Melasmaphyllum*. It seems reasonable to conclude that this corallum was a successful if bizarre mutation living in association with the other distinct colonial forms.

Spongophyllum rosiforme Yoh, 1937, is similar to *Spongophyllum elongatum* Schlüter, 1880, the type species of *Stringophyllum* (*Sociophyllum*) Birenheide, 1962. Although Birenheide (1962, p. 72) refers *S. rosiforme* to *Spongophyllum*, axially isolated trabeculae which it exhibits indicate stringophyllid affinities. The Middle Devonian species from Kwangsi is very similar to *M. mullamuddiensis* apart from phaceloid habit and regularly concave tabulae.

The multipartite parricidal axial increase seems to be close to that seen in *Hexagonaria quadrigemina* (Goldfuss) : Smith (1945, p. 46, Pl. 14, figs 5*a–b*) but the segregating structure extends in that species from the ends of the major septa to the axis rather than from the axis to the walls as in *M. mullamuddiensis*.

Material : Only the holotype corallum 21103 is known ; weathered into three pieces, two have been sectioned as follows whereas 21103A remains whole :—21103B : Text-fig. 10, based on serial cellulose peels of 21103B/8 ; W999 (Text-fig. 4) ; W1000 (Text-fig. 7) ; 21103C : W835 (Pl. xxvi, fig. 2) ; W836 (Text-figs 9*a–b*) ; W869 (Text-fig. 5) ; W870 (Text-fig. 8) ; W1178 ; W1179 (Text-fig. 6) ; W1180.

Type Locality : S.U.G.D. locality number Mu/IV/38, grid reference 26379535 ; in portion 152, parish of Broombee, county of Wellington.

Typical Formation : Sutchers Creek Formation.

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EXPLANATION OF PLATE XXVI.

Fig. 1. *Melrosia rosae*, gen. et sp. nov. Transverse section of holotype. 21104, W1128, ×4.

Fig. 2. *Melasmaphyllum mullamuddiensis*, gen. et sp. nov. Transverse section of holotype. 21103, W835, ×6.

AN EMBRYOLOGICAL STUDY OF FIVE SPECIES OF *BASSIA* ALL. (CHENOPODIACEAE)

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[Read 27th October, 1965]

Synopsis

Development of male and female gametophytes and embryogeny of *Bassia bicornis, B. brachyptera, B. divaricata, B. paradoxa* and *B. patenticuspis* is described.

Plate crystals of calcium oxalate were found in the perianth and ovary wall of all species, and anther filaments of some species.

The anther, which is tetrasporangiate, becomes four to five layered due to irregular divisions in the tapetum. Both amoeboid and secretory tapetum types occurred. Cytokinesis of the microspores is simultaneous and the mature pollen grain is three-celled.

The ovary contains a basal, campylotropous, bitegmic ovule which is crassinucellate. The hypodermal archesporial cell cuts off a parietal cell and the megaspore mother cell undergoes normal megasporogenesis. The chalazal megaspore of a linear tetrad develops into the monosporic eight-nucleate embryo sac of the *Polygonum* type.

Embryogeny conforms to the Chenopodiad type and the mature embryo is elongate and spiral. The endosperm is at first nuclear, but later becomes cellular and is digested by the developing embryo until only a cap remains over the tip of the radicle. In the seed the food storage region is the perisperm.

INTRODUCTION

Representatives of the family Chenopodiaceae are native to Australia in a wide variety of habitats, which include xerophytic and halophytic situations. In semi-arid areas, which are too dry for grasses, many genera such as *Atriplex*, *Bassia*, *Chenopodium*, *Kochia*, and *Rhagodia* are valuable fodder plants. The genus *Bassia*, according to Black (1948), consists of 60 species, of which about 50 are Australian endemics and the remainder occur in Europe and Asia. No indigenous members of the family have been studied embryologically and, although some overseas species of genera represented in Australia have been examined, no previous work of this nature has been carried out on *Bassia*.

MATERIALS AND METHODS

The material used in this investigation was collected in the field by Mr. E. Hoult in May, 1963, or from plants grown in the glasshouse from seeds collected in western New South Wales (Table 1).

Conventional paraffin sections were cut at 9–14 μ and stained with Delafield's Haematoxylin and Johansen's Safranin; supplementary examinations were made by dissections and squashes of fresh and preserved material.

The drawings, unless otherwise indicated, are of *B. paradoxa* and comparative studies were made with the other species.

MORPHOLOGY

Bassia paradoxa is a small shrub with narrow to linear, thick, alternate leaves which, together with the stems, bear a white woolly indumentum (Fig. 1). The hairs are multicellular and uniseriate (Figs 2, 3). The flowers, which are also hairy, are sessile, and 8–20 are united in each dense axillary cluster (Figs 4, 9), although according to Black (1948) clusters of 6–10 flowers are usual. Bisulputra (1960) has shown that the cluster is morphologically a condensed

dichasium. In the remaining species examined, the flowers occurred singly in the leaf axils due to the suppression of the lateral buds of the dichasium (Bisulputra, 1960). The development of the hairs, the perianth tube and the spines is variable (Figs 8–14) but is specifically distinct (Black, 1948).

The ovary is monocarpellary and unilocular with a solitary basal campylotropous ovule (Fig. 5). The elongated style terminates in two elongated stigmatic branches, although in some cases it is trifid due to the presence of

Table 1

List of species and locations from which material was collected

Species	Location	Collected from glasshouse
B. paradoxa (R. Br.) F. v. M.	31 m. W. Broken Hill	May '63—July '64
B. bicornis (Lindl.) F. v. M.	60 m. E. Quilpie, Q'ld.	May '63—Nov. '63
B. brachyptera (F. v. M.) R. H. Anderson	40 m. E. Broken Hill	—
B. divaricata (R. Br.) F. v. M.	70 m. N. Broken Hill	—
B. patenticuspis R. H. Anderson	—	Nov. '64—Feb. '65

a smaller third branch. Its surface is finely papillose and its open stylar canal communicates directly with the loculus (Fig. 6). The five stamens are obdiplostemonous with dorsifixed tetrasporangiate anthers and are at first enclosed within the perianth tube, but with elongation of the filament after maturity of the pollen grains they are displayed outside the woolly mat of hairs surrounding the flowers (Fig. 7). Introrse dehiscence occurs by means of longitudinal slits.

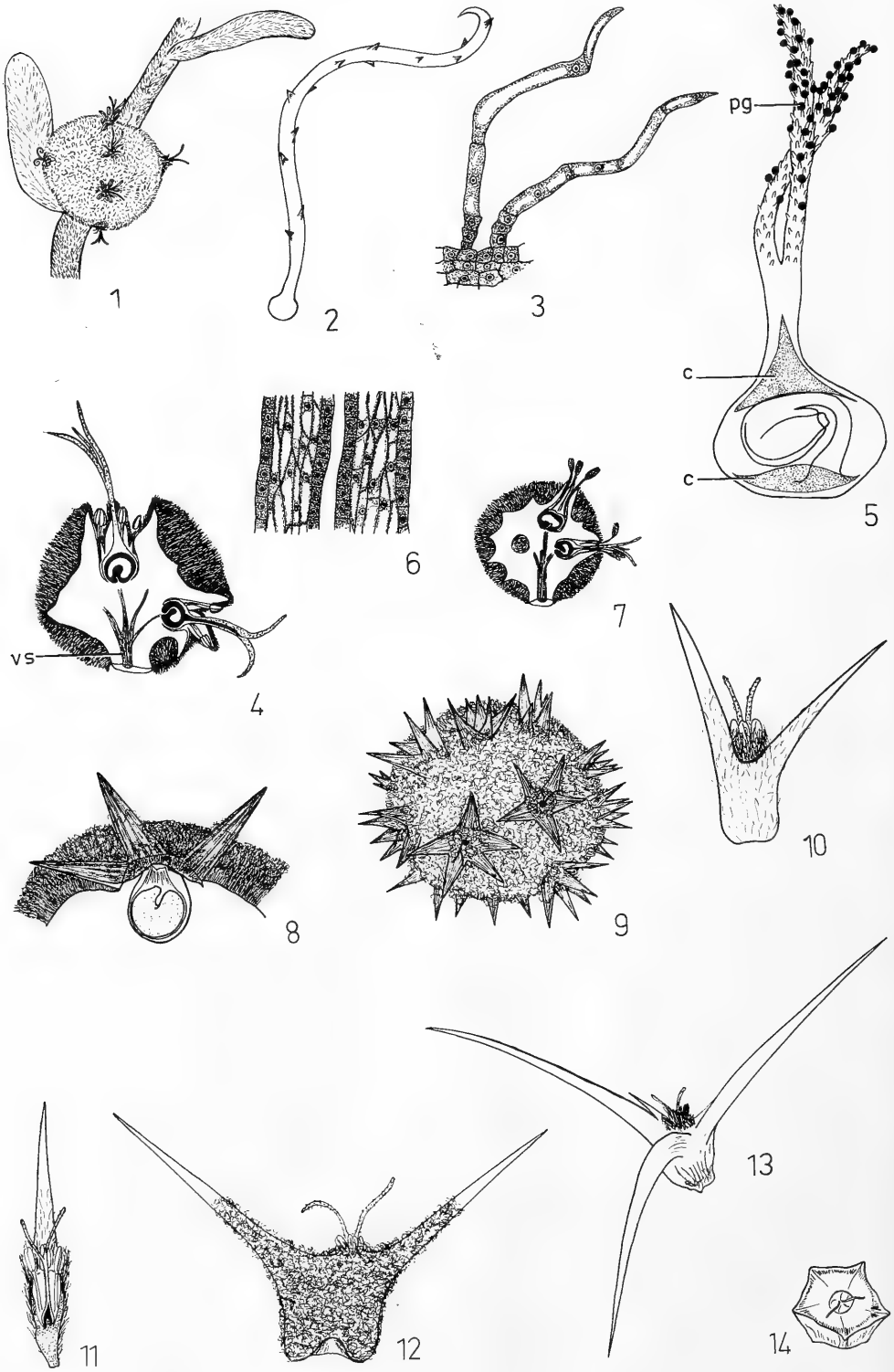
Table 2

Figures in microns indicate the average length of the larger crystals

Species	Top of ovary	Base of ovary	Perianth	Anther
B. paradoxa	20	5	9	—
B. bicornis	25	15	15	15
B. divaricata	12	4	10	4
B. brachyptera	14	13	11	8
B. patenticuspis	17	20	17	—

Crystals

Plate crystals were present in the perianth and ovary wall of all species studied (Figs 15, 16) and were identified as calcium oxalate by their solubility in 2N hydrochloric acid and their insolubility in 20% acetic acid. Although their shape was constant they varied in length from 2 to 30 μ, the average size for the larger ones varying between species and according to their location within the flowers (Table 2). The larger crystals were solitary and almost completely filled the cells, while in other instances there were up to four smaller ones present (Figs 17, 18). In *B. bicornis*, and to a lesser extent in the other species, the crystal-containing cells were larger than those lacking them (Figs



Figs 1–8. Morphology of *B. paradoxa*. 1, 4, 7, 8, Flower clusters of different ages; 2, 3, Hairs; 5, The gynoecium; 6, Stylar canal.
Figs 9–14. Fruits: 9, *B. paradoxa*; 10, 11, *B. patenticuspis*; 12, *B. bicornis*; 13, *B. divaricata*; 14, *B. brachyptera*.
Figs 3, 4, 6–8, 11, 12, in L.S.; remainder whole mounts.
(*c*, crystals; *pg*, pollen grains; *vs*, vascular strand.)
Figs 1, 7, ×3; 2, 3, ×220; 4, 9–14, ×7; 5, ×30; 6, ×130; 8, ×13.

17, 19). In the course of floral development, the crystals were first observed when the ovule was at the megaspore mother stage. They appeared in the inner hypodermal layer of the perianth lobes and tube, connecting with a broad crystal-bearing layer at the base of the ovary. Similarly, crystals were deposited in the upper hypodermal cells of the inner wall of the ovary wall and followed up the hollow style but with reduced size and frequency. A relationship was noted in the ovary between the absence of the crystals in the hypodermis and the radial elongation of the overlying inner epidermal cells (Figs 20, 21), while cells above and below these areas, which contained crystals in the hypodermis, were smaller although still glandular in appearance (Fig. 22). By the time of anthesis, the crystal layers had become thickened through further deposition of crystals in the second to the fourth sub-hypodermal cell layers where they persisted into the fruiting stage.

In *B. bicornis*, *B. brachyptera*, and *B. divaricata* a small number of crystals were also found in the central cells of some anther filaments but their distribution followed no definite pattern.

The Microsporangium

The undifferentiated anther is at first ovoid in cross section, but becomes rectangular due to radial expansion resulting from localized cell divisions. The cells are initially of similar size and non-vacuolate with prominent nuclei, after which four hypodermal, uniseriate rows differentiate as archesporial cells (Figs 23, 24), and initiate the formation of the four sporangia.

(*a*) *Wall Formation*

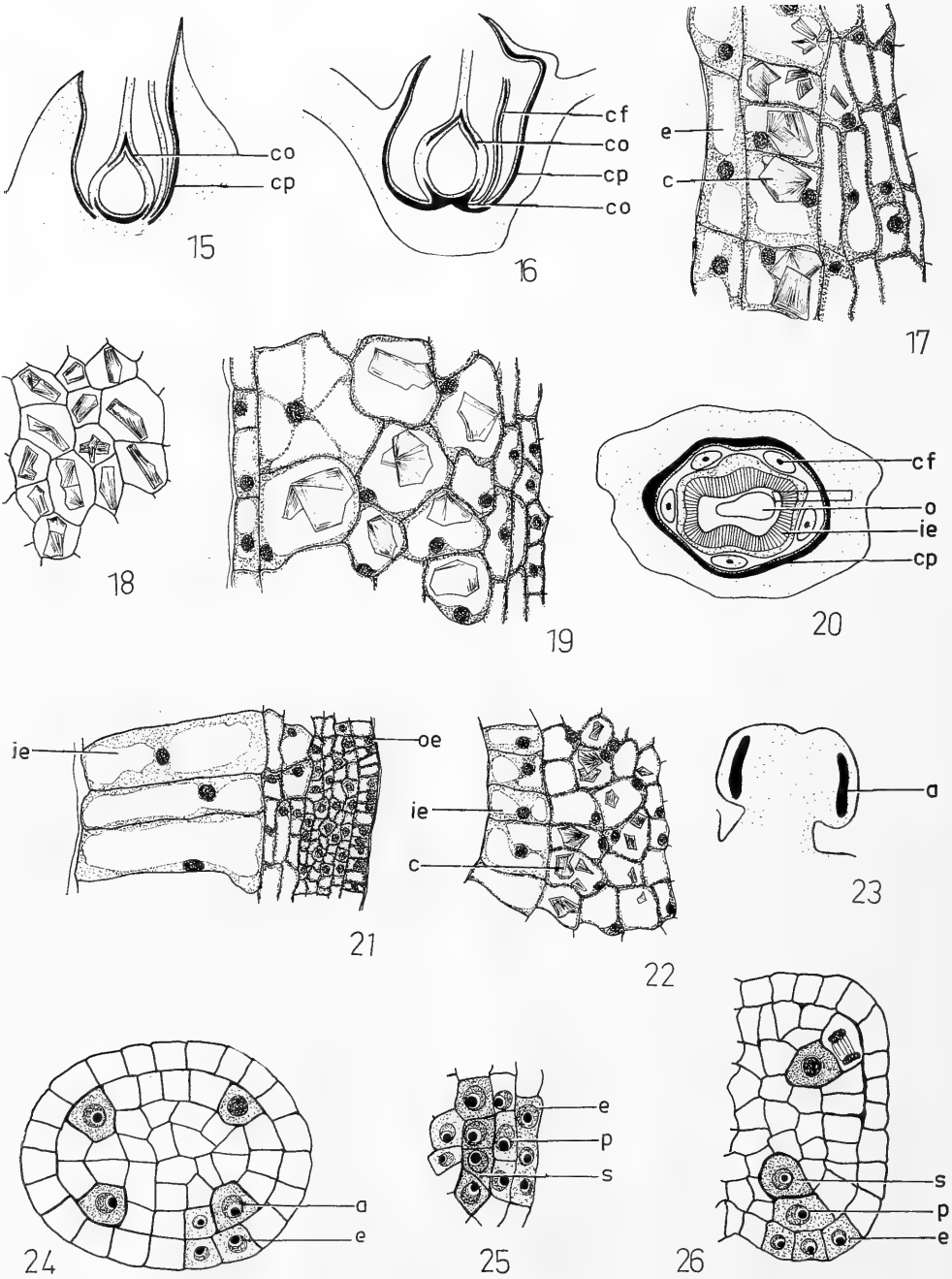
Each archesporial cell divides periclinally to form an inner primary sporogenous cell and an outer parietal cell which undergoes anticlinal divisions and, together with the adjacent cells from the ground tissue, forms the primary parietal layer, which encloses the sporogenous tissue (Figs 25, 26). Periclinal division of the primary parietal layer forms the secondary parietal layer and the outer endothecial layer (Figs 27, 28), whose cells divide only anticlinally. A periclinal division of the secondary parietal layer then gives rise to a single middle layer and to the tapetum, which may become irregularly two-layered due to further periclinal cell divisions (Figs 29–31). At this stage the microsporangium wall consists of four or five layers, the epidermis, the endothecium, the middle layer, and the tapetum which may be irregularly two-layered. The development of the wall layers is the same as that outlined diagrammatically in *Themeda australis* (Woodland, 1964, Fig. 7).

A four-layered wall is the usual condition in members of the Chenopodiaceae ; however, in *Beta vulgaris* (Artschwager, 1947) more than four layers have been described while, according to Miller, Kline and Weber (1959), in *Chenopodium ambrosioides* either one or two middle layers are present.

The pressure exerted by the expanding sporogenous tissue stretches all the wall layers tangentially and, although some anticlinal divisions occur, these cease when vacuolation sets in prior to the differentiation of the wall layers.

After the initial stretching of the tapetal cells rapid cytoplasmic synthesis occurs, and the cells increase in size and become glandular in appearance, with prominent nuclei and dense cytoplasm. When the adjacent microspore mother cells enter Prophase I many of the tapetal nuclei undergo an apparently normal mitotic division, in which the spindles are obliquely orientated within the cells (Figs 32, 33), and the cells become binucleate (Fig. 34), although fusion may occur and result in the formation of a single large polyploid nucleus (Fig. 35).

The tapetal cells first show signs of breakdown just prior to the release of the microspores from the tetrads (Fig. 36). This is indicated by the contraction of the protoplasm, which is followed by disorganization of the bounding



Figs 15–22. Calcium oxalate crystals. 15, Distribution of crystals in *B. paradoxa*; 16, Distribution of crystals in *B. divaricata*; 17, L.S. of *B. paradoxa* perianth; 18, *B. patenticuspis*, surface view of perianth crystals; 19–22, *B. bicornis*: 19, L.S. of perianth; 20, T.S. of flower; 21, Ovary wall as in Fig. 20; 22, T.S. of wall at top of the ovary.

Figs 23–26. Development of the microsporangium. Figs 23, 25 in L.S.
(*a*, archesporium; *c*, crystals; *cf*, crystals in the anther filament; *co*, crystals in the ovary wall; *cp*, crystals in the perianth; *e*, epidermis; *ie*, inner epidermis of ovary wall; *o*, ovary; *oe*, outer epidermis of the ovary wall; *p*, primary parietal layer; *s*, sporogenous tissue.)
Figs 15, 16, 20, ×20; 17, ×320; 18, 19, 24–26, ×540; 21, 22, ×220; 23, ×130.

membrane (Fig. 37). At a later stage, when the pollen grains enter the ' signet ring ' configuration, it is usual in *B. paradoxa* for the inner walls of the tapetal cells to degenerate and so allow the protoplasts to form a continuous mass around the periphery of the loculus. As a result, the pollen grains come into contact with, and lie between, the remaining portions of the tapetal cells (Fig. 38). At this point, the nuclei show signs of degeneration but maintain their identity as dense areas in the tapetal cytoplasm until it is absorbed. Finally, the tapetum is represented by small oval globules on the inner walls of the endothecium (Fig. 39), which disappear before dehiscence (Fig. 44). In *B. brachyptera*, *B. divaricata*, *B. patenticuspis*, as well as *B. paradoxa*, the contents of the tapetal cells break down and are absorbed *in situ*; the tapetum conforms to the secretory or glandular type. In some anthers of *B. paradoxa*, however, after dissolution of the cell walls, the protoplasts become amoeboid and move into the loculus between the recently liberated tapetal microspores, forming a periplasmodium (Fig. 43). The liberated tapetal nuclei maintained their identity, and underwent mitotic divisions, indicating that this was a ' true '

TABLE 3

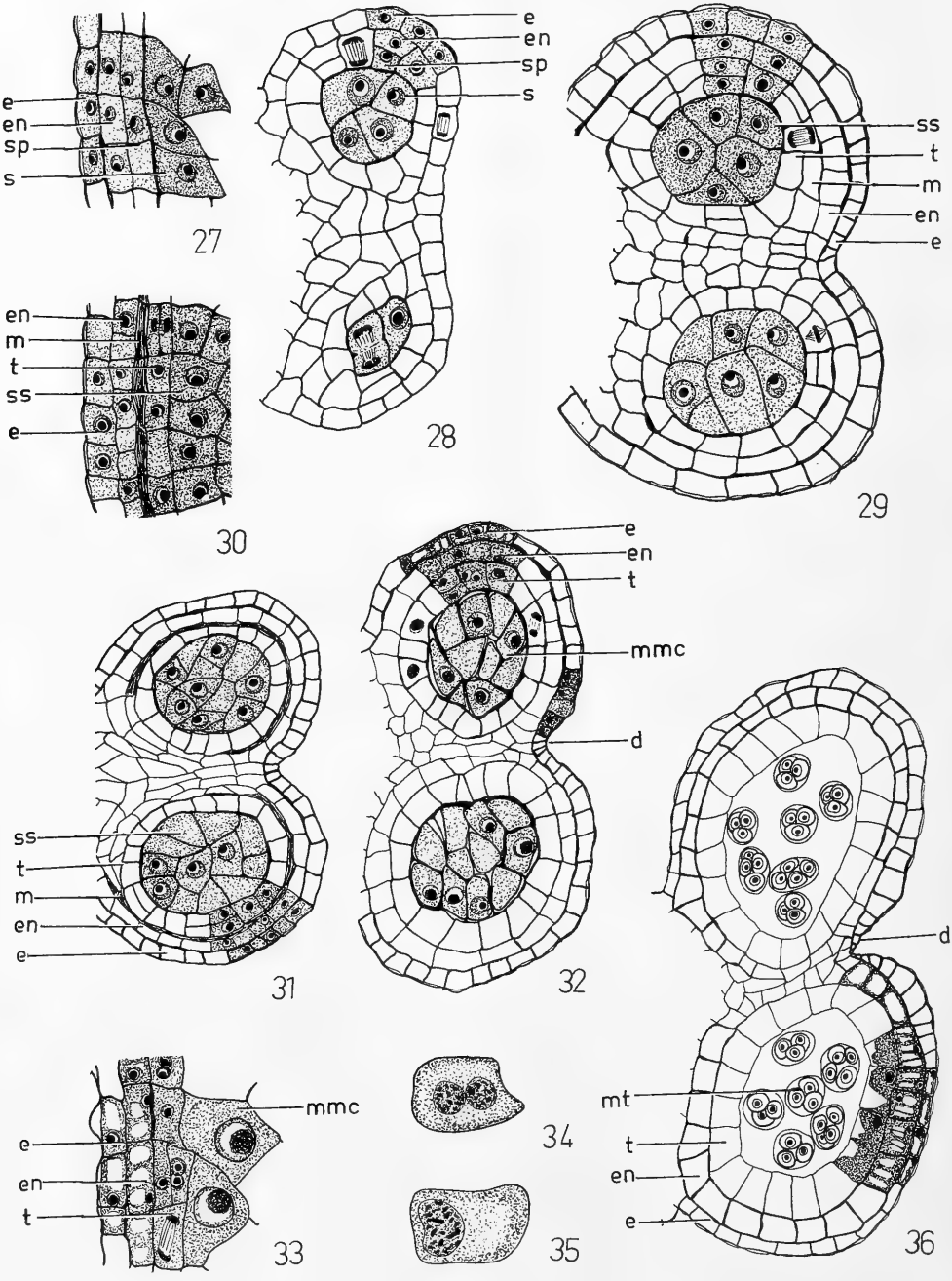
Types of tapetum in the species of Bassia *studied*

	Secretory	Amoeboid	
		Periplasmodium	No Periplasmodium
B. paradoxa	+	+	+
B. bicornis	—	—	+
B. brachyptera	+	—	—
B. divaricata	+	—	—
B. patenticuspis	+	—	—

periplasmodium, although in some sections of *B. paradoxa* the tapetal cells appeared to become detached and lie between the developing pollen grains, forming an apparently ' false ' periplasmodium (Fig. 40). However, on examination of serial sections it was seen that these cells were still in contact with the endothecium, and the pollen grains were merely lodged between the degenerating cells of the glandular tapetum (Fig. 38). An additional variation in *B. bicornis*, and of occasional occurrence in *B. paradoxa*, is the formation of an amoeboid tapetum which does not form a periplasmodium (Table 3). The protoplasts, which maintain their contact with the endothecium, become enlarged and vacuolated, and protrude into the loculus between the developing pollen grains, where they are absorbed (Fig. 41).

The occurrence of both a secretory and an amoeboid tapetum in the same species is unusual and, in some instances in *B. paradoxa*, both types were found in sporangia of adjacent anthers within the same flower, with a higher proportion of aborting microspores being found in the loculi with a secretory tapetum (Figs 42, 43). The only previous record in which both tapetal types occur is in the male-sterile plants of *Beta vulgaris* (Artschwager, 1947) where the periplasmodium is thought to delay pollen abortion, since in those microsporangia with a secretory tapetum the microspores degenerate while still retained in the tetrads. In fully fertile flowers of the same species Artschwager (1927) had previously reported only a secretory tapetum. In the present investigation, about 60% of microspores were degenerating in microsporangia with a secretory tapetum (Fig. 42), as against only about 10% in those with an amoeboid tapetum (Fig. 43).

Variation of tapetal behaviour is common within the family and, according to Mahabale and Solanky (1954*a*) in *Arthrocnemum indicum*, although it is of



Figs 27–36. Development of the microsporangium. Figs 27, 30, 33, in L.S., remainder in T.S. Figs 34, 35, Tapetal cells.

(*d*, region of dehiscence ; *e*, epidermis ; *en*, endothecium ; *m*, middle layer ; *mmc*, microspore mother cell ; *mt*, microspore tetrad ; *s*, sporogenous tissue ; *sp*, secondary parietal layer ; *ss*, secondary sporogenous tissue ; *t*, tapetum.)

Figs 27–30, ×540 ; 31, 32, 36, ×310 ; 34, 35, ×780.

the secretory type, the " walls of the tapetal cells break down and the protoplasts coalesce to form a continuous mass at the periphery of the pollen chamber " which is similar to that reported in *Chenopodium ambrosioides* (Mahabale and Solanky, 1954*b*), *Kochia scoparia* (Mahabale and Solanky, 1953*b*) and *Suaeda fruticosa* (Mahabale and Solanky, 1953*a*). In *Chenopodium album* (Bhargava, 1936), however, although the tapetum is amoeboid it does not form a periplasmodium, and a similar condition is indicated by the illustration of Mahabale and Solanky (1954*c*) in *Chenopodium murale*, although the authors state that a periplasmodium forms.

The middle layer shows signs of stretching and of being crushed when the microspore mother cells are formed (Figs 31, 32), and at the microspore tetrad no remains are visible (Fig. 36).

The endothecial cells contain many starch grains (Fig. 45) which disappear after microsporogenesis, and the cells then become vacuolated, followed by the deposition of dimorphic ' fibrous ' wall thickenings. The cells from the connective region to about a third way around each sporangium are thickened in a scalariform manner (Fig. 46), while those extending to near the region of dehiscence bear numerous ' fibrous ' rods which are united at their bases and extend out along the tangential wall (Figs 47, 48). The first six or seven cells on either side of the point of dehiscence do not bear any thickenings and become highly vacuolated before breaking down completely at dehiscence (Fig. 40).

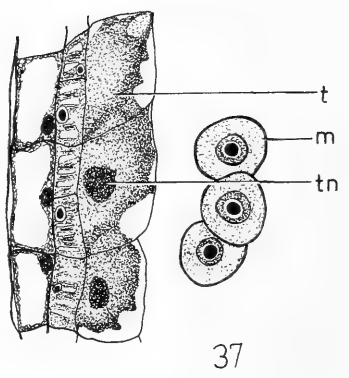
The epidermal cells become vacuolated simultaneously with the rounding off of the microspore mother cells prior to meiosis (Fig. 33), and all except those external to the ' non-fibrous ' cells of the endothecium are greatly stretched tangentially. At dehiscence they form a dead layer of cells over the endothecium, while those in the region of dehiscence increase in size at the same time as the thickenings are laid down in the endothecium (Fig. 48).

Introrse dehiscence takes place by a longitudinal slit in each side of the anther at the junction of the outer wall and the intersporangial septum (Figs 48, 49).

(*b*) *Microsporogenesis and Male Gametogenesis*

The primary sporogenous cells undergo two transverse and one vertical division to form the secondary sporogenous cells which then divide obliquely to form the microspore mother cells (Fig. 32), which round off and enter meiosis (Figs 50–52) followed by simultaneous cytokinesis. The occurrence of secondary spindles is common at telophase II (Figs 53, 54). The microspore tetrads are tetrahedral and isobilateral (Figs 56, 57), but in *B. bicornis* some decussate tetrads were found (Fig. 55). Separation of the microspores is accomplished by centripetal furrows and they are at first angular when liberated by the gelatinization of the enclosing wall of the microspore mother cell (Figs 58, 59). The appearance of a vacuole in the dense cytoplasm represents germination into the one-nucleate pollen grain or male gametophyte, and as this vacuole increases in size the nucleus becomes displaced laterally and the pollen grain assumes the ' signet ring ' configuration (Fig. 61).

Cytoplasmic synthesis reduces, and finally obliterates, the vacuole, and nuclear division is followed by the formation of the small generative cell (Figs 62, 63), which undergoes a further division to form the two male gametes (Figs 64, 65). It is in this three-celled condition that the pollen grain is shed. The deposition of exine is first apparent after the microspores are released from the tetrad and it thickens irregularly as the pollen grain increases in size to give the granular appearance of the mature polyforate pollen grain (Fig. 41).



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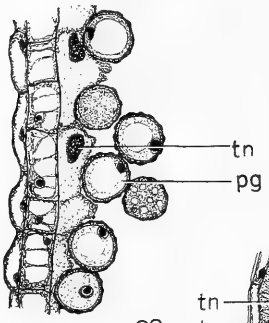

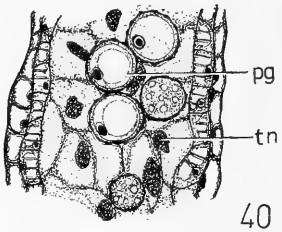

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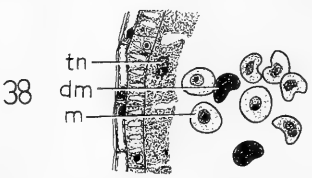

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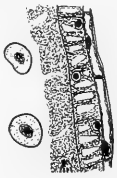

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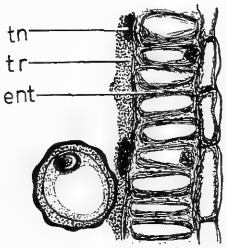

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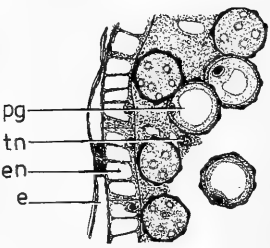

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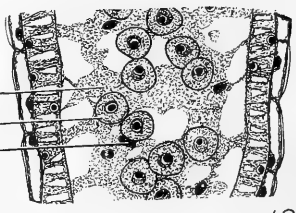

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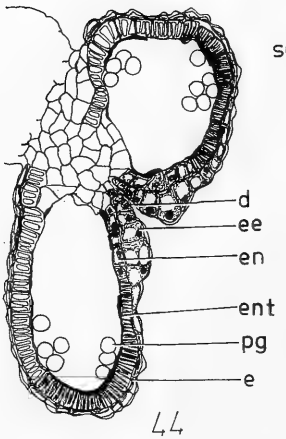

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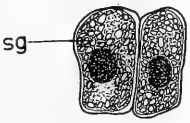

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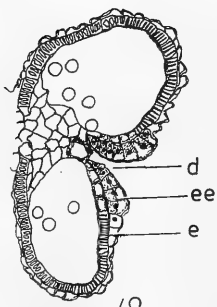

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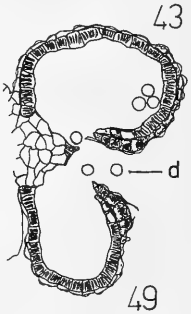

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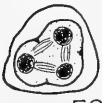

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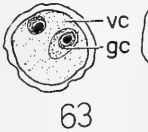

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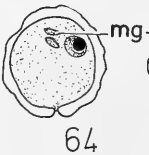

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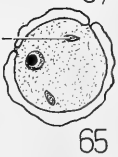

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The Megasporangium

(*a*) *Development of the Ovule*

The primordium of the ovule develops at the base of the ovary when the microsporangium wall is two-layered, and two integumentary primordia appear as folds at the base of the nucellus simultaneously with the differentiation of the archesporial cell (Figs 66, 67). The integuments are at first two-layered, but further cell divisions occur in the inner integument and extend it beyond the slower growing outer one which has no part in the formation of the micropyle (Figs 69, 84). This form of integumentary development is commonly found in this family. A prominent air space was observed in the chalazal region between the integuments. During the differential growth of the ovule, which assumes a campylotropous form, the funiculus becomes elongated and results in the micropylar end of the ovule coming to lie across the base of the funiculus (Figs 68–70). A single vascular strand of annular and spiral vessels differentiates in the funiculus and passes to the chalazal region of the ovule (Fig. 84).

(*b*) *Megasporogenesis*

A single hypodermal archesporial cell makes its appearance at the apex of the ovule (Fig. 71) and divides periclinally to form an outer primary parietal cell and a megaspore mother cell, which is consistent with other records for this family. Mahabale and Solanky (1954*a*) quote Billings (1934) as having reported parietal cell formation in the ovule of *Atriplex hymenelytra* and, while this may well be true, it should be pointed out that Billings' statement referred to the behaviour of the anther archesporium. The parietal cell divides both anticlinally and periclinally and, together with similar divisions in the overlying nucellar epidermis, forms the massive nucellus of the crassinucellate ovule (Figs 72–74).

The megaspore mother cell undergoes meiosis accompanied by cytokinesis and gives rise to a dyad followed by a linear tetrad of megaspores (Figs 73, 74). In the Chenopodiaceae, the chalazal megaspore is invariably functional and, with vacuolation, increases in size at the expense of the three non-functional megaspores until it occupies the place which was filled previously by the tetrad (Figs 75, 76).

(*c*) *Female Gametogenesis*

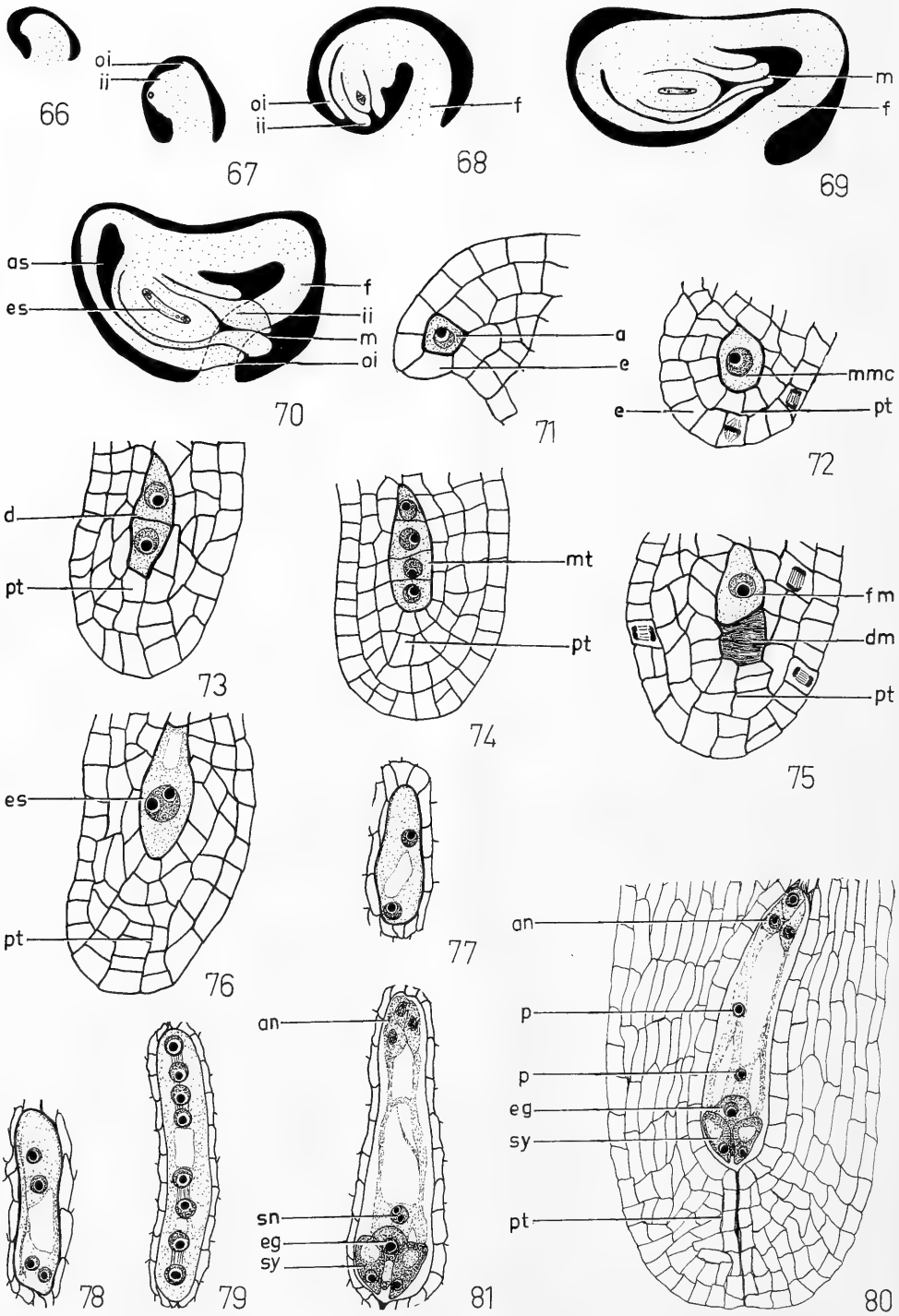
The one-nucleate embryo sac is embedded deeply within the nucellus and, following nuclear division, passes into the two-nucleate stage in which the nuclei are separated by a central vacuole (Fig. 77). Both nuclei then divide simultaneously to form a four-nucleate embryo sac in which the central vacuole is retained (Fig. 78), and a third post-meiotic mitosis gives rise to an unorganized, eight-nucleate embryo sac in which small vacuoles separate the nuclei (Fig. 79). Cytokinesis follows rapidly to form seven cells, of which the central endosperm cell is binucleate (Fig. 80). In its development, the embryo sac is, therefore, of the monosporic, *Polygonum* or 'normal' type which has been reported in all other species investigated in this family.

Legends to figures on opposite page.

Figs 37–43. Types of tapetum. 37–39, Secretory tapetum; 40, 'False' periplasmodium; 41, *B. bicornis*—amoeboid tapetum, but no periplasmodium forms; 42, Secretory tapetum with degenerating microspores; 43, Periplasmodium.

Figs 44–49. Maturation of the anther wall and dehiscence; 45, Endothecial cell; 46, Scalariform thickening; 47, Rod thickening.

Figs 50–65. Formation of the microspores and the male gametes.
(*d*, region of dehiscence; *dm*, degenerating microspores; *e*, epidermis; *ee*, enlarged epidermal cells; *en*, endothecium; *ent*, endothecium with thickenings; *g*, germ pore; *gc*, generative cell; *m*, microspores; *mg*, male gametes; *p*, periplasmodium; *pg*, pollen grains; *sg*, starch grains; *t*, tapetum; *tn*, tapetal nuclei; *tr*, tapetal remains; *vc*, vegetative cell.)
Figs 37, ×780; 38, 40–43, ×320; 39, ×540; 44, ×90; 45–47, 50–65, ×360; 48, 49, ×53.



Figs 66–70. Development of the ovule. Figs 71–81. Megasporogenesis and embryo sac development.

(*a*, archesporium ; *an*, antipodals ; *as*, air space ; *d*, dyad ; *dm*, degenerating megaspores ; *e*, epidermis ; *eg*, egg ; *es*, embryo sac ; *f*, funiculus ; *fm*, functional megaspore ; *ii*, inner integument ; *m*, micropyle ; *mmc*, megaspore mother cell ; *mt*, megaspore tetrad ; *oi*, outer integument ; *pt*, parietal tissue ; *sn*, secondary nucleus ; *sy*, synergids.)

Figs 66–70, ×80 ; 71–81, ×540.

The three antipodal cells are short lived and do not persist after fertilization. The binucleate endosperm cell consists of the original central vacuole surrounded by a thin layer of cytoplasm containing the polar nuclei. Just before fertilization, the chalazal polar nucleus migrates to the micropylar pole of the cell, where it becomes closely associated and then fuses with the micropylar polar nucleus to form the secondary nucleus (Figs 80, 81). The remaining three nuclei of the embryo sac form the egg apparatus which consists of two synergids and the egg (Fig. 80). The synergids, which are situated below the micropyle, are wedge-shaped, and their nuclei are apically situated, while a large vacuole occupies the base of each cell. The synergids commence degeneration as the pollen tube makes its way into the embryo sac, but their remains are still visible at the two-celled stage of the pro-embryo (Fig. 83). The egg cell is overlaid by the synergids and is at first non-vacuolate, but a large vacuole forms in the micropylar region of the cell at maturity.

The mature embryo sac becomes elongated in its chalazal region and it is enclosed by the persisting parietal and nucellar tissues (Fig. 81).

Fertilization

Large numbers of germinating pollen grains were found on the stigma (Fig. 5) and, although they were monosiphonous, branching frequently occurred on the stigmatic papillae to give the appearance of bisiphonous grains (Fig. 82). The pollen tubes grow down the surface of the papillae and between the loosely-packed cells of the stigmatic branches, finally reaching the hollow stylar canal which is in direct communication with the loculus of the ovary. At the base of the stylar canal, the pollen tubes encounter the funiculus of the ovule which is in contact with the upper wall of the ovary, and follow its course to the micropyle (Fig. 83). In some instances pollen tubes passed directly from the stylar canal to the outer integument and then to the micropyle over the surface of the integuments, thereby passing the funiculus and taking, apparently, a longer route. After penetrating the micropyle, the pollen tube makes its way between the elongated cells of the nucellus which encloses the embryo sac and, although more than one pollen tube reaches the ovule, each branching freely and becoming entangled with each other, only one appears to liberate male gametes and effect double fertilization. The pollen tubes do not persist into embryogeny.

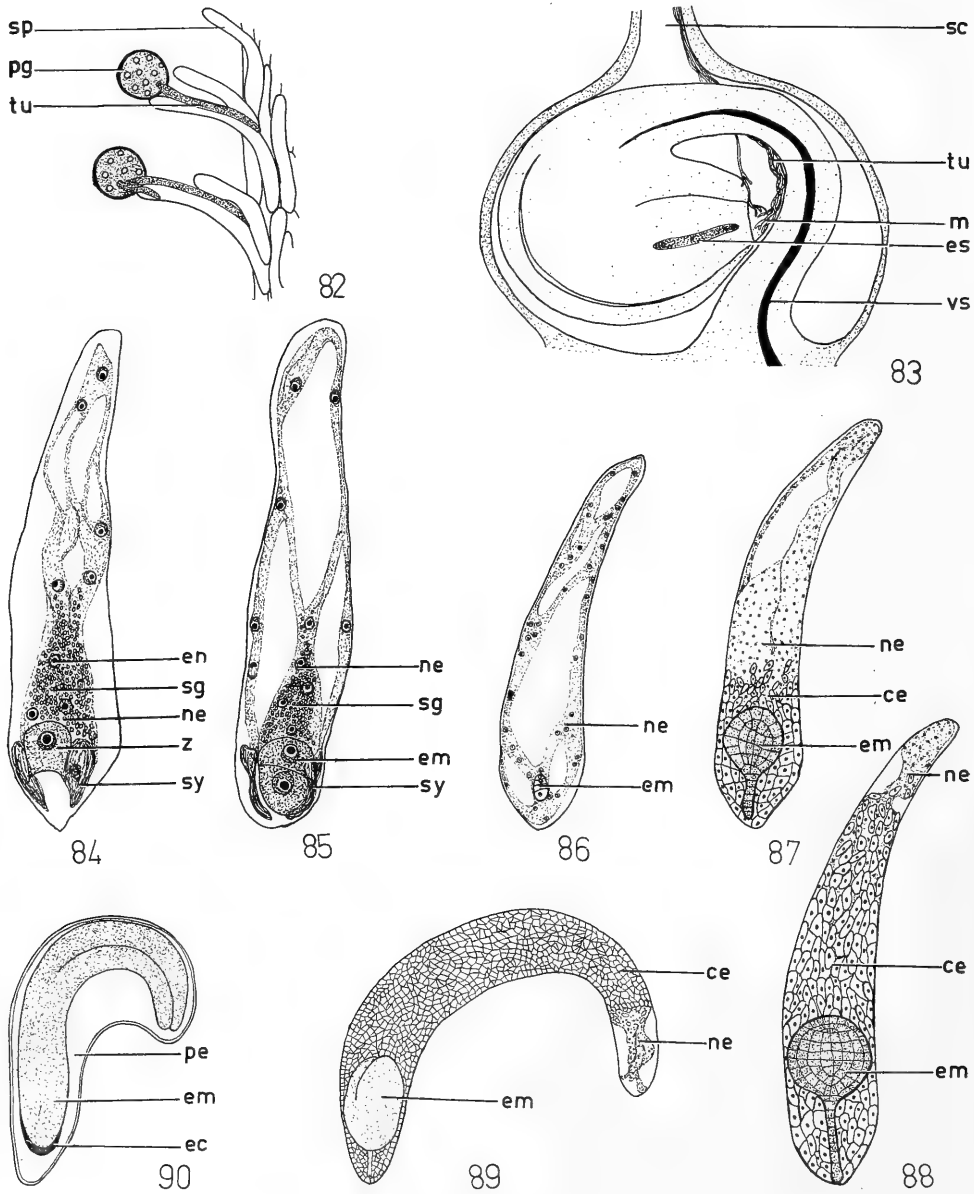
Post-fertilization Changes

(*a*) *Endosperm*

Division of the primary endosperm nucleus precedes that of the zygote and is not accompanied by wall formation, so that the endosperm is of the nuclear type (Fig. 84). After further divisions, the free nuclei are distributed around the proembryo and the periphery of the embryo sac in cytoplasmic strands in which starch grains are also visible (Fig. 85). Nuclear divisions continue until the embryo sac is almost filled with endosperm (Fig. 86), and cell formation is initiated in the micropylar region when the embryo has become spherical (Fig. 87). Wall formation proceeds slowly and free nuclei are still visible in the chalazal region until after the initiation of the cotyledons (Figs 88, 89). The embryo digests the endosperm as it increases in size and finally only a small cap remains over the apex of the radicle (Fig. 90).

(*b*) *Embryogeny*

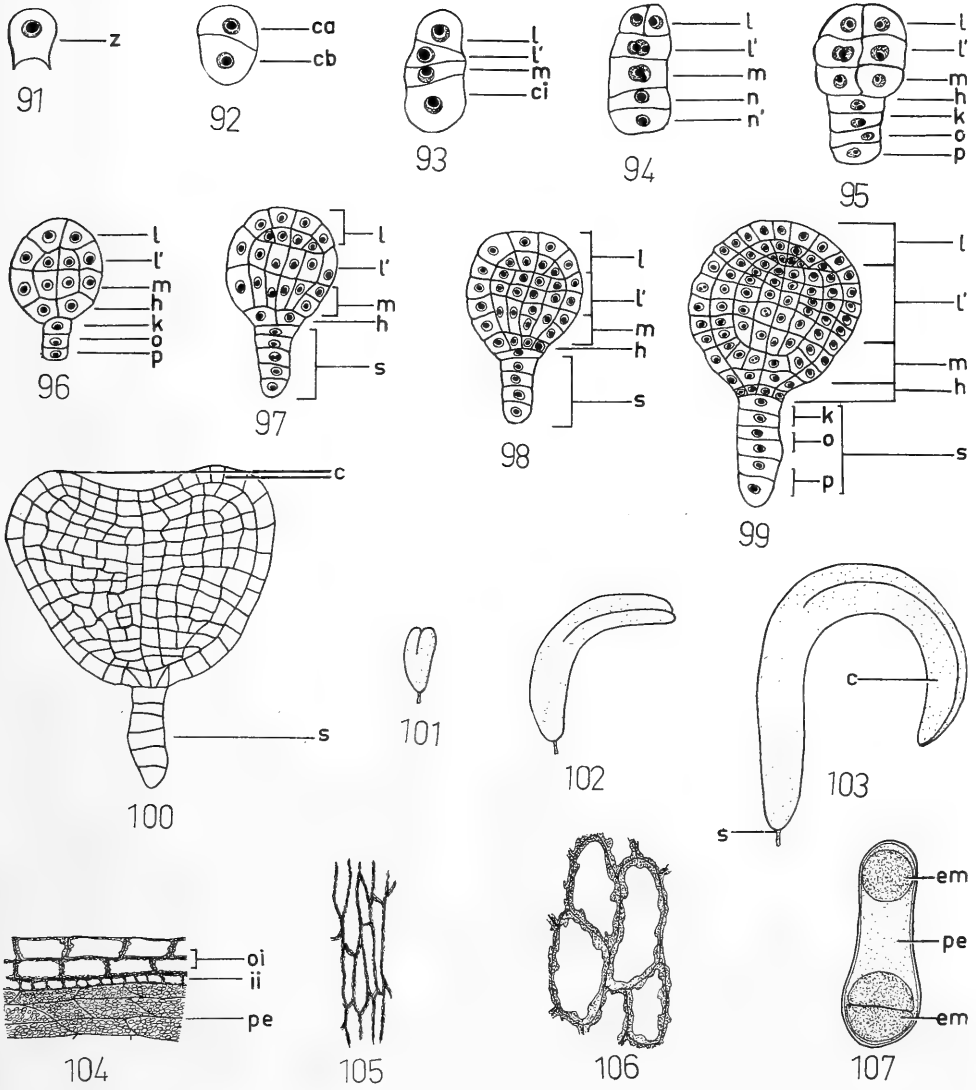
The zygote enlarges but does not divide until after several free endosperm nuclei have formed (Figs 84, 91). A transverse division forms the two-celled proembryos, or first cell generation, which consists of an upper cell, *ca*, and a basal cell, *cb* (Figs 85, 92). These cells divide simultaneously forming the superposed cells *l*, *l'*, *m*, and *ci* of the second cell generation (Fig. 93). Each



Figs 82, 83. Growth of the pollen tubes, drawn from whole mounts. Figs 84–90. Endosperm development.

(*ce*, cellular endosperm ; *ec*, endosperm cap ; *em*, embryo ; *en*, endosperm nuclei ; *es*, embryo sac ; *ne*, nuclear endosperm ; *pe*, perisperm ; *pg*, pollen grains ; *sc*, stylar canal ; *sg*, starch grains ; *sp*, stigmatic papilla ; *sy*, synergids ; *tu*, pollen tubes ; *vs*, vascular strand ; *z*, zygote.)

Figs 82, ×220 ; 83, 86–88, ×130 ; 84, 85, ×540 ; 89, ×50 ; 90, ×20.



Figs 91–107 : 91–103, Embryogeny and changes in shape and dimensions of the embryo ; 104–107, The mature seed ; 104, T.S. of seed wall ; 105, Tangential section of cells of the inner integument ; 106, Tangential section of cells of the outer integument ; 107, T.S. of seed. Lettering of the embryo follows the system of Soueges.

(*c*, cotyledon ; *em*, embryo ; *ii*, inner integument ; *oi*, outer integument ; *pe*, perisperm ; *s*, suspensor ; *z*, zygote.)

Figs 96–100, ×220 ; 101–103, 107, ×20 ; 104–106, ×330.

of these divides to give the eight-celled proembryo of the third cell generation, the lowest cell, *ci*, dividing transversely into *n* and *n'*, while the other three cells divide vertically (Fig. 94). In the fourth cell generation *n* and *n'* both undergo a transverse division to give rise to *h*, *k*, *o*, and *p* (Fig. 95), which is followed by quadrants being produced in tiers *m* and *l'* and, at a later stage, *l* (Fig. 96). The embryo proper develops from *l*, *l'*, *m*, and *h*, while *k*, *o*, and *p* form the uniseriate suspensor which is elongate and usually consists of six superposed cells, which results from further divisions in these cells (Fig. 98). However, in *B. patenticuspis* further divisions may form eight superposed cells. The cells of the suspensor when fully formed are vacuolate and the basal one enlarges slightly, remaining in contact with the nucellus (Figs 87, 99). The hypophysis cell, *h*, divides vertically into two juxtaposed cells (Fig. 96), and a similar division follows in the inner cells, and a transverse division in the outer cells of the tiers *l*, *l'*, and *m* (Fig. 97). The cells of tier *h* divide longitudinally to form the hypophyseal quadrant, which then divides horizontally (Figs 98, 99). The embryo proper is now spherical in form due to the enlargement of cells in tiers *l*, *l'*, and *m*. After further divisions, the embryo becomes heart-shaped and the primordia of the cotyledons differentiate (Fig. 100). The embryo sac meanwhile has continued its growth into the chalazal region of the ovule, becoming spirally curved to accommodate the enlarging embryo which, at maturity, is elongate and spiral (Figs 101–103). This type of embryo development conforms to the Chenopodiad type of Soueges (1920).

Polyembryony

No case of polyembryony was observed in the species investigated, but Cole (1895) reported this to be the normal condition in *Beta rubra*, in which a single seed produced as many as four plants. Favorsky (1928) also described polyembryony resulting from nucellar budding in *Beta vulgaria*, but Artschwager and Starrett (1933) reported that it did not occur in their material.

The Mature Seed

The fully developed integuments are two-layered except in the micropylar region where they are four to six cell layers in thickness. During development the cells of the outer layer of the inner integument gradually lose their contents and disappear, while the inner layer remains intact into the seed stage (Figs 104, 105). Both the cell layers of the outer integument persist and deposition of tannin occurs in their cells, while small areas of thickening develop on the tangential walls of the outer cells and project into the lumina (Figs 104, 106). As the endosperm is digested, starch grains are deposited in the nucellus so that in the mature seed the food storage region is the perisperm (Figs 90, 107), which is characteristic of the Centrospermales.

Acknowledgements

The author wishes to express her thanks to members of the Botany Department and especially to Associate Professor G. L. Davis for her guidance during this investigation.

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STUDIES OF NITROGEN FIXING BACTERIA. IX

Study of Inoculation of Wheat with Azotobacter in Laboratory and Field Experiments

Y. T. Tchan and D. L. Jackson

(Plates xxvii–xxviii)

[Read 27th October, 1965]

Synopsis

Azotobacter used as inoculum on wheat seed can multiply during the germination of the seed. The organic substances exuded by the seed provide the necessary carbon source to support the growth of *Azotobacter*. However, multiplication was subject to competition from other micro-organisms present on the seed coat and in the soil. On agar media or in sand culture, *Azotobacter* was capable of multiplying in the presence of other micro-organisms if combined nitrogen were not added into the media. In soil, the numbers of *Azotobacter* increased during the early germination of wheat seeds but were reduced at later stages.

In field trials our experimental results do not confirm claims that *Azotobacter* inoculation increases crop yields.

Introduction

Agricultural experiments with *Azotobacter* have been carried out since 1902 (Gerlach and Vogel, 1902). Since this date, a considerable amount of data has accumulated; review papers by Cooper (1959) and Rubenchik (1960) have summarized the earlier work. More recently several papers have been published dealing with the use of *Azotobacter* as an inoculum and the development of the organism in the rhizosphere (Brown *et al.*, 1962; Helmeczi, 1963; Katznelson and Strzelczyk, 1961; Macura, 1963; Maliozewska, 1961; Němec and Pecina, 1964; Pochon, 1963; Panosyan, 1964; Rakhno and Rȳȳs, 1963; Rovira, 1963; Samtsevich, 1963; Starkey, 1961; Strzelczyk, 1961; Vancura, 1964).

The literature gives the impression that seed inoculation by non-symbiotic micro-organisms is inconsistent in its effects on plant yields. No logical general explanation has yet been proposed.

In view of the possible importance of *Azotobacter* inoculation to yield increase in the wheat industry of Australia, and since no such experiments on New South Wales wheat soils were available, the authors have examined the effects of *Azotobacter* on the growth of wheat under laboratory and field conditions.

Methods

The effects of *Azotobacter* were examined in laboratory trials using sterile media, sand and soil cultures, and unsterilized cores of soil, and in a number of field trials. Wheat, *Triticum aestivum* L. var. 'Gabo' was used in the laboratory trials; var. 'Festival' was used in the field trials. However, the wheat used in some earlier experimental work done in France was of unknown variety.

(*a*) Laboratory trials

Organisms used: *Azotobacter chroococcum* strains NG241, Veg. B, Veg. 2, Sydney peggy, wheat root (a strain of *Azot. chroococcum* isolated from wheat rhizosphere), IP1, IP2; *Azotobacter macrocytogenes*; *Azotobacter vinelandii* (obtained from Delft, Holland); *Azomonas agilis*; *Azomonas insigne*.

Media

(A) Winogradsky nitrogen free mineral medium: K_2HPO_4, 1 g; NaCl, 0·5 g; $MnSO_4,4H_2O$, 0·01 g; $MgSO_4,7H_2O$, 0·5 g; $FeSO_4,7H_2O$, 0·01 g; tap water, 1,000 ml.
(B) Ammonium nitrate: 1% solution.
(C) Winogradsky mineral agar medium: Solution (A) with 1·5% agar.
(D) Winogradsky sucrose agar medium: Medium (C) with 1% sucrose.
(E) Sand: Coarse river sand, washed with tap water.
(F) Soil cores were collected in tins driven into the soil to a depth of four inches. Samples were taken from a long-cultivated wheat field at Tamworth, N.S.W., (approx. 34 crops) and from an adjacent area that had never been cropped.

Seed sterilization techniques: Seeds were washed in detergent (5% teepol), then in 1% calcium hypochlorite for 10 minutes. The hypochlorite was removed by a series of 10 rinses in sterile distilled water.

Azotobacter counting technique: The number of *Azotobacter* was determined by the method described previously by Tchan (1952).

(*b*) Field experiments

During the 1962 season, field trials of *Azotobacter* inoculation of wheat were carried out in the vicinity of Tamworth, N.S.W.

A 2 × 3 × 2 factorial design was used to examine the effects of *Azotobacter* and the interactions due to added phosphorus and nitrogen fertilizers.

TABLE 1

Chemical analyses of soil samples from the land sown to the factorial trial and from adjacent uncultivated land

	Cultivated Soil (Trial Area)		Adjacent Uncultivated Soil	
	0—4″	4″—8″	0—4″	4″—8″
pH (" sticky point " method)	6·0	6·5	6·0	6·3
Extractable phosphorus				
Truog (p.p.m.) ..	0	0	0·4	0
Olsen (p.p.m.)	0·4	2·6	10·9	1·9
Bray (p.p.m.)	3·7	1·4	4·5	2·1
Organic Carbon				
Tinsley (%)	0·99	0·78	1·69	1·16

The trial was carried out on a solodized Red-Brown Earth soil (Dr2·23—Northcote, 1960) that had been under cultivation for about 20 years, with a rotation based on several years of grazing lucerne (*Medicago sativa* L.) followed by some years of wheat cropping. 1962 was the first year of cropping following a period under lucerne. Table 1 shows a comparison of chemical analyses of the cultivated soil and of samples taken from an adjacent area that had been cleared and grazed, but had never been cultivated.

The decline in organic carbon and extractable phosphorus due to cultivation is typical of the differences found in similar comparisons in this district.

The factors and levels used in the trial were: (1) *Azotobacter* inoculation: not inoculated, inoculated; (2) Superphosphate: 0, 80 and 160 lb/acre; (3) Sulphate of ammonia: 0, 50 lb/acre.

The treatments were fully randomized in each of two replicates.

The inoculation treatment was applied by steeping 5 lb. of seed in 40 oz. of water containing 20 ml. of a 7-days-old *Azotobacter* (strain IP_1) suspension (10^9 cells/ml.) for 30 minutes. After soaking, the grain was spread out in a shaded place. The uninoculated seed was steeped in the same way, in water without the *Azotobacter* suspension.

The seed was sown from a commercial cultivator-drill within a couple of hours from inoculation or soaking. The seed and fertilizer were separate up to the time of sowing, but were brought into contact in the delivery tube of the drill during sowing and were sown together in the drill row in the soil. The sowing rate was 47 lb/acre.

The plots were nine rows wide (4′8″) by 130 ft. long. At harvest the length was trimmed to 124′6″ and the middle five rows were harvested to give the yield from 1/120 acre.

In addition, comparison trials were sown at nine other sites in the district, these consisted of uninoculated and inoculated plots, and were designed to measure the responses to inoculation over a range of farm soils. From these nine and the factorial trial ten sets of data were available for comparison.

Results and Discussion

(1) Multiplication of *Azotobacter* in the presence of wheat seedlings in agar medium.

Wheat seeds (of an unknown French variety) were sterilized as previously described. This simplified the interpretation of the results by eliminating the interaction of the microflora of the wheat rhizosphere. The sterile seeds were inoculated with one drop of a suspension of a culture of *Azotobacter* strain IP_1 (agar culture) and transferred to Winogradsky's mineral agar medium. The seeds were then allowed to germinate at room temperature. After one week the wheat roots were found to be covered with *Azotobacter* (Plate xxvii, *a*, *b*, *c*). This was reisolated and found to be identical with the original inoculum. The experiment was repeated and the results were reproduced. This result indicated that the culture of *Azotobacter* used was capable of multiplication in the rhizosphere of a wheat seedling without added organic substances.

After these preliminary encouraging results, other strains of *Azotobacter chroococcum* (including IP_1) and other species of *Azotobacter* and *Azomonas* as listed above (under Methods, p. 290) were tested in Australia in a similar manner with local wheat varieties. The results were all negative. There was no growth of *Azotobacter* or *Azomonas* in the rhizosphere of the wheat seedling including the strain of *Azotobacter chroococcum* (wheat-root) originally isolated from a wheat rhizosphere.

In spite of the reproducible results of the early experiment it was impossible to repeat the colonization of the rhizosphere of wheat by *Azotobacter*. Close examination of the plates showed that the sites where the seeds were deposited, before their displacement due to germination, contained numerous small colonies of *Azotobacter* and *Azomonas* (Plate xxviii). This suggested that during germination, at least under these artificial conditions, enough organic substances had been exuded to support limited growth of *Azotobacter in situ*. Also, it appears that if the seeds are inoculated, under such conditions, an increase in *Azotobacter* surrounding the seedling at the early stage of germination may be expected without establishing a true rhizosphere association. Such growth could provide some growth factors or plant hormone-like substances (known to be excreted by *Azotobacter*) to influence the growth of wheat. Therefore, it was decided to examine the effects of *Azotobacter* on wheat grown to a more advanced stage in sand culture and in soil.

(2) Multiplication of *Azotobacter* in contact with wheat seeds in plant tube cultures.

To obtain more quantitative information a sand culture technique was used. 10 ml. of Winogradsky mineral solution was added to 50 g. of air dried sand in 3·5 cm. diameter tubes. The tubes were then sterilized at 15 lb. for 20 minutes.

The tubes were inoculated with 5 ml. of suspension of *Azotobacter chroococcum* strain IP_1 containing 500 cells per ml. (a total of 2,500 cells). Immediately after inoculation, 35 ml. of mineral medium was added to the control tube (total volume of 50 ml.) and ten-fold dilutions carried out to estimate the initial number. The other tubes were seeded with six wheat grains either killed (by boiling the seed in water), surface sterilized, or unsterile. In the nitrogen treatment 0·15 ml. of 1% ammonium nitrate was added to the tubes.

At seven and 21 days, the number of *Azotobacter* per tube was estimated and the plant growth was measured by length in cm. The results are summarized in Table 2.

In the absence of added nitrogen there was an increase in *Azotobacter* in all cases. The killed seeds, the surface sterilized and unsterilized seeds all provided an organic exudate for the *Azotobacter* multiplication. Where nitrogen was added, multiplication again occurred in the presence of the killed and surface sterilized seed but not in the case of unsterilized seed.

The multiplication of *Azotobacter* did not influence the growth of seedlings. At seven days level the interpretation is difficult since the length of the seedlings is influenced by the initial germination energy. For all practical purposes, the difference cannot be regarded as having any importance.

The above experiment indicated that the utilization of the organic matter from exudates by *Azotobacter* in the case of unsterile seed is subject to competition from micro-organisms carried by the seed coat.

(3) Multiplication of *Azotobacter* in soil in the presence of wheat seedlings

In soil, the micro-flora could also influence the multiplication and survival of *Azotobacter* in seed inoculation experimentation. Also the amount of available mineral nitrogen can rarely reach 0·01% (100 p.p.m.). Therefore the competition may not be as severe as in the sand experiment with added NH_4No_3

The experiment was repeated using soil from a wheat field in place of sand. Calcium carbonate was added to produce a near neutral pH. The soil was not sterilized and the ammonium nitrate treatment was omitted. The results are included in Table 2.

The seven day count showed an initial increase in *Azotobacter*, but at 21 days the numbers had fallen to less than the original inoculation.

These results suggest that limited growth of *Azotobacter* is possible during the early stages of germination.

(4) Effects of *Azotobacter* in pot trials

Soil cores were collected from cultivated and uncropped soil at Tamworth, N.S.W. Calcium carbonate was added to the surface to bring the pH approximately to neutrality.

A 2^3 *Azotobacter* × phosphorus × nitrogen trial was made. The preliminary result indicated that wheat seed without fertilizer responded very slightly but not significantly to *Azotobacter* inoculation. With fertilizer treatment, there was no response to inoculation. The detailed results are not reported here.

TABLE 2

Multiplication of Azotobacter *in the presence of wheat seeds* (initial number of Azotobacter introduced as inoculum $0 \cdot 25 \cdot 10^4$)

	Wheat Grains		
	Killed	Sterilized	Unsterilized
SAND CULTURE NH_4NO_3 not added			
7 days incubation			
No. of Azotobacter per tube ..	$40 \cdot 4 \cdot 10^4$	$41 \cdot 10^4$	$16 \cdot 7 \cdot 10^4$
Mean value of seedling length			
inoculated ..	—	13 cm.	16
uninoculated* ..	—	6	11·6
21 days incubation			
No. of Azotobacter per tube ..	$31 \cdot 3 \cdot 10^4$	$7 \cdot 10^4$	$4 \cdot 7 \cdot 10^4$
Mean value of seedling length			
inoculated ..	—	21·6	21·5
uninoculated* ..	—	20·7	23·6
	NH_4NO_3 added (final concentration 0·01%)		
7 days incubation			
No. of Azotobacter per tube ..	$20 \cdot 10^4$	$7 \cdot 10^4$	$0 \cdot 1 \cdot 10^4$
Mean value of seedling length			
inoculated ..	—	11·9	12
uninoculated* ..	—	6	10·6
21 days incubation			
No. of Azotobacter per tube ..	$37 \cdot 10^4$	$5 \cdot 10^4$	$0 \cdot 6 \cdot 10^4$
Mean value of seedling length			
inoculated ..	—	26	26
uninoculated* ..	—	26	27
SOIL CULTURE (unsterilized)			
7 days incubation			
No. of Azotobacter per tube ..	$2 \cdot 7 \cdot 10^4$	$17 \cdot 10^4$	$2 \cdot 2 \cdot 10^4$
Mean value of seedling length			
inoculated ..	—	12	13
uninoculated ..	—	9	13
21 days incubation			
No. of Azotobacter per tube ..	$0 \cdot 2 \cdot 10^4$	0	$0 \cdot 002 \cdot 10^4$
Mean value of seedling length			
inoculated ..	—	19	27
uninoculated ..	—	23	25

* No Azotobacter was detected at any stage of seedling growth.

A 2 × 2 trial with eight replications was set out to ascertain the effect of inoculation in cultivated and uncultivated soil. The wheat seeds for the inoculation treatment were soaked in a suspension of *Azotobacter* strain IP_1 for one hour. Seeds for the uninoculated treatment were soaked in water for the same time. The soil cores were manipulated with a minimum disturbance possible to the soil structure. Each pot received six seeds and was later thinned to four seedlings which were allowed to grow for 74 days in glasshouse conditions. The pot arrangement and the results were as indicated in Table 3.

Statistical analysis showed that there were no significant differences of plant weight between the inoculated and the uninoculated treatments.

TABLE 3

Inoculation experiment in cultivated and uncultivated wheat soil. (Dry weight in g. of 4 wheat plants)

	Uncultivated soil				Total	Mean	Cultivated soil				Total	Mean
Inoculated I	1·07	0·94	0·88	0·60	7·19	0·898	0·56	0·56	0·87	0·88	5·84	0·73
Inoculated II	0·870	1·02	0·97	0·84			0·71	0·70	0·78	0·78		
Uninoculated I	0·7	0·95	0·87	0·75	6·34	0·906	0·62	0·78	1·06	0·71	4·80	0·685
Uninoculated II	0·90	0·83	1·34	—			0·56	0·62	0·45	—		

(5) Study of *Azotobacter* inoculation in field trials

To complete the investigation, field trials as described above (under Methods, p. 291) were sown in May, 1962. Inspections of the plots during the growing season and visual scoring for growth revealed no response to the *Azotobacter* inoculation.

At harvest the plots were well grown and free from weeds. There was no damage due to hail, disease, frost or lodging. A summary of the grain yields is presented in Table 4. The accuracy of the results is indicated by the low coefficient of variation (4·9%).

TABLE 4

Field Factorial trial. Grain yields in bushels per acre. (Means of two replicates)

Superphosphate lb/acre	0		80		160		Means
Sulphate of Ammonia lb/acre	0	50	0	50	0	50	
Azotobacter							
Not inoculated ..	19·7	22·3	26·6	27·6	30·0	29·3	25·9
Inoculated.. ..	21·4	19·3	27·8	26·5	29·9	29·8	25·8
Differences due to Azotobacter inoculation	+1·7	—3·0	+1·2	—1·1	—0·1	+0·5	—0·1

In the absence of fertilizers the difference in yield due to inoculation was an increase of 1·7 bushels per acre (on means of two plots). Over the whole trial, however, the mean effect of inoculation was a yield reduction of 0·1 bushels per acre. Neither of these results was statistically significant.

The results indicated that there was an *Azotobacter* × phosphorus × nitrogen interaction. Nitrogen appeared to be the dominant factor in the

interaction. In the absence of nitrogen, the responses to inoculation at 0, 80 and 160 lb/acre of superphosphate were + 1·7, + 1·2 and — 0·1 bushels per acre. In the presence of added nitrogen the corresponding responses were — 3·0, — 1·1 and + 0·5 bushels per acre. None of the interactions were statistically significant.

The experimental data with sand and soil under laboratory conditions (Table 2) indicated that the multiplication of *Azotobacter* in the presence of unsterilized seed was influenced by the available nitrogen. After a week in sand cultures the number of *Azotobacter* had dropped below the inoculum level where the available nitrogen was high. In the absence of added N, the number of *Azotobacter* had significantly increased. The situation was not very different after three weeks. The number of *Azotobacter* was still substantially higher in the no nitrogen treatment.

In the soil under laboratory conditions, with no fertilizer added, the number of *Azotobacter* increased only ten-fold during the first week and dropped well below the inoculated number in three weeks. It would not be unreasonable to speculate that in the presence of nitrogenous fertilizer *Azotobacter* inoculated with the seed would not increase but probably decrease and it could not exercise any influence on the wheat growth. The negative response at 50 lb/acre of sulphate of ammonia of —3·0 (no superphosphate) and of —1·05 (at 80 lb/acre of superphosphate) in the inoculated trial can not be explained on a microbiological basis.

Comparison plots

Inoculated and uninoculated plots were sown at nine other sites in the vicinity of Tamworth, N.S.W. Together with data from the factorial trial these gave ten sets of data. Two of the sites were on Black Earth soils; the others were on Solodized Red-Brown Earths. The data are summarized in Table 5.

Table 5

Grain yield from comparison plots. Bus/ac.

Soil Group	Inoculation treatment		Response
	Uninoculated	Inoculated	
Red-Brown Earth	19·7	21·4	+1·7
	14·0	12·1	—1·9
	8·5	7·8	—0·7
	27·9	25·8	—2·1
	8·6	8·0	—0·6
	19·6	20·7	+1·1
	15·8	23·4	+7·6
	14·0	14·6	+0·6
Black Earth	41·1	34·1	—7·0
	17·8	17·7	—0·1
Total	187·0	185·6	—1·4
Mean			—0·14

The mean response, — 0·14 bushels per acre, shows no benefit from inoculation. In two cases, however, the responses were marked. In the first, there was an apparent response in favour of inoculation (+ 7·6 bushels per acre); an inspection of the harvest records suggests that soil variation was the main reason for this apparent response. In the second, the difference was against inoculation (— 7·0 bushels per acre); no explanation can be given.

From the above data no apparent difference existed between the inoculated and uninoculated treatments.

Conclusions

It has been suggested that plant hormone-like substances or growth factors excreted by *Azotobacter* could be beneficial to the higher plant (see Starkey, 1961, and Pochon, 1963). Under laboratory conditions *Azotobacter* is capable of multiplication by utilizing the organic matter excreted during the germination of the seed. Therefore, such beneficial influence of *Azotobacter* should be noticeable in the early phase of plant growth. Our experiment in the laboratory and in the field failed to show such response by wheat seedling. Also, under our experimental conditions, the multiplication of *Azotobacter* during germination of the seed occurs only when the competition of other micro-organisms was not severe. When the available combined nitrogen is high *Azotobacter* can not compete successfully for the available organic matter. In the pot trials and field experiments, no significant beneficial effect could be obtained. Such conclusion may only apply to our experimental data ; however, when favourable ecological conditions are prevalent it could not be excluded that a possible significant influence of yields could be obtained by *Azotobacter* inoculation. To determine the most suitable ecological factors in this regard a very elaborate programme is needed. This would include the study of soil factors, climatic conditions, the investigation of interrelationship of micro-organism and higher plant, and genetic studies of biotic partners.

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EXPLANATION OF PLATES XXVII–XXVIII.

Plate xxvii.

I*a*. Wheat seed germinated on agar medium. Note the colonies of *Azotobacter* surrounding the roots (arrows).

I*b*. Detail of a root and root-hairs. Note the growth of *Azotobacter* in the rhizosphere (dark areas).

I*c*. Detail of root tip and root-hairs with *Azotobacter*.

Plate xxviii.

II. Wheat seed germinated on agar medium. Micro-colonies of *Azotobacter* (arrows) using the exudate of the seed as organic matter. Note the absence of *Azotobacter* in the rhizosphere.

STUDIES ON THE GENETIC NATURE OF RESISTANCE TO *PUCCINIA GRAMINIS* VAR. *TRITICI* IN SIX VARIETIES OF COMMON WHEAT

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Synopsis

The mode of inheritance of resistance to stem rust was determined for six varieties of *T. vulgare*. In the case of Eureka the type of F_2 segregation obtained in crosses with susceptible varieties was influenced by temperature and by the strain used. The resistance of Eureka to the laboratory strain 103–H–2 was controlled by two independent factors, Sr6 and an incompletely dominant factor which was not temperature sensitive.

In each case a different factor conditioned the seedling resistance of Gabo to the strains 126–Anz–6, 21–Anz–2, 103–H–2 and A20. Three of these factors were also present in Charter, but only one (Sr11) in Yalta. The gene Sr11 in Gabo, Charter and Yalta was differentially transmitted in crosses between these three varieties and the susceptible Mentana and Chinese Spring, and also, apparently, in crosses with Federation and Morocco. Sr11 was closely linked with the factor for leaf rust resistance in Mentana. Another factor, Sr_{G2}, in Gabo and Charter conferred resistance to strains 103–H–2 and 111–E–2, but was ineffective against field strains.

Seedling resistance of Mentana to 21–Anz–2 was controlled by a single factor, Sr8, which, together with another factor, conferred resistance to NR–7.

Kenya 117A was found to possess three factors for seedling resistance of which one, Sr9b, also conferred field resistance, while the other two had only a modifying effect. In the seedling stage Sr9b was dominant with 222–Anz–1, 2, 4, 6 but incompletely dominant with other strains.

Introduction

The task of the plant breeder who is concerned with developing varieties of wheat resistant to *Puccinia graminis* Pers. var. *tritici* (Eriks. and E. Henn.) has been made difficult by the existence of many pathogenic strains of the parasite. Especially in recent years, the rapid spread of virulent strains of the 21 and 34 standard series has been a setback to breeders in New South Wales and Queensland, as these strains rendered susceptible the commonly used sources of resistance. All the six varieties used in this study are no longer resistant to the stem rust strains occurring in the field, while a few years ago the resistances of Eureka and Kenya 117A were still effective against most field strains.

The present study was undertaken to study the mode of inheritance of resistance in six varieties of *Triticum vulgare* to some of the new strains of stem rust, and to correlate results obtained by Australian and overseas workers, which were at variance. A special effort has been made to study the effect of minor or modifying genes as these could be of some use in future breeding work.

Review of Literature

For the purpose of this review the types of resistance carried by the three varieties, Gabo, Charter and Yalta are considered together and the other varieties *seriatim*.

Eureka

In 1941 Macindoe reported that a single factor in Eureka conferred resistance at lower temperatures; this factor was non-allelic to the single factor in the varieties Charter and (Gaza × Bobin²), the latter being a sisterline to Gabo.

Watson and Waterhouse (1945) showed that the resistance factor in Eureka derived from Kenya W 743* C6040 was inherited independently of the single factors for resistance in Kenya W 744 C6041 and Kenya W 745 C6042. Knott and Anderson (1956) have designated this factor Sr6. Studying the mode of inheritance of resistance, they postulated that Sr6 is dominant with race 56 but recessive with race 15B. Recent work by Green *et al.* (1960), using many North American and Australian strains, indicated that Sr_{Kal} (a designation used by Australian workers for the resistance gene in Eureka) and Sr6 are the same and this was also apparent when all F_2 plants from a cross between Eureka and the isogenic Sr6 line proved resistant to races 56 and 15B. Peterson and Campbell (1953) located Sr6 on chromosome XX and this has been confirmed by other workers. The effect of temperature on the breakdown of rust resistance in varieties carrying Sr6 has been described by Green and Johnson (1954) and Forsyth (1956).

A second gene for resistance in Eureka was reported by Athwal (1955) who used race 42 from India. This gene was not temperature sensitive. Race 42 was interesting as it also did not attack the varieties Bencubbin, Mentana, Dundee and Uruguay which are susceptible to Australian strains. Athwal concluded from his studies that in each of these varieties a single factor controlled resistance to race 42 and that the factor in Eureka was allelomorphic with the factor in Bencubbin. This gene in Eureka was inherited independently of two factors in Gabo and a single factor in Mentana. The factors for resistance in Mentana and Dundee were independent of each other: Dundee is one of the parents of Eureka. Athwal also considered that the factor for resistance to race 42 in Eureka was allelic or closely linked with the single factor in Uruguay and with one of the two factors in Kenya 117A which confer resistance to race 42.

Gabo, Charter and Yalta

Watson (1941) showed that Kenya 745 (the parent of Charter and Yalta) possessed a single incompletely dominant factor for resistance, and that seedling resistance and field resistance were highly correlated. In the same year Macindoe obtained a similar result with Charter using North American race 34. When crosses between the resistant variety (Gaza $\times$ Bobin^2) and susceptible varieties were studied with race 34, a single major factor controlled resistance in the seedling and adult plant stage. Seedling tests with race 19, however, indicated at least one additional factor for resistance in Charter and (Gaza $\times$ Bobin^2).

On the basis of F_2 data Watson and Waterhouse (1949) classified many wheat varieties into three groups each carrying a major gene present in Kenya 743, Kenya 744 or Kenya 745 respectively. Into the latter group they also placed Gabo, Charter and Yalta.

In 1948, however, Sears and Rodenhiser suggested that two linked, dominant complementary factors were responsible for resistance in crosses between the resistant Timstein and Chinese Spring monosomic lines. Monosomic analysis located these factors on chromosome X, and they were designated Sr11 and Sr12 (Knott, 1959). Similar conclusions were reached by other workers who used the varieties Gabo and Lee in crosses with monosomic lines of Chinese Spring. Lee originated from a Hope $\times$ Timstein cross, and Watson and Stewart (1956) have shown that the varieties Timstein C.I. 12347 and Lee carry the same resistances as Gabo. They concluded that Timstein probably was introduced into the U.S. as a sisterline of Gabo. More recently, a line from a cross Steinwedel $\times$ *T. timopheevi* and carrying the resistance of the latter has been named Timvera (Watson and Luig, 1958).

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* Refers to the University of Sydney Wheat Accession Register.

Work by Luig (1960) demonstrated that the Gabo-type resistance was due to a single factor and that this factor was differentially transmitted whenever Mentana was used as the susceptible parent. Sears and Loegering (1961) found evidence for a pollen-killing gene in Chinese Spring located on chromosome X.

Watson (1943) found a second factor in Kenya 745 which operated against four out of 22 standard races against which the single incompletely dominant factor reported earlier (Watson, 1941) gave protection. Both factors seemed to be independent of each other. As mentioned above Athwal (1953) explained the segregation in a cross between susceptible Federation and Gabo to Indian race 42 on the basis of two dominant independent factors, and both these factors were found to be inherited independently of single factors for resistance to this race in Mentana, Bencubbin and Eureka.

Kenya 117*A*

In 1953 Athwal reported a single incompletely dominant factor for resistance in Kenya 117A to four strains of stem rust, while two factors were operative in this variety against Indian race 42. Subsequently Athwal and Watson (1954) found that the single incompletely dominant factor in Kenya 117A was allelic to the factor Sr_{Kbl} in Kenya 744. Seedling and field resistance were correlated, but appeared also to be influenced by modifying factors.

More recently Knott and Anderson (1956) reported that Kenya 117A C.I. 13140 carries three independent genes Sr7, Sr9 and Sr10 for resistance to races 56 and 15B. From tests of isogenic lines of Marquis carrying Sr7, Sr9 and Sr10 with 29 North American and eight Australian strains Green *et al.* (1960) concluded that Sr9b is the same as Sr_{Kbl}, this gene being operative against all eight Australian strains. The lines having Sr7 and Sr10 were only moderately resistant or were susceptible to the eight strains.

Aslam and Ausemus (1958) explained the inheritance of seedling resistance to race 15B in a cross of Mida with Kenya 117A C.I. 12568 on the basis of two or three genes for resistance in Kenya 117A and two genes for susceptibility in Mida. That their results did not agree with the previous findings was probably due to a different strain of Kenya 117A being used. Watson and Stewart (1956) stated that Kenya 117A C.I. 12568 and Australian Kenya 117A W 1347 were dissimilar in their reaction to many strains of stem rust, with the former being the more susceptible. Kenya 117A W 1347, however, was indistinguishable from Kenya 117A C.I. 13140. Omar (1959) reported that the seedling resistance of Kenya 117A to 15B was inherited independently of field resistance to many races of rust.

Sears, Loegering and Rodenhiser (1957) located Sr9 on chromosome XIII, and Knott (1959) found that Sr7 was on chromosome VIII.

Mentana

Although Mentana has been used as an extra-differential variety in several countries, the earlier mentioned work of Athwal (1953) with Indian race 42 is the only report on the inheritance of resistance that has been found during the course of this search of the literature.

Materials and Methods

A short description of the six main varieties used in the present study follows.

Eureka II W 1325. A selection from a cross (Kenya C 6040 × Florence F_1) × Dundee. (Macindoe, 1948).

Gabo W 1422. Bred at Sydney University from a cross (Bobin 39 × Gaza (*T. durum*)) × Bobin 39. (Athwal, 1953).

Charter W 1371. Bred by Dr. S. L. Macindoe from a cross Kenya C 6040 × Gular. In 1948, however, Macindoe stated that the cross was probably

made with Kenya C 6042 and not with Kenya C 6040, as Watson had found no segregation for resistance in crosses between Charter and Kenya C 6042 (Macindoe, 1948).

Yalta W 1373. Originated from a cross (Kenya C 6042 × Pusa 4) × Dundee made by Dr. S. L. Macindoe. The spike is square and has short awns, the glumes are pubescent and white, the grain is white.

Mentana W 1124. Athwal and Watson (1957) stated that Mentana W 1124 was different from Mentana Genetic Stock No. 1028. Professor Ugo de Cillis, Italy, has identified Mentana W 1124 as " Ciro Menotti ", also known as Rachael or Awnless Mentana. Ciro Menotti resulted from a cross Akagomuki × (Rieti × Wilhelmina Tarwe) made in 1917. The spike is short awned, semi-compact, somewhat clubby at the tip ; the glumes are glabrous and brown, the grain is white.

Kenya 117*A* W 1347. Accessioned under C.I. 13140 in the U.S.A. The spike is tip-awned, mid-dense, the glumes are glabrous and white and the grain is red.

The following varieties were used in particular crosses as susceptible parents :

Federation W 107. Bred by W. Farrer from a cross between a selection of Improved Fife and Yandilla.

Little Club W 1. One of Stakman's 12 differential hosts. Very susceptible in the seedling and adult plant stage to all Australian strains of stem and leaf rust of wheat, but semi-resistant to hybrid strains from crosses between *P. graminis* var. *tritici* and *P. graminis* var. *secalis*.

Morocco W 1103. Pedigree unknown. This awned pubescent variety was chosen for this study because of its high susceptibility to all Australian field strains of stem and leaf rust.

Chinese Spring W 1806. Obtained from Dr. E. R. Sears. Susceptible in the seedling stage to all Australian field strains of stem and leaf rust, but resistant to all leaf rust strains as adult plants.

Bobin W 39. The pedigree is unknown as Bobin W 39 is distinct from the commercial Bobin which resulted from a cross between Thew and Steinwedel.

Gular W 1101. Originated from a cross between Wagga 13 and a selection from Marshalls No. 3. Gular is one of the parents of Charter.

Insignia W 1989. Originated from a cross Ghurka × Ranee. It does not carry the gene Sr11 which has been incorporated into its derivatives Insignia 48 and Insignia 49.

Kenya C 6042 W 745. An unnamed crossbred introduced from Kenya Colony.

*II*56.48.1.2.1 W 2691. Developed from an F_2 plant from cross (Little Club × (Gabo[3] × Charter)). More susceptible than Little Club to strains of *P. graminis* var. *secalis*.

Mona W 1168. Cross between Plowman's No. 3 (Bunyip selection) and Canberra.

The material under study comprised the following crosses :

(*a*) Reciprocal crosses in all 30 possible combinations between the six abovementioned varieties.
(*b*) Backcrosses involving the abovementioned crosses.
(*c*) Reciprocal crosses between the six varieties and the susceptible Federation.
(*d*) Crosses involving resistant F_3 lines for the purpose of obtaining lines with single genes for resistance.
(*e*) Crosses between certain varieties to solve special problems which had arisen during the course of these studies.

Inoculations were made and reaction types recorded as described by Stakman and Levine (1922). Rust studies in the field were conducted at Castle Hill Research Station under an artificial epiphytotic.

Designation and description of strains used

In a recent paper Watson and Luig (1963) have proposed a new system of nomenclature for strains of stem rust occurring in the geographical region of Australia and New Zealand. Basically the scheme is the same as Watson and Luig (1961) proposed for leaf rust. According to the new system the numbers preceding the regional designation " Anz " refer to the international set of differential varieties, and the numbers following " Anz " to the six extra-differential varieties, which are numbered in a standardized way: McMurachy (Sr6) — 1, Yalta (Sr11) — 2, W 2402 (Sr9b) — 3, C.I. 12632 (W 1656) — 4, Renown W 2346 — 5, Mentana W 1124 (Sr8) — 6. For example, if an isolate which on the international set conforms to 21 attacks McMurachy and Yalta, but is avirulent on the other four supplementals the designation is strain 21–Anz–1, 2.

Twelve strains of stem rust were used to test the material under study. They represent stock cultures and were frequently checked for contamination. A short description of the strains and their origin is given below:

21–*Anz*–0. Accession Number 57043. A field strain, mainly occurring in Tasmania, New Zealand, and in the southern part of the Eastern Australian Wheat Belt. First identified in 1954 (Watson, 1955), its origin is unknown.

21–*Anz*–2. Accession Number 57072. Several years ago the most prevalent strain in Australia. Was first detected in 1956 and could have arisen as a mutation from 21–Anz–0, or as the result of somatic recombination between 21–Anz–0 and a strain capable of attacking the Yalta type of resistance.

21–*Anz*–2, 6. Accession Number 59137. Not widespread. Origin unknown.

126–*Anz*–6. Accession Number 56196. This is probably identical with the rust first isolated by Waterhouse in 1926 and determined as race 34. It has now been replaced by more virulent strains in the field. Origin unknown. A yellow colour mutant found in the stock culture of 126–Anz–6 was also used. It proved to be identical with the stock culture in its reaction types on differential varieties.

126–*Anz*–1, 6. Accession Number 7316. First identified from Eureka at Narrabri in 1942. This strain is now nearly extinct, but was widespread in the years following 1942 when it first heavily damaged crops of Eureka. Could have originated as a mutation from 126–Anz–6. (Watson and Singh, 1952).

126–*Anz*–2, 6. Accession Number 55350. First reported by Watson, 1955. Its spread in the field has been limited. It is closely related to 126–Anz–6 and 222–Anz–2, 6 and could have arisen as a mutation or as a somatic hybrid.

222–*Anz*–1, 2, 4, 6. Found at Hawkesbury Agricultural College, N.S.W., on genetic material carrying Sr6 and *Triticum timopheevi* resistance, and possibly resulted from a mutation of strain 222–Anz–1, 2, 6. It is distinctly lighter in colour than the other Australian field strains and has also a prolonged incubation period.

NR–7. Obtained as a somatic hybrid between Yellow NR–2 and Red 111–E–2 (Watson and Luig, 1958b).

103–*H*–2*. Obtained as a somatic hybrid between Yellow NR–2 and Red *P. graminis* var. *secalis* (57241) in 1958 (Watson and Luig, 1959). Previous designation M9–a.

* The letter H refers to a laboratory strain of hybrid origin, while E indicates a strain of foreign origin.

111–*E*–2. Obtained from Minnesota, U.S.A. A very avirulent strain of *P. graminis* var. *tritici*, which could have arisen from an intervarietal cross between *P. graminis* var. *tritici* and *P. graminis* var. *secalis*. Described by Watson (1957).

A. 20. Obtained from selfing a culture of *P. graminis* var. *secalis* (57241) (Watson and Luig, 1962). This strain is virulent on Black Winter Rye, but gives also a high reaction on the wheat varieties Yalta and Eureka at temperatures above 75°F.

The rust reaction of eight varieties used in this study to 11 strains of *P. graminis* is given in Table 1.

TABLE 1

Reaction of the six varieties under study and of Federation and Little Club to the eleven selected strains of P. graminis*

Variety	21–0	21–2	21–2, 6	126–6	126–1, 6	126–2, 6	222–1, 2, 4, 6	NR–7	103–H–2	111–E–2	A20
Eureka at 60–65°F	;	;	;	;	3+	;	3	;	;	;	;
Eureka at 75–80°F	3+	3+	3+	3	3+	3	3+	3^{c}	;1+	;1+	3^{cn}
Gabo	;1=	3^{c}	3^{c}	;1=	;1=	3^{c}	3^{c}	3^{c}	;1=	;1=	;
Charter	;1=	3+	3+	;1=	;1=	3+	3	3	;1=	;1=	;
Yalta	;1=	3+	3+	;1=	;1=	3+	3	3+	3^{c}	;1++3^{-c}	3^{c}
Mentana	2	2	3	3+	3+	3+	3	;	;	;	;
Kenya 117A	;2^{-c}	;2^{-c}	;2^{-c}	2^{-n}	2^{-n}	2^{-n}	;1≡	;1, 2^{-n}	;2≡	;2≡	;
Federation	3	3	3+	3+	3+	3+	3+	3	$3^{=c}$	3^{+N}	;1
Little Club	3+	3+	3+	3+	3+	3+	3+	3+	2+	3+	2^{-}

* At temperatures 70°–75°F unless otherwise stated.

EXPERIMENTAL RESULTS

A. Inheritance of resistance to stem rust in the varieties under study

1. *Eureka W* 1325

(*a*) Inheritance of resistance to strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7.

F_1 Studies

At temperatures of 60°–65°F Eureka is resistant to all except two of the strains used in this study. The virulent ones are 126–Anz–1, 6 and 222–Anz–1, 2, 4, 6. As mentioned in the literature review and indicated in Table 1, the resistance of Eureka to most of the former strains is ineffective at high temperatures. F_1 seedlings of crosses between Eureka and the susceptible varieties Little Club, Mentana, Federation and Yalta were tested at temperatures of 60°–65°F. The results are shown in Table 2 and indicate dominance of resistance to strains 126–Anz–6, 126–Anz–2, 6 and NR–7 and incomplete dominance where 21–Anz–2 was used.

F_2 and F_3 Studies

Seedlings of five F_2 families from a cross between Eureka (resistant) and Yalta (susceptible) were tested with strain 21–Anz–2 and seedlings of one of these families were tested with strain NR–7. The tests were carried out at temperatures of 60°–65°F. When analysed statistically the data were homogeneous and indicated a single dominant factor for resistance in Eureka (Table 3).

In 1958, F_2 seedlings from a cross between Gabo (susceptible) and Eureka were tested with strain 126–Anz–2, 6 at day temperatures of 60°–65°F. Out of a total of 204 plants, 48 were susceptible (" 3+ " reaction) and the remainder gave a resistant reaction of a " ; 1 = " type. The F_2 seedlings were tagged according to their reaction type and transplanted into the field at Castle Hill. Later in the year a severe stem rust epiphytotic developed which was mainly caused by 21–Anz–2. All plants which had given a resistant reaction in the seedling stage were resistant or semi-resistant in the field, while the plants

TABLE 2

Reaction types of F_1 seedlings of crosses between Eureka and susceptible varieties when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7

Susceptible Parent	Strain used	F_1 Reaction
Little Club	126–Anz–6	" ; "
Federation	126–Anz–6	" ; "
Mentana	126–Anz–6	" ; 1 "
Federation	126–Anz–2, 6	" ; "
Yalta	126–Anz–2, 6	" ; "
Federation	NR–7	" ; "
Federation	21–Anz–2	" X "
Yalta	21–Anz–2	" X+ "

which had been susceptible as seedlings reacted similarly in the adult stage. The resulting F_3 generation was tested with strains 126–Anz–2, 6, 21–Anz–2 and NR–7 (Table 4). A similar result was obtained for each F_3 line and from the data it was concluded that a single, dominant factor in Eureka controlled reaction to these three strains.

The results from studies of crosses involving Eureka with Mentana, Little Club, Charter and Federation are given in Tables 3 and 4 and provide further evidence for a single dominant factor hypothesis.

In the foregoing it has been noted that when F_2 plants of the cross (Gabo × Eureka) were studied at Castle Hill in 1958, the one single, dominant factor

TABLE 3

Segregation of F_2 plants of crosses involving Eureka and susceptible varieties when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7

Susceptible parent	Cross No.	Strain used	Number of seedlings		P-value (3 : 1)
			Resistant	Susceptible	
Yalta	II56.22.1	21–Anz–2	111	41	0·70–0·50
	.2	21–Anz–2	133	55	0·20–0·10
	.3	21–Anz–2	97	27	0·50–0·30
	.4	21–Anz–2	127	55	0·20–0·10
	.5	21–Anz–2	161	60	0·50–0·30
	.1	NR–7	143	47	0·95–0·90
Total			772	285	0·20–0·10
Gabo	II56.9.6	126–Anz–2, 6	156	52	1·00
Mentana	II58.420.1	126–Anz–6	89	32	0·90–0·80
Federation	II58.21.8	126–Anz–6	107	34	0·90–0·80
Charter	II56.24.3	21–Anz–2	146	60	0·20–0·10
Grand Total			1,270	463	0·10–0·05

controlled resistance both in the seedling and adult plant stage. Field studies on F_2 plants of crosses between Eureka and the susceptible varieties Little Club and Federation at Castle Hill in 1960, however, suggested that resistance in Eureka was recessive. In both seasons the field inoculum comprised mainly 21–Anz–2. Of the 147 F_2 plants of cross II58.21.8 (Eureka × Federation), 35 were classified as resistant and 112 as susceptible, while of the 87 F_2 plants of cross II58.84.4 (Little Club × Eureka), 21 were resistant and the remainder susceptible. Classification of adult plants in 1960 was made on the basis of parental reaction: Little Club and Federation were fully susceptible (more than 60% infection) and Eureka was resistant, being less than 15% infected and showing only small pustules.

TABLE 4

Reaction of F_3 lines of crosses between Eureka and three susceptible varieties when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6 and NR–7

Susceptible parent	Cross No.	Strain used	F_3 Behaviour			P-value (1 : 2 : 1)
			Resist.	Segreg.	Suscept.	
Yalta	II56.22.1	21–Anz–2	39	75	47	0·50–0·30
Gabo	II56.9.6	126–Anz–2, 6 21–Anz–2 NR–7	45	106	48	0·70–0·50
Charter	II56.24.3	21–Anz–2	39	68	40	0·70–0·50
Little Club	II58.84.4	126–Anz–6	19	44	24	0·70–0·50
Total			142	293	159	0·70–0·50

When seedling tests with strain 126–Anz–6 were carried out on the progeny of the F_2 plants from the two crosses it was found that the F_2 plants resistant in the field gave only resistant progeny. Approximately two-thirds of the susceptible F_2 plants gave segregating progeny and one-third gave homozygous susceptible progeny. The combined field and glasshouse data from the cross II56.9.6 (Gabo × Eureka) and from the two above crosses (II58.21.8 and II58.84.4) indicate that plants heterozygous for Sr6 were resistant in the field in 1958 but susceptible in the 1960 season. This was probably due to environmental influences, mainly temperature differences.

(*b*) Inheritance of resistance in Eureka to strain 103–H–2.

The results of seedling tests (Table 1) showed that Eureka was resistant to strains 103–H–2 and 111–E–2 at high temperatures whereas the resistance to certain other strains became ineffective. This suggested that the resistance to 103–H–2 might be due to a gene(s) other than Sr6 and studies were carried out to investigate this possibility.

At day temperatures of above 80°F, 78 F_2 seedlings of the cross Little Club × Eureka were tested with 103–H–2 and the results are presented in Table 5.

Little Club, used as the susceptible parent, gave evidence of some resistance to this strain and this could account in part for the variations obtained in both the intermediate and susceptible classes. Our unpublished work shows that many other varieties in addition to Little Club have genes which operate against strains like 103–H–2 which have arisen from inter-varietal crosses in *P. graminis*. From the broad classification used, however, the data suggest a single factor for high resistance in Eureka.

TABLE 5

Segregation of F_2 plants of the cross (Little Club × Eureka) when tested with strain 103–H–2 at temperatures above 80°F

Parent	Parental reaction	F_2 Segregation			P-value (1 : 2 : 1)
		Resistant ("; 2 =")	Intermediate ("2 —, 2, 3 — c")	Susceptible ("2 + +, 3")	
Little Club	"2 + +, 3 + c"	14	42	24	0·30–0·20
Eureka	"; 2 ="				

Correlated studies on F_3 lines of the cross Gabo × Eureka, using strains 126–Anz–2, 6 and 103–H–2 further indicated that Sr6 was not operative against 103–H–2 at high temperatures. The resistance of Eureka to the latter was due to a second major gene tentatively designated Sr_{E1}.

2. *Gabo W 1422, Charter W 1371 and Yalta W 1373*

The varieties Gabo, Charter and Yalta will be discussed together as the data from crosses involving these varieties show that they have common factors for resistance to certain strains.

(*a*) Intercrosses between Gabo, Charter and Yalta.

As indicated in the literature review, Gabo, Charter and Yalta were found to possess the same gene (or genes) for resistance to strain 126–Anz–6. To confirm this, F_2 and F_3 generation material of intercrosses between these three varieties was studied (Table 6) and, as expected, no susceptible segregates were found.

TABLE 6

Reaction of F_2 plants and breeding behaviour of F_3 lines of intercrosses involving Gabo, Charter and Yalta when tested with strain 126–Anz–6

Cross	F_2 Segregation		Upper limit of recombination at ·05 level
	Resistant	Susceptible	
Gabo × Yalta ..	788	—	12·65%
Gabo × Charter ..	169	—	26·62%
Charter × Yalta ..	226	—	23·16%
	F_3 Behaviour		
	Resist.	Segreg. Suscept.	
Gabo × Yalta ..	178	— —	1·72%
Charter × Gabo ..	93	— —	3·26%
Charter × Yalta ..	119	— —	2·54%

(*b*) Crosses between Gabo, Charter and Yalta and susceptible varieties

(i) Inheritance of resistance in Gabo, Charter and Yalta to strains 126–Anz–6 and 126–Anz–1, 6.

F_1 Studies

F_1 seedlings of crosses between the three resistant varieties Gabo, Charter and Yalta and susceptible varieties gave a resistant reaction type ("; 1 +") to strain 126–Anz–6, indicating that resistance is completely dominant in the F_1 generation.

F_2 and F_3 Studies

F_2 and F_3 generation material from crosses between the resistant varieties Gabo, Charter and Yalta and the susceptible varieties Eureka and Bobin W 39 were tested with strain 126–Anz–1, 6. Segregation of a single dominant factor pair for resistance in each cross was indicated (Tables 7 and 8). Likewise, F_2 segregation results of crosses between Gabo and Charter and the susceptible Federation, Insignia and Little Club suggested a single dominant factor for resistance.

Data from some F_2 families of crosses (Gabo × Morocco) and (Morocco × Yalta), however, did not fit a single factor hypothesis and in the crosses (II56.48.1.2.1 W 2691 × Gabo) and (Yalta × Federation) and reciprocal, deviations from a three to one ratio were so great that another explanation

TABLE 7

Results of tests with strain 126–*Anz*–1, 6 *on* F_2 *populations from crosses between the three resistant varieties Gabo, Charter and Yalta and susceptible varieties*

Parents	Cross No. and Family	F_2 Segregation		P-value (3 : 1)
		Resist.	Suscept.	
Gabo × Eureka ..	II56.9.2	335	113	0·95–0·90
Eureka × Gabo ..	II56.20.1	127	48	0·50–0·30
Total		462	161	0·70–0·50
Gabo × Federation ..	II58.42.5	92	32	0·90–0·80
Federation × Gabo ..	II58.32.2	126	47	0·70–0·50
Federation × Gabo ..	.6	310	101	0·90–0·80
Total		528	180	0·80–0·70
Gabo × Morocco ..	II59.345.1	208	73	0·80–0·70
Gabo × Morocco ..	.2	129	59	0·05–0·02
Gabo × Morocco ..	.3	65	15	0·20–0·10
Gabo × Morocco ..	.4	112	44	0·50–0·30
Total		514	191	0·20
Insignia × Gabo ..	II59.358.1	203	82	0·20–0·10
Insignia × Gabo ..	.2	150	50	1·00
Total		353	132	0·30–0·20
II56.48.1.2.1 × Gabo ..	II61.90.5	83	62	<0·001
II56.48.1.2.1 × Gabo ..	.11	111	49	0·20–0·10
Total		194	111	<0·001
Mona × Gabo	II59.383.1	156	50	0·90–0·80
Charter × Eureka ..	II56.40.1	89	31	0·90–0·80
Charter × Federation ..	II58.19.3	279	99	0·70–0·50
Charter × Federation ..	.4	34	12	0·90–0·80
Total		313	111	0·70–0·50
Little Club × Charter	II58.84.3	408	125	0·50–0·30
Yalta × Eureka ..	II58.40.1	59	22	0·70–0·50
Yalta × Eureka ..	.2	96	37	0·50–0·30
Eureka × Yalta ..	II56.22.6	186	61	0·95–0·90
Eureka × Yalta ..	.8	58	19	0·95
Eureka × Yalta ..	II58.419.5	126	44	0·80–0·70
Total		525	183	0·70–0·50

TABLE 7.—*Continued.*

Results of tests with strain 126-*Anz*-1, 6 *on* F_2 *populations from crosses between the three resistant varieties Gabo, Charter and Yalta and susceptible varieties*—Continued

Parents	Cross No. and Family	F_2 Segregation		P-value (3 : 1)
		Resist.	Suscept.	
Yalta × Federation ..	II58.41.2	54	9	0·05–0·02
Yalta × Federation ..	.3	115	43	0·70–0·50
Yalta × Federation ..	.4	64	20	0·80
Federation × Yalta ..	II58.33.1	26	12	0·50–0·30
Federation × Yalta ..	.2	36	3	0·02–0·01
Federation × Yalta ..	.3	54	18	1·00
Federation × Yalta ..	.5	63	10	0·05–0·02
Federation × Yalta ..	.6	42	22	0·10–0·05
Federation × Yalta ..	.7	21	6	0·80–0·70
Federation × Yalta ..	.8	47	9	0·20–0·10
Federation × Yalta ..	.9	56	26	0·20–0·10
Federation × Yalta ..	.10	118	39	0·98–0·95
Federation × Yalta ..	.11	102	18	0·02–0·01
Federation × Yalta ..	.12	71	21	0·70–0·50
Federation × Yalta ..	.13	244	62	0·10–0·05
Federation × Yalta ..	.14	87	26	0·70–0·50
Total		1,200	344	0·02–0·01
Heterogeneity (3·49 : 1) : $\chi^2 = 30·674$; d.f = 15 ; P-value = 0·01–0·001				
Morocco × Yalta ..	II59.355.2	115	36	0·80–0·70
Morocco × Yalta ..	.3	159	64	0·30–0·20
Morocco × Yalta ..	.4	236	71	0·50–0·30
Morocco × Yalta ..	.5	229	56	0·05–0·02
Morocco × Yalta ..	.6	96	38	0·50–0·30
Morocco × Yalta ..	.7	103	22	0·10–0·05
Total		938	287	0·30–0·20

had to be found. Moreover, the test for heterogeneity of the latter reciprocal cross gave a significant χ^2 value.

When Chinese Spring and Mentana were used as the susceptible parents in crosses with three resistant varieties, the F_2 ratios again did not fit a single factor hypothesis (Tables 9 and 10). While the F_2 data of crosses involving Gabo and Charter proved to be homogeneous when analysed statistically this

TABLE 8

Reaction of F_3 *lines of three crosses when tested with strain* 126–*Anz*–1, 6

Cross	F_3 Segregation				P-value (1 : 2 : 1)
	Resist.	Segreg.	Suscept.	Total	
Eureka × Yalta ..	37	79	45	161	0·70–0·50
Gabo × Eureka ..	49	103	47	199	0·90–0·80
Charter × Bobin 39	16	34	16	66	0·98–0·95
Total	102	216	108	426	0·90–0·80

was not so of reciprocal crosses of Yalta with Mentana and the χ^2 value from the cross involving Yalta with Chinese Spring also suggested heterogeneity. The F_2 ratios varied according to the F_1 plant from which they came, and apparently no maternal influences were present in the reciprocal crosses.

It has been suggested that this departure from Mendelian segregation in crosses involving Gabo, Charter and Yalta is due to differential transmission

of gametes containing the alleles for rust reaction (Luig, 1960; 1964). The data which provided the first conclusive evidence to this were obtained mainly from correlated F_3 studies of stem rust and leaf rust resistance. Mentana is resistant to strain 68–Anz–1, 2, 3 of leaf rust, *Puccinia recondita* Rob. ex Desm., and this resistance was found to be closely linked with the stem rust resistance of Gabo, Charter and Yalta. By testing F_3 lines with the two pathogens (Table 11) it was possible to establish the following: (i) a very close linkage in the repulsion phase between leaf rust and stem rust reaction, so that among

TABLE 9

Segregation of plants of F_2 populations from crosses between the three resistant varieties Gabo, Charter and Yalta and the susceptible varieties Chinese Spring and Mentana when tested with strain 126–Anz–6

Parents	Cross No. and Family	F_2 Segregation		Ratio (Res. : Sus.)	P-value (3 : 1)
		Resist.	Suscept.		
Chinese Spring × Gabo	II61.445.1	163	80	2·0 : 1	0·01–0·001
Chinese Spring × Gabo	.2	144	75	1·9 : 1	0·01–0·001
Chinese Spring × Gabo	.3	133	77	1·7 : 1	<0·001
Chinese Spring × Gabo	.4	214	116	1·8 : 1	<0·001
Total		654	348	1·9 : 1	<0·001
Chinese Spring × Yalta	II61.444.1	24	13	1·8 : 1	0·20–0·10
Chinese Spring × Yalta	.2	11	18	0·6 : 1	<0·001
Chinese Spring × Yalta	.4	26	20	1·3 : 1	0·01–0·001
Chinese Spring × Yalta	.5	47	53	0·9 : 1	<0·001
Chinese Spring × Yalta	.6	21	12	1·9 : 1	0·20–0·10
Chinese Spring × Yalta	.7	12	10	1·2 : 1	0·05–0·02
Chinese Spring × Yalta	.8	48	25	1·9 : 1	0·10–0·05
Total		189	151	1·3 : 1	<0·001
Heterogeneity: $\chi^2 = 11·885$; d.fr. = 6; P-value = 0·05–0·02					
Gabo × Mentana ..	II56.7.4	107	51	2·1 : 1	0·05–0·02
Gabo × Mentana ..	.5	83	31	2·7 : 1	0·70–0·50
Mentana × Gabo ..	II56.1.1	85	27	3·1 : 1	0·90–0·80
Mentana × Gabo ..	.2	129	60	2·2 : 1	0·05–0·02
Mentana × Gabo ..	II61.436.1	218	90	2·4 : 1	0·10–0·05
Mentana × Gabo ..	.2	194	95	2·0 : 1	0·01–0·001
Mentana × Gabo ..	.3	118	66	1·8 : 1	<0·001
Total		934	420	2·2 : 1	<0·001
Charter × Mentana ..	II56.37.1	171	80	2·1 : 1	0·02–0·01
Charter × Mentana ..	.2	260	111	2·3 : 1	0·05–0·02
Charter × Mentana ..	.7	69	35	2·0 : 1	0·05–0·02
Total		500	226	2·2 : 1	<0·001

786 F_3 lines none was homozygous resistant to both rusts; (ii) a difference in the segregation ratios according to whether Gabo, Charter or Yalta was used as the parent in crosses with Mentana.

The significance of these results in relation to differential transmission of gametes has already been reported (Luig, 1964).

(ii) Inheritance of resistance in Gabo to strain 21–Anz–2.

The gene Sr11 carried by Gabo, Charter and Yalta is not operative against 21–Anz–2. Gabo gives a "3–c, 3c" type of reaction when tested with this strain while Charter and Yalta are fully susceptible.

When F_2 and F_3 generation material of the cross (Gabo × Charter) was tested with 21–Anz–2, the results suggested that the difference in the reaction

TABLE 10

Reaction of F_2 families of cross Yalta × Mentana and reciprocal to strain 126–Anz–6

Family	F_2 Segregation		Ratio	χ^2 (3 : 1)	P-value (3 : 1)	χ^2 (1·29 : 1)	P-value (1·29 : 1)
	Resist.	Suscept.					
Yalta × Mentana II56.25							
·1	10	8	1·3 : 1	2·722	·10–·05	0·004	·95–·90
·3	25	11	2·3 : 1	0·593	·50–·30	2·516	·20–·10
·4	34	16	2·1 : 1	1·307	·30–·20	2·767	·10–·05
·5	81	43	1·9 : 1	6·194	·02–·01	4·075	·05–·02
·7	122	129	0·9 : 1	93·260	<·001	6·091	·02–·01
·8	142	109	1·3 : 1	45·452	<·001	0·006	·95–·90
·9	119	122	1·0 : 1	84·383	<·001	4·738	·05–·02
·10	129	82	1·6 : 1	21·626	<·001	1·981	·20–·10
Total	662	520	1·27 : 1			22·178*	·01–·001
Mentana × Yalta II56.4							
·1	79	98	0·8 : 1	87·053	<·001	9·858	·01–·001
·2	119	48	2·5 : 1	1·248	·30–·20	15·103	<·001
·3	160	158	1·0 : 1	103·350	<·001	4·679	·05–·02
·4	109	87	1·3 : 1	39·293	<·001	0·041	·90–·80
·5	99	47	1·1 : 1	4·027	·05–·02	7·829	·01–·001
·6	134	132	1·0 : 1	86·020	<·001	3·836	·10–·05
·7	81	47	1·7 : 1	9·375	·01–·001	2·513	·20–·10
·8	92	53	1·7 : 1	10·320	·01–·001	2·985	·10–·05
Total	873	670	1·3 : 1			46·844*	<·001
Grand Total	1,535	1,190	1·29 : 1			69·022*	<·001

* Heterogeneity χ^2 (1·29 : 1) = 69·022 ; P-value (15 d.f.) = <·001.

TABLE 11

Reaction of F_3 lines of the crosses (Gabo × Mentana), (Mentana × Charter), (Mentana × Yalta) and (Yalta × Mentana) to strains 126–Anz–6 of stem rust and 68–Anz–1, 2, 3 of leaf rust

Gabo × Mentana		Reaction to stem rust		
		Resistant	Segregating	Susceptible
Reaction to leaf rust	Resistant	—	—	62
	Segregating	—	121	3
	Susceptible	40	—	—
Mentana × Charter				
Reaction to leaf rust	Resistant	—	—	52
	Segregating	—	88	—
	Susceptible	37	1	—
Mentana × Yalta				
Reaction to leaf rust	Resistant	—	—	62
	Segregating	—	84	2
	Susceptible	24	1	1
Yalta × Mentana				
Reaction to leaf rust	Resistant	—	—	107
	Segregating	1	93	2
	Susceptible	4	1	—

types of these two varieties was due to a single factor pair possessed by Gabo (Table 12). Provisionally, this factor is designated Sr_{G1}.

(iii) Inheritance of resistance in Gabo and Charter to strains 103–H–2, 111–E–2 and A20.

As shown in Table 1, Gabo and Charter are highly resistant in the seedling stage to 103–H–2, while Yalta gives a semi-susceptible reaction. Apparently the gene Sr11 does not operate against this strain. To investigate the nature of the resistance to 103–H–2, F_2 and F_3 generation material from crosses between the three varieties was studied. F_1 seedlings of crosses of W2691 (" 3 " reaction type) × Gabo and Little Club (" 2 + + " reaction type) × Charter were resistant (" ; 1 " reaction type) thus indicating dominance of resistance.

TABLE 12

Reaction of F_2 plants and breeding behaviour of F_3 lines to strain 21–Anz–2 of cross (Gabo × Charter)

F_2 Segregation				P-value (1 : 2 : 1)
Resistant (" 3 — c, 3c ")	Intermediate (" 3c, 3 + c ")	Susceptible (" 3 + ")	Total	
29	62	21	112	0·30–0·20
F_3 Behaviour				
Resistant	Segregating	Susceptible	Total	
5	13	3	21	0·50–0·30

F_2 and F_3 Studies

From a cross (Gabo × Charter), 169 F_2 seedlings were tested with 103–H–2 but no susceptible segregates were found. Likewise, only highly resistant plants were found when 97 F_3 families of this cross were tested. The presence of the same factor pair for resistance to strain 103–H–2 in both varieties is thus suggested. If it is assumed that the genes in Gabo and Charter are non-allelic and dominant, an upper limit of recombination of 3·06% at the 0·95 level of probability could be calculated according to the formula $0{\cdot}05 = \left(1 - p - \frac{p^2}{4}\right)^n$ where p is the recombination value and n the number of F_3 lines tested.

When F_2 populations from a cross Gabo × Yalta were tested with 103–H–2 a single factor difference was obtained. 104 F_2 seedlings gave a reaction as high as that of Yalta or were fully susceptible, while the remaining 306 plants resembled the resistant parent (Table 13).

TABLE 13

Reaction to strain 103–H–2 of F_2 seedlings of the crosses (Gabo × Yalta) and (Charter × Yalta)

Parents or Cross	Parental reaction	F_2 Segregation				Probability (3 Res. : 1 Sus.)
		Resistant		Susceptible		
		" ; 1 = "	" 1 + "	" X +, 3c "	" 3 "	
Gabo ..	" ; 1 = "					
Yalta ..	" 3c "					
II56.10 ..		287	19	80	24	·90–·80
Charter ..	" ; 1 = "					
Yalta ..	" 3c "					
II56.41.7 ..		124	18	30	9	·30–·20

F_2 plants were tagged according to their reaction type and grown to maturity. Subsequently their breeding behaviour to 103–H–2 was studied (Table 14).

The correlated results indicated that a single major factor pair was responsible for the resistance in Gabo. Variations in reaction type in the resistant and susceptible group are probably due to the action of a minor gene (or genes) in Yalta and/or Gabo.

Further evidence for a single dominant factor for resistance to strain 103–H–2 was obtained from F_2 studies of cross Charter × Yalta (Table 13). Studies using monosomic lines of Chinese Spring indicate that this single factor in Gabo and Charter is located on chromosome XVII (Baker and Luig, unpublished ; McIntosh, unpublished).

TABLE 14

F_3 Breeding behaviour of F_2 plants from cross II56.10.3 *(Gabo × Yalta) representing different reaction types, when tested with strain* 103–*H*–2

		F_3 Behaviour			
		Resistant	Segregating	Susceptible	Total
Reaction types in F_2	" ; 1 — "	43	92	—	135
	" 1 + + "	—	2	6	8
	" X +, 3c "	—	1	38	39
	" 3 "	—	—	8	8
	Total	43	95	52	190
χ^2 for a 1 : 2 : 1 ratio = 0·852		P-value = 0·70–0·50			

Studies were also carried out with 111–E–2 and A20 on F_3 generation material of the crosses (Charter × Gabo) and (Gabo × Yalta). Charter and Gabo are fully resistant to these strains, while Yalta at temperatures above 75°F gives a " 3–n " reaction with 111–E–2 and a " 3 " reaction with A20. No susceptible segregates were obtained from 97 F_3 lines of the cross (Charter × Gabo) when tested with the two strains, and this suggested that Charter and Gabo have genes for resistance in common, as was found when testing the same lines with 103–H–2. When 42 F_3 lines of the cross II56.10.3 (Gabo × Yalta) previously tested with 103–H–2 were inoculated with 111–E–2 and with A20 it was evident that the same dominant factor in Gabo was operative against 103–H–2 and against 111–E–2, and that the high resistance to A20 was due to a different single factor. Tentatively these two factors have been designated Sr_{G3} and Sr_{G2}, respectively.

3. *Kenya* 117*A* *W* 1347

F_1 Studies

The F_1 seedlings from crosses between Kenya 117A and susceptible Federation and reciprocal were inoculated with six strains of stem rust and the results are shown in Table 15. The reaction types varied from a " 3 = c " to a " 3 + c " according to the strain used and indicated incomplete dominance of resistance.

F_2 Studies

When F_2 populations of crosses between Kenya 117A and susceptible varieties were tested with strains 126–Anz–6, 126–Anz–2, 6, 21–Anz–2, 222–Anz–1, 2, 4, 6 and NR–7, varying segregation patterns were obtained. It was evident that the resistance of Kenya 117A was conditioned by more than one factor. As tests were not all carried out under similar environmental

conditions it was not possible to make accurate comparisons between segregation ratios obtained with different strains, but there seemed to be fewer susceptible segregates when testing with strains 21–Anz–2 and NR–7.

F_3 Studies

(i) Inheritance of resistance in Kenya 117A in a cross with susceptible Yalta.

Of cross II56.35.2 (Kenya 117A × Yalta) 202 seedlings were transplanted into the field and seed was harvested from 181 plants. When the resulting 181 F_3 families were tested with strain 21–Anz–2, 176 were either resistant or segregated with resistant and susceptible plants and five were susceptible. A ratio of 63 : 1 is proposed (P-value = 0·20–0·10) on the basis of segregation of three independent factor pairs. The detailed results of testing these lines, together with the proposed genotypes, are outlined in Table 16. In two of the eight classes the numbers obtained did not conform to the expected ratio.

TABLE 15

Reaction of F_1 seedlings of crosses between Kenya 117A and the susceptible varieties Yalta and Federation when tested with strains 21–Anz–2, 126–Anz–6, 126–Anz–2, 6, 222–Anz–1, 2, 4, 6 and NR–7

Parents or Cross	Strain used	Reaction of parents and of F_1 plants				
		21–2	126–6	126–2, 6	222–1, 2, 4, 6	NR–7
Kenya 117A		2 =	2 = n	2 = n	2 =	2 −
Federation		3 +	3 +	3 +	3	3 +
Yalta		3 +	—	—	—	—
Kenya 117A × Federation		3 =	3 c	—	3 = c	—
Federation × Kenya 117A		3 — c	—	3 c	—	3 c
Yalta × Kenya 117A		3 — c	—	—	—	—

There were approximately 20 lines in excess in one class (" Segregating Resistant and Susceptible ") and about the same number was lacking in the other class (" Segregating Resistant, Intermediate and Moderately Susceptible "). This is probably due to plants homozygous for the third factor being classified as susceptible.

The inheritance of resistance of Kenya 117A was also studied by testing the same F_3 families of cross II56.35.2 with strain 126–Anz–2, 6 (Table 16). Results were in most cases similar to those observed when testing with 21–Anz–2. This similarity in behaviour is thought to be due mainly to the segregation of Sr9b, a gene which confers resistance to both strains. The other two factors postulated to be effective against 21–Anz–2, seemed to confer a moderate resistance to 126–Anz–2, 6. One of these factors, presumably Sr10 (Green *et al.*, 1960), gave a " 3 — c, 3c " reaction type when homozygous, while the other factor, presumably Sr7 (Green *et al.*, 1960), produced a " 3 + c " reaction type. It is probable that in some instances the moderate susceptibility of lines carrying Sr7 only was mistaken for full susceptibility, and this would explain the discrepancy of observed and expected numbers in some segregation classes. Additive effects of Sr7 and Sr10 in combination with each other and with Sr9b were also in evidence.

Kenya 117A has noticeably more resistance to 222–Anz–1, 2, 4, 6 than to strains 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–2, 6 and NR–7. But comparatively more susceptible or semi-susceptible F_2 plants and F_3 lines were found when crosses of Kenya 117A with two susceptible varieties were tested with 222–Anz–1, 2, 4, 6. Tests on 128 F_3 families from a cross of Kenya 117A with Yalta (" 3 " reaction type) showed that Kenya 117A carries one gene conferring a high degree of resistance, and a second minor gene conditioning a moderately susceptible reaction (" 3c ") to 222–Anz–1, 2, 4, 6 (Table 16).

Correlated F_3 data indicated that the major gene was the same (Sr9b) as that which gave protection against 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–2, 6 and NR–7, but it was evident that against 222–Anz–1, 2, 4, 6 the gene conferred a much higher degree of resistance. Sr9b conditioned a type " ; 2 = " reaction to 222–Anz–1, 2, 4, 6 when homozygous and a type " 2 — " reaction when heterozygous. With the other five strains Sr9b was incompletely dominant.

The minor gene in Kenya 117A for resistance to 222–Anz–1, 2, 4, 6 is probably Sr10. This gene was also operative against 126–Anz–2, 6 and gave a semi-resistant " 3 — cn " reaction to 21–Anz–2. The third gene reported in Kenya 117A, Sr7, apparently does not condition a reaction on its own to 222–Anz–1, 2, 4, 6 which could be easily distinguished from the reaction type of Yalta ; it might, however, act as a modifier in combination with Sr9b or Sr10.

Finally, F_3 families of the cross II56.35.2 of which sufficient seed was at hand were tested with NR–7. This strain originated as a somatic hybrid from two North American strains and one of the objectives for using it was to confirm the previous assumption (Green *et al.*, 1960) that the three factors which condition reaction types in segregating material of cross (Kenya 117A × Yalta) are identical with the three genes Sr7, Sr9b and Sr10. Only 68 F_3 families were tested with NR–7, but it was evident from the results that the three factors which conditioned reaction to the other three strains were also operative against NR–7.

In an attempt to isolate F_3 lines which carry only one of the three factors for resistance in Kenya 117A, seedling tests with the above-mentioned four strains were simultaneously carried out on selected lines of cross II56.35.2 at temperatures ranging from 60° to 70°F. Three lines were found which were homozygous for each of the three genes, and one line which apparently carried both Sr7 and Sr10. The reaction types produced by these lines together with those of their parents, Yalta and Kenya 117A, are shown below :

Proposed genotype	Line or variety	Strain used				
		21–2	126–2, 6	222–1, 2, 4, 6	NR–7	21–2, 3*
Sr7	246	3 c	3 + c	3 + c	3 + c	
Sr9b	256	2 —	2 — c	; 2 =	2 +	3 +
Sr10	244	3 — cn	3 — c	3 c	3 — c	
Sr7, Sr10	2,121	3 = cn	3 = c	3 — c	3 = c	
—	Yalta	3 +	3 +	3 + c	3 +	3 +
Sr7, Sr9b, Sr10	Kenya 117A	2 — n	2 = n	; 2 =	2 —	3 = c

* This strain was obtained from the 1960 Cereal Rust Survey. It is virulent on the isogenic Marquis-line W2402 (obtained from Dr. D. R. Knott) and on the variety Festival, both of which carry Sr9b.

(ii) Inheritance of resistance in Kenya 117A in a cross with susceptible Mentana.

The mode of inheritance of resistance in Kenya 117A to the Australian field strain 126–Anz–6, which has been used extensively in inheritance studies by other workers, was also studied. Yalta, used as the susceptible parent in the cross II56.35.2, is resistant to 126–Anz–6 and therefore the resistance of Kenya 117A to 126–Anz–6 could not be studied in this cross. Cross II56.5.3 (Mentana × Kenya 117A) was used instead as Mentana is susceptible to 126–Anz–6 as well as to 126–Anz–2, 6, 21–Anz–2, 6 and 222–Anz–1, 2, 4, 6. Mentana gives only a semi-resistant " 2 " type of reaction to 21–Anz–0 and 21–Anz–2.

When 126 F_3 lines of cross II56.5.3 were inoculated with 126–Anz–6, the results indicated segregation of two independent and incompletely dominant

TABLE 16

Distribution of F_3 lines of the cross II56.35.2 (Yalta × Kenya 117A) for reaction to strains 21–Anz–2, 126–Anz–2, 6 and 222–Anz–1, 2, 4, 6, and proposed genotypes for the segregation classes

Strain	F_3 Rust behaviour and proposed genotypes								Total
	R	Seg. R, I & MS	I	Seg. I & MS	MS	Seg. R & S	Seg. I, MS & S	S	
21–Anz–2	44	21	6	7	5	74	19	5	181
(Expected numbers)	(45·3)	(39·6)	(5·7)	(11·3)	(2·8)	(50·9)	(22·6)	(2·8)	
126–Anz–2, 6	34	12	6	2	4	54	15	4	131
(Expected numbers)	(32·8)	(28·7)	(4·1)	(8·2)	(2·0)	(36·8)	(16·4)	(2·0)	
Proposed genotypes and fraction of total	AABBCC AABBCc AABBcc AABbCC AABbCc AABbcc AAbbCC AAbbCc AAbbcc	AaBBCC AaBBCc AaBBcc AaBbCC AabbCC	aaBBCC aaBBcc	aaBBCc aaBbCC	aabbCC	AaBbCc AaBbcc AabbCc Aabbcc	AaBbCc aaBbcc aabbCc	aabbcc	
	16/64	14/64	2/64	4/64	1/64	18/64	8/64	1/64	

Strain	F_3 Rust behaviour and proposed genotypes						Total
	R	Seg. R & MS	MS	Seg. R & S	Seg. MS & S	S	
222–Anz–1, 2, 4, 6	30	12	9	54	15	8	128
(Expected numbers)	(32)	(16)	(8)	(48)	(16)	(8)	
Proposed genotypes and fraction of total	AABB AABb AAbb	AaBB	aaBB	AaBb Aabb	aaBb	aabb	
	4/16	2/16	1/16	6/16	2/16	1/16	

Explanation of abbreviations: R —resistant; I —intermediate; MS —moderately susceptible; S —susceptible; Seg.—segregating.

Proposed genes: A—Sr9b; B—Sr10; C—Sr7.

factor pairs (Table 17). The two factors, however, were not equal in the degree of resistance they conferred on the F_3 plants. The major factor, which is later shown to be Sr9b, imparted a high resistance (type "2 —" reaction) when homozygous, while the minor factor conditioned a reaction type ranging only from "3 — n" to "3c". This variation in reaction type of F_3 lines thought to possess the minor gene in the homozygous state could be due to the action of a modifying factor, and/or environmental influences.

Strains 126–Anz–2, 6 and 21–Anz–2, 6 were also used to inoculate these F_3 families. The inheritance of resistance in Kenya 117A to the former in

TABLE 17

Distribution of F_3 lines of cross II56.5.3 (Mentana × Kenya 117A) for reaction to strain 126–Anz–6, and proposed genotypes for the segregation classes

	Behaviour of F_3 lines and their proposed genotypes							
	Segreg. "2—n", "2—"	"2—"	Segreg. "2—n", "3—c"	"3—c"	Segreg. "2—n", "3+"	Segreg. "3—c", "3+"	"3+"	Total
Actual numbers	25	11	15	3	44	20	8	128
Expected numbers	24	8	16	8	48	16	8	128
Proposed genotypes	AABB AABb	AAbb	AaBB	aaBB	AaBb Aabb	aaBb	aabb	

χ^2 for a 3 : 1 : 2 : 1 : 6 : 2 : 1 ratio = 5·688 P-value (6 d.fr.) = 0·50–0·30

cross II56.35.2 has been reported above and Green *et al.* (1960) have shown a close similarity in the reaction types produced by strains 126–Anz–6 and 126–Anz–2, 6 on isogenic Marquis lines carrying genes Sr7, Sr9b or Sr10. As expected, lines tested with 126–Anz–6 and 126–Anz–2, 6 gave the same reactions to each strain, suggesting that the major factor for resistance to 126–Anz–6 was Sr9b, while the minor factor was presumably Sr10. Mentana itself gives a " 3 " type reaction to these two strains and it is possible that F_3 lines carrying only Sr7 were not significantly more resistant than Mentana.

When the reaction types on F_3 lines to strains 126–Anz–6 and 21–Anz–2, 6 were compared two at a time it was evident that several lines carried more resistance to the latter strain than to the former. This was not unexpected, as 21–Anz–2, 6 probably originated from 21–Anz–2 and thus would be similarly constituted in regard to most genes for pathogenicity. When studying cross II56.35.2 it was found that the factor Sr7 conferred a higher resistance to 21–Anz–2 than to 126–Anz–2, 6. Therefore the presence of Sr7 presumably accounted for the higher resistance of some F_3 lines to 21–Anz–2, 6 than to 126–Anz–6.

Field Studies

During the years 1958–1960 segregating material of the two above-mentioned crosses and of other crosses involving Kenya 117A was studied under field conditions at Castle Hill Research Station, strain 21–Anz–2 contributing most of the inoculum. Classification of adult plants was made on the basis of percentage of rust and size of pustules. Plants with less than 30% infection of stem and with pustules small to medium in size were classified as resistant, and plants showing mainly large confluent pustules and/or carrying more than 30% infection were classified as susceptible.

The mature plant reactions of 181 F_2 plants of cross II56.35.2 (Yalta × Kenya 117A) were recorded and the behaviour in the field of the progenies of these plants was studied in the F_3 and F_4 generations. Kenya 117A was resistant in the field, showing only small pustules on stems less than 10% infected, while Yalta was extremely susceptible (summer sowings of Kenya 117A, however, showed a much higher degree of infection). Nine F_2 plants of the cross II56.35.2 susceptible in the seedling stage to 21–Anz–2 were susceptible as adult plants. However, 94 of 172 resistant F_2 seedlings were also susceptible in the adult plant stage and the remainder were resistant.

The results of the F_3 field tests were compared for each line with F_3 seedlings tests with 21–Anz–2 and it was evident that many F_3 lines resistant or segregating to 21–Anz–2 as seedlings were susceptible as adult plants. These findings can be explained by the incomplete dominance of gene Sr9b and by assuming that the other two genes, Sr7 and Sr10, become ineffective in the adult plant. There was, however, evidence which suggested that these latter genes acted as modifiers in combination with Sr9b. The above results would indicate that selection for resistance of Kenya 117A to 21–Anz–2 in the F_2 generation is of only limited value in breeding procedures.

When seedling reactions of F_3 lines to 126–Anz–2, 6 and NR–7 were compared with the behaviour of these lines under field conditions, the same lack of correlation as in the case of 21–Anz–2 was found. This was expected, as many lines reacted similarly to the three strains.

There was, however, good correlation between seedling reaction to 222–Anz–1, 2, 4, 6 of F_3 lines and their behaviour to stem rust in the field. The comparative data are shown in Table 18. In classifying seedling reaction only the major factor for resistance (Sr9b) was considered and it can be seen that all except two of the 32 families classified as susceptible to 222–Anz–1, 2, 4, 6 in the seedling stage were also susceptible in the field to a combination of strains consisting mainly of 21–Anz–2. The two families which were classified

as segregating in the field probably comprised susceptible plants and plants which had escaped infection to a large degree. These results indicate that no gene (or genes) of Kenya 117A other than Sr9b can confer field resistance to 21–Anz–2. Of the 30 F_3 lines which in seedling tests appeared to be homozygous for Sr9b, 25 lines were found to be resistant in the field, a further indication that Sr9b is the main factor for field resistance in Kenya 117A. However, 21 out of 66 families, apparently heterozygous for this gene, were classified as susceptible in the field. It is possible that resistant adult plants were present in the 21 lines, but were not classified as such.

TABLE 18

Distribution of F_3 lines of the cross Yalta × Kenya 117A for reaction to a collection of strains in the field, being mainly 21–Anz–2, and for seedling reaction to 222–Anz–1, 2, 4, 6

Seedling reaction to 222–Anz–1, 2, 4, 6		Behaviour in the field		
		Resistant	Segregating	Susceptible
Resistant	30	25	3	2
Segregating	66	4	41	21
Susceptible	32	—	2	30
Total	128	29	46	53

In 1958, F_2 plants of cross II56.5.3 (Mentana × Kenya 117A) were also studied for their reaction in the field. Mentana was moderately susceptible in the field, showing approximately 40 to 60% infection on stems with pustules of medium size. Of the 122 F_2 plants, 21 were found to be resistant and 101 were classified as susceptible. In some cases, however, difficulties were experienced in making the classification. As mentioned before, the progenies of these F_2 plants were tested in the seedling stage with strains 126–Anz–6, 126–Anz–2, 6 and 21–Anz–2, 6, and when the results of the seedling tests were compared for each F_3 line with the mature plant reaction of the corresponding F_2 plant, it was evident that the same, single, major factor for resistance was operating in the seedling and adult plant stage (Table 19). Of the 21 resistant F_2 plants all, except one, carried the gene Sr9b either in the homozygous or heterozygous condition. Thus the findings on the nature of mature plant resistance in Kenya 117A in this cross are in agreement with those for cross II56.35.2

TABLE 19

Reaction in the field of F_2 plants of the cross Mentana × Kenya 117A and seedling reaction of F_3 lines raised from these plants when tested to strains 126–Anz–6, 126–Anz–2, 6 and 21–Anz–2, 6

Behaviour of F_3 lines	Proposed genotype* of F_2 plant	No. of F_3 lines	Field reaction of F_2 plant	
			Resistant	Susceptible
All 2—n, 2—c, 2—	AABB AABb	25	9	16
All 2—	AAbb	11	3	8
Segregating 2—n, 2—, 3—c, 3c	AaBB	15	3	12
Segregating 2—, 3=c, 3+ ..	AaBb Aabb	44	5	39
All 3—c, 3c	aaBB	3	—	3
Segregating 3—c, 3+	aaBb	16	—	16
All 3+	aabb	8	1	7
Total		122	21	101

* A = Sr9b ; B = Sr10

In 1960, 91 F_2 plants of cross II58.73.3 (Kenya 117A × Federation) were studied for their behaviour to stem rust in the field. Of these plants 25 were resistant or semi-resistant, the remaining 66 were semi-susceptible or susceptible. A ratio of one resistant to three susceptible is indicated (P-value = 0·70–0·50), and this is further evidence for a single major factor for adult plant resistance in Kenya 117A. The semi-resistant and semi-susceptible plants carried approximately 20 to 30 and 40 to 60% infection, respectively, and this variation could be due to the action of the modifying genes Sr7 and Sr10 in combination with Sr9b in the heterozygous condition.

4. *Mentana W* 1124

(i) Inheritance of the resistance in Mentana to strain 21–Anz–2 of stem rust.

F_1 Studies

When tested with strain 21–Anz–2 Mentana gave a semi-resistant "; 2, 3 — c" reaction type. F_1 seedlings from crosses of Mentana with susceptible varieties gave a type "3 — c, 3c" reaction with this strain thus indicating incomplete dominance of resistance.

F_2 and F_3 Studies

The segregation of reaction in F_2 plants to strain 21–Anz–2 in crosses of Mentana with Yalta and Federation are given in Table 20. A single, incompletely dominant factor pair for resistance in Mentana is indicated, as the data fit a ratio of one resistant : two intermediate : one susceptible. The resistant F_2 seedlings gave a type "; 2, 3 — c" reaction similar to that of Mentana, the intermediate exhibited a "3c" reaction type, and the susceptible were as susceptible as Yalta or Federation.

TABLE 20

F_2 segregation to strain 21–Anz–2 of crosses involving Mentana and susceptible varieties

Susceptible parent	Cross No. and family	F_2 Segregation			P-value (3 : 1) (R + I : S)	P-value (1 : 2 : 1)
		Resist.	Inter.	Suscept.		
Yalta	II56.4.1	19	41	22	0·70	0·90–0·80
Federation	II58.86.1	65	112	52	0·50–0·30	0·50–0·30
Federation	II58.86.2	68	133	61	0·70–0·50	0·90–0·80
Total		152	286	135	0·50–0·30	0·70–0·50

Two crosses between Mentana and susceptible varieties were studied in the F_3 generation for their reaction to 21–Anz–2 (Table 21). The data fit a 1 : 2 : 1 ratio and thus provide further evidence for monofactorial segregation in crosses between Mentana and susceptible varieties. Recent work has indicated that this factor is the same as Sr8 (Watson and Luig, 1963).

TABLE 21

Segregation of F_3 lines of crosses between Mentana and susceptible Federation and Yalta for reaction to strain 21–Anz–2

Cross	F_3 Segregation				P-value (1 : 2 : 1)
	Resistant	Segregating	Susceptible	Total	
Federation × Mentana	12	12	8	32	0·30–0·20
Yalta × Mentana	14	31	11	56	0·70–0·50
Total	26	43	19	88	0·70–0·50

(ii) Inheritance of resistance in Mentana to strain NR–7.

F_1 Studies

Mentana is fully resistant to this strain and shows a " ; " reaction type. Yalta is susceptible and Federation and Chinese Spring moderately susceptible (" 3 + cn " and " 3 " type reactions respectively). F_1 seedlings of crosses between Mentana and the latter three varieties when tested with NR–7 gave " X, 3 — c " reaction types, thus indicating that resistance was incompletely dominant.

F_2 and F_3 Studies

The F_2 and F_3 data from a cross between Yalta and Mentana are set out in Table 22, and they can be best explained on the basis of two independent, incompletely dominant factors for resistance present in Mentana. A high correlation between F_2 and F_3 reaction was obtained in spite of the incomplete dominance of resistance indicated by F_1 tests. Eight distinct F_3 behaviour patterns were observed and genotypes were assigned to them by assuming that Mentana possesses two factor pairs for resistance. One factor pair conditions an " X = " reaction in the homozygous and an " X + " reaction in the heterozygous state, while the second produces a moderately resistant reaction of a " 2, 3 — c " type in the homozygous and a semi-susceptible " 3c " reaction type in the heterozygous state. The statistical analysis shows close agreement between the observed numbers of plants and those expected on this hypothesis.

TABLE 22

Correlated data showing reaction to strain NR–7 of F_2 plants of the cross Yalta (susceptible) × Mentana (resistant) and of F_3 lines raised from the F_2 plants

Reaction in F_2	Number of F_2 plants	Behaviour and reaction in F_3								Number of F_3 lines
		" ;1= "	Segreg. " ;1= " and " X = "	" X= "	Segreg. " ;1= ", " X= " & " 3–c "	Segreg. " ;1= " and " 3+ "	" 2, 3–c "	Segreg. " 2 " and " 3+ "	" 3+ "	
" 0 "	3	—	—	—	—	—	—	1	—	1
" ;1= "	9	7	—	1	1	—	—	—	—	9
" ;1 "	22	1	14	2	1	2	1	—	—	21
" X "	51	—	4	2	8	25	3	7	—	49
" 3c "	24	—	—	—	1	12	—	6	4	23
" 3+ "	11	—	—	—	—	5	—	2	2	9
Total	120	8	18	5	11	44	4	16	6	112
Suggested genotype		CCDD	CCDd	CCdd	CcDD	CcDd Ccdd	ccDD	ccDd	ccdd	
Expected number of F^3 lines		7	14	7	14	42	7	14	7	112

$\chi^2 = 4{\cdot}336$ P-value (7 d.fr.) = 0·80–0·70

Further evidence for two factor pairs for resistance to NR–7 in Mentana was obtained in a cross with susceptible Charter (Table 23). The F_2 and F_3 segregations of this cross followed very closely those observed in the cross where Yalta was the susceptible parent, and again a non-significant χ^2-value for the eight segregation classes was obtained.

In order to obtain lines which carry only one of the two postulated major genes for resistance to NR–7, two lines from the cross (Yalta × Mentana) were selected : " 1841 " apparently homozygous for a factor pair giving a " 3 — c " reaction, and " 1843 " which appeared to carry a factor pair conditioning a " X = " reaction. A cross was made between these two lines and each line was also crossed with the moderately susceptible Federation.

The F_1 plants of these crosses when tested with NR–7 gave a reaction similar to that of F_1 plants from crosses between Mentana and susceptible varieties. In the following year F_2 populations from these crosses were tested

TABLE 23

Correlated data showing reaction to strain NR–7, of F_2 plants of the cross Charter (susceptible) × Mentana (resistant) and of F_3 lines raised from the F_2 plants

Reaction in F_2	Number of F_2 plants	Behaviour and reaction in F_3								Number of F_3 lines
		"; 1 ="	Segreg. "; " to "X ="	"X ="	Segreg. "; " to "3–c"	Segreg. "; " to "3+"	"2", "3–c"	Segreg. "2" to "3+"	"3+"	
"; 1 ="	30	12	14	2	2	—	—	—	—	30
"1+"	36	—	7	2	17	7	1	2	—	36
"X"	81	—	2	2	6	45	6	10	—	71
"3c"	6	—	—	—	—	1	—	1	4	6
"3"	7	—	—	—	—	1	—	—	4	5
Total	160	12	23	6	25	54	7	13	8	148
Suggested genotype		CCDD	CCDd	CCdd	CcDD	CcDd Ccdd	ccDD	ccDd	ccdd	
Expected number of F_3 lines		9·25	18·5	9·25	18·5	55·5	9·25	18·5	9·25	148

$\chi^2 = 7{\cdot}731$ P-value (7 d.fr.) = 0·50–0·30

with NR–7 and 21–Anz–2 (Table 24). A single factor segregation was indicated in cross ("1841" × Federation) with both strains. F_2 seedlings of cross ("1843" × Federation) segregated in a ratio of approximately three resistant to one susceptible when tested with NR–7, but were all susceptible to strain 21–Anz–2. F_2 tests with strain NR–7 on cross ("1843" × "1841") gave a similar segregation pattern to that obtained previously in F_2 populations from crosses between Mentana and susceptible varieties. These findings suggest that lines "1841" and "1843" together possess the full resistance of Mentana to NR–7 and that each line carries a single factor pair for resistance to it. "1841" carries the factor pair Sr8 which also gives protection from 21–Anz–2 in the seedling stage, and "1843" possesses the factor pair which confers the higher type of resistance to NR–7 ("; 1 + 3 — n" reaction) but no resistance to 21–Anz–2. This factor is tentatively designated Sr_{M1}.

TABLE 24

Reactions of F_2 seedlings of crosses involving the two resistant lines "1841" and "1843" when tested with strains 21–Anz–2 and NR–7

Parents	Strain used	F_2 Segregation and reaction									Ratio	P-value
		;	$;2^{-n}$	$;2^{-}$	X, 3^{-n}	2^{+cn}	3–c, X+	3–c, 3^{c}	3^{c}, 3+c	3, 3+		
1843 × Federation	21–Anz–2	—	—	—	—	—	—	—	—	69	—	—
1843 × Federation	NR–7	—	—	—	16	—	38	—	—	27	1 : 2 : 1	0·20–0·10
1841 × Federation	21–Anz–2	—	—	—	—	—	—	47	69	40	1 : 2 : 1	0·30–0·20
1841 × Federation	NR–7	—	—	—	—	—	—	56	91	54	1 : 2 : 1	0·50–0·30
1843 × 1841	NR–7	6	18	20	9	25	23	13	15	10	15 : 1	0·70–0·50
Proposed genotype of F_2 plant		CCDD	CCDd	CcDD	CCdd	CcDd	Ccdd	ccDD	ccDd	ccdd		

B. The linkage relationship of genes controlling reaction to stem rust

As indicated in the foregoing, several factors for resistance to stem rust were found in the six varieties under study. The possibility of linkage between these factors was considered and the appropriate tests were carried out. Results from F_2 and F_3 generation material of crosses between Eureka and the varieties Gabo, Yalta and Charter are shown in Tables 25 and 26. Eureka carries a single gene for resistance (Sr6) to strain 126–Anz–6 on chromosome XX (2D) and Gabo, Yalta and Charter all carry the gene Sr11 for resistance to strain 126–Anz–6 on chromosome X (6B). In certain instances Sr11 is differentially transmitted, but this was not the case in crosses with Eureka. The statistical analysis showed that the data agreed with the hypothesis of two dominant independent factors (Tables 25 and 26).

TABLE 25

Segregation in F_2 populations of crosses between resistant varieties

Cross	Strain used	F_2 Segregation		Expected ratio	P-value
		Resistant	Susceptible		
Gabo × Eureka	126–Anz–6	135	6	15 : 1	0·50–0·30
Eureka × Yalta	126–Anz–6	215	14	15 : 1	0·95–0·90
Charter × Eureka . .	126–Anz–6	469	30	15 : 1	0·90–0·80
Kenya 117A × Eureka	21–Anz–2	304	2	255 : 1	0·80–0·70
Gabo × Eureka	103–H–2*	244	13	15 : 1	0·50–0·30

* The testing was conducted at temperatures above 80°F.

No evidence of linkage was found between the gene Sr6 in Eureka and the genes for resistance to 21–Anz–2 in Kenya 117A (Table 25). It has been postulated that three factors operate in Kenya 117A against 21–Anz–2, of which two, Sr7 and Sr9b, have been located by previous workers on chromosomes VIII (4B) and XIII (2A) respectively.

The close linkage of Sr11 with a factor for leaf rust resistance in Mentana was discussed earlier. In Table 26 it is shown that Sr11 in Yalta and the factor for resistance to strain 103–H–2 in Eureka, tentatively designated Sr_{E1}, were inherited independently of each other. No linkage was found between Sr_{E1} and the factor for resistance (Sr_{G2}) to 103–H–2 in Gabo (Table 25).

TABLE 26

Reaction of F_3 lines of the crosses (Eureka × Yalta) and (Gabo × Eureka) when tested with strains 126–Anz–1, 6 and 126–Anz–2, 6 and of the cross (Eureka × Yalta) when tested with strains 126–Anz–1, 6 and 103–H–2

Eureka × Yalta		Reaction to 126–Anz–1, 6				χ^2	P-value (4 d.fr.)
		Resist.	Segreg.	Suscept.	Total		
Reaction to 126–Anz–2, 6	Resistant	10	20	9	39		
	Segregating	19	32	24	75		
	Susceptible	8	27	12	47		
	Total	37	79	45	161	2·597	0·70–0·50

Gabo × Eureka		Reaction to 126–Anz–1, 6				χ^2	P-value (4 d.fr.)
		Resist.	Segreg.	Suscept.	Total		
Reaction to 126–Anz–2, 6	Resistant	10	25	10	45		
	Segregating	25	55	26	106		
	Susceptible	14	23	11	48		
	Total	49	103	47	199	0·903	0·95–0·90

Eureka × Yalta		Reaction to 103–H–2*				χ^2	P-value (4 d.fr.)
		Resist.	Segreg.	Suscept.	Total		
Reaction to 126–Anz–1, 6	Resistant	2	2	1	5		
	Segregating	5	4	4	13		
	Susceptible	3	9	3	15		
	Total	10	15	8	33	2·689	0·70–0·50

* The testing was conducted at temperatures above 80°F.

The two independent factors for resistance to NR–7 in Mentana, Sr8 and Sr_{M1}, did not show any linkage with Sr11 in the cross (Yalta × Mentana).

The three genes for stem rust resistance in Kenya 117A appeared also to be inherited independently of the following genes: Sr11 and Sr_{G2} in the crosses (Gabo × Kenya 117A) and (Kenya 117A × Gabo); and Sr8 in the cross (Kenya 117A × Mentana).

A study was also made of the segregation of two morphological characters, brown chaff colour and glume pubescence, in relation to stem rust reaction.

TABLE 27

Probable genotypes of six varieties of wheat regarding genes for resistance to stem rust

Variety	Genotype										
Eureka	Sr6										Sr_{E1}
Gabo						Sr11	Sr_{G1}	Sr_{G2}	Sr_{G3}		
Charter						Sr11		Sr_{G2}	Sr_{G3}		
Yalta						Sr11					
Kenya 117A		Sr7		Sr9b	Sr10						
Mentana			Sr8							Sr_{M1}	

The single factor for pubescent glume in Yalta was inherited independently of the following genes for stem rust resistance: Sr6, Sr8, Sr9b, Sr11, Sr_{G2} and Sr_{M1}. The factor for pubescent glume has been located on chromosome XIV (1A) (Sears, 1953).

The single factor for brown chaff in Eureka was inherited independently of Sr11 and of Sr6. Unrau (1950) has located a single gene for brown chaff colour on chromosome I (1B).

The following Tables 27 and 28 summarize the results of these studies as to the genetic constitution of the six varieties and as to the nature of the resistance conferred by the different genes.

TABLE 28

Nature of resistance conferred by eleven genes possessed by six wheat varieties

Gene	Dom. or Rec.*	Possessed by Variety	Controls resistance to strain**
Sr6***	D	Eureka	21–Anz–0, 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, NR–7, 103–H–2, 111–E–2
Sr_{E1}	d	Eureka	103–H–2
Sr11	D	Gabo Charter Yalta	21–Anz–0, 126–Anz–6, 126–Anz–1, 6
Sr_{G1}	r	Gabo	21–Anz–0, 21–Anz–2, 126–Anz–6
Sr_{G2}	D	Gabo Charter	103–H–2 and 111–E–2
Sr_{G3}	D	Gabo Charter	A20
Sr7	d	Kenya 117A	21–Anz–0, 21–Anz–2, 21–Anz–2, 6
Sr9b	d	Kenya 117A	21–Anz–0, 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6, NR–7, 222–Anz–1, 2, 4, 6
Sr10	d	Kenya 117A	21–Anz–0, 21–Anz–2, 21–Anz–2, 6, 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6, NR–7
Sr8	r	Mentana	21–Anz–0, 21–Anz–2, NR–7
Sr_{M1}	r	Mentana	NR–7

* D = dominant; d = incompletely dominant; r = recessive.
** Includes only the eleven strains listed in Table 1.
*** Temperature-sensitive.

Discussion

The results of the studies on the nature of resistance to stem rust in six wheat varieties reported herein show that single independent factors were operating to individual strains. In certain cases the segregation ratios were distorted by a differential transmission rate for the gametes carrying genes located on chromosome X (6B). The segregation ratios were also altered by genes which had a cumulative effect in modifying the dominant or recessive condition and by temperature effects changing the expression of the factors for resistance.

The latter was the case with the gene Sr6 of Eureka, which becomes ineffective at temperatures above 80°F. Hence when Eureka is crossed with susceptible varieties and the progenies are studied at low temperatures (60° to 65°F) an F_2 ratio of three resistant to one susceptible is obtained with strains 21–Anz–2, 126–Anz–6 and NR–7. At higher temperatures of 65° to 70°F the heterozygous class can be distinguished from the resistant class when testing with 21–Anz–2. The intermediate, heterozygous F_2 seedlings still give a necrotic reaction, but the type "; 1 =" reaction has changed into a type "1 + +, 3 — n" reaction. A similar segregation pattern is obtained with strains 126–Anz–6 and NR–7 at temperatures of 70° to 75°F. At these temperatures, however, it is no longer possible to decide between intermediate and susceptible seedlings when testing with 21–Anz–2. With this strain the initial ratio of three to one has thus changed into a one to three ratio, with the resistant plants giving the same reaction at 70° to 75°F as the intermediates at temperatures of 65° to 70°F. At temperatures above 75°F, F_2 seedlings are all moderately susceptible or susceptible to 21–Anz–2, and at temperatures above 80°F the gene Sr6 is no longer effective against 126–Anz–6 or NR–7. Hence when testing at temperatures of 70° to 75°F with strains 21–Anz–2, 126–Anz–6 and NR–7 it can be assumed that the gene Sr6 is recessive with 21–Anz–2 and incompletely dominant with the latter two strains. Such has been suggested by Knott and Anderson (1956), who found that Sr6 was dominant with race 56 but recessive with race 15B. The reaction types recorded on Eureka to seven strains listed in Table 1, at various temperatures, suggest that genetic material in which Sr6 segregates would behave similarly to strains 21–Anz–0, 21–Anz–2 and 21–Anz–2, 6. With the other four strains, 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6, and NR–7, the same single factor is operating, but with a somewhat higher degree of resistance.

No differential transmission rate exists for alleles at the Sr6 locus. Eureka possesses no other factors for resistance to Australian field strains. However, when an avirulent laboratory strain, 103–H–2, which had its origin in a somatic cross between *P. graminis* var. *tritici* and *P. graminis* var. *secalis*, was used, segregation of a second, incompletely dominant factor pair was evident. Whether this factor is identical with the second factor for resistance in Eureka, as reported by Athwal (1955), cannot be ascertained. Athwal worked with race 42 from India, and he found that the varieties Bencubbin, Mentana, Dundee, Uruguay and Gabo, which are susceptible to several Australian strains, were resistant to race 42. Strain 103–H–2 is also non-pathogenic on these five varieties. Hence, it is likely that the same factor in Eureka conditions resistance to 103–H–2 and to race 42.

The gene Sr11, possessed by Gabo, Charter and Yalta, has been shown to be differentially transmitted in crosses between each of these three varieties and certain other varieties including Chinese Spring. This finding explains why several investigators using the latter variety as the susceptible parent postulated two, linked, dominant complementary factors for this type of resistance, while other workers who used different susceptible varieties reported a single factor pair. Further results on, and several aspects of, differential transmission have been discussed elsewhere (Luig, 1961 ; 1964).

While it has been known for many years that Gabo, Charter and Yalta carry the same resistance (Sr11) to particular Australian field strains (Watson and Waterhouse, 1949), it was also noticed that when these strains were present in the field Gabo was not as severely attacked as Charter, and Charter was less affected than Yalta (Waterhouse, 1952). It was thought that the early maturity of Gabo enabled this variety to escape infection to a certain extent and, while this may be so, the present study indicates that minor factors can be important once the major factor for resistance is rendered ineffective. Gabo carries one minor factor, tentatively designated Sr_{G1}, for resistance to Australian field strains. This factor gives a " 3 — c " type of reaction in the seedling stage. Charter and Yalta do not possess this minor factor, but it is present in Bobin 39 and Gular.

To strain 103–H–2, seedling resistance of Gabo was governed by a single factor, Sr_{G2}, which is distinct from the two previously mentioned factors in this variety. Sr_{G2} is also present in Charter, but not in Yalta. Whether Sr_{G2} is identical with one of the two factors for resistance found in Gabo by Athwal (1953) cannot be ascertained as Athwal used Indian race 42, as mentioned earlier.

When strain A20 of *P. graminis* var. *secalis* was employed, a fourth factor for resistance, Sr_{G3}, was found in Gabo and this factor was also present in Charter but not in Yalta. Thus, when testing with strains 126–Anz–6, 103–H–2 and A20, no segregation for susceptibility occurs in crosses between Gabo and Charter, but this is in each case due to a different resistance factor. The type of seedling reaction of Gabo and Charter to these three strains, however, is very similar. Yalta carries only Sr11 and is susceptible in the seedling stage to 103–H–2 and A20.

Results on the resistance of Kenya 117A in the seedling and adult plant stage are in agreement with those reported by earlier investigators (Watson and Waterhouse, 1949 ; Athwal, 1953 ; Athwal and Watson, 1954 ; Knott and Anderson, 1956). During the present investigations it was found that the major gene for seedling resistance in Kenya 117A, Sr9b, was the same as that which gives resistance in the mature plant stage. The other two factors, presumably Sr7 and Sr10, had only a modifying influence under Australian field conditions. The modifying effect of these genes was evident when the field reactions of F_1 seedlings from crosses of Kenya 117A and Gamenya* with susceptible varieties were compared. Gamenya apparently carries the factors Sr9b and Sr_{G1} only, the latter factor derived from Gabo and having no influence on field reaction. Because Gamenya does not carry Sr7 or Sr10, F_1 seedlings from crosses with Gamenya are moderately susceptible in the field, while those from crosses with Kenya 117A are intermediate. It was also found that with most strains the genes of Kenya 117A were incompletely recessive in seedlings and in adult plants. The effect of these genes was additive rather than epistatic.

The three genes, when homozygous, produced different reaction types when tested with different strains. This result is in agreement with those of Green *et al.* (1960). Sr9b was very effective against strain 222–Anz–1, 2, 4, 6 at all temperatures, but lines carrying either Sr7 or Sr10 were moderately susceptible when tested with this strain. At temperatures of 65° to 70°F lines possessing Sr9b only were more resistant to 126–Anz–2, 6 than to 21–Anz–2 and NR–7, but became increasingly susceptible at higher temperatures. Lines which carried either Sr7 or Sr10 were more resistant to 21–Anz–2 than to 126–Anz–2, 6 and NR–7 to which they gave identical reaction types. The data suggested that Sr7 gives less protection than Sr10 under Australian conditions. Sr10 would be a valuable gene in combination with other genes, but it is ineffective on its own. As the seedling reaction produced by this

* Bred from a cross Gabo × [(Gabo^5 × Mentana) × (Gabo^2 × Kenya 117A)].

gene is easily discernible from a susceptible type there should be no difficulty in incorporating it into varieties. Although ineffective in adult plants in the field, and hence useless on its own for breeding, Sr10 is apparently operative in the seedling stage against all Australian strains of stem rust. Plants possessing Sr9b, by contrast, react differentially and are rendered ineffective by several strains now well established in the field, e.g., 17 — 2, 3, 21 — 2, 3, 21 — 1, 2, 3, 21 — 2, 3, 4, 21 — 2, 3, 6 and 116 — 2, 3 (Watson and Luig, 1963).

These studies further demonstrate that the strains of stem rust used in this study can be grouped as follows when plants having specific genes from Kenya 117A are inoculated with them:

Group I : 21–Anz–0, 21–Anz–2, 21–Anz–2, 6
Group II : 126–Anz–6, 126–Anz–1, 6, 126–Anz–2, 6
Group III : 222–Anz–1, 2, 4, 6
Group IV : NR–7
Group V : 21–Anz–2, 3

The results from studies on the inheritance of resistance in Mentana to two strains of stem rust can be interpreted on the basis of two apparently independent factor pairs. Against most Australian field strains, like 21–Anz–2, a single factor, Sr8, conferred resistance in the seedling stage, this resistance being of a chlorotic " 2 — " reaction type. The same factor was operative against NR–7, but Mentana also possessed a second factor which conditioned a necrotic type " X = " reaction to this laboratory strain. The combined effect of these two factors, Sr8 and Sr_{M1}, was to make Mentana practically immune at low temperatures (" 0 ; " reaction type).

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THE DISTRIBUTION OF SUBMERGED AQUATIC ANGIOSPERMS IN THE TUGGERAH LAKES SYSTEM

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Synopsis

The submerged communities of Tuggerah Lakes are dominated by the aquatic angiosperms, *Zostera capricorni* Aschers and *Ruppia spiralis* Dumort. The distribution of these species has been mapped and an attempt made to determine the ecological factors underlying their distributional pattern.

Introduction

The Tuggerah Lakes, a system of maritime coastal lakes covering a total area of 24 square miles, are located approximately 60 miles north of Sydney on the central coast of New South Wales (Fig. 1). Physiographically, they appear similar to other coastal lakes or lagoons of Eastern Australia, and have apparently been formed by longshore currents building a series of sand bars across an irregularity or indentation in the coastline (Hutchinson, 1957). This has resulted in eastern foreshores of a coastal sand-dune character, whereas the foreshores on the western perimeter are of typically sandstone-derived soils.

Lake level and salinity, two important aspects of the submerged environment, are considerably influenced by the influx of water from streams, and evaporation from the lake itself. In dry seasons, little fresh water enters the lake from the streams, and with continued evaporation the salinity may rise as high as 3·1%. Conversely, in times of heavy precipitation, the salinity may be as low as 0·5%. Table 1 illustrates these effects in Lake Budgewoi.

By far the most important type of current in the lakes is that caused by winds, the most effective being from the south-east and north-east, in which directions the lakes are relatively exposed. The influx of streams also causes localized turbulence, due to the mixture of water of different densities; however, this is generally of secondary importance. There is no tidal effect, as a result of an extremely small oceanic connection and a relatively large amount of water entry from creeks and streams.

A combination of shallow depth and abundant supply of nutrients from the catchment area has allowed the development of a very extensive macroflora in the lakes. Table 2 lists the major plants of the submerged communities. Of these species, *Ruppia spiralis* and *Zostera capricorni* occupy at least 80% of the colonized areas, and therefore most of the following discussion will be concerned with their distribution.

Previous Studies

Many workers have published accounts of the distribution of submerged plants in freshwater lakes (Misra, 1938; Pearsall, 1920; Penfound, 1953; Pond, 1905) but there are few published accounts of the ecology of brackish water environments, particularly under Australian conditions.

Ferguson Wood (1959*a*, 1959*b*), working in Lake Macquarie, found that *Zostera* is usually confined to water of marine character, although it may at times encroach into less saline waters, and is found from low tide mark to a

depth of 20 feet. He also observed that it appears to require good illumination and can persist in currents of several knots. *Ruppia*, on the other hand, is generally found in waters of low salinity, but does extend into more saline areas where it is associated with *Zostera*. *Ruppia* is also observed to require good illumination, and to be intolerant of strong currents.

Ferguson Wood (1959*a*) includes adequate descriptions of the important marine angiosperms; therefore, no attempt will be made to cover their taxonomic aspect in this paper.

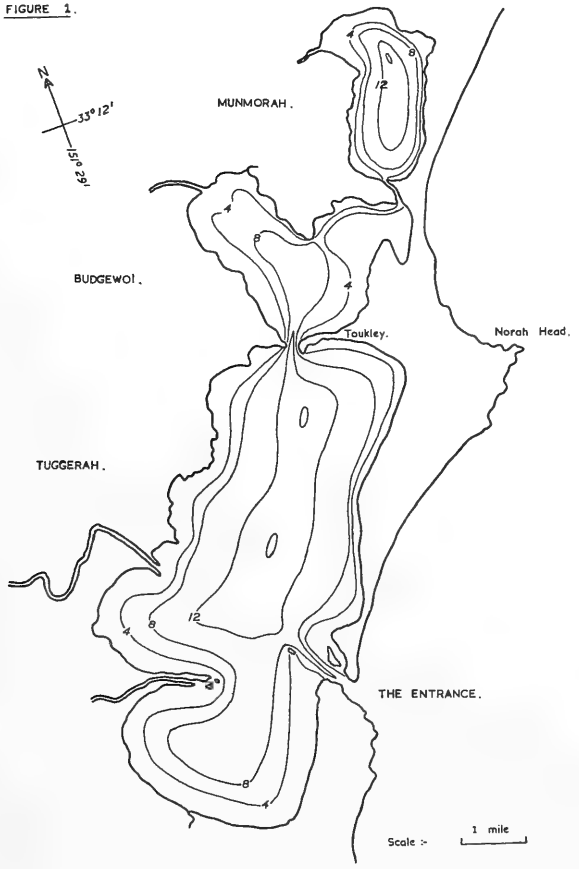

Fig. 1. Bathymetric map of the Tuggerah Lakes system (depth contours in feet), showing locations mentioned in text. The system can be seen to consist of three lakes: Tuggerah, Budgewoi and Munmorah.

Angiosperm Distribution—Observations

The distribution of the three major submerged angiosperms in Tuggerah Lakes is shown in Figure 2. This map is based on that compiled by the Electricity Commission of N.S.W. from aerial photographs (November, 1962), supplemented by skindiver transect observations in 1963. The distribution of *Halophila ovalis* is seen to be restricted to shallow, sandy areas to a depth of approximately three feet.

From general observations at collecting sites, the only characters of the water which vary significantly are salinity and light intensity (determined by depth and turbidity). Although salinity decreases with distance from the ocean entrance it does not appear to affect the distribution of *Zostera* within

the lake. For example, *Zostera* is found 400 yards from the ocean at the Entrance where salinity approaches that of sea-water (3·4% S), and also in Munmorah Lake, 10 miles from the ocean, where the salinity may be as low as 0·3%. Likewise, the distribution of *Ruppia* is not greatly affected by salinity variations as it has been found over a salinity range of 0·02% to 3·1%, although it does not appear to grow as well in strongly saline waters.

Current has a noticeable effect upon plant distribution, *Ruppia* being more prevalent in lentic situations such as sheltered bays, whereas *Zostera* can

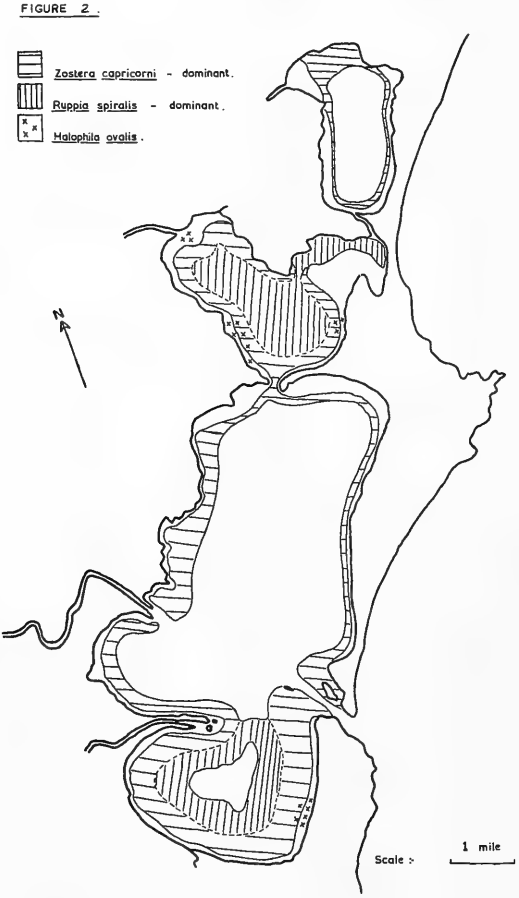

Fig. 2. Map of Tuggerah Lakes system showing distribution of submerged angiosperms.

withstand relatively strong currents, for example, the currents of the ocean entrance and in the constriction between Lake Budgewoi and Tuggerah Lake at Toukley (see Fig. 2).

The plants are generally found at an average depth of five feet, and very rarely at depths exceeding nine feet. *Ruppia* grows quite well in water from two to eight feet, whereas *Zostera* may occasionally be found in depths up to 13 feet.

Although it has been observed that depth and current have a marked effect upon the distribution of *Ruppia* and *Zostera*, these factors alone are clearly not adequate to explain differences in distribution which exist at the same depth, or in similar flow areas. Thus other factors must be examined, the most important being the character of the lake bed.

The Sediment Factor

Methods and Results

Sediment samples were collected at 50 sites within the Tuggerah Lakes, observations on plant growth being taken at each site. A " torpedo " core sampler was used to collect the surface three inches of the sediment.

The sediment samples were analysed for:

(i) % organic matter by a dichromate wet oxidation method (Tinsley, 1950);
(ii) % total nitrogen by the Kjeldahl method;
(iii) % total calcium
(iv) % total potassium
(v) % total magnesium
(vi) % total iron
} Extraction by Hall's method (Piper, 1942) and estimation of individual cations by Atomic absorption spectroscopy.
(vii) Mechanical analysis (size distribution of particles) by the Bouyoucos hydrometer method, using the International convention of particle diameter limits.

All analytical results are expressed on the basis of oven-dry matter (105°C).

The sediment samples were divided into five groups depending on the type of plant cover, and the mean results for each group presented in Table 3.

Discussion

The mechanical analysis shows that there are three major types of sediments: sandy, clayey and intermediate. All the sandy sediments occur close to the lake perimeter, whereas the clayey sediments occur in the centre or in sheltered places. This zonation of sediment type can be explained if we assume that initially the lake floor was sandy, and that subsequently large quantities of soil material have been brought into the lake by fluvial erosion.

Table 1

The effect of precipitation upon lake-water level and salinity in Budgewoi Lake (Toukley)

Month	Surface water temperature (°C.)	Precipitation* on catchment (points)	Lake level at sampling site (ft.)	Salinity % † lake water	Salinity % ‡ sea water
1963 May	15·0	1377	8·0	0·84	3·37
June	12·5	811	7·5	0·54	3·28
July	11·0	216	7·5	0·99	3·34
Aug.	12·0	703	8·0	1·11	3·28
Sept.	15·5	153	7·0	1·84	3·44
Oct.	20·0	142	6·8	2·31	3·44
Nov.	21·0	227	6·5	2·54	3·46
Dec.	21·5	443	6·3	2·79	3·49
1964 Jan.	21·5	186	8·0	2·97	3·50
Feb.	22·0	114	8·0	3·10	3·50
March	21·0	658	8·0	2·63	3·50
April	19·5	424	8·0	2·32	3·49
May	16·5	227	6·5	2·79	3·50

* Precipitation measured in a standard 8″ gauge at Munmorah.
† Salinity values calculated from chlorinity titrations, according to Harvey (1957).
‡ Sea water values inserted for comparison; samples collected at Norah Head.

The smaller particles of this erosional material would tend to be deposited in sheltered positions or in areas of greater depth, whereas the coarse material would be deposited near the stream mouths. Consequently, the substratum would become composed of coarse materials in shallow water, and of progressively finer particles as depth increases.

The results show that *Zostera* tends to favour the sandy sediments and *Ruppia* the clayey sediments, the intermediate sediments having a mixed

community (see Table 3). Differences, however, in the size distribution of particles of the substratum do not seem sufficient to explain differences in associated vegetation unless this can be considered in terms of their possible effects on plant growth.

In all but a few of the 50 soil samples, an increase in clay content was associated with an increase in organic matter regardless of vegetation. Therefore *Ruppia*, as well as being associated with sediments of higher clay content, is normally associated with higher organic matter levels than *Zostera*. Where

TABLE 2

List of the major plants of the submerged communities in the Tuggerah Lakes

Classification	Species name
i. Angiospermae	*Zostera capricorni* Aschers. *Ruppia spiralis* Dumort. *Halophila ovalis* (R.Br.) Hook. f.
ii. Chlorophyceae	*Chaetomorpha linum* (Muller) Kutz. *Enteromorpha clathrata* (Roth.) Grev. *Cladophora* Kutz. sp.
iii. Charophyceae	*Chara*
iv. Phaeophyceae	*Cystophyllum muricatum* (Turn.) J. Ag. *Dictyota dichotoma* var. *implexa* (Desf.) Gray.
v. Rhodophyceae	*Polysiphonia mollis* Hook. and Harv. *Gracilaria verrucosa* (Huds.) Papenfuss.
vi. Cyanophyceae	*Lyngbya majuscula* Harv.

sandy sediments are deposited, peaty matter accumulates on the surface of the substratum and often contains recognizable fragments of plant material, decay and incorporation being extremely slow. Where clayey sediments are deposited, the organic litter is rapidly decomposed and incorporated as humus. This may be an explanation for the increase in mineral content as the percentage of clay rises.

Results show that sediments high in organic matter are also high in total content of estimated minerals except calcium. *Ruppia*, therefore, is associated with substrata of high fertility and *Zostera* with those of lower fertility. The calcium content is approximately the same in all colonized substrata, the highest calcium level being in non-vegetated sands where there are accumulations of

TABLE 3*

Average results of sediment analysis from five vegetation classes

Vegetation class	%† Coarse sand	%‡ Clay	% Organic matter	% N	% Ca	% K	% Mg	% Fe
Zostera growth only	71·5	13·9	2·31	0·11	0·26	0·10	0·11	0·42
Ruppia growth only	25·4	42·3	5·37	0·21	0·27	0·44	0·52	2·11
Zostera and *Ruppia* together	37·6	36·8	6·02	0·27	0·35	0·29	0·50	1·62
Bare clays	9·1	60·8	8·14	0·28	0·66	1·02	0·75	3·59
Bare sands (occasional *Halophila*)	83·7	9·1	0·71	0·06	0·80	0·05	0·09	0·12

* Results condensed from Higginson (1963).
† Coarse sand particle diameter limits: 2·0–0·2 mm.
‡ Clay particle diameter limits: less than 0·002 mm.

marine skeletons. Plant colonization is observed to be associated with a reduction in total calcium content of the sediment, and this may be adequately explained by conversion of calcium carbonate to soluble forms with subsequent leaching from the substratum. The increase in carbon dioxide content of the water, resulting from organic matter breakdown in the sediment, would enable such a conversion to take place.

Average results of sediment analysis (Table 3) show that an increase in clay content is associated with an increase in nitrogen content. Hence it is apparent that a relationship exists between the mechanical properties and the chemical composition of the substrata. The form of available nitrogen in the substratum is important. Nitrates are normally absent from submerged soils (Misra, 1938), nitrogen being available as ammonia. Much of the organic nitrogen is ultimately converted to ammonium ions, and a large proportion is adsorbed onto the colloid exchange complex of the sediment replacing other cations. The cations exchanged would tend to go into solution and be more or less concentrated in the mud where they diffuse into the aqueous system or become available for plant absorption.

TABLE 4

The interaction of depth and sediment type upon the distribution of submerged angiosperms in Tuggerah Lakes

Vegetation	Average depth ft.	Coarse sand %	Clay %
Usually no growth, but with occasional *Halophila ovalis* (sterile sands) ..	2·0	83·7	9·1
Zostera capricorni only	5·4	71·5	13·9
Zostera and *Ruppia* growing together ..	5·0	37·6	36·8
Ruppia spiralis only	6·5	25·4	42·3
No growth (bare muds)	10·0	9·1	60·8

CONCLUSION

An increase in clay content of the sediment is associated with an increase in organic matter, nitrogen and all estimated minerals except calcium. There is, however, no evidence indicating that the greater fertility of sediments of high clay content is due to chemical rather than physical characters, and it is probable that, as in terrestrial soils, the two groups of factors cannot be dissociated.

It seems clear from the results in Table 3 that there is a close relationship between the nature of the sediment and the type of vegetation growing on it. The fact that there are distinct zones of sediments with different physical structure, and that these differ in chemical composition, justifies the assumption that zonation of vegetation is a result of differences in sediment conditions.

On the basis of evidence presented, it appears likely that an interaction of depth and sediment type can adequately explain the distribution of submerged aquatic angiosperms in Tuggerah Lakes. A summary of investigations, presented in Table 4, illustrates this conclusion.

Acknowledgements

The author wishes to acknowledge the assistance of the late Professor R. L. Crocker in the early stages of this project, for without Professor Crocker's help, the project would not have commenced.

For their frequent assistance in sampling and for their observations, I am indebted to Mr. B. Clough and members of the Projects Division of the Electricity Commission of N.S.W.

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NUMERICAL METHODS IN TAXONOMY

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[Read 24th November, 1965]

Synopsis

Some of the advantages of a numerical approach to taxonomy are indicated, also the compatibility of the technique with phylogenetically based taxonomy. Two main avenues for the application of computer techniques are described—the simplification of individual relationships and the detection of group structure. Finally, a means of combining the results of these two techniques is described.

The development of electronic computers has led to the introduction in recent years of numerical methods to the taxonomic process. That the advent of such methods has been the subject of some criticism cannot be denied, and it is the author's hope that this contribution will serve to dispel some misapprehensions, and to indicate some of the facilities offered by differing forms of numerical analysis.

Perhaps the foremost objection of many taxonomists to the introduction of numerical methods is their doubt that any automatic process could replace the extremely complex and flexible mental comparison of individuals and attributes which forms the vital part of the taxonomic process. The second objection is that the use of numerical methods precludes any phylogenetic basis for the final classification, and is hence an essentially retrogressive step. With regard to the first objection, assurance may be given that computers are indeed capable of reproducing the results of mental classifications made by taxonomists, so long as they are provided with the same or comparable information. A number of methodological investigations of numerical techniques have been carried out in which data supplied by monographers have been subjected to numerical analysis, the resulting output being fully in accord with the taxonomic decisions arrived at independently by the monographer (Rogers and Fleming, 1964). In an investigation of the genus *Phyllota* (Leguminosae) the author demonstrated by numerical methods a group structure almost identical with one advocated by Bentham more than a century ago, although in this case the characters used were almost certainly quite different (Jancey, 1965).

The second objection to the use of numerical methods, that they preclude a phylogenetic classification, is quite unfounded though widely held. Such a situation may well be the result of a misunderstanding since, although a number of numerical taxonomists hold strong views on the place of phylogenetic considerations in classification, this in no way makes numerical techniques and a phylogenetic classification necessarily incompatible. Assuming that the term phylogenetic classification implies the interpretation and modification of the groupings of present day phenotypically similar organisms in the light of known or inferred evolutionary trends, then a number of observations may be made concerning the methods by which such a classification can be achieved. In the mental taxonomic process it is possible to keep evidence of evolutionary trends in mind, and to modify taxonomic relationships even as they are being

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constructed, or, alternatively, to construct first an essentially phenotypic classification and then modify this in the light of such other evidence as may be available. Both these possibilities are available with numerical techniques; in the case of concurrent consideration of evolutionary evidence, such data would have to be converted into a subjective numerical form, its relative influence on the final result being entirely in the hands of the taxonomist during the coding process. If it should be asked how one estimates the importance of a hypothetical trend, relative to a given piece of phenotypic data, it may be pointed out that such a subjective estimate must be made, at least subconsciously, in the mental process, and that an attempt to arrive at a visible estimate of such degrees of relative importance could in itself be illuminating. Such a mixing of the factual with the hypothetical is the basis for the objection of numerical taxonomists to the inclusion of evolutionary data in the analyses themselves. The second approach indicated above is perhaps the more satisfactory; the consideration of phylogenetic data after completion of a purely phenotypic grouping would result in the final phylogenetic classification being the same, but it would then be possible to see precisely what changes in a purely phenotypic grouping had been made by the taxonomist in order to achieve a more phylogenetic relationship, thus opening the way for a more informed discussion of the significance of such changes.

Apart from their acceptability as techniques for performing the sorting and group-forming processes of taxonomy, numerical analyses offer a number of additional benefits. Information concerning the homogeneity and relative similarity of the groups is available from most analytical methods, thus enabling the purely taxonomic decisions regarding the status of the groups to be based on rather more precise evidence than usual. The analytical techniques involved are mathematically defined and reproducible, thus the repetition of an analysis with new or differently defined characters is capable of providing additional evidence concerning the validity of the original choice of characters, or classification arrived at, since the computational procedure itself remains constant.

The basis of numerical methods

The taxonomic process is essentially the translation of observations made on individuals into statements of similarity and hence of group structure. The use of mathematical techniques in taxonomy has been largely confined in the past to their secondary applications of describing and substantiating taxa which have been established by subjective processes. Techniques of this type, e.g. Analysis of Variance, Discriminant Functions, still require the prior establishment of groups by some means or other before they can be applied. It is only with the advent of electronic computers that it has become practicable to carry objective translations of information concerning individuals into statements of group structure. While such analyses almost all start by computing some measure of similarity between all possible pairs of individuals, they differ greatly in the way in which this information is used to detect group structure.

One of the first results of the use of numerical methods of data analysis is an increased realization of the multidimensional nature of taxonomic relationships. A single dimension is sufficient to describe the relationships of two points. If a third point is added, a statement of its relationship to the first point will necessarily fix its position relative to the second point, a position which may well not represent its true relationship. This is a difficulty which may be overcome by the addition of a second dimension. Clearly, the addition of a fourth point may require the addition of a third dimension, so that in general terms it may be said that n–1 dimensions will be needed to describe fully all possible relationships of n points. This statement will be obviously as true for taxa or individuals as for points, though it must be emphasized that this is the maximum number of dimensions which may be needed, particular cases

may well require fewer, the simplest situation being a straightforward clinal variation with n points arranged in a straight line.

It should be pointed out before proceeding further that not all analytical methods employ the multidimensional Euclidean space foreshadowed above. Indeed, the advantages of an entirely non-metric space for the detection of group structure are considerable (Rogers and Fleming, 1964). It is felt, however, that the concept of similarity between individuals or groups is intuitively considered in terms of real spatial relationships, and that for this reason the concept is worthy of retention and consideration in greater detail, even though it involves excursions beyond three dimensions.

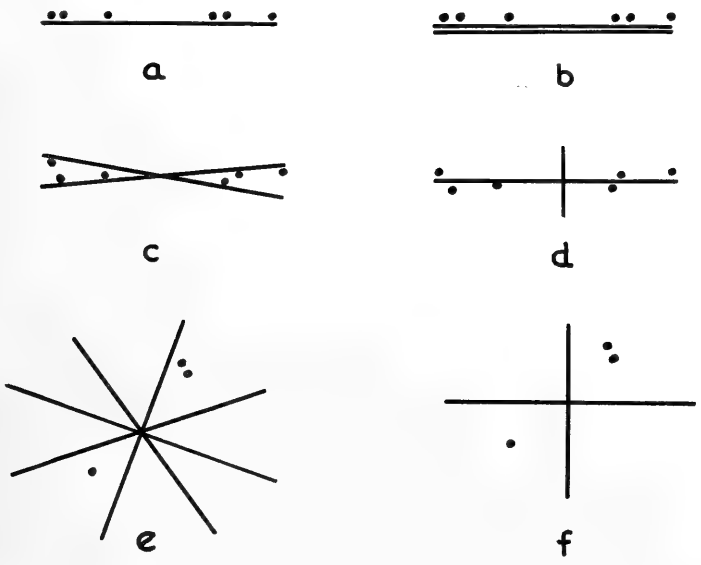

Fig.1. The representation of correlated characters by oblique axes.

a, Six individuals arranged according to their mutual phenotypic similarities, as revealed by a single character. *b*, As in *a*, but with two perfectly correlated characters. *c*, The same six individuals, now showing their phenotypic similarities as revealed by two highly, but not perfectly correlated characters (the cosine of the angle enclosing the points is equal to the correlation between the characters). *d*, As in *c*, but with two orthogonal axes now replacing the two oblique axes of the correlated characters. The positions of the points remain unchanged relative to each other. *e*, Three individuals described in terms of four correlated characters (the four axes are not necessarily confined to two dimensions). *f*, As in *e*, but re-expressed without loss of information in terms of two orthogonal axes (the maximum number needed to express the relationships of three individuals).

Information as collected by the taxonomist is expressed in terms of a number of reference variables, i.e. the characters observed and recorded for each specimen, the variables being more or less correlated. Thus the phenotypic relationships of a collection of individual plants for which x characters have been recorded may be thought of as being described in terms of x oblique axes (oblique because of the character correlations), the axes being located in a space of at most n–1 dimensions where n equals the number of individuals included in the analysis. Thus the relationships of the individual specimens could equally well be represented by n–1 orthogonal axes as by the x oblique ones. If x is less than n–1 then x represents the maximum number of dimensions required to represent the information available, the extent to which this number of dimensions can be reduced depending on the extent to which the characters are correlated (see Fig. 1).

While n–1 dimensions represent the maximum number of dimensions needed for complete description of the population, in practice far fewer

dimensions are needed to contain the information available. Indeed, a further reduction in the number of dimensions may be achieved with a level of distortion which would be quite acceptable in the interests of simplicity of description. Thus one of the main objects of a taxonomic computer programme is to take a population whose interrelationships are described in terms of a large number of correlated characters, and to re-express the interrelationships in terms of a relatively small number of dimensions, while allowing the taxonomist to nominate the level of distortion, if any, which is acceptable. At the same time, and unlike classical taxonomic methods, the processes to which the data have been subjected are completely definable. There are then four further steps in the taxonomic process, all of which will have been simplified by the re-expression of the characters. Firstly, an examination of the spatial relationships of individuals for evidence of group structure; secondly, the assignment of individuals to groups; thirdly, an evaluation of the relationships between the groups; and finally, the setting up of characters, or linear compounds of characters (cf. discriminant functions) to discriminate between the groups.

The technique of factor analysis is particularly well adapted to performing the first part of this process. It is a technique first used by Spearman (1904 et seq.) to describe the results of a large number of different tests of human ability in terms of a relatively small number of special aptitudes, e.g. manual, visual, numerical, etc., each special aptitude being described by a linear compound of the original tests. This is clearly the same as the first part of the taxonomic process, and by a slight extension, can be used as such. The analysis is based on the formation of a correlation or similar matrix from the original characters, from which is extracted a series of vectors or factors compounded from the characters. Since these factors when extracted from the matrix are made up of varying contributions from the original characters, it is possible to re-state the population relationships in terms of factor scores rather than characters (for a full account of factor analysis, see Harman, 1960). The relative information content of the factors depends on the method used for extracting them from the matrix, and for taxonomic purposes particular requirements for information distribution apply. The prime purpose of factor analysis of taxonomic data, as has been stated, is to reduce as far as possible the number of dimensions used in taxonomic description, so that as small as possible a number of meaningful factors is desirable. The Principal Axes method of factor analysis is such that the residual variance of the matrix is minimized with the extraction of each factor, thus the first factor extracted will contain the most information, and although in the Principal Axes method the number of factors extracted is equal to the order of the original correlation matrix, the information content of succeeding factors falls off rapidly and becomes non-significant. In graphic terms, the analysis examines a population described in terms of a number of oblique axes set in a multidimensional space, and computes the one axis best able to describe the spatial relationships of the population, the axis being composed of a linear compound of the original characters used. The analysis then investigates the position of the axis best able to represent the spatial relationships undescribed by the first axis. By definition, these axes and the succeeding ones must be orthogonal to each other. Knowing the contributions of the original characters to each factor, it is possible to re-express the data in terms of factors. By expressing the relationships of the individuals in terms of the first three factors only, a loss of information is incurred, but because of the rapid fall off in information content of the factors this is not usually serious, but has the advantage that limitation to three factors enables the spatial relationships of the individuals to be expressed graphically using isometric graph paper.

While factor analysis does not, in itself, delimit groups, it does present data in a far more comprehensible form as a basis for the establishment of such

groupings by other means. Methods are available which do make an objective demonstration of group structure, notably those of Goodall (1953), Michener and Sokal (1957), Sneath (1957), Williams and Lambert (1959), and Rogers and Fleming (1964). A fuller account of these methods will be found in Sokal and Sneath (1963), but for the purposes of this discussion it is sufficient to say that while considerable differences exist between the respective techniques, they all depend essentially on the calculation of some measure of association between all possible pairs of individuals, based on the characters measured. Such a measure of association can take many forms, being usually based on the ratio of character matches to mismatches between pairs of individuals, since such a measure is particularly well suited to data in a presence or absence, or limited class form. Having computed some measure of association, groups may be established by a synthetic process, the agglomeration of individuals possessing mutually high levels of association, discontinuities in the agglomerative process indicating group structure. The actual delimitation of groups may be performed automatically in response to some parameter involving the discontinuities—essentially a relationship between variation within the group and that of the whole population.

The techniques of Goodall (1953) and of Williams and Lambert (1959) are rather different in that they are analytic processes designed primarily for ecological use, whereby the population is subjected to successive divisions into the most homogeneous sub-groups. Such methods are particularly adapted to two-state character data, and provide a monothetic classification with hierarchical ordering of groups.

The methods of detecting group structure which have been described above do not by themselves give any obvious indications of the inter-relationships of the groups demonstrated. Levels of similarity at which groups form from individuals submitted to analysis are usually shown in the form of a dendrogram. Such diagrams have the advantage of illustrating clearly the discontinuities between groups. They cannot, however, represent in graphic form the similarity relationships between all pairs of individuals. Such a representation is not possible in two dimensions for the reasons described previously. A pictorial representation approximating to group inter-relationships may be obtained by the combination of factor analysis with one of the techniques of group detection described. The centres of gravity of the groups can be calculated in terms of three-dimensional space from the factor scores of individuals on the first three axes of a factor analysis. Knowing the individual co-ordinates of members of a group, a value for the standard deviation from the mean can be calculated for the group on each axis. It is thus possible to construct a perspective diagram of the group relationships on isometric graph paper, in which the groups are represented as ellipses drawn at one standard deviation from the mean of the group on each factor axis, the ellipses serving to indicate both the spatial relationships and the amount of variation found within and between the groups. It might be argued that more real information could be obtained from a perspective diagram showing the positions of all the individuals on which the analysis was based. Such a diagram is impracticable, since the illusion of three dimensions is lost when a large number of points need to be shown, and in addition no advantage would have been gained from the objective discrimination of groups made previously. An example of a perspective diagram of the former type is shown in Jancey (1966).

Conclusions

Numerical methods of data analysis are considered by the author to represent a valuable new technique available to the taxonomist. It is unfortunate that some taxonomists have looked upon the technique as an isolated field of endeavour, together with chemotaxonomy and cytotaxonomy,

and bearing no close relation to taxonomy as practised in the herbarium. While for purely practical reasons classification must continue to be based largely on morphological data, it would seem unreasonable to ignore any additional information concerning the living organisms which might be available. Similarly, a technique which enables the maximum amount of information to be extracted from a mass of raw data by a defined process would seem to be worthy of consideration by all taxonomists. The nature of the results yielded by numerical methods should be emphasized, since they are a frequent source of misunderstanding. The computations do not produce classical taxa, but group the individuals for which data was provided. Precise information is provided concerning the membership, distinctness, and diagnostic characters of the groups produced, but the status of any group in terms of orthodox taxonomic nomenclature, and its relationship to other taxa, are entirely in the hands of the taxonomist, the only difference being that he is provided with rather more information than usual on which to base his decision.

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AN INVESTIGATION OF THE GENUS *PHYLLOTA* (DC.) BENTH. (LEGUMINOSAE)

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(Plates xxix–xxx)

[Read 24th November, 1965]

Synopsis

The generic status of *Phyllota* has been retained, pending a more extensive examination of the taxonomic relationships of *Pultenaea* with *Phyllota*, *Dillwynia*, *Aotus*, and possibly other related members of the Podalyrieae. At the moment the generic distinction between *Phyllota* and *Pultenaea* rests almost wholly on the differing form and texture of the bracts, a distinction of comparable magnitude existing between east coast species of *Phyllota* with leafy bracteoles and persistent petals, and the remaining species, in which the bracteoles are predominantly small, linear, and in some species scarious or coriaceous. A detailed study, using quantitative techniques, demonstrated a number of phenotypically differentiated groups within *P. phylicoides*. As a result of this, specific rank has been restored to *P. grandiflora*, *P. squarrosa*, and *P. humifusa*. A number of other groups retain the identity of *P. phylicoides*. The need for an investigation of the breeding behaviour of these groups is shown, also the need for an investigation of the ecological factors connected with their distribution, in particular an investigation of possible variation in the mineral composition of the sandstones of the Sydney district. Lectotypes are named for *Phyllota luehmannii* and *Phyllota pleurandroides*.

Introduction

The genus *Phyllota*, which is endemic to Australia, was first described by A. P. de Candolle in his Prodromus Regni Vegetabilis, as a section of the genus *Pultenaea*. It was established as a genus in its own right by Bentham in 1838.

In the present study, the genus was investigated from several viewpoints, firstly an evaluation of its taxonomic relationships with other genera, in particular with the genus *Pultenaea*, an association first recognized by de Candolle, but also with the genera *Aotus* Sm. and *Dillwynia* Sm. Secondly, an investigation of the taxonomic relationships within the genus, particularly in the Sydney region, where considerable variation occurs in a relatively small area, and finally an attempt to correlate the variation in the Sydney district with environmental factors.

The distribution of the genus (see Fig. 1) extends around the southern part of Australia from Bundaberg on the Queensland coast, through New South Wales, Victoria, Tasmania, South Australia and the south-west of Western Australia. Figure 1 is based on herbarium records and, particularly in the case of Western Australia, the distribution shown may be incomplete.

The genus is confined largely to a sandy substrate, either in the form of fixed sand dunes or of sandstone, depending on the species. With the exception of two Western Australian species, the genus is also confined to temperate regions with a rainfall in excess of 20 inches per annum (Burbidge, 1960).

Since it appeared that infraspecific variation in the Sydney region was much greater than elsewhere, it was decided to devote particular attention to this area, where, in recent years, all variations have generally been included

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within the species *Phyllota phylicoides* (Sieber ex DC.) Benth. (e.g. Thompson, 1961). In the past these variants have been recognized as being of specific rank, there being eight specific epithets presently included as synonyms of *P. phylicoides*. It is proposed to deal with the investigation carried out in the Sydney region in a first section, and to consider later the taxonomy of the genus as a whole.

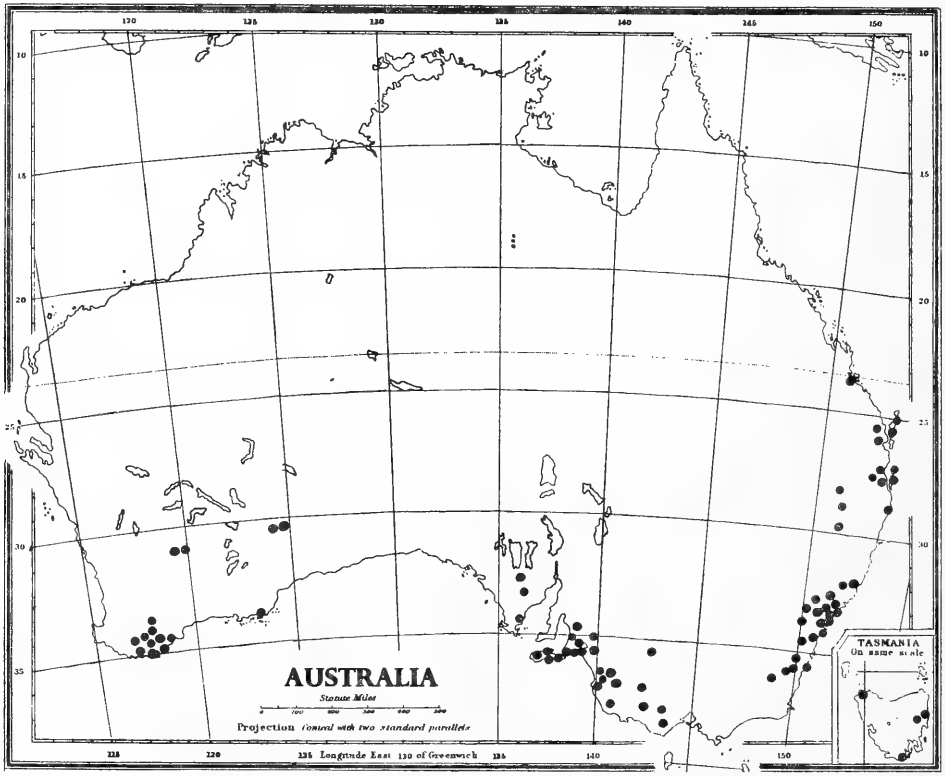


Fig. 1. Distribution map of the genus *Phyllota*

Variation in the Sydney Region

Introduction

This section of the study formed the basis of an investigation using numerical taxonomic methods. The numerical aspects of the investigation have been reported elsewhere (Jancey, 1966). In the course of this investigation a number of groups were established on the basis of phenotypic similarity. In the present account it is proposed to describe the relationships of these groups in terms of geographic distribution, breeding behaviour, and cytology, in addition to phenotypic characters, and, in the light of the total information available, establish the taxonomic rank, if any, to which they may be entitled. While it is not proposed to introduce any discussion of numerical techniques into this account, for convenience of reference the variants in the Sydney region will be referred to by the group numbers used in the investigation previously referred to.

Methods

Collection of specimens

All the specimens of *P. phylicoides* from the National Herbarium of New South Wales and the Queensland Herbarium were examined in detail, and a

series of measurements on soaked material were also made on all the specimens from the National Herbarium of New South Wales with the object of selecting an area for investigation which would include all the sites of major variation within the species. A further object of this examination was the selection of phenotypic characters to be recorded on living material.

As a result of these preliminary investigations coupled with observations in the field, the area selected for study was one bounded by Lake Macquarie in the north, Jervis Bay in the south, and Lithgow in the west. It was felt desirable to collect specimens as evenly as possible from the area under investigation, since this would yield additional information concerning the geographic and ecological range of the variants, apart from the location of any possibly transitional forms. The method chosen was to take specimens at one-mile intervals along roads and fire trails in the area, with the precaution of making the collection 100 yards or more from the road to avoid plants distributed by passing traffic. Detailed measurements were made on 313 specimens, and additional field trips made and specimens examined to establish more precisely the distributional limits of the groups.

Recording of data

Data recorded at the time of collection included height of specimens, the formation in which they were growing (heath, dry sclerophyll forest, etc.), soil type, amount of shading, exposure to wind, and the presence of other plants where it was felt that these were indicative of a change of habitat.

On returning to the laboratory, a number of records of characteristics were made on the fresh material, and are listed below. Use was made of a number of subjective scales for recording characters not amenable to objective measurement; illustrations of scale values are included where applicable. All measurements of floral parts were made on flowers which had just opened, and could hence be considered to be in a comparable state of development.

Data recorded in the laboratory may be summarized as follows:

Inflorescence length

The longest inflorescence of any specimen was stripped of its flowers, and the length of the inflorescence axis measured in millimetres. While there was considerable variation within individuals, there appeared to be some constancy in the maximum inflorescence length which an individual could attain.

Number of flowers per inflorescence

As could be expected, this character was correlated with inflorescence length. The correlation was not a necessary one, however, since independent variation of these characters occurred. It served, in conjunction with the other two inflorescence characters, to demonstrate affinities which could otherwise be described only in extremely subjective terms.

Number of flowers per millimetre

A character derived from the two previous inflorescence observations. It showed a high correlation with both, but demonstrated differences which would have otherwise been difficult to describe, and was hence treated as an independent variable.

Bracteole length and breadth

Both these two characters were measured to the nearest half millimetre. Since all floral measurements were made on flowers which had just opened, the characteristic enlargement of bracteoles after the death of the petals did not constitute a source of variation between specimens.

Calyx and bracteole indumentum

For flowers of the same age on the same plant this character was quite constant. The epidermal hairs responsible were similar to those associated with the bullae on the leaves. In flowers of the age examined, the hairs were still present, obviously so in the case of the calyx, but the relationship between bracteole and calyx indumentum was always the same. A subjective assessment of this indumentum was made on a 1–4 scale of abundance (see Pl. xxix).

Bracteole colour

Bracteole colour appeared from preliminary observations to be far less dependent on environmental factors than stem colour, and considerably more constant within individuals. It was preferred consequently as a character. It was difficult to assess, and may, like calyx colour, have represented the outcome of a number of contributing forces. It was recorded on a subjective scale, with green represented by 1, and varying through yellow to almost wholly red at 4.

Calyx colour

This was recorded in a similar way to bracteole colour. The colour of the calyx and bracteoles was frequently similar but not always so. For this reason both characters were retained.

Calyx length

This character was measured by dissecting out the calyx tube at its point of attachment to the receptacle, and measuring the length of the tube plus one of the posterior calyx lobes to the nearest half millimetre.

Standard length

It was found that within the species *P. phylicoides*, the petals did not vary in relative lengths, consequently standard length was taken as representative of corolla length. After dissecting the flower, the total length of the standard was measured, including the claw. The length of the standard was extremely constant within individuals, such variation as occurred, some 0·5 mm. within individuals, was almost certainly due to the difficulty experienced in flattening reflexed standards prior to measurement.

Standard pigmentation

Three separate patterns were found on the standards of living specimens. The three pigmented areas were recorded on subjective 1–4 scales, the four values being illustrated in Figure 2.

Leaf spacing

The number of leaves produced within the 10 mm. of axis immediately behind an inflorescence was counted. This character was somewhat susceptible to environmental factors.

Leaf weight per millimetre of length

The character was measured by determining the air-dried weight of 20 leaves immediately below an inflorescence, and dividing this weight by 20 times the average leaf length as found in the previous character, thus giving a value for leaf weight per millimetre of length. Given the assumption that all leaves of all individuals were of equal density, this character would have provided a comparable measure of the cross sectional area of the leaves, a character which was seen in the preliminary investigation to have a marked constancy within individuals, and an equally marked variation within individuals. No attempt

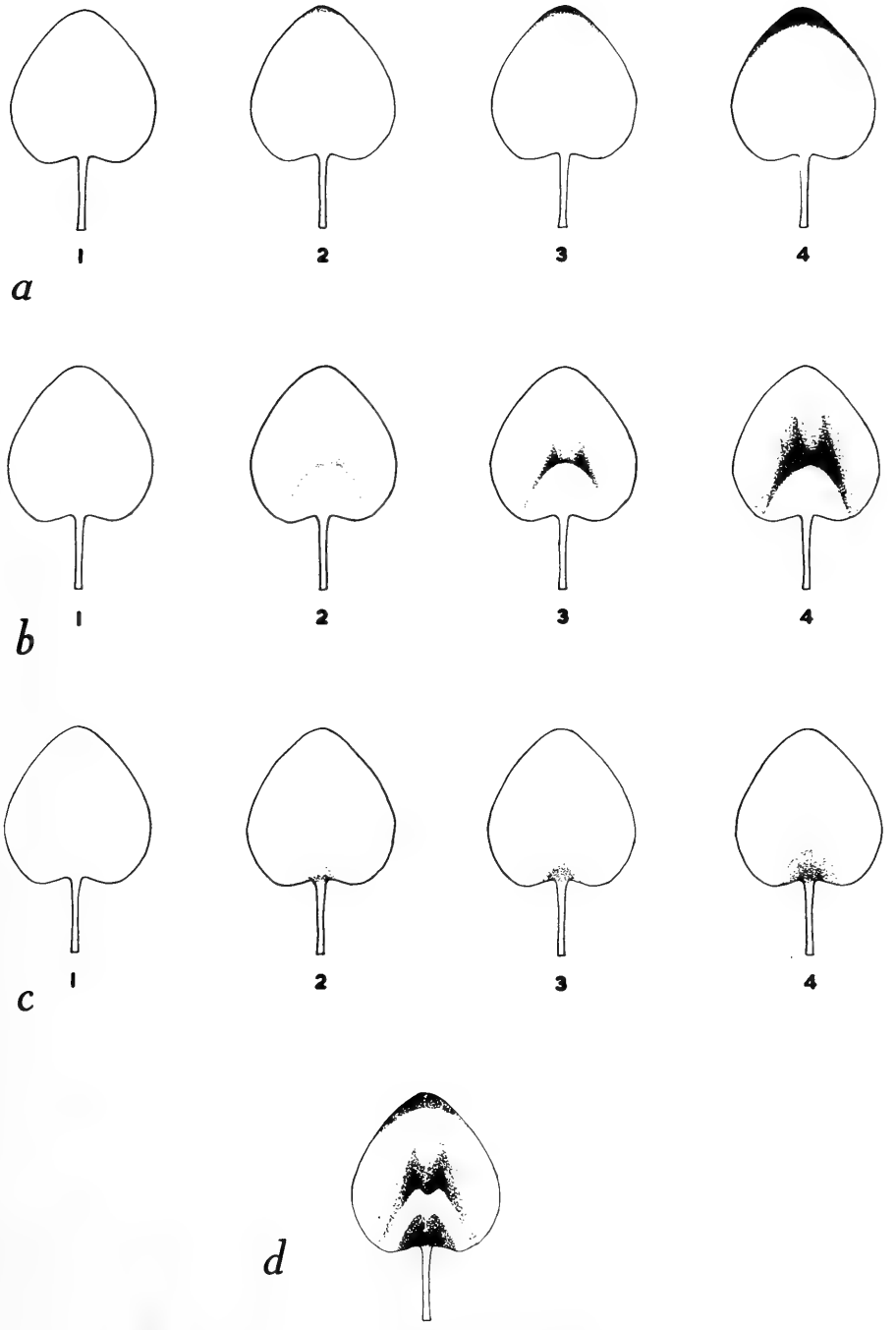


Fig. 2. Illustrating the values from 1 to 4 on the subjective scale for pigmentation of the standard. Upper, middle and lower zones are shown in *a*, *b*, *c* respectively. The composite form is shown in *d*, which also illustrates the alternative form taken by the lower edge of the middle zone.

was made to confirm the assumption of equal density, since the differences in cross sectional area were so large and so consistent as to be quite distinct despite any possible variation in leaf density.

Leaf length

Measures of leaf length were based on the average of 10 fresh leaves taken from immediately below the inflorescence, the leaves being measured to the nearest millimetre.

Leaf tips

Leaf-tip shape varied from obtuse and rounded, bearing a very small, deciduous, black mucro, to an acuminate structure in which the greater part of the tapering leaf tip was yellow, merging into a still tapering black mucro. This character was remarkably constant within individuals, and proved to be of considerable taxonomic worth. The character was recorded subjectively on a 1–4 scale since no objective measure could readily be applied (see Pl. xxix). Frequently associated with a value of 4 on this scale was a recurved state of the leaf tip. This feature was also recorded.

Decurrence of leaf bases

There was a variation in the extent to which leaf bases were decurrent on the stem, some individuals showing bases decurrent for three to four millimetres, others on leaf abscission leaving no more than a small tubercle. There was considerable variation within individuals, but the subjective decision was made that this was sufficiently less than the variation between individuals, when assessed on a 1–4 scale, to be of possible taxonomic value.

Leaf bulla number

Leaf bullae were found to be the persistent bases of epidermal hairs; the number of bullae on the adaxial surface of the leaf was assessed on a 1–4 scale (see Pl. xxix).

Leaf bulla size

The size of leaf bullae was effectively constant on any given specimen, but showed considerable variation between specimens. While there appeared to be a strong negative correlation between this and the previous character, it was shown not to be a necessary correlation by one group of individuals and, at least in this one case, leaf bulla number is of taxonomic significance.

Indumentum of style

Variation of stylar indumentum fell into two classes; in all cases hairs were of the same type, in one class covering the ovary and lower part of the style, while in the other class, apart from covering the ovary and lower part of the style, they continued along the upper edge of the style, around the hook, and almost reached the stigma.

Continued growth of the inflorescence axis

A marked division existed between individuals in which the axis bearing the inflorescence died back to the apex of the inflorescence, after having produced no more than 1–10 mm. of fresh growth, and those in which at least some of the axes continued to grow on unimpaired (see Pl. xxx).

A number of characters used previously in the taxonomy of this complex were rejected after a preliminary survey of living material, on the grounds that the character concerned was essentially constant within the species under investigation. Characters coming within this category were the shape of calyx lobes, their length relative to that of the calyx tube, the relative length of the

petals and their shapes, and also the shape of the style. Other characters were rejected because of excessive susceptibility to environmental factors; these included stem and leaf indumentum.

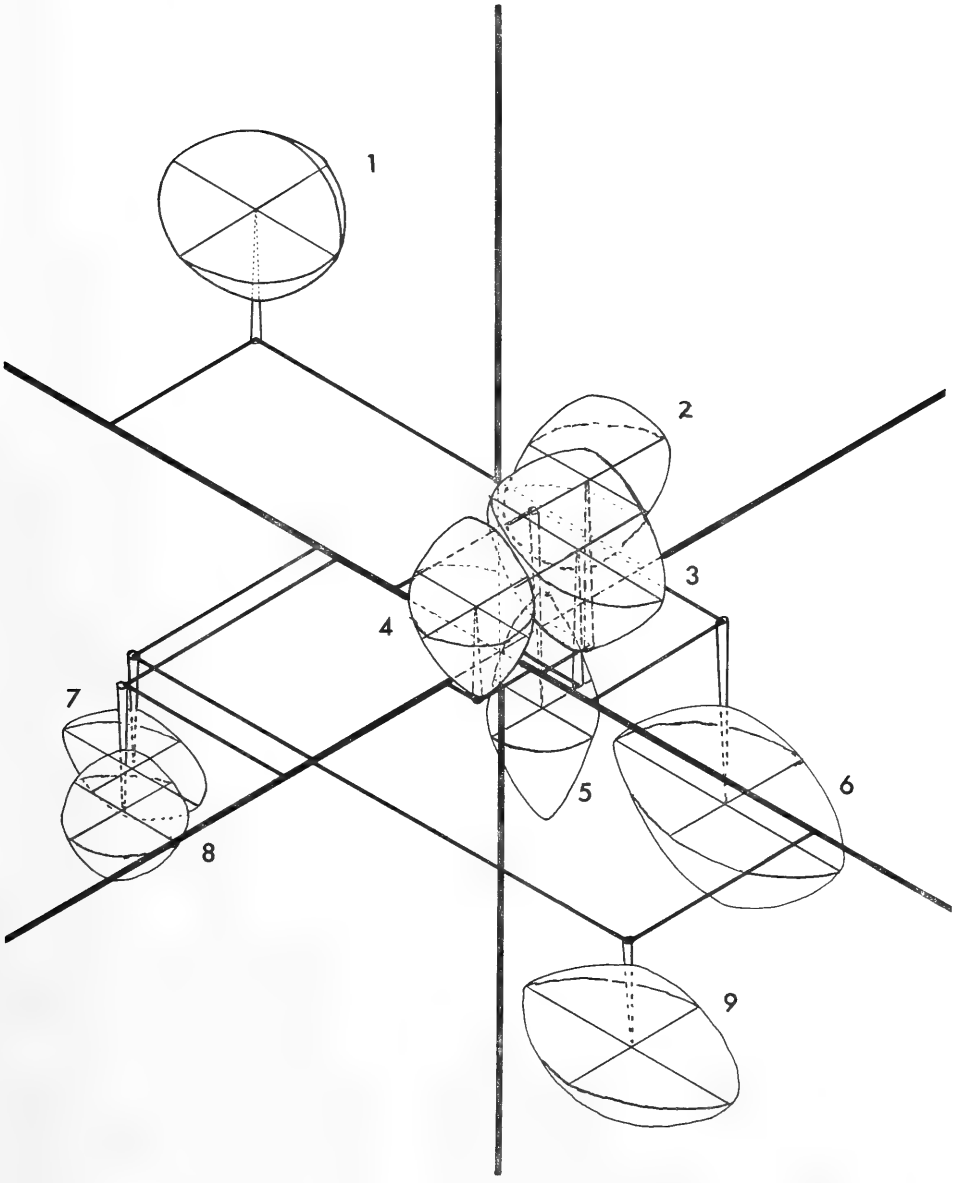


Fig. 3. Perspective illustration of the relationships of morphologic groups in three dimensions

Morphologic groups established within P. phylicoides

Figure 3 shows a perspective illustration in three dimensions of the phenotypic relationships of the groups. It is not proposed to consider the numerical techniques by which the groups were delimited in this taxonomic account, but it may be said briefly that the three axes represent the first three axes of a principal axes factor analysis of the correlation matrix of characters. Thus each axis is composed of varying contributions from the characters used

in the study. The groups have been discriminated by another multidimensional analytical technique, but for clarity of expression have been represented in terms of factor scores of their members. This was achieved by calculating the mean on each axis for the members of a group, calculating the standard deviation and drawing the ellipse at one standard deviation from the mean. The acceptability of the groups from the biological point of view obviously differs considerably and will be considered later in the text. While it is possible to relate the axes as drawn to particular combinations of characters, it would seem more useful in the present account to consider the diagram purely as an illustration of the overall phenotypic relationships of the groups. For an account of the quantitative aspects of this study, see Jancey (1966). Discriminating features of the morphology of the groups will be considered in conjunction with the non-morphologic data which follows.

Other data relevant to the taxonomy of Phyllota *in N.S.W.*

It is proposed to consider the geographical distribution of the groups, followed by ecological and other factors which may be concerned in group distribution and relationships; finally, in the light of these observations, the taxonomy of the N.S.W. groups of *Phyllota* will be considered.

Geographical Distribution of the Groups

From Figure 4, it will be seen that group 1 is of extremely limited distribution. Herbarium material suggested that similar individuals might be found in the Bundanoon-Penrose area, but field examination failed to reveal any such individuals. It is felt that if this group occurs elsewhere it must be of extremely local distribution to have escaped detection. It will be seen from the geological map (Fig. 11) that no other form of *Phyllota* occurs in the same area, and that a continuous area of apparently suitable mineral composition extends to link the group with other forms of *Phyllota*, in particular groups 2, 3 and 4. This question will be discussed further in connection with the ecological and systematic relationships of the forms.

The distribution of group 2 seen in Figure 4 is around the edges of the Sydney Basin; it appeared more prolific in the area to the north of the Hawkesbury River, elsewhere being locally abundant, but rather discontinuous in its distribution. The distribution of group 3 shown in Figure 5 is similar to that of group 2 in general terms, but differs in local habitat. This is particularly interesting in the light of their very close morphologic relationship.

Group 4, which from the perspective diagram is also seen to belong to the central complex of groups, has been collected from a limited area of the southern ramp in the region of Mt. Keira (see Fig. 6). Additional material not included in the distribution map would suggest that the group extends southwards into the Bundanoon area.

The relationship of group 5 to the other central groups is less close than would appear from Figure 3, since an additional character is available for the discrimination of the group, that of possessing wholly terminal inflorescences. The terminal position of the inflorescence is caused by the die-back of the very short continuation of the axis after flowering. It will be seen from Figure 6, that the group is largely confined to the region south of Botany Bay, having its centre in the Royal National Park; a small number of individuals from other areas have been assigned to the group. Of these, one individual from the near north shore of Sydney, and the two from the Blue Mountains, are similar to those found in the main distribution area of group 5, their isolated position possibly being due to distribution by man. The remaining isolated individuals do not show the terminal inflorescences characteristic of group 5, and may now be better assigned to groups 2 or 3, an assignment which would be more in keeping with their distribution.

Group 6 is confined to the north shore of Sydney Harbour (see Fig. 7). The two individuals from the Royal National Park could be assigned subjectively with greater confidence to group 5 in the light of data concerning terminalization of the inflorescence. It will be seen from a comparison of the distribution of this group (Fig. 7), with the combined distribution of groups 2 and 3 (Figs 4 and 5), that their areas are contiguous, but that there is virtually no overlap.

Very closely associated with each other, but quite distinct from other groups, groups 7 and 8 differ only in the characters dealing with red pigmentation of the standard, group 7 having dark red standards and those of group 8 being

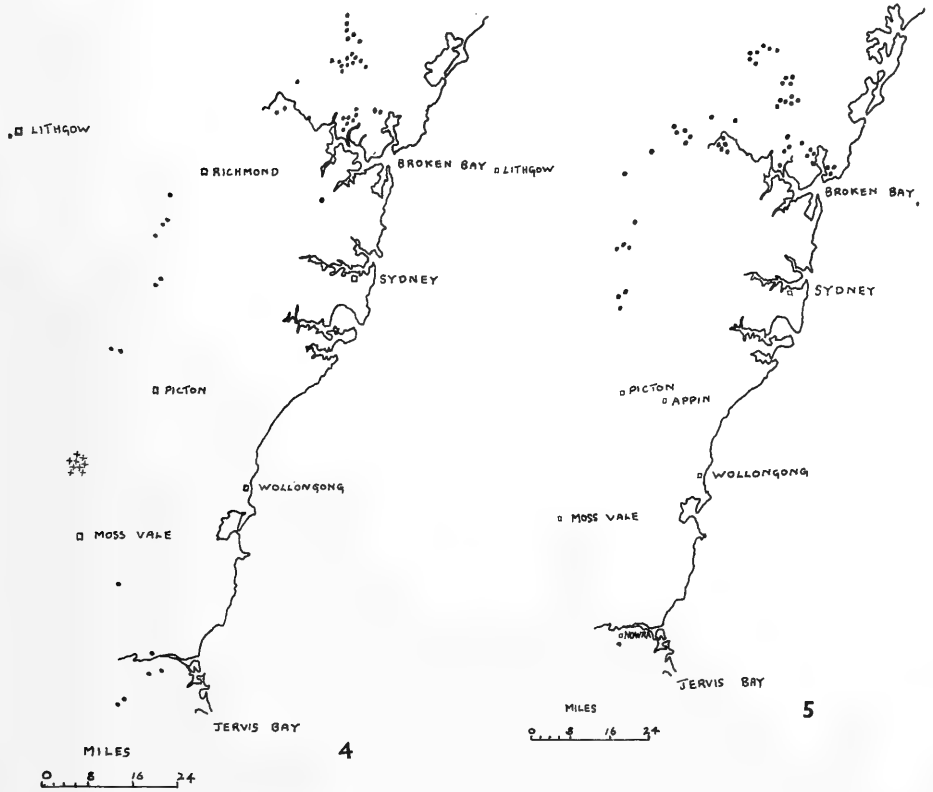


Fig. 4. Distribution map of group 1 (*P. humifusa* in the taxonomic treatment), and of group 2 (part of *P. phylicoides* in the taxonomic treatment). Group 1 is indicated by crosses, and group 2 by solid dots.

Fig. 5. Distribution map of group 3 (*P. phylicoides* in the taxonomic treatment).

almost wholly yellow. The distribution of these two groups (see Figs 8 and 9) overlaps in the region of Blackheath to Mt. Victoria ; indeed plants with yellow and red standards have been found growing next to each other in this region. Group 7 contains two individuals isolated geographically from the rest of the group, one at Mt. Keira, and the other south of Nowra. Group 8 contains one individual from the Nowra region, but is otherwise confined to the Upper Blue Mountains. Examination of these three specimens confirmed that their assignment to groups 7 and 8, like the assignment of two individuals from the same region to group 5, was almost certainly a misclassification as a consequence of the small number of individuals from the region. It will be seen from the combined distribution of groups 7 and 8, that the groups are confined to the

higher parts of the Blue Mountains. Comparison with Figures 4 and 5 would suggest that the groups are geographically isolated from groups 2 and 3. However, the anomalous records for group 5 individuals at Wentworth Falls and also two Herbarium records for plants of the group 2, 3 type in the same area would suggest that the geographic isolation may not be complete. The ease with which plants of the group 2, 3 type can be found in the foothills of the Blue Mountains, and their absence despite careful searching higher in the ranges would suggest that their distribution in the latter area must be very discontinuous and limited. The north-south distribution of groups 7 and 8 is less easy to establish than their east-west distribution. Figures 8 and 9

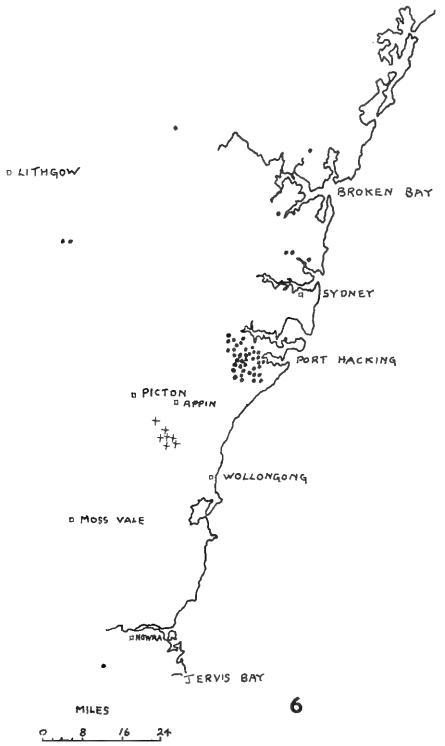


Fig. 6. Distribution map of group 4 and group 5 (both are part of *P. phylicoides* in the taxonomic treatment). Group 4 is indicated by crosses and group 5 by solid dots.

Fig. 7. Distribution map of group 6 (part of *P. phylicoides* in the taxonomic treatment).

show the distribution to be confined to the highest parts of the Blue Mountains, and from further observations it may be said that the northerly distribution extends at least as far as the inner end of the Wolgan Valley, north of Clarence, but has ceased before the Capertee Beds east of Rylstone are reached. This absence of *Phyllota* is paralleled to the east by the absence of groups 2 and 3 going north along the Colo-Putty-Singleton road (see Figs 4 and 5). The southerly extension of groups 7 and 8 appears to be limited by the available high ground of suitable mineral composition. South of the Blackheath-Katoomba area there is little continuous high sandstone ground, apart from the neck running out to Mt. Solitary. This area has not been examined for the presence of *Phyllota*, but individuals of group 8 have been collected from Kanangra Walls, where they were found growing on Permian sandstones. Their presence in this area would imply either great age to the discreteness of group 8, followed by no evolutionary change, or alternatively, that even

assuming a route via Mt. Solitary, colonization and genetic interchange over considerable distances of unsuitable country were possible. No *Phyllota* has been found on the non-sandstone rocks surrounding Kanangra Walls. To the east of the walls, groups 2, 3 have been found at Oakdale, though at a very much lower altitude. South of Kanangra, the first sandstone examined lies south of the Wollondilly River, to the east of Mt. Bullio, where the altitude is also much lower. Here no *Phyllota* is found at all, though some 10 miles to the east lies the limited area containing group 1.

Group 9 follows the distribution of group 6 (see Figs 10 and 7). The small group of individuals from group 9 in the region of Appin, are rather different from the bulk of the group found north of Sydney Harbour, being rather less

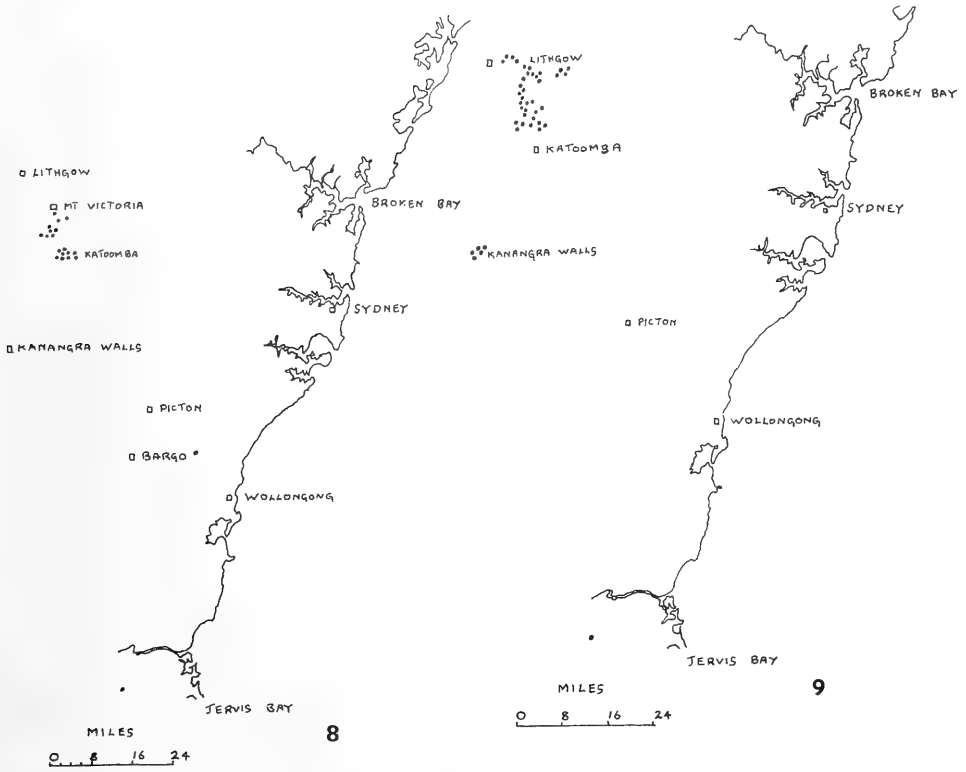


Fig. 8. Distribution map of group 7 (part of *P. squarrosa* in the taxonomic treatment).
Fig. 9. Distribution map of group 8 (part of *P. squarrosa* in the taxonomic treatment).

robust, and possessing rather fewer flowers per inflorescence. However, these distinctions will be considered in more detail in the section dealing with the taxonomy of the New South Wales forms of *Phyllota*. The two individuals found on the Hume Highway south of Bargo correspond very well to the character values for group 9. Their presence in this area could possibly have been the result of human distribution, but if so, the distribution must have taken place in early colonial days or before, as a specimen of the group 9 type was collected by MacArthur from Bargo, and is at present in the Kew Herbarium. Failure of the plants to spread may have been due to unsuitable substrate. Herbarium records show specimens of the group 9 type to be growing immediately south of Botany Bay in the region of Como. Careful searching has failed to reveal any living examples in this area, an absence which may be due to urban development.

Factors affecting Distribution and Variation

Geological and Ecological

Figure 11 shows the distribution of all the individuals used in the analysis, superimposed on the areas of sandstone in the region. It will be seen that, while no records fall outside the sandstone areas shown on the map, there are large areas of sandstone in which no *Phyllota* of any group is found. While no quantitative study has been made of this problem, it may be said that the presence or absence of *Phyllota* is to some extent associated with small changes in altitude. In view of the small changes in altitude involved, this would suggest stratigraphic changes, and hence possible changes of a mineralogical nature. Changes in iron content of the Hawkesbury Sandstone certainly occur

Fig. 10. Distribution map of group 9 (*P. grandiflora* in the taxonomic treatment).

(David, 1950), and it would seem reasonable to suppose that other metals at least would be present in varying abundance. Cases where discontinuities of *Phyllota* occur without changes in altitude would not necessarily refute this basis for variation since, in the case of dipping strata, movement over the surface would bring about the same changes as changes of altitude in the case of horizontally bedded strata. A particularly clear case of the correlation of strata with distribution is found in the region north of Wiseman's Ferry, where, although *Phyllota* is apparently absent from the slopes of the sandstone plateau, it may be found at the top of the plateau. Equally flat, although slightly lower, areas of the plateau are however once again devoid of *Phyllota*. Similarly, individuals of group 5 disappear from the Princes Hghway just south of the Woronora Dam turnoff as the highway climbs up towards the Bulli Pass, and, although not included in Figure 6, the distribution of group 5 continues around the lower contour as far as the western limit of the exposed sandstone to the north-east of Appin.

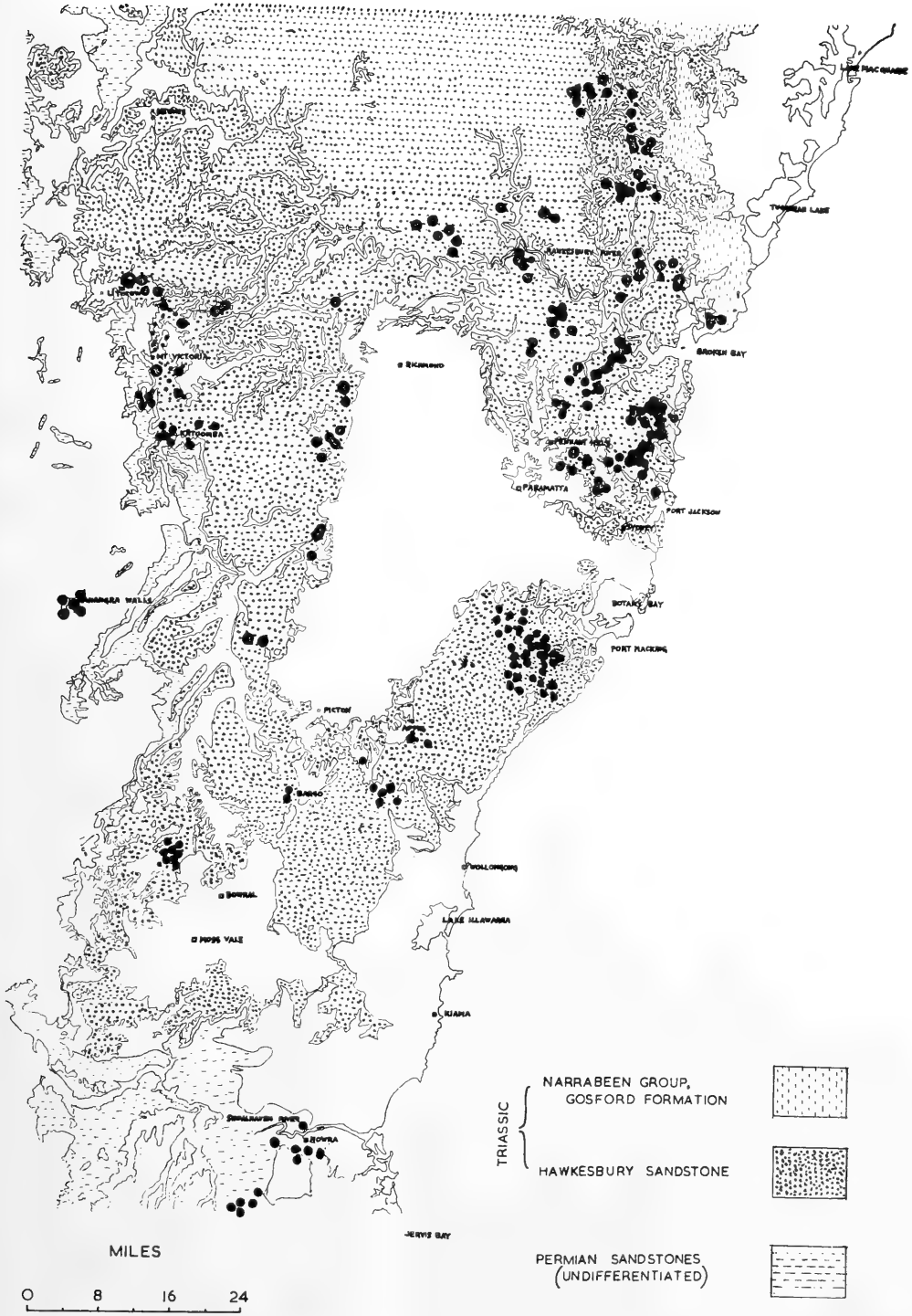


Fig. 11. Map of total distribution relative to areas of sandstone. The westernmost areas shown as Hawkesbury Sandstone are, according to Standard (1963), Narrabeen Sandstone but are mineralogically different from that in the Gosford area.

The geological basis for discontinuous distribution as described above is supported by the observation that *Phyllota*, at least in the Sydney region, is not unduly sensitive to such environmental factors as shading or exposure, and appears able to survive under a range of water availabilities. Plants of the same group have been found in very moist shaded situations, and in cracks in rocks with scarcely any soil and fully exposed to the sun, in the same area. Several facts tend to discount the importance of geological factors on distribution. Firstly, even single groups of *Phyllota* are found growing on a relatively wide range of sandstone types, thus groups 2 and 3 are found on the Permian, Nowra and Hawkesbury Sandstone, and on the mineralogically much richer Narrabeen Sandstone in the Gosford region. Secondly, it is found that while *Phyllota* is characteristically confined to sandstone, it is capable of extending for short distances on to shale soils, where small cappings of such soils remain in areas of sandstone, or where lenses of shale occur within the sandstone strata. Finally, *Phyllota* of group 8 will grow both on Hawkesbury Sandstone, as in the Katoomba area (though this is considered to be Narrabeen Sandstone by Standard, 1963), and also on the mineralogically richer Permian Sandstone of the Kanangra Walls region. Evidence such as this, that *Phyllota* is able to grow on such sandstones, even extending into the margins of the shale, would make it seem more probable that if distribution were being affected mineralogically, then, at least within sanstone soils, it would be by paucity of supply or by imbalance, rather than by general superfluity.

Cytology and barriers to interbreeding

Since the forms of *Phyllota* growing in the Sydney region showed a variety of types of genetic isolation, a number of investigations were carried out with the object of establishing the possibilities which existed for gene interchange between the groups.

A number of inflorescences were covered with muslin bags on representative plants from all the groups. The bags were attached prior to the opening of the flowers, and the plants revisited later in the year when seed could have been expected to have been set. The muslin-covered inflorescences were harvested, together with other inflorescences from the same plants which had not been so covered. In no case did any of the flowers covered with muslin set seed, from which it would appear that self-pollination is unlikely to occur in the field. Seed production from cross-pollination was variable, however, and at a low level, rather less than 5% of the exposed flowers producing seeds.

Isolation due to different flowering times

Absolute flowering times varied from year to year, but in the observation of three flowering seasons, the relative flowering times of the groups remained reasonably constant. The first groups to flower were 2, 3 and 5, doing so simultaneously during early August. These were followed by group 6 about three weeks later. In October or early November group 9 began flowering north of Sydney Harbour. This coincided with the end of the flowering season of group 6 although sufficient overlap occurred to permit of possible cross-pollination. With very few exceptions groups 2, 3 and 5 had ceased flowering by this time, so were isolated from direct genetic exchange with group 9. A possible bridge in time might exist however in the form of group 6, whose flowering time coincided with groups 2, 3 and 5 and with group 9. This would present no problem in the case of groups 2, 3, 6 and 9 since their geographical distributions are contiguous, but with the exception of the individuals mentioned in connection with the descriptions of geographical distribution, groups 5 and 6 are isolated from each other by both Sydney Harbour and Botany Bay. The members of group 9 occurring in the Appin region are in geographic contact with group 5. However, the members of group 9 in the Appin region, apart from the slight differences from the rest of group 9 already mentioned, also

differ in flowering time, since they do not flower until much later, usually in January, and are thus quite isolated temporally from the group 5 individuals with which they are in contact. Late flowering was also found to be characteristic of groups 1, 4, 7 and 8, all of which flowered in late December or January onwards. Group 4 and the Appin members of group 9 possessed a flowering period of similar length to that of the groups already described, i.e., groups 2, 3, 5, 6 and 9, the precise length appearing to be dependent on the season, but extending over about eight weeks. Thus group 4 and the Appin members of group 9, by commencing flowering in the beginning of January, experienced a temporal isolation from groups 2, 3 and 5 with which they may possess geographic contact (as was found to exist certainly between group 5 and the Appin members of group 9), while at the same time they are isolated geographically from the groups with contemporaneous flowering periods, i.e., groups 1, 7 and 8.

TABLE 1

Flowering periods, and geographic contacts of groups

Group	Flowering period								Geographic contact with groups
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mch.	
1						———	———	→	None.
2	———	———							3 5, 6 and 9.
3	———	———							2, 5, 6 and 9.
4						———	———		2, 3, 5 and 9 (Appin).
5	———	———							2, 3 and 9 (Appin).
6		———	———	———					2, 3 and 9.
7						———	———	→	8, possibly 2, 3 and 5.
8						———	———	→	7, possibly 2, 3 and 5.
9				———	———				2, 3 and 6.
9 (Appin)						———	———		2, 3, 4 and 5.

The flowering period of the remaining groups, 1, 7 and 8, while beginning in January, differed from the other groups described in being more extended, continuing until the autumn, but with fewer and fewer flowers being produced per inflorescence as the season progressed, a characteristic which is particularly marked in group 1, where one-flowered inflorescences were frequently produced late in the season. Groups 7 and 8 are virtually identical, apart from the pigmentation of the standard, and group 1 exists in geographic isolation.

The possibility that flowering periods were determined by environmental factors was investigated by transplanting members of the various groups to sites in the grounds of Sydney University. It was established that flowering occurred at times characteristic of the group, rather than in response to local climatic conditions. There was a tendency for flowering to be two to three weeks later than plants of similar groups in their natural habitats, also the flowering seasons were much shorter with far fewer flowers produced by all plants than would have been expected under natural conditions.

Information from field observations which would support the view that flowering times are controlled genetically rather than purely environmentally comes from two sources. Groups 2 and 3, which have an extremely wide distribution, flower at virtually the same time regardless of their position, and group 1 flowers at the same time as groups 7 or 8, although growing at a very much lower altitude, and in a much lower rainfall area.

Cytological Examination

All cells examined were found to have a chromosome number of $2n=14$. No differences were observed in the morphology of the chromosomes. The need for artificial breeding experiments is clear but, owing to the time required

to produce flowering progeny, and the difficulties experienced in raising seedlings, no attempts at artificial crossing were made. Voucher specimens were placed in the herbarium of Sydney University, and are listed in the formal taxonomic section of this work.

Growth Habit

Apart from the differing propensities for terminalization of the inflorescence as mentioned earlier, a number of further habit differences exist between the groups which for various reasons it was not possible to utilize in the construction of the model of phenotypic groups.

Branching pattern

The extent to which plants branched was characteristic of the different groups, and appeared to be related in some way to the tendency towards inflorescence terminalization. Groups 2, 3 and 5 branched most profusely, the branches emerging and remaining at an angle of about 45 degrees to the parent axis. Such branching tended to be, but was not invariably, associated with the formation of inflorescences. The resulting appearance tended to be of a rather compact bushy shrub. Groups 4, 6 and 9 showed less tendency towards branching and, associated with this, a more vigorous growth of existing stems, and a greater mean plant height, at least in the case of groups 6 and 9. Groups 7 and 8, although showing virtually no tendency towards inflorescence terminalization, and branching relatively infrequently, nevertheless showed a distinct limitation in the height to which they would grow, even in sheltered situations. Joined with them in the matter of height limitation was group 4, though to a rather lesser extent. The most extreme case of height limitation was found in group 1, in which the production of the characteristically few flowered inflorescences appeared in no way to interfere with the continued growth of the stem. Plant height seldom exceeded three to six inches, however.

Rooting system

Some explanation of plant height variations not apparently relatable to branching characteristics may be found in the form of the plant at and below ground level. In setting up the transplant experiments described previously, stolon-like structures were discovered while digging up plants in the field. Since the presence of runners had been used as a diagnostic character in the case of a South Australian species of *Phyllota* (Willis, 1957), their occurrence among the groups under discussion was investigated. Horizontal underground structures linking two or more aerial stem systems were found in groups 2, 3, 4, 7, 8 and 9. Microscopic examination showed that these possessed the anatomical structure of a root. The extent to which the root system developed suckers varied considerably among the groups, being most marked in groups 7 and 8, considerably less extensive in groups 4 and 9, but with the suckering roots much thicker in the latter though occurring rather less frequently. Suckering was very infrequent among groups 2 and 3, though short horizontal roots, about six inches long and rather thicker than the normal rooting system, were encountered frequently, even in seedlings about 12 months old. No examples of suckering were found in groups 5 or 6, though group 6 showed occasional examples of short horizontal roots similar to those found in groups 2, 3. No such roots were found in group 5, nor were any other indications of a tendency to produce suckers. Group 1, while showing no tendency to produce root suckers, achieved a similar, though lower, growth habit to groups 7 and 8 through an extensive prostrate stem system, from which arose short erect branches, bearing in turn a few even shorter lateral branches (see Pl. xxx). Continued growth of some aerial shoots caused them to become procumbent, finally forming part of the prostrate stem system. Apart from the presence of leaf bases, anatomical investigation confirmed the distinction of group 1 in

possessing a prostrate stem system, as opposed to the suckering root system of some other groups. The free and extensive suckering of groups 7 and 8, and to a lesser extent of group 4 (see Pl. xxx, *c* and *a*), would appear to be related in some way to the limited height achieved by their aerial parts, a situation paralleled in some degree by group 1. The stimulation of suckering by burning off the aerial parts during bush fires is a possibility, but since bush fires are prevalent throughout the areas of Hawkesbury Sandstone, it is not felt that this would account for the observed differences. The plant shown in Plate xxx was collected from an area believed not to have been burnt for some years, yet numerous young suckers were emerging. Examination of group 5 plants from areas known to have been burnt showed no trace of suckering, while among plants of groups 6 and 9 growing within a few feet of each other, plants of group 9 bearing suckers were easily found, while none were found on plants of group 6.

The Taxonomy of Phyllota *in New South Wales*

As was stated previously, the forms of *Phyllota*, presently referred to *P. phylicoides*, which occur outside the area covered by the investigation are remarkably uniform, and correspond in fact to groups 2, 3 in Figure 3. Some herbarium material from sites in Queensland might be referable to group 5 but, in the absence of non-terminal inflorescences, the distinction between the groups rests mainly on inflorescence characters which can be established only by destruction of the inflorescence. In any case, at least in the light of present knowledge, the entities recognized on the basis of information from the area under investigation include the whole range of variation found within what has been recognized hitherto as the species *P. phylicoides*.

Taxonomic status of the groups

The groups which have been described are, for the most part, easily recognizable in the field by a trained observer. A considerable amount of additional data exists supporting the status of the groups, but in many of the groups there is a lack of suitable discriminatory characters on which the confident allocation of some herbarium material might be made.

The difficulty described above presents the problem of purpose in erecting formal taxa. Barriers to gene interchange appear to exist between all groups with the exception of groups 2, 3 and 7, 8. The barriers, as described in an earlier section, apparently being distance, differing flowering times or, at least in the case of groups 6 and 9, genetic incompatibility. In this latter case, the two groups are found within six feet of each other, and the flowering periods overlap sufficiently to permit the possibility of frequent cross pollination. The absence of intermediate forms is so complete that no difficulty was experienced in distinguishing flowering individuals of the two groups at a glance; it was scarcely more difficult in the vegetative condition. Clearly information of this sort is not a satisfactory basis for decisions concerning barriers to gene interchange, and should be substantiated by controlled breeding experiments. The length of time involved, however, placed such a programme beyond the scope of this investigation. The probability of partial or complete barriers to gene flow between the groups is relevant to their taxonomic status but, even were complete genetic isolation demonstrated, the utility of erecting taxa not readily discriminated on morphologic grounds seems doubtful. A more appropriate vehicle for describing a number of the morphologically similar groups would appear to be the deme system of terminology (Gilmour and Heslop-Harrison, 1954), in which groups of plants characterized, for example, by geographic distribution or potentialities for gene interchange are described in such terms, without any implication of orthodox taxonomic rank.

Considering the group relationships in the light of all the available information, it is clear that the distinction least capable of substantiation is

that between 2 and 3. Their separation was the result of small consistent differences on a number of characters. The distinction was so slight as to be undetectable by subjective means, and even now cannot be confidently discriminated at sight. Such a distinction is clearly of little utility for taxonomic purposes, particularly in view of the common flowering time and distribution of the two groups. Consequently their distinction will not be maintained.

The combined groups 2 and 3 have, as their closest related form, group 5. Discrimination between these two groups in morphologic terms rests on the number of flowers per inflorescence, number of flowers per mm. and the number of leaves per 10 mm. respectively. A further distinction is given by the invariable inflorescence terminalization in 5 as opposed to the continued growth of the stem in 2, 3. Other distinctions lie in the production of occasional root suckers in 2, 3 and, rather less infrequently, short, thickened horizontal roots resembling abortive attempts at sucker production, as compared with the complete absence of anything approaching sucker formation in 5. Finally, the group distributions may be considered; apart from a small number of herbarium specimens from Queensland whose identity with 5 was doubtful, the group is confined to an area south of Sydney Harbour and, as far as can be determined, is isolated geographically from the possibility of gene interchange with 2, 3. Whether any incompatibility barriers also exist is not known, but the effective isolation might well be sufficient to account for the observed morphologic differences. While the magnitude of these differences is not sufficient to make a formal taxonomic distinction either necessary or practicable, recognition may nevertheless be given to 5 by describing it as a phenogamodeme. This term indicates at one time the spatial, temporal, and genetic possibility of interbreeding within the group and also the existence of phenotypic distinction from other groups.

The status of 4 is to some extent analogous to that of the members of 9 occurring in the Appin area. Both are represented by small numbers of individuals, and occur in a limited geographical area. In both cases the large flowers occurring in lax inflorescences suggest affinities with 7, 8 and 9. However, the inflorescences of Appin individuals are both shorter and contain fewer flowers than other members of 9. Those of 4 are quite typical of 7 and 8. Despite the similarity of inflorescence with 7 and 8, in almost all other characters, 4 shows greatest affinity with the central complex of groups as may be seen in Figure 3. As a consequence of this, it has been decided to unite 4 with 2, 3 and hence with 5 for taxonomic purposes. Individuals at Appin can best be left as members of 9 since, although differences exist, they are associated most closely with this group and, in the absence of further information concerning their origin, cannot be separated reasonably from it. Both group 4 and the Appin members of 9 may be given some recognition in the deme terminology as phenotopodemes, though absence of sufficient evidence precludes the use of the distinction gamodeme.

Groups 6 and 9 show greater morphologic distinction from each other and from group 2, 3 than other groups described so far. They differ also in having superposed distributions, though that of group 9 is more restricted in area. Both groups 6 and 9 tend to be characterized by taller growing plants than group 2, 3, though this may be obscured by the age of the plants. As in the groups described already, flower and inflorescence characters are of particular discriminatory value. Inflorescence length is least in group 2, 3, followed by group 6, and finally group 9 has the longest inflorescence. Inflorescence density serves to distinguish groups 2, 3 and 9 with lax inflorescences, from group 6 in which the number of flowers per millimetre is much greater, though not equal to that found in group 5. A suspected connection between inflorescence density and tendency towards inflorescence terminalization was not borne out by group 6, since, although possessing denser inflorescences than group 2, 3, it shows a considerably greater tendency towards vigorous continued growth

of the stem after inflorescence production. Above average length of inflorescence, coupled with great density, results in group 6 having the highest value of any group for the number of flowers per inflorescence. Apart from the characters already described, group 9 is distinguished from group 2, 3 and from group 6 by high values for weight per millimetre of leaf length ; indeed, this character distinguishes group 9 from all groups other than groups 7 and 8, where other distinctions apply. The absence of root suckers in group 6 provides a further link with group 5, while at the same time distinguishing it from group 9 in which such suckers are frequently found, and group 2, 3 in which they are occasionally present.

TABLE 2

Summary of major discriminating characters

Presence of	Characteristic of groups
Procumbent stems	1.
Consistent and prolific production of root suckers	7, 8.
Consistent terminalization of inflorescence	5.
Large flowers	4, 7, 8, 9.
Lax inflorescence	4, 7, 8, 9.
Long inflorescence	6, 9.
Recurved leaf tips	7, 8.
Numerous flowers in inflorescence	5, 6.
Massive leaves	9.

This qualitative table is by no means exhaustive, and should be interpreted in conjunction with the text. Quantitative values have been omitted in the interests of simplicity, but may be found in the formal taxonomic descriptions.

Information concerning breeding behaviour on the north shore of Sydney Harbour may be summarized as follows : Temporal isolation precludes direct gene flow between group 2, 3 and group 9, though group 6 represents a possible temporal bridge. In the absence of direct experimental evidence, no final conclusions on gene flow can be reached ; it may be said, however, that in view of the distributions and flowering times of the groups, the absence of intermediate forms, particularly between groups 6 and 9, would suggest inter-group sterility.

In the light of the above considerations, group 9 will be restored to specific rank. The status of 6 is less clear ; while this group shows sufficient differentiation from groups 2 to 5, when these are considered as individual groups, to merit infra-specific distinction, the increase in range of character variation resulting from the combination of 2 to 5 is such that confident discrimination between this combined group and 6 can no longer be achieved. Group 6 will be merged, therefore, with these groups for formal taxonomic purposes, though it undoubtedly represents a phenotopodeme of rather greater distinction. In the absence of spatial or temporal breeding isolation, a decision regarding its status as a gamodeme must be reserved until direct experimental evidence is available.

The two groups occurring in the Upper Blue Mountains, 7 and 8, show little morphologic differentiation from each other, except in pigmentation of the standard. Geographic distributions are not identical, but show considerable overlap. Since flowering times are identical, little can be said concerning the breeding behaviour of the two groups other than that there is no obvious barrier to interbreeding. The contrary evidence provided by the absence of intermediate forms is of rather less weight than in other groups, since the phenotypic distinction is confined to characters which might have a very similar genetic origin. While the differences in pigmentation enable the two groups to be recognized as separate phenodemes, it is not felt to be a distinction meriting formal taxonomic status. Consequently, these two groups will be considered together ; in this combined form ready discrimination from other groups is

still possible. In qualitative terms it may be said that the group differs from the 'central complex' of Figure 3 in possessing lax inflorescences of larger flowers (though see previous remarks concerning group 4), and the much greater leaf weight per mm. It is distinct from group 9 in its lesser plant height, number of flowers per inflorescence, rather smaller flowers and narrower bracteoles. Characters separating 7 and 8 from all other groups are the consistently recurved and acuminate leaf tips, and the abundance of root suckers produced by unspecialized roots. With the exception of two apparently anomalously located individuals from other groups, geographic isolation would appear to be complete from all other groups and, even if the two individuals mentioned should be representative of others as yet undetected, breeding isolation would still be maintained by virtue of the differing flowering times. In the light of the above considerations, the combined groups 7 and 8 will be restored to specific rank.

The remaining group, group 1, shows considerable morphologic differentiation from other groups. It differs from the combined groups 7 and 8 in its smaller flowers, absence of acuminate recurved leaf tips, and in having a lower value for leaf weight per mm. It can be distinguished from 9 by size of floral parts, pigmentation of standard, inflorescence length and flower number, length and weight per mm. of leaves, plant height and number of leaf tubercles. From the 'central complex' of groups, group 1 differs in respect of plant height, inflorescence length, bracteole breadth, pigmentation of standard, and leaf length. Group 1 differs from all other groups in its low creeping habit and prostrate stem, and also in geographical distribution. In view of the degree of differentiation indicated above, it is felt that group 1 should be restored to specific rank.

Thus in this area, specific rank is given to the following four assemblages: 1; 9; 7, 8; 2, 3, 4, 5, 6.

The Relationship of Specific Epithets previously applied to Phyllota *in New South Wales, to the Groups described*

In view of the considerable synonymy of the New South Wales species of *Phyllota* it is proposed to consider the specific epithets available, the groups to which they refer, and hence the synonymies of the species, prior to the formal descriptions of the species occurring in New South Wales as determined by this investigation.

PHYLLOTA HUMIFUSA A. Cunn. ex Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

Features of the holotype of this species which are of importance in relating the type specimen to the groups described in the preceding section are as follows: Stems prostrate, thin and wiry. Leaves 6 mm. long, 0·5 mm. wide, apex recurved with a small mucro. Inflorescence few–flowered (*ca.* 3), loose, not terminal. Bracteoles linear-lanceolate, 3 mm. long, 1 mm. wide. Calyx hirsute with appressed hairs, *ca.* 4 mm. long (lobes 2 mm.). Ovary villous, style glabrous.

Holotype: Wombat Brush, Argyle County, N.S.W. A. Cunningham No. 8 (K).

These characters, combined with the locality of the type specimen, leave no doubt as to the identity of *P. humifusa* with group 1.

PHYLLOTA SQUARROSA (Sieber ex DC.) Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

Basionym: *Pultenaea squarrosa* Sieber ex DC. *Prod.*, II: 113 (1825).

Leaves divergent, recurved, with distinct recurved, acuminate yellow tips, leaves *ca.* 1·3 mm. long. Flowers few in spike, axis growing on while still in flower. Standard *ca.* 9·5 mm. long.

Holotype: Sieber No. 406 (GEN). The isotype at Kew bears Sieber's original label, and is localized as Blue Mountains; there are also two sheets bearing this number at MEL. This specific epithet will be applied to the combined groups 7 and 8.

Two names are available for the species represented by group 9: *Phyllota pilosa* Benth. and *Phyllota grandiflora* Benth. Both species were erected by Bentham in *Ann. Wien. Mus.*, II: 77 (1838), but included by him in *Phyllota phylicoides* in *Fl. Austr.*, II: 95 (1864). The latter epithet will be adopted, since it describes the more striking and constant feature of the species.

PHYLLOTA PILOSA Benth.

There are three sheets of Huegel's collection at Vienna, two of which correspond to group 9; the remaining sheet differs in a number of respects from both the two preceding sheets and Bentham's description of the species, corresponding more closely to the type of *P. comosa*. In particular this last sheet possesses rather more slender, erect leaves, the hairs over the whole plant being more appressed. The flowers are smaller and the calyx much less pilose. It corresponds most closely to NSW 7226, Gordon West, M. Tindale, except for slightly longer, yellowish hairs.

P. GRANDIFLORA Benth.

Only one sheet bearing this name exists at Vienna, and none at Kew. The specimen corresponds to Bentham's diagnosis of *P. grandiflora*, but this does not differ sufficiently from that of *P. pilosa* to differentiate the two species; thus for *P. grandiflora*, '. . . foliis supra tuberculoso-scabris subtus pubescentibus . . .', and '. . . bracteolisque pilosis flore brevioribus . . .', while for *P. pilosa*, '. . . foliis tuberculoso-scabris muticis, novellis calicibusque pilosis, floralibus flores aequantibus . . .'; the type specimens, with the exception referred to in the case of *P. pilosa*, all being referable to group 9.

P. COMOSA (Sieber ex DC.) Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

Basionym: *Pultenaea comosa* Sieber ex DC. *Prod.*, II: 113 (1825).

Holotype: Sieber No. 407. Locality, Nov. Holl. Two sheets of this material are at Vienna, and one at Kew, all bearing Sieber's original label, and also two at MEL. The Kew isotype is similar to the specimen NSW 7226 Gordon West, M. Tindale. The vigorous continued growth of the axis is characteristic of groups 6 and 9, while the size of the floral parts satisfactorily establish *P. comosa* as a binomial associated with group 6. This is also in accord with the isotypes at MEL.

P. ASPERA (Sieber ex DC.) Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

Basionym: *Pultenaea aspera* Sieber ex DC. *Prod.*, II: 113 (1825).

Holotype: Sieber No. 408. Locality, Nov. Holl. There are two sheets of this material at Vienna, one of which was acquired via Reichenbach fil., possibly in 1889. Since Bentham described the species while in Vienna, it would seem possible that his diagnosis of *P. aspera* was derived from the other sheet, previously at Vienna; this deduction would be in accord with the fact that Bentham's description '. . . bracteis glabris . . . . calycibus vix pubescentibus . . .' fits the specimen at Vienna. The sheet at Kew bearing Sieber's number 408 is also labelled Wm. Mac Arthur, No. 13, *Pultenaea asperata* (sic); no precise location is given, but another specimen of this is labelled Bargo Brush, Mac Arthur. It does not agree with Bentham's diagnosis with respect to the bracteoles and calyx quoted above, but resembles the specimen W. F. Blakely, The Valley, Hornsby, NSW 36368. These observations would place the Kew sheet in group 9, in contrast to the specimen seen by Bentham in Vienna, and the three sheets at MEL, which have been identified with group 6.

P. BILLARDIERI Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

The holotype of this binomial is at Vienna, having been collected by Labillardière, with no record of the locality. The predominantly glabrous nature of the plant '. . . ramulis vix puberulis, foliis glabris . . . . bracteolis glabris . . . . calycibus glabrisculis . . .' would all seem to prohibit reference of the name to group 9, all the members of which tend to be moderately to markedly hirsute, at least in the calyx, and never wholly glabrous. The size of the leaves, 10·0 mm. long, 1·5 mm. broad, pedicels 1 mm. long, bracteoles nearly ovate, with a breadth of 3 mm., and an overall flower length of 9 mm., which would correspond to a standard length of 8·5–9·0 mm., all tend to exclude the possibility of reference to group 9. A photograph of the holotype excluded the possibility of groups 1 and 7, 8, though group 1 was in any case excluded on the basis of the measurements. The diagnosis 'Spica oblonga subterminali' excludes group 5 from consideration, thus leaving the conclusion that this epithet properly belongs with group 2, 3 or group 6, though insufficient data are available to differentiate between these two groups.

P. PHYLICOIDES (Sieber ex DC.) Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

Basionym: *Pultenaea phylicoides* Sieber ex DC. *Prod.*, II: 113 (1825).

Holotype: Sieber No. 405. Locality, Nov. Holl. There are three sheets of this collection, all bearing Sieber's original number, two at Vienna (one via Reichenbach fil.) and one at Kew. There are three sheets at MEL and a second sheet at Kew, which does not bear Sieber's original label, but is marked 'ex Herb. Mus. Vind.'. It bears no flowers, but is mounted with a specimen labelled '14, Pultenaea, Sydney, Hooker 1845', which corresponds to group 5. The Kew isotype possesses leaves of length 13 mm., which are not mucronate. This feature is characteristic of members of group 5, the leaves being obtuse and with an extremely small black mucro which is very deciduous; this characteristic appears in Bentham's diagnosis as '. . . foliis obtusis'. The diagnosis also states 'spicis brevibus terminalibus', a distinctive characteristic of group 5 since any growth of the axis following production of an inflorescence rapidly dies back, leaving the inflorescence effectively in a terminal position. Finally, the numerous and small flowers (length overall 6 mm.) are both characteristic of group 5, which is in accord with the MEL isotypes.

P. BAUERI Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

Now at Kew and ex Herb. Mus. Vind., the holotype is mounted on the same sheet as another specimen collected by the U.S. Exploring Expedition, under Wilkes, at Sydney, this second specimen also being labelled *P. baueri.* The small leaves with minute mucro, and the small flowers in a subterminal inflorescence, identify this name with group 2, 3. It consequently becomes synonymous with *P. phylicoides.*

P. STURTII Benth. in *Fl. Austr.*, II: 95 (1864).

Holotype: C. Sturt, South Australia (K). Personal examination of the holotype of this species identified it with groups 2, 3 although it is described by Bentham as being between *P. phylicoides* and *P. barbata.* It is surprising that no similar collections have been made in South Australia subsequent to that of Sturt; possibly the location refers in fact to southern New South Wales, though it is unlikely that Sturt collected in this region. There is, however, no doubt as to the identity of the specimen with groups 2, 3, and hence synonymous with *P. phylicoides.*

TAXONOMIC DISCUSSION

Intrageneric relationships of Phyllota *Benth.*

The species of *Phyllota* occurring on the east coast of Australia are distinguished from the remaining species of the genus in a number of respects.

Adnation of the petals and stamens is well marked in the New South Wales species, usually all 10 stamens being firmly united to the petals along the length of the claws. In addition, the claws of one or both wings are not uncommonly fused to that of the standard. In the remaining species, adnation is much less common, being confined to 5 or fewer of the stamens attached to the base of the petal claws, connation of the petal claws not occurring at all.

A distinction which may bear some relation to adnation of stamens is seen in the persistence of petals and stamens after flowering in the east coast species. This persistence was such that the remains were still present at maturity of the legume, while in other species petals and stamens were deciduous soon after enlargement of the legume began.

Final distinguishing features of the east coast species are seen in the shape and texture of the bracteoles. The lanceolate, herbaceous bracteoles, common to all these species with the exception of *P. humifusa*, are not found in the remaining species. Many possess scarious or coriaceous bracteoles, e.g. *P. diffusa*, *P. remota*, and *P. pleurandroides*, while those of the Western Australian species are very similar to foliage leaves, except in *P. luehmannii*, the bracteoles of which were found to approach the expanded leafy form found in the east.

P. barbata and *P. gracilis* in Western Australia represent another distinct group of species, being distinguished by barbulate styles, and acute, narrowly lunate keels. The relationship of these species is obscure, due to the lack of material of *P. gracilis*, a species represented solely by the type collection.

Apart from the larger discontinuities in the genus described above, interspecific distinctions within the genus appear, at least from a subjective approach, to be at approximately the same level of significance, with size, shape and texture of the bracteole being most useful in taxonomic discrimination, followed by size and shape of the standard.

The relationship of Phyllota *to the genera* Pultenaea, Dillwynia, *and* Aotus

Discriminating characters

Leaves : A satisfactory distinction exists between *Phyllota* and *Dillwynia* in that the leaves of *Dillwynia*, while being narrow-linear, are, without exception, involute as opposed to revolute. The leaves of *Aotus* and of some species of *Pultenaea* are similar to those of *Phyllota*.

Stipules : The presence or absence of stipules is not a reliable distinguishing character between the genera quoted, though it has been used as such in the past. All species of *Phyllota* have been found to possess minute stipules, stipules of the same size being found in at least some species of *Dillwynia* and *Aotus*. While *Pultenaea* has been characterized frequently as having more or less obvious stipules, in many species they are minute, and in others quite absent.

Bracts : Clear intergeneric distinctions are afforded by the form and texture of the bracts, these being small, brown and scarious in *Pultenaea*, *Dillwynia* and *Aotus*, also deciduous in the latter two genera. In *Phyllota*, however, the foliage leaves subtending the flower are unaltered, except in two instances : *P. pleurandroides* shows what may be an approach to the formation of differentiated bracts in the virgate clusters of leaves with altered bases which surround the flower ; on the specimen of *P. georgii*, now referred to *P. luehmannii*, the floral leaves, and those immediately below the inflorescence, no longer show the characteristic revolute form, but are nearly flat, with recurved margins.

Bracteoles : The range of bracteole form in the genus *Phyllota* has already been discussed. The presence, in at least some of the species, of minute scarious bracteoles removes this character as a source of intergeneric distinction, at least from *Pultenaea*, since such bracteoles are also characteristic of the latter genus. *Dillwynia* possesses similar bracteoles, but they are remote from the calyx and deciduous, while *Aotus* is without bracteoles.

Petals : No satisfactory distinctions may be made on the basis of petal shapes or relative sizes, due to the variation within genera, the biggest distinction existing between *Phyllota* and *Dillwynia*, where the orbicular to almost reniform standard of *Dillwynia* is only approached by some species of *Phyllota.*

Stamens : Adnation of stamens to the petals is confined to the genus *Phyllota*, though it has not been possible to establish the complete absence of this phenomenon in the other three genera. It has been possible to show, however, that there is considerable variation in the extent to which adnation occurs within the genus *Phyllota*, varying from fusion of stamens to petals and also of the petal bases themselves in *P. phylicoides* and the other New South Wales species, to the situation found in *P. diffusa* where the adnation is so slight as to be virtually undetectable, and certainly comparable with the situation occurring in at least some members of the genus *Pultenaea.*

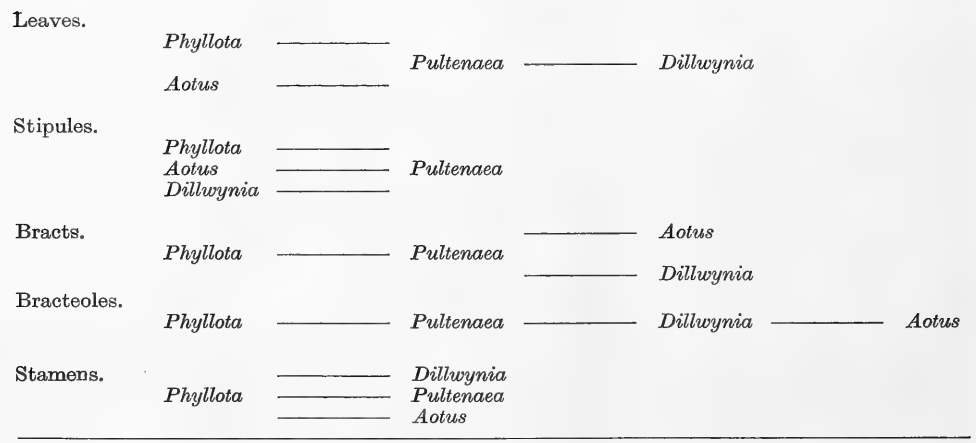
Style : As a result of the intrageneric variation associated with stylar characteristics, and also the range of intraspecific variation associated with this character, little discriminatory value attaches to it, except in the case of *Dillwynia* which differs from the other genera in possessing a thicker, more truncate style, and *Aotus* in which the style is generally filiform.

Seed : All the genera under discussion possess two ovules per ovary, of which characteristically only one develops into a mature seed. The genera are also united in possessing reniform seeds of similar size ranges. The strophiole is a distinguishing character of limited value, being wholly absent from *Phyllota*, wholly present as far as is known in *Dillwynia* and, with some exceptions, present in *Pultenaea* and absent in *Aotus.*

The intergeneric relationships described above may be summarized as follows :

The genus *Pultenaea*, by virtue of its greater size and more diverse nature, appears to act as a central link joining the other three genera considered. Thus, in the form of its bracteoles, *Phyllota* appears to be linked to *Dillwynia* and *Aotus* via *Pultenaea.* A similar series may be seen in the form of the bracts, though there is much greater discontinuity in this case, in which no species of *Phyllota* shows any leaf modification comparable with that found in *Pultenaea.*

In leaf form *Phyllota* and *Aotus* appear to be alike, and linked to *Dillwynia* via *Pultenaea.* The small size or absence of stipules in *Phyllota*, *Dillwynia* and *Aotus* would unite them with relation to the greater part of the genus *Pultenaea*, though without creating any discontinuity, since similar forms are also found in the latter genus. Since stamens are free in all the genera except *Phyllota*, the positions of *Phyllota* and *Pultenaea* are the reverse of those obtaining in the case of stipules.



Status of the genus Phyllota

The relationships of the genus have been considered in the previous section; whether these relationships are sufficiently distant to warrant generic rank is debatable. It will be seen that the association is particularly close between *Phyllota*, *Aotus* and *Pultenaea*. The distinction between *Phyllota* and *Aotus* is acceptable at the generic level in that the two genera differ quite clearly in the form of their bracts and of their bracteoles. These structures bear a relationship to each other which leaves these two distinguishing characteristics with rather less weight than might have been carried by a more dissimilar pair of characters, but when considered in conjunction with a number of correlated but less constant characteristics, for example, those concerned with the shape of the standard and of the style, there is a dissimilarity which is of satisfactory generic rank. The distinction between *Phyllota* and *Pultenaea* is less satisfactory; founded originally on differences in stipules, bracts, bracteoles, stamens and seeds, discrimination can now be based only on the bracts. It would seem doubtful if generic distinction could properly be based on one such character, without support from a number of other, more or less constant character differences. That the distinction is narrow is emphasized by some Western Australian species of *Pultenaea*, e.g. *P. dasyphylla* (Turcz.) C. A. Gardn., *P. lycopodioides* (S. Moore) and *P. capitata* (Turcz.) C. A. Gardn., none of wnich possess strophioles, and whose only apparent common difference from *Phyllota luehmannii* rests in the recurved rather than revolute form of the leaves, a distinction which, it will be recalled, was largely bridged by the specimen of *P. luehmannii* originally attributed to *P. georgii*.

While there is no doubt that such doubtful generic limitations are unsatisfactory, the generic status of *Phyllota* has been maintained in this study, since it is felt that an evaluation of the generic status of *Phyllota* should form part of an overall review of the Podalyrieae, or at least those members of the tribe already mentioned and known to be allied to *Pultenaea*.

Formal Descriptions of Taxa

Characters used in formal descriptions have been largely confined to those of value in intrageneric discrimination, those of generic distinction being considered in the section dealing with the status of the genus.

Of the specimens examined, only those belonging to collections known to have been lodged in European herbaria, or which are readily identifiable by accession numbers to Australian herbaria, have been included in the citations of specimens following the formal descriptions.

Taxonomy

Phyllota (DC.) Benth.

Fl. Austr., II: 93 (1864); Engler et Prantl, *Nat. Pflanz. Fam.*, III, 3: 210 (1894); Benth. et Hook., *Gen. Pl.*, I: 470 (1865); Moore et Betche, *Handb. Fl. N.S.W.*, 135 (1893); Ewart, *Fl. Vic.*, 640 (1931); Black, *Fl. S. Aust.*, II: 442 (1948); Thompson in *Contrib. N.S.W. Nat. Herb., Fl. N.S.W.*, No. 101: 45 (1961).

As *Pultenaea* sect. *Phyllota* DC., *Prod.*, II: 113 (1825); Curtis, *Stud. Fl. Tasm.*, I: 132 (1956).

Shrubs, with stems terete, pubescent at least in the upper parts, echinate with decurrent leaf bases. Leaves alternate, simple entire, linear, the margins revolute; stipules minute or absent. Flowers axillary, solitary or crowded towards the ends of the branches, sometimes appearing terminal by death of the distal axis; pedicels 1–5 mm. long; bracts identical with, or scarcely differing from, foliage leaves; bracteoles 1–15 mm. in length, scarious, coriaceous or frequently herbaceous, inserted at the base of the calyx. Calyx with the two upper lobes broader than the lower, and connate higher up.

Corolla: petals all clawed, the standard ovate to orbicular, equal to or somewhat exceeding the others. Stamens adnate to petals or scarcely so in some species. Ovary sessile, pubescent to villous, ovules 2, on short funicles, the style dilated or thickened at the base, incurved and subulate above, the stigma small and terminal. Legume inflated, twice as long as the calyx at maturity, containing 1–2 seeds. Seed reniform, not strophiolate.

A genus of 10 species, endemic in Australia.

Key to the Species of Phyllota

A. Style bearded upwards on inner edge
  B. Flower 12 mm. long, pedicel less than 1·5 mm. long .. .. .. *P. barbata*
  B′. Flower 5 mm. long, pedicel 4 mm. long, exceeding the calyx .. *P. gracilis*
A′. Style not bearded on inner edge
  C. Bracteoles herbaceous, linear or lanceolate
    D. Stem, bracteoles and calyx yellow tomentose, flowers in dense heads, keel purple, petals and stamens deciduous after flowering .. .. *P. luehmannii*
    D′. Stem glabrous to pubescent, bracteoles and calyx glabrous to villous, if flowers in dense heads then keel not purple, petals and stamens persisting until maturity of legume
      E. Flowers in lax spikes towards the ends of the branches, leaf tips acuminate and recurved, numerous root suckers formed .. .. *P. squarrosa*
      E′. Flowers scattered, in lax spikes or dense terminal heads, leaf tips never acuminate and recurved, root suckers absent or few from a thickened root-stock
        F. Procumbent shrub with purple-red corolla; flowers solitary or few together, bracteoles linear .. .. *P. humifusa*
        F′. Erect shrub with flowers in dense spikes at or towards the ends of the branches
          G. Leaves massive, 1·25–2·25 mm. broad, standard 10–15 mm. long, calyx densely villous .. .. *P. grandiflora*
          G′. Leaves slender, 0·75–1·25 mm. broad, standard 5–11·5 mm. long, calyx glabrous or pubescent .. .. *P. phylicoides*
  C′. Bracteoles scarious or coriaceous, not green
    H. Bracteoles oblong-ovate, as long as the calyx, keeled, mucronate .. *P. remota*
    H′. Bracteoles ovate, less than 2 mm. long, not keeled
      I. Flowers solitary or in pairs, in virgate clusters of leaves along the stem; leaves recurved and acuminate.. .. .. *P. pleurandroides*
      I′. Flowers in spikes towards the ends of the branches; leaf tips not recurved, obtuse .. .. *P. diffusa*

Phyllota phylicoides (Sieber ex DC.) Benth.

In *Ann. Wien. Mus.*, II: 77 (1838); Benth., *Fl. Austr.*, II: 95 (1864); Moore et Betche, *Handb. Fl. N.S.W.*, 135 (1893); Thompson in *Contrib. N.S.W. Nat. Herb., Fl. N.S.W.*, No. 101: 45 (1961).

Nomenclatural synonym: Pultenaea phylicoides Sieber ex DC., *Prod.*, II: 113 (1825). BASIONYM.

Taxonomic synonyms: Phyllota baueri Benth. in *Ann. Wien. Mus.*, II: 77 (1838); *Phyllota billardieri* Benth. in *Ann. Wien. Mus.*, II: 77 (1838); *Phyllota comosa* (Sieber ex DC.) Benth. in *Ann. Wien. Mus.*, II: 77 (1838); *Phyllota aspera* (Sieber ex DC.) Benth. in *Ann. Wien. Mus.*, II: 77 (1838); *Phyllota sturtii* Benth. *Fl. Austr.*, II: 95 (1864).

A shrub 90 cm. (15–165 cm.) high, with stems terete, pubescent at least in the upper parts. Leaves linear, 10 mm. (5·5–19 mm.) long, 1 mm. (0·75–1·25 mm.) broad, bullate, obtuse to acute (1–3 on the subjective scale); stipules minute. Flowers 23 (11–83), crowded together into leafy spikes 13 mm. (8–45 mm.) long towards the ends of the branches. Pedicel 1 mm. (0·5–1·5 mm.) long. Bracts identical in appearance with foliage leaves; bracteoles lanceolate, 7·5 mm. (4·0–11·5 mm.) long, 1·7 mm. (0·5–3·5 mm.) broad, herbaceous with scattered or numerous short appressed silky hairs, borne on the base of the calyx. Calyx 5·3 mm. (3·5–9·0 mm.) long, almost glabrous

or with scattered to numerous short appressed silky hairs; lower lobes acuminate, longer than, or equal to, or shorter than the tube; upper lobes broader connate higher up and less acuminate. Corolla: keel equal in length to standard, broadly lunate to semi-circular, obtuse, yellow to yellow-green; wings equal in length to standard, oblong to semi-circular, laciniate at base, obtuse and rounded, sometimes almost acute, yellow; standard 8 mm. (5–11·5 mm.) long, ovate, obtuse and rounded, yellow or yellow with red markings. Stamens 10, some or all adnate to petals at base, both persistent after flowering. Ovary villous, style dilated or thickened at base, incurved or subulate above, pubescent with short appressed silky hairs below the curve. Legume 1–2 seeded, 1–2 times as long as the calyx. Seed reniform.

Distribution: Coast and tablelands of New South Wales and Queensland to Bundaberg.

Habitat: Sandstone heath and dry sclerophyll forest.

Chromosome number: 2n=14, voucher specimens R. C. Jancey No. 2; R. Carolin No. 3933; R. C. Jancey No. 3; V. Sands sine num.; R. C. Jancey No. 4; R. C. Jancey No. 5 (SYD).

Typification: Holotype: Sieber No. 405 GEN. Isotypes K, WIEN.

Selected specimens examined: New South Wales: Neutral Bay, J. B. Cleland, 9/1910, (AD 96311325); Port Jackson, R. Schomburgk, 8/1896, (AD 96311334); Shoalhaven, W. Bäuerlen, No. 396, 9/1883, (MEL); Kurrajong, Miss Atkinson, No. 13, —, (MEL); Richmond River, Mrs. Hodgkinson, 1874, (MEL); Long Bay, Miss C. Cowle, 1907, (MEL); Sandy Cape, R. Brown, —, (MEL); Fl. Nov. Holl., Sieber, No. 407, (MEL); Fl. Nov. Holl., Sieber, No. 408, (MEL); Mitchell's Expedition of 1836, Mitchell 291, 8/1836, (MEL); Nov. Holl., Lambert, —, (MEL); Nov. Holl., Sieber, No. 405, —, (MEL); Caloundra, L. J. Brass, 10/1934, (CANB 24244); French's Forest, G. H. Clarke, 9/1920, (CANB 4535); Middle Harbour, G. H. Clarke, 12/1920, (CANB 4534); Oxford Falls, K. Mair, 26/8/1953, (NSW 36444); Wahroonga, L. A. S. Johnson, 23/6/1945, (NSW 36445); Terrey Hills, M. Tindale, 12/8/1961, (NSW 55356); Dural, D. C. Cross, 5/9/1945, (NSW 15668); Cheltenham, N. C. Ford, 4/7/1945, (NSW 36421); Castlecrag, M. Tindale, 1/8/1948, (NSW 7227); Mount Colah, G. Chippendale, 18/8/1953, (NSW 36398); Berowra, R. H. Cambage, No. 499, 9/1901, (NSW 36429); Asquith, F. J. Thomas, 24/8/1951, (NSW 36434); Currockbilly, J. L. Boorman, 2/1910, (NSW 36393); Snowball, F. A. Rodway, No. 11734, 12/1940, (NSW 36395); Cooma, J. L. Boorman, 12/1915, (NSW 35391); Nerriga, F. A. Rodway, No. 13467, 3/1944, (NSW 36394); Como, J. L. Boorman, 9/1916, (NSW 36412); Gymea Bay, A. Cahill, 10/1938, (NSW 36409); National Park, Anderson and Boorman, 9/1921, (NSW 36413); Glenbrook, A. A. Hamilton, 10/1914, (NSW 36432); Blaxland, Blakely and Chisholm, 10/1929, (NSW 36426); Bundanoon, H. E. Ellen, 3/1917, (NSW 36448); Pigeon House Ra., Nerriga, E. F. Constable, 10/1957, (NSW 45273); Jervis Bay, F. A. Rodway, 10/1931, (NSW 36403); Wentworth Falls, W. F. Blakely, 11/1938, (NSW 36480); Box Point to Barber's Creek, J. H. Maiden, 10/1896, (NSW 36450); Appin, J. H. Maiden, —, (NSW 15662); Wiseman's Ferry, J. L. Boorman, 4/1908, (NSW 36433); Gosford, Blakely and Shiress, 1/1927, (NSW 15665); Woy Woy, Blakely and Buckingham, 10/1939, (NSW 15667); Somersby, G. Chippendale, 8/1953, (NSW 36418); Maroota, W. F. Blakely, 9/1929, (NSW 36439); Corindi, E. J. Constable, 11/1956, (NSW 4221); Bulladelah, J. Garden, 10/1951, (NSW 36379). *Queensland:* Sunnybank nr. Brisbane, C. T. White, No. 985, 9/1921, (NSW 36390); Sunnybank, L. A. S. Johnson, 6/1951, (NSW 36385); Mt. Gravatt, L. A. S. Johnson, 6/1951, (NSW 36386); Moreton Island, C. T. White, 9/1907, (NSW 36388); Stradbroke Island, H. S. McKee, No. 8725, 9/1961, (NSW 56450); Burrum, M. E. Watson, 10/1929, (BRI 036876); South Brisbane Cemetery, F. M. Bailey, 3/1875, (BRI 036889); Apsley, C. T. White, No. 6133, 7/1929, (BRI 036875); Coolum, Miss

M. S. Clemens, 4/1945, (BRI 036871); Mt. Gravatt, C. T. White, No. 7409, 3/1931, (BRI 036868); The Blunder, nr. Brisbane, C. E. Hubbard, No. 3584, 8/1930, (BRI 036863); Plunkett, C. E. Hubbard, No. 3784, 8/1930, (BRI 036862); Tingalpa, D. A. Goy, No. 134, 9/1936, (BRI 036860); Maryborough, Miss M. S. Clemens, 9/1948, (BRI 036857); Capalaba, L. Pedley, No. 426, 8/1959, (BRI 024332); Keppel Bay, C. T. White, No. 8032, 9/1931, (BRI 036882); Bundaberg, J. Keys, No. 336, —, (BRI 036887).

Phyllota grandiflora Benth.

In *Ann. Wien. Mus.*,, II: 77 (1838).

Taxonomic synonym: *Phyllota pilosa* Benth. in *Ann. Wien. Mus.*, II: 77 (1838).

A shrub 90 cm. (60–150 cm.) high, stems pubescent at least in the upper parts. Leaves linear, 13 mm. (6–17·5 mm.) long, 1·25–2·25 mm. broad, densely minute-bullate, obtuse or acute (1–3 on the subjective scale); stipules minute. Flowers 23 (6–59) in lax leafy spikes towards the ends of the branches. Pedicel 1–2 mm. long. Bracts identical in appearance with foliage leaves; bracteoles lanceolate, 11 mm. (8·5–15·0 mm.) long, 2·7 mm. (2·0–4·0 mm.) broad, herbaceous, with scattered to numerous appressed silky hairs, borne on the base of the calyx. Calyx 8·2 mm. (6·0–10·0 mm.) long with numerous appressed silky hairs; lower lobes acuminate, equal to or shorter than the tube; upper lobes broader, connate higher up, acuminate. Corolla: keel equal in length to standard, broadly lunate to semi-circular, obtuse, yellow occasionally tinged with green; wings shorter than or equal to the standard, semi-circular, laciniate at the base, obtuse and rounded, yellow; standard 12·4 mm. (10·5–15·0 mm.) long, broadly ovate, obtuse and rounded, yellow or yellow with red marking. Stamens 10, some or all adnate to petals, both persistent after flowering. Ovary villous, style dilated and thickened at base, incurved or subulate above, pubescent with short silky appressed hairs, often extending along upper edge around the hook. Legume 1–2 seeded, 1–2 times as long as the calyx. Seed reniform.

Distribution: Between Sydney Harbour and the Hawkesbury River, also Appin and Bargo regions (see Fig. 10).

Habitat: Sandstone heath and dry sclerophyll forest.

Chromosome number: 2n=14, voucher specimen R. C. Jancey, No. 7 (SYD).

Typification: Holotype: Loc. non cit. F. Bauer, WIEN.

Specimens examined: New South Wales: Parramatta, W. Woolls, —, (MEL); Parramatta, W. Woolls, —, (MEL); Elanora Heights, V. May, 10/1934, (NSW 36366); Port Jackson, F. J. Sargood, 10/1911, (NSW 36362); Berowra, W. F. Blakely, 10/1940, (NSW 36369); Narrabeen, M. Mills, 10/1940, (NSW 36365); Narrabeen, J. J. Fletcher, 8/1887, (NSW 36364); The Valley, Hornsby, W. F. Blakely, 11/1939, (NSW 36368); Hornsby, E. Betche, 12/1886, (NSW 36436); "West Australia", Maxwell, —, (NSW 36359); St. Ives, Blakely and Anderson, 9/1936, (NSW 36357); Manly, E. Cheel, 10/1898, (NSW 36363); Hornsby, W. F. Blakely, 10/1914, (NSW 36371); Cheltenham, L. A. S. Johnson, 10/1945, (NSW 36370); Field of Mars, H. Deane, —, (NSW 36367); National Park, W. F. Blakely, 11/1938, (NSW 36361); Cataract Dam, J. H. Maiden, 11/1906, (NSW 36360).

Phyllota squarrosa (Sieber ex DC.) Benth.

In *Ann. Wien. Mus.*, II: 77 (1838).

Nomenclatural synonym: *Pultenaea squarrosa* Sieber ex DC., *Prod.*, II: 113 (1825). BASIONYM.

A shrub 30 cm. (15–60 cm.) high, suckering freely from the roots, stems pubescent at least in the upper parts. Leaves linear, 9 mm. (6·6–13·8 mm.)

long, 0·75–1·25 mm. broad, minutely bullate, acuminate and recurved (4 on the subjective scale), stipules minute. Flowers 8 (3–12) together towards the ends of the branches in lax leafy spikes 8 mm. (2–18 mm.) long. Pedicel 0·75–1·75 mm. long. Bracts identical in appearance with foliage leaves; bracteoles lanceolate, 8·25 mm. (5·5–13·0 mm.) long, 1·25 mm. (1·0–2·5 mm.) broad, herbaceous, glabrous or with scattered to numerous short appressed silky hairs, borne on the base of the calyx. Calyx 7·5 mm. (5·5–9·0 mm.) long, almost glabrous or with scattered to numerous short appressed silky hairs; lower lobes acuminate, equal to or longer than the tube; upper lobes broader, connate higher up, acuminate. Corolla: keel equal in length to standard, semi-circular, obtuse, yellow occasionally tinged with red; wings shorter than or equal to the standard, broadly lunate, obtuse and rounded, yellow; standard 10·3 mm. (8·0–12·0 mm.) long, broadly ovate, obtuse and rounded, yellow to red. Stamens 10, some or all adnate to petals, both persistent after flowering. Ovary villous, style dilated and thickened at base, incurved or subulate above, pubescent with short appressed silky hairs to below the hook. Legume 1–2 seeded, 1–2 times as long as the calyx. Seed reniform.

Distribution: Upper Blue Mountains, central tablelands.

Habitat: Sandstone heath and open dry sclerophyll forest.

Chromosome number: 2n=14, voucher specimen R. C. Jancey, No. 6 (SYD).

Typification: Holotype: Blue Mountains, Sieber, No. 406 (GEN).

Selected specimens examined: New South Wales: Clarence, F. H. Rodway, —, 1908, (AD 96311374); Mt. Tomah, W. Woolls, —, (MEL); Blackheath, Althofer, 8/1945, (MEL); Nov. Holl., Sieber, No. 406, (MEL); Bell, L. A. S. Johnson, 5/1951, (NSW 36470); Eskbank, A. A. Hamilton, 1/1915, (NSW 36485); Mt. Victoria, J. H. Maiden, 12/1896, (NSW 36452); Mt. Victoria, J. L. Boorman, 12/1917, (NSW 36457); Bell, A. A. Hamilton, 1/1915, (NSW 36458); Mt. Wilson, J. H. Maiden, 4/1896, (NSW 36459); Clarence Tunnel, W. F. Blakely, 11/1938, (NSW 36463); Newnes Junction, Blakely and Buckingham, 11/1938, (NSW 36483); Mt. Piddington, Mt. Victoria, Blakely and Buckingham, 1/1939, (NSW 15660); Mitchell's Ridge, Blakely and Buckingham, 1/1939, (NSW 36472); Katoomba, W. Forsyth, 12/1899, (NSW 15659); Katoomba, J. H. Camfield, 12/1908, (NSW 36469); Blackheath, J. H. Maiden, 1/1905, (NSW 36471); Narrow Neck, G. Chippendale, 1/1951, (NSW 36474); nr. Bald Trig., Clarence, W. F. Blakely, 1/1939, (NSW 36462).

Phyllota humifusa Benth.

Fl. Austr., II: 95; Moore and Betche. *Handb. Fl. N.S.W.*, 135 (1893).

A prostrate shrub 8–15 cm. high, with stems pubescent at least in the upper parts. Leaves linear, 4·5 mm. (3·0–8·0 mm.) long, 0·25–0·75 mm. broad, minutely bullate, obtuse to acute (1–3 on the subjective scale); stipules minute. Flowers 8 (2–15) in lax leafy spikes, 7 mm. (1–14 mm.) long, towards the ends of the branches. Pedicel 0·5–1·25 mm. long. Bracts identical in appearance with foliage leaves; bracteoles identical in appearance with foliage leaves, 3 mm. (2–4·5 mm.) long, 0·5 mm. (0·25–0·6 mm.) broad, glabrous or with scattered short appressed silky hairs, borne on the base of the calyx. Calyx 5·0 mm. (4·0–5·5 mm.) long, almost glabrous or with scattered short appressed silky hairs; lower lobes acuminate, shorter than or equal to the tube; upper lobes broader, connate higher up and acute. Corolla: keel equal in length to standard, semi-circular, obtuse and rounded, yellow to yellow-red; standard 7·5 mm. (7·0–8·0 mm.) long, broadly ovate, obtuse and rounded, red to deep red. Stamens 10, some or all adnate to petals, both persistent after flowering. Ovary villous, style dilated and thickened at base, incurved or subulate above, pubescent with short appressed silky hairs to below the curve. Legume 1–2 seeded, 1–2 times as long as the calyx. Seed reniform.

Distribution : Southern tablelands of New South Wales, between Mittagong and Mt. Bullio (see Fig. 4).

Habitat : Deep sandy shale soil in dry sclerophyll forest and in open sparsely grass covered areas.

Chromosome number : 2n=14, voucher specimen R. C. Jancey, No. 1 (SYD).

Typification : Holotype ; Wombat Brush, Argyll County, A. Cunningham, No. 8 (K).

Specimens examined : Mittagong to Bullio, E. Cheel, 11/1919, (NSW 36449) ; Penrose, Blakely and Buckingham, 11/1939, (NSW 36447).

Species of Phyllota not occurring in New South Wales

All observations on interstate material were based on herbarium specimens on loan from the various State herbaria. A list of material examined, and its origin, is included in the description of each species.

Methods

Since the material in question was on loan from other herbaria, some of the measurements which had been carried out on material collected personally could not be repeated, owing to the amount of destruction involved. In other cases, specimens were so small that it was felt that any further disintegration would be undesirable and, consequently, such specimens were only examined superficially under a dissecting microscope.

Measurements were made on material soaked in a mixture of detergent and water, scored values referring to the same scales as those used in connection with the New South Wales material. To avoid undue destruction of loaned material, the whole range of material was first examined, then measurements made on a limited number of individuals. In many cases, variation in floral parts was negligible, and in these cases single values have been quoted. Where this was not the case, or in the case of other more variable structures, values are quoted for the range of variation, and one for an individual apparently representative of the mean for that particular character. A number of observations other than those employed in the case of the New South Wales taxa were introduced after preliminary examination of the interstate species.

Phyllota barbata Benth.

In *Hueg. Enum.* 33 (1837), and in *Ann. Wien. Mus.*, II : 78 (1838), and in *Fl. Aust.* II : 94 (1864).

Taxonomic synonyms : Pultenaea andrewsii Gardn. ex Blackall and Grieve ' How to know West Australian Wildflowers ', 234 (1953). NOM. NUD. ET ILLEGIT.

A shrub with stems terete, pubescent at least in the upper parts. Leaves linear, 8 mm. (6–10 mm.) long, scabrous, with revolute margins, obtuse and rounded, some also bearing a minute deciduous black mucro (1 on the subjective scale) ; stipules minute. Flowers scattered along the branches, sometimes crowded into leafy spikes towards the ends of the branches. Pedicel 0·5–1·0 mm. long. Bracts identical in appearance with foliage leaves ; bracteoles linear, 8 mm. long, 1 mm. broad, almost identical in appearance with foliage leaves, borne on the base of the calyx. Calyx 5 mm. long, almost glabrous to heavily tomentose ; lower lobes acuminate, longer than, or equal to, or shorter than the tube ; the upper lobes broader connate higher up and less acuminate. Corolla : keel 12 mm. long, tapering to an acute point, red ; wings 7–8 mm. long, cuneate-oblong in their upper parts, yellow red ; standard 12 mm. long, elliptic, yellow-red. Stamens 10, some adnate to petals at base, both deciduous after flowering. Ovary villous ; style villous below and barbulate in the distal half on the upper edge with persistent white hairs. Legume 1–2 seeded, as long as or longer than the calyx. Seed reniform.

Distribution : Coastal south-western area of Western Australia.

Habitat : Sandy heath.

Chromosome number : 2n=14. Voucher specimen, V. Sands, No. 638/19/4. Determined by V. Sands (unpublished).

Typification : Holotype.

Discussion : P. barbata is distinguished from all other species of *Phyllota* with the exception of *P. gracilis* Turcz. by the bearding of the distal half of the style. From *P. gracilis* it differs in the length of the peduncle, and in the flowers which are almost sessile in *P. barbata* but borne on a pedicel 4 mm. long in *P. gracilis*. These latter two species also differ in leaf length. Only one specimen of *P. andrewsii* was available for examination (Gardner, 2219). Having been collected by the author of the manuscript name, and bearing his determination, it may be taken, however, as an authoritative example of the intended taxon. The specimen examined was bearded on the inner edge of the style, as is characteristic in *P. barbata* and *P. gracilis*, whereas, in ' How to Know West Australian Wildflowers ', *P. andrewsii* is distinguished by two characters, one of which is the absence of bearding. The position of the inflorescence, however, was found to be in agreement with the text quoted, being terminal in the specimen of *P. andrewsii*, as opposed to the rather lax and interrupted spikes characteristic of *P. barbata*. Since the distinction proposed between the species was based, at least in the case of the specimen examined, on one character, it is not proposed at this stage to give formal status to the name proposed by Gardner. There seems little doubt that the range and degree of morphologic differentiation in this section of the genus in Western Australia is not as yet fully represented in herbarium collections.

Specimens examined : Cape Riche, R. T. Lange, No. 13, 3/1958, (PERTH) ; Albany, W. E. Blackall, 12/1937, (PERTH) ; Mt. Manypeaks area, S. P. Pfeiffer, No. 12, —, (PERTH) ; Narrikup, R. T. Lange, No. 13, 3/1958, (PERTH) ; Cheyne Beach, J. M. Storr, No. 3900, 5/1959, (PERTH) ; King George's Sound, B. T. Goadby, No. 92, 2/1899, (PERTH) ; Sand heath south of Stirling Range, W. E. Blackall, 4/1939, (PERTH) ; Nr. West Mount Barren, C. A. Gardner, 10/1928, (PERTH) ; Nr. Albany, Maxwell, No. 33, 7/1858, (MEL) ; King George's Sound, A. Hugham, No. 22, 1869, (MEL) ; South West Australia, Mills, 6/1861, (MEL) ; Cape Riche, Preiss, No. 846, 1843, (MEL) ; Sand Plains, Wilson's Inlet, Oldfield, No. 766, —, (MEL) ; Bremer River, Webb, 1884, (MEL) ; Phillip's River, C. R. Andrews, 10/1903, (NSW 36498) ; King River Road, F. Staer, 2/1911, (NSW 36519) ; King George's Sound, Rev. R. Collie, 1898, (NSW 36513) ; Western Australia, Drummond, No. 84, —, (NSW 36514) ; Torbay, A. E. Sheath, 1/1903, (NSW 36515) ; Warejinup, —, —, (NSW 36517) ; South West Plantagenet, E. Pritzel, No. 207, 1/1901, (NSW 36518) ; Western Australia, Drummond, No. 85, (4th collection), 1848, (NSW 36512).

Phyllota gracilis Turcz.

In *Bull. Soc. Nat. Mosc.*, XXVI : 1267 (1853) ; Benth, *Fl. Austr.*, II : 94 (1864).

Nomenclatural synonym : Pultenaea gracilis (Turcz.) Gardner, *Enum. Pl. Austr. Occ.*, 59 (1930).

A shrub, with stems terete, pubescent with short white hairs (densely so in the upper parts) ; scarcely rugose with decurrent leaf bases (1 on the subjective scale). Leaves linear, minute, 1–3 mm. long, 0–5 mm. broad, with a scattered pubescence, revolute margins, obtuse and rounded bearing a deciduous black mucro (1 on the subjective scale) ; stipules minute. Flower solitary, near end of branch. Pedicel 4 mm. long. Bracts identical in appearance with foliage leaves ; bracteoles linear-lanceolate, 1–5 mm. long, herbaceous, sparsely pubescent, borne on the base of the calyx. Calyx 3 mm. long, densely villous with pale yellow simple hairs ; lower lobes acute, equal to or longer

than the tube; upper lobes acute, equal to or shorter than the tube. Corolla not seen dissected; 5 mm. long from receptacle to apex of keel; keel dark red; wings dark red; standard dark red. Ovary not seen; style bearded in distal half. Legume not seen. Seed not seen.

Distribution: Not known.

Habitat: Not known.

Chromosome number: Not known.

Typification: Holotype: Swan River, Western Australia, Drummond, No. 91, *ca.* 1845. KW. Isotypes MEL, K.

Discussion: While this species shows affinities to *P. barbata* in the bearded style and boat-shaped keel, it shows striking morphologic distinction in the very much smaller bracteoles, the lesser overall length of flower, very much longer pedicel and much shorter leaves. The differentiation from *P. barbata* is such as to merit specific rank.

Specimen examined: Swan River, Western Australia, Drummond, No. 91, *ca.* 1845, (MEL).

Phyllota luehmannii F. Muell.

Fragm. Phytogr. Austral., X: 33 (1877), as *Phyllota luehmannii.*

Nomenclatural synonym: Pultenaea luehmannii (F. Muell.) Gardner, *Enum. Pl. Austr. Occ.*, 59 (1930).

Taxonomic synonym: Phyllota georgii Hemsl. in *Hook. Ic. Pl.*, t. 2778 (1905). *Pultenaea luehmannii* var. *georgii* Gardn. ex Blackall and Grieve 'How to Know West Australian Wildflowers', 234 (1953). NOM. NUD. ET ILLEGIT.

A shrub with stems terete, covered with a pale gold tomentum at least in the upper parts. Leaves linear, 6 mm. (4–10 mm.) long, scarcely scabrous, bearing a sparse pale golden tomentum, with revolute margins; leaf tips acuminate recurved (4 on the subjective scale); stipules minute. Flowers crowded into spikes at the ends of the branches becoming terminal by die-back of the axis. Pedicel 0·5–1·0 mm. long. Bracts identical in appearance with foliage leaves, occasionally with somewhat less revolute margins; bracteoles linear-lanceolate, 4–6 mm. long, 0·5 mm. broad, herbaceous, with a pale golden tomentum, borne on the base of the calyx. Calyx 6 mm. long, densely tomentose with a pale golden tomentum; lower lobes acuminate, about equal in length to the tube; the upper lobes broader connate higher up and less acuminate. Corolla: keel 8 mm. long, obtuse, purple; wings equal to or (more usually) 1 mm. shorter than the keel, cuneate-oblong in upper parts, yellow; standard orbicular, 11 mm. long, yellow with a red marking at the base. Stamens 10, some slightly adnate to the petals, both deciduous after flowering. Ovary densely villous; style villous below, glabrous in the distal half, Legume 1–2 seeded, as long as or longer than the calyx. Seed reniform.

Distribution: The Victoria Desert region of Western Australia.

Habitat: Sand plain.

Chromosome number: 2n=14, also n=7. Voucher specimen V. Sands, No. 639/1/5 (SYD). Determined by V. Sands (unpublished).

Typification: Syntypes of *Phyllota luehmannii* F. Muell.: Near Waring, Western Australia, F. Mueller; Elder Exploring Expedition, Victoria Desert Camp 58, R. Helms sine num., 21/9/91. Lectotype: Elder Exploring Expedition, Victoria Desert Camp 58, R. Helms sine num., 21/9/91. MEL. Isolectotypes: K., AD.

Phyllota georgii Hemsl. Holotype: Railway between Cunderdin and Dedari, G. H. Thistleton-Dyer, K.

Discussion: There appear to be no features distinguishing *P. georgii* from *P. luehmannii*, at least among the specimens examined. The short, obtuse

leaves quoted in ' How to Know West Australian Wildflowers ' as characteristic of *P. luehmannii* var. *georgii* were found to be so variable within specimens as to be unsatisfactory for discriminatory purposes.

Specimens examined : Karalee, C. A. Gardner, 9/1934, (PERTH) ; East-west railway, C. French, —, (MEL) ; No. 15 Pumping Station, Yerbillon, M. Koch, No. 2892, 10/1923, (MEL) ; Victoria Desert Camp 58, Elder Exploring Expedition, R. Helms, 9/1891, (MEL) ; Karoling, Elder Exploring Expedition, R. Helms, 11/1891, (MEL) ; Victoria Springs, Young, 10/1875, (MEL).

Phyllota pleurandroides F. Muell.

In *Trans. Phil. Soc. Vic.*, I : 38 (1833) ; Benth., *Fl. Austr.*, II : 96 (1864).

A shrub, suckering freely from the roots. Stems terete, more or less pubescent. Leaves scattered to virgate, linear, 8 mm. (6–10 mm.) long, 0·75–1·25 mm. broad, bullate, tip acuminate and recurved ; stipules minute. Flowers scattered among the virgate clusters of leaves. Pedicel 0·5–1·0 mm. long. Bracts similar in appearance to foliage leaves, somewhat narrowed and villous towards the base, as are other leaves of the virgate clusters ; bracteoles ovate-obtuse, 1–5 mm. long, 1 mm. broad, coriaceous, pubescent, borne on the base of the calyx. Calyx 4 mm. long, villous with white hairs ; lower lobes acute, equal in length to the tube ; upper lobes broader and connate higher up. Corolla : keel 6 mm. long, obtuse, yellow-red ; wings slightly exceeding the keel, oblong in upper parts ; standard broadly ovate, 5 mm. long, yellow. Stamens 10, some adnate to petals at base of claw, both deciduous after flowering. Ovary villous ; style villous below, glabrous in upper parts. Legume 1–2 seeded, 1–2 times as long as the calyx. Seed reniform.

Distribution : South-eastern parts of South Australia, and south-western Victoria.

Habitat : Deep sandy soil on sand ridges of sand plain.

Chromosome number : Not known.

Typification : Syntypes : Kangaroo Island, F. Mueller, Herb. W. Sonder : Grampians, Wilhelm, F. Mueller, 1857 : Mount Abrupt, F. Mueller, MEL, K. It is proposed to select Mount Abrupt, F. Mueller, MEL as lectotype of this species. Isolectotype : Mount Abrupt, F. Mueller, K.

Selected specimens examined : South Australia : Bool Lagoon-Lucindale, D. Hunt, No. 796, 5/1962, (AD 96227095) ; Southern Mt. Lofty Range, nr. Mt. Compass, —, 1/1882, (AD 96311376) ; South Australia, —, —, (AD 96311378) ; Kangaroo Island, —, No. 1217, 3/1884, (AD 96311375) ; Lower Mt. Lofty Range, nr. Strathalbyn, E. C. Black, 2/1944, (AD 96311330) ; Malinong, 45 km. south of Murray Bridge, R. D. Sharrad, No. 13, 8/1960, (AD 96149180) ; Encounter Bay, J. B. Cleland, 11/1924, (AD 96311377) ; Kangaroo Island, Mt. Pleasant, —, 1/1883, (AD 96311380) ; Bordertown, D. Hunt, No. 748, 3/1962, (AD 96220087) ; Mt. Abrupt, F. Mueller, —, (MEL) ; Square Waterhole, O. Tepper, No. 30, 7/1882, (MEL) ; Gawler Ranges, Dr. Sullivan, —, (MEL) ; Lacepede Bay, Herschel and Babbage, —, (MEL) ; Penola, Rev. Tenison-Woods, No. 15, —, (MEL) ; N.W. of Lake Albacutya, C. French, 10/1887, (MEL) *Victoria :* Grampians, H. B. Williamson, 4/1904, (MEL) ; Grampians, J. W. Audas, 11/1920, (MEL) ; Mt. Zero, C. Wilhelmi, 2/1857, (MEL) ; Wimmera, D'Alton, No. 16, 1890, (MEL) ; West of Wimmera, D'Alton, 7/1892, (MEL) ; Shire of Dimboola, F. M. Reader, 1/1893, (MEL) ; Keith, R. L. Crocker, 9/1943, (CANB 11633).

Phyllota remota J. H. Willis

In *Vic. Nat.*, LXXIII : 191 (1957).

A shrub, with stems terete, tomentose at least in the upper parts, rugose with decurrent leaf bases (2 on the subjective scale). Leaves linear, 8 mm. (5–10 mm.) long, distant, occasionally becoming virgate, tomentose when young,

papillose with age, revolute margins, acute to obtuse, sometimes bearing a minute black mucro (2 on the subjective scale); stipules minute. Flowers scattered, solitary or occasionally in pairs. Pedicels 0·5–1·0 mm. long. Bracts identical in appearance with foliage leaves; bracteoles ovate, 4 mm. long, scarious, keeled and with a mucronate apex, almost enveloping the calyx. Calyx 3–4 mm. long, glabrous to villous; lower lobes acute, more or less equal to the tube; upper lobes broader and connate higher up. Corolla: keel 6 mm. long, obtuse, yellow; wings slightly exceeding the keel, oblong in upper parts; standard broadly ovate, 5 mm. long, yellow. Stamens 10, some adnate to petals at base, both deciduous after flowering. Ovary villous; style villous below, glabrous in upper parts. Legume 1–2 seeded, twice as long as the calyx. Seeds reniform.

Distribution: South-eastern South Australia and south-western Victoria.

Habitat: In shallow sandy soil between sand ridges of mallee heath.

Chromosome number: Not known.

Typification: Holotype: Keith, R. L. Specht and P. Rayson, 1954, (MEL).

Specimens examined: Boston Point, Spencer's Gulf, Wilhelmi, —, (MEL); Lillimur, nr. Wimmera, A. J. Hicks, 9/1954, (MEL); Eyre Peninsula, 85 km. north of Port Lincoln, R. L. Specht, No. 2602, 11/1960, (AD 96109031); Dark Island, 14 km. east of Keith, Specht and Rayson, 2/1950, (AD 96311331); 11 km. east of Meningie, on Lake Albert, M. C. R. Sharrad, No. 486, 12/1959, (AD 96150850); Keith, Specht and Rayson, 1954, (MEL).

Phyllota diffusa (Hooker f.) F. Mueller

Fragm., I: 8 (1877).

Nomenclatural synonym: Pultenaea diffusa Hooker, f., *Fl. Tasm.*, I: 91, t. 14 (1860); Benth., *Fl. Austr.*, II: 119 (1864); Curtis, *Stud. Fl. Tasm.*, pars 1, 132 (1956).

A small diffuse shrub, much branched and ascending, 10–30 cm. high, and spreading 30–50 cm. Stems terete, glabrous to pubescent with short appressed hairs. Leaves linear, 7 mm. (5–10 mm.) long, bullate, acute (3 on the subjective scale); stipules minute. Flowers scattered along the stem, solitary or in pairs, sometimes crowded towards the ends of the branches. Pedicel 2–2·5 mm. long. Bracts identical in appearance with foliage leaves; bracteoles lanceolate, 1·75 mm. long, 0·75 mm. broad, scarcely herbaceous, glabrous or a few scattered short silky hairs, borne on the base of the calyx. Calyx 3–4 mm. long, almost glabrous or with a few scattered silky hairs; lower lobes acute, shorter than or equal to the tube; upper lobes broader connate higher up, obtuse. Corolla: keel equal in length to the standard, broadly lunate to semi-circular, obtuse, yellow-red; wings equal in length to the standard, oblong to obovate, obtuse and rounded, yellow; standard 6–8 mm. long, orbicular, yellow. Stamens 10, almost wholly free, deciduous with the petals after flowering. Ovary pubescent to villous, style dilated or thickened at base, incurved or subulate above, pubescent with short appressed silky hairs to below the hook. Legume 1–2 seeded, 1–2 times as long as the calyx. Seed reniform.

Distribution: Tasmania, endemic. Local near the east coast and in the extreme north west.

Habitat: Sandy heaths.

Chromosome number: Not known.

Typification: Holotype: Loc. non cit. J. D. Hooker, (K).

Specimens examined: Coast Rd. to George's Bay, A. Simson, No. 1325, 11/1878, (MEL); St. Paul's River, nr. Broadshead, —, 1/1858, (MEL); Coast nr. Scamander River, A. Simson, 11/1878, (MEL); South Port, Stuart, —, (MEL); South Port, —, No. 1515, 1/1856, (MEL); George's Bay, L. Rodway, 6/1900, (NSW 36497); Tasmania, A. H. S. Lucas, 1910-1930, (NSW 36499).

Acknowledgements

The writer is greatly indebted to Dr. R. C. Carolin of the University of Sydney, for his help and advice during the course of this investigation, for detailed descriptions of type specimens lodged in European herbaria, and also for reading the manuscript. Thanks are also expressed to the Directors of the following institutions for the loan of herbarium specimens: The Department of Agriculture, Government of Western Australia; The State Herbarium of South Australia; The National Herbarium of Victoria; The National Herbarium of New South Wales; Queensland Herbarium.

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EXPLANATION OF PLATES XXIX–XXX

Plate xxix

A, Illustrating from left to right, the subjective values from 4 to 1 for calyx and bracteole indumentum. B, Leaves showing values of 1 to 4 on the subjective scale for size of leaf bullae. C, Leaves showing values of 1 to 4 on the subjective scale for number of leaf bullae. (In both B and C cases it will be seen that many of the epidermal hairs are still present, while these are lost with increasing age of the leaf, the bullae remain.) D, Four leaf tips of *P. phylicoides* showing examples of the values from 1 to 4 on the subjective scale for leaf tip shape.

Plate xxx

A, Growth habit of group 1. B, Growth habit of group 4. C, Growth habit of groups 7 and 8. (Scales equal 12 inches.)

ABSTRACT OF PROCEEDINGS

ORDINARY MONTHLY MEETING

31st March, 1965

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

The minutes of the last Monthly Meeting (25th November, 1964) were taken as read and signed.

The following were elected Ordinary Members of the Society: Mr. K. R. Ayers, Fairfield, N.S.W.; Mr. R. Basden, M.Ed., B.Sc. (Lond.), F.R.A.C.I., A.S.T.C., Hamilton, N.S.W.; Miss Phillipa A. Croucher, B.Sc., Canberra, A.C.T.; Mr. D. J. McGillivray, B.Sc.For. (Syd.), Dip.For. (Canb.), Castle Hill, N.S.W.; Mr. D. R. Murray, B.Sc., Brookvale, N.S.W.; Dr. F. H. Talbot, M.Sc., Ph.D., Australian Museum, Sydney; and Dr. R. Tucker, B.V.Sc., Dr.Vet.M., University of Queensland, St. Lucia, Queensland.

The Chairman announced that library accessions amounting to 42 volumes, 472 parts or numbers, 13 bulletins, 18 reports and 14 pamphlets, total 559, had been received since the last meeting.

The Chairman announced that the Conservation Photographic Exhibition which the Society has arranged is now on view at the Australian Museum. The Exhibition, which consists of photographs and diagrams, illustrates the need for nature conservation, particularly in New South Wales. Members are invited to view and to draw the attention of others to this Exhibition. The Society particularly wishes to acknowledge the help given by various members of the staff of the Australian Museum, Dr. Eric Bird (A.N.U.) and Mr. R. Schodde (C.S.I.R.O.) for help in the production.

PAPER READ

(By title only, an opportunity for discussion to be given at the April Ordinary Monthly Meeting)

1. Chromosome numbers in some Australian leafhoppers (Homoptera: Auchenorrhyncha). By M. J. Whitten. (With an Appendix by J. W. Evans, Australian Museum, describing a new genus and species of Eurymelidae.)

ORDINARY MONTHLY MEETING

28th April, 1965

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

The minutes of the last Monthly Meeting (31st March, 1965) were read and confirmed.

Lecturette

A lecturette, illustrated by colour transparencies, entitled "Some aspects of coastal morphology in New South Wales", was delivered by Mr. J. R. Hails, Geography Department, University of Sydney.

Dr. T. E. Woodward, M.Sc. (N.Z.), Ph.D. (Lond.), D.I.C., University of Queensland, St. Lucia, Queensland, was elected an Ordinary Member of the Society.

The Chairman announced that the Council had elected the following office-bearers for the 1965–66 session: Vice-Presidents: Miss Elizabeth C. Pope,

Mr. G. P. Whitley, Professor J. M. Vincent and Dr. T. G. Vallance ; Honorary Treasurer : Dr. A. B. Walkom ; Honorary Secretaries : Drs. A. B. Walkom and W. R. Browne.

The Chairman announced that library accessions amounting to 10 volumes, 111 parts or numbers, 2 bulletins, 6 reports and 1 pamphlet, total 130, had been received since the last meeting.

The Chairman reminded members and their friends of the Conservation Photographic Exhibition now open for inspection at the Australian Museum, College Street, Sydney.

The Chairman reminded members that there will be no Ordinary Monthly Meeting in May.

PAPERS READ

1. A note on blood preferences of *Anopheles farauti*. By Margaret Spencer.

2. Malaria in the D'Entrecasteaux Islands, Papua, with particular reference to *Anopheles farauti* Laveran. By Margaret Spencer.

3. The distribution of the Notonectidae (Hemiptera) in south-eastern Australia. By A. W. Sweeney.

4. The reproduction and early life histories of the gastropods, *Notoacmaea petterdi* (Ten.-Woods), *Chiazacmaea flammea* (Quoy and Gaimard) and *Patelloida alticostata* (Angas) (Fam. Acmaeidae). By D. T. Anderson.

5. The histology and anatomy of the reproductive system of the littoral gastropod, *Bembicium nanum* (Lamarck) (Fam. Littorinidae). By Lynne Bedford.

Dr. I. V. Newman, a Trustee of the Muogamarra Sanctuary, appealed to the younger members of the Society of both sexes to join the Sanctuary's Volunteer Fire Brigade. The extent of the devastation caused by the recent bushfires would have been greatly lessened had more fire fighters been available. Applications should be made to the Hon. Secretary, Miss Monaghan (Tel. Evenings only, 44 2624), Box 2770, G.P.O., Sydney.

ORDINARY MONTHLY MEETING

30th June, 1965

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

The minutes of the last Monthly Meeting (28th April, 1965) were read and confirmed.

The following were elected Ordinary Members of the Society : N. E. Milward, B.Sc.(Hons.), M.Sc., Queensland ; Mrs. I. M. Straughan, B.Sc.(Hons.) Queensland ; and B. D. Webby, Ph.D., M.Sc., Sydney University.

The Chairman announced the death of Miss Florence Sulman, M.B.E., on 15th June, 1965, aged 89 years. Miss Sulman had been a member of the Society since 1911.

The Chairman announced that library accessions amounting to 26 volumes, 269 parts or numbers, 6 bulletins, 2 reports and 1 pamphlet, total 304, had been received since the last meeting.

PAPERS READ

1. Australian larval Carabidae of the subfamilies Harpalinae, Licininae, Odacanthinae and Pentagonicinae (Coleoptera). By B. P. Moore.

2. Some Laelapid mites of syndactylous marsupials. By R. Domrow.

3. The occurrence and composition of manna in *Eucalyptus* and *Angophora*. By Ralph Basden.

4. Comparative studies on the external acoustic meatus. 1. The morphology of the external ear of the echidna (*Tachyglossus aculeatus*). By Richard Tucker.

5. Studies on the inheritance of rust resistance in oats. III. Genetic diversity in the varieties Landhafer, Santa Fe, Mutica Ukraine, Trispernia and Victoria for crown rust resistance. By U. M. Upadhyaya and E. P. Baker.

LECTURETTE

A lecturette, illustrated by slides and exhibits, entitled " Trace fossils : their classification and palaeoecological significance ", was delivered by Dr. B. D. Webby, Lecturer in Palaeontology, University of Sydney.

ORDINARY MONTHLY MEETING

28th JULY, 1965

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

The minutes of the last Monthly Meeting (30th June, 1965) were read and confirmed.

Professor W. Stephenson, University of Queensland, Brisbane, was elected an Ordinary Member of the Society.

The Chairman announced that library accessions amounting to 18 volumes, 170 parts or numbers, 8 bulletins, 5 reports and 10 pamphlets, total 211, had been received since the last meeting.

The Chairman reminded members that there will be no August Ordinary Monthly Meeting.

The Chairman announced that a lecture on Radio-carbon Dating in the Quaternary will be given by Professor H. Godwin on Wednesday, 8th September, 1965, at 8 p.m., in the Chemistry No. 1 Lecture Theatre, University of Sydney.

The Chairman announced that a Conversazione will be held on Saturday, 18th September, 1965, from 2 to 5.30 p.m., in the Zoology Department of the University of New South Wales. Members engaged in scientific research who have material or apparatus considered suitable for exhibition are invited to communicate with Mr. R. Strahan, Department of Zoology, School of Biological Sciences, University of New South Wales.

The Chairman also announced the proposed formation of a Mycological Society of New South Wales. Interested persons or representatives of institutions please communicate with Professor N. H. White, Department of Agriculture, University of Sydney.

PAPERS READ

1. The Devonian tetracoral *Haplothecia* and new Australian phacellophyllids. By A. E. H. Pedder.

2. Some mite parasites of Australian birds. By R. Domrow.

3. Development of the eggs and early larvae of the Australian smelt, *Retropinna semoni* (Weber). By N. E. Milward. (*Communicated by Mr. G. P. Whitley.*)

4. The vertebrate fauna of " Gilruth Plains ", South-west Queensland. By M. C. Brooker and G. Caughley. (*Communicated by Dr. Mervyn Griffiths.*)

5. The first zoea of the soldier crab, *Mictyris longicarpus* (Grapsoidea : Mictyridae). By Ann M. Cameron. (*Communicated by Dr. E. J. Reye.*)

6. Plant parasitic nematodes in fruit tree nurseries of New South Wales. By E. J. Anderson. (*Communicated by Dr. C. D. Blake.*)

7. Diurnal variation in the release of pollen by *Plantago lanceolata* L. By J. M. Matthews. (*Communicated by Dr. Donald Walker.*)

LECTURETTE

A lecturette, entitled " Ecology of *Ruppia* and *Zostera* ", was delivered by Mr. R. Higginson, B.Sc.Agr., School of Biological Sciences, University of Sydney.

SPECIAL GENERAL MEETING

29th September, 1965

The recommendation from the Council, of which the required notice had been given to members, that Rules V and VI be altered to read as follows, was read :

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

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

The President explained that these changes in the Rules, if adopted, would provide for (*a*) abolition of the entrance fee of one guinea, (*b*) increase of the annual subscription from two guineas to three pounds ten shillings (seven dollars), and (*c*) abolition of the provision for subscription for Life Membership.

A letter from Mr. A. F. Batley, a member absent from Australia, was read, in which he stated, *inter alia*, that the Society at present is living well within its annual income, and suggested that members would be interested to know if there is a specific purpose in the proposed increase of subscription, other than the increased cost of publication.

In explanation the Hon. Treasurer reminded members that from 1886 to the end of 1950 the Society had a full-time paid Secretary. At the beginning of 1951 the Council was faced with the position that the income of the Society was no longer sufficient to permit employment of a Secretary *and* publication of the Proceedings. To alleviate this position two members of the Council undertook to carry on in an honorary capacity the work of the Secretary (set out in Rule XLIX) in the hope that gradual accumulation of surplus income would, in due course, make it possible for the Society to consider the appointment of a full-time Secretary. This stage appears to have been reached, and recent events have emphasized the need for the Council to give the matter serious consideration.

The Hon. Treasurer then proposed that the recommendation of the Council, as set out in the notice to members, be approved. This was seconded, and was carried unanimously.

ORDINARY MONTHLY MEETING

29th September, 1965

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

The minutes of the last Monthly Meeting (28th July, 1965) were read and confirmed.

LECTURETTE

An illustrated lecturette on Opossums was delivered by Dr. M. P. Marsh, School of Biological Sciences, University of Sydney.

The Chairman announced that Dr. N. G. Stephenson, Mr. L. A. S. Johnson and Dr. Erik Shipp have been elected members of Council in place of Professors B. J. Ralph, W. L. Waterhouse and I. A. Watson, who had resigned.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1966, 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, 3rd November, 1965.

The Chairman announced that library accessions amounting to 39 volumes, 293 parts or numbers, 8 bulletins, 7 reports and 8 pamphlets, total 355, had been received since the last meeting.

PAPERS READ

1. Observations on the fine structure of the meristem of root nodules from some annual legumes. By P. J. Dart and F. V. Mercer.

2. Cerioid Stringophyllidae (Tetracoralla) from Devonian strata in the Mudgee district, New South Wales. By A. J. T. Wright.

3. Further observations on the life histories of littoral gastropods in New South Wales. By D. T. Anderson.

SPECIAL GENERAL MEETING

27th October, 1965

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

The minutes of the Special General Meeting of 29th September, 1965, were read and confirmed.

The recommendation of the Council that Rules V and VI be altered, as approved at the Special General Meeting of 29th September, 1965, was confirmed, and carried unanimously.

ORDINARY MONTHLY MEETING

27th October, 1965

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

The minutes of the last Monthly Meeting (29th September, 1965) were read and confirmed.

LECTURETTE

A lecturette entitled "Some Problems of Evolutionary Theory" was delivered by Dr. Paul Ehrlich, Stanford University, Stanford, U.S.A.

The lecturer raised many controversial issues and much vigorous discussion ensued.

Miss Alison Kay Dandie, Women's College, Newtown, N.S.W., and Dr. David Michael Griffin, M.A., Ph.D. (Cantab.), Sydney University, were elected Ordinary Members of the Society.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1966, 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 Hon. Secretary, who will give further details and information, not later than Wednesday, 3rd November, 1965.

The Chairman announced that library accessions amounting to 25 volumes, 227 parts or numbers, 31 bulletins, 9 reports and 8 pamphlets, total 300, had been received since the last meeting.

The Chairman drew the attention of members to the portrait of Linnaeus, a recent gift from the Linnean Society of London. This painting from the Roslin portrait, presented to the Linnean Society of London in 1814 by Joseph Sabine, one of the original Fellows of the Society, hung for many years in the meeting room of the Society behind the President's chair.

PAPERS READ

1. An embryological study of five species of *Bassia* All. (Chenopodiaceae). By Gwenneth J. Hindmarsh.

2. Studies of nitrogen-fixing bacteria. IX. Study of inoculation of wheat with *Azotobacter* in laboratory and field experiments. By Y. T. Tchan and D. L. Jackson.

3. Studies on the genetic nature of resistance to *Puccinia graminis* var. *tritici* in six varieties of common wheat. By N. H. Luig and I. A. Watson.

ORDINARY MONTHLY MEETING

24th November, 1965

Mr. G. P. Whitley, Vice-President, in the chair.

The following were elected Ordinary Members of the Society: Derek John Anderson, Ph.D., Drummoyne, N.S.W., and David Robert Selkirk, Mosman, N.S.W.

The Chairman announced that library accessions amounting to 15 volumes, 133 parts or numbers, and 9 pamphlets, total 157, had been received since the last meeting.

PAPERS READ

1. Numerical methods in taxonomy. By R. C. Jancey.

2. An investigation of the genus *Phyllota* Benth. By R. C. Jancey.

3. The distribution of submerged aquatic Angiosperms in the Tuggerah Lakes system. By F. R. Higginson.

NOTES AND EXHIBITS

Dr. T. G. Vallance drew attention to two significant tercentenaries in Natural Science which have occurred during 1965. In 1665, Dr. Robert Hooke (1635–1705), encouraged by the newly-established Royal Society, issued *Micrographia*. Sir Geoffrey Keynes has recently commented " . . . that Hooke was almost, if not quite, the most prolific inventive genius that has ever lived and that at least one of his books, the *Micrographia*, is among the most important books ever published in the history of science ". Hooke's scientific career was outlined briefly and a copy of the original issue of *Micrographia* was exhibited together with a modern facsimile reproduction. Dr. John Woodward (1665–1728) was a much less distinguished scientist than Robert Hooke but he has some claim to our attention for his work in pioneering the concept of an organic origin for fossils and through his bequest to the University of Cambridge which led to the establishment of a Chair of Geology—the first of its kind in the world. Copies of the first (1695) and second (1702) editions of Woodward's *An Essay toward(s) a Natural History of the Earth* were exhibited.

Mr. A. Mahmood, a visitor (introduced by Dr. I. V. Newman), exhibited two electronmicrographs of phloem tissue of *Pinus radiata* as seen in transverse section, revealing the parental primary wall. Looking centrifugally in the first photograph, each of the three cells showed the secondary wall, the primary wall, and broken pieces of " parental wall " of uneven thickness on the outer side of the radial face of the primary walls of the cells. The intercellular substance between the tangential faces of the primary walls is seen as a dark line, but its identity as such is obscure where the cells are rounded at their corners due to tissue differentiation. In the second photograph two cells are seen, more enlarged. The stretching of the " parental wall " is more pronounced opposite the cell corners where the intercellular space has appeared. The black material lining the intercellular space may be intercellular substance which was displaced from its original position due to the splitting of the two primary walls as described by some workers. It looked as if the secondary wall is composed of more than one layer. The cell cavity showed plasmalemma, mitochondria, golgi bodies and vesicles. The consequences of formation of new cell wall with each division were discussed.

Mr. M. V. Ramji, a visitor (introduced by Dr. I. V. Newman), exhibited slides illustrating a study of embryogeny of *Stellaria media* showing the following features : (1) the four terminal cell tiers of a proembryo of six cells produce the globular embryo while the basal cells produce the stalk with the suspensor below ; (2) the cotyledons, the lateral protoderm, pith and procambium of embryonal axis arise from the second, third and fourth original tiers of cells and *not* from the terminal tier ; (3) the terminal tier gives rise essentially to the shoot apex ; (4) the terminal hemisphere of the embryo cannot be considered to be the first shoot apex of the plant as is usually done in many books, since the shoot apex arises exclusively from the terminal tier ; (5) the cotyledons cannot be considered as the first leaves of the plant.

Miss J. L. Jacobs exhibited, on behalf of Mr. R. Selkirk, a specimen from Kiandra, N.S.W. Many of these specimens are found associated with epiphyllous and leaf-parasitic fungi on the surface of small myrtaceous leaves from lignite at Kiandra. They are visible as small dots under a dissecting microscope, becoming visible only after maceration of the leaves to leave clear cuticular preparations. The specimen is apparently fungal in nature but, out of thousands so far examined, no form of mycelium, spores or usual fungal structures is exhibited. Three mycologists have so far examined it, but it remains as much a mystery as ever, Other fossil fungi occurring with it are tentatively assigned to Asterinaceae. Meliolaceae and Trichopeltaceae, a number of Cookson's types (Proc. Linn. Soc. N.S.W., 72 : 207–214, 1947) being present.

Mr. R. K. Bamber exhibited a specimen and photographs of fossil wood found in Mount Royal State Forest, New South Wales, on the roadside following road construction. The specimen is highly silicified, being almost completely soluble in hydrofluoric acid. The cell formation is fairly well preserved and under incident light a great amount of detail is visible on the broken faces. From the pattern of the cells it is estimated that the tree from which the specimen originated was at least $7\frac{1}{2}$ inches in diameter. The fossil wood has only tracheids and ray parenchyma. Growth rings and resin canals are absent. The tracheids have an average diameter of 83μ radially by 72μ tangentially and an average length of 8 mm. The radial walls are profusely pitted with from 2 to 4 rows of alternate bordered pits. The ray parenchyma is multiseriate, ranging from 2 to 5 cells wide and from 6 to 43 cells high. All the ray parenchyma cells are procumbent. Pitting in the ray parenchyma could not be observed. This structure appears generally to be similar to that described in the literature as cordaitean wood. It is almost identical with a specimen from Wallarobba described as *Pitys ? sussmilchi* by A. B. Walkom in 1928 (Proc. Linn. Soc. N.S.W., 53 : 255–269). The specimen also shows some similarity to a fossil wood from Upper Devonian rocks at Mansfield, Victoria, described by I. C. Cookson (*Proc. Roy. Soc. Vict.*, 1937, vol. 50 : 182–189).

LIST OF MEMBERS.

(15th December, 1965.)

ORDINARY MEMBERS.

(An asterisk (*) denotes Life Member.)

1940 Abbie, Professor Andrew Arthur, M.D., B.S., B.Sc., Ph.D., c.o. University of Adelaide, Adelaide, South Australia.
1940 *Allman, Stuart Leo, B.Sc.Agr., M.Sc., 99 Cumberland Avenue, Collaroy, N.S.W.
1965 Anderson, Derek John, Ph.D., School of Biological Sciences, Botany Building, Sydney University.
1959 Anderson, Donald Thomas, B.Sc., Ph.D., School of Biological Sciences, Department of Zoology, Sydney University.
1964 Anderson, Mrs. Jennifer Mercianna Elizabeth, B.Sc.Agr., Macleay Museum, Sydney University.
1922 Anderson, Robert Henry, B.Sc.Agr., Kareela Road, Chatswood, N.S.W.
1963 Ardley, John Henry, B.Sc. (N.Z.), School of Public Health and Tropical Medicine, Sydney University.
1927 *Armstrong, Jack Walter Trench, "Cullingera", Nyngan, N.S.W.
1952 Ashton, David Hungerford, B.Sc., Ph.D., 92 Warrigal Road, Surrey Hills, E.10, Victoria.
1912 Aurousseau, Marcel, B.Sc., 229 Woodland Street, Balgowlah, N.S.W.
1965 Ayers, Kenneth Robert, 9 Livingstone Street, Burwood, N.S.W.

1962 Bailey, Peter Thomas, B.Sc., C.S.I.R.O., Division of Wildlife Research, P.O. Box 109, City, Canberra, A.C.T.
1961 Bain, Miss Joan Maud, M.Sc., 18 Onyx Road, Artarmon, N.S.W.
1949 Baker, Eldred Percy, B.Sc.Agr., Ph.D., 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, F.S.T.C., 113 Lucinda Avenue South, Wahroonga, N.S.W.
1950 *Barber, Professor Horace Newton, M.S., Ph.D., F.A.A., School of Biological Sciences, Department of Botany, University of N.S.W., P.O. Box 1, Kensington, N.S.W.
1960 Barber, Ian Alexander, B.Sc.Agr., School of Biological Sciences, Department of Zoology, Sydney University.
1955 Barlow, Bryan Alwyn, B.Sc., Ph.D., c/- Waite Agricultural Research Institute, Private Bag, Glen Osmond, South Australia.
1965 Basden, Ralph, M.Ed., B.Sc. (Lond.), F.R.A.C.I., A.S.T.C., 183 Parkway Avenue, Hamilton, N.S.W.
1960 Batley, Alan Francis, A.C.A., 123 Burns Road, Wahroonga, N.S.W.
1954 Baur, George Norton, B.Sc., B.Sc.For., Dip.For., 3 Mary Street, Beecroft, N.S.W.
1935 *Beadle, Professor Noel Charles William, D.Sc., University of New England, Armidale, 5N, N.S.W.
1946 Bearup, Arthur Joseph, B.Sc., 66 Pacific Avenue, Penshurst, N.S.W.
1940 Beattie, Joan Marion, D.Sc. (*née* Crockford), 2 Grace Avenue, Beecroft, N.S.W.
1964 Bedford, Geoffrey Owen, B.Sc., c/- C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1961 Bedford, Miss Lynette, B.Sc., School of Biological Sciences, Department of Zoology, Sydney University.
1952 Bennett, Miss Isobel Ida, Hon. M.Sc., School of Biological Sciences, Department of Zoology, Sydney University.
1964 Bertus, Anthony Lawrence, B.Sc., Biology Branch, N.S.W. Department of Agriculture, Private Mail Bag, No. 10, Rydalmere, N.S.W.
1948 Besly, Miss Mary Ann Catherine, B.A., School of Biological Sciences, Department of Zoology, Sydney University.
1961 Bishop, James Arthur, School of Biological Sciences, Department of Zoology, Sydney University.
1964 Blackmore, John Allan Philip, LL.B. (Syd. Univ.), 25 Holden Street, Ashfield, N.S.W.
1958 Blake, Clifford Douglas, B.Sc.Agr., Ph.D., Faculty of Agriculture, Sydney University.
1941 Blake, Stanley Thatcher, D.Sc. (Q'ld.), Botanic Gardens, Brisbane, Queensland.
1960 Bourke, Terrence Victor, B.Sc.Agr., c/- Department of Agriculture, Stock and Fisheries, Popondetta, Papua.
1946 Brett, Robert Gordon Lindsay, B.Sc., 7 Petty Street, West Hobart, Tasmania.
1960 Brewer, Ilma Mary, D.Sc., 7 Thornton Street, Darling Point, Sydney.
1955 Briggs, Miss Barbara Gillian, Ph.D., 13 Findlay Avenue, Roseville, N.S.W.
1924 Browne, Ida Alison, D.Sc. (*née* Brown), 363 Edgecliff Road, Edgecliff, N.S.W.
1911 Browne, William Rowan, D.Sc., F.A.A., 363 Edgecliff Road, Edgecliff, N.S.W.
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, Coff's Harbour, N.S.W.

1960 Cady, Leo Isaac, P.O. Box 88, Kiama, N.S.W.
1959 Campbell, Keith George, D.F.C., B.Sc.For., Dip.For., M.Sc., 17 Third Avenue, Epping, N.S.W.
1927 Campbell, Thomas Graham, Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
1934 *Carey, Professor Samuel Warren, D.Sc., Geology Department, University of Tasmania, Hobart, Tasmania.
1949 Carne, Phillip Broughton, B.Agr.Sci. (Melb.), Ph.D. (London), D.I.C., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1956 Carolin, Roger Charles, B.Sc., A.R.C.S., Ph.D., School of Biological Sciences, Department of Botany, Sydney University.
1957 Casimir, Max, B.Sc.Agr., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag, No. 10, Rydalmere, N.S.W.
1936 *Chadwick, Clarence Earl, B.Sc., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W.
1956 Chambers, Thomas Carrick, M.Sc. (N.Z.), Ph.D., Botany School, University of Melbourne, Parkville, N.2, Victoria.
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., "Shady Trees", Clarktown Avenue, Mount Eliza, Victoria.
1946 Clark, Laurance Ross, M.Sc., c.o. C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
1961 Clarke, Miss Lesley Dorothy, 4 Gordon Crescent, Eastwood, N.S.W.
1947 Clarke, Mrs. Muriel Catherine, M.Sc (*née* Morris), 122 Swan Street, Morpeth, N.S.W.
1901 Cleland, Professor Sir John Burton, M.D., Ch.M., C.B.E., 1 Dashwood Road, Beaumont, Adelaide, South Australia.
1957 Clinton, Kenneth John, School of Public Health and Tropical Medicine, Sydney University.
1956 Cogger, Harold George, M.Sc., Australian Museum, College Street, Sydney.
1946 Colless, Donald Henry, Ph.D. (Univ. of Malaya), c.o. Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
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.
1964 Craddock, Miss Elysse Margaret, 36 Lyons Road, Drummoyne, N.S.W.
1950 Crawford, Lindsay Dinham, B.Sc., c/- Victorian Plant Research Institute, Department of Agriculture, Burnley Gardens, Melbourne, Victoria.
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.
1965 Croucher, Miss Phillipa Audrey, B.Sc., Department of Zoology, Australian National University, P.O. Box 4, Canberra, A.C.T.

1965 Dandie, Miss Alison Kay, Women's College, Carillon Avenue, Newtown, N.S.W.
1960 Dart, Peter John, B.Sc.Agr., c/- Mr. H. F. Dart, 53 Smith Street, Wollongong, N.S.W.
1957 Davies, Stephen John James Frank, B.A. (Cantab.), C.S.I.R.O., Private Bag, Nedlands, Western Australia.
1945 Davis, Professor Gwenda Louise, Ph.D., B.Sc., Faculty of Science, University of New England, Armidale, 5N, 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., c/- The Keith Turnbull Research Station, Private Bag, Frankston, Victoria.

1946 Durie, Peter Harold, M.Sc., C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Brisbane, Queensland.
1952 Dyce, Alan Lindsay, B.Sc.Agr., 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.

1964 Facer, Richard Andrew, "Moppity", Parsonage Road, Castle Hill, N.S.W.
1955 *Fairey, Kenneth David, Box 1176, G.P.O., Sydney.
1957 Filewood, Lionel Winston Charles, c/- Department of Agriculture, Stock and Fisheries, Konedobu, Papua.
1964 Florence, Ross Garth, M.Sc.For., Ph.D., Forest Research Station, Beerwah, Queensland.
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., Forestry Office, Wauchope, N.S.W.
1935 *Garretty, Michael Duhan, D.Sc., Box 763, Melbourne, Victoria.
1958 Green, John William, B.Sc. (Adel.), Department of Botany, Australian National University, Box 197, P.O., Canberra City, A.C.T.
1944 Greenwood, William Frederick Neville, 11 Wentworth Avenue, Waitara, N.S.W.
1965 Griffin, David Michael, M.A., Ph.D. (Cantab.), School of Agriculture, Sydney University.
1946 *Griffiths, Mrs. Mabel, B.Sc. (*née* Crust), 50 Amourin Street, Brookvale, 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, 68 Cliff Avenue, Northbridge, 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.), A.R.A.C.I., Department of Chemistry, University of Malaya, Kuala Lumpur, Malaya.
1963 Hewson, Miss Helen Joan, B.Sc. (Hons.), School of Biological Sciences, Department of Botany, Sydney University.
1964 Higginson, Francis Ross, B.Sc.Agr. (Hon.), 3 Benson Street, West Ryde, N.S.W.
1938 Hill, Miss Dorothy, M.Sc., Ph.D., Department of Geology, University of Queensland, Brisbane, Queensland.
1964 Hindmarsh, Miss Gwenneth Jean, B.Sc., Botany Department, University College of Townsville, Pimlico, Townsville, Queensland.
1943 *Hindmarsh, Miss Mary Maclean, B.Sc., Ph.D., 4 Recreation Avenue, Roseville, N.S.W.
1956 *Holder, Miss Lynette Anne, B.Sc., 48 Rutledge Street, Eastwood, N.S.W.
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., 7 Ramsay Road, Pennant Hills, N.S.W.

1957 Jackes, Mrs. Betsy Rivers, B.Sc., Ph.D. (Univ. Chicago) (*née* Paterson), 120 Wellington Street, Aitkenvale, Hermit Park, North Queensland.
1963 Jacobs, Miss Janice Lorraine, B.Sc., School of Biological Sciences, Department of Botany, Sydney University.
1938 Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., Australian Forestry School, Canberra, A.C.T.
1961 Jacobson, Miss Constance Mary, M.Sc., Ph.D., School of Biological Sciences, Department of Zoology, Sydney University.
1960 James, Sidney Herbert, M.Sc., 54 Holmfirth Street, Mt. Lawley, Western Australia.
1964 Jancey, Robert Christopher, M.Sc., Ph.D., 5A Phoebe Street, Balmain, N.S.W.
1963 Jefferies, Mrs. Lesly Joan, 14 Denman Street, Hurstville, N.S.W.
1960 Jenkins, Thomas Benjamin Huw, Ph.D., Department of Geology and Geophysics, Sydney University.

1952 Jessup, Rupert William, M.Sc., 6 Penno Parade North, Belair, South Australia.
1956 Jobson, Arthur Edgar, 3 Wellington Road, East Lindfield, N.S.W.
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., Metropolitan Water, Sewerage and Drainage Board, 314 Pitt Street, Sydney.
1958 Jones, Edwin Llewelyn, B.A., P.O. Box 196, Leeton 6S, N.S.W.
1963 Jones, Leslie Patrick, Department of Animal Husbandry, Sydney University.
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., Summer Institute of Linguistics, P.O. Ukarumpa, E.H.D., Territory of New Guinea.
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., The Institute for Cancer Research, 7701 Burholme Avenue, Fox Chase, Philadelphia, Pa., 19111, U.S.A.
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.
1964 Lanyon, Miss Joyce Winifred, B.Sc., Dip.Ed., 35 Gordon Street, Eastwood, N.S.W.
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.
1964 Levy, Miss Margery Olwyn, B.Sc., Dip.Ed., Katoomba High School, Martin Street, Katoomba, N.S.W.
1964 Littlejohn, Murray John, B.Sc., Ph.D. (W.A.), Department of Zoology, University of Melbourne, Parkville, N.2, Victoria.
1943 Lothian, Thomas Robert Noel, Botanic Gardens, Adelaide, South Australia.
1957 Luig, Norbert Harold, Ph.D., 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, 20 Ordnance Avenue, Lithgow, 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., Department of Botany, University College of Townsville, P.O. Box 499, Townsville, North Queensland.
1922 Mackerras, Ian Murray, M.B., Ch.M., B.Sc., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
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., School of Biological Sciences, Department of Botany, Sydney University.
1953 Martin, Mrs. Hilda Ruth Brownell, B.Sc. (*née* Simons), c/- Mrs. H. F. Simons, 43 Spencer Road, Killara, N.S.W.
1964 Martin, Peter Marcus, M.Sc.Agr., Dip.Ed., School of Biological Sciences, Department of Botany, Sydney University.
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LIST OF PLATES

PROCEEDINGS, 1965

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New Genera

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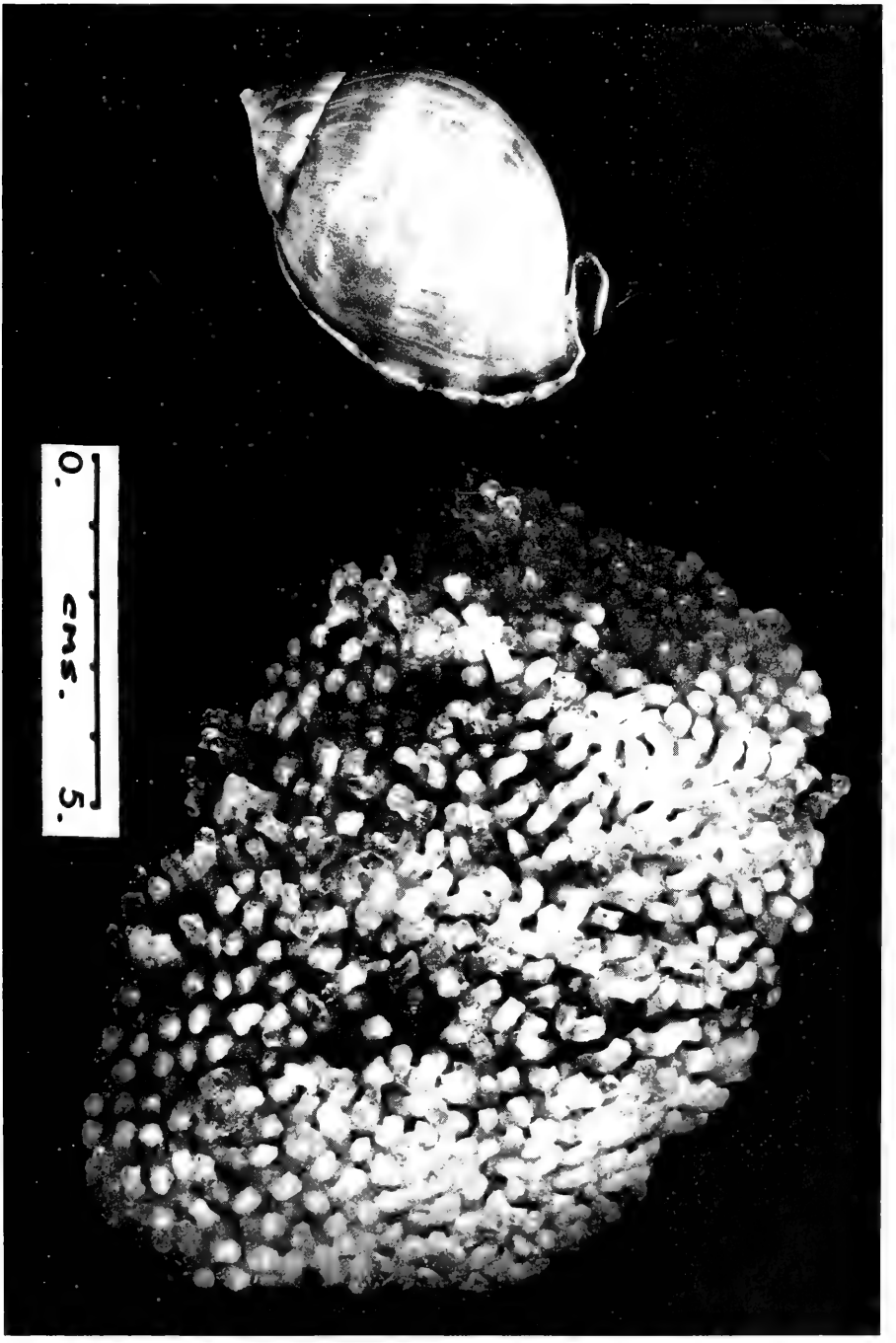
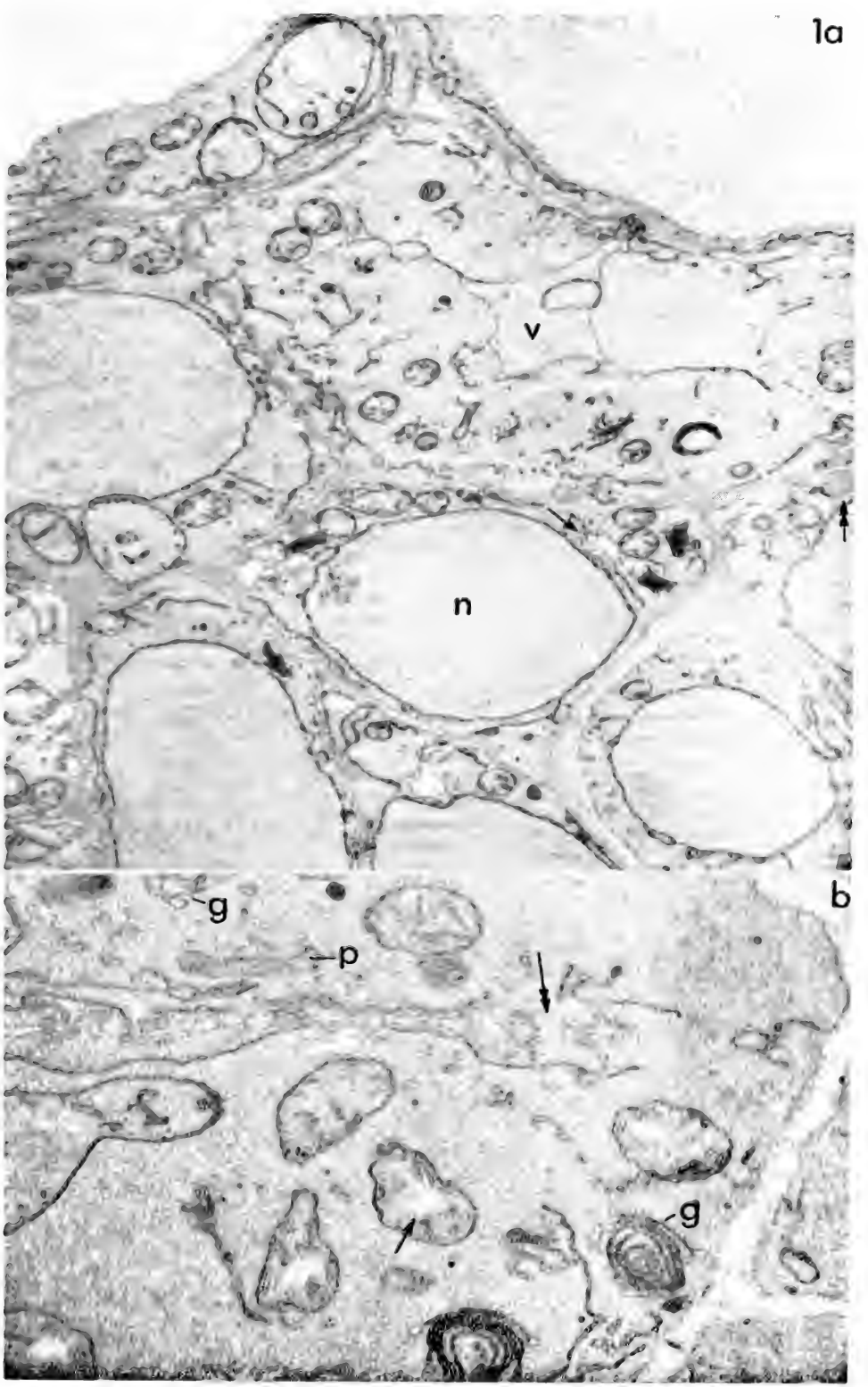
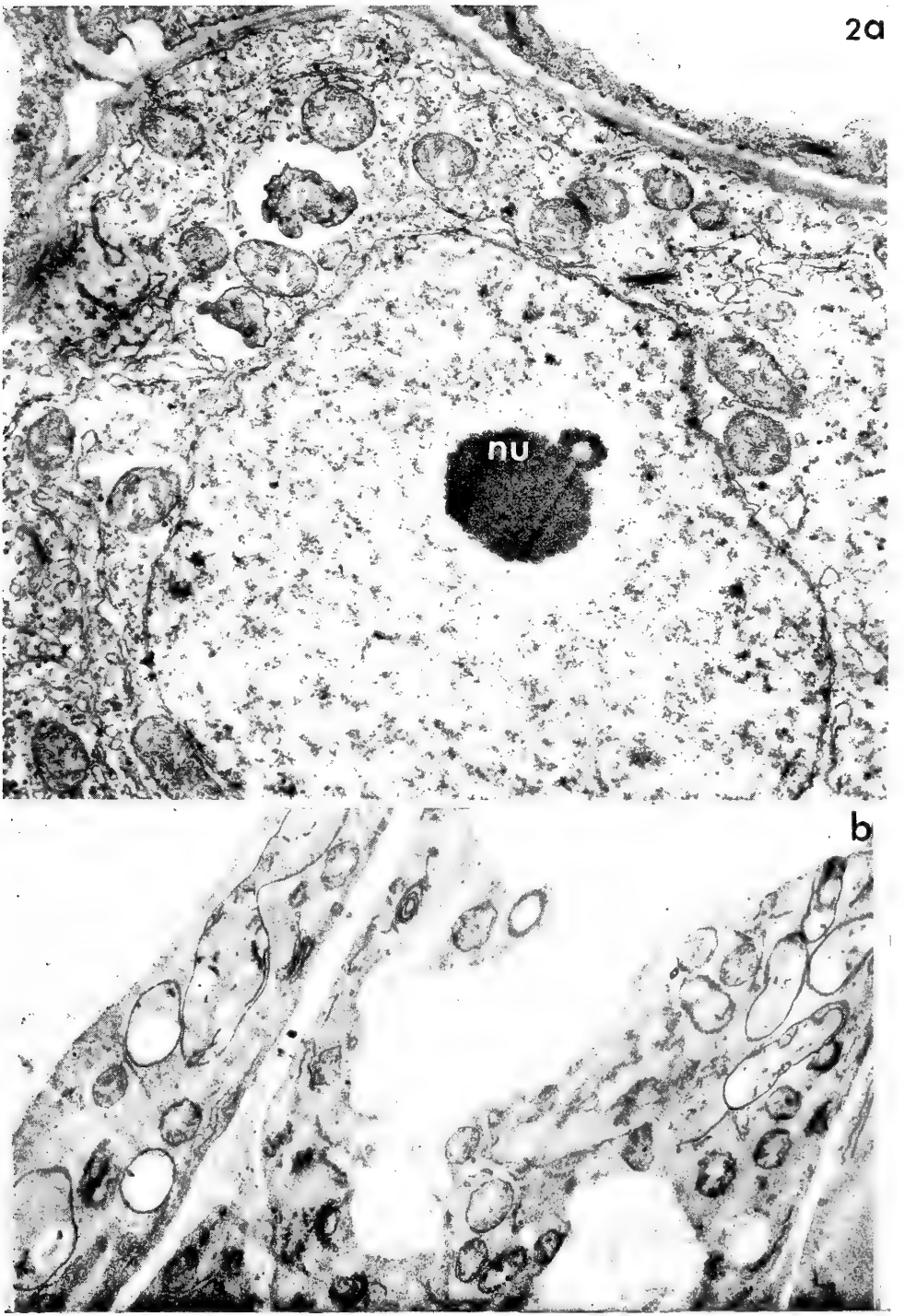


Xenogalea labiata : Shell and part of egg mass.



Fine structure of the meristem of root nodules from some annual legumes.



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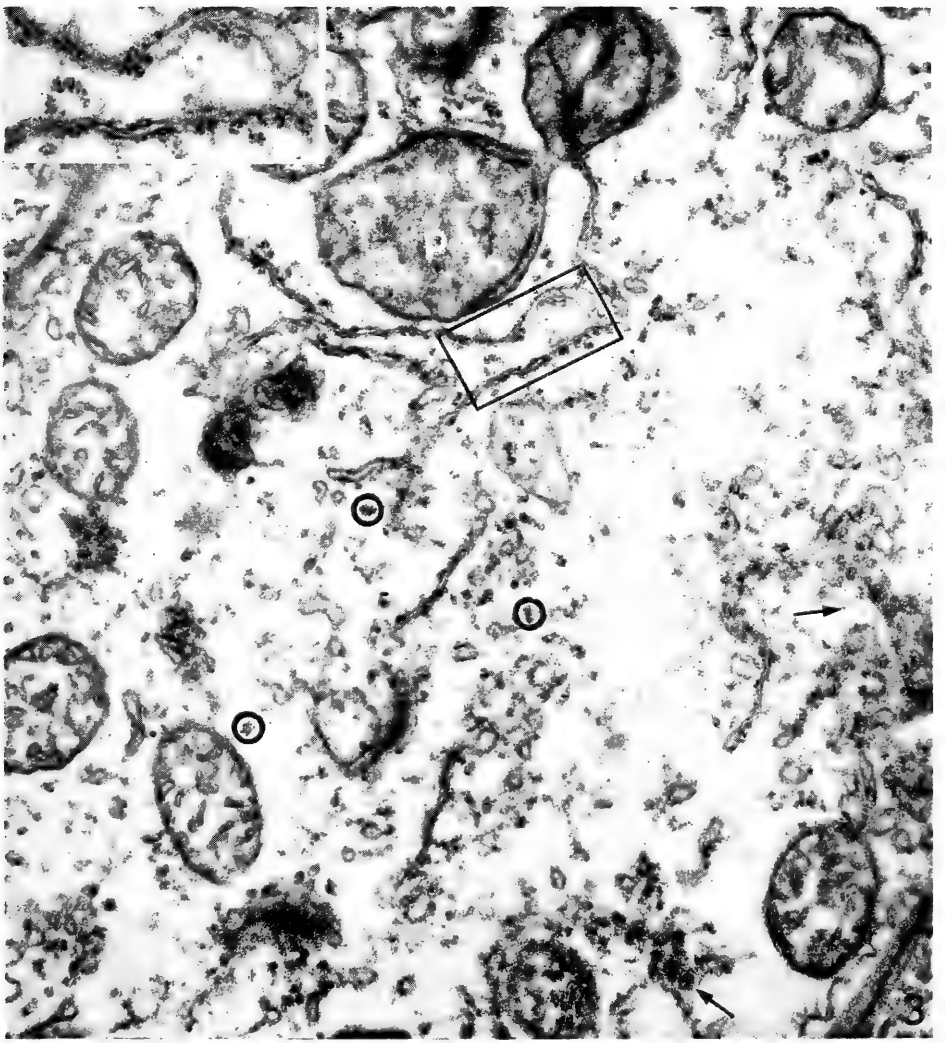

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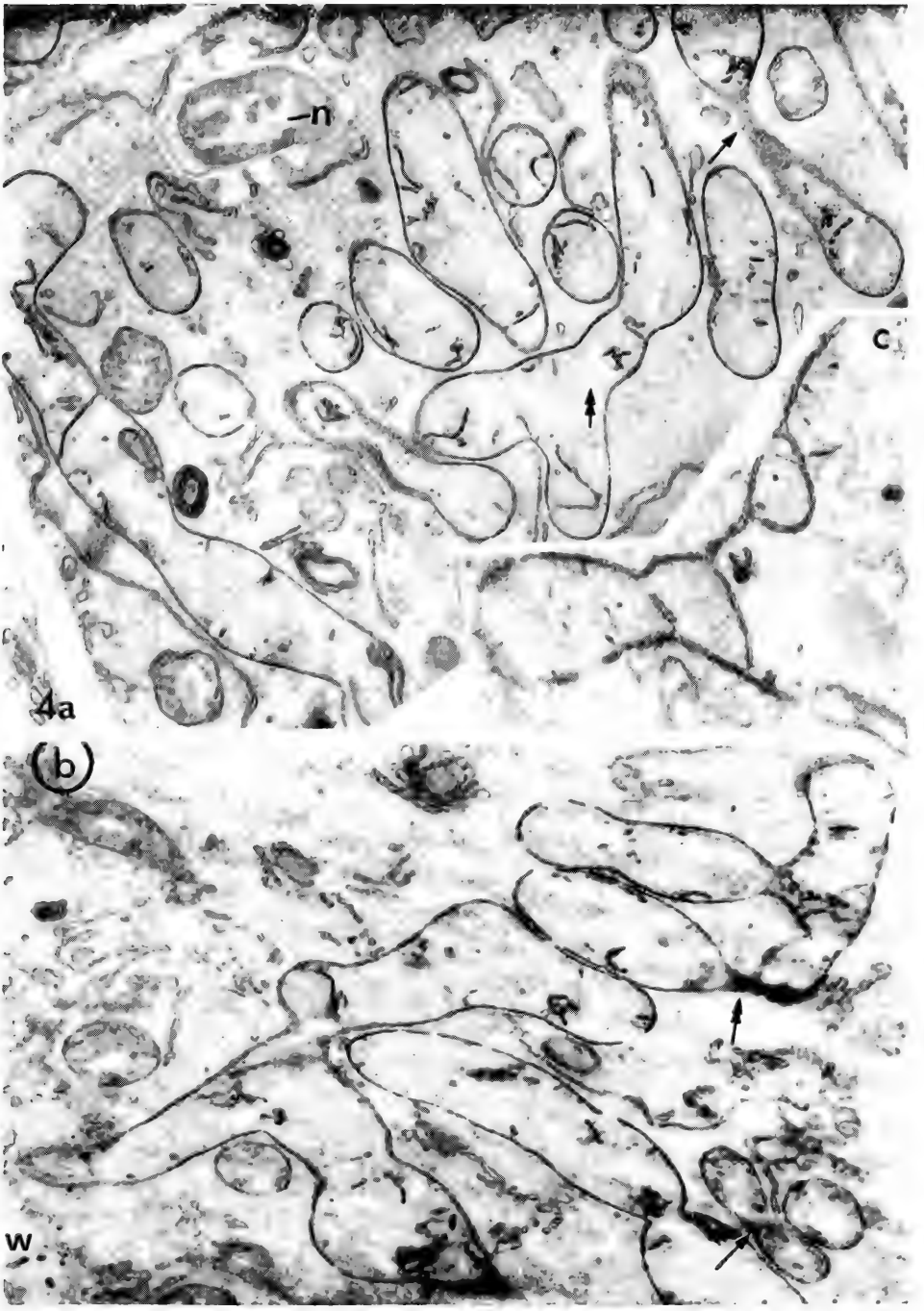

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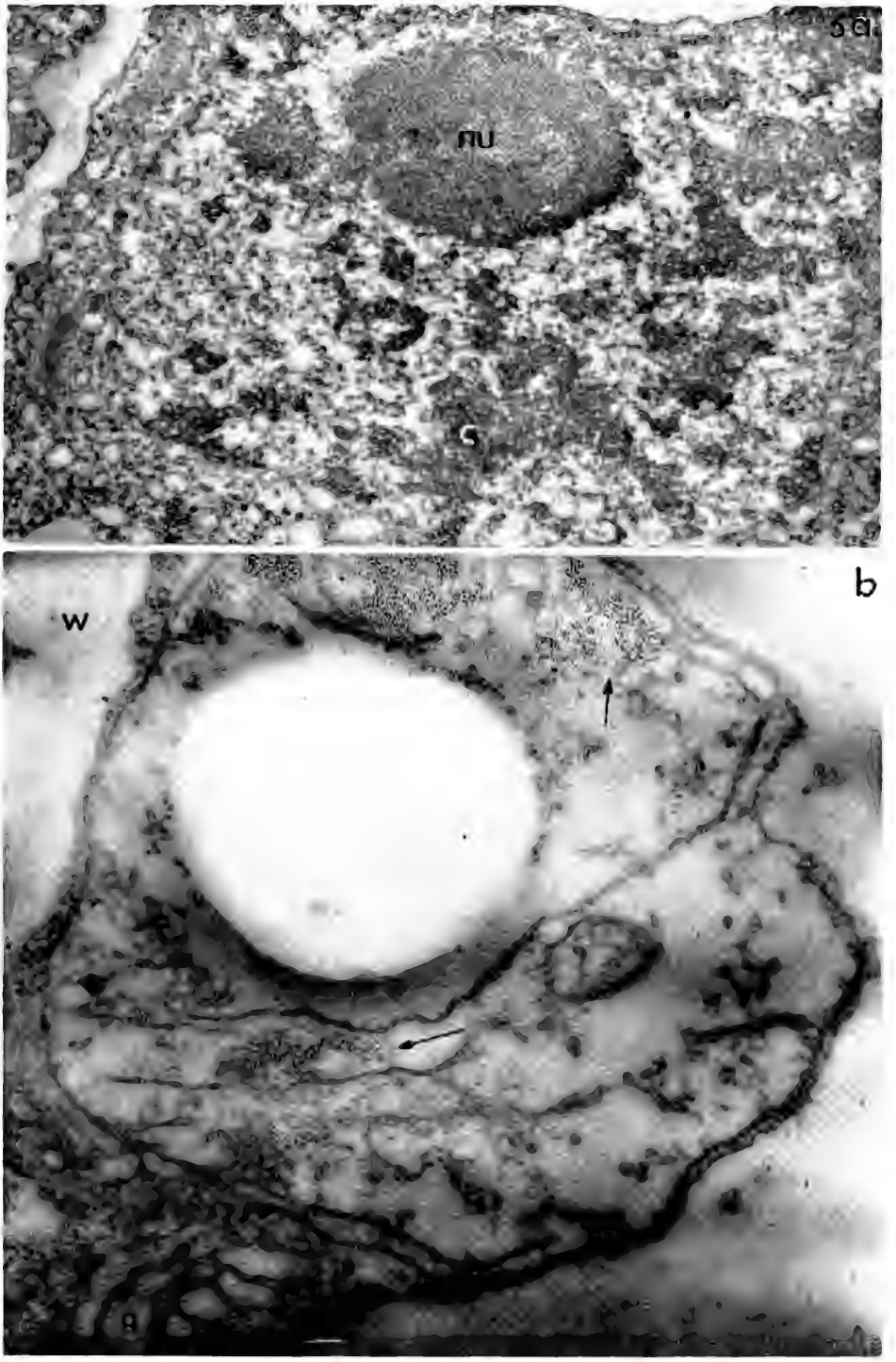

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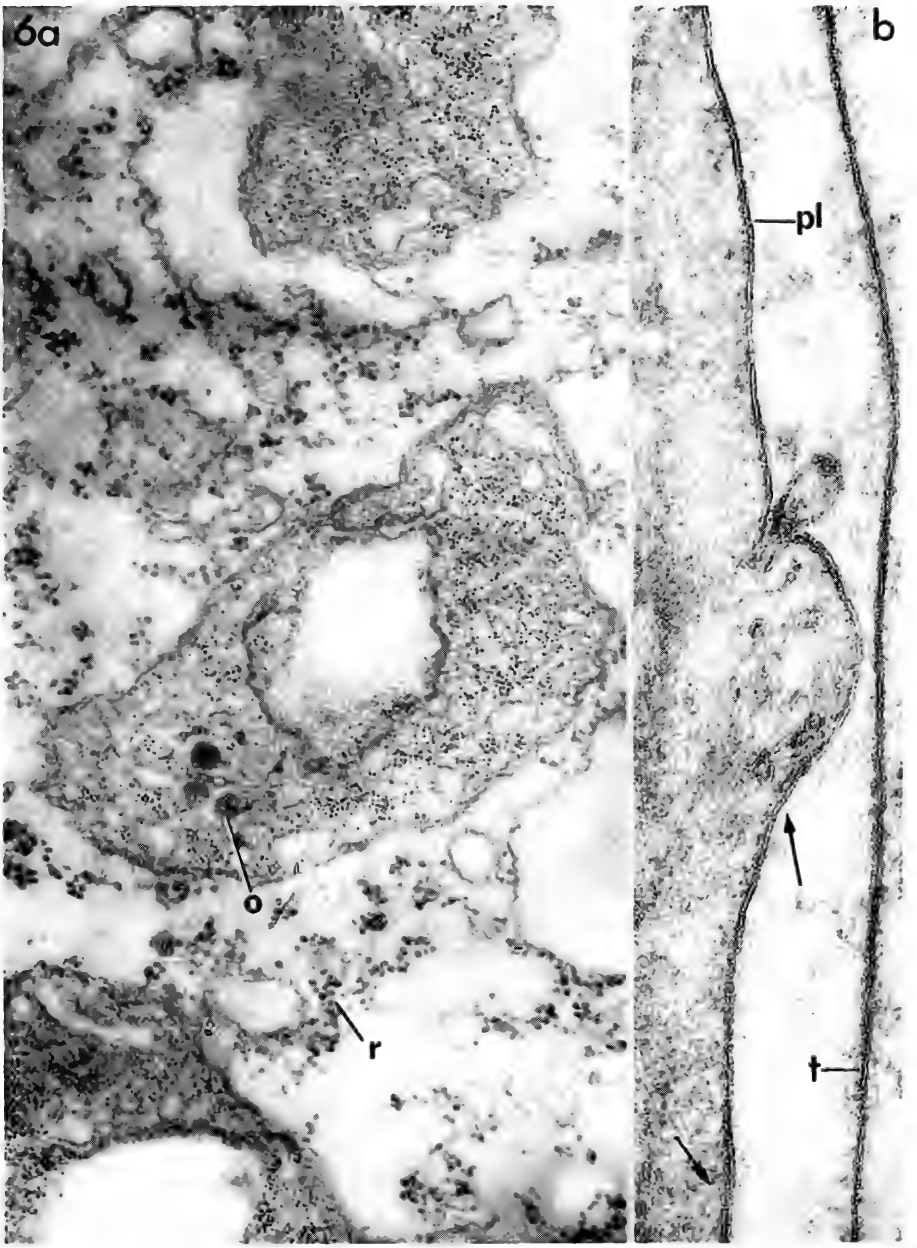

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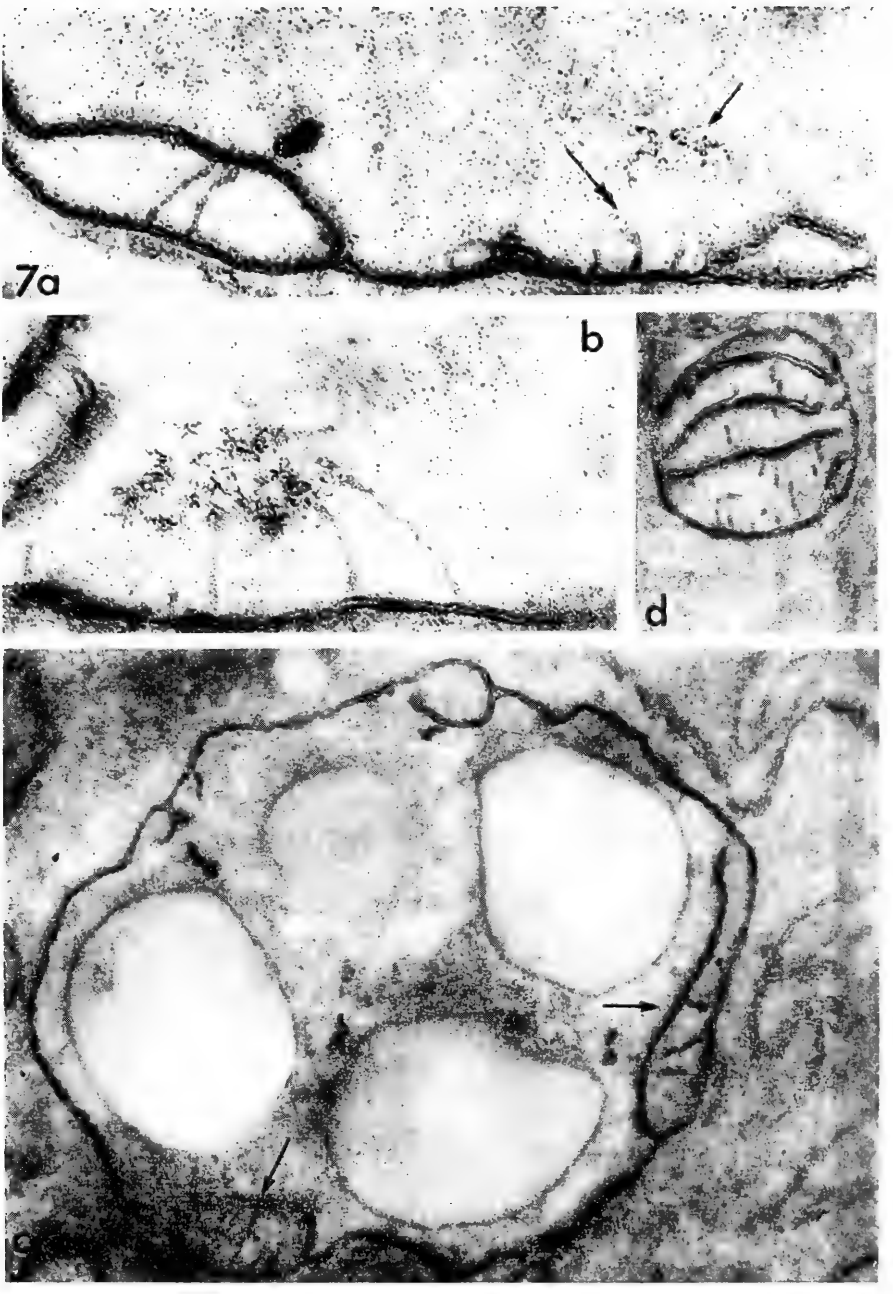

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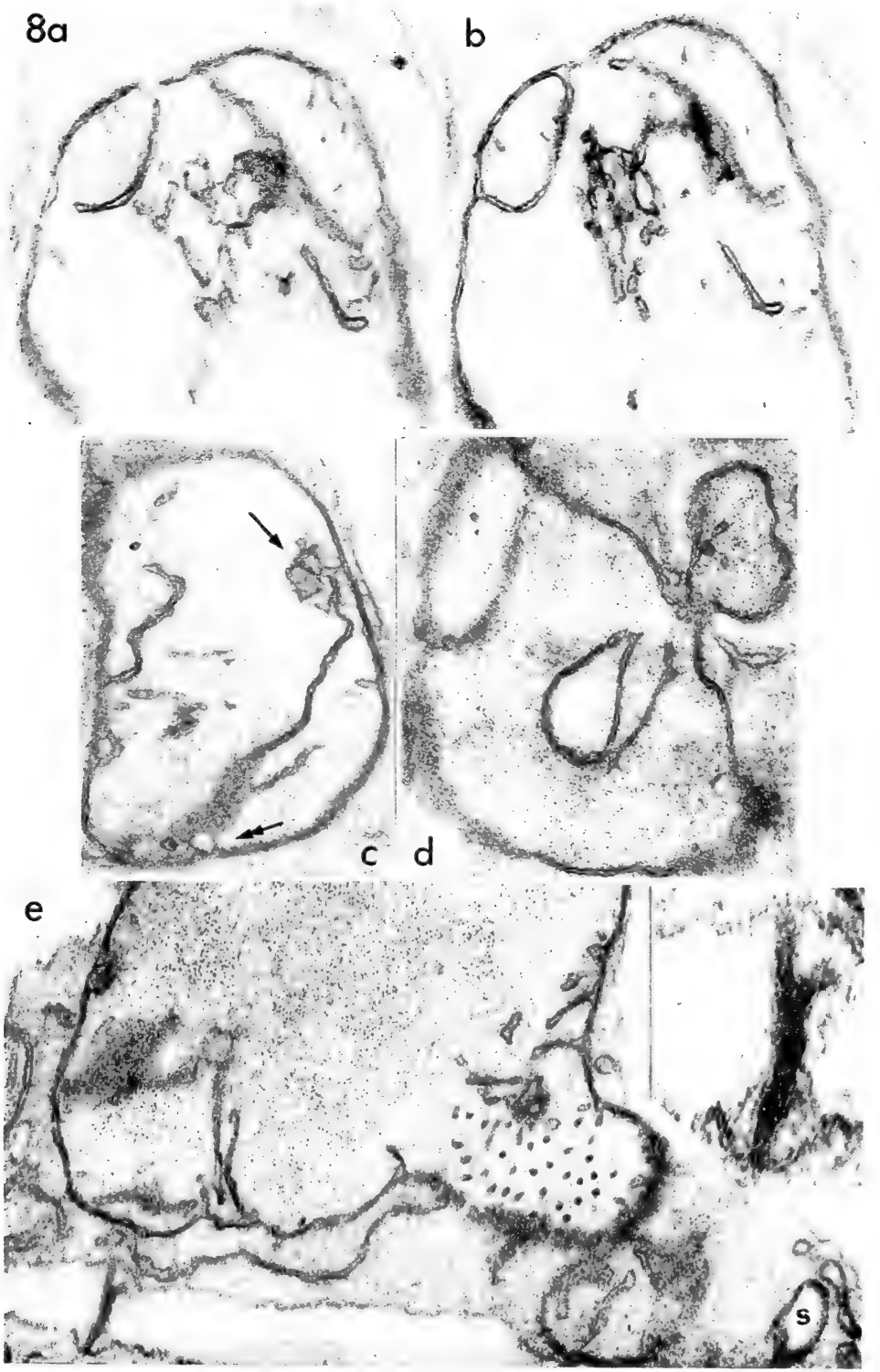

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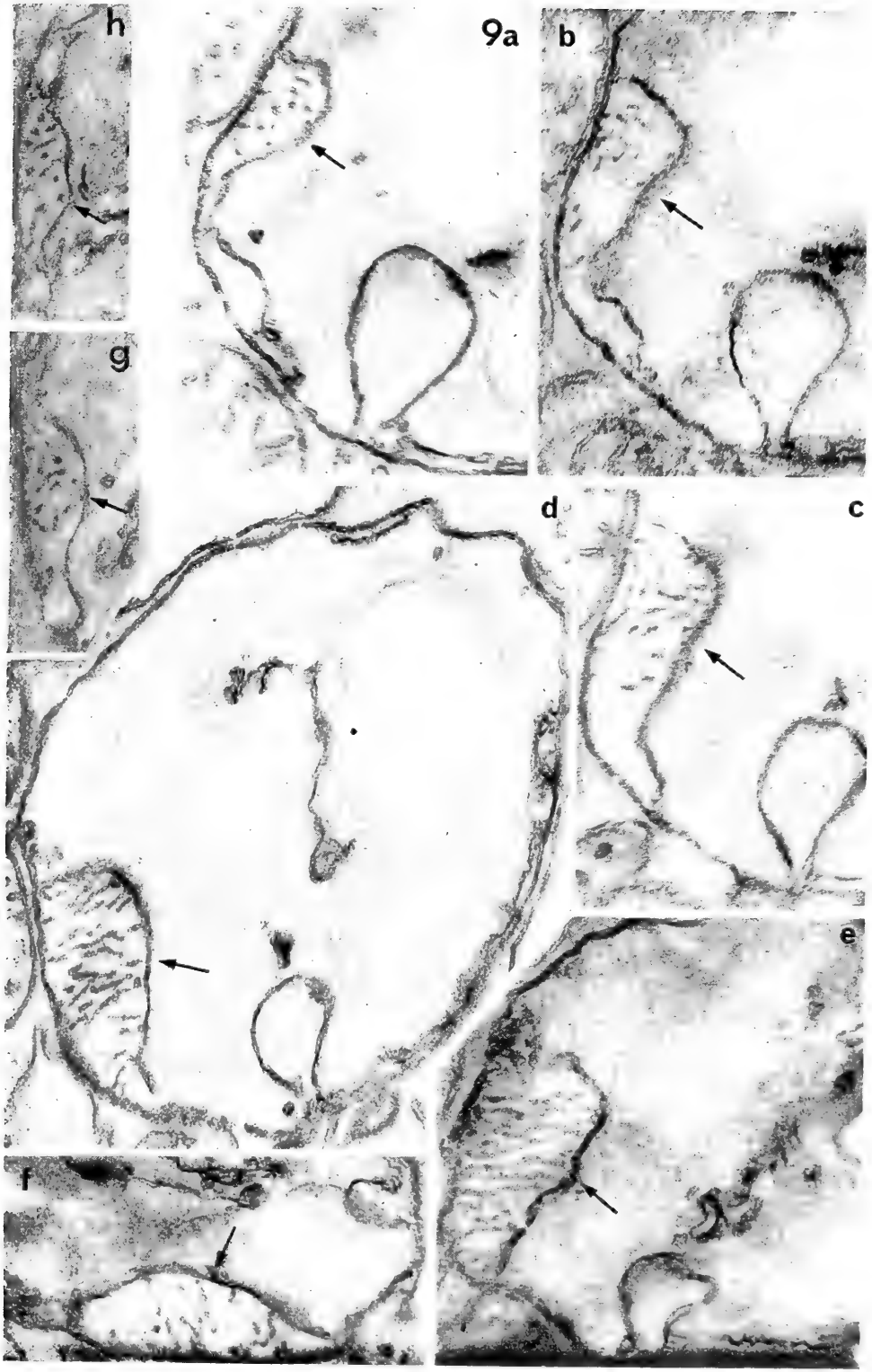

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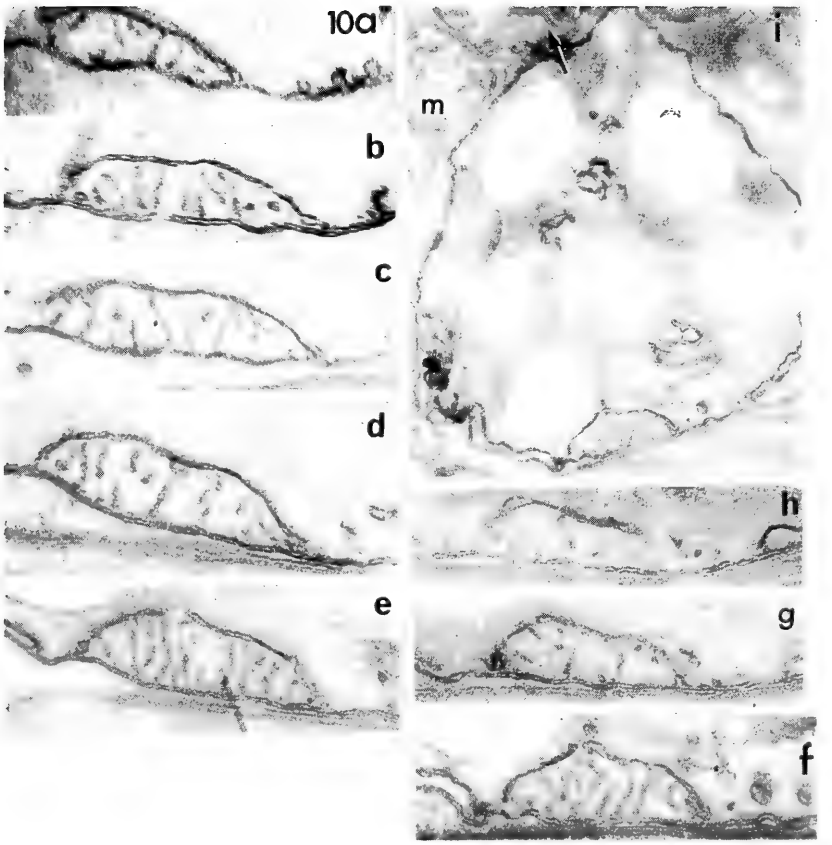

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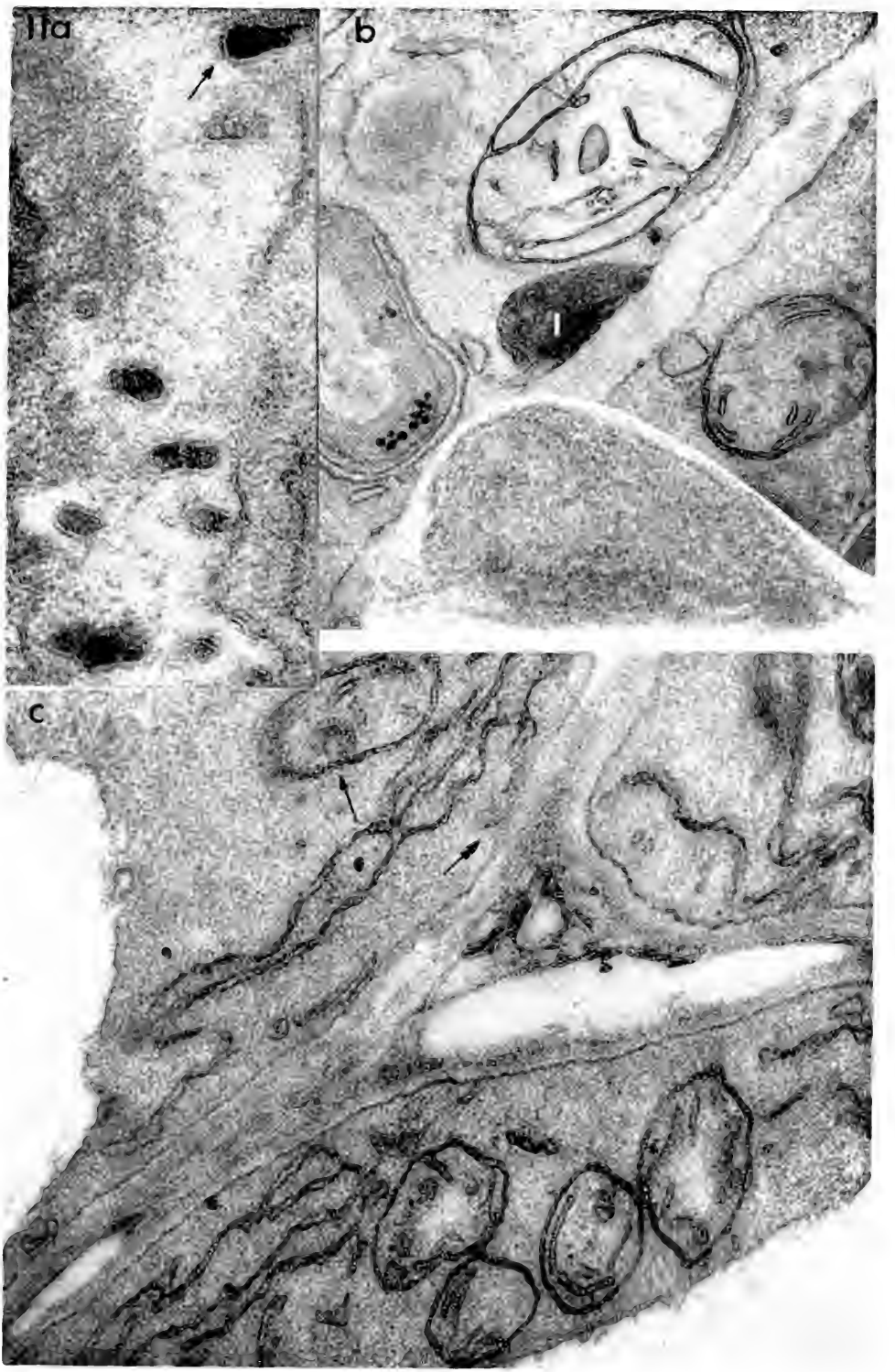

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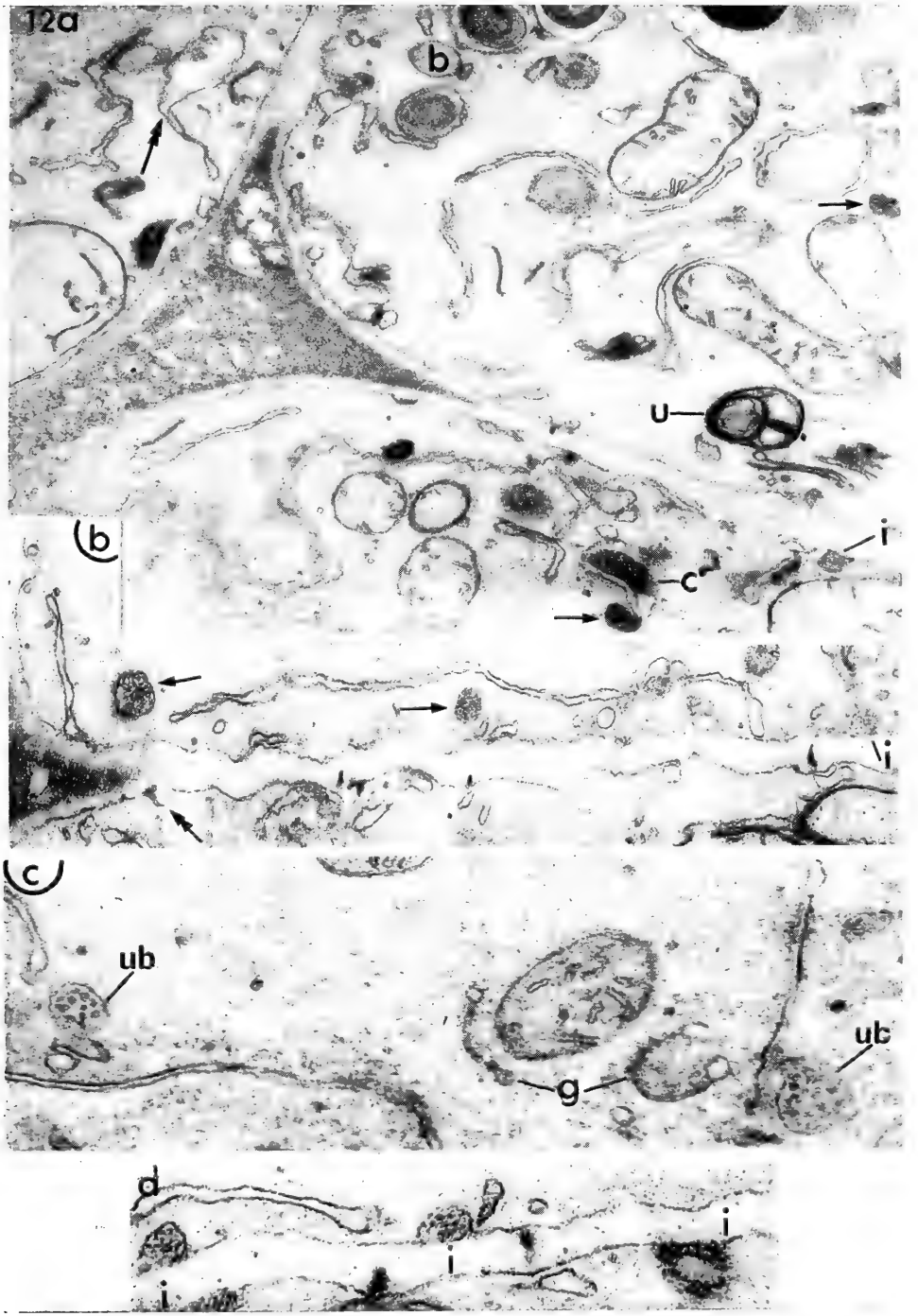

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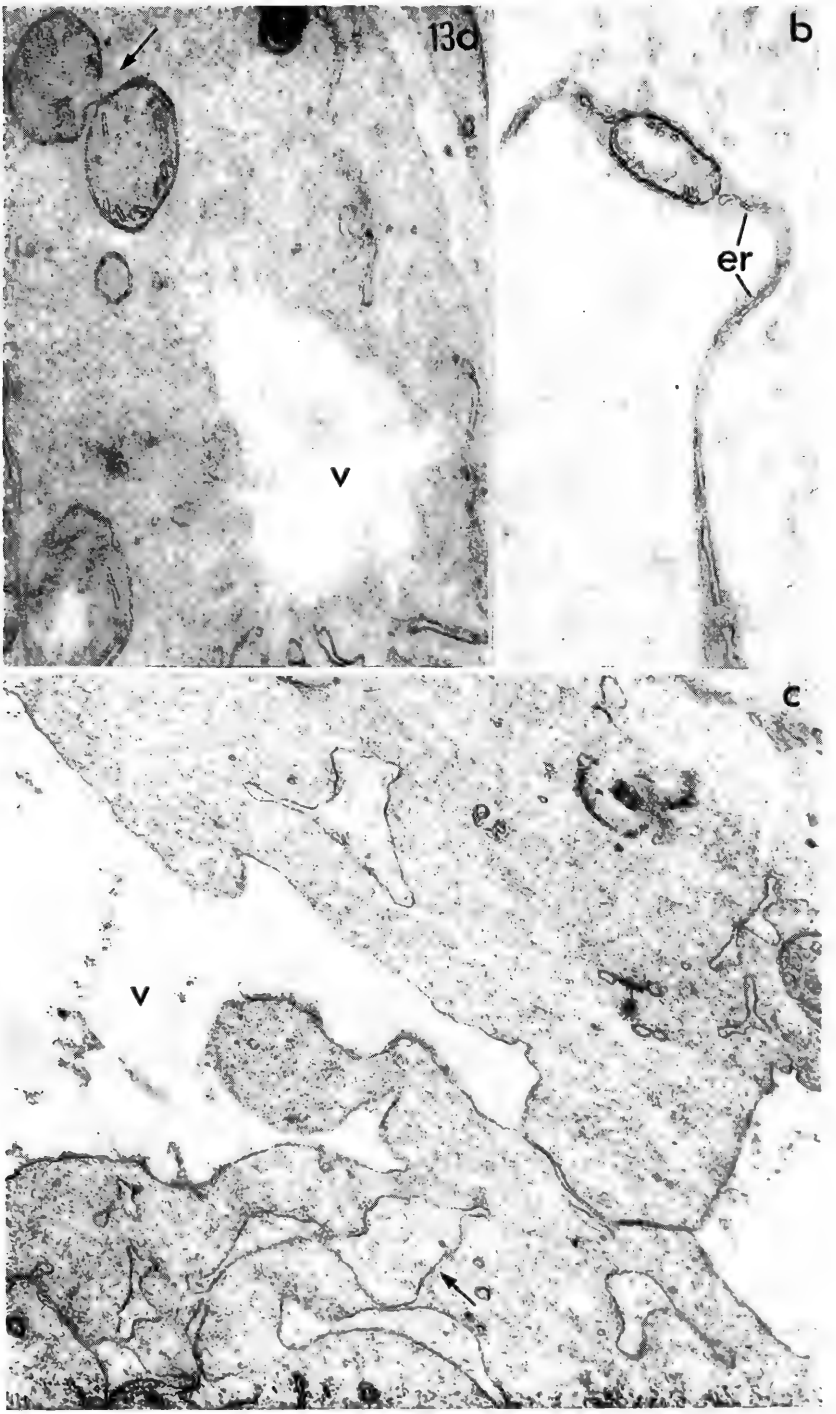
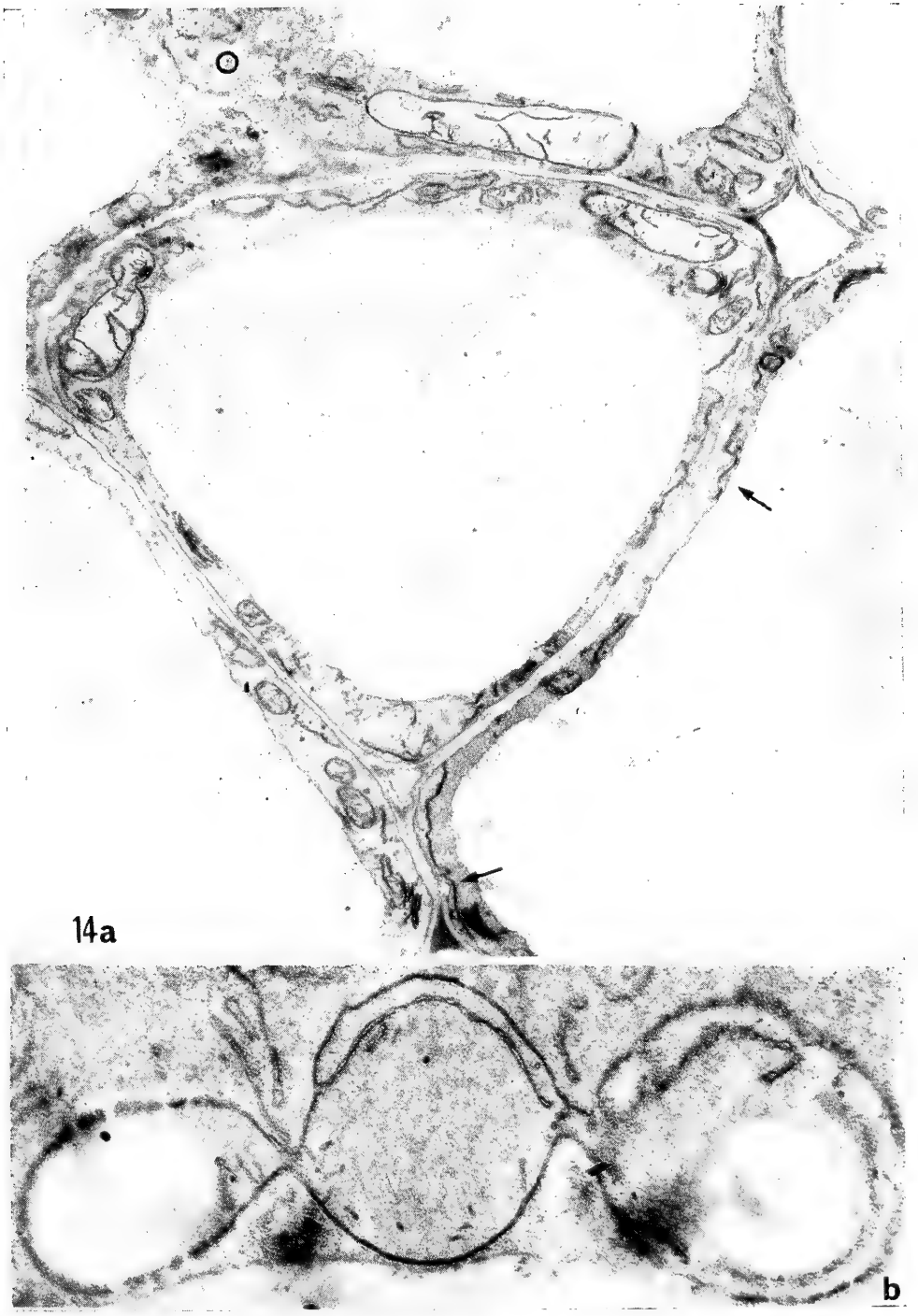
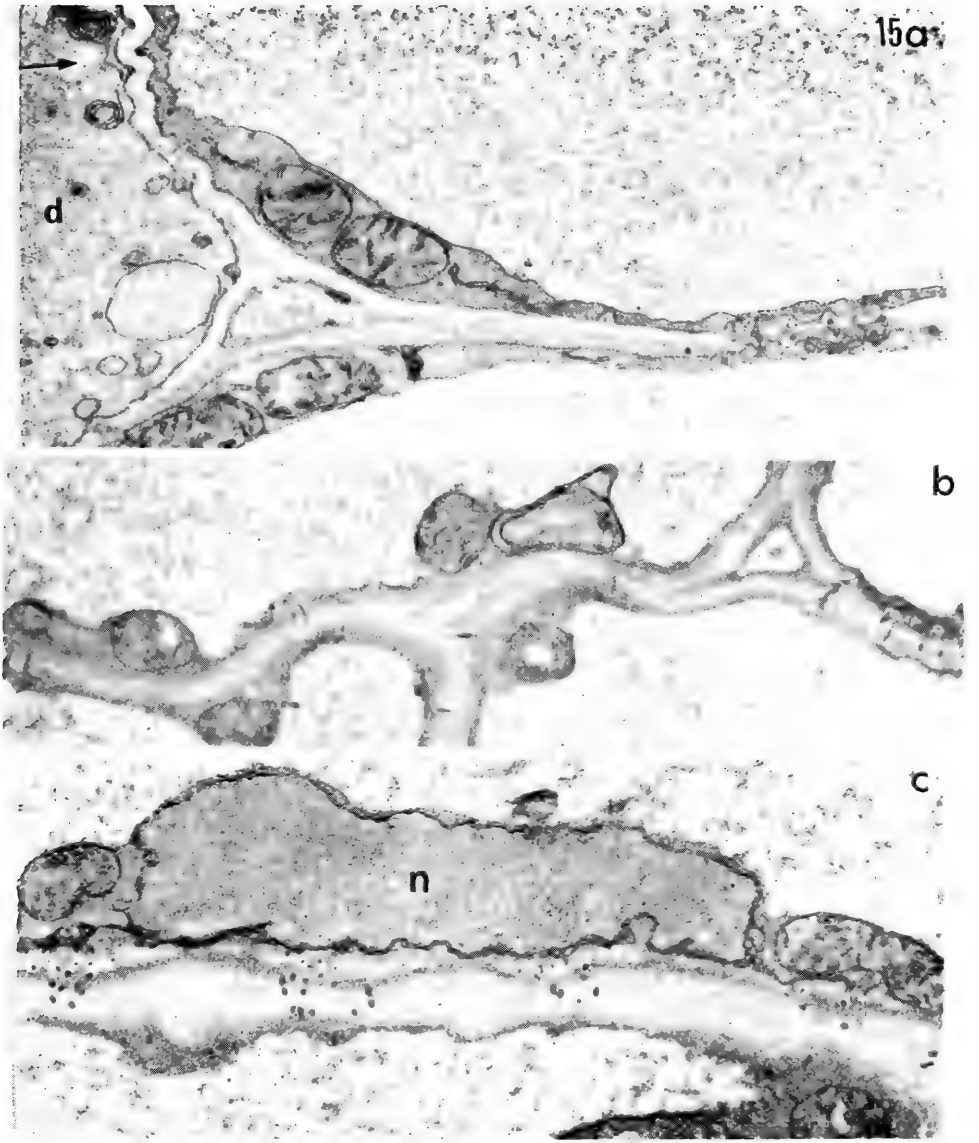


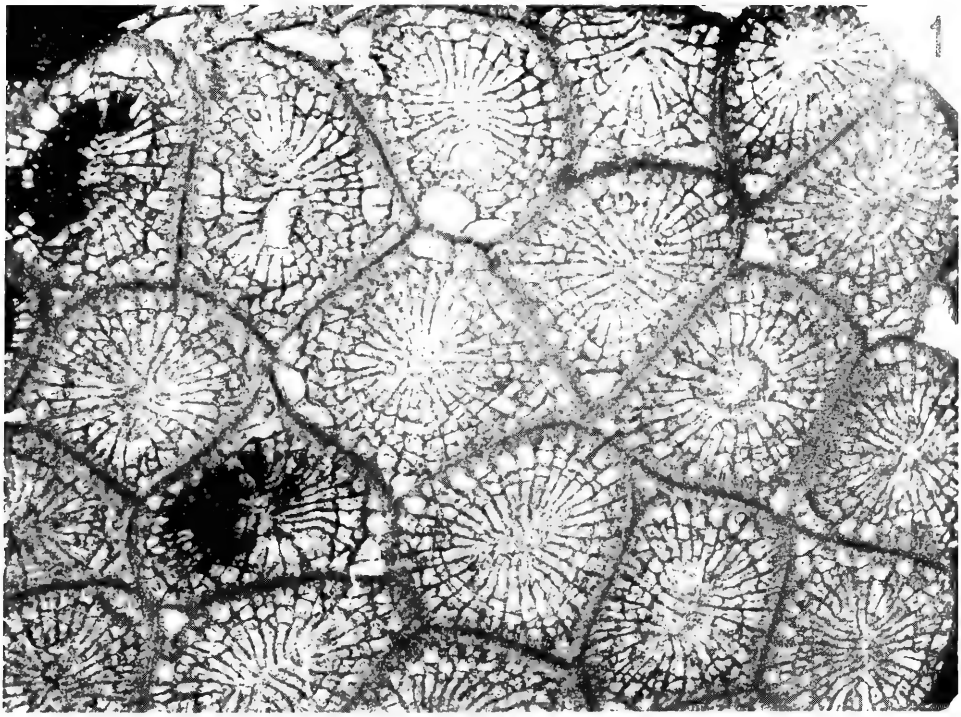
Fine structure of the meristem of root nodules from some annual legumes.

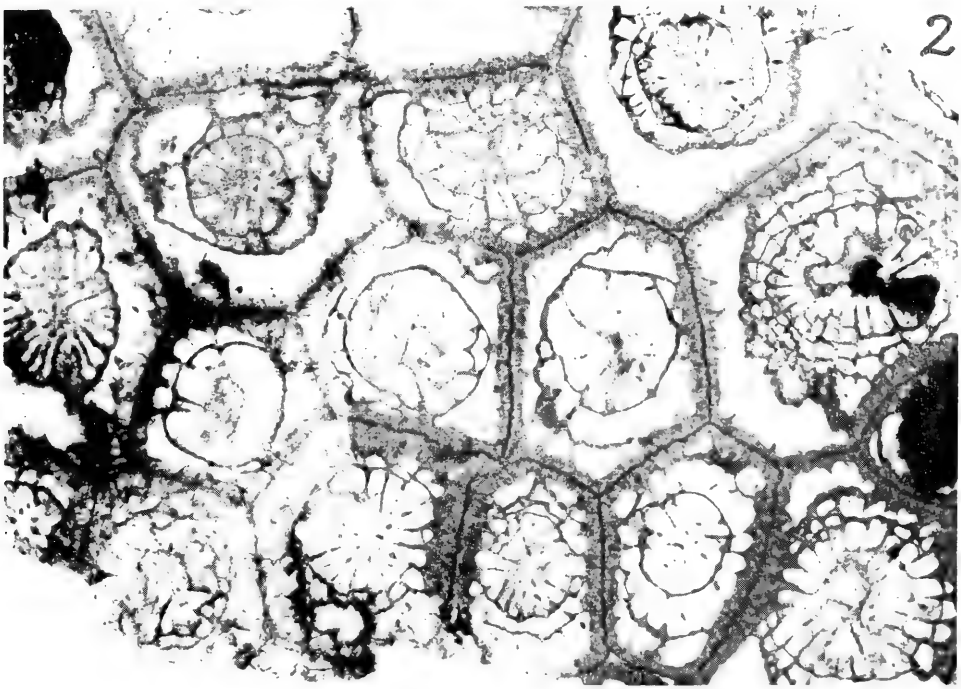


Fine structure of the meristem of root nodules from some annual legumes.



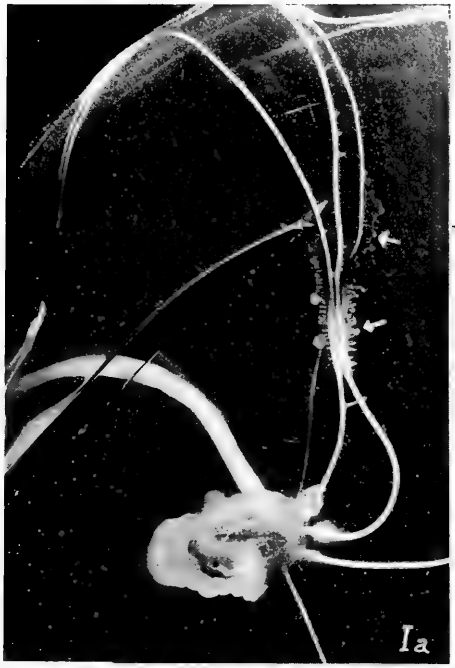
Fine structure of the meristem of root nodules from some annual legumes.

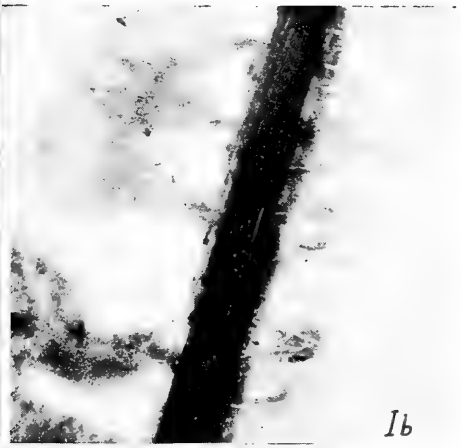


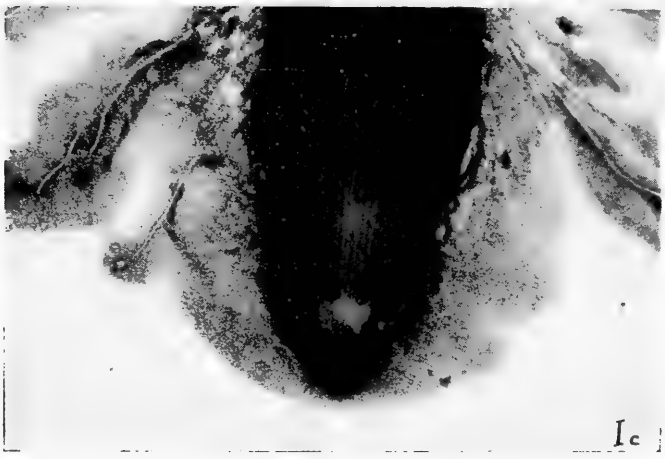


1. *Melrosia rosae.*

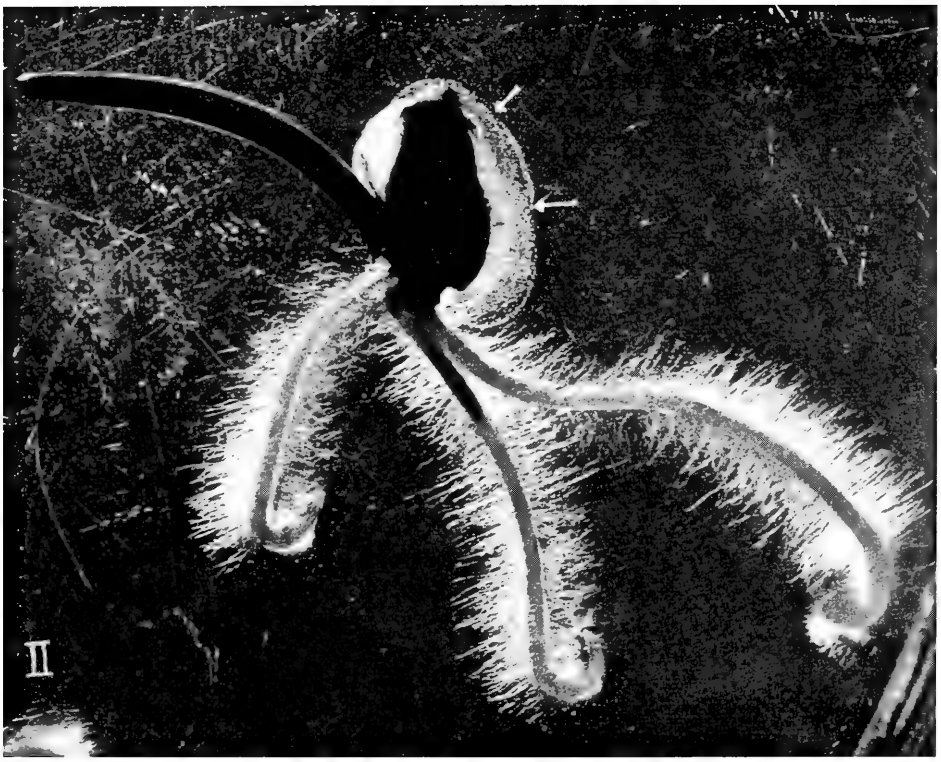
2. *Melasmaphyllum mullamuddiensis.*



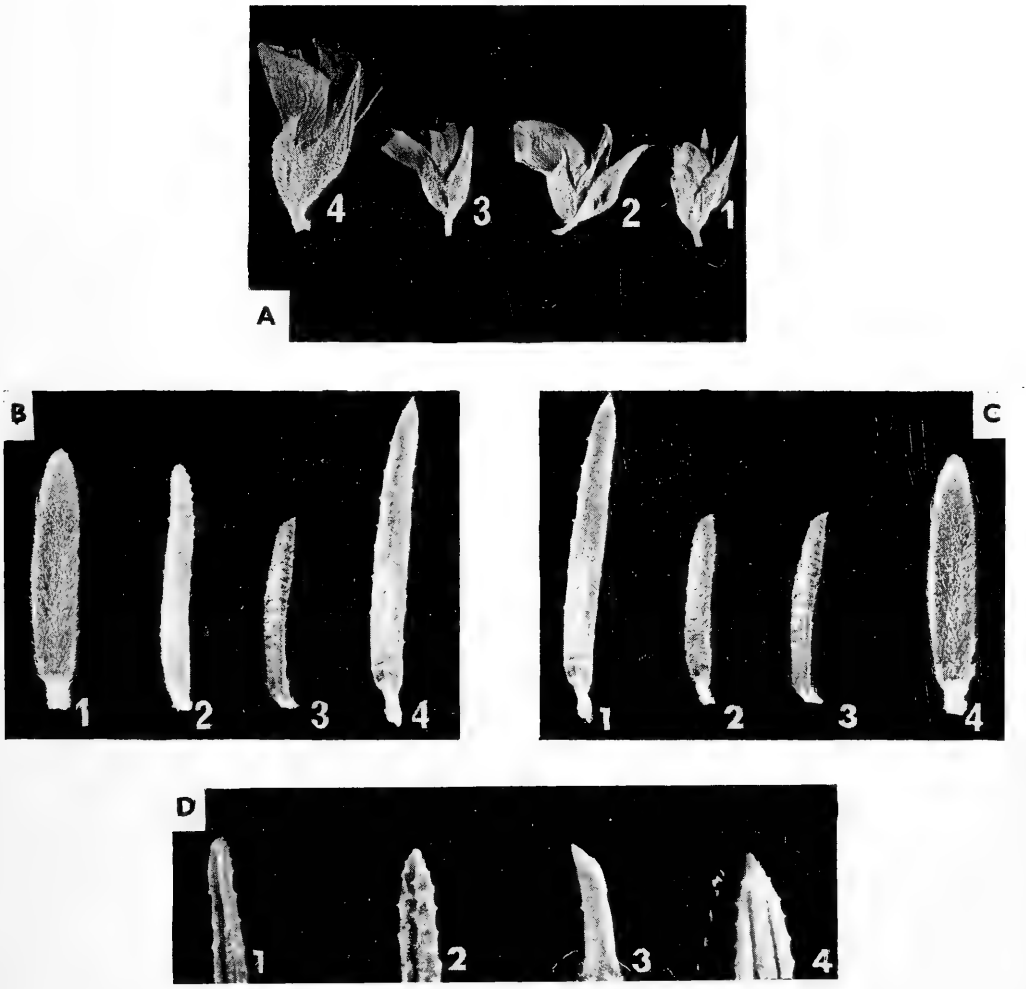




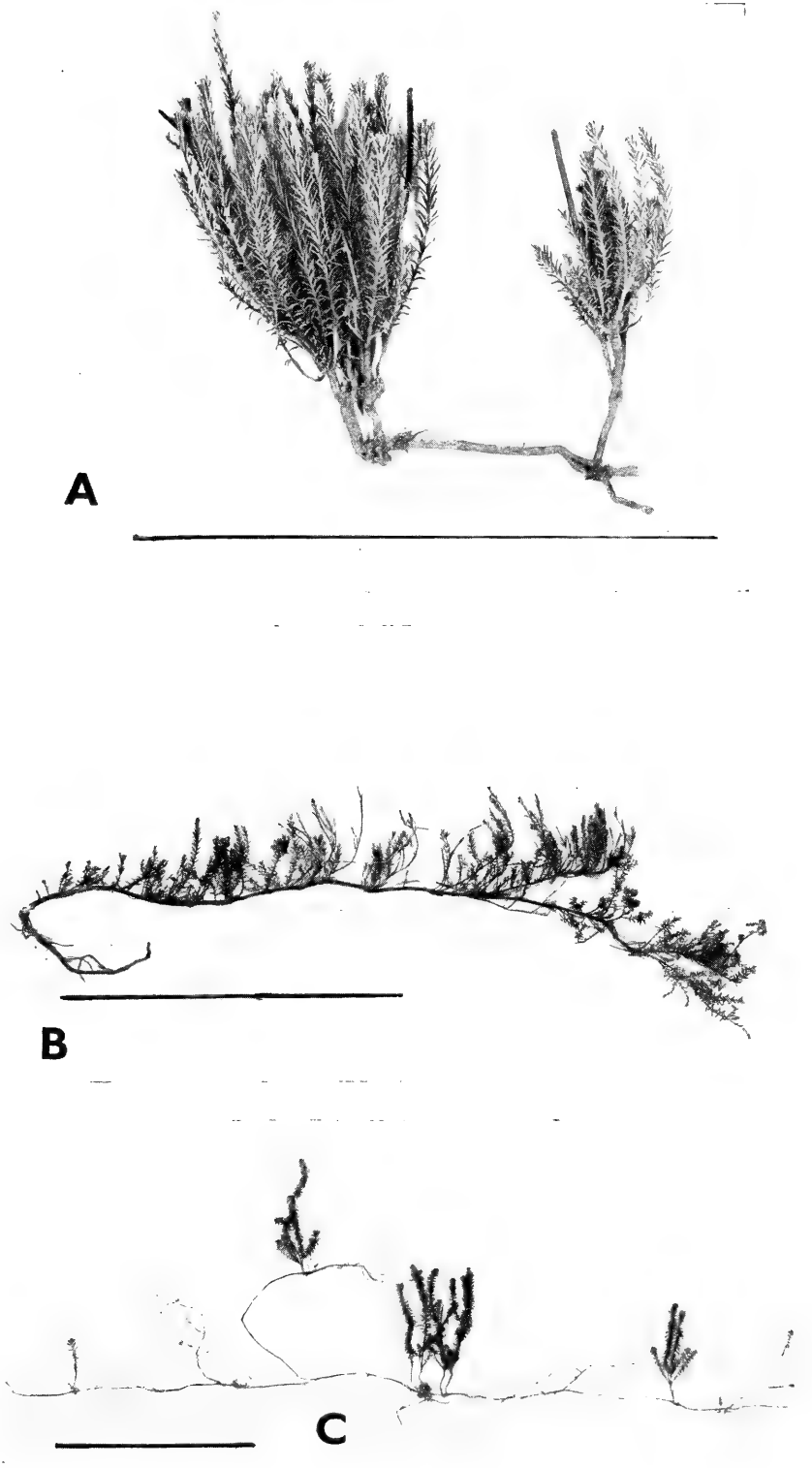
Wheat seed germinated on agar medium.



Wheat seed germinated on agar medium.



Scales of subjective values for parts of *Phyllota*.



Growth habit in groups of *Phyllota*.