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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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Janet Donald, B.A., Dip.Lib.

The Society's Headquarters are in Science House, 157 Gloucester Street, Sydney,
N.S.W. 2000, Australia

ANNUAL GENERAL MEETING

26th March 1975

The one-hundredth Annual General Meeting was held in the Society's Rooms, Science House, 157 Gloucester Street, Sydney, on Wednesday, 26th March 1975, at 8.00 p.m.

Professor T. G. Vallance occupied the chair. The minutes of the ninety-ninth Annual General Meeting (27th March 1974) were read and confirmed.

Report on the Affairs of the Society for the Year 1974

Publications

The Society's *Proceedings* were published on the following dates during the year:

1974 Vol. 98, Part 4	25th May 1974
1974 Vol. 99, Part 1	11th November 1974
1975 Vol. 99, Part 2	25th February 1975
1975 Vol. 99, Part 3	5th March 1975

The cost of publishing the *Proceedings* was as follows:

	$		$
Blockmaking (Illustrations)	794.81	Subscriptions ..	5,279.76
Printing	3,487.60	Miscellaneous Sales	2,266.69
Postage	167.12		

Cost of Reprints: Printing—$556.00; Sales—$356.25.

All four parts were published behind schedule, owing to labour difficulties experienced by the printer. Reprints were likewise slow in appearing. Therefore the figures for printing (above) represent the cost of Part 4 (Vol. 98) and Part 1 (Vol. 99), and the cost of the reprints from Parts 3 and 4 (Vol. 98), only.

Membership

During the year 21 new members were admitted to the Society; 11 resigned and one died. The numerical strength of the Society as at 1st March 1975 was Ordinary Members 278; Life Members 28; Corresponding Members 4; total 310.

Meetings

Ordinary monthly meetings were held in March, June and September, the first at Science House in the Linnean Society Rooms and the latter two in the Botany Department, University of Sydney, and in the Australian Museum, College Street, respectively.

Two centenary functions were held during the year, the first being the Sir William Macleay Memorial Lecture and Centenary Dinner held in April at the Wentworth Building, University of Sydney, and the second an exhibition of the Society's archives and cocktail party held in October at the Mitchell and Dixson Galleries, Library of New South Wales.

A Special General Meeting was held in the Society's Rooms, Science House, in November in order to alter the Society's Rules as provided under Rule 59 of the old Rules.

The Notes and Exhibits Evening took place as usual in November after the Special General Meeting. (Details of these may be found in Vol. 99, Part 4 of the *Proceedings*).

Library

Requests for photocopies of reference material from libraries in Australia, New Zealand and Malaysia have again shown a steady increase. In addition many requests for references to be used in the library have been received during the year.

The cumulative author and subject index to the Society's *Proceedings*: 1926 to date, is now complete and being kept up to date as each issue is published.

The completion of the serials cataloguing and the index has enabled the services of the Linnean Society's librarian to be made available to the Royal Society three mornings a week to undertake the re-cataloguing of serials and up-dating of entries in *Scientific Serials in Australian Libraries.*

A very successful exhibition of maps, notes, manuscripts and portraits relating to the Society and held by the Mitchell Library was opened in the Dixson Gallery by the Hon. W. L. Morrison, Minister for Science, on 25th October 1974, as part of the Society's centenary year celebrations.

Despite assurance from the University of Sydney that progress is being made on the organisation and cataloguing of the Society's monographs, which are being held by the University as a special collection, as yet no catalogue cards have been received.

As the result of a Library Appeal for the Royal and Linnean Societies, the N.S.W. State Government donated $10,000 towards the building project.

Linnean Macleay Lectureship in Microbiology

The appointment continues to be held by Dr. K. Y. Cho. During 1974 he spent his sabbatical leave in the University of Texas at Austin and at the New York University Medical Center. The work in the former was concerned with factors affecting the formation of protoplast in *Azotobacter vinelandii* and isolation and characterisation of its wall and membrane. A paper based on these results was published in *Arch. Microbiol.* (Vol. 101, 1974), another was accepted for publication in *Reports of Texas Biology and Medicine* and a third is in preparation.

The work at the New York University Medical Center was concerned mainly with the phospholipid turnover of *Gonococcus*, isolation and characterisation of lipids in *Streptococcus faecalis* and *Streptomyces* as well as the effect of antibiotics on the composition of bacterial membranes.

Obituary

Mr. Ellis Le Geyt Troughton, F.R.Z.S., C.M.Z.S., President of the Society 1943–4 and a councillor 1939–1972, died in Sydney on 30th November 1974. Mr. Troughton was born at Darlinghurst on 29th April 1893 and, following appointment as a Cadet at the Australian Museum early in 1908, studied zoology first at the Sydney Technical College and then at the University of Sydney.

On his return to the Museum after service in France with the Fourth Australian Field Ambulance he became (October 1919) Curator of Mammals. That position he occupied until his retirement though, as a Research Associate, his connection with the Museum continued to the end.

Mr. Troughton was the author or joint author of some 168 papers, articles and books, the best known of the latter being *Furred Mammals of Australia* which has already passed through nine editions. That record bears witness to his industry in the field of mammalogy and conservation. His other interests—in theatre, in ballet, in music—were cultivated with a like devotion and fresh enthusiasm.

His genial personality, his skill as a raconteur, added to a wide and sympathetic learning, earned for Mr. Troughton a wide circle of friends. Despite failing health he managed to attend our centennial meeting last October and there plainly showed his joy at seeing again so many firm friends. Those friends now salute the delightful character known to all as " Troughtie " and mourn his passing.

Staffing Arrangements

During the year a number of changes were made in the staffing arrangements.

Although the Secretary, Mrs. Inall, was originally employed by the Society on a full-time basis, her functions and responsibilities have continued to widen and increase. Apart from taking on the planning of the new Science Centre in 1971 on behalf of the two Societies, she was asked to take on the management of the present Science House in 1972 when the Institution of Engineers was no longer able to do so. Increasingly her time has been taken up with the new project and towards the end of 1973 Science House Pty. Ltd., on the recommendation of its advisers, appointed her as Project Director for the building project (a function which had previously been assigned to paid consultants) with the additional responsibilities of finding the finance and later letting the building.

In consequence, the Company felt that it should assume responsibility for the major portion of Mrs. Inall's salary, and as from the 1st October 1974, Mrs. Inall became Secretary of the Linnean Society with an honorarium only. In reality it has not made any difference to her relationship with Council or the Society—she still carries full responsibility as set out in the Rules.

The Society has had the services on a part-time basis of an Assistant Editor, Mrs. Donald, since February 1974. Mrs. Donald is a graduate librarian and has also had editorial experience. It is envisaged that many more societies will avail themselves of professional editorial services in the Science Centre, and it seems from the enquiries received that this will be one of the most useful facilities the new Centre will offer.

During the year work on the reorganisation of the library was completed, as is the index to the Society's *Proceedings* except for Volume 100. It was therefore agreed that our librarian, Mrs. McKay, should be made available to the Royal Society to catalogue its library. This arrangement has been in operation since October 1974 which means that the Society now meets only two-fifths of the librarian's salary, the rest being met by the Royal Society.

Due to the increasing work load, the Company decided to appoint an Assistant Secretary and a typist during the latter part of 1974. The Linnean Society buys secretarial services from the Company amounting to $1,000 per annum.

From this review it can be seen that considerable rationalisation has occurred in staffing arrangements. It illustrates clearly that by sharing personnel costs can be considerably reduced and a better standard of services offered to participating societies.

Finance

In the General Account, the Balance Sheet reveals that we ended the year with a deficiency of $3,823.73. While this in itself is no cause for satisfaction, when one recalls that the past year has seen even greater inflationary costs, that we received no income from Science House but had to pay out rent for our rooms for the full year to Science House and that last financial year our deficiency was $6,043.00, it does give some hope that our costs are being contained. In large measure this is due to the changes in the staffing arrangements between the Linnean Society and Science House Pty. Ltd. of which you have already been informed ; the Society has benefited from these changes for only a portion of the past financial year. The Balance Sheets show that our total funds in the General Account stand at $508,664.79. These are represented by our Fixed Assets, Investments and Current Assets as detailed on the right hand side of your sheet.

The Income and Expenditure Account details the nature of our expenses and the sources of our income. At the present time the most disturbing feature of our expenditure relates to greatly increased costs of printing our *Proceedings*. Last year our printer experienced delays in printing the first part of the *Proceedings*; in the interval wages in the trade increased considerably and by the time we were invoiced the bill for one part accounted for a very high proportion of our year's budget. That is why Part 2, which you have recently received, had to be reduced to a slimmer volume than usual. Unfortunately it is becoming increasingly necessary to ask authors of papers to make some contribution towards the cost of printing their work. You will note that several other costs, such as cleaning, electricity, postage, maintenance and telephone, all essential services, have increased noticeably.

We have substantially increased the subscription cost demanded from non-members for the *Proceedings* and some extra $1,200.00 has been received from this source. Due to the turnover of a proportion of our investments and the higher interest rates available last year we have received over $600.00 more in interest from investments in the General Account. This factor applied also to the Fellowships Fund, so that we have transferred about $500.00 more than last year from the surplus in the Fellowships Account.

In the Fellowships Account we have added $1,333.38 to Accumulated Funds which now stand at $127,078.38. Last year our Linnean Macleay Fellow resigned at the end of September to take up a more permanent position. The salary which was not paid to him for the balance of the year was therefore transferred to Accumulated Funds as stipulated in the Will of Sir William Macleay. The balance of the income in this fund was then transferred to the General Account, namely $4,653.88.

The Bacteriology Account is straightforward. We were able to send $2,200.00 to the University of Sydney towards the salary of the Linnean-Macleay Lecturer in Microbiology, an increase of $200.00 since last year.

The Scientific Research Fund has been augmented by interest amounting to $583.63 and donations totalling $2,003.00 and now stands at $8,140.73. If you believe that the Society should do more for research in Natural History, this tax-deductible fund is open for you to give practical expression to your views and obtain a deduction from your income tax for any donation of $2.00 or over.

The Library Fund account appears for the first time this year. This is another tax-deductible fund established for the housing and maintenance of the Society's valuable library. Donations to the fund during the year totalled $5,850.00 including $5,000.00 received from the State Government. This, together with accrued bank interest of $16.00, has been loaned to Science House Pty. Ltd. for the purpose of providing in due course a new home for the library.

You will recall that a few years ago Council seriously considered disposing of the Society's library to one or more other libraries better equipped than the Society to house and preserve it fittingly. Members of the Society vigorously opposed this proposal. Its retention has been and will be an expensive exercise. It appears to me therefore that members should feel an obligation to give practical expression to their convictions and by giving generously to the Library Fund.

Report on Science Centre

The past twelve months have been an exciting period in the development of the new Science Centre. At the last Annual General Meeting of the Society you were informed that the Directors of Science House Pty. Ltd. had resolved to proceed with a proposition to acquire and renovate an existing building in an attractively central and accessible city site. Conditional contracts were exchanged on 25th June 1974 between Science House Pty. Ltd. and F. T. Wimble Pty. Ltd., conditional upon satisfactory terms of approval to our development application being received from the City Council.

To commemorate this historic event, a joint meeting between the respective Councils of the Linnean Society and Royal Society and the Board of Directors took place on 29th July at which our architects, Messrs. Jackson, Teece, Chesterman and Willis, displayed and explained photographs and preliminary sketches of the proposed alterations to the building.

Development approval was received from the City Council during September but further clarification had to be sought on some of its terms, causing consequential delays. Indeed some aspects are still the subject of negotiation. However, the Directors decided to proceed.

The contract with F. T. Wimble was settled on 5th November 1974, when the building in Clarence Street became entirely the property of Science House Pty. Ltd., but subject to a mortgage from the Commonwealth Savings Bank.

Between December 1974 and February 1975 the Board met frequently with its architects who led it through the various stages of planning and decision-making. I do not propose to describe the plans in detail tonight but I am sure that Members will be pleased to hear that, as well as meeting rooms of assorted sizes, it is proposed to include a conference floor with an auditorium seating about 250 persons and a restaurant in which you can have a meal and meet others informally prior to your evening meetings.

The work of the architects is proceeding according to programmed dates and the Board hopes that it will be in a position to call tenders early in May. It is now expected that all existing tenants will have vacated the premises by the end of June which will enable the builders to work unhampered and therefore more quickly and economically.

The Board greatly appreciates the services of our Solicitors and Architects who have worked unstintingly in our interests during the year.

On 13th November a deputation from the Board waited upon Mr. Fife, then Minister assisting the Treasurer and deputising on this occasion for the Premier, at Parliament House. Mr. Fife had taken the trouble to inform himself fully regarding the previous representations made by the Societies and the Board to the Premier and the other Ministers under whom our activities have come over the last few years, and received the deputation with sympathy and interest. Following upon this meeting the two Societies each received from the State Government a donation of $5,000 (total $10,000) towards their respective Library Funds. Mr. Fife has also ensured that the Public Service Board will negotiate to rent a floor in the new Science Centre and that we shall be enabled to purchase certain equipment and furnishings for the building through Government Stores. These concessions are expected to be of considerable value to the project and the Board is delighted that this support evidences the interest of the State Government in our activities.

Contact has been maintained with the Commonwealth Foundation in London. The Foundation, which is financed by some 31 Commonwealth Governments, was formed in 1965 to stimulate the development of professional organisations and Professional Centres, especially in developing countries, and to encourage the interchange of scientific and professional knowledge among the Commonwealth nations. Its Director, Mr. John Chadwick, paid his second visit to Sydney between 4th and 6th February. Mr. Chadwick was delighted with the progress that has been made since his last visit towards the development of our Science Centre in Sydney which he described as the most sophisticated and satisfactory of any he was aware of in the southern hemisphere. The Board took the opportunity of having informal discussions with him on matters of mutual interest. From Sydney, Mr. Chadwick proceeded to Canberra where, at our request, he raised matters concerning the Science Centre with the Governor-General, the Prime Minister's Department, the Department of Foreign Affairs and the Australian Aid Agency. These matters are of mutual interest to the Commonwealth Foundation, the Australian Government and Science House Pty. Ltd. The Board feels that the progress of scientific and professional organisations in the Pacific area is an objective worth encouraging and that Sydney is geographically ideal as a major centre of activity as long as the cost of providing the facilities envisaged is not an expense to the Societies or to their Company.

Science House Pty. Ltd.

The first Annual General Meeting of Science House Pty. Ltd. was held on 3rd October 1974, when the Director's Report, Balance Sheet and Profit and Loss Account to the 30th June 1974 was presented to the Shareholders.

Dr. P. J. Stanbury resigned from the Board of Directors during July owing to pressure of other duties and your Council appointed Dr. L. A. Moffat as a Director in his place.

Mr. D. Edwards resigned from the Board in November owing to the pressure of other unavoidable commitments and your Council appointed Mr. E. Selby as a Director in his place.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Balance Sheet as at 28th February 1975

1974 $		$	$
	Accumulated Funds—		
	Balance, 1st March 1974		511,345.86
	Less Deficiency for Year		3,823.73
511,346	Balance, 28th February 1975		507,522.13
	Reserves—		
418	Science House Management	—	
1,143	Bookbinding	1,142.66	
			1,142.66
449	Bank Overdraft		—
$513,356			$508,664.79

1974 $		$	$
	Fixed Assets—		
	Furniture, Fixtures and Fittings—At Cost	370.91	
304	*Less* Depreciation written off	89.92	
			280.99
	Office Machines—At Cost	984.00	
858	*Less* Depreciation written off	201.30	
			782.70
	Investment—At Cost—		
1	Share—Science House Pty. Limited		1.00
1,163	Total Fixed Assets		1,064.69
	Investments—		
	Deposits—		
10,522	N.S.W. Permanent Building Society	5,657.71	
—	Australian Resources Development Corp.	36,700.00	
30,000	Commonwealth Loans—At Cost	1,000.00	
	Debentures—At Cost—		
4,990	Colonial Sugar Refining Co. Limited	4,990.00	
39,700	Metropolitan Water, Sewerage and Drainage Board	39,700.00	
5,000	Commercial & General Acceptance Limited	—	
—	Mutual Acceptance Limited	12,750.00	
6,000	Sydney County Council	—	
3,004	Science House—At Cost (One-third Interest)	3,004.60	
4,750	Loan on Mortgage	—	
103,966	Total Investments		103,802.31
	Current Assets—		
407,500	Loan—Science House Pty. Limited	400,000.00	
720	Sundry Debtors	1,377.79	
7	Cash on Hand	19.87	
—	Cash at Bank	2,400.13	
408,227	Total Current Assets		403,797.79
$513,356			$508,664.79

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Income and Expenditure Account for the Year Ended 28th February 1975

EXPENDITURE

1974 $		$
325	Audit Fees	425.00
523	Cleaning	869.30
176	Depreciation	112.08
266	General Expenses	776.15
836	Illustrations	751.58
76	Insurance	98.86
240	Library	115.49
250	Life Assurance Premium	250.00
77	Light and Power	118 83
720	Postages	864.54
2,870	Proceedings—Printing Costs	4,145.30
513	Printing and Stationery	713.62
146	Referees' Fees	70.00
191	Repairs and Maintenance	288.20
961	Reprints	556.00
13,857	Salaries and Honorarium	10,023.62
3,778	Science House Rent	4,448.75
160	Telephone	224.57
$5,965	Total Expenditure	$24,851.89

INCOME

1974 $		$	$
	Subscriptions—		
	Members'	478.00	
	Proceedings	5,279.76	
4,452			5,757.76
	Science House Management Reimbursement—		
1,384	Salaries	868.50	
750	Management Fees	375.00	
			1,243.50
6,075	Interest Received		6,720.58
	Fellowships Account—		
4,135	Surplus Income for the year ended 28th February 1975		4,653.88
59	Rents Received		29.50
762	Reprints Sales		356.25
713	Sales		2,266.69
	Science House—		
1,592	Share of Surplus		—
19,922	Total Income		21,028.16
6,043	Deficiency for Year Transferred to Accumulated Funds		3,823.73
$25,965			$24,851.89

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1975 and are of the opinion that the above Balance Sheet and accompanying Income and Expenditure Account correctly set forth the position of the financial affairs as at 28th February 1975, according to the explanations given to us and as disclosed by the books of the Society.

W. SINCLAIR & CO.,
Chartered Accountants,
Registered under the Public Accountants Registration Act 1945,
as amended.

DATED at Sydney this thirteenth day of March 1975.

13th March 1975

JOYCE W. VICKERY,
Hon. Treasurer.

LINNEAN SOCIETY OF NEW SOUTH WALES

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT

Balance Sheet as at 28th February 1975

1974 $		$	$
	Accumulated Funds—		
	Balance, 1st March 1974:		
	Amount Bequeathed by Sir William Macleay	70,000.00	
	Transfers from Income Account	55,472.98	
	Increase in Value of Assets	272.02	125,745.00
	Add Transfer from Income and Expenditure Account		1,333.38
125,745	Balance, 28th February 1975		127,078.38
$125,745			$127,078.38

1974 $		$
	Fixed Assets—	
59,500	Commonwealth Loans—At Cost	52,200.00
	Debentures—At Cost—	
200	British Petroleum Company of Australia Ltd.	200.00
6,000	Electricity Commission of New South Wales	1,000.00
1,263	F.N.C.B. and Waltons Corporation Limited	1,262.90
37,700	Metropolitan Water, Sewerage and Drainage Board	36,700.00
800	Mutual Acceptance Limited	13,250.00
1,800	Rural Bank of New South Wales	1,800.00
15,750	Loans on Mortgage	11,000.00
	Deposits—	
—	Australian Resources Development Bank	8,300.00
123,013	Total Investments	125,712.90
	Current Assets—	
2,732	Cash at Bank	1,365.48
$125,745		$127,078.38

Income and Expenditure Account for the Year Ended 28th February 1975

1974 $		$
533	Salary of Linnean Macleay Fellow	1,866.62
2,667	Transfer to Capital Account	1,333.38
4,134	Surplus for the year transferred to General Account	4,653.88
$7,334		$7,853.88

1974 $		$
7,334	Interest Received	7,853.88
$7,334		$7,853.88

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1975, and are of the opinion that the above Balance Sheet and accompanying Income and Expenditure Account correctly set forth the position of the financial affairs of the Linnean Macleay Fellowships Account as at 28th February 1975, according to the explanations given to us and as disclosed by the books of the Society.

W. Sinclair & Co.
Chartered Accountants,
Registered under the Public Accountants Registration Act 1945,
as amended.

DATED at Sydney this thirteenth day of March 1975.

13th March 1975

Joyce W. Vickery,
Hon. Treasurer.

LINNEAN SOCIETY OF NEW SOUTH WALES

BACTERIOLOGY ACCOUNT

Balance Sheet as at 28th February 1975

1974 $		$	$	1974 $		$
	Accumulated Funds—				Investments—	
	Balance, 1st March 1974—			26,900	Commonwealth Loans—At Cost	26,900.00
	Amount Bequeathed by Sir William Macleay	24,000.00			Debentures—	
	Transfers from Income Account Etc.	13,811.57		200	British Petroleum Company of Australia Ltd. ..	200.00
			37,811.57	1,800	Metropolitan Water, Sewerage and Drainage Board—At Cost	1,800.00
	Add Surplus for Year		40.39	8,000	Loan on Mortgage	8,000.00
37,812	Balance, 28th February 1975		$37,851.96	36,900		36,900.00
					Current Assets—	
				912	Cash at Bank	951.96
$37,812			$37,851.96	$37,812		$37,851.96

Income and Expenditure Account for the Year Ended 28th February 1975

1974 $		$	1974 $		$
2,000	University of Sydney—Salary of Lecturer..	2,200.00	2,220	Interest Received	2,240.39
220	Surplus for the Year	40.39			
$2,220		$2,240.39	$2,220		$2,240.39

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1975, and are of the opinion that the above Balance Sheet and accompanying Income and Expenditure Account correctly set forth the position of the financial affairs of the Bacteriology Account as at 28th February 1975, according to the explanations given to us and as disclosed by the books of the Society.

W. Sinclair & Co.,
Chartered Accountants,
Registered under the Public Accountants Registration Act 1945,
as amended.

DATED at Sydney this thirteenth day of March 1975.

Joyce W. Vickery,
Hon. Treasurer,

13th March 1975.

LINNEAN SOCIETY OF NEW SOUTH WALES

SCIENTIFIC RESEARCH FUND ACCOUNT

Balance Sheet as at 28th February 1975

1974 $		$	$
	Accumulated Funds—		
	Balance, 1st March 1974	5,554.10	
	Interest Received	583.63	
	Donations Received	2,003.00	
5,554	Balance, 28th February 1975		8,140.73
$5,554			$8,140.73

1974 $		$
	Investments—	
	Debentures—At Cost—	
1,200	British Petroleum Company of Australia Ltd.	1,200.00
—	Commercial and General Acceptance Limited	1,400.00
1,021	F.N.C.B.—Waltons Corporation Limited	1,021.00
1,200	Industrial Acceptance Corporation Limited	1,200.00
—	Mutual Acceptance Limited	1,200.00
2,000	Loans on Mortgage	2,000.00
5,421		8,021.00
	Current Assets—	
133	Cash at Bank	119.73
$5,554		$8,140.73

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1975, and are of the opinion that the above Balance Sheet correctly sets forth the position of the financial affairs of the Scientific Research Fund Account as at 28th February 1975, according to the explanations given to us and as disclosed by the books of the Society.

W. Sinclair & Co.,
Chartered Accountants.
Registered under the Public Accountants Registration Act 1945,
as amended.

DATED at Sydney this thirteenth day of March 1975.

Joyce W. Vickery,
Hon. Treasurer.

13th March 1975.

LINNEAN SOCIETY OF NEW SOUTH WALES

LIBRARY FUND ACCOUNT

Balance Sheet as at 28th February 1975

	$	$		$
Accumulated Funds—			Current Assets—	
Donations Received	5,850.00		Loan Account—	
Interest Received	16.00		Science House Pty. Limited	5,866.00
Balance, 28th February 1975		5,866.00		
		$5,866.00		$5,866.00

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1975, and are of the opinion that the above Balance Sheet correctly sets forth the position of the financial affairs of the Library Fund Account as at 28th February 1975, according to the explanations given to us and as disclosed by the books of the Society.

W. Sinclair & Co.,
Chartered Accountants.
Registered under the Public Accountants Registration Act 1945,
as amended.

DATED at Sydney this thirteenth day of March 1975.

Joyce W. Vickery,
Hon. Treasurer.

13th March, 1975.

PRESIDENTIAL ADDRESS

ORIGINS OF AUSTRALIAN GEOLOGY

by T. G. VALLANCE

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Synopsis

One hundred years ago, when the Linnean Society of New South Wales began, geology in this country was a ' colonial ' science—its base of authority still lay largely in Europe. For almost a century, geology in Australia had been dominated by concepts originating in Europe and transported, more or less uncritically, to a land being explored. European precedent is seen as having exerted, in many cases, a counter-productive influence on geological progress here in the years before 1875.

At the start of our centennial session the Macleay Lecturer, Sir Rutherford Robertson, reminded us of the Society's history, of its achievements and of its aspirations (Robertson, 1974). He spoke of a loyalty to the Linnean tradition and how, especially through the *Proceedings* and the work of our Linnean Macleay Fellows, the Linnean Society of New South Wales has contributed to the cause of natural science in Australia.

Recalling that Linnean tradition I am struck by your sense of history in choosing a geologist to preside at this time. Carl Linnaeus [1707–1778] in his first essay of the *Systema Naturae* (1735) placed Regnum Lapideum first among the equal kingdoms of nature. Perhaps our successors will see fit to remember Regnum Vegetabile in 2074. For the present, however, it is my privilege to speak for the stones and I thank you for the opportunity of doing so.

This historic occasion arouses thoughts of time and, being no prophet, I am constrained to turn retrospectively. Sir Rutherford has tidied the last one hundred years; I propose to cast further for some of the earlier sources of Australian geology and to examine how geology, a European creation, fared in its transfer to a distant land.

The year 1875 is an interesting point at which to pause for review. In Adelaide the third Australian university was about to open its doors. Ralph Tate [1840–1901], foundation professor of natural science there, joined colleagues in Sydney (Archibald Liversidge [1846–1927], one of our first members) and Melbourne (Frederick M'Coy [1817–1899]), teaching aspects of geological science in a context of general educational rather than professional training. Something of the organization of science at the time is evident in Branagan's (1972*b*) recent survey. By 1875 the colonial governments of New South Wales and Queensland had followed the lead of Victoria and moved to establish geological surveys that continue to function. The sorry record of capricious parsimony shown by all the colonial governments towards geological surveys in the period before 1875, however, is best passed in silence. Only the first Geological Survey of Victoria (1852–1869), directed by A. R. C. Selwyn [1824–1902], was given any real opportunity to demonstrate its worth. Few now seem to be aware of what Australian geology lost when that survey was disbanded in 1869. Selwyn's contributions place him in the first rank of our geological pioneers, yet how many remembered the sesquicentenary of his birth?

I believe it is time we gave more attention to the rise of Australian geology. The past record is still not seen by many geologists as a source of useful or even interesting experience. To them that record is one merely of the out-of-date

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and superseded. In fairness they have had few guides. There are, of course, useful contributions to the history of particular subject or geographical areas as, for instance, the presidential addresses of Drs Charles Anderson (1933) and Ida Brown (1946) to this Society. But I can recall only two major historical reviews of Australian geology, those of Tate (1894) and Andrews (1942). Unfortunately, the usefulness of Andrews's study is limited by its poor documentation and his evident failure to examine many of the early primary sources. To underline the failure of scholarship in the twentieth century may I point to the last bibliography of Australian geology—that of Etheridge and Jack (1881).

Tate's history remains essential to anyone seeking a way to the beginnings of geological activity in this country. His concern was achievement in discovery rather than intellectual influences. Tate saw his science moving splendidly along a fine broad highway. There is nothing in Tate about wrong turnings, about blind alleys or those lost in them. " No prejudices or scholastic disputations have retarded our progress, for those who have aided in the work were disciples in the modern school of geology " (Tate, 1894, p. 3). The more I delve in the record of Australian geology the more extraordinary I find that claim to be. It seems to me that most of the disputations of European geology found their way here to be compounded with others of local origin.

A Science of the Earth

The 1780's for us were significant years ; they saw not only the foundation of Sydney but also the publication of statements by Abraham Gottlob Werner [1749–1817] and James Hutton [1726–1797] concerning the materials, processes and history of the earth. These men were to exert profound influence on geology, indeed they are accounted founders of the science. For a recent detailed analysis of Werner's work in geology the reader may refer to Wagenbreth (1967) and other papers in that *Gedenkschrift.* Ospovat (1971) supplies an edited translation of Werner's treatise of 1787. James Hutton is treated succinctly by Eyles (1972) who provides a select bibliography. Hutton's *Theory of the Earth* was issued by the Royal Society of Edinburgh in the year of Sydney's birth ; an extended statement, in two volumes, followed in 1795.

The charges of irreligion and wild speculation hurled against Hutton remind one of the cries raised against Darwin some seventy years later. The comparison has even greater interest in that both Hutton's and Darwin's theories came to achieve after long and painful debate the status almost of received opinion. Werner, a popular teacher and effective synthesizer of information, made an immediate impact.

To Hutton more than to any other belongs the credit for first emphasizing the vast span of geological time. From his demonstration of the significance of unconformities geologists gained an essential tool for unravelling earth-history. Hutton also saw that, with time, processes such as those of erosion presently operative could be efficient causes of profound changes in the earth's surface. This model that called not only for operation in the past of the same causes as act at present but also for action throughout at similar levels of intensity received from the philosopher W. Whewell [1794–1866] the name *uniformitarianism.* It is a special case of *actualism* (cf. Hooykaas, 1970), the general term attached to schemes that depend on the operation of known or actual causes though not necessarily at present levels of intensity.

Roughly actualistic models long antedate Hutton but most tend to be strongly non-uniformitarian. That of G. L. L. Buffon [1707–1788] issued in 1749 in his *Histoire & Théorie de la Terre* offers a useful example. Buffon relied on observable processes but postulated their action in the past at levels sufficient to cause sudden and violent revolutions or catastrophes. Catastrophic action is explicit in the scheme outlined by P. S. Pallas [1741–1811] of St. Petersburgh, one of the first great naturalist-travellers, in his *Observations sur la formation des montagnes* of 1771 (Mather and Mason, 1939, pp. 123–5). There Pallas adopted a three-fold chronology of mountains (Primitive or Primary, Secondary and Tertiary) devised earlier in Italy and Germany. The oldest and greatest (Primitive) mountains, according to Pallas, formed chains with granite the oldest of all rocks as typical core material. Younger mountains were lesser structures and consisted of bedded rocks. The most recent mountains that Pallas recognized in Asia he called Tertiary ; these he attributed to the action of violent floods of water displaced by great volcanic eruptions in the South Seas.

Werner's scheme contains borrowings from Pallas and indeed from a wide range of sources. From these sources Werner produced a synthesis that was not even actualist but to his contemporaries had the great merit of being at once practical and essentially conservative. The oldest mountains stood highest and had granite cores but the Primitive, indeed all, crystalline rocks he argued had formed not from a molten state but by precipitation from an early ocean chemically different from that of the present. For this reason his model acquired the nickname *neptunian* and his followers *neptunists.* By contrast, Hutton urged that heat was a profoundly important geological agent and interpreted crystalline rocks as derived by cooling from melts—hence the label *plutonist* or *volcanist* attached to his ideas and his supporters. These names that in fact refer to limited aspects only of the two systems came to be identified by many with the respective wholes.

By his own claim Werner eschewed speculation. The emerging term *geology* he rejected in favour of his invention *geognosy*—a statement of factual knowledge. As befitted a teacher in a mining school (at Freiberg in Saxony), Werner's approach was pragmatic and his classificatory systems generally easy to apply. Minerals were sorted, for instance, according to their gross external characters. Mountains and their constituents he had by the 1790's grouped (Wagenbreth, 1967) in terms of the old three-fold arrangement modified by insertion of a Transition class between the first and second terms the latter of which he called Flötz (stratified).*

According to Werner, sea-level had diminished as time passed and this occasioned deposition of younger rocks at progressively lower levels on the flanks of Primitive mountains. As he postulated no operations of uplift and folding in earth-history, the observed altitude of a rock ought to offer a clue as to its age—a notion that doubtless helped the sale of travelling barometers. Werner's system of stratigraphy was exclusively lithological. He argued further that any particular formation of, say, limestone or sandstone should have a world-wide extent. Stratigraphic correlation ought thus to be possible by matching rock-types.

The period 1790–1820 is termed the Heroic Age of Geology in Zittel (1901), which remains one of the more judicious accounts of the history of geology. It is popularly represented as a time dominated by conflict between the disciples of Hutton and those of Werner. In fact, Hutton himself founded no school and apart from signs of an increasing acceptance of heat and fusion as geological agents one does not find much evidence in Europe of the spread of Huttonian ideas during the Heroic Age. But then whereas all neptunists might be identified as Wernerians, far from all volcanists subscribed to Huttonian doctrine. I get the impression that the practical advances in European geology during this period came mainly from two sources, namely, from Wernerians testing their master's propositions in the field and from that numerous and scattered band, rather

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* This Flötz of Werner embraces the succession of European strata from the Coal Measures to the Chalk.

strong in France, that stood apart. The observations of volcanic regions by F. H. A. von Humboldt [1769–1859] and Leopold von Buch [1774–1853], both of them distinguished former students at Freiberg, led to their early defection from the ranks of strict neptunists, though each persisted with other Wernerian methods (e.g. Humboldt, 1823). Within Werner's lifetime the labours of such as the Abbé R. J. Haüy [1743–1822] in Paris had taken mineralogy far from the simple Wernerian system on its course to the purely physical science of modern times. One must add, however, that for long the term *mineralogist* accommodated many whose interests lay in the collection and natural history of minerals. In Australia the term was often enough to be equated with prospector.

In the field of stratigraphy, too, a method was emerging that was to effect profound modification of Wernerian practice. By the late 1790's William Smith [1769–1839], an English engineer, had discovered that order in stratified sequences of rocks was reflected not only in the spatial, depositional relations of beds but also in their fossil contents, so that fossils afforded a means of correlating strata (Cox, 1942 ; Eyles, 1969). J.L.N.F. (Georges) Cuvier [1769–1832] and Alexandre Brongniart [1770–1847] appear to have discovered something of the same principle, independently. Smith is not even mentioned in the revised edition of their account of the Paris Basin (Cuvier and Brongniart, 1822) issued after the great map of the strata of England and Wales (Eyles and Eyles, 1938) had helped to make Smith's discovery known. Despite their careful work on fossils the Frenchmen betray a tendency to emphasize lithological characters in correlating formations. We see much the same in Brongniart's (1829) later classification of terrains. By then in England Smith was gaining his recognition. Conybeare and Phillips (1822) give an early exposition based on Smith's method and one in which the Wernerian stratigraphic method, as distinct from Wernerian terminology, is specifically rejected.

Strict neptunian ideas were in retreat by the 1820's but the growing acceptance of igneous action came most commonly in notional contexts that harked back to Buffon. Catastrophism in some form had a place in most eighteenth century systems, not least, of course, in that of Werner. Cuvier's vigorous promotion of catastrophism in the *Discours Préliminaire* to his researches on vertebrate fossils published first in 1812 ensured its survival during his lifetime. Catastrophism in England turned to a preoccupation with Noah's Deluge. The biblical flood became the last great catastrophic event in earth-history and Diluvial Geology, the study of physical evidences of the Flood, arose through the efforts of the Rev. William Buckland [1784–1856] and others like-minded.

Uniformitarianism eventually found an able and devoted exponent in Charles Lyell [1795–1875]. His *Principles of Geology* (1830–33), despite its seemingly contentious message, was remarkably influential from the start. Lyellian uniformitarianism may never have been universally accepted by geologists but there is no denying its role in determining much of the later course of the science (Bailey, 1962 ; Wilson, 1972).

Lyell (1833) also outlined a subdivision of Tertiary successions and Tertiary time using the terms Eocene, Miocene, Pliocene, still employed. Of the fifteen terms now taken to constitute the Phanerozoic time-scale, only Carboniferous, Jurassic and Cretaceous antedate the year 1833. By 1841 all the others with the particular exceptions of Ordovician and Oligocene had been defined. Definition does not, of course, imply acceptance but the record is surely a measure of the great activity in European geology during those eight years. It was a time when the so-called British (William Smith's) method of stratigraphy and Lyellian doctrine spread across Europe. Even in the German regions where Wernerian geognosy had been most firmly entrenched the impact of the new influences was no less remarkable for being delayed.

TOWARDS AN AUSTRALIAN GEOLOGY

PASTURES NEW

Before considering the context in which geology began in Australia, it may be useful to notice how and when the science took hold in another new land. Commentators on the history of North American geology (Merrill, 1924 ; Hazen, 1974 ; Ospovat, 1967) all agree on assigning its beginnings there to the very period when Hutton and Werner were active.

Geology went to an established community in eastern North America, one much after the English provincial style of the time. The devotees of geology were amateurs drawn mainly from the learned professions—teachers, lawyers, physicians and surgeons, and clergymen. Those with a university education most likely had been instructed in classics and mathematics and not, as a rule, in the observation of nature, though it is impressive to note a letter of 1799 (Cohen, 1950, p. 117) claiming that mineralogy had become a favourite branch of study among the young men at Harvard. Of the British universities only those in Scotland could then have matched that (Ritchie, 1952 ; Scott, 1966). There is, indeed, a geological chair at Cambridge founded in 1724 but no instruction in the subject was offered there until the appointment of Adam Sedgwick [1785–1873] in 1818. Mineralogy began at Cambridge a few years earlier through the enthusiasm of Dr. E. D. Clarke [1769–1822]. Oxford was not long in following its rival. Graduates, many of them clergymen, appear among the 'learned' geologists of Australia but not until the cruder aspects of frontier existence had begun to disappear.

At the time of Hutton and Werner, Australia was almost as unknown geographically as it was geologically. Had Australia repeated the pattern of earlier exercises in European colonisation there might have been from the outset a dominating commercial interest. From ancient times Europeans entertained great hopes of riches, mineral and otherwise, in new lands. The fascination of Africa was old ; South America had yielded treasures to Spain and Portugal. The first emigrants to Virginia in 1607 had lively expectations of finding gold and precious stones (Wright, 1949, pp. 31–32), as did Dampier coming to New Holland in 1699 (Dampier, 1703, p. 138). We find them in 1785 pressed upon the British government as a reason for colonizing New Holland (Barton, 1889, p. 430). But considerations of social rather than commercial advantage prevailed. The greater need was to find a remote place to lose an increasing number of convicts. In such a colony discoveries of mineral treasure might be highly disturbing. As late as 1844 we find expression of fears of dire consequences, were reports of gold discoveries to become public (Jervis, 1944, p. 394). Indeed for almost the first forty years of settlement no private exploitation of minerals was permitted (cf. Branagan, 1972*a*).

All the infant colony at Sydney required from the earth in 1788, apart from safe anchorage and a supply of fresh water, was material for shelter. Geology enters at its humblest level, that of usefulness. Sandstone and clay occurred locally in abundance ; only limestone for mortar was lacking. The first geological observations reported by a resident come from Arthur Phillip [1738–1814], first governor of New South Wales, and relate to these materials. His remarks (Vallance and Branagan, 1968, p. 265) are observational and practical, of a type not unexpected of an intelligent layman. Few would think of Phillip as a geologist or even as a naturalist yet he represents the first of a long line of colonial officials who contributed to our geological knowledge. Most of them in the early years at least were serving or former naval or military officers. From their ranks came the first explorers and surveyors (Spate *in* Feeken and Feeken, 1970, pp. 4–32). Many demonstrate in their journals a geological interest to the extent of a practical familiarity with earth-materials ; some, for instance T. L. Mitchell [1792–1855] and Charles Sturt [1795–1869], possessed a rather more sophisticated knowledge of the subject. There must be few parts of the world more liberally endowed with topographical features named in honour of prominent European geologists than Australia—names like Buckland, Cuvier, Dolomieu, Faujas, Fitton, Haüy, Hutton, Lonsdale, Lyell, Murchison, Owen, Sedgwick and Sowerby. Not one of these worthies visited Australia, yet each was sufficient of a hero to some explorer to be thought worthy of remembrance.

Observations of the transit of Venus in 1769 began a fashion for scientific exploration. That event was the reason for Pallas's first excursion in Siberia and, of course, had relevance to Captain Cook's *Endeavour* voyage during which he discovered the coast of New South Wales. The achievements of those expeditions need no emphasis ; their very success encouraged emulation by other European nations. The French, in particular, showed great interest and activity. Between 1788 and 1840 no fewer than eight French naval/scientific expeditions visited Australia ; in that time there had been calls too from Russian, Spanish and American parties as well as several British expeditions. Most were accompanied by trained observers, equipped to consider nature in Australia in terms of current scientific thought.

Those from Europe brought with them the experience of a longer tradition of scientific and technical education than was to be found in England. The Mining Academy at Freiberg has a continuous history from the year 1765. Not long after that date mining schools were active in Russia, in the Austrian Empire and in France ; the earliest such institution in Britain opened in 1851. Nowhere in the eighteenth century was the range and quality of technical education greater than in post-revolutionary Paris. Furthermore for its time that education was remarkably democratic—strict entrance examinations ensured that (Aguillon, 1889 ; Birembaut, 1964). The first trained geological observers in Australia represented that French tradition. Unfortunately they were confined to coastal areas for the interest of their remarks stands in great contrast with those of the first inland explorers. The so-called mineralogists or geologists who accompanied some of the latter, for example John Oxley [1785?–1828], were generally little more than collectors.

Joseph Banks [1743–1820] had returned home with Cook in 1771 enriched with specimens and accounts of strange new plants and animals from the Pacific region. He returned to an instant scientific fame that his wealth and social place helped him to maintain for the rest of his life. By 1788 he had achieved considerable political influence. Banks's power as well as his genuine interest in the new country and its productions ensured that, despite the practical difficulties of existence in a remote penal settlement, colonial officials did their best to keep him informed and supplied with natural novelties.

Among various specimens sent by Phillip was one that attracted unusual interest although it had been despatched for a highly practical reason, namely the possible establishment in Sydney of a pottery. The Abbé J. A. Mongez [1751–1788], distinguished scientist and sometime editor of the *Journal de Physique*, while at Botany Bay with the La Pérouse expedition suggested that Phillip ought to have the local clay tested by a ceramist. Banks was asked to arrange this and passed a sample to his friend the potter-chemist Josiah Wedgwood [1730–1795] who, in addition to having a handsome medallion made (Rathbone, 1886), announced discovery of a new elementary substance to which he gave the name Sydneia (Wedgwood, 1790). Another part of the sample Banks gave to the Göttingen naturalist J. F. Blumenbach [1752–1840] ; his observations (Blumenbach, 1791) generally agreed with Wedgwood's. Blumenbach, incidentally, is credited by several writers (e.g. Lang, 1834) with a view that implies the ultimate in Australian novelty—that the continent arose by a cometary impact with the earth. I have failed to discover the original reference. But to return to Sydneia, the new element quickly found its way under that name or one of its synonyms Sydney Earth, Terra Australis or Terre Australe, Australa, Australsand and even Cambria (the latter, Forster, 1795) into treatises on systematic chemistry and mineralogy.

Its fame was short. In 1797 the Berlin chemist M. H. Klaproth [1743–1817] reported his failure to confirm the earlier observations and for his trouble was attacked by Nicholson (1797). The argument ceased with the publication of Charles Hatchett's [1765–1847] study of another moiety of Banks's stock (Hatchett, 1798). Impure reagents seem the most likely cause of the brief Sydneia affair; Wedgwood had been thus deceived on other occasions (Schofield, 1963, p. 302). Blumenbach must have had like trouble though his results suggest a less contaminated acid. The nature of the impurity remains uncertain; the responses observed would be compatible with the presence of bismuth in the hydrochloric acid.

Over the years Banks became a sort of scientific agent for the colony. The young Robert Jameson [1774–1854], later one of Werner's staunchest disciples in Britain, recalled seeing at Banks's house in August 1793 a sample of 'Sporadic Zeolite' (i.e. the mineral in its host rock) just arrived from Van Diemens Land (Sweet, 1965). The Irish chemist Richard Chenevix [1774–1830] obtained from Banks the Australian mineral sand in which he discovered (Chenevix, 1801) the mineral menaccanite, a variety of ilmenite. Unfortunately the exact provenance of the sample is unknown; the locality Providence Island mentioned by Chenevix arises from confusion with another new source in North America (cf. Leonhard, 1808, pp. 244–5).

Banks in fact went far beyond merely sitting in receipt of communications from government officers. Within ten years of the first settlement he had arranged, at his own expense, for a naturalist-collector George Caley [1770–1829] to work about Sydney (Currey, 1966). Caley's concerns were principally botanical but one finds scraps of geological information among his notes. The incomparably more scientific Robert Brown [1773–1858] owed his place as naturalist to Matthew Flinders's [1774–1814] expedition in Australian waters to the interest of Banks. In 1816 Allan Cunningham [1791–1839], another botanical protégé of Banks, arrived here to begin a notable career that included some of the first scientific exploration of the Australian inland. His journals contain much of interest to a geologist (Lee, 1925).

Among the affluent savants of Europe who did not share Banks's privileged position a rising passion for cabinets of natural history had to be satisfied by dealers. Few devotees of science were quite as detached as the celebrated French geologist Nicolas Desmarest [1725–1815]. According to Cuvier (1819, p. 370), Desmarest, when told of Cook's encounter with the Australian barrier reef, merely asked was the reef basalt or limestone. The demands of collectors led the more enterprising dealers to issue instructions to travellers about how and what to gather (e.g. Mawe, 1804). Within a few years topaz from 'Botany Bay' was cheaper and more easily obtained in London than its Scottish rival (Thomson, 1814). The availability of such material led to its scientific study. Brewster's (1827) optical study of Australian topaz is but one example; Brewster claims that the mineral was analysed by the great J. J. Berzelius.

When in 1803 the British government responded to requests from Sydney that a mineralogist be appointed to the civil establishment of the colony to assist a search for useful materials, the place went, on the recommendation of a wealthy collector, the Rt. Hon. C. F. Greville, to Adolarius W. H. Humphrey [1782?–1829], one of a family of dealers in natural history (Whitehead, 1973). Humphrey's contract permitted him to collect on his own account and ship samples free of charge. None of this material has yet been identified. We really know little of his work in the period 1803–12 that he enjoyed the office of His Majesty's Mineralogist but, if we may judge from the repeated requests for appointment of a successor, Humphrey cannot have destroyed faith in the value of his profession. No action, in fact, was taken until John Busby [1765–1857] in 1823 secured the post of civil engineer and mineral surveyor with particular responsibility for the coal mines and water supply. It is worth noting that a geological survey was not established in the United Kingdom until 1835.

National and provincial institutions appear to have been as eager as private collectors to acquire foreign material. The greater museums even followed the example of dealers. No fewer than five editions of *Instructions pour les Voyageurs* were issued by the Museum d'Histoire Naturelle, Paris, between 1825 and 1860. The collections made by the French expeditions passed mainly to the Paris museums ; the British Museum, the Geological Society and various local museums in Britain gained by way of donations and purchases from colonial officers and travellers. Acquisitions listed in the annual reports of the Geological Society provide a useful key to the collecting side of Australian geology.

Interest in museums and cabinets was no less strong in those states that had not yet manifested their naval pretensions by sending expeditions to distant parts. The German Travelling Union for Promoting Natural History (Hooker, 1827, 1830) which despatched collectors on behalf of subscribers offered one sort of solution. We know that P. E. de Strzelecki [1797–1873], J. Lhotsky [1795–*c.* 1870] and J. Menge [1788–1852] who were active in Australia during the 1830's and 1840's all had connections with European collectors. Income from the sale of specimens enabled them to pursue their valuable work as private scientific explorers.

Through the study of Australian collections in Britain and Europe many notable mineralogists and palaeontologists, some whose names appear on the maps of this country, came to a vicarious involvement in the growth of Australian science. Indeed their contributions were essential in the early years. The first skilled palaeontologist to settle here arrived at the end of 1854 !

By 1800 the colony was sufficiently established to attract free settlers who, with a few retired officials, set up as landed proprietors assisted by a plentiful supply of assigned convict labour. Jukes (1867) comments sharply on the 'landed manner' of the first councillors of the Geological Society of London (founded 1807). These amateurs of science were men of property and social standing like Banks himself. The record of early nineteenth century geology in England shows that some were genuinely concerned with scientific enquiry and did notable work. One might expect that such gentlemen of science and their more affluent professional colleagues, were they to remove to the colonies, would find much to catch their interest. The first of them in Australia was a sad disappointment.

Dr. Robert Townson [1763–1827] came to Sydney as a settler in 1807. He arrived not only with a letter of recommendation from Banks to the governor (William Bligh [1754–1817]) but with a library, a laboratory (at least he had a grant to establish one) and the promise of free land. Townson had studied at Edinburgh and Göttingen and, moreover, was author of three books as well as several scientific papers. His *Travels in Hungary* (1797) includes a coloured map showing the distribution of different sorts of rocks in that country. He called the information *petrography* ; I know of no earlier use of the term. The *Philosophy of Mineralogy* (1799) and *Tracts and Observations in Natural History* (1799) demonstrate both his close awareness of the state of mineral science and his skill as an observer.

Despite this promise, letters written in 1800 (Pinkerton, 1830, Vol. II) suggest that Townson had already retired from science to the country. Why he decided a few years later to re-assert the scientist-image and move to Australia remains a mystery though he did have a military brother in the colony. In New South Wales it is plain he was far less enthusiastic for science than for farming and for the factional disputations that then consumed so much of colonists' time and energies. The select list of Townson's library (*Sydney Gazette*, Nov. 2, 1827) offers a mute commentary on a scholarly resource that might have been of great value in a remote community. But it may not be fair to blame Townson only for this failure. After all, Bligh writing to Banks in November 1807 and remarking on these very books said " many can be of no general benefit here, as they are written in the German tongue ". Such a society was no congenial place for scholarship.

The fate of the Philosophical Society of Australasia, founded in 1821 and expiring little more than twelve months later in " the baneful atmosphere of distracted politics " (Field, 1825, p. v), shows how small was the improvement since the time of Townson's arrival. Yet during its brief existence the Society had listened to original papers, of which a selection is preserved in Field (1825), and set about arranging a museum and exchanges with institutions abroad (Branagan, 1972*b*), though with what success is unknown. At least the idea of a museum did not die for in the year (1827) that James King [1800–1857] arrived in Sydney and reported so scathingly on the lack of science here (King, 1828) provision was made for the establishment of a Colonial Museum. This became, by 1834, the Australian Museum, the oldest existing institution in this country devoted to the natural sciences. To our shame, a history of the Museum compiled by Mr. G. P. Whitley remains unpublished ; it is a record that deserves to be known. But we must not exaggerage the Museum's contribution to geology in its early years when the greatest problem was survival. In fact the main advances in New South Wales in the two decades from 1830 came from the slowly increasing number of learned amateurs, at last drawn to a colony beginning to shed its convict image.

During that period, as Hoare (1968) has shown, the focus of organization of Australian science shifted from the old colony to Van Diemens Land (Tasmania). Even there the active students of geology were few, the most notable perhaps being the surveyor-general George Frankland [1800–1838] and Joseph Milligan [1807–1884]. Many of the select band who supported the Van Diemens Land Scientific Society and its successors may have been as much attracted by considerations of society as by considerations of science. Despite its own share of distracted politics that impinged on science, Tasmania has the proud record of the longest tradition of scientific serial publication in Australia. Since the first issue of the *Tasmanian Journal of Natural Science* appeared in August 1841 (Plomley, 1969), the societies of the island colony/state have continued to provide means of disseminating knowledge. Comparable journals did not emerge on the mainland before the 1850's. Until then resident scientific observers had to make do with local newspapers, almanacs and the few ephemeral literary magazines—or publish overseas. These local sources of information merit close study but are still quite inadequately explored.

Unlike the other colonies in which scientific societies emerged slowly and survived with difficulty, South Australia had a Literary and Scientific Association two years before the colony was proclaimed in 1836. This London group appears for a time to have been active ; among the addresses listed for 1834 was one by W. M. Higgins on the geology of Australia (Hale, 1956). An insufficient number of these philosophical gentlemen must have moved to the new colony for the Association seems not to have continued in Adelaide. But from the first settlement there was a particular geological interest in South Australia. The South Australian Company briefly (1836–8) employed a geologist, Johann Menge, a strange character if we believe Cawthorne (1849). Menge's (1841) treatment of South Australian geology is certainly original. Papers on local geology by Binney (1842) and Finniss (1843) belong to the first few years of the colony as does the first book on geology published in this country (Burr, 1846). The discoveries of lead and copper deposits in 1841 and the years following (Price, 1924, p. 231) rewarded such interest. On the other hand the early success of mining in a region where few fossils had been found probably helped maintain in South Australia the themes of prospecting and mineralogical geology at a time when the search for stratigraphic order was beginning to yield results in the coalfields of eastern Australia. That search and indeed practically all activity—political, commercial and scientific—in Australia underwent profound change with the advent of gold-fever in 1851. To the years following belong establishment of the first universities and the beginnings of geological survey. Both subjects have been discussed by Andrews (1942) and, in the palaeontological context, by Brown (1946).

European Prejudice and Geology in Australia

I turn now to consider how a few of the concepts and methods of geology, derived from European experience, fared in translation to a part of the world not only remote but largely unknown. Even in the more sophisticated society of eastern North America there seems to have been a certain reticence to theorize. Ospovat (1967) points to an apparent reluctance among the pioneers of American geology to take sides in the neptunist-volcanist dispute but emphasises the profound influence on them of Werner and his school in the period from 1785 to *c.* 1830. A recent commentator on early Australian geology (Seddon, 1973) makes a case for Wernerian influences in this country and goes so far as to claim that some of our early naturalists preferred the ' cold-bath ' of neptunism. I believe, however, that we must exercise care in seeking to identify influences of particular schools of thought on our pioneers. After all, their knowledge of science was most likely to have arisen through accidents of experience related to travel and conversation more than to special reading and conscious study.

When we encounter an observer inferring volcanic action, it is unwise to pronounce the person a follower of Hutton. Ideas of heat and fusion in the earth existed long before Hutton's time. Similarly, one who used terms favoured by the Freiberg professor need not have been an advocate of neptunian precipitation. Long after support for that model had waned in Europe many geologists continued to employ the language of Werner's stratigraphic and mineralogical systems—some of his mineral names still continue to be used though one would search long and hard for a modern believer in the ' cold-bath '.

It is convenient, however, to begin a search for European influences among the crucial areas of the neptunist-volcanist debate, a debate that involved interpretations of earth-processes, how rock masses originated, how they came to be disposed as now seen and how the earth's present configuration arose. I shall start with the obvious question of igneous phenomena and go on to consider a few other aspects of what we now term physical geology before ending with a look at the way a search for order in time was developed in Australia. Throughout, I believe, we shall see European prejudices dominating Australian experience.

The very idea that Australia was somehow a land of anomalies, an idea still not lost from popular thought and for long expressed in serious geological literature (e.g. Rattray, 1869), derives from such prejudice. The early explorers found a continent the physical features of which differed utterly from those of Europe; instead of a great median mountain axis in Australia there were low arid plains, the mountains of Australia followed the east coast. Such physical anomalies presumably matched the equally ' anomalous ' flora and fauna. Despite recognition of such differences, the geologists of Australia long continued to fit their science into the European mould.

Igneous Action

Here was a central issue of dispute between the schemes of Hutton and Werner. Hutton with his belief in heat as a geological agent found no difficulty in accepting the possibility of fusion of rock matter and the possibility that such action could take place from time to time in the earth's history. The Wernerian neptunist by force of observation accepted the existence of volcanoes but assigned to them a recent and superficial role and regarded them as due to local fusion occasioned by the ignition of combustible matter such as coal or sulphur. The term *basalt*, as used by Werner, implied no synonymy with *lava*, only the latter was associated with volcanic phenomena ; crystalline rocks in general (basalt, granite, etc.) resulted from aqueous precipitation. Let us now look at some examples of the way the subject was treated in Australia ; they suggest that strict neptunian opinion arrived late and had little influence.

Matthew Flinders, in his journal of a voyage to the Furneaux group in Bass Strait during 1798, offers some remarkable opinions that merit quotation. After describing granite insinuated among strata of slate on Cape Barren Island, he says :

> " Granite being the heaviest of all stones, must, according to geologists, have been placed nearer than any other to the center of the earth, in its primitive state ; and being situate so near the fountain of heat and fire, might be dissolved, when the more light bodies, such as slate, were not, or perhaps could not. When the universal burst happened, which some suppose to have taken place in consequence of the sudden rarefaction of the air and water, which had gained admission to this internal region of fire, these bodies might naturally become thus compounded ; the liquid substance filling up every interstice, which its fluidity and superior gravity enabled it to penetrate " (Flinders, 1798 (1974, p. 11)).

Despite the insinuation of granite melt there is nothing of Hutton and uniformitarianism here. In the passage Flinders seems to hark back to Buffonian catastrophism or perhaps to John Michell [1724–1793] and his theory of earthquakes. Where would a naval officer who had gone to sea as a boy acquire such ideas ? Is there a hint to be found in his old chief William Bligh ? Bligh's remarks on the vicinity of Adventure Bay, Tasmania, written in 1792 when Flinders was there as a midshipman, indicate his acceptance of heat as a geological agent (Lee, 1920, p. 26). At any rate Flinders's later writings (Flinders, 1814) show his continuing faith in igneous action, a faith that makes his membership of the Wernerian Society of Edinburgh somewhat unexpected (Sweet, 1967, p. 211).

The French expedition of 1800–04 sent out under the command of Nicolas Baudin [1754–1803] is of particular interest because of the presence of two trained mineralogists, Louis Depuch [d. 1803] and J. C. Bailly [1777–1844], in the scientific party. Baudin (1974, p. 232) quotes a report of the naval engineer Ronsard who led a party ashore on what was to be called Depuch Island, off the coast of Western Australia. Ronsard identified basalt, which he also terms lava, on the island. Depuch's description of a sample is given by Péron (1807, p. 131).

The two mineralogists were both recent graduates, Depuch of the Paris École des Mines where he had studied under Haüy, and Bailly of the École Polytechnique. It is reasonable to expect them to express informed and up-to-date opinions. That Depuch Island was not the scene of some aberration is clear from their later remarks on the volcanic nature of the Tasmanian basalts (dolerites). Although readers of the official account of the voyage (Péron, 1807 ; Péron and Freycinet, 1816) might be forgiven for thinking that Bailly, like his colleague Depuch, had succumbed before the record was written, he survived to follow a most distinguished career as a naval hydrographer. Furthermore, Bailly's account of extinct volcanoes on the island of Mauritius contributed to a book by his friend J. G. Milbert and published at Paris in 1812 leaves no doubt of his igneous beliefs. Bailly (1825) is derived from a German translation of Milbert issued in that year.

These French reports of volcanic rocks in Australian localities where no volcanoes and no combustible materials had been observed created some stir in Europe. The most usual response by neptunists was to ascribe the rocks to Werner's Trap Formation. Perhaps it was with the French work in mind that Karsten (1808, p. 83) placed basalt of the Trap Formation at Botany Bay—to someone in Europe that place and New Holland may have seemed much the same. On the other hand, it is not hard to find other German writers of the period accepting volcanic action in Australia despite the seeming absence of volcanoes (e.g. Zimmermann, 1810, p. 848); several were clearly aware of Pallas's scheme that required volcanic action in the South Seas.

Although recent work has not confirmed the volcanic nature of Depuch Island—the dark rocks there (Ryan, 1966) like those seen by the French in Tasmania are now regarded as intrusive dolerites—we may recall that F. T. Gregory [1821–1888] in 1861 claimed to have found evidence of volcanic action on the adjacent mainland. Gregory (Gregory and Gregory, 1884, p. 71) believed that volcanic heat had there been " sufficient to convert the trap and sandstone into a deep bluish-grey scoria " even though no " actual overflow of lava " was observed. In this area southeast of Roebourne, dolerites like those of Depuch Island as well as Proterozoic lavas are now recognized.

A much earlier instance of faith in fusion is expressed by H. C. Antill [1779–1852] in an account of a journey across the Blue Mountains in 1815. Antill saw on King's Tableland what he took to be evidence of a violent volcanic eruption that had produced material like melted sand (Mackaness, 1965, pp. 88–89). The occurrence elicited a different response from Fedor Ivanovich Stein [d. *c.* 1845], surgeon and naturalist to the northern section of the Russian Pacific expedition of 1819–21, who visited it in the company of Allan Cunningham (Aurousseau, 1972). Stein (1842) made no secret of his respect for Werner, whose name together with those of two Russian mineralogists he attached to topographical features that cannot be identified. The phenomena observed by Antill and Stein are now ascribed to diagenetic cementation. In this case the model involving aqueous precipitation has fared better than that of fusion. The example is not unrelated to the problem of flints to which Hutton (1795) gave misdirected attention.

If Stein is one of the few avowed Wernerians among early observers of Australia, Alexander Berry [1781–1873] emerges as an equally rare professed Huttonian. His comment " Dr. Hutton would have given much for a single day's walk along this shore " south of Lake Macquarie (Berry *in* Field, 1825, p. 235) bespeaks an attachment probably formed while a medical student at Edinburgh. Throughout that paper, the first geological work prepared and presented (March 6, 1822) in Australia, Berry expresses Huttonian doctrine.

Stein for all his attachment to Werner was no strict neptunian.* He mentions volcanoes in the Pacific region conformable to the beliefs of that earlier Russian resident, Pallas, and has left an account of an active volcano in Kamchatka. Stein was certainly a catastrophist but in that he differs little from the majority of our geological pioneers.

Despite the various reports of volcanic rocks in Australia no one had found an active volcano. The Burning Mountain or Mount Wingen, found in 1828 in the Upper Hunter district of New South Wales, was therefore bound to attract attention though it came too late to comfort many but the most persistent neptunists. Long before, in 1801, James Grant [1772–1833] had examined the Hunter River as far as Singleton and remarked, for reasons undisclosed, that the

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* Dr. John Henderson (Hoare, 1968) seems to be a more worthy candidate. Henderson (1832) not only employs Werner's stratigraphic terminology (many non-neptunists did that) but his discussion of crystalline rocks of the Wacke Stratum in Australia is distinctly neptunian.

minerals " about the river in general are volcanick " (*Hist. Rec. N.S.W.*, IV, p. 408). It is highly doubtful if the Rev. C. P. N. Wilton [1795–1859] was aware of this when he visited the Burning Mountain in 1829 and, indeed, the two matters are unrelated. Wilton wrote an account of his visit for the *Sydney Gazette* (March 14, 1829) ; see also Wilton (1830). " That celebrated mountain of the southern world " (Wilton, 1832, p. 186) was mapped by T. L. Mitchell (1838, Plate 9) in the very month of Wilton's first visit though neither in their published remarks acknowledges the other. The only authorities worth mentioning apparently lived in Europe. At least Mitchell and Wilton both agreed on the cause of the phenomenon at Mount Wingen, combustion of a coal seam, though Wilton's slight attempt to consider the occurrence in the context of known volcanic regions may betray a vestigial Wernerian attitude.

Reference to this pseudo-volcano of Australia will be found in a few geological treatises of the period. Pseudo-volcanic action of a different sort was invoked by Menge (1841, No. 7) to account for opaline silica and siliceous tufa in South Australia. As a young mineral collector, Menge had been to Iceland in 1819 where he was impressed by the hot springs ; the siliceous deposits of his new home he ascribed to a like cause. On Iceland, Menge (1820) was essentially Wernerian though apparently not pure enough for his editor Jameson, who added his own remarks to the paper. In Australia the hermit Menge praises Werner for his mineralogy but develops a line all his own.

Mitchell's explorations of 1836 in western Victoria revealed the existence of well-preserved craters and cones (Mitchell, 1838). Examples, such as Mount Napier, are described without any particular effort to justify their diagnosis as extinct volcanic centres. To Mitchell, who knew Lyell's *Principles*, trap and amygdaloid were simply igneous rocks. The distinctive features known to the settlers of that region as *Stony Rises* are considered by Westgarth (1846) as products of extinct volcanism. In the southeastern corner of South Australia Mounts Gambier and Schank were recognized as extinct eruptive centres by Burr (1844). Thomas Burr [fl. 1839–1860], for a time deputy surveyor-general of South Australia and then superintendent of the Burra Burra mines, is an interesting figure who deserves further study ; I know only of his career in South Australia. Another South Australian resident, B. T. Finniss [1807–1893], in his account of local geology (Finniss, 1843) considers evidence of volcanism far more ancient than that represented by the craters and cones seen by Mitchell and Burr.

From that time forward one finds few if any signs of hesitation in recognizing igneous rocks in Australia. In some forty years treatment of such rocks here had passed from an old-fashioned approach derived from the days before Hutton and Werner to one influenced by Lyell. That development had taken almost twice as long originally in Europe. The telescoping of the process in this country was achieved by a diminished attention to both strict neptunism and Huttonian volcanism.

Relative Sea-Level Changes

J. R. Forster [1729–1798], naturalist with his son Georg to Cook's second voyage, reminds us that even in his time diminution of sea level and emergence of land were subjects of interest (Forster, 1778, p. 145). Forster had spent some years in Russia and probably was aware of Pallas's work ; indeed he may have known the man. Forster's suggestion that the steep rocky southerly terminations to the southern continents resulted from a violent flood from the southwest seems to owe much to Pallas.

Our record of inferred coastal changes based on direct observation begins with a visit of George Vancouver [1757–1798] to King George's Sound in 1791. There he found calcareous material (he called it coralline limestone) capping hills well above the present level of the sea (Vancouver, 1798, I, p. 49). No doubt the ‘ coral ’ was fossilized vegetable matter but our interest lies in Vancouver’s conclusion that the land had only recently emerged. Some ten years later both Baudin’s and Flinders’s expeditions examined that and many other localities along the western and southern coasts of the continent and noted the considerable extent of the calcareous rock known still as the coastal limestone.

The French, in particular, were impressed to find in the limestone remains of organisms like those inhabiting adjacent waters. Some, for instance *Trigonia*, were known in Europe only as fossils. The discoveries reinforced others made earlier by R. P. de Lamanon [1752–1787], one of La Pérouse’s naturalists. Lamanon’s descriptions of living terebratulids and nautiloids from the eastern seas survive to remind us of the scientific potential in that ill-fated expedition (Milet Mureau, 1798, II, pp. 321–339). François Péron [1775–1810], one of Baudin’s zoologists, quickly seized on the point that the Australian region was a habitat for ‘ living fossils ’. That theme has been repeated many times since and there is no denying the relevance of observations of Australian habitats and life-styles of such as the Port Jackson Shark, the marsupials, various molluscs, brachiopods and corals, not to mention elements of the extant Australian flora, in the development of European palaeoecology. The title of Unger’s little treatise on aspects of the Tertiary flora of Europe—*Neu-Holland in Europa* (Unger, 1861)—indicates something of this return influence.

Soon after Péron’s return to France he read a paper on zoological facts applicable to geology (Péron, 1804). It stands as ancestor to Chapter XXVIII of Péron and Freycinet (1816), but with some interesting differences. For one thing, the tortuous argument later offered to justify ignoring place names given by Flinders is all the stranger when one finds that Péron in 1804 was content to follow the English navigator. Again, Bailly the mineralogist, acknowledged as a source in the earlier issue, is dropped from the revision where only the dead Depuch is praised. Over the years Péron has been covered with glory ; Tate (1894) adds his share. For an alternative view I suggest a reading of Baudin’s (1974) journal and the translator’s preface to Dégérando (1969).

But no matter how we regard the man, Péron (1804) provides many useful details on the distribution of organisms, especially of corals, in warm seas. He argues that the coastal limestone of Australia must be of recent origin because its fauna so closely resembles that still extant nearby. Indeed both the French and Flinders* believed the material was still being formed at sea-level. Those occurrences now above the sea Péron saw as evidence that the land had emerged from the sea, an emergence he attributed to sudden and violent revolution. His catastrophism harks back to Buffon and Pallas and brought him wide notice, the more so after Cuvier’s espousal of the doctrine. Cuvier cited Péron and New Holland in support of his argument (e.g. Cuvier, 1813, 1825) but gave no prominence to the ‘ living fossils ’. His revolutions wiped out populations so living organisms ought not to be too closely related to fossils.

Péron’s catastrophist model was taken up by J. B. Lamarck [1744–1829] whose great work *Histoire Naturelle des Animaux sans Vertèbres* (1815–22) was to include details of both living *Trigonia* gathered by Baudin’s naturalists and fossil forms (cf. Deshayes, 1831) hardly supportive of Cuvier. Lamarck (1805) follows a geological theme outlined in a highly original but neglected treatise (Lamarck, 1802). Lamarck saw no need to postulate violent action. Indeed

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* Flinders (1814, II, pp. 115–6, 336) also made valuable observations on the coral reefs off the northeastern coast. His scheme of gradual progressive growth of the reefs is not unlike that suggested by Forster (1778, p. 150) for the origin of the so-called low islands of the Pacific. Both works were recognized as important by later students, notably Jukes (1847, 1850), of the subject in Australia.

his broadly uniformitarian view would hardly have affronted Hutton though there is no evidence that he even knew of the man or his theory. Lamarck commented on various ways of achieving gradual decline of sea level (Péron had not concerned himself with the cause of his revolution). Consumption of water by organisms or through volcanic action Lamarck rejected as insufficient and concluded that sea level varied from place to place through time consequent on migration of the earth's equatorial protuberance—a sort of embryonic model of polar wandering—and adduced astronomical detail in support. E. M. L. Patrin [1742–1815] joined the discussion (Patrin, 1805) as a protagonist of volcanic consumption while sharing a preference for gradual adjustments as opposed to catastrophic revolutions.

These alternative schemes passed practically unnoticed. Catastrophism was a received doctrine in Europe ; its persistence in Australia, as we shall see, was longer and at least equally strong. Nevertheless, after this active beginning the investigation of relative sea-level changes in Australia faded in popularity although valuable observations were made during the marine surveys (King, 1826) of P. P. King [1791–1856], during the visit of J. R. C. Quoy [1790–1869] and his companions to Shark Bay with the French expedition of 1817–20 (Freycinet, 1828, pp. 471–476) and in the course of the voyage of H.M.S. *Fly* (Jukes, 1847). Remarks of a general nature are to be found in Mitchell (1838, II, pp. 368–9) and in Dana (1849, pp. 533–6). Sommer (1848, p. 45) comments on the evidence of apparently rapid changes in coastal configuration in the Hutt River estuary of Western Australia and Gregory (1861, p. 482) mentions the natural uncovering of a ship buried further south on the same coast. I can find no earlier map of old shorelines than that of the lower Macleay River area, N.S.W., compiled by E. W. Rudder (1867).

The Formation of Valleys

Both Hutton and Lamarck had argued for fluvial agencies as sufficient causes in the formation of valleys but early nineteenth century opinion still favoured concepts popularized by Pallas, that valleys were carved by the action of catastrophic floods. Wernerians found nothing there with which to take exception and neither did the Cuvierian catastrophists.

From the early days travellers in New South Wales have been impressed by the valleys of the Blue Mountains. These vast features bounded by near-vertical cliffs seem to be entirely out of scale with the small streams that inhabit them. Gregory Blaxland [1778–1853], one of the first party to succeed in crossing the mountains in 1813, suggested that the valleys were manifestations of " an earthquake or some dreadful convulsion of Nature " (Mackaness, 1965, p. 7). R. P. Lesson [1794–1849], naturalist to Duperrey's expedition of 1822–5, reflects a like catastrophist view in his notes of a visit in 1824 : " It must have required a very great movement to rend so perceptibly this section of the Blue Mountains " (Mackaness, 1965, p. 152). Earthquakes rather than floods were the more popular cause. A few tremors had been felt about Sydney since the first was reported in June, 1788 ; Mann (1811), with remarkable hyperbole, even claimed the colony was menaced with destruction by an earthquake on January 17, 1801. Perhaps knowledge of these aided adoption of the particular catastrophist model.

By the time of the visit of Charles Darwin [1809–1882] in 1836, opinions in Europe were changing. Lyell and Murchison (1829) had revived the case for fluvial agencies in their account of valleys in the Auvergne. Aware of his regard for Lyell, we might expect Darwin to follow this line but his conclusion is very different. Darwin found the valleys among the few aspects of Australia with which he could be impressed but decided that " to attribute these hollows to alluvial action, would be preposterous " (Darwin, 1844, p. 136). In his notebook (Barlow, 1945, p. 251) Darwin merely asks the question " Cause of great precipice ? ". In 1844 he comments that cliffs limiting the valleys reminded him of sea-cliffs, an observation conformable to the model of marine denudation he was to offer.

Marine currents as agents of erosion had long held appeal. Surely, we may ask, Darwin was too familiar with Lyell to enter such a catastrophist trap. Chorley *et al.* (1964) point to a likely explanation. Lyell himself had gone off at a non-uniformitarian tangent. The fifth edition of the *Principles* issued in the year of Darwin's return from the *Beagle* voyage (1837) presents a case for marine denudation in the origin of valleys. This Darwin appears to have swallowed whole. Darwin on Australian geology is no shining original.

In this department he is deservedly overshadowed by James D. Dana [1813–1895], geologist to the U.S. Exploring Expedition of 1838–42. Dana spent nearly four months of 1839–40 in and about Sydney making visits to the Illawarra district, of which he prepared a geological sketch map, and to the Hunter River area. He did not, in fact, cross the Blue Mountains but had the benefit of the experience of a colleague, Horatio Hale, who went to Wellington ; Dana himself examined the Kangaroo Valley. He provides (Dana, 1849, p. 526ff) a thoroughly fluvial account of the history of the valleys and in so doing supports the earlier brief exposition of Mitchell (1838, II, pp. 351–2). In view of the inordinate rarity of Dana (1849)—see Haskell (1942, pp. 67–68)—it may be worth noting that the substance of his case is available elsewhere (Dana, 1850). With geologists of the calibre of Dana we see a reason for the remarkable development of North American geology in the second half of the nineteenth century. Would that he had found greater opportunity to explore Australia.

Reading Dana's argument one might expect that there the matter of the valleys and catastrophist notions also would rest. Only one later example must suffice to show the error of such expectation. W. S. Jevons [1832–1882], later famous as logician and economist, worked for some years at the Sydney Mint and while here interested himself in geology. In an unsigned article Jevons (1858, pp. 90–91) dilates on a thought that the valleys represent regions of collapse in ranges raised by volcanic action. That reminds one of Strzelecki (1845, p. 150) and his volcanoes of ' elevation ' ; and those he borrowed from European geology of the 1830's.

Diluvial Geology and Glaciation

It was mentioned earlier that especially in England the Flood of Noah came to have a geological dimension. Buckland's first major work (Buckland, 1823) deals with the remains of fossil vertebrates preserved in caves known as osseous caverns. These animals, argued Buckland, were victims of the great inundation.

The Flood caught up with Australia very quickly. In a popular account of the roads of New South Wales, Raymond (1832, p. 101) notes the natural feature called 'ploughed ground ' in the colony as possibly " impressed on the earth when it first emerged from the Deluge ". C. P. N. Wilton (1828), in fact, introduced the subject of Diluvial Geology in a journal he started soon after his arrival in 1827. Wilton had taken a pass degree at Cambridge the year before Sedgwick became professor, though later correspondence indicates their acquaintance. Wilton's connection with the Oxford Ashmolean Society suggests also the attraction of Buckland. The Flood must have interested Wilton before he came to Australia for there are references (Boué, 1832, p. 145 ; Melleville, 1842, p. 5) attributing to him a commentary dated 1826 on the fundamentalist work of a British M.P., Granville Penn. Penn (1822) had claimed that what he termed Mineral Geology and Scriptural or Mosaic Geology were antipathetic and irreconcilable. Despite much search I have failed to trace Wilton on Penn ; I imagine he essayed a moderate Bucklandian position. Lang (1846) and Rudder

(1854) provide later Australian accounts of Mosaic or Bible Geology before it ceased to have any pretension to science and passed to the pulpiteers.

Wilton (1828, p. 193) remarked presciently that bone deposits like those described by Buckland might be found in this country. " In or about 1830 " (Anderson, 1933, p. x) bone deposits in the Wellington Caves were brought to notice. Anderson gives an account of the discovery and subsequent study of these remains, a study that involved some of the leading comparative anatomists of Europe.

Apart from the purely palaeontological interest, the discovery of these osseous caverns had other implications, not least those relating to the age of Australia. Referring to the cave deposits, Henry Dumaresq [1792–1838] said in a letter from Sydney " it has been ascertained that the hypothesis, with regard to its [Australia's] post-diluvian formation, is as groundless as that of its absorbent interior marshes " (Barrow, 1832, p. 2). The shaken hypothesis was that based on the coastal limestone, that Australia had recently risen from the sea. As that emergence had been represented as violent there would appear to have been room for conflict between post-diluvial catastrophes and belief that the Flood (which had wiped out terrestrial animals) was the last such disaster. However, no one seems to have been greatly concerned. The German geographer Carl Meinicke [1803–1876], in an interesting review of Australian geology (Meinicke, 1837, I, ch. 4), simply concluded that the cave deposits indicated Australia was of greater antiquity than had been thought hitherto. Less than forty years later we find F. von Hochstetter [1829–1884], geologist to the Austrian *Novara* expedition of 1857–9, stating that Australia was one of the world's oldest continents and that most of the region had been subject to little disturbance since the end of Palaeozoic times (Hochstetter, 1864, p. XLVI). Behind that shift lie other revolutions—of thought and experience.

Diluvial theory in its heyday offered an explanation not only for the cave deposits but for the great spread of boulder clay across northern Europe. Hutton's first fluent disciple John Playfair [1748–1819] had pointed to the effectiveness of glaciers in transporting blocks of stone (Playfair, 1802, p. 388). By the 1830's a few Swiss geologists revived thoughts of glacial action ; the best-known though not the first of them, J. R. L. Agassiz [1807–1873], won some converts in Britain following his visit in 1840. Buckland, once the prince of Diluvialists, had already abandoned most of his catastrophist views (cf. Buckland, 1836) through Lyell's influence, so for him the step to acceptance of glacial action was not great. Geologists being a conservative lot continued to use the term Diluvium practically as a synonym for Pleistocene long after belief in the Flood as a pervasive geological agent had disappeared.

Thoughts of glaciers spread to Australia with remarkable swiftness. Murray (1842, p. 203) claimed to have seen evidence of moraines and other glacial features in the Pyrenees, WNW of Melbourne. The example has greater interest for its date than for its conviction. The Rev. W. B. Clarke [1798–1878] appears to have been the first to express belief that the Snowy Mountains bore evidence of glaciation (Clarke, 1860, pp. 225, 230). In that year A. R. C. Selwyn reported signs of glacial action in the striated pavements of the Inman Valley of South Australia (Selwyn, 1860, p. 4). Before coming to Australia Selwyn had assisted A. C. Ramsay [1814–1891], one of the first British students of terrains affected by the Quaternary glaciation. Selwyn seems not to have suspected that the glacial features of the Inman Valley belonged to a far older event but then who at the time thought the (Quaternary) Great Ice Age was other than unique? Without realizing it Selwyn had come across one of those geological features that unite the southern continents and India and which caused so many difficulties to those with European prejudices. How close Selwyn came to breaking from this strait-jacket may be seen in his notion that glacial agencies had operated during deposition of what he took to be late Palaeozoic rocks at Bacchus Marsh, Victoria (Selwyn, 1861; Selwyn and Ulrich, 1866). One result of Selwyn's enforced removal to Canada and the triumph for a time of office-geology in Melbourne was a ' revision ' of the stratigraphy at Bacchus Marsh. Indirectly it saved for the geologists of India the credit for establishing the non-European character of late Palaeozoic successions in the southern lands. But here I trespass upon my final topic.

THE SEARCH FOR STRATIGRAPHIC ORDER

Whereas Werner's process of neptunian precipitation may not have been invoked by many of our pioneers there is no denying the influence of the method of lithological stratigraphy that was part of the Wernerian system. The search for order of succession in this country began, from the accidents of landfalls and settlement, in a distinctly haphazard way. But according to the concept of world-wide formations that Werner had made his own that need not have caused difficulties. The significant point was to recognize the characteristic lithologies.

Leopold von Buch took the trouble while in Paris during 1810 to examine the collections made by Bailly and Depuch; he found samples that generally matched rocks known in Europe. But what, Buch (1814) asked, was to be made of materials like the coastal limestone that bore fossils so like organisms still living? The rock could be assigned a place in the European order but there no such association with related living organisms was known. Were there, in fact, formations of local extent? The Paris collections supplied no answers. Buch's rhetoric is left undeveloped but it strikes at the core of the doctrine of universal formations by hinting that a particular sort of rock may not everywhere occupy the same stratigraphic position. Although once a student of Werner, Buch was no typical disciple; he had already abandoned belief in the neptunian origin of basalt and his interest in fossils was for the time quite unusual.

The Problem of Australian Coal

Buch knew that coal with sandstone, as in Europe, had been found near South Cape, Tasmania, during the second visit (1793) of the d'Entrecasteaux expedition (Labillardière, 1799, II, pp. 21–22) and suggested the fossil plants collected near North-West Bay by Baudin's naturalists might also belong to the coal measures. Here his European experience prevailed, the term used, *Steinkohlengebirge*, was that applied to the coal measures that in Europe lay just above Werner's Transition series.

Stratigraphic order in Australia really begins with coal, as it did in Europe. When Ludwig Leichhardt [1813–1848?] observed (Leichhardt, 1849, p. 45) that the geology of Australia in general started at Newcastle, N.S.W., we know what he implied. Coal had been found by runaway convicts on the coast north of Sydney in 1791. London papers reported the find (e.g. *The European Magazine*, July 1792, p. 77) but the news does not appear to have reached Sydney before the next discoveries were made in 1796. George Bass [1771–1803], sent by the governor to examine the occurrence at Coalcliff, south of Sydney, found the coal there to lie below the sandstones that abounded near the settlement. In a letter written from Sydney in August 1797 to a colleague then in London, Bass evinces the first signs of belief in a coal basin in the region (*Hist. Rec. N.S.W.*, III, p. 289).

Depuch and Bailly (Péron and Freycinet, 1816) saw in 1803 that shales lay above the sandstone near Parramatta and predicted that older (primitive) rocks must be exposed in the area drained by the Hawkesbury system. A few years before, in 1798, explorers to the southwest of Sydney returned with claims that salt, coal and limestone existed there (*Hist. Rec. N.S.W.*, III, pp. 820–8;

Cambage, 1920). The salt was said to form cliffs and veins (Collins, 1802, pp. 88, 98); from such reports arose stories of mountains of salt in Australia. In fact, the salt merely occurred as incrustations. Not long after, Humphrey the mineralogist found salt in the midlands of Tasmania, another area where coal was known.

To the lithological stratigrapher these finds appeared to offer scope for correlation. In Europe salt deposits existed in what came to be called the New Red Sandstone. Below this, in order, came first Magnesian Limestone then, as a rule separated from it by an unconformity, came the coal, shales and sandstones of the Coal Measures, the quartzose sandstones of the Millstone Grit and finally limestones known as the Mountain Limestone. The latter in England rests on Old Red Sandstone. A valuable contemporary treatment of this sequence is given by Conybeare and Phillips (1822); in more modern terms the succession ranges from Triassic to Devonian. The Old Red with the slates and greywackes below were grouped in Werner's Transition series.

These various terms appear in the early literature of Australian geology. Predictably, red sandstones became Old or New depending on their relation to the coal or, where that was unknown, on individual choice. Mitchell and Sturt, for instance, seem to have preferred the Old as a matter of course. Those who relied on collections made by others were no less arbitrary. The report of Humphrey's examination in Sydney of samples gathered by F. L. Barrallier [1773–1853] on his journeys of 1802 into the Blue Mountains allows us to glimpse the limitations of local science. Humphrey decided that Barrallier had not really reached far into the mountains because no granite had been brought back (*Hist. Rec. Austr.*, ser. I, vol. V, p. 589). The argument might have interested Pallas or Werner but Humphrey had evidently failed to examine the explorer's journal (*Hist. Rec. N.S.W.*, V, Appendix A). In that document the explorer not only reports the occurrence of granite but also notices the presence of fossil shells in the Kowmung River area. These fossils are now recognized as the first Devonian remains found in Australia. Perhaps Humphrey had no French and so was unable to study the journal.

N. J. Winch [1768–1838] of Newcastle-upon-Tyne decided from a study of collections made by the Rev. T. H. Scott [1783–1860] that apart from diluvium there was nothing in Tasmania younger than the European Magnesian Limestone and in New South Wales nothing more recent than the Coal (Winch, 1823). Scott (1824) himself offered some notes on the supposed distribution of the various units identified on the basis of lithological features. The stratigraphy recognised by W. H. Fitton [1780–1861] from a study of P. P. King's collection and from published sources depends also on what had become almost standard lithological criteria (Fitton, 1826). By that time, however, workers in Europe had started to recognize the value of fossils in correlation.

Buckland (1821) from an examination of Robert Brown's collections made in 1803–5 decided plant fossils in the Australian coal were like those of England and that marine fossils from near Hobart resembled those of the Mountain Limestone. Yet it was among samples in Buckland's possession that Adolphe Brongniart [1801–1876] recognized *Glossopteris browniana* (Brongniart, 1828), a plant he found also in Indian coal but quite unknown in the European coal measures. This distinctive southern coal plant appears earlier to have been confused with *Eucalyptus* (cf. Scott, 1824). R. P. Lesson (Lesson and Garnot, 1826, p. 6), in fact, went so far as to postulate a Tertiary age for the sandstones of the Blue Mountains, presumably because of the apparent relation of the fossil plants to living types—an interesting example of the then newly-emerging palaeontological method foundering on erroneous identification.

Quoy in 1826 collected casts of spiriferids from near Jervis Bay, N.S.W., that were deemed to resemble those of the " période Phylladienne ou intermédiaire " in Europe (Dumont d'Urville, 1830, pp. cix–cx), i.e. Devonian. Fossil shells from below the coal in the Hunter Valley are noted by Wilton (1832) and Mitchell (1838). Mitchell, in particular, took the enterprizing step of enlisting help from the palaeontologist J. de C. Sowerby [1787–1871] (cf. Cleevely, 1974). The spirifers suggested a correlation with Mountain Limestone. G. B. Sowerby [1788–1854] assigned a like place to the brachiopods gathered by Darwin during his visit to Tasmania (Darwin, 1844). Darwin's corals from the same area were thought by William Lonsdale [1794–1871] to be of Devonian or Carboniferous age. Another interesting collection of rocks and fossils from New South Wales and Tasmania is listed by Chevalier (1844). P. E. de Verneuil [1805–1873] referred the Tasmanian fossils to Carboniferous types (Verneuil, 1840). Although a few years earlier H. T. De la Beche [1796–1855] had warned there was no real evidence that the coal of Australia must be of an age with that in England (De la Beche, 1835, p. 306), the palaeontologists by suggesting correlation of marine beds below the Australian coal with the Carboniferous Mountain Limestone can only have strengthened belief in a European-type succession at the antipodes. Any distinctive features associated with the Australian coal perhaps came within the province of ' wayward sports ' that Nature here turned up to ' amuse ' the geologist just as she did in the animal kingdom (Wilton, 1833, p. xviii).

As yet no one had attempted to examine relations of strata in the field or to map the distribution of units including the coal. Credit for the first such work belongs to P. E. de Strzelecki [1797–1873]. His map, of which a reduced version accompanies his important book on Australia (Strzelecki, 1845), has been examined recently by Branagan (1974). The man himself still presents many problems. We know for instance almost nothing of where he learned his geology (Heney, 1961, pp. 41–2) yet clearly he had a good working knowledge of the subject. The particular systems of geognostic divisions he adopted for Australia (Strzelecki, 1841, 1845) reflect continental influences but these are treated with unexpected independence. His approach incidentally is followed almost in its entirety by Grange (1854). There is catastrophism in Strzelecki's grouping of epochs each separated by a revolution but it is not Cuvierian catastrophism. I see it rather as reflecting the evolved model by which Elie de Beaumont [1798–1874] and others were leading geology towards concepts of orogenesis.

Strzelecki's (1845) attributions of rocks in particular localities to particular epochs do not in every case bear close examination but the wonder is that he covered so much ground during the four years of his stay here and furthermore managed on his own resources. His treatment of geology in the book is largely lithological and distributional ; apart from the map the main interest now lies in the work of John Morris [1810–1886] on Strzelecki's fossil plants and of Lonsdale and Morris on the fossil fauna. Morris's remarks (Strzelecki, 1845, pp. 252–3) on the apparent differences between the coal floras of the northern and southern hemispheres and the contrast of these differences with similarities exhibited among fossils from the older rocks of both hemispheres may seem to us obvious ; in his time they represented a necessary recognition. Some more rational answer than wayward sports of nature had to be found.

For all the interest of his mapping Strzelecki did not succeed in establishing any detailed positional relations between his units. Berry (*in* Field, 1825) had long ago demonstrated that on the south coast of New South Wales the sandstones that underlie the coal strata rest, at an angle, on older deformed rocks. Little more was done until 1840 when the Rev. W. B. Clarke, who had arrived in Sydney soon after Strzelecki in 1839, joined J. D. Dana in the field at Wollongong. Dana and Clarke observed there a comformable succession from marine fossiliferous sandstones upwards into the coal measures—strata that Strzelecki had assigned to different epochs separated by a revolution. From Dana we have a carefully argued resumé (Dana, 1849, pp. 493–5) of his ideas on the age of the coal. His experience of field relations and the fossil flora and fauna, both vertebrate and invertebrate, led to a conclusion that the whole succession of sandstones, shales and coal belonged to the " upper carboniferous or partly the lower Permian era ". His suggestion of a Permian age had in fact been anticipated by a throwaway remark on the invertebrates that occurred just below the Australian coal in a paper (Koninck, 1846) dealing with fossils from Spitzbergen written by the Belgian chemist and amateur palaeontologist L. G. de Koninck [1809–1887].

Dana's clarity and directness stand in marked contrast with Clarke's responses to the coal problem. Clarke is commonly represented as a staunch advocate of a Carboniferous age for the coal and, until his last years, of the whole succession in what is now called the Sydney Basin. Certainly he maintained, with no little combativeness, such views for many years. I believe they came in part from his failure to recognize differences between the two hemispheres ; he expected an angular break, as in Europe, separating coal measures from Permian and Mesozoic strata.

In the light of Clarke's later position it is strange to find that, soon after Dana's departure, he began to argue an Oolitic (Jurassic) age for the coal. Jervis (1944, p. 428–9) quotes from a letter dated 28 June 1842 from W. S. Macleay [1792–1865] to Clarke stating objections to the case for Oolitic coal expounded anonymously that day in the *Sydney Morning Herald.* It may be noted by the way that Macleay, best remembered as a zoologist, had no mean grasp of geology. He had attended E. D. Clarke's course in mineralogy at Cambridge (Vallance, 1974) and had contributed a discussion on trilobites to Murchison's classic *The Silurian System* (1839). W. B. Clarke's reply (1 July 1842) to Macleay has turned up among some papers preserved by the late J. J. Fletcher and passed to me by Dr. A. B. Walkom. Clarke never actually acknowledged authorship of the newspaper article but the reply leaves no doubt that he was responsible and further that he was not then the devoted adherent of William Smith he later claimed to be. His justification to Macleay rests chiefly on lithological argument. He was evidently roused by Macleay's queries for he returned to the subject in a long rambling memorandum finished at midnight 5 July 1842. He there persists : " if the Sydney sandstone be *New Red*, where are the red and green marls—and the gypsum ? ". To which Macleay responded with the blunt annotation " not necessary ". One wonders whether the excellent paper by J. B. Jukes [1811–1869] warning geologists of the problems of lithological correlation (Jukes, 1843) arose from the author meeting Clarke in Sydney during 1842.

Both Jukes and Clarke had been students of Sedgwick. Jukes evidently did not share Clarke's Oolitic view for in a letter dated 31 May 1843 among the Clarke Papers at the Mitchell Library, Sedgwick tells Clarke that Jukes regarded the Australian coal as stratigraphically lower than that of England. In 1845 H.M.S. *Fly* with Jukes aboard returned to Sydney and during that visit he and Clarke went to the Illawarra district. By then Clarke had gone Carboniferous but Jukes's letter of 1 February 1846 (Jervis, 1944, pp. 381–2) throws light on another aspect of the problem. Jukes there argues to Clarke that what the latter called the Wyanamatta beds must lie above the Sydney or Hawkesbury sandstone and not below as he said Clarke had represented. It must be added, however, that the other side of this correspondence has not been examined. Jukes may have misunderstood his host, for a sketch section accompanying the memo of 5 July 1842 has what Clarke then termed ' Brownlow beds ' clearly above the ' Hawkesbury beds '.

In his important review of Australian geology Jukes (1850) adopted a conservative view as to geological age that agrees generally with that argued by Clarke after 1847. That year saw the publication of M'Coy's palaeontological researches on the collections sent by Clarke to Sedgwick (M'Coy, 1847). By a delicious irony, M'Coy took the Oolitic position abandoned by Clarke. He had been roused by Macleay's criticism in 1842, now Clarke was really stirred. His unfortunate propensity to defend himself with more enthusiasm than prudence became all too evident. For instance, he soon set about proving his Carboniferous model by an attack on Strzelecki's claim that *Lepidodendron* did not occur in the Australian coalfields (Clarke, 1848*a*). Clarke must have seen this fossil plant as required by his case ; the localities he adduced by way of contradicting Strzelecki do not, in fact, belong to the coal areas.

The accidents of the gold discoveries in eastern Australia during and after 1851 deflected geological attention for a time to rocks older than the coal measures. Not until about 1860 did coal problems reassert themselves and by then M'Coy had come to Melbourne as a professor in the new university, a post he combined with that of palaeontologist to Selwyn's geological survey. Fifteen years later there was no general agreement. If we examine Brough Smyth's map of Australia or his explanatory notes (Smyth, 1876) we find a category *Carbonaceous* placed below the Cretaceous ; together they constitute the Mesozoic. Of the strata in the Sydney Basin everything from the coal upwards is lumped in the Carbonaceous. The argument outlined by Smyth (1876) is really that of M'Coy. It was, in fact, as thoroughly determined by European prejudice as was Clarke's. The Australian coal could not be of Palaeozoic age, M'Coy (1867) argued, because certain distinctive (northern) Carboniferous coal plants were not found here. He did, however, admit that fossil fish in the local succession had a Permian or Triassic character, thus taking a point first developed by Dana. And it is only reasonable to admit the validity of his argument that plants from the higher units of the Sydney Basin were of Mesozoic types. In that work of 1867 M'Coy claimed credit for suggesting the existence of Triassic and Permian rocks in Australia—in places remote from the Sydney Basin. Unfortunately knowledge of Permian and Triassic successions in Europe was little help in Australia.

Clarke's side of the argument may be followed through the four editions of his *Sedimentary Formations*, issued between 1867 and 1878 (Vallance, 1969). He ought to be granted the final advantage in the debate. For all the hastiness of his field-work, Clarke at least did examine the succession as it occurs. Indeed the order of strata outlined by Clarke (1866) is now generally recognized if in somewhat different terms. Those like William Keene [1798–1872] and Richard Daintree [1832–1878] who took the trouble to visit the rocks agreed with Clarke. In his important work on Queensland, Daintree (1872) points to the occurrence there of both late Palaeozoic (Carboniferous) coal measures and others of Mesozoic (Carbonaceous) age. Charles Gould [1834–1893], government geologist in Tasmania 1859–69, followed Clarke (Johnston, 1888) but posterity has favoured a Mesozoic attribution for most of the Tasmanian coal. Final sorting of the coal problem in New South Wales came with the advent of men like C. S. Wilkinson and T. W. Edgeworth David, careful field geologists less bound to the primacy of European experience than Clarke and M'Coy and so better able to develop the sort of independence expressed in the work of the Geological Survey of India whence came the germ of the Gondwana concept.

Before leaving the matter of coal we should look at the record in other parts of the continent, if only to see how slight was the rapport between the separate colonies. In both Western and South Australia the need for coal arose before discovery. Moore (1884, p. 376) notes the discovery by J. A. L. Preiss [1811–1883] in 1839 of a fossil 'encrinite' in the west. This was seen as indicating the presence of a Transition or Secondary formation and prompted the government to offer a reward to the first discoverer of workable coal. A few years later, surgeon Joseph Harris in an addendum to remarks by J. W.

Gregory [1815 ?–1850]* on iron ore found near the Swan River argued that as coal and iron usually occurred together in England, coal was to be expected in Western Australia (Gregory and Harris, 1843). Gregory's brother Augustus Charles [1819–1905] in fact found coal at the Irwin River in 1846 (Gregory and Gregory, 1884, p. 8).

The earlier work of the Gregory brothers, like that in eastern Australia some twenty years before, was almost entirely lithological. New Red Sandstone and the like appear, as they do in the reports of F. von Sommer (1848, 1849*a*, 1849*b*) who was employed briefly by the government as a mineralogist. J. W. Gregory (1849), however, notes the presence of fossils in what he calls upper carboniferous limestone at Gingin (was it the Chalk ?) and F. T. Gregory (1861) also reports fossils ; indeed, he is credited with the first clear evidence of Mesozoic rocks in Australia (Moore, 1870). Sommer (1849*c*) offers an idiosyncratic classification of Australian rocks. Perhaps its main interest lies in the (unsupported) claims that Silurian and Devonian rocks exist in South Australia and Triassic rocks in the west. All these pioneers united in regarding the coal as Carboniferous but supply rather than age was the main problem in Western Australia. With the removal of A. C. and, later, F. T. Gregory to the eastern colonies geological activity almost ceased in the west. Not until 1870, with the arrival of the Rev. C. G. Nicolay [1815–1897] and the appointment of H. Y. L. Brown [1844–1928] as government geologist on a two-year contract, did geology begin to revive.

In southern Australia the discovery of order began with the recognition of the Tertiary age of strata along the lower reaches of the River Murray (Sturt, 1833). A more detailed account of Tertiary geology may be found in the work of the Rev. J. E. (T.) Woods [1832–1889] and others (e.g. Woods, 1862). Limestones from about St. Vincent's Gulf, Sturt referred to the Primitive Transition or Transition. Nothing of intermediate age had been recognized by the time Finniss (1843) announced that no secondary rocks existed in South Australia. But as mining activity grew and began to consume the local supply of wood at an alarming rate the need to find other fuels became urgent. Dutton (1846, pp. 311–3) quotes the opinion of C. D. E. Fortnum [1820–1899] on the possibility of finding coal in the colony. Fortnum, remembered as a benefactor at Oxford, spent the years 1840–5 as a settler in South Australia. The remarks and ideal section attributed to him by Dutton are the work of a person with a deal of geological commonsense. On the assumption that any coal would be of Carboniferous age he pointed to places where such strata might exist below the surface. Fortnum's advice to test his model by drilling was not followed but in 1848 surface exploration for coal began on a subscription basis. Dr. G. H. Bruhn of Dresden (Lodewyckx, 1932, pp. 77–8) had come to Adelaide with a party of German miners and, claiming experience of prospecting for coal, offered his services to colonial proprietors. Although disappointed at the response he nonetheless essayed a search. One wonders about his experience for the report (Bruhn, 1849) might suggest that coal geology in Germany had not yet shed Wernerism.

It is interesting to contrast Bruhn with a contemporary German coal expert, Friedrich Odernheimer [1808–1885], employed 1853–6 as mineral surveyor in the Newcastle coalfield by the Australian Agricultural Company. Odernheimer's reports, privately printed for the company, contain much information of value.

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* Joshua William Gregory, at the age of 14 arrived with his family at the Swan River in 1829 ; he died there 21 September 1850 [information kindly supplied by the Battye Library, Perth]. By some he has been confused with the unrelated John Walter Gregory [1864–1932], Professor of Geology in the University of Melbourne 1899–1904. The Gregory brothers must be accounted pioneers of geology in the west ; J. W. and F. T. Gregory (1847) prepared the first geological map of Western Australia.

Admittedly there is not much discussion of stratigraphical detail, apart from that relating to coal seams, but no doubt the employers made their requirements clear. Odernheimer was no mere prospector. He came to Australia on the strength of highly-regarded consulting work in Scotland; his early training included studies at Göttingen, Heidelberg and Clausthal. Of Bruhn's career I know nothing except that after his failure in South Australia success came with a reward of £500 for his part in the discovery of gold in Victoria. But the 'physician Dr. G. H. Bruhn' had left the country before the first part of his prize was paid in 1855. The short account he wrote of Australia (Bruhn, 1855) does little for his reputation as a geologist. On the other hand those that followed him in South Australia during the years to 1875 met with no more success in finding coal. Apart from the Tertiary rocks, the discovery of order in South Australia is an achievement of the last century.

Order Among Older Palaeozoic Rocks

No doubt R. I. Murchison [1792–1871], whose researches in Wales led to his definition of the Silurian System in 1835, was gratified that another Peninsular War veteran reported evidence of Silurian rocks in the Murrumbidgee region of New South Wales so promptly (Mitchell, 1838). He was not to know that graceless posterity deems them Devonian. Verneuil (1840) and Chevalier (1844) also attributed a Silurian age to fossils from the Murrumbidgee hills. Among Strzelecki's collection from the same region Lonsdale (Strzelecki, 1845, p. 296) found material with what he saw as Devonian characters. Two years later de Koninck attributed a Devonian age to a spirifer from Tasmania. These examples and others like Clarke (1848*b*) and Leichhardt (1847, p. 212) mark the first, halting steps towards finding order among those rocks lumped under the Wernerian label *Transition* by earlier investigators. No real progress was made, however, until the discoveries of gold drew attention to the older, folded terrains.

The work of Elie de Beaumont and others in Europe had popularized the notion that mountain ranges sharing a common trend consisted of rocks of similar character and similar age. On that basis it had been argued the mountains of eastern Australia match those of New Zealand and the Pacific coast of South America. Murchison, recently returned from Russia and doubtless influenced by such concepts, offered the suggestion (Murchison, 1844) that the Australian mountains were likewise of a type with the Ural Mountains. More significantly, as the Urals had yielded gold and other precious materials so should the Australian ranges. Two years later Murchison claimed success for his long-range forecasting. W. B. Clarke took up the same line in the *Sydney Morning Herald* for 28 September 1847—and later collided with Murchison in claiming credit for the discoveries of gold in Australia. Neither, in fact, had much substance for his claim but the history of gold discovery as such does not concern me here. It is worth noting, however, that while Clarke was dilating on the Urals, an area of which he had no personal knowledge, there lived in South Australia a man who not only had been there but had written at least two scientific articles dealing with the Urals (Menge, 1826; 1842). Such was the parochial state of Australia that no one seems to have thought of seeking his views.

By 1849 mineral discoveries in New South Wales had become sufficiently numerous to move the colonial government to seek the services of a mineral surveyor. Samuel Stutchbury [1798–1859], the man finally appointed, had been in Australia briefly some 25 years before he reached Sydney again late in 1850. He had scarcely commenced his work when the madness of gold erupted and disrupted his survey. Between 1851 and 1855 when the government terminated his appointment he reconnoitred geologically some 80,000 km^2 of the northern part of the colony including part of what since 1859 has been Queensland. Sixteen quarterly reports furnished with maps and sketches to the Colonial

Secretary in Sydney state the results of his work. While Stutchbury was thus engaged Clarke secured a commission to examine other goldfields in the colony. Clarke by collecting and reprinting his reports (Clarke, 1860) avoided the neglect Stutchbury has suffered.

Returning to stratigraphy, we find Stutchbury in his Second Report (dated July 18, 1851) writing of limestones with probable Devonian faunas and in the Fourth Report (January 26, 1852) he presents a case for Devonian rocks at Wellington, N.S.W., on the basis of fossils from limestone and the nature of associated red sandstones. This was the area of the first Australian geological map (Mitchell, 1838) and as far as I am aware Stutchbury offers here the first clear statement on an occurrence of Devonian rocks in this country. Clarke's report of 6 March 1852 from Twofold Bay discloses that he also was then having Devonian thoughts (Clarke, 1860). But whereas Stutchbury went quietly on his way with little opportunity to revise his work, Clarke perhaps erred by writing too much ; from the goldfields reports through the various editions of *Sedimentary Formations* it is possible to trace his difficulties with the Devonian and his susceptibilities to shifts in European opinion.

During the 1860's Clarke's friend Jukes, then attached to the Geological Survey of Ireland, expressed strong doubts as to the validity of the concept of a Devonian System. Briefly, he found difficulty in accepting the Old Red Sandstone and certain slaty rocks of SW England and southern Ireland as belonging to the same system (e.g. Jukes, 1868). The slates he regarded as equivalent to the Irish Carboniferous slates. Clarke, ever sensitive to what he regarded as higher authority, entered a stage of coolness to the Devonian from which he did not finally emerge until reassured by de Koninck in 1876 (Koninck, 1898). Meanwhile, M'Coy was also suffering Devonian problems. Whereas in 1861 he proclaimed pontifically there were no Devonian formations in Australia, a few years later he could announce " with great pleasure " that Devonian limestone existed in Gippsland, Victoria (M'Coy, 1867).

In 1852 the new colony of Victoria, already beset with gold-fever, moved to emulate its northern neighbour and secure the services of a mineral surveyor. Stutchbury was sound ; the man chosen for Victoria was brilliant. A. R. C. Selwyn, as we have seen earlier, came to Australia fresh from the old rocks of North Wales. No more appropriate training-ground could have been found for a man who was to investigate the slates of Victoria. And fortunately, unlike the later Palaeozoic successions in Australia, our older sequences were more approachable by way of European precedent. Starting with little more support than Stutchbury had, Selwyn slowly acquired and trained a staff of assistants (Dunn, 1910). The period 1852–1869 of Selwyn's Geological Survey of Victoria saw the foundation of systematic geological mapping in this country. Hitherto the record had been essentially one of scattered observations. In those 17 years the Victorian survey issued more than 50 district map sheets, a geological map of the colony in eight sheets as well as numerous reports. The papers contributed to the then fashionable international and intercolonial exhibitions provide important reviews of progress (e.g. Selwyn and Ulrich, 1866).

The older Palaeozoic successions in Britain had been argued over since the 1830's when Sedgwick introduced his Cambrian System and Murchison, working stratigraphically higher, his Silurian System. The problem of how the two were related was not helped by Murchison's enthusiasm for his creation. Sedgwick came to believe that Murchison had trespassed on his property. Lapworth's solution of 1879, the erection of an Ordovician System to cover the disputed middle ground, is now generally adopted but does not concern us here. Selwyn the Survey man naturally showed a preference for Murchison and Silurian. The auriferous slates of Victoria on the basis of their graptolite faunas he demonstrated to be of an age with Lower Silurian (Murchison) of North Wales. Here M'Coy's work as palaeontologist to the survey was invaluable. But M'Coy had been for a time Sedgwick's assistant and colleague and it is not surprising to find he called these slates Cambrian.

Establishment of the Cambrian/Lower Silurian System in Australia stands entirely to the credit of Selwyn's survey. Well after 1875 its existence was still limited to Victoria. In New South Wales, Silurian rocks were consistently labelled Upper Silurian. There and elsewhere the sorting of older rocks had to await the attentions of geologists during the past century. Those areas marked as Metamorphic on Brough Smyth's map were all but unknown.

Finale

Geology in Australia to 1875 followed no fine, forward march. Many disputed matters were still unresolved although solutions had begun to emerge. The greatest difficulties concerned those areas in which the European experience gave least guidance and in particular the ordering of the late Palaeozoic to Mesozoic successions. Clarke and M'Coy, who loom so large in this story, strike me as the last of the European school in Australia. Both achieved much of lasting value but their attitudes so firmly shaped by European experience and precedent seem at times to have stultified rather than promoted enquiry. Were they really the founders of Australian geology or, with Selwyn and perhaps Dana, the great forerunners?

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DROUGHT DAMAGE ON MOUNT TOWRONG, VICTORIA

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(Plate I)

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Synopsis

The vegetation on Mount Towrong in south-central Victoria was severely desiccated in the widespread drought of 1967–68. Severe damage was inflicted on trees and shrubs in woodlands on the hot rocky western slopes and in tall forests along gully margins. A study of the ecotones between the various communities allowed a relative drought resistance ranking of species to be compiled. Amongst the dominants *Casuarina stricta* was the most drought resistant, followed by *Eucalyptus goniocalyx*, *E. radiata* and *E. obliqua*. This order corresponds to their site ranking along moisture gradients in Victoria. Damage was more severe in dense than in open stands.

Studies on the water relations of seedlings of the dominant species confirm this ranking of resistance. Most of the resistance of the species is concerned with drought avoidance and with the efficient reduction of cuticular transpiration. In addition *C. stricta* appears to be more inherently resistant to tissue desiccation and high temperatures. It also develops deep-striking tap roots at an early stage. Seedlings of *E. goniocalyx* and *E. radiata* are closely matched although the former species appears to endure higher tissue dehydration, resists water loss from stems and develops an early robust root system. The adult foliage of *E. radiata* has a lower cuticular control and poorer resistance to desiccation than the juvenile foliage. The development of its seedling tap root is also very slow. *E. obliqua* transpires relatively rapidly and has poor cuticular control of water loss. It is sensitive to tissue dehydration and its tap root development is relatively poor. It is suggested that many of these characteristics may have adaptive value in determining which particular sites the species will occupy. It is likely that the distribution of the species depends not only on the level of average rainfall and soil moisture storage but also on the frequency of extremes.

DESCRIPTION

In 1967 and in the summer of 1968 a drought of unprecedented severity gripped most of Victoria and caused the death or damage of native vegetation, mostly in areas in the 50–100 cm rainfall belt. This followed the 1965 drought in New South Wales and in the Australian Capital Territory which had caused damage to forests on a scale hitherto unknown (Pook *et al.*, 1966). In April 1968, after the drought in Victoria had broken, the western slopes of Mount Towrong looked as though they had been swept by a patchy fire. By the spring of 1968 many drought-damaged trees had developed epicormic and coppice shoots. In the following autumn the field study described in this paper was carried out by senior ecology students of the Botany Department, Melbourne University.

Physiography and Soils

Mount Towrong (800 m) is the highest part of the spur which runs 5 km south-westerly from the Macedon massif on the Great Dividing Range, to a point 1 km east of the Upper Macedon township. The end of the spur rises 150–240 m above Stony Creek on the west and the Gisborne uplands on the east (Pl. I, bottom). The slopes vary from 11° to 25°, depending on the presence of small gullies and more or less resistant rock. The spur, like most of Mount Macedon, consists of well jointed Upper Devonian dacite (Skeats and Summers, 1912) (Fig. 1). Zones of deeper soils carrying forest run diagonally across the western slopes. These are flanked by broad areas of rock outcrops and rocky soils which

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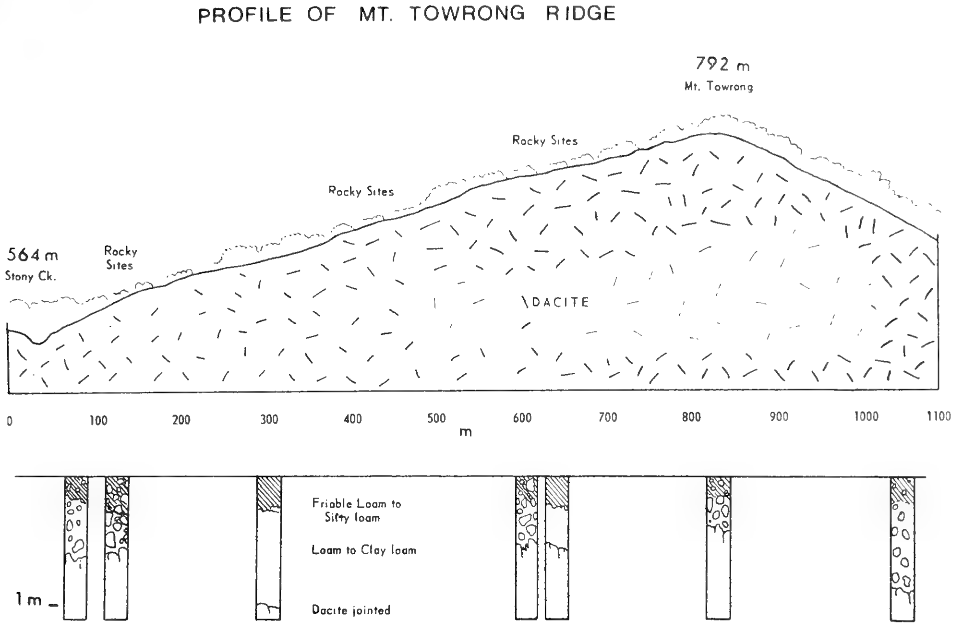

Fig. 1. Profile of Mount Towrong ridge with soil profiles (westerly to easterly).

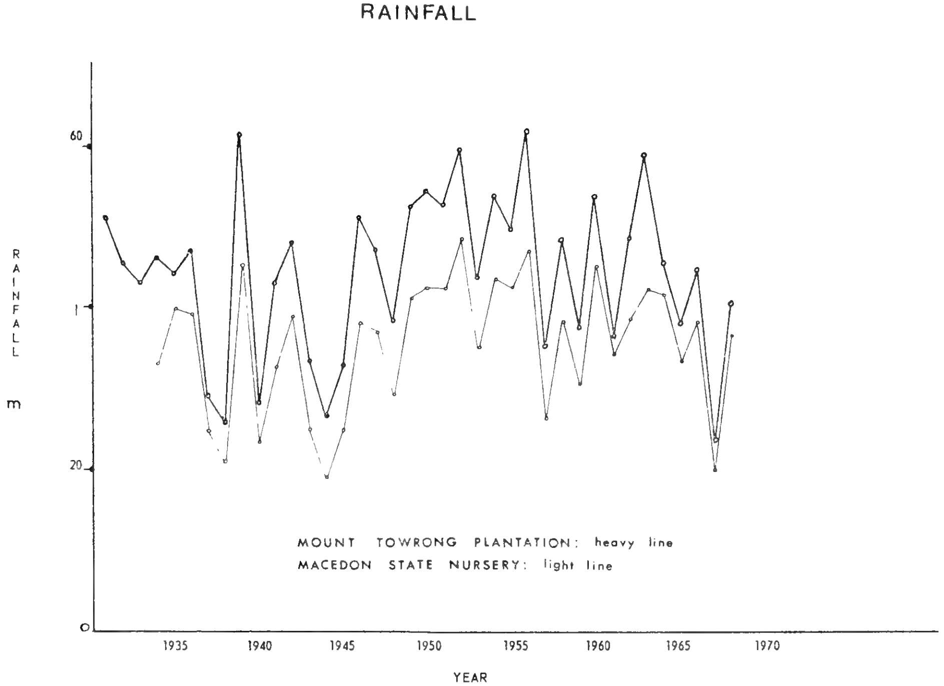

Fig. 2. Annual rainfalls of nearby stations. Mount Towrong 1109 mm and Upper Macedon 846 mm (average).

carry low woodland. The north-south trend of these zones may reflect a major joint system in the dacite. These deeper soils, which are of the krasnozem type, are friable red-brown silty to fine sandy loams increasing in clay content with depth. On the eastern aspect and on the gentler slopes of the mid-western aspects the soils are relatively deep (120–500 cm); elsewhere they are shallow (30–45 cm) with numerous rock floaters 7–30 cm in diameter which become more frequent with depth and merge with the parent rock. The skeletal soils around areas of rock outcrop on the ridge top and close to Stony Creek contain between 20% and 33% rock by volume in the top 30 cm of soil. In other areas rocks are absent in the top soil or the volume is less than 10%. The moisture storage capacity of soil in the top 45 cm ranged between 20% and 25% over most of the area but increased to 35–40% towards Stony Creek.

Fig. 3. Decile ranges in Australia during the drought period.

Climate

The climate of the area is normally relatively mild and moist. The rainfall occurs mainly from late autumn to mid-spring and is fairly reliable (Australian Bureau of Meteorology, 1968). The annual rainfall ranges between that at Upper Macedon (81·6 cm at 610 m) to that at the Mount Towrong plantation (110·9 cm at 840 m). At each station the maximum deviation observed over 35 years is about 50% of the mean. In 1967 the rainfall was half of normal and was the same as that of the bad drought years of 1938 and 1944 (Fig. 2). Virtually the whole of the south-east of Australia suffered rainfalls within the lowest 10% frequency of all records. Such a rainfall range has been termed " decile 1 " by Gibbs and Maher (1967) and is indicative of severe drought (Fig. 3). The monthly rainfall was consistently low and only the August 1967 rainfall was above average. The spring rains failed badly and the following summer was dry and hot. The drought did not break until April 1968 (Fig. 4). The seasonal distribution of the rainfall and the blisteringly hot winds of February 1968 probably contributed to the severity of the drought symptoms.

Local variations in climate on the Towrong spur are likely to include greater incidence of mist and fog above 600–750 m and, in addition, the westerly slopes are likely to be warmer than the easterly due to the position and altitude of the

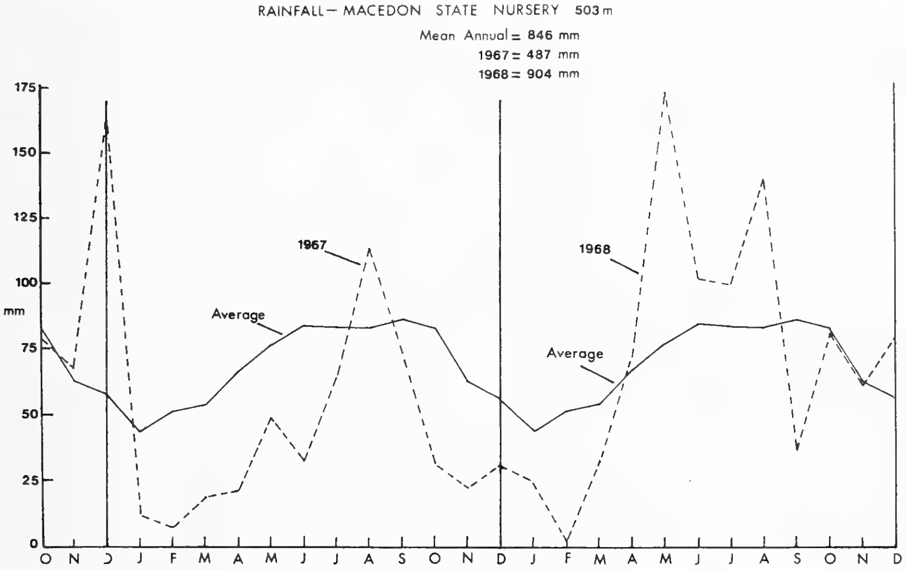

Fig. 4. Seasonal rainfall 1967–68 compared with 30-year mean.

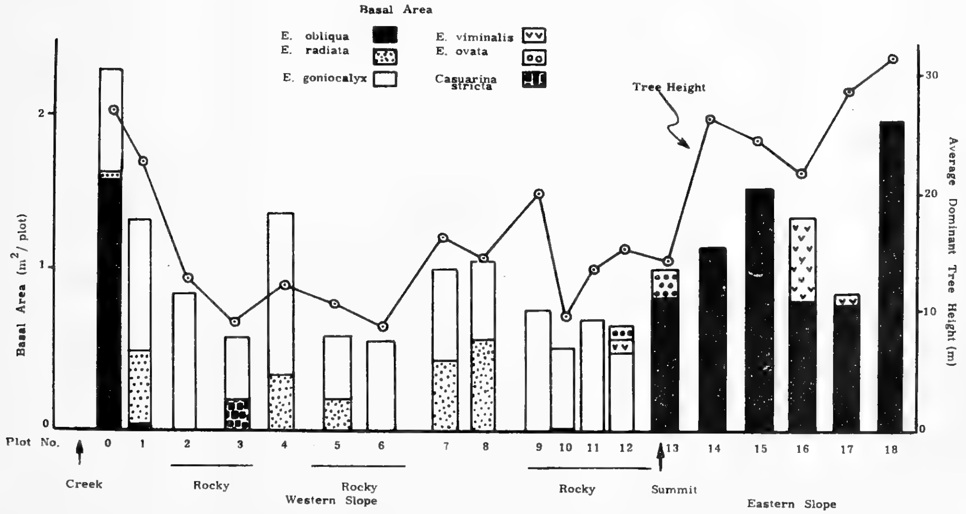

Fig. 5. Basal area and height of eucalypts.

sun in the hottest part of the day. Evaporation is also likely to be greater on the westerly slopes due to the north-west to south-west direction of the prevailing winds.

Method of Study

The vegetation was studied by means of offset plots at 30–90 m intervals along a 900 m transect line from Stony Creek up the west, south-west and west-north-west slopes to the summit, thence down the east-south-east slope. At each site tree heights and girths were measured over 0·022 ha plots (Fig. 5) and the drought recovery assessed on a 5-point scale (Fig. 6). Species were assessed in cover classes in sub-plots measuring 10 × 1 m. The results are summarised in Table 1 and Figs 7–9. At each site rocks were collected from several excavations of 25 cm cubes of soil. Rock volume was later determined by water displacement.

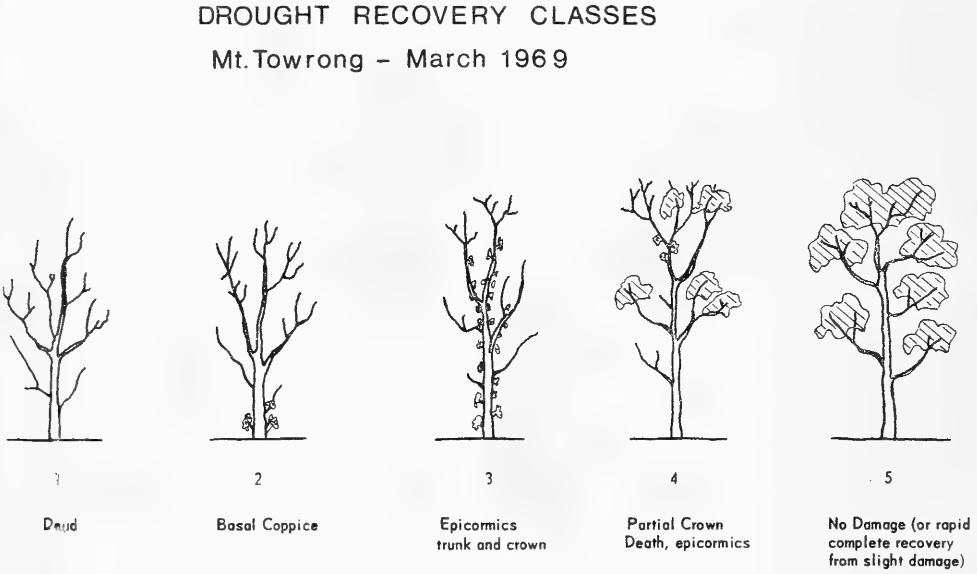

Fig. 6. Drought recovery categories of eucalypts.

Vegetation

The vegetation of the Mount Towrong area varies widely from a fern gully along Stony Creek to a low woodland of almost " mallee " habit on the rockiest sites. Moisture supply appears to be the most important factor controlling vegetation distribution ; hence such features as aspect and slope, the depth and volume of soil, depth to water table and altitude of cloud condensation are likely to be important. The terms used in the description are largely those defined in Leeper (1970). Except where indicated, the nomenclature of species follows that of Willis (1970, 1972).

OPEN FOREST

Wet Sclerophyll Forest Type[1]

This open forest occurs as a ribbon along Stony Creek and on the lower eastern slopes of the Towrong spur. Along the creek mature *Eucalyptus obliqua* and *E. viminalis* reach heights of 27–31 m with occasional *Acacia melanoxylon*

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[1] This is a well-entrenched term in Australian ecology ; hence it is proposed to keep it within the framework of formations defined by Specht in Leeper (1970).

TABLE 1

The distribution and cover of major species along the Mount Towrong transect

Aspect	SW–W	SW	Summit	E	Gully and Lower E
Moisture status	Dry		to		wet
Formation	Low grassy woodland	Grassy woodland	Open grassy forest	Open bracken forest	Wet sclerophyll open forest
Associations	*E. goniocalyx*; *Themeda*	*E. goniocalyx*; *Poa*	*E. obliqua*; *Lomandra*	*E. obliqua*; *Pteridium*	*E. obliqua*; *E. viminalis*; *Prostanthera*
No. plots	4	4	4	4	3
Mean tree height (m) ..	10	13	16	25	26
Mean tree basal area (m²)	0·08	0·14	0·11	0·17	0·26
Mean tree drought score	2·0	4·0	3·5	5·0	4·3
Species (Trees and shrubs) *Eucalyptus goniocalyx* ..	+115	2245	+5		1
Acrotriche serrulata ..	+	11	+++		++1
Acacia dealbata ..		2225	++		+
A. verticillata	+				+1
Casuarina stricta ..	1				
E. radiata		122	+		1
E. obliqua		+	45	+15	+23
E. ovata			1		
E. viminalis				+	+
Prostanthera lasianthos					12
Olearia argophylla ..					++1
Coprosma quadrifida ..					+1
(Monocot. herbs and ferns) *Cheilanthes tenuifolia* ..	+12				
Themeda australis ..	+124				
Stipa hemipogon ..	+13				
Microlaena stipoides ..		3		+	+++

TABLE 1.—*continued*

The distribution and cover of major species along the Mount Towrong transect

Aspect	SW-W	SW	Summit	E	Gully and Lower E
Moisture status	Dry		to		wet
Formation	Low grassy woodland	Grassy woodland	Open grassy forest	Open bracken forest	Wet sclerophyll open forest
Associations	*E. gonio-calyx*; *Themeda*	*E. gonio-calyx*; *Poa*	*E. obliqua*; *Lomandra*	*E. obliqua*; *Pteridium*	*E. obliqua*; *E. viminalis*; *Prostanthera*
Poa labillardieri . .	1244	3344	1233	45	234
Danthonia spp. . .	+++1	+++1	4	11	+++
Pteridium esculentum . .		1	+122	+222	+2
Lomandra longifolia . .		++	2223	1	
Echinopogon ovatus . .				+1	+1
Tetrarrhena juncea . .				2	+12
Polystichum proliferum . .				2	1
Adiantum aethiopicum . .					+1
(Dicot. herbs) *Dichondra repens* . .	+1				++
Anagallis arvensis . .		+1			
Senecio linearifolius . .		++1			++
Hydrocotyle hirta . .	+	+2		1	++1
Glycine clandestina . .	+1		+11		++
Oreomyrrhis eriopoda . .	+	+	+1		+
Poranthera microphylla		++3			+
Geranium '*pilosum*' . .		+1	+1	+11	+1
Plantago varia		+11			+1
Viola hederacea . .		+1	+++1	11	+++
Oxalis corniculata . .	++11	++11	++11	1	+1
Clematis aristata . .		++1		2	+11
Acaena anserinifolia . .		+111		12	+1
Stellaria pungens . .		+++2		223	++1
Galium sp.				12	+
Mentha laxiflora . .				1	
Asperula scoparia . .				+2	+1

Cover values assessed as : +(1%), 1(1–5%), 2(5–25%), 3(25–50%), 4(50–70%), 5(70–100%). Species recorded with covers of + *only* were not included.

trees of 15–20 m (Fig. 7). *E. radiata* and *E. goniocalyx* are also present but are chiefly found on the margins of this community. A lateral zonation also occurs in the subordinate vegetation. Within 30 m of the stream broad-leaved notophyll to microphyll shrubs (Webb, 1959) such as *Pomaderris aspera*, *Olearia argophylla*, *O. lirata*, *Hedycarya angustifolia* and *Prostanthera lasianthos* are common with ferns (*Polystichum proliferum*) and wiregrass (*Tetrarrhena juncea*) on the ground.

STONY CREEK

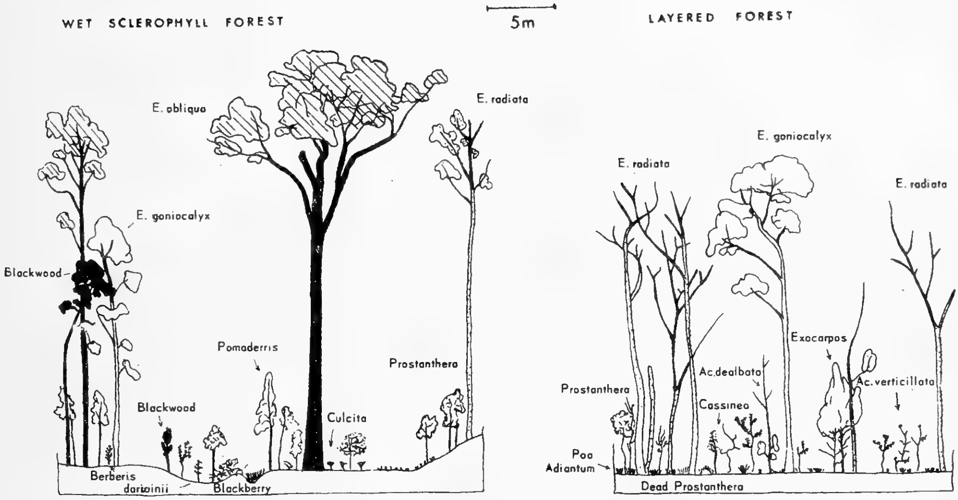

Fig. 7. Vegetation profiles of wet sclerophyll and layered forest.

Between 30 and 60 m from the stream only *Prostanthera lasianthos* and *Olearia lirata* still persist but the undergrowth is dominated by small-leaved shrubs such as *Acacia verticillata* and *Cassinia aculeata* with tussock grass (*Poa labillardieri* Steud.) and maidenhair fern (*Adiantum aethiopicum*) on the ground. The low scrambling shrub, *Bossiaea obcordatum*, is common in the "layered forest" ecotone region between forest and woodland. The nature of this community is likely to be altered in the future due to the great success with which foreign fleshy-fruited species, such as *Arbutus unedo*, *Cotoneaster pannosa* Franch, *Berberis darwinii* and *Rubus fruticosus agg.*, as well as the winged-seeded ubiquitous *Pinus radiata*, have invaded this site from nearby garden estates. On the cool eastern slopes the main forest of *E. obliqua* and *E. viminalis* is an even-aged stand 20–26 m high with mature emergent trees up to 33 m. The woody undergrowth is almost exclusively *Olearia argophylla* with ferns and wiregrass on the floor. The wing-fruited sycamore (*Acer pseudoplanatus*) is actively invading this forest.

Open Grassy-Bracken Forest

This somewhat shorter open-forest occurs on and near the summit of the spur and on the deeper soils of the mid-western aspect. On the upper slopes, where the rockiness of the soil is probably compensated for by the greater incidence of mist, *E. obliqua* dominates a forest of mixed ages up to 15–26 m high. Bracken (*Pteridium esculentum*) is common and is associated with *Poa labillardieri* tussocks and herbs such as *Stellaria flaccida* and *S. pungens*.

On the mid-west aspect the forest consists of mixed ages of *E. radiata* and *E. goniocalyx.* Scattered shrubs occur—*Acacia dealbata* being frequent and *Olearia lirata* quite rare—and the ground stratum consists of the grasses *Poa labillardieri* and *Microlaena stipoides.*

WOODLANDS

Grassy Woodland

These more open stands are 12–18 m high and occur in sites of lower moisture status than that of the forest. They are found in the zone surrounding the forests on the western aspect. On the lower slopes they are dominated by *E. goniocalyx* with some *E. radiata* with a grassy floor of *Poa labillardieri*, *Danthonia* and *Stipa* species. On the upper slopes *E. obliqua* is dominant with a rather unexpected occurrence of swamp gum, *E. ovata. E. pauciflora* is found in this community but is very rare. The floor of these stands is covered with tussocks of *Lomandra longifolia* together with *Dianella tasmanica*, *Poa labillardieri* and herbs such as *Stellaria pungens* and *Asperula scoparia* (Fig. 8).

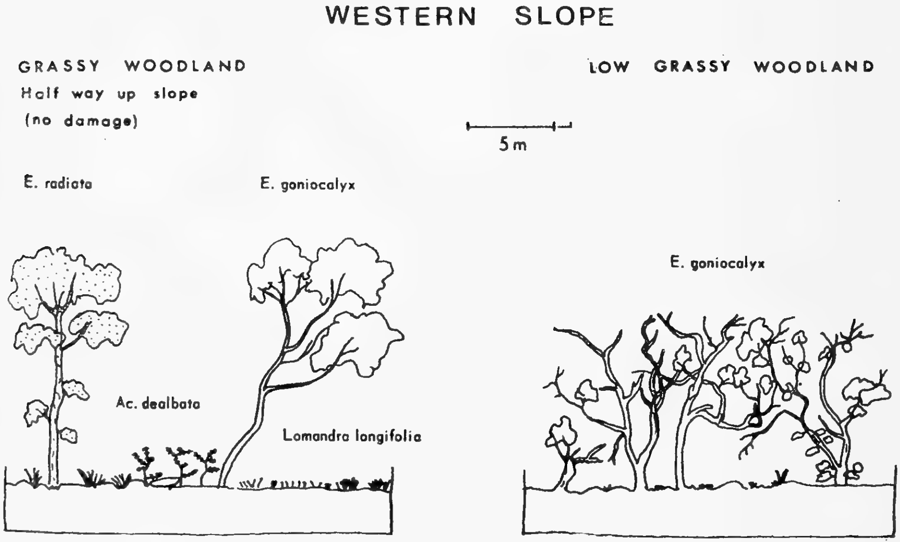

Fig. 8. Woodlands and low woodlands.

Low Grassy Woodland

These relatively open stands occur on the westerly aspects and range in height from 8–11 m. They occur on rocky shallow soils with rock volumes in the upper foot between 25% and 33%; hence drainage and run-off are excessive and the total water storage very low. *E. goniocalyx* is the dominant tree and frequently assumes a twisted mallee-like habit. On the upper slopes the trees are denser although the canopy is sparse. The floor of the stand consists of the grasses *Poa* and *Danthonia* spp. together with occasional low shrubs of *Acrotriche serrulata* and *Bossiaea prostrata.* At lower elevations, where rainfall is lower and amelioration of the climate by fog drip is less frequent, *Casuarina stricta* is often co-dominant (Fig. 9). The floor of these stands is dominated by the grasses *Themeda australis*, *Stipa hemipogon* and *Danthonia* spp. with frequent occurrences of the rock fern, *Cheilanthes tenuifolia*, and the prostrate shrub, *Astroloma humifusum.*

In sites with massive rock outcrops trees are sparse and stunted and the vegetation consists of xerophytic lichens, mosses, rock ferns, grasses and low shrubs in micro-communities which suggest stages of primary succession. The low woodlands follow the north-south trend of the rocky soil across the western aspect and to a limited extent onto the south-western aspect. Sheet erosion is occurring in most of these stands and has possibly been aggravated by the exposure of bare ground during the recent prolonged drought.

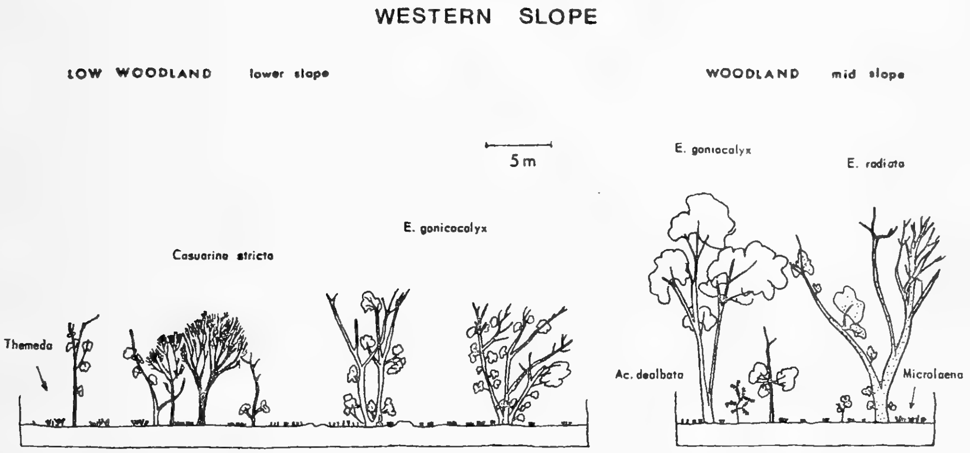

Fig. 9. Woodlands and low woodlands.

The Pattern of Drought Damage

The drought damage of 1967–68 on Mount Towrong was patchy and chiefly confined to the exposed westerly slopes and to the zones marginal to creeks and dry gullies (Fig. 10). No damage occurred on the cooler east and south-east slopes and only occasional damage occurred on the ridge top. Low woodlands were severely damaged on the western aspect below altitudes of about 730 m where rock volumes in the upper 30 cm of soil exceeded 20% but were much less damaged above this level due probably to the modifying effects of low cloud. Damage also occurred in tall woodlands on the mid-western slope and in a belt of tall forest parallel to, and slightly above, Stony Creek.

The forests of the southern, eastern and mid-western slopes were not damaged, due probably either to the greater amount of soil water storage and joint plane seepage at depth or to lower radiation loads. Undamaged forests also occurred on the rocky ridge summits where the low soil moisture could have been compensated by the greater incidence of mist and fog. Trees rooted in rocky soils up to 6 m above Stony Creek were undamaged due to the proximity of the water table to the root zone. Many trees and shrubs between 6 and 18 m above Stony Creek were severely damaged. At 18 m such forest gave way to undamaged woodland. It is likely that in this marginal forest zone the water table and its capillary fringe fell below the root zone of most of the species during the 1967–68 drought. The degree of drought damage of trees tended to increase with density of stems on any given site (Fig. 11). In an area north of the transect line, well spaced mature *E. radiata* trees were little damaged whereas young dense stands nearby were killed or severely damaged. The worst affected stands of *E. goniocalyx* on rocky sites were without exception very stunted and often multi-stemmed. Since fire scars are very rare, the " mallee " habit of these trees is likely to have resulted from dieback of the mainshoot caused by drought. It would appear that the high density of apparently old trees on many of the poor sites is due to the curtailment of height growth and the failure of potentially superior individuals effectively to suppress and eliminate those nearby which are weaker. The partitioning of available water supplies amongst a large number of individuals could result in severe stress, particularly if the leaf area is high and leaf cast is ineffective in sufficiently reducing water demand. The resilience of a species on these sites will depend not only on its inherent resistance to water stress and subsequent regeneration from lignotubers but also on the persistence of such regrowth in spite of such factors as animal browsing, insect attack and fungal infection. The coppice growth of *E. ovata* one year after the drought, for example, was selectively browsed very heavily, presumably by wallabies. Many trees in the gully coppiced after the drought but succumbed to the fungal parasite, *Armillaria mellea* (Vahl) Fr., in the following year.

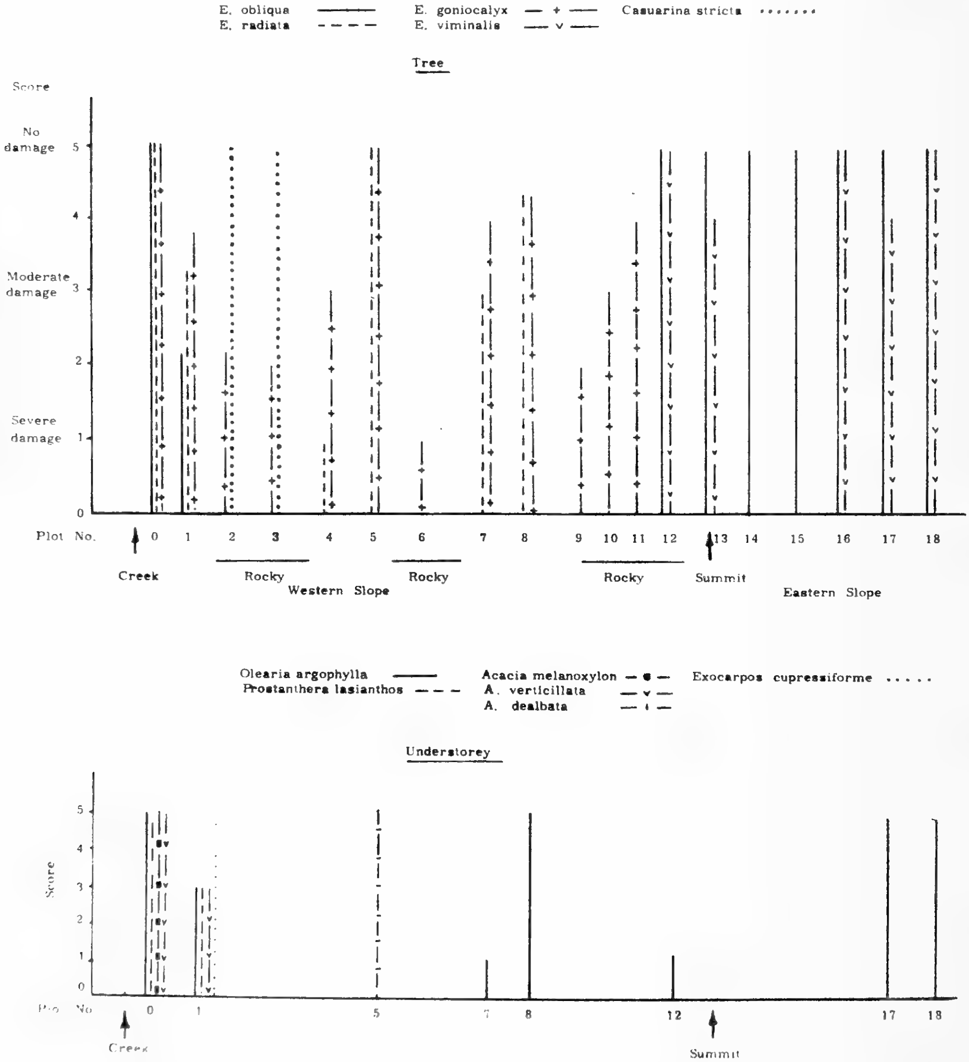

Fig. 10. Drought recovery distribution of trees and shrubs along transect using 0–5 scale (from no recovery to full recovery).

There was marked differential drought damage between species on the one site. Such differences have been recently noted by Kirkpatrick (1970) between

E. sideroxylon and *E. bicostata* at Airey's Inlet, Victoria. In general the order of damage was similar to that predicted from the distribution of the species along moisture gradients. *E. goniocalyx* is the most ecologically widespread species in the area and ranges from wet sclerophyll forests along Stony Creek to the hottest and driest sites on north-westerly aspects. In the marginal areas of the wet sclerophyll forests it was much less severely damaged than any of the other eucalypts. In the forest-woodland ecotone on the mid-western slopes *E. radiata* was clearly more severely damaged than was *E. goniocalyx*. In this site *E. radiata* has been able to establish 40–50 m into the woodland area but now could be placed at a competitive disadvantage with *E. goniocalyx* as a result of this exceptional drought. The permanence of this effect will depend on the frequency of such catastrophes in the life time of the trees. Differential resistance also occurred between understory species. In the Stony Creek forest a lateral gradation of drought damage occurred up the western slope. The most mesic species (e.g. *Pomaderris aspera*) were damaged 1·5–3 m above the creek in sites where little or no damage of *Prostanthera lasianthos* and *Olearia argophylla* occurred. Further above the creek at 12–15 m these latter species and *Olearia lirata* were extensively damaged whilst *Acacia verticillata*, *Exocarpos cupressiformis* and *Cassinia aculeata* were undamaged. On the margin of this forest these species were damaged whilst the low scrambling shrub, *Bossiaea obcordatum*, was undamaged. The latter species however was killed where it had grown out onto the rocky soils of the woodlands on the slope above. A similar understory differentiation occurred in the mid-western slope where *Olearia lirata* was badly damaged in comparison with *Acacia dealbata*. The drought resistance of *Pinus radiata* in a small plantation in the low woodlands on the south-west slope was far superior to that of the surrounding *E. goniocalyx*. The general vigour of the swards of *Themeda australis*, *Stipa hemipogon* and *Cheilanthes tenuifolia* in 1969 suggests that these species were little affected by the drought.

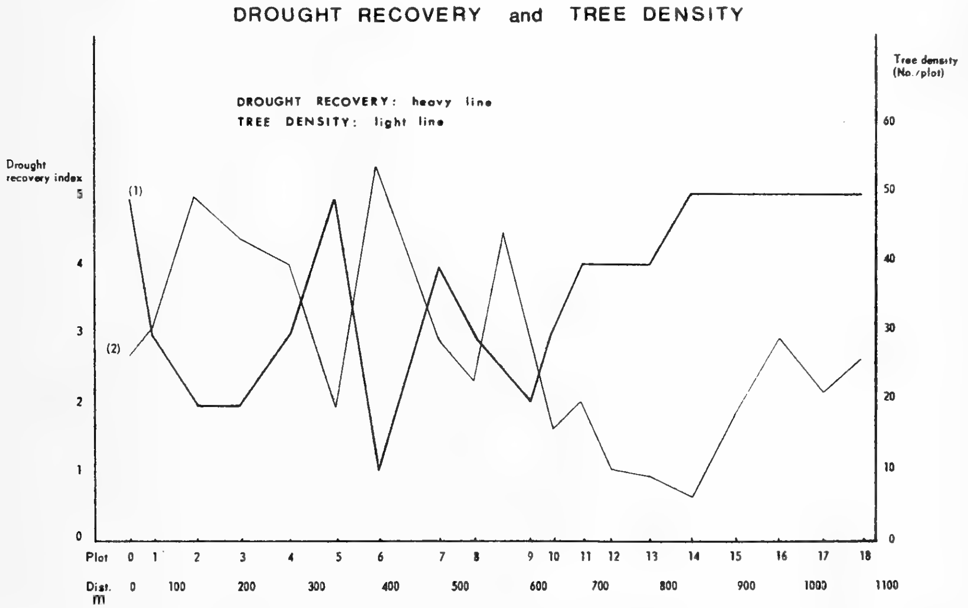

Fig. 11. Relationship between tree recovery and tree density. Line (1) : Drought recovery ; line (2) : Tree density.

Other patches of forest on the Mount Macedon massif up to the summit at 997 m were also damaged in the drought. On northern catchments *E. obliqua* was observed to have been more damaged than *E. viminalis* in mixed stands (Pl. I, top). In the Mount Towrong area *E. viminalis* was little damaged and was not considered of sufficient importance to be included in the experimental work.

EXPERIMENTAL WORK

In order to gain further insight into the relative behaviour of the dominant species on Mount Towrong and their particular distribution in relation to probable moisture gradients, limited experiments on the water relations of seedlings were undertaken. It would have been preferable to have measured the water potentials of tree species and their seedlings during the whole period of the drought and to have referred these to precise measurements of soil moisture and microclimate. The detailed work of Pook *et al.* (1966) shows the efficiency of such an approach. The resistance of the species to drought, whether by endurance or avoidance, would have enabled definitive statements to be made concerning their physiological and ecological adaptations. However, since no such work has been done on these species, the resistance of the plant to wilting treatment, the control of cuticular transpiration, the desiccation of leaf tissues and the resistance to high temperatures were investigated. Since establishment of seedlings is often difficult in dry environments, the development of the initial root system was also investigated. The seed sources were confined to areas within 70 km of Melbourne and ranged from the Brisbane Ranges to Kinglake.

Preliminary Droughting Experiments (1969-70)

METHOD

It was decided to base these experiments on a recognisable state of the plant in the cycle of desiccation—namely, the permanent wilting point. The length of wilting period, the age and condition of the plant and the environmental conditions throughout will all affect the severity of the symptoms developed. Because of the uncertainty of weather, plants which had been hardened in the open for several weeks were transferred to a well-lit glasshouse for desiccation treatment. The plants all had young growing tips and wilting was easily observed. In the first experiment a dwarf cultivar of sunflower, *Helianthus annuus*, were grown with the test plants to facilitate the recognition of the droughted condition. In general the test plants wilted at about the same time as this standard mesophyte and the permanent wilting condition generally occurred one day after the first signs of tip wilting. The wilting of *Casuarina* was not so obvious but could be recognised by curving of the branchlets and a deepening of the longitudinal furrows. In the first experiment eight replicates of 4 month old seedlings (one per pot) 18–30 cm high were droughted in 15 cm diameter plots of sandy loam under mild sunny conditions in autumn 1969. Different batches were wilted for one and four days after which they were watered and assessed for leaf and axillary bud damage some weeks later.

In the second experiment large lignotuberous plants 18 months old and 0·5–1 m high were grown in two-gallon buckets of sandy loam and allowed to wilt for four days under hot dry glasshouse conditions in late summer 1970. The buckets were heavily insulated from evaporation by Alfoil and daily weighing of pots enabled some estimates of transpiration to be made during the process of desiccation.

RESULTS

In the first experiment, the ranking of species according to their seedling's resistance to glasshouse desiccation was exactly the same as the relative drought resistance observed for trees on Mount Towrong following the 1967–68 drought, viz. *C. stricta*, *E. goniocalyx*, *E. radiata* and *E. obliqua* (Table 2). In all species the younger leaves were the more resistant and in *E. goniocalyx* there was a tendency for stressed leaves readily to absciss and for the stems to show little die-back. In the second experiment the order of drought resistance between species remained much the same. However, one plant of *E. radiata* showed exceptional resistance to drought and failed to wilt and finally turned pale green and became brittle. It was omitted from the assessments since it could not be compared readily with other individuals. The transpiration of the different species varied greatly. When water supply was abundant on the first day of the experiment, *E. obliqua* with its large intermediate leaves transpired much faster per unit area than any of the other species. *Casuarina* transpired more slowly and was barely affected by the wilting treatment. The superior drought resistance of the branches of *E. goniocalyx* was again apparent when compared with the other eucalypts.

TABLE 2

Desiccation damage in preliminary glasshouse experiments 1969–70

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
Expt. 1 May 1961 : 14–19°C, 54–93% R.H.				
Av. height (cm)	26	25	32	18
% damage (leaf and stem) ..				
1 days wilting	7	0	0	0
4 days wilting	63	42	23	14
No. plants/10 killed	1	2	0	0
No. plants/10 undamaged ..	0	1	3	4
Expt. 2 Feb. 1970 : 25–36°C, 40–85% R.H.				
Av. height (cm)	132	99	148	61
Av. leaf area (dm^2)	19·7	18·9	18·1	3·2*
Transpiration at field capacity				
g/day	1138	792	754	462
g/dm^2/day	63·3	32·0	42·0	36·3*
% damage after 4 days wilting				
% leaf killed	85·3	90·2	68·8	no leaves
% branch killed	51·3	52·1	9·4	0·9
Lignotuber development (cm)				
Max. width at lignotuber ..	2·1	3·1	3·7	1·6†
Stem width above lignotuber	1·4	1·1	1·5	1·1

* ½ cylinder area.

† carroty swelling

Droughting Experiments: Assessment of Relative Turgor, Water Potential and Transpiration Rates. December 1971 to January 1972

METHODS

In this major experiment a wilting period of four days was again employed and disc samples were removed from leaves at intervals to assess the changes in relative turgor (=relative water content) (Barrs and Weatherley, 1962). *Casuarina* seedlings were pre-pruned to various levels so that internode samples for relative turgor encompassed a range of branchlet sizes. Eight replicates of seedlings 15–20 cm high were grown in plastic pots of 15 cm diameter in sandy loam. The pots were carefully insulated from direct sunlight by Alfoil and the soil surface covered with 2 cm of white plastic pellets to minimise direct evaporation. Controls proved these measures to be effective. The pots were weighed before sunrise and a control set watered up to their initial field capacity each day. A further set of pots were sown with dwarf sunflowers to check on the uniformity of wilting response. Transpiration of seedlings was expressed per unit leaf area although for *Casuarina* half cylinder area was used. Transpiration of stems was studied by pruning a number of plants of each species to about four leafless branches of about the same diameter range. The cut ends were sealed and the pots insulated and weighed on several consecutive days. The weight loss was expressed per unit surface area.

The relationship between relative turgor and water potential was obtained by allowing cut shoots to dry out for varying lengths of time in the laboratory. The foliage was sampled for relative turgor by floating discs on water for four hours and obtaining fresh and dry weights. Short pieces of shoot were placed in a Scholander pressure bomb and the air pressure necessary to force water from the cut stem recorded. It was thus hoped to infer the kind of internal conditions developed by the seedlings during the wilting treatment.

TABLE 3

Damage and stress of species in major experiment December 1971–January 1972

Damage	*E. obliqua*	*E. radiata*	*E. goniocalyx*	*C. stricta*
Species alone (8 replicates)				
% leaf killed	92·4	32·2	53·7	no leaves
% branch killed	87·4	12·4	2·5	0·7
Wilting score (1–5) ..	5·0	3·7	4·7	4·5
% plants killed	66	12	0	0
In presence of sunflower				
% leaf killed	100·0	100·0	52·7	no leaves
% branch killed	100·0	100·0	1·0	3·0
% plants killed	100·0	100·0	0	0
% sunflowers killed ..	0	0	30·0	0
Relative turgor (%)				
At field capacity	90	89	88	93
At permanent wilting ..	75	70	70	80
After 4 days wilting ..	46	43	38	63
Water potential (–bars)				
At field capacity	10·8	13·4	16·7	10·9
At permanent wilting ..	19·9	24·1	24·4	18·4
After 4 days wilting ..	27·7	36·4	37·5	27·5
Lowest water potential corresponding to 50% damage	24·1	34·1	38·2	not achieved
Water content foliage (% O.D.W.)				
At field capacity	250	260	170	413
At permanent wilting ..	215	228	135	285
After 4 days wilting ..	136	100	84	171
% *water content drop/unit water potential from field capacity to wilting point*	3·7	3·3	2·2	1·4
Soil moisture (% O.D.W.)				
At field capacity	30·0	30·0	30·0	30·0
After 4 days wilting ..	6·8	5·4	5·0	5·1

RESULTS

The ranking of the seedlings according to severity of damage was again much the same as that in the preliminary experiments (Table 2). *C. stricta* was extremely resistant and *E. obliqua* extremely susceptible to the stress imposed by wilting for four days in average diurnal temperature ranging from 16–29°C. Many *E. obliqua* plants were killed whereas only some of the finer branchlets of *C. stricta* died. The damage to *E. radiata* and *E. goniocalyx* was intermediate in severity. In this experiment *E. radiata* foliage was less damaged and the stems more damaged than those of *E. goniocalyx*. The population of *E. radiata* proved very variable—some plants died rapidly whilst others wilted only slightly and remained grey-green and resistant for a relatively long time. The onset of wilting of all the species was not greatly dissimilar from that of the sunflowers. The rapid loss of water caused by the additional leaf area of the sunflowers caused a dramatic increase in the death rate in *E. radiata* seedlings (Table 3 ; Fig. 12). The extremely mesophytic sunflowers largely recovered from their severely wilted condition.

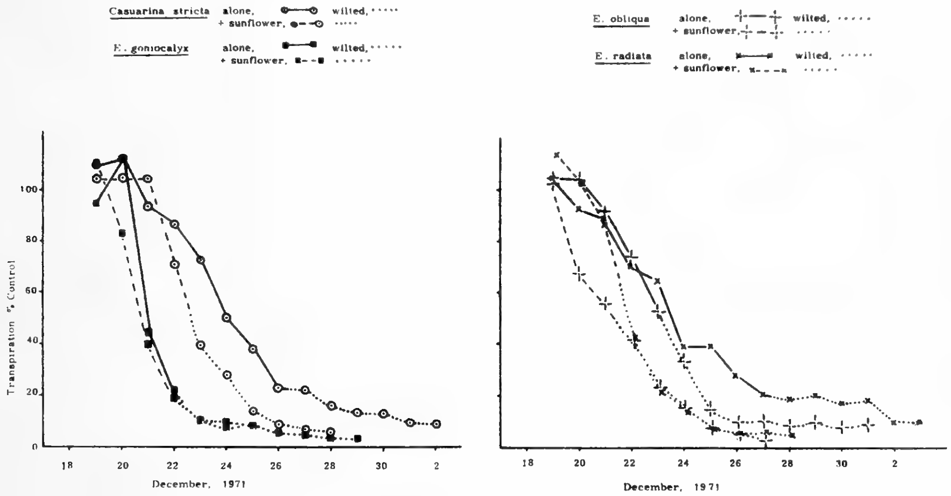

Fig. 12 Transpiration during wilting experiment.

The larger plants of *E. goniocalyx* depleted their moisture supply at the fastest rate of any species ; however, on the basis of water loss per unit area at field capacity, *E. goniocalyx* transpired less than the other eucalypts (Table 4). No plants of this species were killed. *E. obliqua* tended to transpire faster per unit area than any of the other species (Fig. 13). The average time taken for plants to reach wilting point was shorter in *E. goniocalyx* and *E. obliqua* than in *E. radiata* and *C. stricta*.

TABLE 4

Transpiration rates during major experiment 1971–72

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
Mean height (cm)	37	28	61	54
Leaf area (dm²)	2·48	2·77	7·31	2·31(4·62)*
Transpiration (g/dm²/day)				
Controls 11 day average ..	20·5	19·1	17·0	30·4 (15·2)*
Desiccating plants				
initial rate (wet)	29·0	23·6	19·5	23·7 (11·8)*
after 10 days (dry) ..	2·1	4·8	0·7	4·2 (2·1)*
Branch transpiration (2–4 mm diam.)				
g/cm²	0·50	0·64	0·32	0·97
Transpiration control plants				
Alone (g/day)	74·4	66·5	143·0	69·6
+Sunflowers (g/day) ..	134·0	125·5	153·5	91·8
Av. no. days taken to reach wilting point (range in brackets)				
Tree seedlings	5·0	8·4	4·2	7·1
	(3–8)	(4–16)	(3–6)	(4–9)
Tree seedlings+Sunflowers ..	3·6	3·2	3·4	4·6
	(3–5)	(3–4)	(3–5)	(3–5)

* *Casuarina* : calculated on ½ cylinder and (full cylinder) basis.

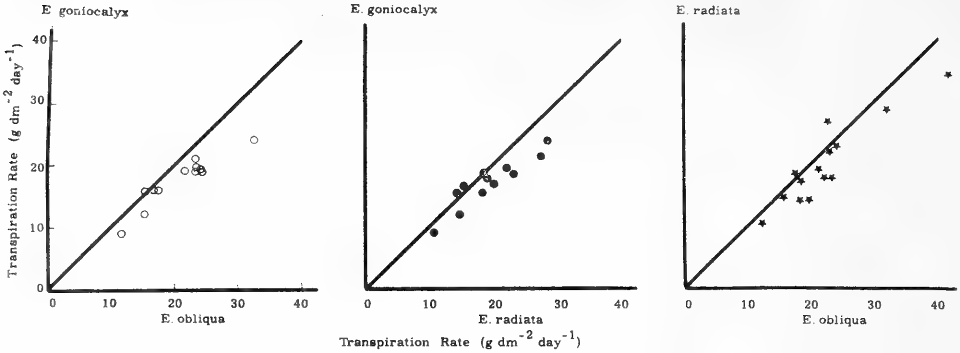

Fig. 13. Comparative transpiration of species at or near full turgor. Diagonal line indicates equal rates.

The relationship between relative turgor and water potential (Fig. 14), although variable, is similar for *E. goniocalyx*, *E. radiata* and *C. stricta*. *E. obliqua* does not reach the correspondingly low water potentials of the other species. During desiccation certain similarities and differences were apparent in water relations in these species. *E. obliqua*, which was so readily damaged, showed similar trends to *C. stricta*, which was hardly affected by the treatment. Both *E. obliqua* and *C. stricta* develop a similar range of relatively low water potentials on wilting, although *C. stricta* has a much higher moisture content throughout (Table 3). Likewise *E. radiata* and *E. goniocalyx* develop a similar

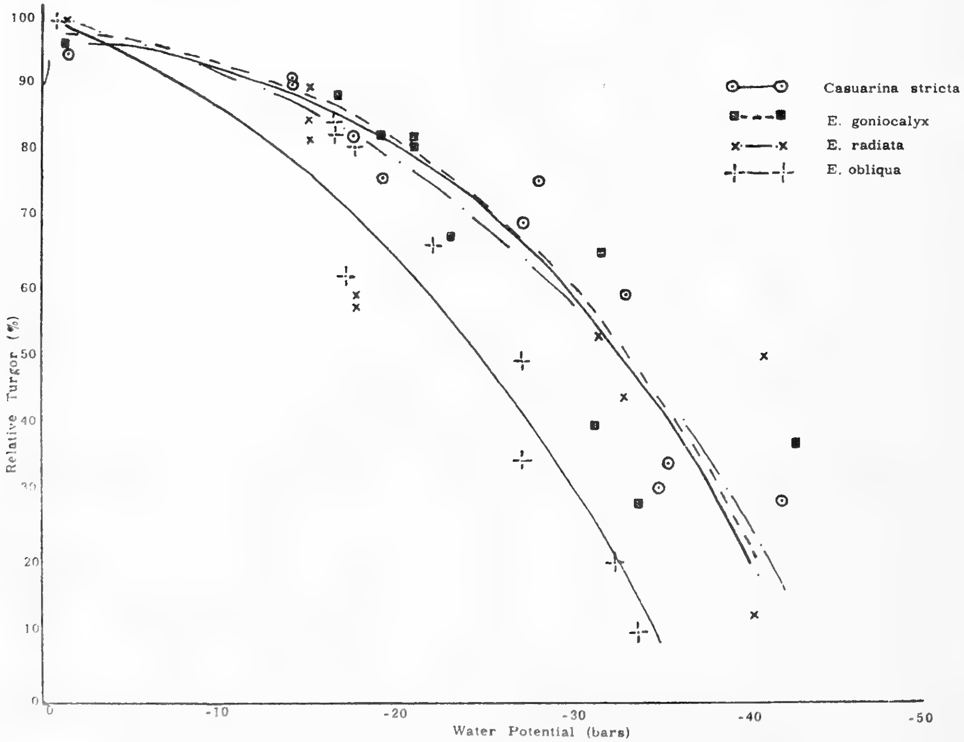

Fig. 14. Relationship between relative turgor and water potential.

range of relatively low water potentials during desiccation. The moisture content of *E. goniocalyx* is relatively low throughout and the relative transpiration rates per unit area for foliage and stems is markedly less than *E. radiata*.

Detached-leaf Dehydration

METHOD

In these experiments tree foliage was obtained from Mount Towrong and juvenile foliage from glasshouse seedlings hardened outside for more than one month (Fig. 15). The aim of the experiment was to investigate any differential cuticular control of water loss when stomata had closed. Twenty replicates of leaves were placed at random on 1 cm mesh wire netting in the laboratory in January 1972 for up to 20 hours. The temperature was 28°C and relative humidity 72%. Batches of leaves were weighed at intervals, their relative turgor determined and any damage due to desiccation assessed. Water potentials were derived from the relationship shown in Fig. 14.

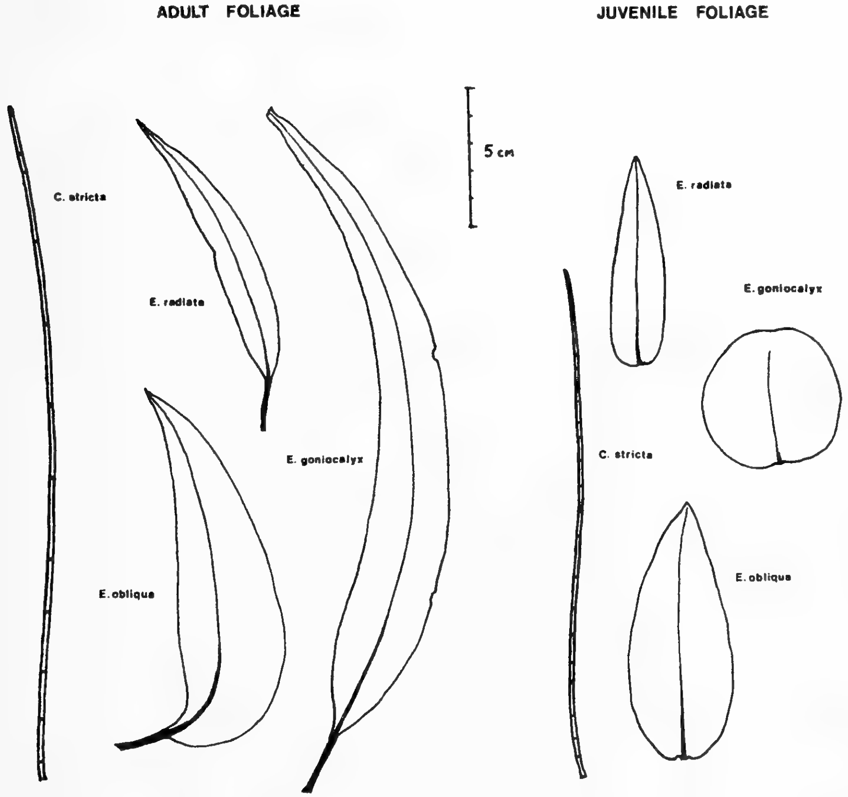

Fig. 15. Juvenile and adult foliage of the test species.

RESULTS

The results of relative moisture loss from juvenile leaves showed a general similarity to the relative rates of transpiration of glasshouse seedlings. Both adult and juvenile leaves of *E. obliqua* lost water rapidly during their stomatal transpiration phase and developed low water potentials. Severe damage occurred after only five hours. Juvenile and adult *E. goniocalyx* and juvenile *E. radiata* leaves controlled water loss efficiently by early stomatal closure and significant damage did not occur until 20 hours of drying. *C. stricta* was extremely efficient at preventing water loss and it would appear that stomata shut early in the drying treatment. It was quite undamaged after 20 hours drying. It also possessed an initially high water content and owing to the slight water loss did not develop low water potentials.

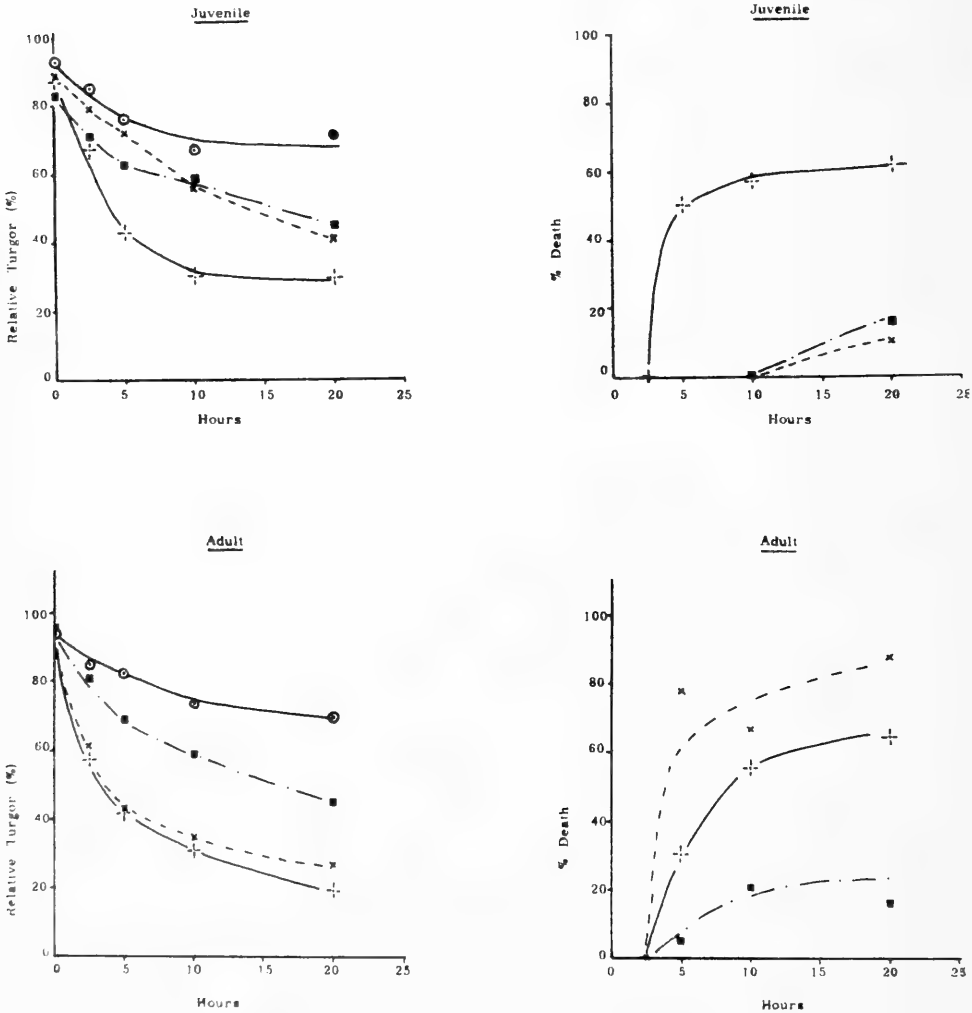

Fig. 16. Relative turgor and death of drying detached leaves.
○=*C. stricta* ; +=*E. obliqua* ; ×=*E. radiata* ; ■=*E. goniocalyx*.

A most marked difference in behaviour occurred between the adult and juvenile foliage of *E. radiata* (Fig. 16). The adult foliage lost water rapidly and was severely damaged and was thus similar to both types of *E. obliqua* foliage. The juvenile foliage on the other hand behaved similarly to *E. goniocalyx*. The behaviour of adult and juvenile leaves of the other species did not differ greatly. The cuticle thickness of the juvenile foliage showed only slight differences—*E. goniocalyx* being the thinnest (5–6 μm) and *E. radiata* and *C. stricta* the thickest (7–9 μm). However, the relative order of cuticle thickness of the adult foliage was reversed—*E. goniocalyx* being the thickest (9–18 μm) and *E. radiata* the thinnest (6–9 μm). The cuticle of the longitudinal ridges of *C. stricta* was thicker (9–12 μm) than that of the grooves (3–5 μm). The mass of thickened hairs, which arise amongst the stomata in the grooves and extend up to 75 μm beyond the cladode periphery, are likely to increase the depth of the boundary layer and thus minimise transpiration rates (Slatyer, 1964). The " needle " form of the cladode could also increase the rate of heat dissipation and lead to a better conservation of water by this species (Slatyer, 1967). The relative sclerophylly, as expressed by area per unit dry weight of foliage, differs between the four species studied. It also increases from juvenile to adult foliage and the amount of increase is roughly in the order of the drought resistance of the species.

TABLE 5

Foliage area/dry weight ratios (cm^2/g)
(The half cylinder area calculated for Casuarina*)*

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
Juvenile ..	92·5	110·2	100·3	67·7
Adult ..	64·4	70·9	53·7	37·7
Juvenile/adult	1·46	1·56	1·87	1·80

Tissue Resistance of Juvenile Leaves to Dehydration

METHOD

In order to assess the relative resistance of the foliar tissues to different degrees of desiccation, discs were suspended on a small mesh cradle above 20 ml of H_2SO_4 so as to produce relative humidities of 99%, 98%, 97%, 96% and 95%. A somewhat similar method was used by Weatherley and Slatyer (1957) to determine the relationship of diffusion pressure deficit and relative turgor. The phials used were as small as practicable. Ten 7 mm discs were cut by cork borer from the eucalypt leaves and 15 internode segments were cut from *Casuarina* using a sharp razor. The samples were weighed daily until equilibrium had been obtained in 4–5 days. The experiment was carried out at 25°C under a light intensity of 1000 lx. The relative turgor was assessed and the percentage of area damaged was noted for each species.

RESULTS

The results suggested that the order of resistance to desiccation was similar to that obtained from other experiments, although there was a tendency for the species to pair into two groups—the more " mesophytic " *E. obliqua* and *E. radiata* and the more " xerophytic " *E. goniocalyx* and *C. stricta*. It is apparent that the former two species were more damaged by slight reductions in relative humidity and that the damage increased rapidly with decrease in water potential. The latter two species develop low water potentials without appreciable damage up to a critical level beyond which damage increases very rapidly indeed (Fig. 17). A water potential of −30 bars in leaf tissues causes 100% death of *E. obliqua*, 40% death of *E. radiata* and 1–5% of *E. goniocalyx* and *C. stricta*. The water potential necessary to kill 50% of the area is −28 bars for *E. obliqua*, −34 bars for *E. radiata*, −37 bars for *E. goniocalyx* and −40 bars for *C. stricta*. These values are fairly close to those obtained during the wilting experiments (Table 2) although for *Casuarina* such water potentials were never reached under the conditions of glasshouse wilting.

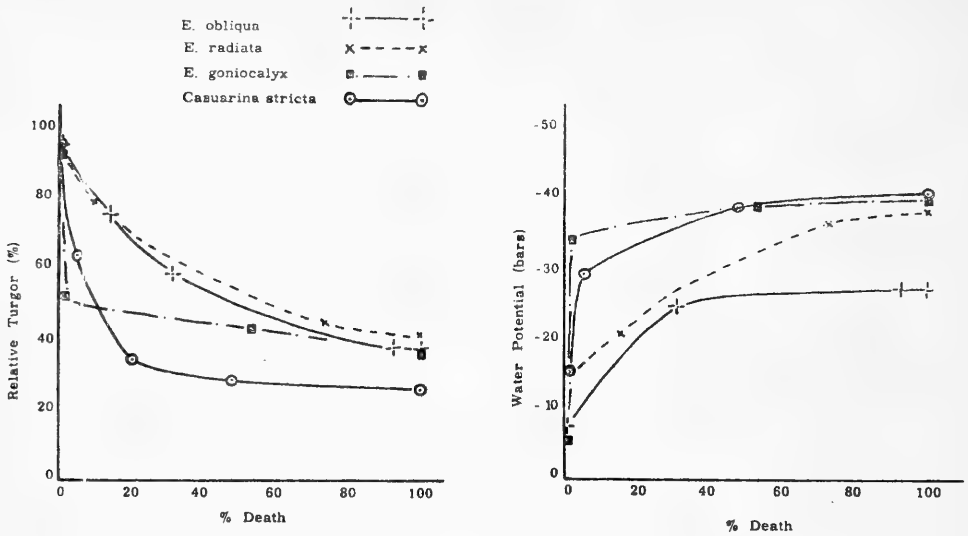

Fig. 17. Death of tissue in equilibrium with various relative humidities. Relative humidities were produced by equilibrium with aqueous solutions of H_2SO_4.

Leaf Temperatures and Heat Resistance

METHODS

Henckel (1964) showed that overheating of leaves during desiccation in bright sunlight could be a factor contributing to drought damage. The relative temperatures of turgid and wilted leaves of each species were measured in the glasshouse during the major experiment (1971–72). A thermocouple needle was held firmly against the leaf surface away from the direct sunlight. Only leaves facing the sun at an angle of less than 10° and greater than 75° to the horizontal were investigated.

The relative resistance of leaves to wet heat was briefly investigated by plunging them into controlled well-stirred water baths at different temperatures for two minutes. Longer times were avoided in order to minimise the possibility of water penetration into the leaves. In one experiment, wilted leaves were sheathed in thin plastic sheeting prior to immersion. The damage sustained was qualitatively assessed after 24–48 hours (Table 6).

RESULTS

As expected, the temperatures of leaves in still, warm, sunny conditions were markedly affected by both their moisture status and the orientation of their laminas to the direct sunlight. Turgid, transpiring leaves developed temperatures 3–6°C higher than ambient under these conditions. However wilting leaves developed temperatures 6–14°C greater than ambient. Horizontal leaves were as much as 6°C warmer than vertical or near vertical leaves. Thus *E. goniocalyx* developed high leaf temperatures because most of the sessile orbicular juvenile leaf remains horizontal on wilting. Most of the wilted foliage of *E. obliqua* and *E. radiata* hangs vertically and therefore avoids much of the excessive heat of midday. If *E. goniocalyx* juvenile leaves had not been glaucous it is likely that their temperatures would have been much higher.

The effect of hot water immersion of the foliage suggests that *E. obliqua* juvenile leaves were more sensitive than the other eucalypts and that *Casuarina* was the most resistant of the four species studied. In general, the tree adult foliage was more sensitive than the juvenile, particularly that of *E. radiata* and

TABLE 6

(a) Leaf temperatures °C, 24.12.71. Glasshouse experiment

Leaf orientation	Plant watered		Plant wilted	
	Horizontal	Vertical	Horizontal	Vertical
E. obliqua	33·3	30·2	38·4	32·8
E. radiata	30·2	30·2	36·4	35·0
E. goniocalyx	32·2	29·2	38·5	32·4
C. stricta				
diam. 1 mm	28·3		30·0	
2 mm	30·2		34·0	

Ambient temperature 26·5°C, ventilating breeze 0·2 m/sec.

(b) The relative heat tolerance of leaves. Preliminary experiment

Water temperature (°C)	% Leaf damage to seedling (a) and tree (b)							
	E. obliqua		*E. radiata*		*E. goniocalyx*		*C. stricta*	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
50	0	0	0	0	0	0	0	0
55	45	16	36	12	38	30	0	4
60	92	75	44	80	60	100	30±	35
65	100	100	100	100	100	100	80	100
70	100	100	100	100	100	100	100	100
Leaf thickness and cladode diam. (mm)	0·27	0·27	0·21	0·20	0·28	0·35	1·12	1·26

E. goniocalyx. Heating wilted leaves in closely appressed thin plastic sheaths considerably increased the damage sustained; however, the relative order of species' susceptibility was not greatly altered.

The Development of Seedling Root Systems

METHOD

It is clear that the depth and extent of the root systems of the various species at different stages of their development need to be known before any work on the mechanisms of drought avoidance can be assessed (Johnson *et al.*, 1968).

TABLE 7

Comparative root and shoot growth. Glasshouse trials 1969–72

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
1. *Two weeks old*				
Autumn 1969				
Root depth (cm)	2·8	1·8	5·3	6·6
2. *Four weeks old*				
Spring 1971				
Root depth (cm)	21·5	18·3	29·4	32·1
Shoot height (cm)	1·7	1·7	3·2	10·5
No. leaves	2·0	2·0	3·6	3·3*
Root/shoot	12·6	10·8	9·2	3·1
3. *Twelve weeks old*				
Summer 1972				
Root D. wt. (g)	0·089	0·069	0·140	0·189
Shoot D. wt. (g)	0·140	0·070	0·102	0·201
Root/shoot	0·64	0·99	1·37	0·94

* branchlets.

Such laborious field work was beyond the scope of the present study. However, the early development of the root and shoot may permit valuable inferences to be made about the likely success of seedling establishment in the environment of the seed source (Toumey and Korstian, 1947 ; Zimmer and Grose, 1958). Seeds were sown in large pots or plastic pipes (10 × 100 cm) containing either sandy loam or krasnozem soil. Three experiments were set up at different times from winter to summer from 1969 to 1972.

RESULTS

The results set out in Table 7 clearly show consistent relative differences in behaviour of the species. *C. stricta* produced the longest tap root and heaviest root system in the first few weeks of growth, probably due to the fact that this species has by far the largest seed weight. Of the eucalypts, *E. goniocalyx* consistently produced the largest tap root and the heaviest total root weight. Both *E. obliqua* and *E. radiata* were relatively slow to produce a sizeable tap root and those of *E. obliqua* were slightly longer than those of *E. radiata*, a feature which may have reflected the slightly heavier seed.

DISCUSSION

The study of the distribution of damage amongst the various species on Mount Towrong has shown that the vegetation on both the hot dry slopes with shallow soils and the gully margins with deeper soil was the worst affected. The pattern is therefore similar to that described for New South Wales and the Australian Capital Territory in 1965 by Pook *et al.* (1966). From an examination of the relative damage of trees and shrubs in the various ecotones between different vegetation types, the species could be ranked in order of their relative drought resistance.

The severe damage along creeks could be attributed to the development of a large demand for water under a normally reliable regime. It is probable that the water table was lowered beyond the reach of roots in this zone and hence dramatic damage occurred in these communities. The severe damage to the low vegetation on the worst hot and rocky sites could not be attributed to a lower resistance on the part of the dominant *E. goniocalyx* but rather to its being the only species capable of enduring such recurrent stress. *C. stricta*, which characteristically occupies such sites, only occurs on the lower slopes and was virtually undamaged. Its restricted distribution on Mount Towrong could be due to the proximity of its upper altitudinal limit in this area. The ranking of the species according to their relative drought damage in the field is compatible with general ecological observations on their broader relationships to moisture gradients in southern Victoria.

The glasshouse and laboratory experiments, although artificial and dealing mainly with seedlings, point to several possible mechanisms by which these dominant species have become adapted to their several well-circumscribed sites. When seedlings of these dominant species are allowed to wilt for various times the amount of damage they sustain is directly proportional to the order of their ranking of field drought resistance.

From every point of view *C. stricta* seems to be the best adapted species to drought stresses. This highly xerophytic plant is able to avoid desiccation for long periods by efficient stomatal and cuticular control of water loss. With good water supply its transpiration per unit area is high on a half cylinder basis but low on a total surface area basis. Water loss is curtailed at relatively high relative turgors and high water potentials. The tissues have a high water content, possibly due to the core of central parenchymatous pith. However, the contribution of cell wall water to the water balance of the leaf (Carr and Gaff, 1962) may prove to be important in this xeromorphic species. When its " cladode " tissues are dehydrated they endure more stress than the more mesophytic eucalypts. In the wilting experiments of seedlings, its conservation of tissue water was so efficient that the limit of endurance was never reached. The development of a rapidly descending tap root would be an undoubted advantage in dry sites where excessive evaporation from the surface soil takes place.

Conversely, *E. obliqua* was the most mesophytic species studied. Its transpiration rates per unit leaf area were higher than the other eucalypts and only moderate water potentials were developed with the onset of dehydration. The water content of the foliage was reduced to a low level and tissues were incapable of withstanding much stress. The great majority of plants died following sustained wilting. Detached leaves, both juvenile and adult, rapidly lose water and appear to have little stomatal and cuticular control of water loss. If this behaviour occurs in the field it would allow rapid loss of water supplies and continued dehydration of tissues early in the drought period, thus minimising its chances of survival. Moreover, the leaves are large, relatively poor dispersers of heat and appear fairly susceptible to high temperatures. The relatively slow descent of the seedling tap root would be a disadvantage to establishment on dry sites.

The other two species, *E. goniocalyx* and *E. radiata*, appear to have different strategies for survival under dry conditions. *E. goniocalyx* is the most conspicuously dimorphic species studied. The waxy glaucous seedling has the ability to control transpiration during the onset of desiccation and cuticular transpiration is low. The general water content of the foliage is relatively low and the plant develops low water potential under prolonged stress. The tissues appear to be able to withstand a relatively high stress and then, like those of *C. stricta*, suddenly succumb. It is apparently not as efficient as *C. stricta* in avoiding drought but it has the capacity readily to shed older stressed leaves, thereby reducing its transpirational load. In spite of their high reflectivity, wilted leaves may heat up considerably under high radiation due to the maintenance of a horizontal orientation. The leaves, however, appear to have a relatively high heat resistance. The long leathery adult leaves are also efficient controllers of cuticular water loss but appear to be more sensitive to high temperatures. *E. radiata* also has markedly dimorphic foliage and was the most physiologically variable species in this study. Some seedlings were mesophytic and, like those of *E. obliqua*, transpired rapidly and died. Others were like those of *C. stricta* and controlled transpiration efficiently, hardened and occasionally resisted desiccation for a long time. This ability by some individuals to regulate water use was completely negated by the association of a wastefully transpiring mesophyte such as the dwarf sunflower. Under these conditions all the seedlings of *E. radiata* died. The ecological implication from such an observation could be that the behaviour of a species to drought in pure stands could be very different from its behaviour in a mixed community, especially if important associated species had different regimes of water use. The juvenile leaves were much more efficient in controlling cuticular transpiration than the adult leaves and were more resistant to experimental desiccation. If such characteristics occur in the field it is possible that the seedlings of this species may be more drought resistant than the tree. However, the early establishment of the seedling in dry sites is likely to be jeopardised by the very tardy development of the root system. This particular feature could differentiate between otherwise equally resistant genotypes of *E. radiata* and *E. goniocalyx*.

In general these studies support the conclusions of Jarvis and Jarvis (1963*a* and *b*), in that the most drought resistant tree species are often those which respond quickly to small changes in relative turgor, close stomata and avoid further water loss by efficient cuticular control. Sanchez-Diaz and Kramer (1971) have stated that more drought resistant species permit less reduction of water content for a given reduction of water potential. In support of this idea, the water content loss per unit decrease in water potential for the Mount Towrong species form a graded series compatible with all aspects concerned with their relative drought resistance. Quraishi and Kramer (1970) found that seedlings of eucalypt species derived from flood plain environments are less drought resistant than those from rocky hillsides and that the ability to avoid drought stress by stomatal control was of great importance. Grieve and Hellmuth (1970) stressed the importance of diversity of adaptation in Western Australian sclerophyll species and the drought escape by the development of deep root systems was a significant feature of some species such as *E. marginata.* Lamb and Florence (1973) have pointed out the subtleties that exist between the local distribution of some eucalypts, such as *E. robertsonii* and *E. fastigata*, and physical features of the soils, such as total moisture storage, pore space and the acceptance of light summer showers.

Hopkins (1964) has shown that the growth rate of eucalypt seedlings could be a crucially important factor in survival in habitats prone to drought. Fast growing species in rich soils in such environments require a correspondingly large moisture supply to meet their demands. Thus *E. regnans* may die if it is encouraged to outgrow the ability of the site to supply sufficient moisture. Parsons (1968) likewise stressed the importance of slow growth rates as a survival mechanism in mallee species in southern Australia. The Mount Towrong observations are analogous to those made by Martin and Specht (1962) in the Mount Lofty Ranges, South Australia. Their studies showed that the soil moisture was depleted faster under the more mesophytic *E. obliqua* forest on southerly slopes than was that under the more xerophytic *E. goniocalyx* forest on the hot northerly slopes. They suggest that tree seedlings and understory species in the *E. obliqua* forest may in fact suffer more prolonged water stress than those in the *E. goniocalyx* woodlands on a warmer slope. It is possible that a similar situation could occur on Mount Towrong. The total leaf area on the eastern aspects certainly appears to be greater than that on the western aspects and experiments suggest that there is an inherent tendency for *E. obliqua* to transpire faster than *E. goniocalyx* on a leaf area basis. However, the local climate attending the development of water stress on these contrasting aspects could be decisive in dictating the degree of damage inflicted. The cool eastern slopes may permit a diurnal replenishment of moisture supply above the lethal limit, whereas the hot western slopes may be subjected to increasingly severe stress due to the high air and soil temperatures and the impact of hot dry winds that blow from that quarter. It is clear that the tolerance limits of *E. goniocalyx* have been reached in shallow soils on this aspect. It is notable that the lignotuber of seedlings is much better developed in *E. goniocalyx* than in *E. obliqua*, a feature that could be important in aiding survival on droughted sites (Table 2).

The ecological distribution of the dominants on Mount Towrong suggests a response to two general modes of the environment; the average or median conditions and the rare extremes. A species may spread along a moisture gradient on to dry sites in periods of adequate rainfall and then be eliminated or greatly reduced in importance by the occurrence of rare extreme drought. Thus *E. radiata* has spread up to 50 m beyond its " safe " limit on the western aspect of Mount Towrong where it has been severely damaged. As has been pointed out by Jones (1945) the frequency of catastrophes or favourable periods within the life span of the tree is of great importance. It is probable that such testing of species distribution has gone on for thousands of years. The ability of a species to develop ecotypes and thus increase its distributional range may well depend on catastrophes which eliminate competing species.

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EXPLANATION OF PLATE

Plate I

Top. Dead *E. obliqua* and living *E. viminalis* on shallow soils, north slopes of Mount Macedon.

Bottom. Mount Towrong from Upper Macedon showing drought damaged areas 60 km north-west of Melbourne.

TERTIARY FOSSIL FUNGI FROM KIANDRA, NEW SOUTH WALES

D. R. SELKIRK*

(Plates II–XII)

[Accepted for publication 28th August 1974]

Synopsis

Leaves in lower Miocene lignites exposed near Kiandra, New South Wales, bear abundant fossil epiphyllous fungi. The fungal flora includes members of the Meliolaceae and Asterinaceae, together with numerous types referable to the Microthyriales. Other fungi whose taxonomic affinities are less clear are also present. The fossil fungi and the associated pollen flora and plant macrofossils point to moist conditions in the forests from which the plant fossils were derived.

INTRODUCTION

The fungi described here form the bulk of a fossil epiphyllous flora from Lower Miocene sub-basaltic sediments near Kiandra, New South Wales, Australia. The geological occurrence of the flora and several fossil species belonging to the family Entopeltaceae have been discussed previously (Selkirk, 1972). Fossil members of the Meliolaceae and several forms of uncertain affinity are also present. Most of the species recognised, however, are similar to modern fungi grouped in the Microthyriales.

Most fossil epiphyllous fungi described by previous authors have been assigned to the Microthyriales and most have been included in the family Microthyriaceae as understood by Stevens and Ryan (1939). More recent taxonomic treatments of modern species of this group of fungi (von Arx and Müller, 1954 ; Müller and von Arx, 1962) have led to considerable changes in understanding of the group. In the case of some fossil genera referable to the Microthyriaceae, the more recent work indicates that the characters used to separate the fossil genera are of doubtful validity and that a number of fossil genera may be best lumped together.

DESCRIPTION OF SPECIMENS

All fossil specimens described are held in the Herbarium, New South Wales Department of Agriculture, Rydalmere, New South Wales (cited in text as DAR).

All cell measurements are given in the following form : minimum—(mean ; standard deviation ; number of measurements)—maximum. Measurements are based on camera lucida drawings at ×1750.

Order MELIOLALES
Family Meliolaceae
1. *Meliolinites* gen. nov.

Generitype. *Meliolinites spinksii* (Dilcher) Selkirk, comb. nov.

Fossil fungal colonies. Mycelium and spores with general characteristics of members of Meliolaceae. Mycelial setae absent. Information regarding perithecial structure and nature of perithecial appendages uncertain or lacking.

(a) *Meliolinites spinksii* (Dilcher) Selkirk, comb. nov.

Basionym. *Meliola spinksii* Dilcher, *Palaeontographica*, 116B, 8, Pl. II, figs 9–11 ; Pl. 3, figs 12–17. Eocene, Western Tennessee, U.S.A.

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* School of Biological Sciences, University of Sydney, New South Wales, 2006.

(b) *Meliolinites nivalis* Selkirk, sp. nov.

Pl. VII, figs 1–6

Fossil. Colonies up to 3 mm across. Hyphae straight, branches alternate (unilateral where crowded), antrorse, forming dense reticulum. Hyphal cells 19–(27·8 ; 3·2 ; 50)–34 μm long × 7–(9·2 ; 1·0 ; 50)–11 μm wide. Capitate hyphopodia alternate, unilateral where crowded, antrorse at *ca* 60° to hyphae or widely spreading, 22–(29·0 ; 3·4 ; 66)–39 μm long. Stalk cells cylindrical, often slightly expanded distally, rarely almost cuneate, 5–(8·9 ; 1·9 ; 66)–15·5 μm long × 6–(8·1 ; 1·1 ; 66)–11 μm wide ; head cells irregularly globose, 14–(20·1 ; 2·1 ; 66)–26 μm long × 11–(15·8 ; 2·2 ; 66)–23 μm wide. Spores smooth, straight, oblong with rounded ends, 3–septate, slightly constricted, 62–(66·7 ; 3·1 ; 17)–72·5 μm long × *ca* 18 μm wide. Modified Beeli formula ?101·6230.

Holotype. DAR 17201 (slide) ; cuticle of leaf of ?Myrtaceae, Kiandra, N.S.W., Lower Miocene. Pl. VII, figs 1–6.

Remarks. Individual colonies are easily visible to the naked eye. Colonies are often confluent and considerable areas of cuticle may be covered by mycelium. The hyphae are straight but long branches may show considerable flexure. About 20% of the hyphal cells bear branches. Most branches are at 60–70° but the angle varies from 40–90° and a few recurved branches also occur. Hyphal walls are 1·5–2·5 μm thick and cross-septa have a distinct pore 2–2·5 μm diameter.

Approximately 50% of hyphal cells bear capitate hyphopodia at the distal end. Most are antrorse but many are widely spreading and a few recurved. Most head cells are globose but the wall is often sinuate and the head cell is occasionally almost lobate. A distinct septal pore is present between head and stalk cells. No mucronate hyphopodia occur.

Head cells have a distinct pore in the lower surface (Pl. VII, fig. 5). A hyaline process extending through the cuticle from the pore presumably represents the remnant of a haustorial filament which penetrated the host (Pl. VII, fig. 6). Hansford (1961) described haustoria of the Meliolaceae as ovate to globular, but no expanded portion has been seen in fossil specimens.

A single poorly preserved fructification is present in one colony, appearing as an almost structureless black body 286 μm diameter. The perithecium may originally have been globose but is cupulate in the specimen. Hansford (1961) reports that perithecia of some modern species of Meliolaceae often become cupulate-collapsed on drying. The perithecium is borne on a radiate disc of hyphae and a number of hyphal discs occur in other colonies (Pl. VII, fig. 3). Hyphae of the disc lack the capitate hyphopodia of the normal vegetative mycelium.

Germinated spores persist in the centre of colonies (Pl. VII, fig. 4). The end cells (av. length = 15·3 μm) are slightly shorter than the central cells (av. length = 18 μm) and have thinner walls. The spore is slightly arched away from the surface of the leaf. Spores have a germinal capitate hyphopodium produced from each end cell, both directed to the same side of the spore. Hyphae are produced from all cells of the spore, from the ends of the end cells and from the lower face of the central cells.

Several perithecia of a form provisionally ascribed to the Trichothyriaceae occur in close contact with hyphae of *Meliolinites nivalis* and many hyphae are invested by narrow pale hyphae of another form. Some hyphal cells appear to have been attacked and it seems possible that the fossil colonies have been attacked by a hyperparasitic form.

Hansford (1961) listed 1,814 species in the Meliolaceae. Of those growing on leaves of Myrtaceae the only species with 3–septate ascospores and lacking setae is *Asteridiella eucalyptorum* (2101·6240). This species differs from the fossil material in mycelial branching and shape of the capitate hyphopodia.

(c) *Meliolinites* sp.

Pl. VIII, figs 3–4

Fragmentary remains of this form occur on the lower cuticle of leaves of ?Lauraceae (DAR 17208, 17210). Hyphae are straight and most branches are opposite, although sometimes unilateral. Hyphal cells are 12–(15·5 ; 2·1 ; 39)–21 μm long × 6–(6·9 ; 0·6 ; 39)–9 μm wide and most bear capitate hyphopodia at the distal end. Hyphopodia are alternate (10% opposite) and antrorse, 12·5–(17·6 ; 1·7 ; 63)–23 μm long. Stalk cells are shortly cylindrical or almost cuneate, 2–(3·9 ; 0·8 ; 63)–17 μm long × 5–(6·6 ; 0·9 ; 63)–8 μm wide. Head cells are mostly obtuse conoid, 9–(13·8 ; 1·4 ; 63)–17 μm long × 7–(8·9 ; 1·0 ; 63)–12 μm wide (Pl. VIII, fig. 3). A few head cells are cylindrical with broadly rounded ends. An indistinct pore is present at the apex of the head cell in most specimens.

A single spore is attached to the hyphae (Pl. VIII, fig. 4). The spore is 46 μm long × 16·5 μm wide, 3-septate, slightly constricted, smooth. The end cells (*ca* 8·5 μm long) are markedly shorter than the central cells (*ca* 14 μm long). A single germinal hyphopodium is developed from each end cell. Mucronate hyphopodia are absent.

2. Sterile mycelia, probably Meliolaceae

Two other forms with mycelia similar to those described above occur on leaves of ?Lauraceae and *Podocarpus*.

(a) Type 1

A single colony occurs on the lower surface of a leaf of ?Lauraceae (DAR 17209). The colony is 1·5 mm diameter and remains of four fructifications are present. Hyphae are straight when growing free from each other but may be considerably bent when crowded. Hyphae branch alternately forming a dense reticulate network (Pl. VIII, fig. 1). Hyphal cells are 19–(23·2 ; 2·9 ; 19)–29 μm long × 7–(8·2 ; 0·7 ; 19)–10 μm wide. Most cells bear antrorse capitate hyphopodia which are alternate, or unilateral where crowded. Hyphopodia are 22–(25·5 ; 2·1 ; 16)–29 μm long. The stalk cell is cylindrical, often slightly wider distally, 4–(7·8 ; 2·1 ; 16)–11 μm long × 7–(8·4 ; 0·8 ; 16)–10 μm wide. Head cells are subglobose to cylindrical with a broadly rounded apex, 15–(17·8 ; 1·2 ; 16)–20 μm long × 11–(12·4 ; 1·0 ; 16)–15 μm wide (Pl. VII, fig. 7). No mucronate hyphopodia are present. The central part of the fructification has fallen away and the portions which remain possibly represent the margin of a radiate hyphal disc on which the perithecium is borne in modern Meliolaceae.

(b) Type 2

Fragments of this form occur on the upper surface of leaves of *Podocarpus* sp. and on bilateral leaves of *Podocarpus praecupressinus* (DAR 17200).

Hyphal branching is opposite. The cells are 18–(23·0 ; 3·0 ; 31)–32 μm long × 7–(9·7 ; 1·3 ; 31)–13 μm wide. Hyphal walls are 1·5–2 μm thick and distinct pores *ca* 2 μm diameter are present in the cross-septa. Capitate hyphopodia are alternate or unilateral and seem to have no preferred orientation. The stalk cells are shortly cylindrical, 3–(6·5 ; 1·7 ; 43)–10 μm long × 6–(8·9 ; 1·5 ; 43)–12 μm wide. Head cells are globose, 13–(15·8 ; 1·4 ; 43)–29 μm long × 10–(13·7 ; 1·7 ; 43)–19 μm wide. Many head cells have a distinct pore in the lower face *ca* 2 μm diameter (Pl. VIII, fig. 2). Total length of the hyphopodia is 17–(22·3 ; 2·3 ; 45)–26 μm. No mucronate hyphopodia are present.

3. Classification of fossil Meliolaceae

Hansford (1961) recognised a number of genera in the Meliolaceae, placing all species with mycelial setae in *Meliola*. Species in which mycelial setae are absent were placed in different genera on the basis of perithecial wall structure and appendages.

Fossil specimens with mycelial setae can thus be readily assigned to *Meliola*. Fossil specimens without setae pose problems. Unless well-preserved perithecia are present so that one can decide what type of appendage (if any) is present, they cannot be placed with any certainty in any of the other genera. Specimens described by Dilcher (1965) as *Meliola spinksii* and all the specimens from Kiandra lack setae and hence cannot be included in *Meliola* (*sensu* Hansford, 1961) with certainty. The lack of well-preserved fructifications in the same specimens precludes their inclusion in the other genera recognised by Hansford. A form genus, *Meliolinites*, has been created to contain such fossil material.

It is possible that some fossil specimens placed in *Meliolinites* may represent species of *Meliola*. In some *Meliola* spp. setae are present in some colonies only and even the majority of colonies may lack them (Hansford, 1961). In other species setae may be developed only around the base of the perithecium. Under these circumstances examination of a wide range of material may be necessary for correct identification. Development of setae, and even of perithecia, may be suppressed if a colony is attacked by hyperparasites (Stevens, 1927 ; Hansford, 1961). The presence of a possible hyperparasite associated with *Meliolinites nivalis* may be of significance in this respect.

In fossil specimens absence of setae may be due to : 1. absence of hyphal setae in the organism ; 2. insufficient material for determination of whether setae occur or not ; 3. suppression of seta formation by hyperparasites. In rather scanty fossil material it would be impossible to decide with certainty between the first two of the above alternatives. There may be some evidence of hyperparasitic attack in other specimens. As a result, it seems preferable to exclude fossil material without setae from *Meliola*.

Gordon and Shaw (1960) recognised a further genus, *Diporotheca*, as belonging to the Meliolaceae. The single species is parasitic on roots of *Solanum* in North America. On the basis of habitat and spore structure this genus can be excluded in considering the fossil material.

The two types of sterile mycelium described above very probably are members of the Meliolaceae, but two-called hyphopodia occur in *Asterina* and its allies. In the absence of spores and fructifications definite assignation to the Meliolaceae is inadvisable.

Order MICROTHYRIALES

Family Microthyriaceae

4. *Asterina* Léveillé

Asterina kosciuskensis Selkirk, sp. nov.

Pl. II, figs 1–9 ; Pl. III, fig. 7

Fossil. Colonies up to 4 mm diameter, amphigenous. Mycelium dark. Hyphae straight, cells 19–(30·5 ; 4·5 ; 84)–47 μm long × 4·5–(6·2 ; 1·2 ; 84)–10 μm wide, branches at 90°, alternate or unilateral. Hyphopodia one-celled, alternate or unilateral, sub-globose to cylindrical with broadly rounded apex, 9–(11·4 ; 1·6 ; 36)–15 μm long × 5–(8·0 ; 1·3 ; 36)–10 μm wide ; mostly at right angles to cells bearing them, often slightly antrorse, occasionally reflexed ; distinct pore up to 2·5 μm diameter towards distal end, usually surrounded by a thickened rim. Perithecia scattered or crowded, up to 450 μm diameter, composed of radiating hyphae ; margin fimbriate, paler than central area. Central portion of wall multilayered, margin single layered. Spores ovate-elliptical, 1–septate, constricted, cells of unequal length, walls thin, granular. Walls of spore become thick and dark after germination and further septa may develop.

Holotype. DAR 17253 (slide), cuticle of ?myrtaceous leaf, New Chum Hill, Kiandra, N.S.W., Lower Miocene. Pl. II, figs 7–9 ; Pl. III, fig. 7.

Remarks. Colonies are often confluent and the surface of some leaves is almost entirely covered by mycelium. Cells in hyphae on the lower surface of leaves are generally longer than those on the upper surface. Walls of individual hyphal cells are often sinuate. Branches usually arise from cells without hyphopodia. If a hyphopodium is present the branch arises opposite it. Hyphal walls and cross-septa are *ca* 1·5 μm thick with a distinct pore 1·5 μm diameter in septa. Pores in hyphopodia presumably represent the position of penetration of the host by haustoria, but no haustorial structures are visible beneath the cuticle.

Many large perithecia have cracks radiating from the centre, or else the wall is irregularly broken. In modern *Asterina* spp. spores escape through radial or irregular fissures (Doidge, 1920) and splits in fossil perithecia may represent dehiscence. In two cases split perithecia contain spores, but it is possible that splits may be due to mechanical damage to the brittle fossil material. Often the entire central portion of a perithecium has broken away and its position is marked by the persistent paler marginal hyphae.

A complete series of stages in fructification development is often present in a single colony. Fructifications first appear as small lobed outgrowths of medial hyphal cells or terminal on short lateral branches. Older fructifications form a plate of radiating hyphae under, or to one side of, the hyphae (Pl. II, figs 2–4).

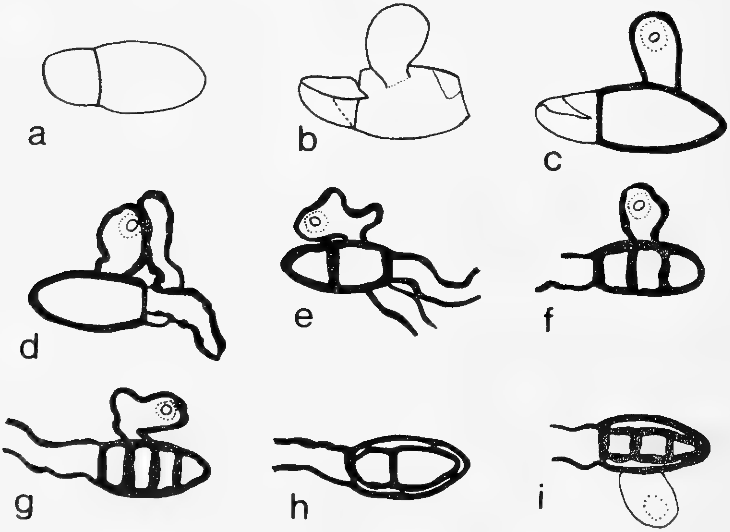

Fig. 1. Spore germination in *Asterina kosciuskensis*. An initially 2-celled, thin-walled spore (a) develops a germinal hyphopodium (b). Once penetration of the host has been effected the large cell of the spore becomes thickened (c). Hyphae then develop from the thickened cell which may remain unicellular (d) or else become variously septate (e–g). " Spore-in-spore " structure (h, i) may also develop. Camera lucida drawings ×500. See also Pl. II, figs 5–9 and Pl. III, fig. 7. (a) DAR 17219 ; (b–i) DAR 17253.

Germinated spores persist attached to hyphae even when a colony is of considerable size and has apparently mature perithecia. One hundred and ninety-two such spores were studied. A few broken perithecia contain apparently immature thin walled spores but only a few are in a position to show the structure clearly (Pl. II, figs 6, 7). Spores are ovate-elliptical, 37 μm long × 18 μm wide, slightly constricted at the septum which is much more distinct than the almost colourless slightly granular spore wall. The septum divides the spore into a large cell *ca* 25 μm long and a small cell *ca* 12 μm long. Spores may have been shed from the perithecia in this condition as several similar spores occur on the cuticle not obviously associated with fructifications. A thin-walled spore which had germinated to form a germinal hyphopodium is shown in Pl. II, fig. 7. The reconstructed pattern of spore germination is shown in Figure 1.

" Spores " found attached to hyphae in fact represent only the thickened large cell of the two-celled ascospore. They are ovate, with one end truncate, 21–(26·8 ; 2·6 ; 73)–40 µm long × 12–(14·5 ; 1·1 ; 73)–17 µm wide. The walls are thick (*ca* 1·5 µm) and dark. Spores vary from 0–3 septate. Measurements of thickened large cells and component cells are given in Table 1. The dimensions of the large cell in the thin-walled spores agrees with those of the thickened large cells in Table 1.

TABLE 1

Measurements of thickened large cell in spores of Asterina kosciuskensis

Cell Septation	Number Examined	Mean Length	Mean Width	Mean Length Component Cells*
1-celled ..	44	26·5 µm	13·8 µm	
2-celled ..	122	26·4 µm	14·6 µm	11·0 µm 15·0 µm
3-celled ..	25	28·8 µm	14·2 µm	10·4 µm 8·9 µm 9·5 µm
4-celled ..	1	28·0 µm	15·0 µm	

* measured in succession from the rounded end of large cell.

Similarly, the dimensions of the 1-celled " spores " are similar to those of 2-, 3- and 4-celled specimens. Many fungal spores which penetrate the host before production of free hyphae may become variously modified, development of further septa being fairly common, and it appears that this is the case in the fossil form.

In many germinated spores the remains of the small cell of the spore are visible at the base of the hypha produced from the truncate end of the thickened cell. In some specimens the developing free hypha appears within the almost hyaline small cell (Pl. II, fig. 9 ; Pl. III, fig. 7). In some spores where thickening of the large cell is not extreme the granular pattern of the wall is still apparent. More than one hypha may be produced from a thickened large cell, usually from the truncate end, but in some specimens hyphae arise from both ends of the cell. Almost all spores have a germinal hyphopodium similar to those of the mycelium but more irregular in shape.

5. Other fossil species probably belonging to *Asterina* or related genera

Species 1

Pl. x, fig. 6 ; Pl. xi. figs 1–3

DAR 17217, 17226, cuticle of ?myrtaceous leaf, Kiandra, N.S.W., Lower Miocene.

This form closely resembles *Asterina*. Fructifications are scattered on a dark hyphopodiate mycelium (Pl. X, fig. 6). The outer wall of the fructification is multi-layered in the centre, single-layered towards the margin. The straight to slightly sinuous septate hyphae grow out at the edge to give a fimbriate margin. Older fructifications are ovate-elliptical, the largest 313 × 205 µm. Large fructifications have a longitudinal paler zone in the central area and in one specimen there are indications of a longitudinal fissure. The free mycelium consists of straight to sinuous hyphae, indistinctly septate. Branches are alternate or unilateral and cells are 24–(31·5 ; 5·2 ; 40)–46 µm long × 4·5–(6·2 ; 0·8 ; 40)–8·5 µm wide. Hyphopodia are alternate or unilateral, sparse, subglobose to elongate cylindrical with a rounded or pointed apex. They are 10–

(12·4 ; 2·0 ; 40)–18 µm long × 5–(7·6 ; 1·1 ; 40)–10 µm wide. Pores 0·5–1·5 µm diameter occur at the apex of hyphopodia. They are not surrounded by a thickened rim (Pl. XI, fig. 3). Hyphae tend to be more obviously septate in the vicinity of young fruiting bodies, with shorter cells than elsewhere in the hyphae.

Development of young fructifications is very similar to that described above for *Asterina kosciuskensis*. Young fructifications are borne beneath, or lateral to, hyphal cells (Pl. XI, fig. 1). A single two-celled spore has been seen associated with this form, lying close to a hypha and fragments of a fruiting body (Pl. XI, fig. 2). The spore is pale, with a smooth wall, conglobate, constricted, *ca* 32 µm long × 16 µm wide, and divided into approximately equal cells. A germinal hyphopodium very similar to hyphopodia on the free mycelium described above occurs on one cell. A process from the other end of the spore may represent a germinal hypha. The structure of the spore and germinal hyphopodium makes it possible that the spore belongs to this species but no specimens have been seen in a fructification or in connection with hyphae and any assignation to this species must be doubtful.

Species 2

Pl. XI, figs 4–6

DAR 17221 (slide), cuticle of leaf of ?Lauraceae, Kiandra, N.S.W., Lower Miocene.

Fructifications of this form are rounded, often with a wavy outline due to the irregularly lobed and fimbriate margin. The largest seen is 460 µm diameter. The wall is one layer thick, of radiate, straight to slightly wavy hyphae. Cells are 12–(19·6 ; 3·4 ; 60)–26 µm long × 2–(4·0 ; 0·8 ; 60)–5·5 µm wide. Towards the margin of the fruiting body the hyphae may be wavy, forming a sinuous plectenchyma. Free hyphae are darker than those of the fructification and are badly fragmented in all specimens. They appear to have been straight to sinuous, exhyphopodiate, with opposite or unilateral branches. Cells are 17–(25·7 ; 3·1 ; 50)–34 µm long × 4–(5·2 ; 0·7 ; 50)–7 µm wide. A few hyphal cells have a small pore in the lower face, possibly representing the position of haustoria. Such pores are rare.

A number of young stages of fructifications have been recognised, resembling those described above for *Asterina kosciuskensis*. Young fructifications are borne laterally on the hyphal cells (Pl. XI, fig. 6).

6. *Euthythyrites* Cookson

Euthythyrites morenoinitis Selkirk, sp. nov.

Pl. III, figs 1–6

Free mycelium sparse. Hyphae straight, branched, without hyphopodia, arising from marginal cells of the fructification. Fructifications linear when mature, dehiscing by a longitudinal slit. Wall of fructification composed of radiating, dichotomously branched hyphae ; cells square to rectangular, 1·5–(3·9 ; 0·8 ; 210)–6·5 µm long × 1–(2·2 ; 0·6 ; 102)–3·5 µm wide, walls 0·5 µm thick. Spores two-celled, smooth, almost colourless.

Holotype. DAR 17231 (slide), cuticle of ?myrtaceous leaf, New Chum Hill, Kiandra, N.S.W., Lower Miocene. Pl. III, figs 1–6.

Remarks. Measurements of fructification size have not been included in the diagnosis owing to the small number of specimens. They range in size from 56 × 34 µm to 280 × 64 µm in an old dehisced specimen. Smaller frutifications are ovate-elliptical with a distinct radial arrangement of the wall (Pl. III, fig. 3). Larger fructifications are elongate. The radiate structure of the first-formed part is visible even in old dehisced specimens.

A distinct longitudinal band of pale cells occurs in the midline of the fructification (Pl. III, fig. 3). The hyphal walls are markedly thinner than elsewhere in the fructification and this band almost certainly represents a zone of weakness along which the fructification dehisced at maturity. Up to three adjacent hyphae are involved in formation of the band.

A group of six spores is present in one fructification but only one spore is in such a position as to show the structure clearly. The spore is 7 μm long, divided into two equal cells 3 μm wide. The spore is constricted at the septum (Pl. III, fig. 2).

The margin of the fructification is fimbriate, some of the marginal cells giving rise to free hyphae (Pl. III, fig. 1). Hyphae are 2–3 μm wide, almost colourless, and extend widely over the cuticle, branching at irregular intervals. Very indistinct septa occur at intervals. There appears to have been no penetration of the leaf either through the cuticle or stomatal cavities. One small pore has been seen in a hypha but this is the only indication of a possible penetration point.

A series of stages in fructification development is present. Large numbers of small circular fruiting bodies occur scattered over the cuticle, developed beneath free hyphae. Organic connection of these with linear fructifications has been shown in two cases. The earliest stage is a small lobed outgrowth of the hypha. Further growth leads to development of a small circular plate beneath the hypha (Pl. III, figs 5, 6). The structure at this stage is distinctly radial but no distinct cross-septa are visible in the dichotomously branched hyphae. Larger specimens have distinct septa (Pl. III, fig. 4). There is no sign of spores or dehiscence in these small fruiting bodies and they are regarded as stages in development of linear fructifications.

Müller and von Arx (1962) list eight genera in the Asterinaceae with linear ascomata opening by a longitudinal slit. The fossil form appears closest to *Lembosina*, *Echidnodella* and *Morenoina*. *Lembosina* has a hypostroma which may develop just beneath the cuticle, in the epidermis, or deeper within the leaf. The presence or absence of such a structure is almost impossible to determine in fossil specimens where the cuticle is the only part of the leaf structure remaining. There is always the possibility that a hypostroma may have originally been present but has been either not preserved or lost in preparation of specimens.

Many members of this group of genera form dark hyphal complexes in the stomata. These do not occur in the fossil specimens, although hyphae often grow around or across a stoma. There is no indication of penetration of the cuticle either by free hyphae or beneath the fructifications and the supposed absence of such penetration has been taken to indicate absence of a hypostroma.

Echidnodella contains parasitic forms with a dematoid mycelium. *Morenoina* contains saprophytic forms in which the mycelium is delicate and sometimes evanescent. The ascospores are very small and hyaline (Müller and von Arx, 1962). The mycelium of the fossil form is certainly not dematoid and best fits the description of hyphae of *Morenoina*. Some larger fossil fructifications have no free hyphae associated with them and the mycelium may have been evanescent or at least very indistinct. The spores appear to be very faintly coloured and are transparent. The size of the single spore measured points to *Morenoina* rather than to *Echidnodella*, in which the ascospores are larger, as the closest affinity of the fossil specimens.

7. *Notothyrites* Cookson

Notothyrites kiandrensis Selkirk, sp. nov.

Pl. IX, figs 1–3

Fructification rounded, margin entire to crenate, irregularly lobed. Central ostiole up to 17 μm diameter. Cells in the ostiole pale, thin-walled, isodiametric, surrounded by a prominent raised border of dark, thick-walled cells, square to rectangular, 1·5–(3·5 ; 0·8 ; 31)–5 μm long × 1·5–(2·8 ; 0·5 ; 31)–3·5 μm wide ; border up to six cells wide. Walls of fructification of radiating hyphae, cells 2–(6·9 ; 1·5 ; 175)–11 μm long × 1–(3·2 ; 0·9 ; 175)–7 μm wide.

Holotype. DAR 17266 (slide), lower cuticle, leaf of ?Lauraceae, Kiandra, N.S.W., Lower Miocene. Pl. IX, figs 1–3.

Remarks. This species occurs in close association with *Callimothallus pertusus.* The fructifications fall away from the cuticle very readily and the specimen illustrated has been removed from the cuticle. Fructifications studied range from 140 to 330 μm diameter. The hyphae of the wall are attached along their entire length, but groups of adjacent hyphae may extend slightly beyond the others to form a crenate margin, and in most specimens the fructification is irregularly lobed (Pl. IX, figs 1, 2). Hyphae towards the margin of the fructification are often contorted and many hyphal branches end blindly against adjacent hyphae. In young specimens the wall is fairly pale with thin-walled hyphae but in older, larger specimens the hyphal walls are very much thickened, except at the margin (Pl. IX, fig. 2).

The raised border surrounding the ostiole is much darker than the rest of the wall in young specimens (Pl. IX, fig. 3). In older specimens the border is difficult to discern against the dark thickened wall (Pl. IX, fig. 1). Cells within the border break down to form the ostiole opening and fragments of them can be seen within the opening in some specimens.

Notothyrites setiferus is recorded from Kiandra in palynological residues (Cookson, 1947). *N. setiferus* is much smaller than *N. kiandrensis*, with up to eight setae produced from cells of the raised border of the ostiole.

8. *Phragmothyrites* Edwards

Synonym. *Microthyriacites* Cookson, PROC. LINN. SOC. N.S.W., 72, 210, 1947
Asterothyrites Cookson, PROC. LINN. SOC. N.S.W., 72, 209, 1947
Microthallites Dilcher, *Palaeontographica*, 116B, 16, 1965

(a) *Phragmothyrites fimbriatus* comb. nov.

Basionym. *Microthyriacites fimbriatus* Cookson, PROC. LINN. SOC. N.S.W., 72, 211, Pl. XIII, fig. 17, 1947.

(b) *Phragmothyrites grandis* comb. nov.

Basionym. *Microthyriacites grandis* Cookson, PROC. LINN. SOC. N.S.W., 72, 211, Pl. XIV, figs 20, 21, 1947

(c) *Phragmothyrites sinuatus* comb. nov.

Basionym. *Asterothyrites sinuatus* Cookson, PROC. LINN. SOC. N.S.W., 72, 209, Pl. XII, fig. 8, 1947.

(d) *Phragmothyrites delicatissimus* comb. nov.

Basionym. *Asterothyrites delicatissimus* Cookson, PROC. LINN. SOC. N.S.W., 72, 210, Pl. XII, fig. 9, 1947.

(e) *Phragmothyrites minutus* comb. nov.

Basionym. *Asterothyrites minutus* Cookson, PROC. LINN. SOC. N.S.W., 72, 210, Pl. XII, fig. 10, 1947.

(f) *Phragmothyrites ostiolatus* comb. nov.

Basionym. *Asterothyrites ostiolatus* Cookson, PROC. LINN. SOC. N.S.W., 72, 210, Pl. XII, fig. 11, 1947.

(g) *Phragmothyrites kiandrensis* Selkirk, sp. nov.

Pl. IX, figs 4–6

Fructifications dimidiate, rounded, flattened-hemispherical, the central area often slightly depressed ; astomate. Upper wall of radiate dichotomously branched hyphae. Cross-septa often indistinct, more or less at the same level but not forming concentric rings, markedly thinner than the lateral walls ; cells proximal to dichotomous branching 5–(7·1 ; 1·1 ; 78)–10 μm long × 5–(6·9 ; 1·0 ; 78)–9 μm wide ; cells between dichotomies and at periphery of ascoma 2–(6·3 ; 1·3 ; 207)–10 μm long × 3–(4·6 ; 0·9 ; 207)–7 μm wide. Margin entire, thick. Central cells often darker than rest of the upper wall, rectangular to polygonal, often arranged irregularly, same size as peripheral cells, often slightly above general level of the wall. Basal layer of fructification hyaline, of radiate dichotomously branched hyphae which may have indistinct cross septa. Free hyphae uncertain.

Holotype. DAR 17207 (slide), cuticle of ?myrtaceous leaf, Kiandra, N.S.W., Lower Miocene. Pl. IX, fig. 4.

Remarks. This species occurs on leaves of both ?Myrtaceae and ?Lauraceae in the sediments. Fructifications are 25–(70·8 ; 18·8 ; 39)–116 μm diameter. A fragmentary specimen probably *ca* 130 μm diameter has been seen. Fructification diameter has not been included in the diagnosis as there is no evidence that any are mature. The central cell is often surrounded by a narrow zone of irregularly arranged cells which separate it from the radial portions of the wall. In some specimens the zone of irregular cells is absent. Hyphae have walls 0·5–1 μm thick. Cells proximal to branching are polygonal with an apex in the direction of growth of the hypha. Cells between dichotomies are square to rectangular. The rather indistinct septa are apparently absent in some young specimens (Pl. IX, fig. 6). Hyphal extremities are very slightly inflated.

Small pores *ca* 0·5 μm diameter occur in some fructifications, occasionally surrounded by a thickened rim which may be very dark brown. The pores have no definite arrangement and may be due to hyperparasitic attack. The lower layer of the fructification is hyaline or very pale brown, composed or radiating hyphae the same width as those in the upper wall. The hyphae are dichotomously branched and may show very indistinct cross-septa (Pl. IX, fig. 5). Some fructifications are in very close contact with hyaline to pale brown hyphae. In some cases hyphae encircle the fructification in very close contact with the margin and occasionally give the impression of radiating from beneath it. However the relation of hyphae to fructifications is problematical as no actual organic continuity has been demonstrated.

Phragmothyrites kiandrensis closely resembles fructifications described by Cookson (1947) as *Microthyriacites* sp. on leaves of *Oleinites willisii* (Oleaceae) from Yallourn. The measurements of the latter, in so far as they are comparable, agree with those given for *Phragmothyrites kiandrensis*. In both the centre of the ascoma is slightly depressed. Cross-septa, particularly towards the margin of the fructification, are indistinct and markedly thinner than the lateral walls of the hyphae.

(h) *Phragmothyrites delicatus* Selkirk, sp. nov.

Pl. VI, figs 3–6

Colonies amphigenous. Fructifications scattered, circular, composed of radiate dichotomously branched hyphae, margin entire ; astomate. Central cells polygonal, mostly thick walled ; peripheral cells square to rectangular, 1–(3·2 ; 0·7 ; 67)–5 μm long × 1–(2·2 ; 0·6 ; 67)–4 μm wide, cross-septa and hyphal walls thin. Free hyphae straight to sinuous, 2–3 μm wide, widely spreading, pale, exhyphopodiate, indistinctly septate, pores present in hyphae. Branching opposite at a wide angle. Free hyphae attached to fructifications either centrally or peripherally. Fructifications develop beneath hyphae.

Holotype. DAR 17234 (slide), cuticle of ?myrtaceous leaf, Kiandra, N.S.W., Lower Miocene. Pl. VI, figs 3–5.

Remarks. Fructifications seen are up to 91 μm diameter. Individual hyphae of the wall have thin walls and indistinct cross-septa (Pl. VI, fig. 6). In most specimens the central cells of the fructification have thick walls but in a few specimens the central cells are very indistinct and cross-septa towards the periphery appear to be absent. There is a progressive increase in hyphal width between branchings. Cells proximal to a branch are polygonal with an apex in the direction of growth of the hypha. The margin of the fructification is entire to very slightly fimbriate. Ends of the individual hyphae are thin and all at the same level, although they are occasionally slightly invaginated (Pl. VI, fig. 6). Several fructifications have irregular fissures in the wall, possibly due to mechanical damage.

Free hyphae are often almost hyaline (Pl. VI, fig. 4). On the upper cuticle hyphae are straight and have distinct opposite branches. On the lower cuticle hyphae are more extensively developed and are sinuous, probably as a result of cuticle sculpture. Hyphae have indistinct cross-septa but distinct " cells " are occasionally recognisable. Small pores occur in the lower face of hyphae, sometimes with a slightly thickened rim, and probably represent the position of penetration of the host leaf by haustoria (Pl. VI, fig. 5).

Several young fructifications occur on DAR 17234. Fructifications arise as outgrowths of the lower face of hyphae and show radiate structure at an early stage (Pl. VI, fig. 3). One large fructification has free hyphae attached centrally but in other specimens they are attached at the margin.

Phragmothyrites delicatus closely resembles *Asterothyrites sinuatus* Cookson in structure of the fructification. The stellate fissures in *Asterothyrites sinuatus* which Cookson (1947) regarded as evidence of dehiscence may be due to mechanical damage as also may those in *Phragmothyrites delicatus. Asterothyrites sinuatus* (holotype : P26028, National Museum, Melbourne, Victoria) lacks the hyphal pores seen in *Phragmothyrites delicatus,* nor are there any young fructification stages present.

(i) *Phragmothyrites* cf. *fimbriatus*

Pl. VIII, fig. 5

Two poorly preserved fructifications similar to those of *Microthyriacites fimbriatus* Cookson occur on DAR 17240, the upper cuticle of a leaf of ?Lauraceae. The fruiting bodies are confluent with large polygonal central cells *ca* 8 μm diameter. The radial structure extends right to the central cell which is surrounded by a number of polygonal cells 5–8 μm long × 5–8 μm wide. Towards the periphery of the fructification cross-septa are indistinct. Most of the margin is missing but in one of the pair the margin varies from thick, smooth and entire with very slightly inflated hyphal extremities to slightly crenate and thin. No definite fimbriate section of the ascoma is visible. The specimens appear to be very similar to those described by Cookson (1947) but are only doubtfully referred to the species due to lack of material and poor preservation.

(j) *Phragmothyrites* sp. 1

Pl. IX, figs 7–9 ; Pl. X, fig. 1

Some fifteen specimens of this form are present on the upper surface of leaves of ?Myrtaceae and ?Lauraceae (DAR 17240, 17247). The fructifications are 28–(34·9 ; 5·5 ; 15)–48 μm diameter, rounded and flattened-hemispherical. The upper wall is dark reddish brown and in many specimens has flaked away revealing a pale or hyaline lower layer on the cuticle (Pl. IX, fig. 9 ; Pl. X, fig. 1). The upper wall has a group of central cells 3–(4·7 ; 1·1 ; 37)–8 μm long × 3–(4·0 ; 0·7 ; 37)–5 μm wide, rectangular, square or polygonal with walls *ca* 0·5 μm thick. One specimen has a distinct square central cell with a pore *ca* 1 μm diameter in the outer face.

Peripheral to the central zone of distinct cells the radiate structure of the wall is obvious. The hyphae have very indistinct cross-septa, apparently completely absent in most specimens. The hyphae are 3–6 μm wide proximal to branching and 3–3·5 μm wide at the base of a newly formed branch.

The margin of fructifications is very characteristic. Hyphal extremities are often slightly invaginated and are capped by a distinctly fimbriate or crenulate zone, up to 3 μm wide, of amorphous brown material. Individual lobes of this material may be entire (Pl. IX, fig. 7) or very finely divided (Pl. X, fig. 1). Where fructifications have flaked away from the cuticle this brown marginal material remains, forming a ring marking the position of the fruiting body and often surrounding the apparently structureless lower layer.

The specimens probably represent young stages of microthyriaceous fructifications and are not described as a new species pending the discovery of further material.

(k) *Phragmothyrites* sp. 2

A few fragments of a very large form apparently belonging to *Phragmothyrites* occur on leaves of ?Lauraceae (DAR 17259, 17260, 17261). The fructification appears to have been circular, *ca* 1 mm diameter in one specimen and 0·5 mm in another fragmentary specimen.

The wall is dark, composed of radiating hyphae which are occasionally branched. Hyphal walls are very dark, *ca* 1·5μm thick. Individual hyphal cells are 9–(14·0 ; 2·7 ; 26)–18 μm long × 4–(5·9 ; 0·9 ; 26)–7 μm wide. Cells towards the centre of the wall are very dark, almost opaque, often with a colourless area at the proximal end. Cells towards the margin are markedly lighter in colour.

The margin varies from entire to fimbriate. Individual hyphae are often divided at the apex or the end may be slightly inflated. Some hyphae project a short distance from the margin or else the margin is distinctly fimbriate. Some areas of the margin have a structure resembling the margin in *Phragmothyrites* sp. 1 described above. The hyphae are capped by a zone of amorphous dark material *ca* 3 μm wide, sometimes lobed (Pl. X, fig. 2).

9. Classification of Fossil *Microthyrium*—like fungi

TABLE 2

Form-genera in the Microthyriaceae

Microthyriaceae *Phragmothyrites* Edwards, 1922 *Microthyriacites* Cookson, 1947	
Subfamily Microthyrieae (free hyphae evanescent)	Subfamily Asterineae (free hyphae persistent)
Notothyrites Cookson, 1947	*Asterothyrites* Cookson, 1947
Microthallites Dilcher, 1965	*Euthythyrites* Cookson, 1947
Callimothallus Dilcher, 1965	

Table 2 lists form-genera within the family Microthyriaceae (*sensu* Stevens and Ryan, 1939) recognised by previous authors. Several of these have fructifications similar to those of modern *Microthyrium* spp.

Edwards (1922) instituted the genus *Phragmothyrites* for " fossil forms belonging to the Microthyriaceae, the exact position of which is uncertain, but which appear closely related to *Phragmothyrium* as defined by von Höhnel ". Edwards' specimens consisted of radiate thyriothecia with entire to slightly crenate margins, associated with structures he described as stigmocysts.

Edwards thought that spores associated with the fruiting bodies might belong to the same species but pointed out that this was based only on association and was therefore questionable. The presence or otherwise of a free mycelium was also uncertain. Cookson (1947) established the genus *Microthyriacites* for microthyriaceous fruiting bodies of uncertain affinities. Fructifications described by Cookson as *Microthyriacites* are very similar to those of *Phragmothyrites*. Sah (1967) regarded *Microthyriacites* Cookson as a synonym of *Phragmothyrites* Edwards and the same classification is adopted here.

Dilcher (1965) described fossil forms very similar to those included by Cookson in *Microthyriacites* and included them in a new genus, *Microthallites*. In *Microthallites*, fruiting bodies " definitely lack free hyphae and so cannot be placed in the genus *Microthyriacites* " (Dilcher, 1965). In *Microthyriacites* " information regarding the presence of a free mycelium " is " either uncertain or wanting " (Cookson, 1947).

All the species of *Microthyriacites* described by Cookson were based on fructifications found in palynological residues, thus giving no indication of whether free hyphae were present or not. Under these circumstances one cannot assign the fossil forms to either subfamily recognised by Stevens and Ryan (1939). The specimens described by Dilcher as *Microthallites*, on the other hand, were found *in situ* on cuticle. Since they lacked hyphae, Dilcher included them in the subfamily Microthyrieae, equating absence of hyphae in fossil specimens with evanescent hyphae in modern species. *Microthyriacites* and *Microthallites* thus differ basically in the interpretation of the significance of the absence of free hyphae. In *Microthyriacites* there are no free hyphae and one does not know whether they were originally present or not. In *Microthallites* there are no free hyphae and it is assumed that this is because they were evanescent.

Absence of hyphae in fossil specimens may be due to : (1) absence of free hyphae at any stage in the living organism ; (2) preservation of fruiting bodies in which free hyphae had degenerated (i.e. evanescent hyphae) ; (3) non-preservation of free hyphae or destruction of hyphae during the maceration process used to prepare the specimen for study. It seems difficult to determine which of these is responsible for the observed state in fossil material, particularly if material is sparse and fragmentary.

Evanescence of hyphae can only be determined if the same specimens are studied at different developmental stages. This is impossible with fossil material. Some evidence may be gained if apparently mature fruiting bodies lack hyphae but it may be difficult to determine if fossil fructifications are mature or not. One cannot discount mechanical damage as the cause of apparent dehiscence and so dehiscence has to be used as evidence of maturity with great caution.

In at least some fossil forms from Kiandra absence of hyphae in a particular series of specimens is due to non-preservation of hyphae. Many specimens of *Plochmopeltinites masonii* (see below) lack free hyphae, while they are well-developed in other specimens. If insufficient material of this form had been available for study, a series of fruiting bodies which lacked free hyphae could have been described. In this case absence of free hyphae in a particular series of specimens is insufficient basis for a statement that they do not occur at all. I suggest that the absence of free hyphae in *Microthallites* is equivalent to insufficient information regarding the presence of free hyphae and I regard *Microthallites* as a synonym of *Microthyriacites* and hence of *Phragmothyrites*.

Cookson (1947), discussing form-genera created for fossil microthyriaceous fungi stated : " In order to minimise their number, generic descriptions are made as broad as possible ; distinctions, which amongst living species would be certainly considered of generic rank, being regarded as only of specific value."

This advice is worth heeding in the light of more recent taxonomic work on microthyriaceous fungi (von Arx and Müller, 1954 ; Müller and von Arx, 1962), particularly in cases where presence or absence of free hyphae has been used to separate form-genera. Müller and von Arx's classification in many instances cuts across the separation of genera into subfamilies used by Stevens and Ryan (1939).

Within the family Microthyriaceae, Stevens and Ryan (1939) separated genera into subfamilies on mycelial characters. Genera with evanescent free hyphae were placed in the Microthyrieae; those with a persistent superficial mycelium in the Asterineae. Both Cookson (1947) and Dilcher (1965) equated absence of hyphae in fossil specimens with evanescent hyphae in the fossils as living organisms.

In view of the difficulty of using hyphal characters with any degree of certainty for classifying microthyriaceous fungi, the structure of the fruiting bodies is the most important character. On this basis it seems impossible to distinguish between *Phragmothyrites* Edwards, *Microthyriacites* Cookson and *Microthallites* Dilcher. Dilcher (1965) commented that *Microthyriacites* "is very useful for classifying the poorly preserved and isolated fruiting bodies often found in palynological investigations." If, however, the separation of *Microthyriacites* and *Microthallites* were retained, it would be possible for specimens of the same form to be placed in different genera depending on whether found isolated in palynological residues or on the surface of cuticle. The scattering of closely related and perhaps identical forms in a number of artificial genera appears to me to be undesirable.

The fossil forms included by Cookson (1947) and Dilcher (1965) in *Asterothyrites* Cookson all have delicate free hyphae. The fruiting bodies are very similar to those of *Phragmothyrites* and would certainly be included in that genus if found without attached hyphae. Several fruiting bodies of *Phragmothyrites delicatus* described above lack free hyphae, while others have them. I have preferred not to maintain the separation of *Microthyriacites* Cookson and *Asterothyrites* Cookson on the basis of hyphal presence alone, and both genera are here regarded as synonyms of *Phragmothyrites* on the basis of fruiting body structure. The two fossil species described above as probably belonging to or related to *Asterina* could be included in *Asterothyrites* Cookson. However, the difference in fructification structure between them and the species described by Cookson is so great as to make such a classification undesirable.

10. *Callimothallus* Dilcher

Callimothallus pertusus Dilcher

Fructifications indistinguishable from those described by Dilcher (1965) from the Eocene of Tennessee are common on the lower surface of leaves of ?Lauraceae from Kiandra, often associated with *Plochmopeltinites masonii.*

Specimens from Kiandra are rounded, often slightly lobed, composed of radiating dichotomously branched hyphae (Pl. VI, fig. 1). Individual cells are 3·5–(11·0 ; 1·6 ; 100)–15 μm long × 3–(5·1 ; 1·0 ; 100)–7·5 μm wide, dimensions which agree with those originally given by Dilcher.

Callimothallus was defined as lacking free hyphae. Several specimens from Kiandra appear to have delicate superficial free hyphae, usually poorly preserved. In some specimens the hyphae radiate from beneath the fruiting body and in some, where the upper wall has fragmented, free hyphae can be seen apparently attached to a pale basal layer (Pl. VI, fig. 2). The hyphae are very pale brown to colourless and stain readily with methylene blue. They are indistinctly septate, composed of rectangular, thin-walled cells, often with slightly bulging walls. Most cells have a distinct pore 1–2 μm diameter in the lower face, often surrounded by a darker rim in stained specimens. The pores probably represent the position of penetration of the cuticle by haustoria and in a few cases small processes extend into the cuticle from the pore.

The only difference between *Callimothallus* and species of *Phragmothyrites* lies in the presence of pores close to the proximal end of the cells. Rao (1958) described *Microthyriacites sahnii* as having " one or more small aperture-like areas ". This name is invalidly published as Rao did not cite type material. Re-examination of the material would be necessary to determine whether Rao's specimens could be included in *Callimothallus*. Sen (1966) described a microthyriaceous fructification in which each cell has a pore-like structure towards the centre.

11. *Plochmopeltinites* Cookson

Plochmopeltinites masonii Cookson emend.

Pl. xi, figs 7–8 ; Pl. xii, figs 1–4.

Fructifications superficial, scattered, occasionally crowded and confluent, rounded, glabrous, ostiolate, up to 200 μm diameter ; margin entire-sinuate or irregularly lobed. Covering membrane radiate, prosenchymatous, composed of slender wavy hyphae 2–5 μm thick, those of the central area often thicker-walled than those towards the periphery. Some hyphae may extend beyond the ascoma as free hyphae. Ostiole up to 25 μm diameter, surrounded by slightly raised border of small, thick-walled cells. Free hyphae, if present, indistinctly septate, sometimes forming a pellicle.

Holotype. P26034, National Museum, Melbourne, Victoria. Cookson, Proc. Linn. Soc. N.S.W., 72, 212, Pl. XIII, fig. 14, 1947. Specimens showing hyphae : DAR 17236 (slide), DAR 17238 (slide), cuticle of ?Lauraceae, Kiandra, N.S.W., Lower Miocene.

Remarks. Cookson (1947) recorded this species from Kerguelen Is., Kiandra, and Traralgon, Victoria. Specimens from Kiandra were recorded on fragments of unidentified cuticle. Comparison of the type specimen with those described here leaves little doubt that the same species is involved.

Fructifications in which the ostiole is fully developed are 68–(112 ; 20·5 ; 54)–157 μm diameter, which considerably extends the range for the species given by Cookson. The wall of the fruiting body is convex and often folded. It is composed of a single layer of hyphae which branch repeatedly forming a sinuous plectenchyma (Pl. XII, figs 1, 2). The fructification is, however, distinctly radiate. Many hyphal branches end blindly against adjacent hyphae. The cells are variable in size and shape, usually 1–3 μm wide at the septa and 2–4 μm wide in the expanded portion of the hypha proximal to branching. The ostiole is surrounded by a slightly raised rim of small rectangular to irregular cells with walls *ca* 1 μm thick. In many specimens the centre of the ostiole is occupied by pale cells with very thin walls (Pl. XII, fig. 3). These cells are mostly 2–4 μm long × 2–3 μm wide. The ostiole opening presumably developed as a result of breakdown of these delicate cells.

Many fructifications have free hyphae but specimens lacking a free mycelium are common. This is probably a preservational feature. Individual colonies may be up to 2 mm across and are often confluent. Hyphae are 2–4 μm wide, straight, and widely spreading with opposite or alternate branches at irregular intervals. In some specimens the hyphae form a pellicle. Indistinct cross-septa divide the hyphae into cells 7–(12·0 ; 2·7 ; 50)–21 μm long. Hyphae towards the periphery of a colony are generally paler than those in the centre, with thinner walls. Many hyphal cells have a small indistinct pore in the lower face. In one specimen a thin hyaline process extends through the cuticle and possibly represents haustorial penetration of the host leaf. There is no evidence of hyphal ramification under the cuticle.

Numerous young fruiting bodies are scattered along the hyphae, often in close proximity to each other. The fructification first appears as a small outgrowth of radiate hyphae either from a medial hyphal cell or terminal on a short lateral branch. Young fructifications are almost hyaline, often with a slightly thickened margin (Pl. XI, fig. 7), but become darker in colour as size increases. The ostiole with its thickened rim is not apparent until the fructification is of considerable size.

Two-celled spores occur in close association with some fruiting bodies (Pl. XII, fig. 4). They are light brown, conglobate, 1-septate, constricted, *ca* 14 μm long × 8 μm wide. Spores have been seen lying on the outer face of fructifications close to the ostiole, and scattered on the cuticle, but none have been seen attached to hyphae or within a fructification and their assignation to this form is questionable.

Cookson (1947) included *Phlochmopeltinites* in the family Micropeltaceae. Alvin and Muir (1970) pointed out that the radiate nature of the thyriothecium in *Plochmopeltinites* points to the Microthyriaceae rather than to the Micropeltaceae in which the thyriothecium is strictly non-radiate.

Family Trichopeltaceae

12. *Trichopeltinites* Cookson

Trichopeltinites kiandrensis Selkirk, sp. nov.

Pl. IV, figs 1–6 ; Pl. V, fig. 1.

Mycelium a radiate prosenchymatous membrane one cell thick ; no free outgrowths from the margin. Mycelial membrane linear, branched, often almost circular where crowded. Individual hyphae dichotomously branched, septate ; cells square to rectangular, 4–(11·8 ; 3·7 ; 143)–26 μm long × 2–5 μm wide ; hyphal walls straight, *ca* 0·5 μm thick. Fructifications formed centrally under the mycelial membrane, 50–(106 ; 34·4 ; 21)–185 μm diameter. Cells above fructifications markedly shorter than elsewhere in the membrane, 4–(6·4 ; 1·6 ; 151)–10·5 μm long, thick-walled. Upper wall of fructification of radiate dichotomously branched hyphae.

Holotype. DAR 17205 (slide), leaf of ?Myrtaceae, Kiandra, N.S.W., Lower Miocene. Pl. IV, figs 1–4.

Remarks. Cookson (1947) commented on the close similarity of *Trichopeltinites pulcher* to the modern *Trichopeltis retans* Speg. The fossil form described above is very similar. The taxonomy of the modern species is somewhat confused. Hughes (1953) regarded *Trichopeltis* Speg. as a synonym of *Trichothyrium* Speg. (Trichothyriaceae). Batista *et al.* (1957) proposed the name *Trichopeltum* to replace *Trichopeltis* and several species of *Trichopeltum* have been described. In these, as in the fossil form, the fructification is developed beneath the mycelial membrane. In *Trichothyrium* the ascomata are superficial.

Colony shape in *Trichopeltinites kiandrensis* is very variable. All gradations from narrow linear thalli to almost circular colonies with tongue-like lobes occur (Pl. IV, figs 1, 2).

There are no indications of development of colonies from recognisable spores. Some small colonies have a zone of irregularly arranged rectangular to isodiametric cells from which the radiate structure of the membrane originates. Ultimate divisions of hyphae at the membrane margin are approximately at right angles to hyphae in the centre. These ultimate segments sometimes give a characteristic fringed appearance to the membrane (Pl. IV, fig. 6). Such fringing growth is common in comparable modern species.

Fructifications occur in most colonies. They appear as darker areas in the membrane, due to the thickened walls of cells over the fruiting body (Pl. IV, fig. 2). In some specimens traces of the upper wall of the fructification developed beneath the vegetative membrane are present. The radiate dichotomously branched hyphae of the wall appear to be outgrowths of the lower face of cells of the membrane (Pl. IV, fig. 5). One fructification from which the overlying mycelial membrane is missing shows hyaline cells which may represent a basal layer of a fructification (Pl. IV, fig. 4).

Many fructifications have a small centrally placed hole which probably represents a lysigenous pseudo-ostiole as developed in modern species (Stevens, 1925). The presence of such a structure may mean that a fructification is mature but as no spores have been seen in any fruiting bodies this interpretation is questionable. The pseudo-ostiole is first visible when a few central cells of the membrane have broken down (Pl. IV, fig. 3). More and more cells are involved and the original position of the fructification is eventually represented by a hole in the thallus, as in *Trichopeltinites fusilis* (Dilcher, 1965). Separation of all the cells above a fructification as described in *Trichopeltinites fusilis* also occurs in Kiandra specimens but a small pseudo-ostiole is always present in the centre and simultaneous separation of all cells does not appear to be a regular feature in this species.

A few specimens on DAR 17254 appear to have been attacked by a parasitic form. Small hyphae *ca* 1 μm thick occur in many of the membrane cells and frequently pass through the lateral walls into adjacent cells (Pl. V, fig. 1). Pores *ca* 0·5 μm diameter in the upper surface of the membrane appear to represent points of entry of the parasite. There does not seem to be any modification of the growth pattern of the membrane in response to penetration by the parasite.

Trichopeltinites kiandrensis appears to be intermediate between *Trichopeltinites pulcher* (Cookson, 1947) and *Trichopeltinites fusilis* (Dilcher, 1965) (see Table 3).

TABLE 3

Comparison of Trichopeltinites pulcher, Trichopeltinites fusilis *and* Trichopeltinites kiandrensis

	T. pulcher	*T. fusilis*	*T. kiandrensis*
Mycelial Membrane Shape	Narrow-elongate to Leaf Like	Circular to Tongue-shaped	Narrow-elongate to Circular
Mycelial membrane width	18–150 μm	30–500 μm	34–188 μm
Cell size	5–8 μm × 3–7 μm	8–25 μm × 2–4 μm	4–26 μm × 2–5 μm
Fructification diameter	72–90 μm	25–50 μm	50–185 μm

On the basis of cell length *Trichopeltinites kiandrensis* appears very similar to *Trichopeltinites fusilis* although no statistical comparison is possible since Dilcher gave only upper and lower limits for cell size. There is some overlap with *Trichopeltinites pulcher* but cells of the latter species are generally smaller. Hyphal widths are comparable in all species. On the basis of fructification diameter, *Trichopeltinites kiandrensis* is closer to *Trichopeltinites pulcher* but there is considerable overlap with *Trichopeltinites fusilis* if small fructifications, lacking a pseudo-ostiole, are included in the measurements. Measurements of fructification diameter in the three species may not be based on comparably mature specimens and the character is best used with caution for distinguishing the species. *Trichopeltinites kiandrensis* may easily be distinguished from the other species because of the difference in size between cells over the fruiting bodies and those elsewhere in the mycelial membrane. In the absence of such qualitative characters there are difficulties in separating fossil specimens on the basis of thallus shape and quantitative characters. Modern species are most easily distinguished on ascus and spore characters. Shape of the mycelial membrane is probably of minimal value.

Family Micropeltaceae

Sub-family Dictyopeltoideae

13. *Dictyotopileos* Dilcher

Dictyotopileos sp.

Specimens. DAR 17241, 17242, 17244, leaves of ?Lauraceae, Kiandra, N.S.W. Lower Miocene.

Remarks. The specimens from Kiandra closely resemble those described as the basal portion of the subiculum in old specimens of *Dictyotopileos yalensis* (Dilcher, 1965). The largest specimen is considerably larger than those described by Dilcher. In *Dictyotopileos yalensis* the subiculum is covered by a reticulate network of anastomosing hyphae and the whole structure is polyostiolate. Specimens from Kiandra are comparatively poorly preserved, with only fragments of a reticulate network in some specimens. Owing to the poor preservation of the Kiandra specimens they are not assigned to a species within *Dictyotopileos* although they clearly represent a form very similar to *Dictyotopileos yalensis*.

Colonies are linear to circular with irregular lobes (Pl. V, figs 2–4). Large specimens have irregular holes in the thallus. Colonies are superficial and there is no evidence of parasitic action on the leaf bearing them. The smallest specimens cover only a few epidermal cells (Pl. V, fig. 7). The largest is 1 mm across.

In most specimens only the basal portion of the subiculum is present, superficially very similar to the mycelial membrane of *Trichopeltinites*. The subiculum is distinctly radiate (Pl. V, figs 3, 4), composed of very pale brown to colourless hyphae forming a membrane one cell thick. Hyphae are dichotomously branched and septate but septa are only distinct in specimens which have been stained in methylene blue. Cells are 2–(3·9 ; 1·0 ; 65)–7 μm long × 2–(2·7 ; 0·4 ; 65)–5 μm wide, square to rectangular.

The subiculum is bordered by 1–2 rows of dark thick-walled (*ca* 1 μm) cells and thickened cells also occur around holes in the subiculum. Small areas of thick walled cells may occur where different lobes of the subiculum meet, or an indistinct line of contact of the lobes may be visible. In areas of most recent growth of the subiculum thick-walled cells are absent or thinner-walled, and small lobes grow from the older areas (Pl. V, fig. 5). The thick-walled cells at the margin of the subiculum are above the pale hyphae of the radial thallus and appear to represent the remains of an upper layer.

Free hyphae occur at the margin of the subiculum and where the subiculum is interrupted (Pl. V, fig. 6). Hyphae are pale brown to almost colourless, irregularly septate and branched. They are produced only from areas of thick-walled cells and are not developed from small lobes of new growth. Hyphae do not extend far over the cuticle. Dark ring-like areas formed by proliferation of dark hyphae on the upper surface of the subiculum are present in one specimen (Pl. V, fig. 2). The hyphae form an irregular pseudoparenchyma and darker free hyphae extend over the surface of the thalloid membrane. In a small area of one specimen dark hyphae form a reticulate network over the subiculum close to the margin.

14. Fossil forms of doubtful affinity

(a) ?Family Trichothyriaceae (Capnodiales)

Fructifications of a form closely resembling the Trichothyriaceae occur on the upper surface of leaves of ?Myrtaceae, associated with hyphae of *Asterina kosciuskensis* and *Meliolinites nivalis* (DAR 17253). The fruiting bodies are often crowded, circular, or flattened on one side if in close contact (Pl. XII, figs 5, 6). The largest specimen is 108 μm in diameter. The wall has distinct upper and lower layers (Pl. XII, fig. 5). The fructification is often split along the junction of upper and lower walls and the isolated lower layer is occasionally found on the cuticle (Pl. XII, fig. 7).

The upper wall is much darker than the lower layer and consists of radiate, dichotomously branched hyphae with distinct cross-septa (Pl. XII, fig. 5). Cells are square to shortly rectangular, 1·5–(3·4 ; 0·9 ; 213)–8·5 μm long × 1·5–(3·2 ; 0·6 ; 213)–5·5 μm wide. Cells towards the centre of the fructification are often slightly irregular in shape. The paler lower layer has a similar structure to the upper wall. The hyphae radiate from an apparently structureless central area and are divided by very indistinct cross-septa, often visible only towards the margin. Most of the margin is smooth and entire but some marginal cells may have small projections.

All specimens over 60 μm diameter have a distinct ostiole in the centre of the upper wall. The ostiole appears to have formed by breakdown of some central cells of the upper wall and varies from 7–17 μm diameter. In many specimens the remains of cells can be seen within the ostiole cavity. The ostiole is slightly raised above the general level of the upper wall but is on the same level as the margin of the fructification.

A few almost colourless young fructifications have been recognised. There are indications of the ostiole at an early stage, although the differentiation of the two layers of the wall is not obvious. One of the small specimens has a distinct slightly darker square cell close to the centre of the upper wall (Pl. XII, fig. 8). The youngest specimen seen is almost colourless.

Many fructifications have fragmentary pale hyphae in contact with the lower wall, resembling those seen in close contact with hyphae of *Asterina* and *Meliolinites*. I have been unable to demonstrate organic continuity between hyphae and fructifications.

Remarks. All modern members of the Trichothyriaceae are hyperparasites on other epiphyllous fungi, the hyphae forming a plate-like thallus over the host hyphae or a reticulum over the surface of the leaf between the host hyphae (Hughes, 1953).

Perithecia of modern Trichothyriaceae and Microthyriaceae appear to be very similar. The perithecia of the Microthyriaceae are dimidiate, those of the Trichothyriaceae complete. Gaumann (1928) regarded the Trichothyriaceae " as Microthyriaceae which have become specialised for parasitism on other, especially asterinoid, fungi . . . As the members of this family do not themselves directly parasitise leaves, their fructifications lie on their own mycelium unprotected beneath by the cuticle of the host. Consequently the basal stromatic parts attain a more marked cover layer character ; they become brown and pseudoparenchymatic . . ."

The only fossil member of the Trichothyriaceae is *Trichothyrites pleistocaenicus* from lower Pleistocene deposits in Minnesota (Rosendahl, 1943). This species was described as having free hyphae attached to the stems and leaves of moss plants. No organic connection between the fructifications and hyphae was proved and the possibility remains that the hyphae are those of the host fungi growing on the moss rather than those of the fructification. Rosendahl commented on the similarity of fructifications of *Trichothyrites pleistocaenicus* to those of *Microthyrium* spp. Godwin and Andrew (1951), discussing an unidentified ascoma apparently belonging to the Microthyriaceae, list *Loranthomyces* (Trichothyriaceae) as a possible identification of the form. Rosendahl (1943) commented that it is next to impossible to determine from the surface aspect alone whether the fruiting bodies are dimidiate or complete. All specimens from Kiandra are seen in surface view and the small number of fructifications has precluded sectioning. The basal layer of the fructification is well-developed and the structure of the entire fruiting body resembles that of the Trichothyriaceae.

In *Trichothyrium reptans* the lower wall of the fructifications is composed of brown, radiating, septate hyphae but is paler than the upper wall and not so distinctly septate (Hughes, 1953). The upper and lower walls often separate at the margin, a conspicuous feature of the fossil specimens from Kiandra. In modern *Trichothyrium* spp. and in *Trichothyrites pleistocaenicus* the ostiole is borne on a small papilla, above the general level of the upper wall (Hughes, 1953 ; Rosendahl, 1943). The ostiole in the Kiandra specimens is similarly above the general level of the wall but in the absence of sections the presence of a papilla cannot be verified.

In *Trichothyrium asterophorum* the upper wall of the young fructification bears short erect hyphae from a couple of the central cells (Hughes, 1953). The small darker cell near the centre of the small fructification in the fossil form may represent the base of such an erect hypha. In the modern species all hyphal connections to the thyriothecium are with the lower wall. The hyphae seen in contact with the fossil fructifications all appear to be in contact with the lower wall and no hyphae have been seen in contact with the upper wall in any specimens.

The fossil fructifications thus appear to be very close to those of the Trichothyriaceae but a final assignation of the form will depend on better preserved material and sectioning of the ascoma to determine whether it is complete or dimidiate.

(b) cf. *Trichopeltheca*

A single specimen of this form occurs on the upper surface of a ?myrtaceous leaf (DAR 17205).

The mycelium forms a long strap-shaped thallus one cell thick. Individual hyphae are laterally adpressed and are composed of square to rectangular cells 6–(8·9 ; 1·5 ; 55)–14 μm long × 5–(7·0 ; 0·9 ; 55)–8·5 μm wide. Hyphae are very pale brown to almost hyaline. Aggregation of the hyphae into a thallus is not complete. At the edge of the thallus some hyphae grow out at an angle. Similar separate hyphae appear at the growing face of the thallus. In places the thallus is broken up and the individual hyphae are separate from each other but grow parallel (Pl. X, fig. 4). Hyphae are occasionally branched, the two hyphae formed as a result of branching growing parallel in close contact. Branching appears to be lateral. Where an obstacle such as a hair base occurs in the path of the hyphae they grow around it.

Fragments of dark brown septate filaments occur scattered over the surface of the thallus (Pl. X, fig. 5). Septa divide the filament into cells 8–22 μm long × 4–8 μm wide. Some filaments show an expanded terminal cell and the cell of the filaments next to this expanded cell is generally much longer than the other cells, which are usually almost square. The dark filaments appear to have been aerial portions, borne on the surface of the prostrate thallus. I have been unable to determine whether the expanded " terminal " cells are basal or apical since no filament has been seen definitely attached to the thallus.

Some cells of the thallus have a pronounced dark thickened ring on the upper face. From this, in some cases, can be seen projecting portion of what appears to be an aerial filament. Thallus cells bearing these projections appear normal in other respects. There is no definite thickening of the walls of the cell, which are the same colour as the other hyphal cells.

The thallus has a superficial resemblance to that of *Trichopeltheca* (Hughes, 1965). In this genus the thalli are variously shaped and free hyphae occur at the edges and growing tip of the thallus. Hughes' figures show setae of *Trichopeltheca* arising from thickened cells of the thallus which have the same ring-shaped thickening as in the fossil specimens, although the cells in the modern form have thick walls and are darker in colour than the rest of the thallus. These basal cells in *Trichopeltheca* resemble the " terminal " cells in the aerial filaments of the fossil. Setae and phialophores of *Trichopeltheca* are multiseptate and distinguished only by presence/absence of phialides.

Whether the aerial filaments of the fossil form are setae or have a spore-bearing function is not known.

(c) Mycelial setae cf. *Vitalia*

Pl. XII, figs 9–12

Specimens of this form occur in large groups on the upper surface of leaves of ?Myrtaceae. Occasional isolated specimens also occur on the lower surface. The setae are borne on a multicellular base, 17–(29·8 ; 5·7 ; 100)–49 μm diameter.

The " cells " radiate from a central, polygonal to circular cell (Pl. XII, fig. 10). In larger specimens the radiate nature of the central portion of the base may be obscured. There is a progressive increase in number of cells with increasing size of the base. The cell walls in the centre of the base are thick and dark, becoming paler towards the margin. The periphery of the base is irregularly invaginated and the margin is very finely fimbriate, the extensions of the cells being almost colourless (Pl. XII, figs 10, 11).

Many cells, particularly those at the margin, have small pores *ca* 0·5 μm diam. in the upper wall (Pl. XII, fig. 9). More than one pore may be present in a single cell.

In side view the base appears as a small mound *ca* 9 μm high. The apex is slightly depressed and the structure has concave slopes from the centre towards the margin.

The thick-walled central cell represents the base of the seta which is broken off in most specimens. Complete setae have a size range of 44–(77·5 ; 15·4 ; 40)–119 μm. Fragments of setae apparently longer than this upper limit have been seen. The seta is dark brown, 4–11 μm wide at the base, and tapers gradually to an acute apex which may be slightly bent (Pl. XII, figs 11, 12). The base of the seta is slightly expanded and appears to extend almost to the lower surface of the base. The walls of the seta are *ca* 3·5 μm thick at the base, becoming thinner towards the apex. The apex has a continuous thick wall. One specimen has the seta divided by thin transverse septa (Pl. XII, fig. 12). In a few specimens the seta bases are associated with poorly preserved hyaline hyphae which may represent hyphae bearing the setae.

The seta bases and setae are very similar to those of *Vitalia rickiana* (Batista, pers. comm.). However, in the absence of fructifications and spores no exact identification can be made. Some *Chaetothyrium* spp. have very similar mycelial setae. The fossil form is also very similar to the setae figured for *Vitalia eckmanii* (Marasas and Rabie, 1966).

Mycelial setae very closely resembling the fossil form, if not identical with it, have been found on leaves of *Ackama* and *Bosistoa* from a number of localities in New South Wales. The setae are borne on much-branched, septate hyaline hyphae which form a pellicle over the surface of the cuticle. The hyphae associated with some of the fossil specimens appear to be similar. There are no fructifications or spores present in the modern material and no identification has been possible. The fossil specimens can be regarded as mycelial setae of a sooty mould closely allied to *Chaetothyrium* or *Vitalia.*

Ecological Significance of the Epiphyllous Flora

Fossil fungi which cannot be related to modern genera or species whose ecological requirements are known are of minimal value as climatic indicators. Fossil microthyriaceous fungi have often been regarded as indicating warm, moist conditions, but such interpretations need to be accepted with caution. Isolated microthyriaceous fruiting bodies occur over a wide latidudinal range in Pleistocene deposits of North America (Wilson, cited in Dilcher, 1965) and in deposits, including interglacial deposits, formed under a wide range of climatic conditions in Britain (Godwin and Andrew, 1951). Many isolated fossil fructifications resemble thyriothecia of *Microthyrium.* In New South Wales members of the genus are common in subtropical rain forest in coastal areas, but extend into sub-alpine areas and into low rainfall areas. Poorly identifiable fossil material belonging to form-genera such as *Phragmothyrites* may not reasonably be expected to indicate any specific climatic conditions. Dilcher (1965) concluded that generalised ecological arguments should not be based on such isolated fossil fungi but that such reports could be useful if used in conjunction with evidence derived from macrofossils and pollen.

The foliicolous ascomycetes are best developed in tropical and subtropical areas, but extend into other regions where conditions are suitable. There are wide geographic gaps in our knowledge of some of the groups (e.g. Meliolaceae) and detailed knowledge of distribution of genera and species is far from complete. Very little work has been done on Australian members of the group. Arnaud (1918) regarded the group as confined to areas where rainfall exceeds 1000 mm per annum and Cookson (1947) commented on the moisture dependence of the microthyriaceous fungi.

There is very little autecological data available on any members of the group but the work of Fraser (1937) on the distribution of sooty mould associations in New South Wales shows the moisture dependence of such fungi. She found that many species are highly resistant to extremes of temperature but that most are markedly affected by desiccation. Some of the associations Fraser studied contained members of the Trichopeltaceae and she regarded these associations as best developed in moist well-shaded situations. *Trichopeltis reptans* is resistant to extremes of temperature but colonies could not survive two weeks without water. Similar results were obtained with *Brefeldiella brasiliensis*, another member of the same family. *Trichopeltinites kiandrensis* and other fossil members of the family can probably be regarded as indicating moist conditions but the possibility that they may represent extinct taxa with greater tolerance should be borne in mind. A survey of hosts of Trichopeltaceae based on specimens in DAR shows that most are species which grow in rainforests or around their margins, while many occur along stream banks in drier areas.

A survey of hosts of *Asterina* spp. yields a similar pattern. Many hosts are rainforest species, while others occur in wet forests, rainforest margins and along creek banks. Australian species of *Asterina* have not been extensively studied and details of distribution are probably far from complete. However, the presence of *Asterina kosciuskensis* and related forms in the fossil flora probably indicates moist conditions.

Hansford (1953) gave host lists for all the then known species of Meliolaceae in Australia. Most hosts are species which grow in rainforests or moist gullies. The Meliolaceae, although best developed in the tropics and subtropics, extend into temperate regions. Arnaud (1946) recorded *Meliola* spp. in the high mountains of Europe. Ciferri (1954) reported members of the family in moist patches in xerophytic forests in the Dominican Republic.

Forms resembling members of the modern genus *Vizella* are represented in the fossil epiphyllous flora (Selkirk, 1972). *Vizella* has a wide range in Australia. Hansford (1956) recorded *Vizella gomphispora* on *Trochocarpa laurina* in the McPherson Range, southern Queensland. Swart (1971) described two species; one on *Banksia integrifolia* (near Tanja, N.S.W.), the other on *Olearia argophylla* (Kinglake National Park, Victoria). *Vizella interrupta* has been collected on *Tieghemopanax* in brush forests of the Hastings River Valley in New South Wales (DAR 4413). I have collected fungi which appear to be referable to *Vizella* on several hosts in subtropical rainforest in north-eastern New South Wales, as well as in temperate rainforests (on *Nothofagus*) and in moist gullies in the Sydney region. Swart (pers. comm.) has found *Vizella* on leaves of plants in dry sclerophyll forest near Geelong, Victoria, and on leaves of *Hakea* from Lake King, north of Esperance in Western Australia.

In New South Wales *Nothofagus* forests occur in areas where precipitation exceeds 1800 mm per annum and where winters are long and severe with occasional snowfalls (Baur, 1957). *Vizella* extends from such areas into the warmer subtropical forests, as well as into much drier areas. The area near Lake King in Western Australia is semi-arid with an annual rainfall of 250 mm to 350 mm. *Vizella discontinua* and the various species of *Entopeltacites* reported from Kiandra would not appear to be very useful climatic indicators in themselves.

The macrofossil and pollen flora from Kiandra indicates moist conditions. Gill and Sharp (1957) listed species present in a number of deposits in the Kiandra area. These lists are by no means a complete record of all forms present. The fossil flora contains elements which today would be typical of New Guinea lower montane rainforests, New Caledonian forests and temperate rainforests in Tasmania. In all these forests *Nothofagus* spp. are associated with members of the Podocarpaceae. Such forests are developed in regions of fairly high precipitation.

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EXPLANATION OF PLATES

PLATE II

Figs 1–9. *Asterina kosciuskensis* Selkirk, sp. nov. 1. DAR 17257, ×160, perithecium and free hyphae. 2. DAR 17216, ×500, young fructification. 3. DAR 17215, ×500, initial stage of fructification. 4. DAR 17216, ×500, young fructification. 5. DAR 17246, ×500, germinated spore with young hypha. 6. DAR 17219, ×1000, thin-walled spore in fructification. 7. DAR 17253, holotype, ×1000, thin-walled spore with germinal hyphopodium. 8. DAR 17253, holotype, ×1000, spore with thickened large cell. 9. DAR 17253, holotype, ×1000, spore with septate thickened large cell and developing hypha in small cell.

PLATE III

Figs 1–6. *Euthythyrites morenoinitis* Selkirk, sp. nov. DAR 17231, holotype. 1. ×285, linear ascoma with free hyphae. 2. ×1120, spores in ascoma. 3. ×500, young ascoma showing pale central band and radiate nature of wall. 4. ×500, young ascoma. 5. ×500, initial stage of fructification attached beneath hypha. 6. ×500, very young fructification.

Fig. 7. *Asterina kosciuskensis* sp. nov. DAR 17253, holotype, ×1000, germinated spore showing young hypha within small cell of spore.

PLATE IV

Figs 1–6. *Trichopeltinites kiandrensis* Selkirk, sp. nov. Figs 1–4, DAR 17205, holotype. 1. ×30, ribbon-like thalli. 2. ×120, crowded thalli. Note darker patches of thick-walled cells over the fructifications and distinct pseudo-ostioles. 3. ×510, detail of cells above fructification showing development of pseudo-ostioles. 4. ×510, fructification in which overlying thallus has broken away to reveal paler hyphae of basal layer. 5. DAR 17204, ×900, dichotomously branched hyphae beneath thallus, possibly representing upper wall of fructification. 6. DAR 17211, ×510, portion of linear thallus showing fringing lateral growth of hyphae.

PLATE V

Fig. 1. *Trichopeltinites kiandrensis* sp. nov. DAR 17254, ×600, parasitic hyphae within cells of thallus.

Figs 2–7. *Dictyotopileos* sp. Figs 2–6, DAR 17244. 2. ×45, large circular thallus with distinct edge of thick-walled cells. 3. ×225, ribbon-like thallus showing radiate nature of subiculum and thick-walled margin. 4. ×225, circular thallus showing radiate construction. 5. ×510, lobe of new growth produced from beneath thick-walled marginal cells. Note dichotomous branching of hyphae. 6. ×510, margin of subiculum with free hyphae produced from proliferating thick-walled cells. 7. DAR 17242, ×510, very young thallus.

PLATE VI

Figs 1–2. *Callimothallus pertusus* Dilcher. 1. DAR 17222, ×510, fructification. 2. DAR 17233, ×600, fragmentary fructification with associated free hyphae. Stained methylene blue.

Figs 3–6. *Phragmothyrites delicatus* Selkirk, sp. nov. Figs 3–5, DAR 17234, holotype. 3. ×900, early stage of fructification beneath hypha. 4. ×360, fructification and free hyphae. Note radiate construction of wall and thicker-walled cells towards centre of fructification. 5. ×900, portion of fructification showing central cells and pore in free hypha. Phase contrast. 6. DAR 17224, ×900, portion of fructification showing thin-walled cells towards margin.

PLATE VII

Figs 1–6. *Meliolinites nivalis* Selkirk, sp. nov. 1. DAR 17201, holotype, ×50, portion of colony showing hyphal branching and central hyphal disc. 2. DAR 17202, ×210, detail hyphae. 3. DAR 17201, holotype, ×110, hyphal disc. 4. DAR 17201, holotype, ×500, persistent spore attached to hyphae. 5. DAR 17201, holotype, ×900, detail hyphopodium. Note pore in lower face of head cell. 6. DAR 17201, ×900, haustorium.

Fig. 7. Sterile mycelium, probably Meliolaceae : Type 1. DAR 17209, ×510, detail mycelium.

PLATE VIII

Fig. 1. Sterile mycelium, probably Meliolaceae : Type 1. DAR 17209, ×120, portion of colony. Fig. 2. Sterile mycelium, probably Meliolaceae : Type 2. DAR 17200, ×510, detail hyphae. Note pore in lower face of head cell. Figs 3–4. *Meliolinites* sp. 3. DAR 17210, ×390, detail hyphae. 4. DAR 17208, ×510, spore. Fig. 5. *Phragmothyrites* cf. *fimbriatus.* DAR 17240, ×570.

PLATE IX

Figs 1–3. *Notothyrites kiandrensis* Selkirk, sp. nov. DAR 17266, holotype. 1. ×410 isolated fructification. 2. ×510, detail margin of fructification. 3. ×510, portion of fructification showing raised collar of dark, thick-walled cells surrounding ostiole.

Figs 4–6. *Phragmothyrites kiandrensis* Selkirk, sp. nov. 4. DAR 17207, holotype, ×600, fructification. 5. DAR 17214, ×600, fructification showing pale hyphae of basal layer. 6. DAR 17227, ×600, small fructification showing dichotomous branching of hyphae of the wall. Note absence of cross-septa.

Figs 7–9. *Phragmothyrites* sp. 1. 7. DAR 17247, ×900, fragmentary specimen. Note projections of amorphous material from margin. 8. DAR 17242, ×750, fructification. 9. DAR 17247, ×950, possible basal layer of fructification.

PLATE X

Fig. 1. *Phragmothyrites* sp. 1. DAR 17240, ×950, material left on cuticle after fructification has flaked off. Note lobing of marginal material.

Figs 2–3. *Phragmothyrites* sp. 2. DAR 17260. 2. ×900, detail of margin. Note protruding hyphae capped with zone of amorphous material. 3. ×165, fragment of large fructification.

Figs 4–5. cf. *Trichopeltheca.* DAR 17205, ×180. 4. general view of thallus. 5. septate filaments on thallus surface.

Fig. 6. *Asterina* or related genera : Species 1. DAR 17266, ×120, fructifications and hyphae.

PLATE XI

Figs 1–3. *Asterina* or related genera : Species 1. 1. DAR 17266, ×510, young fructification. 2. DAR 17266, ×600, spore associated with fragments of fructification. 3. DAR 17217, ×600, detail hyphae.

Figs 4–6. *Asterina* or related genera : Species 2. DAR 17221. 4. ×120, fructifications and hyphae. 5. ×510, detail portion of fructification. 6. ×510, fragments of hyphae with attached young fructification.

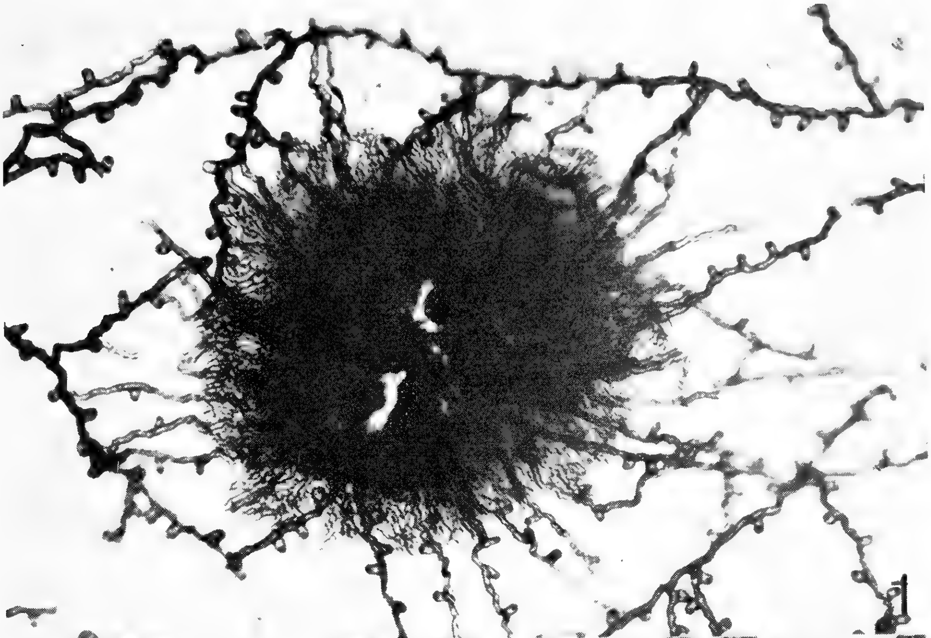
Figs 7–8. *Plochmopeltinites masonii* Cookson. 7. DAR 17262, ×900, hyphae with attached very young stages of fructifications. 8. DAR 17237, ×900, young fructification.

PLATE XII

Figs 1–4. *Plochmopeltinites masonii* Cookson. 1. DAR 17236, ×510, fructification. 2. DAR 17237, ×900, detail portion of fructification wall. 3. DAR 17237, ×900, detail of ostiole. 4. DAR 17237, ×900, spore-type associated with fructifications.

Figs 5–8. ?Trichothyriaceae. DAR 17253. 5. ×400, fructification with upper wall broken away revealing lower layer. 6. ×400, intact fructification. 7. ×480, isolated lower layer of fructification. 8. ×480, young fructification.

Figs 9–12. Seta bases and setae cf. *Vitalia.* DAR 17239. 9. ×1120, margin of seta base showing pores in marginal cells. 10. ×510, seta bases. 11. ×510, base with attached non-septate seta. 12. ×510, base with attached septate seta.



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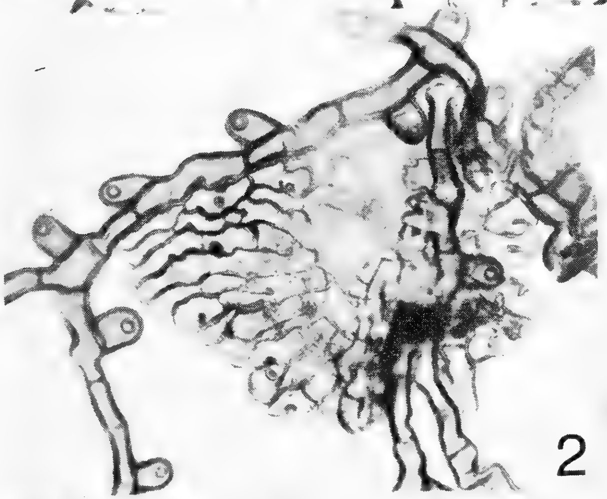

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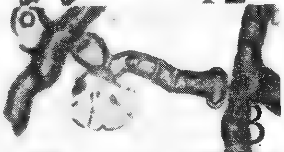

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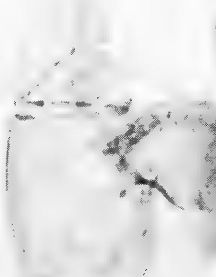

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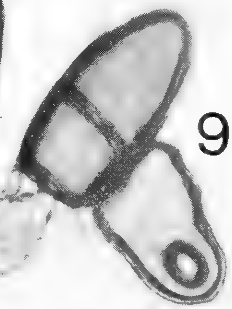

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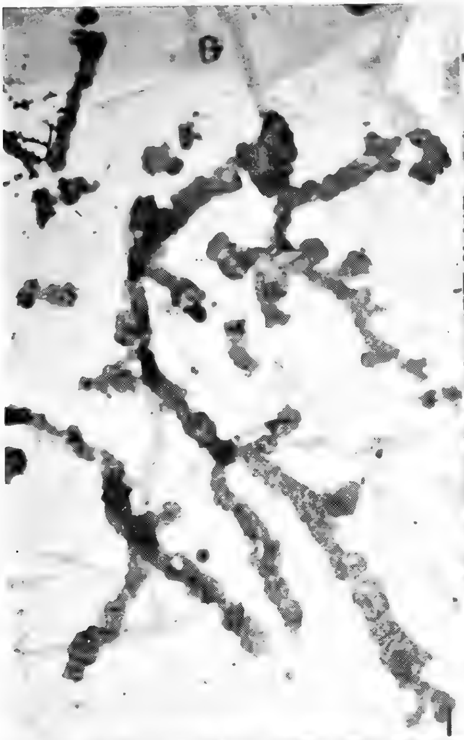

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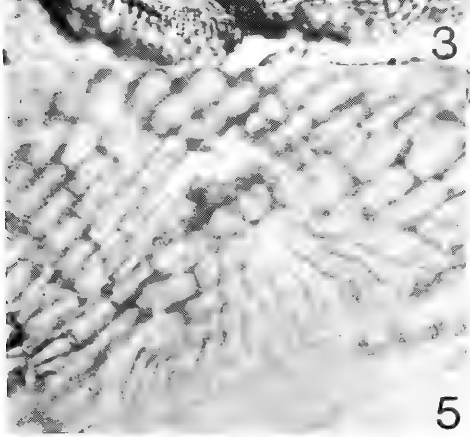
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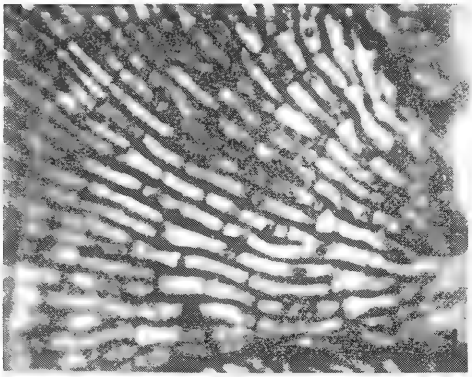

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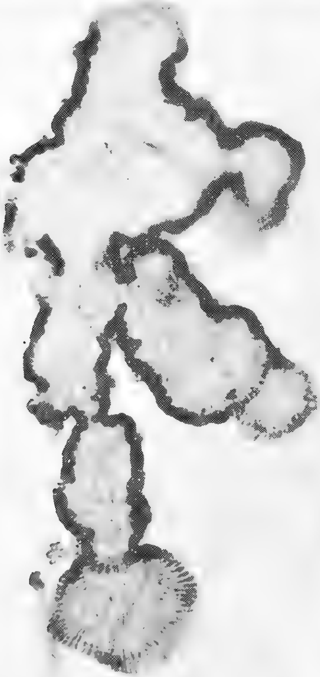

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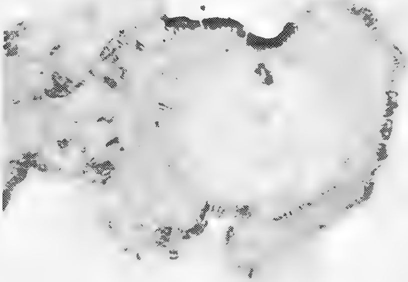

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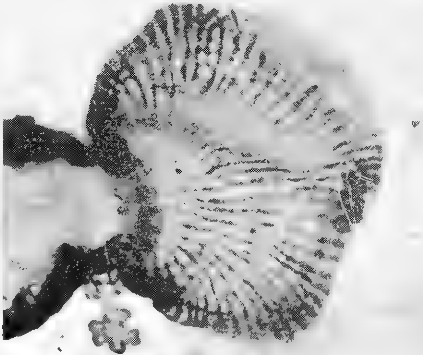

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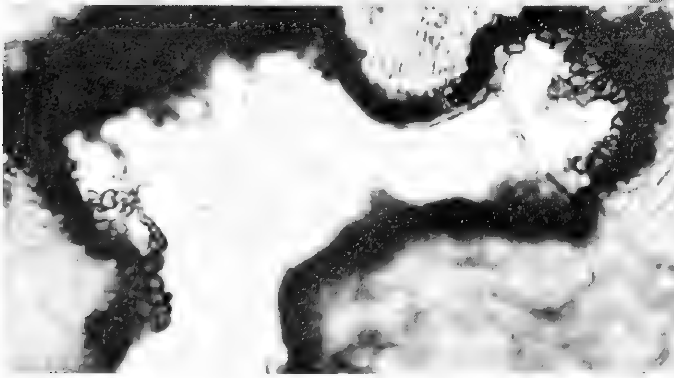

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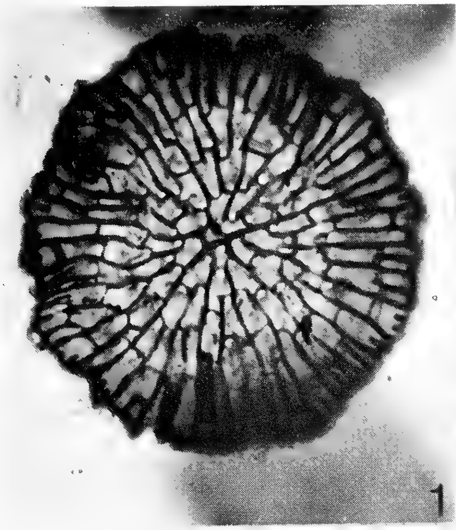

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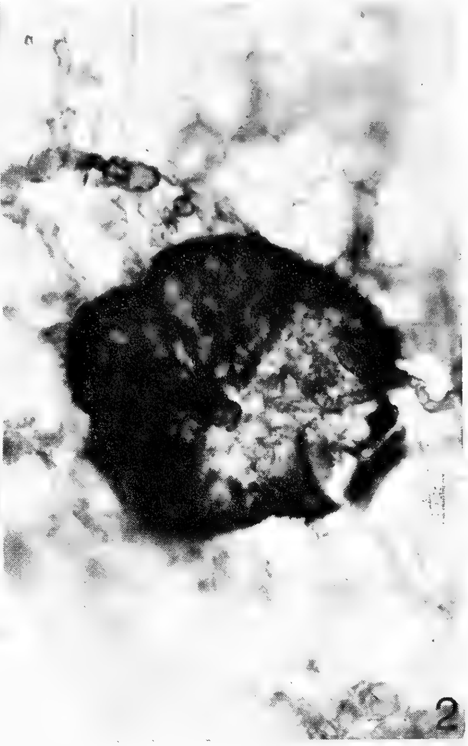

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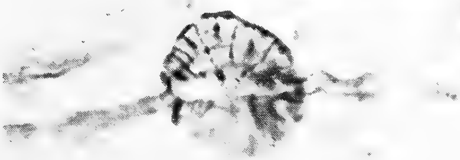

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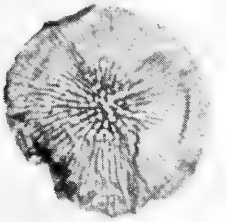

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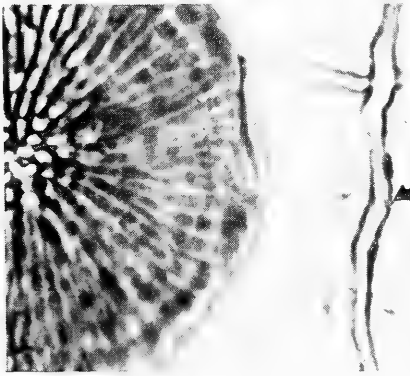

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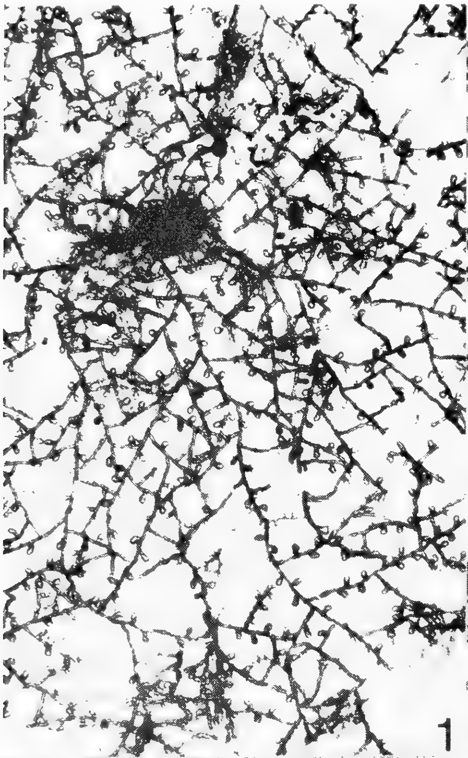
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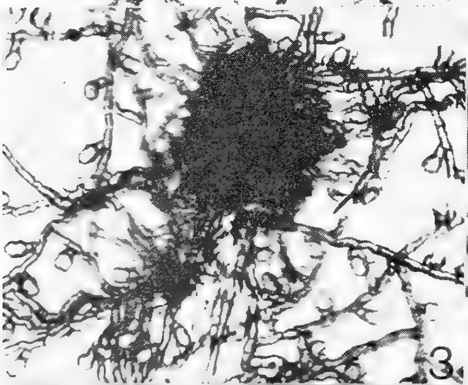
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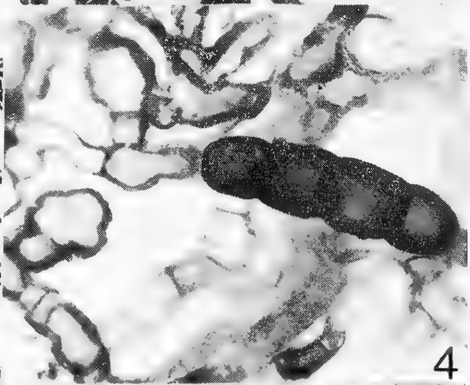
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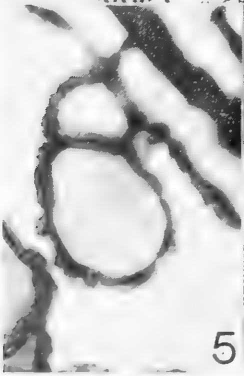
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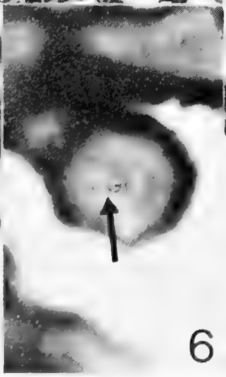
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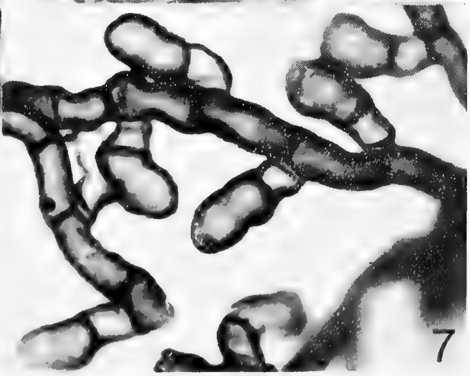
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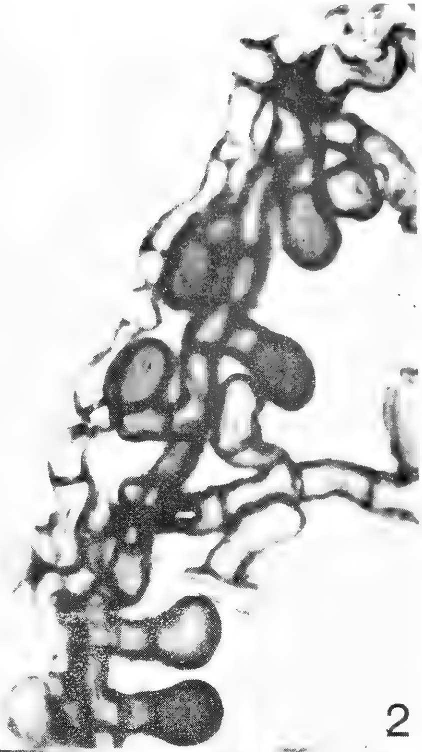
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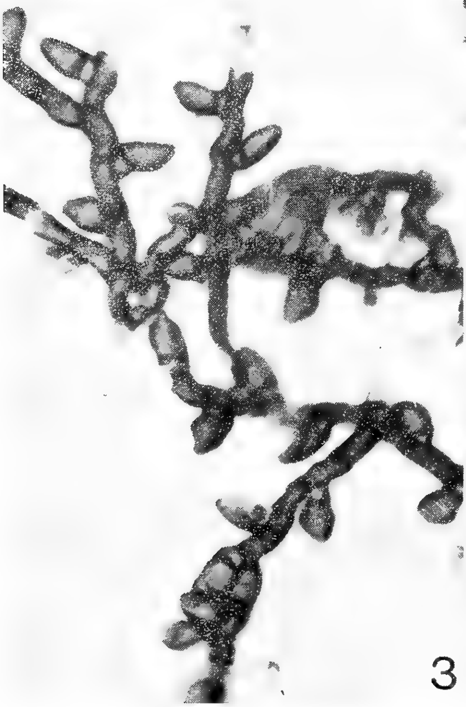
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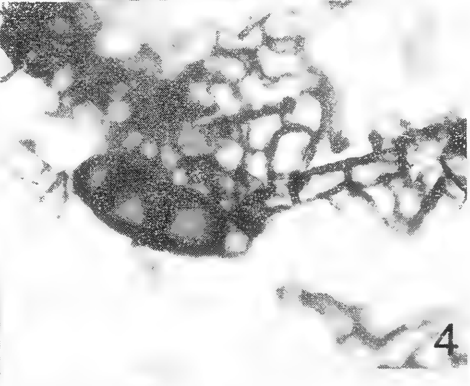
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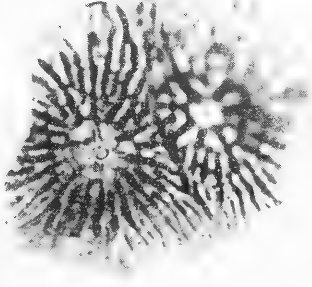
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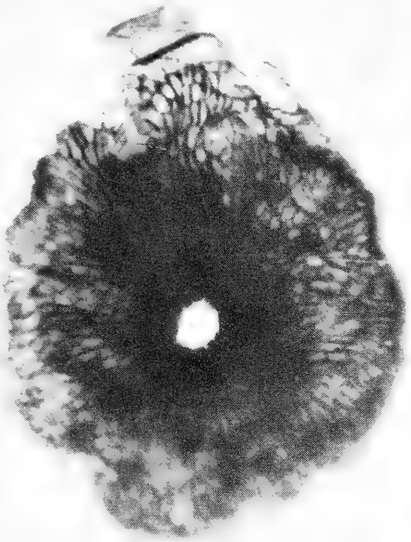

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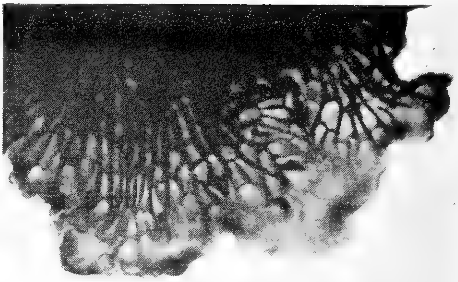

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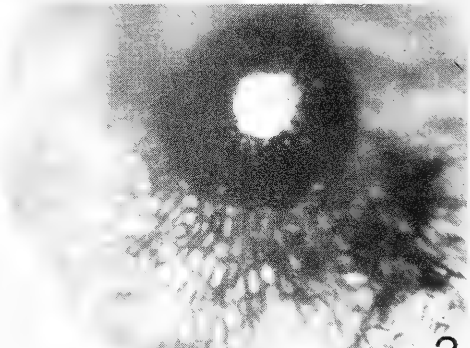

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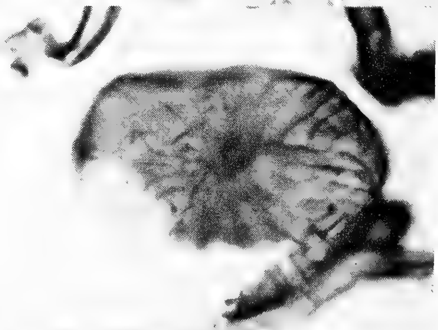

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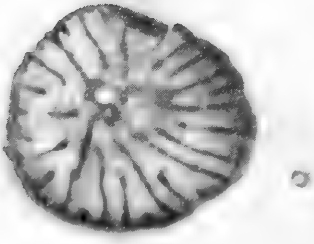

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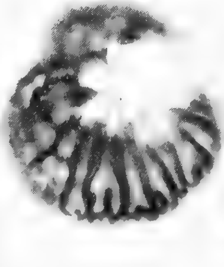

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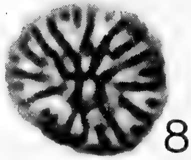

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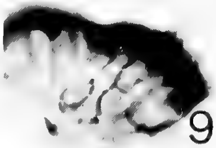

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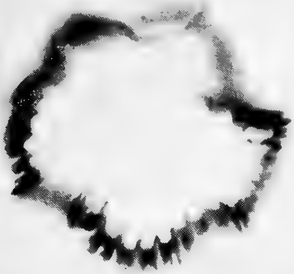

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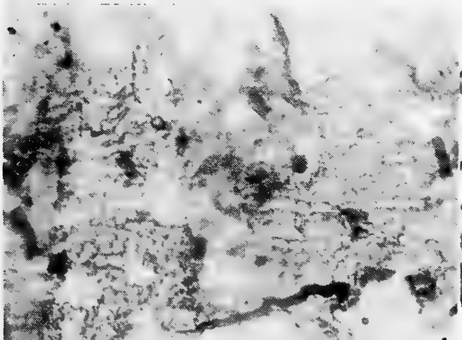

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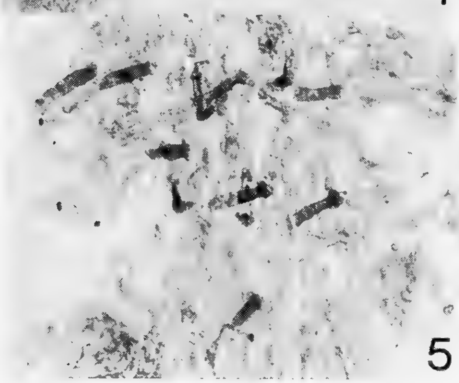

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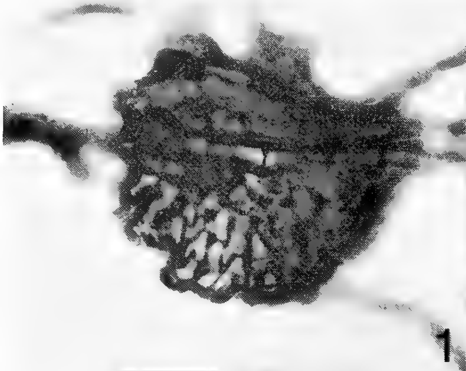
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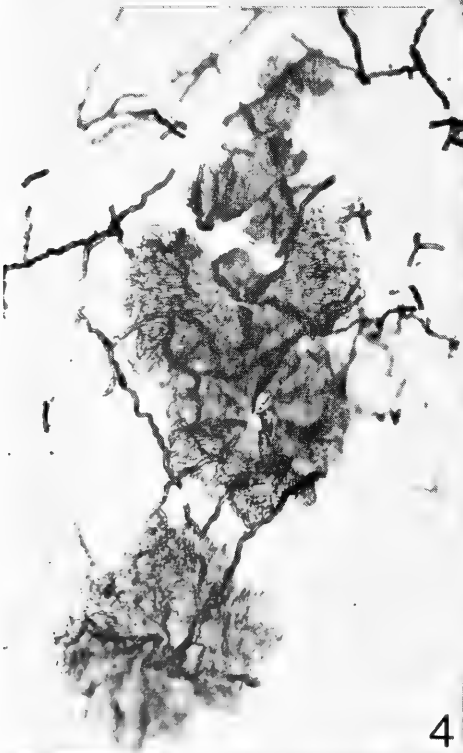
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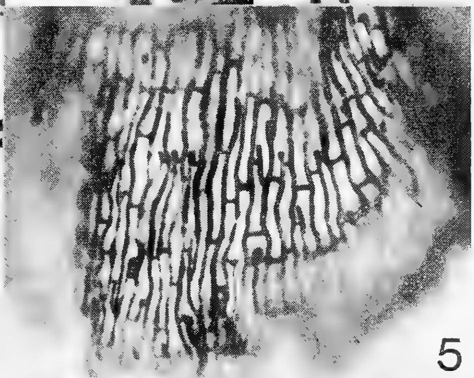
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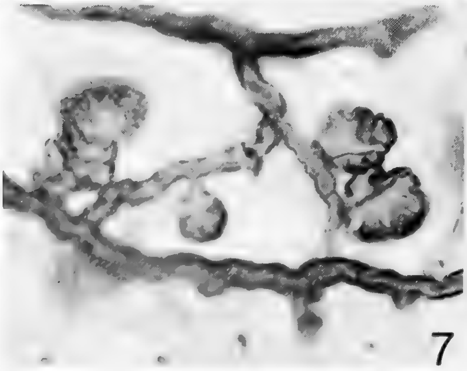
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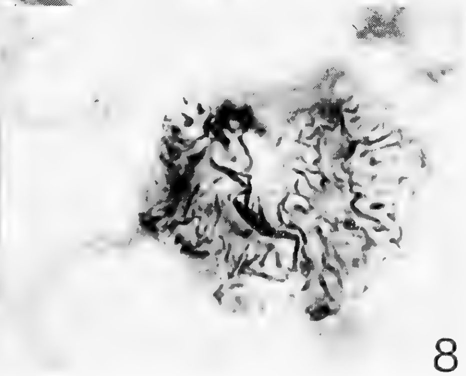
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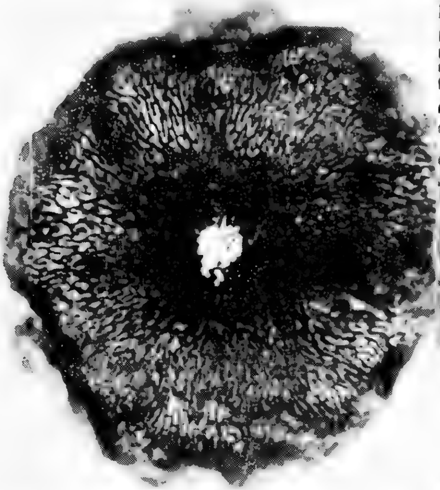
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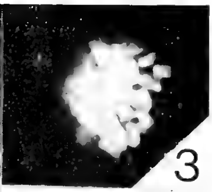
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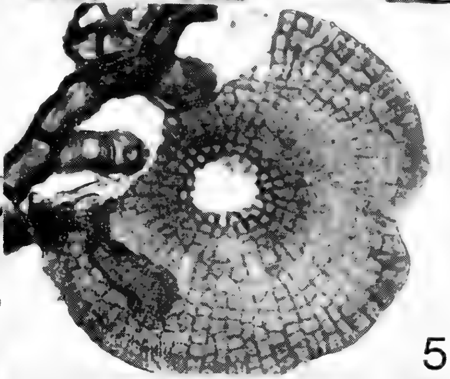
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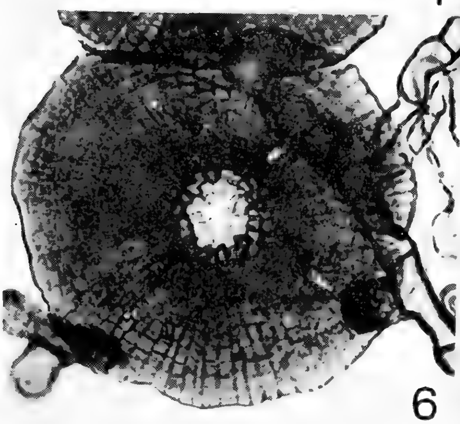
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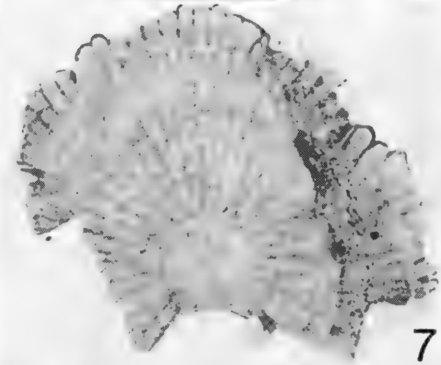
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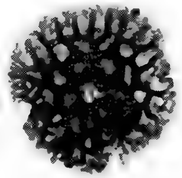

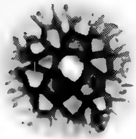

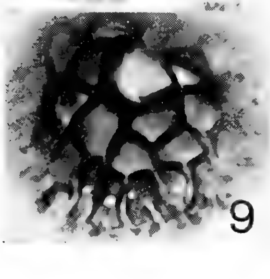
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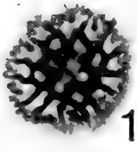
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THE FRUITS AND SEED PRODUCTIVITY IN *XANTHORRHOEA*

Ian A. Staff*

(Plates XIII and XIV)

[Accepted for publication 28th August 1974]

Synopsis

A study of the productivity of the tricarpellary fruits in species of *Xanthorrhoea* was made. Seed counts of a total of 3,992 fruits of *Xanthorrhoea resinosa*, *X. australis* and *X. preissii* showed an overall average of 2·1 per fruit. Notice was taken of fruit productivity in relation to linear position on the inflorescence axis and it was apparent that seed productivity was lowest at each end of the inflorescences. As flowers open late in these positions, ovule abortion is thus higher in late opening flowers. Seed output was well below the possible maximum that could be produced by flowers reaching anthesis—only 0·1 to 5·2 per cent—and even these figures are greater than total ovule abortion by more than 50 per cent when the loss before anthesis of six to seven out of eleven flower primordia in each floral cluster is considered.

The production of more than one seed per loculus occurred in 24·5 per cent of fruits counted, but fruits with one set of twins accounted for 18·5 per cent of this figure. Maximum seed number per fruit was seven while the greatest number of seeds found in one loculus was four. Speculations concerning greater seed output in a single season by shaded, arborescent plants than by more frequently flowering non-arborescent plants were made. Factors such as arborescence, high food storage capacity and shading could contribute to the production of more polymorphic seeds. High abortion rates of seeds in plants growing in open habitats may be increased by water stresses in drier habitats. The mechanism of staggered times of anthesis in combination with production of excessive numbers of flower primordia and high ovular abortions provides a dynamically fluid strategy that could overcome problems such as intermittent water stresses and insect predations with ease.

INTRODUCTION

Over a period of several years, the author has been interested in various aspects of the biology of the Australian grass tree *Xanthorrhoea* (Staff 1968, 1970, 1974, 1975). Although most interest has centred on the anatomy of the plant, data have been collected from time to time on the seed productivity of fruits of some of the plants.

Salisbury (1942) presents detailed records of fruit and seed counts of large numbers of British plants and makes the generalisation that plants growing in intermittently open habitats produce most seeds. Next in productivity are those that grow in permanently open, semi-open and closed unshaded habitats, which, in turn, produce more seeds than those growing in shaded communities. However, comparison between these groups was rendered difficult by the presence of large numbers of annuals in the first three community types and by the preponderance of perennials in the closed communities. Harper and White (1974) have reviewed much of the pertinent literature on reproductive output of perennials, including a treatment of the great fluctuations that can occur in seed output by such plants from year to year and of fluctuations resulting from differences in age and vigour of the plant. It is difficult to generalise about seed productivity of perennial monocotyledons, however, as wide ranges have already been recorded. Schwerzel (1967) has shown a mean seed number of 40 per plant for *Cyperus rotundus* and 820 for *C. esculentus* in one season. In the orchids, seed productivity is much greater—Salisbury (1942) recorded an average output of 56,000 seeds per plant, for *Orchis maculata*. This figure has been exceeded by

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Darwin (1882) who recorded 1,756,440 seeds in a single capsule of *Maxillaria* sp, and as these plants often produce six capsules, a seasonal total of the order of ten million seeds would result. Hager (1952) found 929,000 viable seeds in a single capsule of a *Cattleya labiata* hybrid which had a total seed production of between two and three million seeds. These plants are all relatively small in size compared to the arborescent monocotyledons, which also have a wide but not as great a range of seed productivity. Annual productivity of 300 plants of the polycarpic *Cocos nucifera* (the coconut palm) (Manthriratna, 1973) was between 50 and 100 seeds. Ellis (1913) found a range of 20 to 719 perfect seeds per plant in *Yucca glauca*, while Tomlinson and Soderholm (1975) found an estimated 250,000 seeds in the inflorescence of the monocarpic palm *Corypha elata*.

Waterhouse (1967) describes the tricarpellary fruits of *Xanthorrhoea* species as having up to eight ovules per carpel. This means that each fruit has the potential to produce a maximum of 24 seeds. In reality, the seed number rarely exceeds six, showing an abortion rate of at least 75 per cent of ovules. As many fruits have been found to produce only one seed, the abortion rate in these cases is 96 per cent, assuming eight ovules were present initially in each carpel. Additional information on abortion of ovules was sought by counting seeds present in each unilocular carpel. As the plants produced large, columnar, terminal unbranched inflorescences (Pl. XIII) that may reach 4·5 metres in length in *X. resinosa*, it should be possible to see if any correlation exists between high ovule abortion rate and great distance distally from the vegetative axis. This condition could be expected as the distal tip of the inflorescence is most distant from the food supplied by the vegetative axis.

MATERIALS AND METHODS

Collections of the inflorescences of species of *Xanthorrhoea* were made from the localities listed :

Xanthorrhoea australis R. Br. : Port Welshpool, Victoria—open habitat ; Mt Slide, Victoria—shaded habitat.

X. resinosa Pers. : Top of Bulli Pass, New South Wales—open habitat.

X. preissii Endlich : Perth, Western Australia—open habitat.

RESULTS

Species of the polycarpic woody monocotyledon *Xanthorrhoea* produce ovoid, capsular fruits that are slightly zygomorphic by virtue of a sharp point on the distal end which represents the persistent base of the style and which is situated eccentrically in the mature fruit (Pl. XIII, fig. *b* ; Pl. XIV, fig. *a*). The fruit's surface is smooth and hard, with three longitudinal furrows opposite the septa of the ovary that alternate with three furrows at the lines of dehiscence (Pl. XIII, fig. *b* ; Pl. XIV, fig. *a*). They are slightly upturned *in situ*, are about 11 mm long by 5 mm wide and dehisce loculicidally (Pl. XIV, fig. *b*). As pointed out by Waterhouse (1967) and Lee (1966) the outer three perianth members are rather glumaceous, with terminal tufts of hairs in *X. resinosa* (Pl. XIV, figs *a*, *b*) and are slightly shorter than the petalloid, near-white inner members.

The seeds are shiny, jet black, about 7 mm long by 3 mm broad, with a small white hilum at one end (Pl. XIV, fig. *c*). They usually have a longitudinal ridge with two sloping sides on one face and a flat third face, being triangular in cross section. Both Brown (1810) and Bentham (1878) described the embryo as situated in a position transverse to the long axis of the seed but Waterhouse (1967) showed that this position arises as a result of excessive growth in the short axis of the ovules, which he formerly termed amphitropous but are correctly described as hemitropous (Waterhouse, pers. comm. 1974). Several seeds which did not conform to the general form just described were found to have been formed in loculi with more than one mature seed present. Plate XIV, fig. *d* shows a pair of seeds that were taken from a single loculus; the dimorphy is quite evident. Seed length is only 1 mm less in single seeds but the tapered ends are lost in some. Also, an extra transverse ridge is prominent where one seed was pressed against the other in the loculus (Pl. XIV, fig. *d*). Further variations are evident in the rarer instances in which loculi contained three or four seeds, and the seed polymorphism seen is a natural result of crowding within the single loculus. Harper *et al.* (1970) list examples of somatic polymorphism in which seeds differ morphologically on the basis of presence or absence of ornaments such as a pappus or a wing-like bract, on texture or colour in the testa, or on

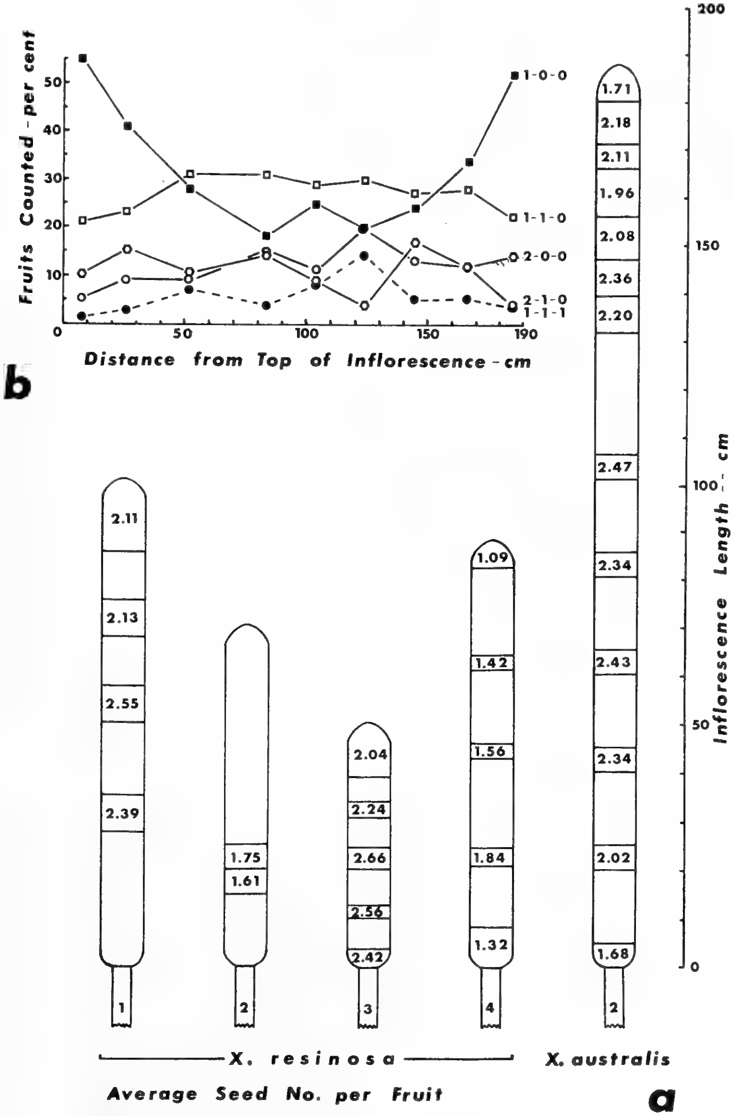

Fig. 1. Fruit productivity in relation to position on the inflorescence axis. a. Relation of average seed numbers in fruits to position on the inflorescence axis. b. Frequency of the most common fruit types with relation to position on the inflorescence axis of *X. australis* in Fig. 1a.

the basis of size. Although the distinction between singly-occurring seeds of *Xanthorrhoea* and twins is not as marked as in some of the examples of Harper *et al.* (1970), the different forms in themselves are distinct enough to fall within the limits of the term somatic polymorphism.

Table 1 provides data collected from three species of *Xanthorrhoea* which involved the opening and examination of 3,992 fruits and the recording of the positions of just over 10,000 seeds. From the results it is apparent that the fruit types with seed arrangements per loculus (1–0–0) and (1–1–0) are most common, occurring in 34·5 per cent and 30·1 per cent respectively of all the material examined. The next most frequent fruit types were those with seed arrangements (1–1–1) and (2–1–0, 2–0–0 and 2–1–1, in all of which one twin was present), having an overall occurrence in 11·0 per cent, 7·9 per cent, 7·2 per cent and 3·7 per cent respectively of those specimens examined. Other fruit types each contributed to about 1 per cent or less of the specimens examined. Two of the three plants of *X. australis* produced most fruits having multiple seed numbers per loculus, while other specimens had predominantly the combinations of (1–1–1), (1–1–0) and (1–0–0). All possible variations of seed groupings were seen in fruits with from one to four seeds, but above that number possible combinations involving 4, 5, 6, or 7 seeds per loculus were lacking except for one example of (4–1–0).

In the examination of five inflorescences, seed counts of fruits were made at measured intervals along the spikes (Fig. 1*a*). Average seed numbers per fruit were marked on the diagram next to the corresponding part of the inflorescence. It is apparent that seed number per fruit is lowest in an inflorescence at its extremities and higher toward the central part of the inflorescence. This applies even to *X. resinosa* (No. 2), where fruit set was very poor.

A plot of the various fruit types in the inflorescence with most complete data (*X. australis*—No. 2, Fig. 1*b*) reveals no great fluctuations except in fruits with a single seed and two empty carpels. The incidence of these is high at each extremity of the inflorescence and drops off by half in the centre. This accounts for the low seed number per fruit in the extremities of the inflorescence.

DISCUSSION

Before considering abortion rates in the ovules, the method of production of flowers should be briefly stated. Waterhouse (1967) describes the arrangement of floral clusters, which contain from 2 to 11 flowers, depending on the species, as follows : " The sessile flower-clusters in surface aspect have essentially the appearance of juxtaposed parallelograms arranged in helices around the spike ". He states that, in a spike of *X. resinosa*, 11 flower primordia are formed, 6 of which usually abort before anthesis. Allowing for this loss, some 7,500 flowers may still develop in one metre length of inflorescence. If each of these flowers grew to maturity and each ovule (eight maximum per loculus) survived, this would mean a potential of 180,000 seeds per metre length of inflorescence. Although the five surviving flowers per cluster mature at differing rates, providing a mechanism that increases the chances of fruit set by presentation of stigmas over an extended period of time, fruit and seed set is still low. Anthesis is always later at each extremity (10 cm) of an inflorescence than it is in the middle. At each end of an inflorescence there is usually an increase in fruits with only one mature seed (Fig. 1 and Table 1). It thus seems likely that food supply from the vegetative axis is not a factor limiting seed set but rather that the time of anthesis is a more significant controlling factor. With an overall average of 2·1 seeds per fruit of all species examined, it is clear that higher abortion of ovules in late opening flowers is a common phenomenon in these plants. Therefore extension of time of anthesis, although of advantage to the plant if early flowers are harmed in any way, results in high abortion rates of late developers.

TABLE 1

Fruit fertility in Xanthorrhoea

Seed per fruit	Number per loculus	*X. resinosa*								*X. australis*						*X. preissii*		Totals	Per-centages
		1		2		3		4		1		2		3		1			
		I*	II†	I	II	I	II	I	II	I	II	I	II	I	II	I	II		
7	3–3–1	—	—	—	—	—	—	—	—	—	—	2	0·1	—	—	—	—	2	0·1
7	3–2–2	—	—	—	—	—	—	—	—	—	—	2	0·1	—	—	—	—	2	0·1
6	3–3–0	—	—	—	—	—	—	—	—	1	0·1	2	0·1	—	—	—	—	3	0·1
6	3–2–1	—	—	—	—	—	—	—	—	1	0·1	10	0·6	—	—	—	—	11	0·3
6	2–2–2	—	—	—	—	—	—	—	—	3	0·3	8	0·5	—	—	—	—	11	0·3
5	4–1–0	—	—	—	—	—	—	—	—	—	—	1	0·1	—	—	—	—	1	0·0
5	3–2–0	10	1·9	—	—	—	—	—	—	7	0·8	6	0·4	—	—	—	—	23	0·6
5	3–1–1	—	—	—	—	—	—	—	—	1	0·1	6	0·4	—	—	—	—	7	0·2
5	2–2–1	—	—	—	—	—	—	—	—	18	2·0	35	2·1	—	—	—	—	53	1·3
4	4–0–0	—	—	—	—	—	—	—	—	—	—	1	0·1	—	—	—	—	1	0·0
4	3–1–0	—	—	—	—	—	—	—	—	5	0·6	26	1·5	—	—	—	—	31	0·8
4	2–2–0	9	1·7	—	—	—	—	—	—	10	1·1	29	1·7	—	—	—	—	48	1·2
4	2–1–1	25	4·8	—	—	6	2·4	—	—	46	5·1	72	4·2	—	—	—	—	149	3·7
3	3–0–0	—	—	—	—	—	—	—	—	8	0·9	20	1·2	—	—	—	—	28	0·7
3	2–1–0	50	9·6	—	—	2	0·8	—	—	79	8·8	186	10·9	—	—	—	—	317	7·9
3	1–1–1	124	23·8	26	13·0	113	45·2	14	12·6	43	4·8	103	6·1	12	12	4	1·9	439	11·0
2	2–0–0	23	4·4	2	1·0	1	0·4	—	—	72	8·0	189	11·1	—	—	1	0·5	288	7·2
2	1–1–0	206	39·5	82	41·0	100	40·0	39	35·1	259	28·7	436	25·6	46	46	34	16·5	1,202	30·1
1	1–0–0	75	14·4	90	45·0	28	11·2	58	52·3	348	38·6	568	33·4	42	42	167	81·1	1,376	34·5
Total		522	100	200	100	250	100	111	100	901	100	1,702	100	100	100	206	100	3,992	100
Average seed number per fruit		2·4		1·7		2·4		1·6		2·0		2·1		1·7		1·2		2·1	

* I=Number of fruits counted with condition in column on far left.

† II=I expressed as a percentage of total fruits counted for that plant.

Actual seed output for the specimens of *X. resinosa* counted in Fig. 1 ranged from a low of 336 in a plant with high floral abortion (No. 2) to a high of about 2,600 in a plant (No. 1) with high floral success. When an adjustment is made for length of spike (relative to data for 1 metre above), these two figures represent 0·1 per cent and 1·4 per cent seed productivity of the maximum potential seed output. When the estimated seed production of 7,500 for the single specimen of *X. australis* is adjusted for a possible maximum of four developed flowers per cluster (instead of the five in *X. resinosa*) and for spike length, a higher seed productivity of 5·2 per cent of the maximum possible is found.

Tomlinson (In press) described a comparable situation of high floral productivity but low seed set in *Corypha elata.* The monocarpic palm produced in the order of ten million flowers but only 250,000 seeds. As each tricarpellary ovary usually produces only a single seed from its three ovules, this means a seed productivity of 0·8 per cent of the maximum potential seed output and again a huge loss of potential seeds by floral and ovular abortions.

Several major points may be made from these results. The abortion rate of ovules from a maximum possible of 24 per fruit reduces final seed number most frequently to two (37·3 per cent) followed by one (34·5 per cent), three (19·6 per cent) and four (5·7 per cent). The highest success of ovules in a single loculus was four, although only five seeds were produced by that fruit. The maximum number of seeds in a fruit was seven–(3–3–1) and (3–2–2). Somatic seed polymorphism results from crowding of more than one developing seed in a loculus. The most frequent polymorphism resulted from twinning and the incidence of fruits with one set of twins as their only polymorphic seeds accounted for 18·8 per cent of the total counts made, the remainder of fruits with polymorphic seeds being found only in 5·7 per cent of all counts made. According to Harper *et al.* (1970) somatic polymorphism is determined not by genetic segregation but by the internal (or external) environment of the maternal parent. The different morphs may also have different ecological roles, dormancies, weights and dispersal mechanisms. In *Xanthorrhoea*, seeds in pairs are generally smaller than single seeds and this leads one to suggest that different dispersal rates in wind would apply between the larger and smaller seeds. Greatest abortion rates of ovules as evidenced by a high frequency of (1–0–0) fruits occurred at both ends of inflorescences, a situation somewhat similar to abortion of ovules in pea fruits (Linck, 1961).

A comparison of these results with those of other workers can only be limited because of the small sample of plants examined. However, some comments will be made with regard to differences seen as a result of habitat, frequency of flowering and predation. All specimens of *X. resinosa* examined were growing in an open habitat with very little shading and were subject to frequent burning in the dry summer months. This leads to flowering annually as fire stimulates this process in these plants. The specimens of *X. preissii* and the first and third specimens of *X. australis* were growing in a similar habitat but were not subject to frequent burning. Finally, the second specimen of *X. australis* was growing in a shaded area as an understory plant in a dry sclerophyll *Eucalyptus* forest and was one of a group of plants studied (Staff, 1975) in which a maximum rapid growth rate of inflorescence of 49 cm over seven days was recorded, and a maximum length of inflorescence of 300 cm was estimated to have reached that length in 75 days—an overall average elongation rate of 4 cm per day. This plant also had not been subjected to burning for several years and was one of a group that flowers infrequently (inflorescences were not produced by this stand in the four years following the measurement of growth rates).

It appears likely that, on an individual plant basis, total seed output of the more frequently flowering *X. resinosa* plants in an open habitat is less than seed output in the unburnt, shaded *X. australis* plants. If, however, the infrequency of flowering of the latter plants is taken into consideration, this apparent surfeit of seeds may not necessarily apply in the long term. More measurements are needed to quantify this relation properly.

Limited seed predation has been observed in *X. australis*. The small moth *Hylaletris latro* Zell reproduces on inflorescences of this species and Britton *et al.* (1970) state that the larvae tunnel in the flower spikes. I have observed young larvae inside fruits and older larvae living in the spikes. Evidence of damage of seeds was seen but it was not extensive. The escape of seeds from predators by release from the dehiscing capsules, a mechanism aiding survival against heavy predation by insects in legumes (Janzen, 1969), must apply here, although seeds may be entrapped in open fruits for several months.

Differences in abortion of ovules as evidenced by average seed number per fruits showed no discernable trends but the plants that possessed most polymorphic seeds in the form of twins, triplets and quadruplets were the *X. australis* inflorescences. This phenomenon could be a reflection of genetical differences between species, or a reflection of greater success of ovules in a physically long structure, or a reflection of the greater size and therefore energy storage capacity of the vegetative stems of *X. australis*, which were the only specimens examined with arborescent stems. Williams and Attwood (1971) and Tripathi and Harper (1973) found that low seed production in perennial monocots such as *Agropyron repens* could be caused by the allocation of considerable energy towards vegetative reproduction in the form of rhizomes that are good food storage organs. So, too, could the infrequently flowering arborescent plants of *X. australis*, which store large amounts of starch in their stems in non-flowering years, then be able to summon vast food reserves when the sexually reproductive event occurs, producing consequently a higher average seed output than the non-arborescent plants. Finally, high abortion rates of ovules could be a reflection of high water stress prevailing at the times of inflorescence initiation and development. In the oil palm, *Elaeis guineensis* Jacq., Hartley (1969) states that, although little is known about abortion of inflorescences, both he and Broekmans (1957) have found some correlations between particularly dry seasons, inflorescence abortions, retarded inflorescence growth and minimum yields of fruits. Meteorological data on rainfall that occurred prior to and during the period of flowering of the *X. australis* plant with high seed polymorphism (No. 2) (Staff, 1975) suggest no dearth of water in that specimen. Unfortunately comparable data are not available for the other specimens examined but it seems reasonable to expect a greater chance of water stress in plants growing in open habitats than in those in shaded areas.

In conclusion it has been shown that seed output in species of *Xanthorrhoea* is well below the possible maximum. Abortion of flowers and ovules is thus very high and the average seed number per fruit is 2·1, although seven seeds have been found in one fruit. Twinning is the most frequent polymorphism, quadruplets were the highest multiple seeds produced. Abortion rates are highest at each end of the inflorescence and reflect the late opening of flowers in these positions. This condition differs from that initially predicted on the basis of the possible limiting effect of nutritional supplies to the distal end of the inflorescence. High abortion rates could be particularly aggravated by water stress in dry open habitats. Frequent flowering tends to produce fewer seeds in the short term but more seeds in the long term. Insect predation is not thought to be a big factor in seed output reduction.

The mechanism in the polycarpic *Xanthorrhoea* of staggered times of anthesis in combination with the production of excessive numbers of flower primordia and high ovular abortions provides a dynamically fluid reproductive stratagem similar to that in the monocarpic palm *Corypha elata*. Its effect is to overcome problems such as intermittent water stresses and insect predations while still providing the plant with an adequate number of disseminules for survival.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

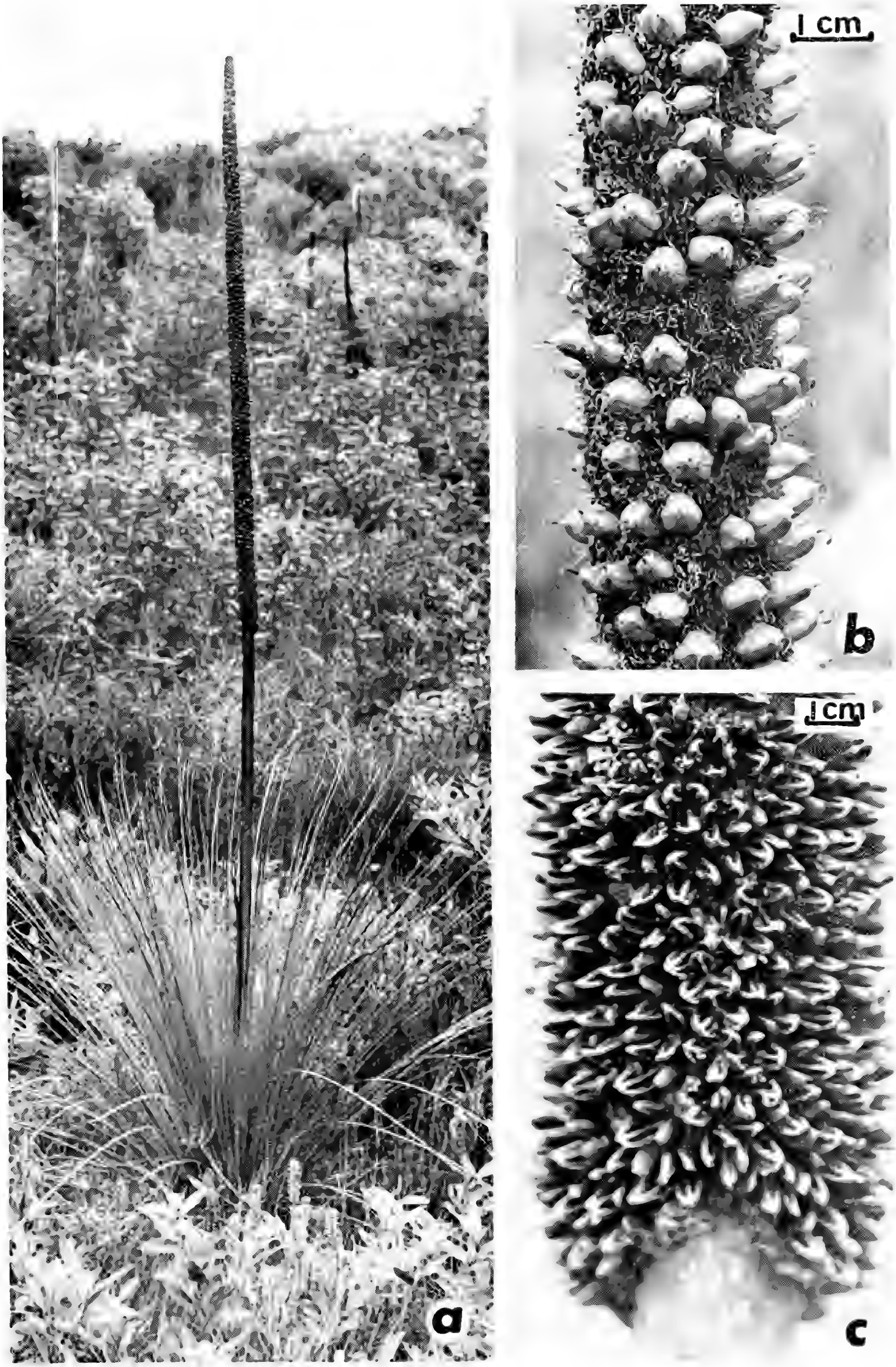
PLATE XIII

Figs a–c. Inflorescences of two species of *Xanthorrhoea*. a,b. *X. resinosa* with maturing fruits about two weeks before dehiscence. Length of inflorescence in the centre = 2·2 m. c. *X. australis* after dehiscence of the capsules.

PLATE XIV

Figs a–b. Fruits of *X. resinosa*. a. Immature fruit with perianth members still attached. b. Open capsule with one wall removed, exposing seeds.

Figs c–d. Seeds of *X. resinosa*. c. Solitary seed from a single loculus. d. Twinned seeds from a single loculus.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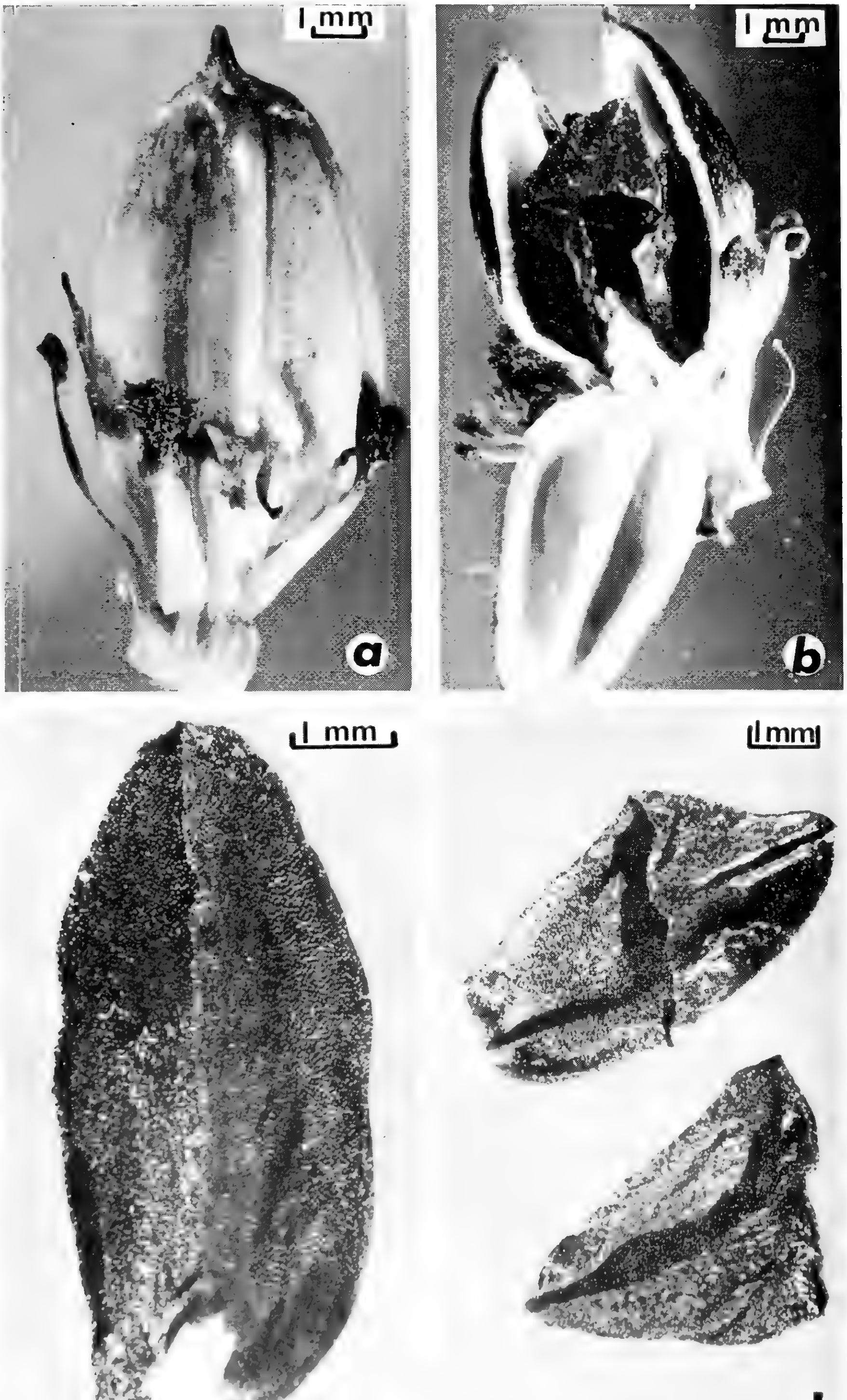
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References should be cited in the text by the author's name and date, e.g., Bullough (1939) or (Bullough, 1939) according to context, and listed alphabetically under References thus :

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A NEW GIANT DEEP-WATER ISOPOD OF THE GENUS *BATHYNOMUS* (FLABELLIFERA: CIROLANIDAE) FROM EASTERN AUSTRALIA

D. J. G. Griffin*

(Plate XV)

[Accepted for publication 23rd October 1974]

Synopsis

A new species of *Bathynomus* is described from 19 specimens taken in depths of 270–540 m off New South Wales. It is distinguished mainly by the armature of the telson and the shape of the uropods.

Introduction

In 1878 naturalists working aboard the *Blake* in the Gulf of Mexico obtained an isopod 23 cm in length from a depth of almost 1,720 m (955 fms). Although a juvenile, this specimen was larger than any similar animal caught before. It was described by A. Milne Edwards (1879) as a new genus and species *Bathynomus giganteus.* This species is now known to be quite common in the Gulf of Mexico and Caribbean and adults have been obtained up to 35 cm in length.

The genus, now including five living species, is placed in the family Cirolanidae of the sub-order Flabellifera. Four species, *B. doderleini* Ortmann, *B. affinis* Richardson, *B. propinquuis* Richardson and *B. decemspinosus* Shih occur in the Japan–Philippine Islands–South China Sea area (Ortmann, 1894; Richardson, 1910; Shih, 1972); *B. giganteus,* the largest species, has been recorded from the Bay of Bengal as well as from the Gulf of Mexico (Wood-Mason and Alcock, 1891). The genus is now known from the continental shelf and slope in depths of 70 to almost 2,000 m. Work by Imaizumi has suggested that the genus existed as early as Cretaceous times around Texas and in Japan during the Miocene (Shih, 1972). Holthius and Mikulka (1972) have recently reviewed the genus.

Since 1971 the New South Wales State Fisheries have been carrying out experimental trawling operations in deep water along the New South Wales coast. These trawls have produced quite large numbers of giant isopods, clearly belonging to the genus *Bathynomus,* from depths down to 585 m.

Only once has a giant isopod been recorded from Australia. Hale (1940) dealt with a single specimen collected off Gabo Island, Bass Strait, in 360 m, which he tentatively identified as *Bathynomus affinis.* Hale did note two differences between his specimen and Richardson's (1910) original description of *B. affinis.*

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* The Australian Museum, College Street, Sydney, New South Wales, 2000.

In this paper the New South Wales specimens are described and figured as a new species; they are considered to be the same as that described by Hale. The new species is compared with other living species of the genus. Terminology follows that of Wolff (1962). All specimens are in the collections of the Australian Museum, Sydney (AM).

Systematics

Bathynomus kapala n. sp.

Pl. XV; Figs 1–8

Bathynomus ?affinis.—Hale, 1940: 292–293, pl. 18. Not *Bathynomus affinis* Richardson, 1910.

Holotype. Female, 110 mm (AM P.17947), off Wollongong, 34°24′S., 151°20′E. to 34°29′S., 151°17′E., 351 m, prawn trawl, FRV *Kapala,* 6 July 1971.

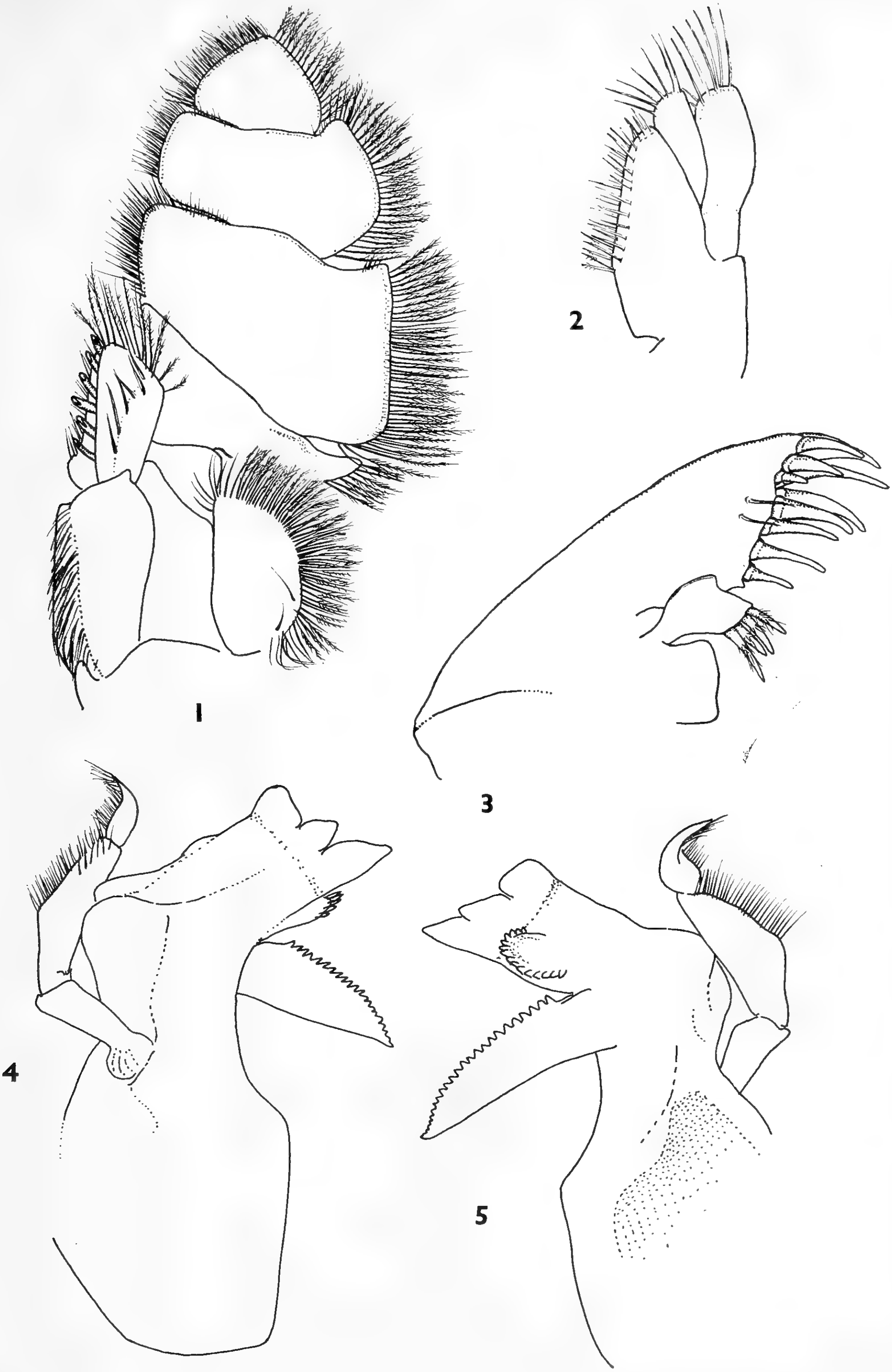
Paratypes. 7 ♂♂, 11 ♀♀, 82·5–110 mm, all collected by FRV *Kapala* as follows: off Port Stephens, 32°46′S., 152°46′E. to 32°51′S., 152°42′E., 585–576 m, sandy mud, prawn trawl, 7 July 1971, 1 ♀ (AM P.17949); north of Sydney, 33°41′S., 151°55′E. to 33°44′S., 151°53′E., 540 m, prawn trawl, 20 April 1971, 2 ♂ (AM P.17948); off Broken Bay, 33°34′S., 152°03′E. to 33°43′S., 152°59′E., 558 m, smooth bottom, prawn trawl, 21 April 1971, 1 ♀ (AM P.18086); south-east of Broken Bay, 33°40′S., 151°55′E. to 33°35′S., 151°58′E., 540 m, prawn trawl, 14 July 1971, 1 ♀ (AM P.17954); 40 km east of Sydney, 33°40′S., 151°52′E. to 33°44′S., 151°49′E., 270–360 m, 6 April 1971, 1 ♀ (AM P.18010), 1 ♂, 1 ♀ (AM P.17952); off Sydney, 33°40′S., 151°53′E. to 33°44′S., 151°50′E., 405 m, 1 August 1972, 2♂, 1 ♀ (AM P.19389); off Botany Bay, 34°00′S., 151°43′E. to 33°54′S., 151°47E., 420 m, 6 November 1972, 1 ♀ (AM P.19390); south of Port Hacking, 34°19′S., 151°24′E. to 34°13′S., 151°28′E., 360 m, prawn trawl, 28 June 1971, 1 ♀ (AM P.17951); north of Jervis Bay, 34°56′S., 151°10′E. to 35°01′S., 151°07′E., 558–522 m, trawled 7 July 1971, 2 ♂, 1 ♀; (AM P.17946); south of Ulladulla, 35°31′S., 150°45′E. to 35°37′S., 150°42′E., 423-405 m, prawn trawn, 8 July 1971, 2♀ (AM P.17953).

Description.

Body spindle shaped, ratio of length to width 2·4:1.

Head broadly oval, width about twice length, frontal margins ridged, medial anterior projection meeting frontal lamina. Eyes widely separated, situated laterally on antero-inferior surface of head and concealed in dorsal view, elongate triangular; base lateral, concave. Frontal lamina triangular. Clypeus anteriorly rounded, projecting anteriorly beyond frontal lamina, lateral margins with a "shoulder" anteriorly, posteriorly expanded laterally beyond saddle-shaped labrum.

Pereon just over half total length. Pereonites 1–5 of about equal length, pereonite 6 slightly shorter than others, pereonite 7 half length of pereonite 1. Pereonites 3–7 about equal width, about twice width of head, first two pereonites decreasing in width anteriorly to posterior margin of head. Coxal plates laterally ridged, last two with weak central ridge, first two quadrate, remainder produced posteriorly, last coxal plate reaching to midway along pleonite 2.



Figs 1–5. *Bathynomus kapala* n. sp., female (Paratype, AM P.17953), 96 mm. 1. Maxilliped (right), dorsal aspect. 2. Maxilla (right), dorsal aspect. 3. Maxillula (right), ventral aspect. 4. Mandible (right), ventral aspect. 5. Mandible (right), dorsal aspect.

Figs 6–8. *Bathynomus kapala* n. sp., female (Holotype) 110 mm. 6. Second (left) pereopod, posterior aspect. 7. Sixth (left) pereopod, anterior aspect. 8. Uropod (right), ventral aspect.

Pleon about one-fifth length, pleonites subequal in length, pleonite 1 extending laterally to half way along last coxal plate, pleonites 2–5 laterally produced, pleonites 2–4 curved posteriorly, pleonite 3 terminating just anterior to pleonites 4 and 5 which terminate at the same level posteriorly.

Telson barely exceeding pleon in length, roughly shield-shaped, subtruncate posteriorly, dorsal surface with a weak longitudinal carina along midline, posterior margin with three acute teeth laterally (and sometimes a small fourth tooth) and a slightly broader and longer medial tooth, the tip of which is truncate or bifid; intervals between teeth setose.

Antennula short, reaching to distal end of antennal peduncle; peduncle of three segments. Antenna long, extending to anterior margin of pereonite 2, peduncle of five segments, first two short; flagellum multisegmented.

Inner endite of maxillula with four distal spines which are centrally plumose and apically naked. Outer endite of maxillula with eleven stout spines on medial margin, seven in a group distally and five in a line in proximal half.

Maxilliped endite with six coupling hooks on medial margin.

All other mouthparts generally similar to those of other species of genus.

Pereopod 1 with long basis almost equal to half total length, naked except for few setae distally; ischium expanded distally with few short spines mid-ventrally and around distal edge; merus dorsally produced and tipped by stout spines distally, ventrally bilobate with a few stout spines; carpus with a few short spines ventrally; propodus weakly compressed, ventrally carinate with a few short, stout spines; dactyl with weak lateral ridge, terminating the claw.

Pereopods 2 and 3 similar to pereopod 1 except dorsal distal projection of merus longer, extending to midway along propodus.

Pereopods 4–7 similar to each other; no segment with special projections, ischium, merus and carpus similar in shape, slightly expanded distally; basis about two-fifths total length of leg; stout setae around distal margins of ischum, merus, carpus and propodus, and in a transverse group midway along ventral surface of ischum, merus and carpus and in 2–4 groups along ventral surface of propodus.

Pleopods generally similar to those of other species of genus.

Uropod exopod of about equal width throughout its length, oblong; lateral and distal edges setose, short spines along lateral and distal edges; posterolateral corner with a small tooth. Endopod larger than exopod, subtriangular; posterolateral corner acute but not produced, bearing a small tooth; edges setose, short teeth along distal part of lateral edge and along distal edge.

Discussion

The new species is similar to *Bathynomus doderleini, B. affinis* and *B. decemspinosus* in most features. The outer endite of the maxillula possesses 11 spines as is usual in the genus.

The principal differences concern the shape and ornamentation of the uropods; there are also differences in the armature of the legs and of the telson. This species has a narrower body than *B. affinis* and is rather similar to *B. doderleini* in shape. The medial carina of the telson is lower than in most other *Bathynomus* species.

The number of teeth on the lateral edge of the exopod of the uropod ranges from 8 to 12 (thirteeen specimens with 9-10 teeth) and the number of teeth on the distal edge is generally 3 (seventeen specimens) but sometimes 2 (two specimens). The number of teeth on the lateral edge of the endopod of the uropod ranges from 3 to 6 and is most commonly 4 or 5 (fourteen specimens); there are 6–10 teeth on the distal edge but usually 8 or 9 (fourteen specimens).

On the posterior edge of the telson the medial tooth is truncate or bifid (notched) in all but one specimen. Nine specimens possess a small tooth lateral to the usual three on each side of the midline.

Pereopods 4–7 are slightly stouter than in *B. doderleini* and there are setae and spines around the distal edge of the carpus and propodus whereas in *B. doderleini* setae occur only on the ventral half of the distal edge of the carpus and are absent from the propodus.

The endopod of the uropod is not prominently produced at the postero-lateral corner as in *B. decemspinosus* and *B. affinis* and the exopod is about as wide distally as proximally, whereas in other species the exopod narrows noticeably towards the distal edge.

Finally, the copulatory organ (attached to the second pleopod) of the male slightly surpasses the distal edge of the endopod and is apically expanded. These are obvious differences from *B. doderleini* (see Milne Edwards and Bouvier, 1902); however, this structure has not been described for most species.

The new species is named after the N.S.W. State Fisheries Research Vessel *Kapala* in recognition of the assistance that this ship and its crew have given to recent scientific programmes on the deep water marine fauna off eastern Australia.

ACKNOWLEDGEMENTS

I have pleasure in thanking Dr. D. D. Francois, Director of the New South Wales State Fisheries, and his staff, particularly the crew of the F.R.V. *Kapala,* for making these specimens available.

I thank Mrs. Janet Holloway and especially Miss Diane Brown of the Department of Marine Invertebrates, Australian Museum, for their special assistance in checking specimens and literature and Dr. T. E. Bowman, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C., for reviewing the manuscript.

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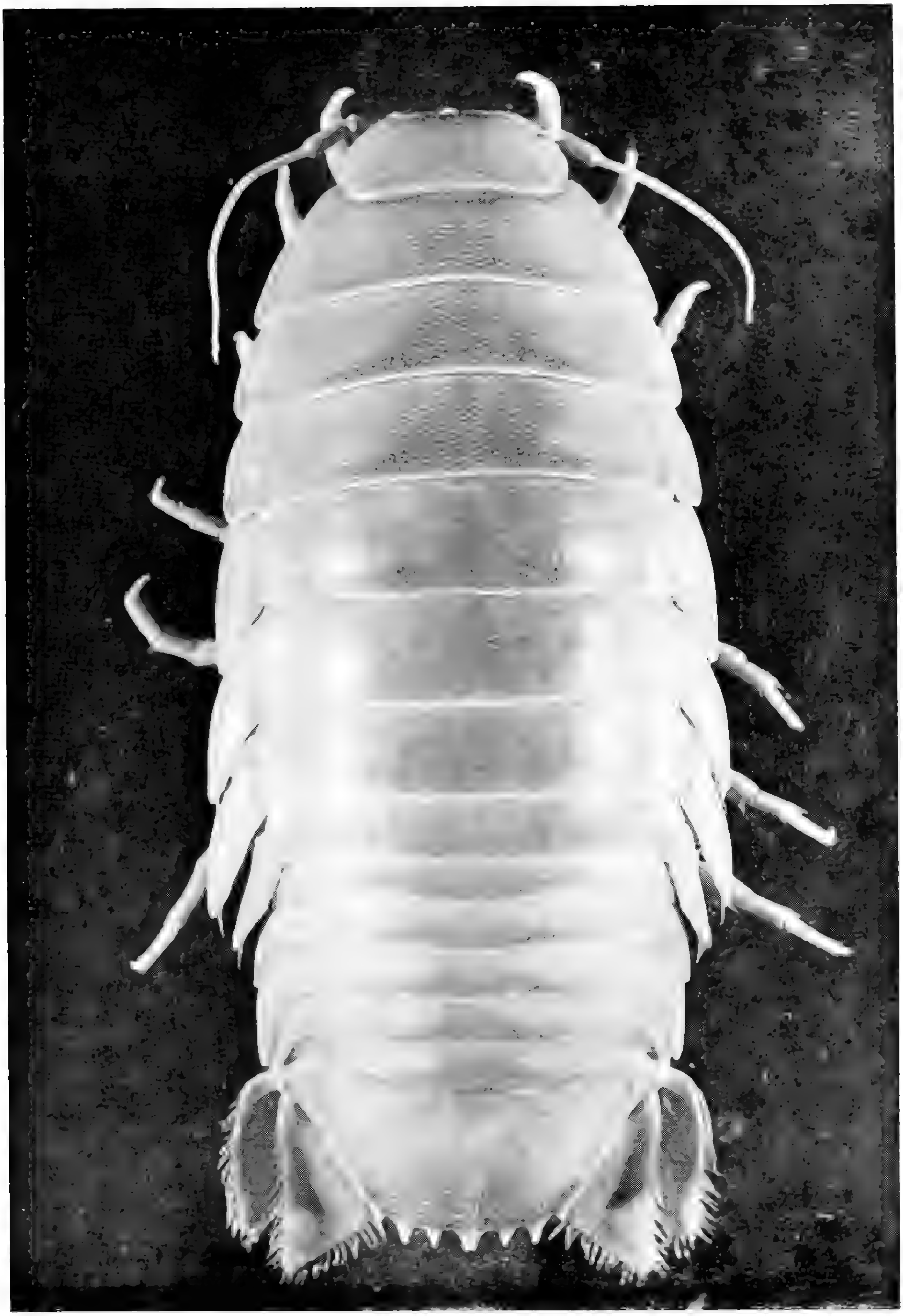

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EXPLANATION OF PLATE XV

Bathynomus kapala n. sp., female (Holotype), 110 mm, dorsal view.

NOTES ON SOME FISHES OF THE FAMILIES URANOSCOPIDAE, SCORPAENIDAE, OPHICHTHIDAE AND MURAENIDAE FROM TORRES STRAIT

Patricia J. Kailola*

[Communicated by J. L. Maclean]

[Accepted for publication 11th December 1974]

Synopsis

A specimen of the striped stargazer, *Ichthyscopus fasciatus*, is described from Torres Strait. Nine other specimens are recorded from northern Australia and southern New Guinea, of which one is a new record for Western Australia. A specimen of *Paracentropogon longispinis* from Torres Strait is described; *Paracentropogon vespa, P. indicus* and *P. zonatus* are probable synonyms. The eel species *Ophichthus evermanni* and *Gymnothorax reticularis*, not previously recorded from Australian waters, are described from specimens obtained off Darnley Island. The eels were part of the stomach contents of seasnakes.

INTRODUCTION

The Fisheries Research and Survey Station in Port Moresby, Papua New Guinea, has in recent years received two collections of fishes from Torres Strait off North Queensland. The first was trawled at depths of 9·1–18·3 m in May 1970, in the vicinity of Cocoanut Island (10°03′S., 143°06′E.) by Mr. E. Whitten. The second consisted of partly digested fishes comprising part of seasnake gut contents. The snakes were trawled off Darnley Island (9°36′S., 143°50′E.) by Mr. C. O'Brien on November 11, 1972 and their gut contents delivered to the Fisheries Research Station by Mr. F. Parker for identification.

Descriptions of and remarks on the most noteworthy specimens are presented. Measurements expressed in thousandths of standard length (SL) are presented in tables. All specimens are registered in the Fisheries Research fish collection (FO) in Port Moresby. Specimens of *Ichthyscopus fasciatus, Paracentropogon vespa, P. vespa livingstoni, P. longispinis* and *P. rubripinnis* from the Australian Museum (AMS), Sydney, were examined, as were specimens of *P. vespa* from the Western Australian Museum, Perth, and the Queensland Museum, Brisbane.

Ichthyscopus fasciatus Haysom

Fig. 1

Ichthyscopus fasciatus Haysom, 1957: 139, fig. 1

Mees (1960) lists five species of *Ichthyscopus* from Australia: three from Western Australia and two from eastern Australia. At that time

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I. fasciatus was known only from the holotype, 102 mm standard length (SL), trawled in Cleveland Bay near Townsville, Queensland (19°15′S., 146°48′E.), in 1955.

Ten other specimens have since been collected, as follows: one specimen (AMS IB. 7172), 113 mm SL, coll. G. P. Whitley, Gulf of Carpentaria (14°00′S., 138°36′E.); two specimens (AMS I. 15557–214), 92 mm and 146 mm SL, coll. I. S. R. Munro, October 1, 1963, off Bentinck Island, Gulf of Carpentaria (16°51′S., 139°23′E.), 9·1 m, trawl; one specimen (AMS IB. 5851), coll. G. Coates, 1962, off Townsville, Queensland, trawl; three specimens, none held in any collection, between mid-1970 and mid-1971, between Townsville and Princess Charlotte Bay (14°20′S., 144°00′E.), prawn trawl (Grant, personal communication, 1972); one specimen in the fish collection of Rijksmuseum van Natuurlijke Historie, Leiden, from the "south coast of (Dutch) New Guinea" (Mees, personal communication, 1970); one specimen, held in the fish collection of the Western Australian Museum, Perth, April 26, 1968, Admiralty Gulf (14°20′S., 125°53′E.), 14·6–18·3 m, trawl, a new record for Western Australia, "agrees well with Haysom's . . . description of the holotype . . . . The belly and the base of the pectoral fin are darker than illustrated in figure 1 of Haysom, and the caudal fin lacks the small brown patch near the base of the two uppermost rays. A strong humeral spine is present." (McKay, personal communication, 1973); one specimen (FO 2344), Cocoanut Island, Torres Strait, compares with the holotype as follows:

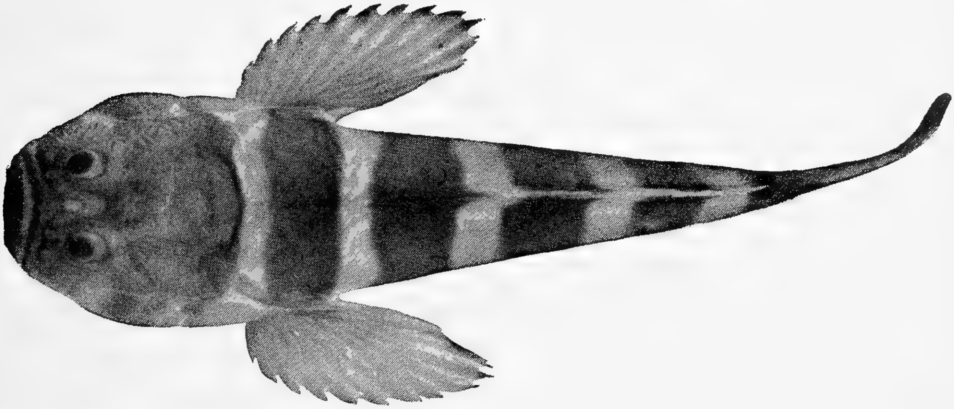

Fig. 1. *Ichthyscopus fasciatus* Haysom from Cocoanut Island, Torres Strait. Standard length 124 mm.

Total length 158 mm; standard length 124 mm. D.20; A.18; P.i,13,i; V.1,5; C.i,10,i; L.lat. approximately 60. Depth 3·6. Head 3·1 in SL. Eye 7·1 in head, 1·4 in interorbital and 1·6 snout length (see Table 1). On upper and lower lips transverse ridges broken into papillae, with branched filaments at their ends. Filaments more developed on lower lip. Villiform band of sharp teeth in upper jaw and on vomer. In lower jaw, row of small pointed teeth near symphysis and inside of this one row of larger canine-like teeth well-spaced towards symphysis. Nostrils oval and fringed. Humeral spine strong but blunt, largely concealed in fringed dermal flap.

Coloration similar to Haysom's (1957) description and figure except that, as with the Western Australian specimen, there is no brown patch at the base of the caudal fin. In addition, there is an oval, brown-edged white ocellus on the naked interorbital and several smaller ones on the dark chin. Brown shading near the base of the pectoral fin and on the edges of all fins except the dorsal.

TABLE 1

Measurements expressed in thousandths of standard length for Ichthyscopus fasciatus *and of total length for* Gymnothorax reticularis *and* Ophichthus evermanni

	Ichthyscopus fasciatus	*Gymnothorax reticularis*	*Ophichthus evermanni*
Total length (mm)	158	356	604
Standard length (mm)	124	—	—
Depth	277	44	32
Head	315	158	104
Eye	44	17	8
Snout	27	21	19
Interorbital	61	14	13
Snout to anus	—	457	458
Snout to dorsal fin origin	—	101	116
Trunk	—	299	353
Tail	—	545	543
Gill-opening	—	9	11
Snout to rictus	—	42	32
Pectoral fin	293	—	22
Above gill opening to dorsal fin origin	—	—	17

Paracentropogon longispinis (Cuvier and Valenciennes).

Apistus longispinis Cuvier and Valenciennes, 1829: 408.
Synonyms: *Centropogon indicus* Day, 1875: 157, pl. 38, fig. 2.
Paracentropogon vespa Ogilby, 1910: 116 (a suppressed publication); McCulloch, 1921: 173, pl. 10, fig. 2.
Prosopodasys zonatus Weber, 1913: 502.
Paracentropogon vespa livingstoni Whitley, 1933: 94.

One example (FO2293), SL 64 mm, was obtained from Cocoanut Island. D.XIV,7; A.III,4; P.i,9; C.ii,5+4,ii (ignoring rudiments); V.I,4; L.lat. tubules 19 or 20, plus one on base of caudal fin.

Because this specimen agreed well with descriptions of several species of *Paracentropogon*, it was decided to measure the variation in as many specimens as possible to ascertain whether those species were synonymous. In all, 30 specimens of *P. vespa*, 5 of *P. vespa livingstoni* (shown to be a synonym of *P. vespa* by Mees, 1964), 2 of *P. longispinis* and 7 of *P. rubripinnis* (Temminck and Schlegel) were examined. Descriptions of these species and of *P. indicus* (Day) and *P. zonatus* (Weber) were also studied. *Paracentropogon rubripinnis* emerged as a valid species, differing from the others in having longer anterior dorsal spines (see Table 2), scarcely developed scales, fewer pored scales in the lateral line and slightly different coloration (as pointed out by McCulloch, 1921, p. 174).

Among the other four nominal species there was little variation. The key characters used by Herre (1952) and de Beaufort (1962) to separate the species are the number of caudal rays, the relative lengths of the dorsal spines, and the direction of the anterior preorbital spine. In the species studied, the anterior preorbital spine was invariably directed down and back in all specimens and figures examined. (Note however that Herre, p. 459, states that this spine is pointed forward in *P. zonatus,* though de Beaufort says it points downwards). The caudal fin normally contained 8–11 divided rays (3–6+3–5) and 2 well-developed simple rays on the upper and lower edges, plus several rudimentary rays. In two specimens of *P. vespa,* one of them a type, there were abnormal caudal fin ray counts, possibly caused by regeneration after damage (type—AMS IA. 139: C.ii,5+5,ii,4,ii, and AMS IA. 4258: C.x,5+3,ii). The second and third dorsal spines are the longest in all species. As well as other characters, Table 2 gives the measurements of dorsal and anal spines expressed in thousandths of standard length. From these it can be seen that there is no appreciable difference between the relative spine lengths of different species (except for *P. rubripinnis*). No figures for *P. indicus* or *P. zonatus* are given therein. However, Herre (1952, p. 448) states that in *P. indicus* the second and third dorsal spines (the longest) go twice in the head length and those of *P. longispinis* 1·1–1·3. In the specimens of *P. longispinis* and *P. vespa* (and *P. vespa livingstoni*) measured, the second dorsal spine went 1·5–2·2 in the head length, which embraces Herre's figure for *P. indicus* (note also that for the *P. longispinis* specimens measured, the second and third dorsal spines went 1·6 and 1·4–1·6, respectively, in the head). In *P. zonatus* the second spine is "equal to head without snout and longer than third spine. Fourth and following spines shorter, . . ." (de Beaufort, 1962, p. 82).

TABLE 2

Range of measurements expressed in thousandths of standard length for four species of Paracentropogon

Character	*P. vespa* (30 specimens)	*P. vespa livingstoni* (5 specimens)	*P. longispinis* (2 specimens)	*P. rubripinnis* (7 specimens)
Standard length (mm) . .	19–88	37–59	46–67	44–62
Depth	301–403	330–359	327–357	304–357
Head length	338–437	379–408	339–396	342–388
Eye diameter	98–138	119–132	97–117	84–116
Snout length	81–120	76–119	93–107	82–105
Interorbital length . .	63–105	70–80	63–74	58–74
Anterior preorbital spine . .	22–48	24–39	28–46	18–27
Posterior preorbital spine	79–133	92–112	88–104	92–118
First dorsal spine	102–152	107–150	124–128	98–127
Second dorsal spine . .	180–237	181–239	210–241	205–315
Third dorsal spine . .	172–266	198–229	241–246	225–323
Fourth dorsal spine . .	156–235	166–212	176–200	170–295
Last dorsal spine	168–243	155–217	187–206	152–185
First anal spine	84–164	81–168	100–102	90–125
Second anal spine	148–218	146–216	143–159	145–173
Third anal spine	185–256	202–236	187–191	169–198
Soft dorsal fin height . .	179–268	203–256	174–252	169–213
Soft anal fin height . .	169–269	229–264	191–242	144–195
Ventral fin length	248–313	268–320	285–342	238–272
Pectoral fin length . .	313–389	339–371	322–376	316–368
Longest preopercular spine	69–108	73–97	72–106	68–104
Snout plus eye	182–232	203–246	193–220	180–248
Head without snout . .	278–342	308–336	282–304	292–339
Postorbital part of head . .	173–221	189–227	185–191	189–208

Of *P. indicus,* Day (1875, p. 154) notes that all the pectoral rays (10) are branched. The usual pectoral count for the specimens examined was 1 simple ray and 9 branched rays, but two specimens had all rays branched on one fin each, and one specimen had one fin with i, 10. *P. zonatus* has i,10 (de Beaufort) or ii, 9 (Herre) (probably i, 10 here too). The number of rays in the dorsal and anal fin of each species varies in descriptions between 7 and 8, and 4 and 5, respectively. I found that the last ray is always split to a common base which is enlarged and that the usually thin secondary ray is well-developed, branched, and generally diverges widely from the primary ray. The last ray thus appears as 2 entire rays.

Description. The salient features of *P. longispinis* based on the 37 specimens studied are: D.XIV–XV,6–7; A.III,4 (de Beaufort notes a specimen of Bleeker's with A.IV,4); P.i,9–10 (rarely P.10–11 or i,10); V.I,4 (I,2 in one specimen); C.ii,8–11,ii plus several rudimentary rays (see also discussion above); 18–22 tubules in lateral line plus one on base of caudal fin; G.R. 1–2+1+5–6.

Anterior profile of head steep; dorsal fin origin above middle of eye. Maxillary reaches more or less below middle of eye. Anterior preorbital spine small, directed down and back, two to four times shorter than posterior preorbital spine which equals or is slightly shorter than eye diameter. Posterior preorbital spine reaches almost to hind border of eye or extends past it as far as half-way to preopercular margin. Hind border of preopercle with strong spine 0·9–1·5 in posterior preorbital spine, and with four short, blunt spines below it. Two weak divergent spines on opercle with blunt tips.

First dorsal spine slightly longer than snout, or 0·8–1·2 in eye (average 0·9). Second dorsal spine 1·4–1·9 longer than first, and 1·5–2·2 in head length. Third dorsal spine 1·4–1·9 in head length and usually longer than head without snout. Third spine longest, rarely shorter than or equal to second spine. Last dorsal spine approximately equals third anal spine which is 1·2–2·0 in head; both subequal to longest dorsal spine. Ventral fins equal to head without snout (occasionally more or less), 1·0–1·5 in head. Ventrals fall short of, or reach, anus and sometimes extend as far as second anal spine. Pectorals longer than ventrals, slightly less than head length, though sometimes equal to or longer than head.

Colour of preserved specimens mottled with dark brown over a pinkish or light brown background. Ventrals are dark brown or black distally (in only a few was a white spot present) and often a dark band extends across posterior half of caudal. Only *P. indicus* lacks a white spot above the lateral line below the tenth and eleventh dorsal spines according to descriptions, although in specimens of other species this white spot is occasionally absent, often faded or often conspicuous. The presence of a large black patch between the fifth and eighth dorsal spines is apparently also variable. It is described as present in *P. vespa, P. zonatus* and *P. longispinis* (Herre, 1952; Günther, 1860) and absent in *P. indicus* and *P. longispinis* (de Beaufort, 1962; Day, 1875). Yet Day's figures (pl. 38) of *P. indicus* and *P. longispinis* both show a dark area on the spinous dorsal. In the preserved specimens of *Paracentropogon* examined, this patch varies in intensity from black to faded or light brown and in two specimens is absent altogether.

Conclusion. From the specimens and descriptions studied, I have found no single character, or combination of characters, which distinguishes any of these species (*P. vespa, P. zonatus, P. longispinis* and *P. indicus*) from each other. Therefore, *P. vespa, P. zonatus* and *P. indicus* are regarded as synonyms of *P. longispinis.* De Beaufort, Herre and McCulloch have all remarked on the similarity to *P. longispinis* of *P. zonatus, P. indicus* and *P. vespa,* respectively

Marshall (1964) records *P. longispinis* (as *P. vespa*) from Queensland and North Australia, where it is occasionally trawled. It also occurs in Western Australia, at least between Broome (18°00′S., 122°10′E.) and Shark Bay (25°30′S., 113°40′E.) (Mees, 1964). The species has not been recorded from Papua New Guinea.

Ophichthus evermanni Jordan and Richardson

Fig. 2A

Ophichthus evermanni Jordan and Richardson, *Mem. Carnegie Mus.*, 4(4), 1909, p. 172, pl. 67.

One specimen (FO3796) obtained from Darnley Island, Torres Strait. This specimen was among the gut contents of the snake *Hydrophis (Leioselasma) elegans* (Grey). The posterior half of the tail is partly digested, with the tip missing. Total length approximately 604 mm.

Depth 31 in total length, 3·2 in head. Head 9·6 in total length, 3·4 in trunk. Eye 12·5, snout 5·6, snout to rictus 3·3, interorbital 8, pectoral fin 4·8, all in head. Space between dorsal fin origin and vertical line from gill opening 6 in head. Eye 2·2 in snout. Snout to dorsal fin origin 8·7 in total length. Snout to anus 1·2 in tail and 2·2 in total length. (See Table 1.)

Anterior nostril in broad tube, posterior nostril labial, below front border of eye, hidden by bulge of skin. Two thin skin flaps on lips: smaller below middle of eye, larger midway between nostrils. Lips fold into mouth. Eye above posterior half of mouth gape. Lower jaw begins slightly in advance of large skin flap. Numerous pores on head: along upper and lower jaws, behind rictus, around eye and along snout, which is pointed. Body thick and cylindrical. Dorsal fin origin behind head, above tip of pectoral fin. Deep predorsal groove extends to occiput. Pectoral fin rounded with about 16 rays, base restricted. Teeth sharp, curved, uniserial. Part of intermaxillary tooth patch before lower jaw.

Colour in formalin greyish white below, pale brown above, with irregular dark brown bands or blotches on back reaching to middle of sides. Area from snout to rictus dark brown, separated by white patch from broad black band across nape, which in turn followed by thinner white band. Anal and pectoral fins pale, dorsal light brown.

This species was previously known to extend from Japan and Taiwan to the Philippines (Fowler, 1932; Chen and Weng, 1967). It is similar in coloration and dentition to *Ophichthus retifer* Fowler and *O. bonaparti* (Kaup) (Smith, 1962*b*; Weber and de Beaufort, 1916) but differs in some body proportions, in the position of the dorsal fin origin and in relative jaw lengths. *Ophichthus evermanni* is also close to *O. cephalozona* Bleeker, but differs in possessing numerous irregular cross bands along the body, whereas *O. cephalozona* has only one nuchal band and a plain body. The specimen is a new record for Queensland and Australia. Although not yet found in Papua New Guinea, it is likely that it occurs there also.

Gymnothorax (Priodonophis) reticularis Bloch

Fig. 2B

Gymnothorax reticularis Bloch, *Ausl. Fische* IX, 1795, p. 85. pl. 416.

One specimen (FO3794) was obtained from the gut contents of a gravid female snake, *Hydrophis (Leioselasma) elegans* (Gray) trawled off Darnley Island. The specimen is complete except for the skin on the tail. Total length 356 mm.

Depth 22·7 in total length, 3·6 in head. Head 6·3 in total length and 1·9 in trunk. Eye 9·4, snout 7·6, interorbital 11, snout to rictus 3·7, all in head. Snout to dorsal fin origin 1·6 in head, 9·9 in total length. Snout to anus 2·2 in total length and 1·2 in tail. (See Table 1.)

Anterior nostril in short tube, posterior nostril pore above front of eye. Snout bluntly rounded. Eye in posterior half of mouth gape. Lips with several rows of tiny papillae. Strong, pointed, triangular teeth uniserially arranged in jaws and vomer. No median intermaxillary canines. Edges of most teeth distinctly and finely serrated. Gill openings oblique, slightly below middle of sides. Dorsal fin thin, origin about halfway between eye and gill opening.

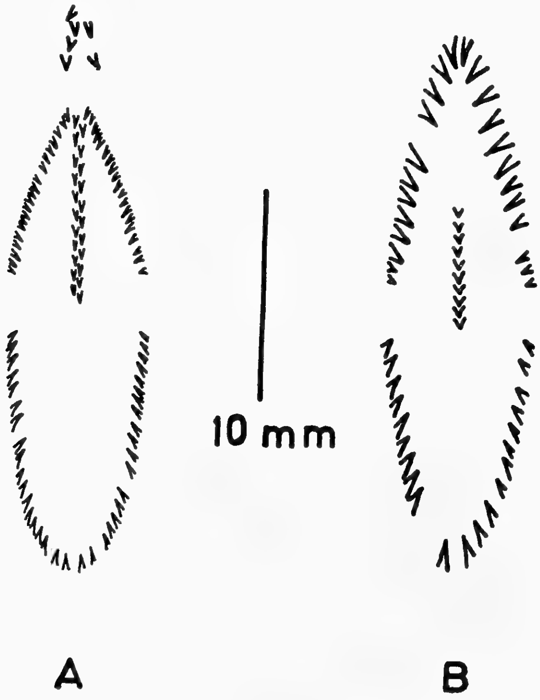

Fig. 2. Dental pattern of two eels from Darnley Island, Torres Strait. A. *Ophichthus evermanni* Jordan and Richardson. Total length approx. 604 mm. B. *Gymnothorax reticularis* Bloch. Total length 356 mm.

Colour in isopropyl alcohol greyish white below, pinkish above, with about 20 dark brown crossbands narrower than interspaces, first on nape. Bands darker ventrally and on fins. Head and upper half of body between bands covered with small brown spots of various sizes.

Gymnothorax reticularis is distinguished from other moray eels by its serrated teeth and coloration. The species is also known from India (Day, 1875), Taiwan and Japan (Chen and Weng, 1967), Mozambique (Smith, 1962*a*), Fiji (Whitley, 1926) and the New Hebrides (Fowler, 1934). As well as the specimen from Darnley Island, the Kanudi collection contains two small tails of *G. reticularis* coloured similarly to the whole specimen, taken from the gut contents of a seasnake, *Aipysurus duboisii* Bavay, trawled off Weipa (12°40′S., 141°58′E.), Gulf of Carpentaria, June 20, 1972 (FO4133). These tails and the Darnley Island specimen are the first records of *G. reticularis* from Australia. *Gymnothorax reticularis* has also recently been found in Papua New Guinea (Kailola, in press).

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THE CYTOEVOLUTION OF THE AUSTRALIAN PAPILIONACEAE

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(Plate XVI)

[Accepted for publication 23rd October 1974]

Synopsis

Evolutionary development in the Australian Papilionaceae is analysed with special reference to the tribe Podalyrieae, through an integration of data on chromosome numbers, inflorescence morphology and geographic distribution.

Chromosome determinations are reported for 242 species of 22 genera in the Podalyrieae, together with 51 species of 13 genera from other tribes. The Podalyrieae is here divided into three groups on chromosome number and inflorescence morphology and the evolutionary pattern of each group has been analysed.

Base chromosome numbers of 7, 8 and 9 in the Podalyrieae originated prior to the development of the genera, which appear to have achieved pan-Australian distribution before mid-Miocene isolation of east and west. Only *Pultenaea* and *Dillwynia* developed strongly in the east. Polyploidy, including triploidy with variable pollen sterility in two species, is shown to be a minor factor in the evolution of the tribe. As in other hardwood families, aneuploid change of base chromosome number has been important.

In *Pultenaea* aneuploidy is associated with considerable morphological diversity, and ten groups of species are defined. Chromosome loss or gain was more frequent in regions where fluctuations in aridity had most profound effect, as in South Australia, while Victoria appears to have been a centre of survival and dispersal for most $x = 8$ species. On morphological evidence, this was the basic chromosome number of the genus, while $x = 7$ and $x = 9$ apparently had multiple origins in both east and west. The pattern of rapid speciation suggested for one *Pultenaea* group may indicate that "catastrophic" evolution permitted the success of *Pultenaea* above the other genera with more stable chromosome number.

INTRODUCTION

The family Papilionaceae of the Leguminosae comprises ten tribes according to Bentham (1864), but Hutchinson (1964) elevates most of Bentham's subtribes to tribes, bringing the total to fifty. The numerous genera are widely dispersed throughout both hemispheres in a great diversity of habitats and are well represented in Australia. In particular, the tribe Podalyrieae has shown extensive development in this country with 21 (according to Bentham (1864)) or 24 (according to Hutchinson (1964)) of its genera being endemic.

In the present paper an attempt is made to elucidate the probable evolution, or historical development, of the tribe Podalyrieae within Australia. The data from which the evolutionary inferences have been developed include cytological, morphological and distributional analyses.

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MATERIAL AND METHODS

Cytology

Cytological studies were made on anthers, ovaries and leaf buds fixed in acetic-alcohol (1:3) and stored in absolute alcohol at 4°C. Most mitotic counts were made from ovule wall tissue following three minutes hydrolysis in N.HCl at 60°C and staining with aceto-orcein. Some embryo and leaf bud mitoses were also studied. Meiotic observations were made on pollen mother cell divisions from aceto-orcein squash preparations. Pollen fertility was assessed by using acid fuchsin in a stain mountant of the formula proposed by Zirkle (1940).

Morphology

Of the approximately 475 species which are currently recognised in the Podalyrieae in Australia, all but 28 have been examined from specimens in the following herbaria: National Herbarium of New South Wales, Sydney (N.S.W.); Herbarium of the School of Biological Sciences, University of Sydney (SYD); Herbarium of C.S.I.R.O., Canberra and Waste Point (CANB); Herbarium of the Parks and Gardens Section, Department of the Australian Capital Territory, Canberra; National Herbarium of Victoria, Melbourne (MEL); State Herbarium of South Australia, Adelaide (AD); State Herbarium of Western Australia, Perth, (PERTH). Wherever possible use of fresh material has been preferred, particularly in determining whether absence of an organ is real or the result of abscission occurring at maturity.

A complete voucher collection is housed in SYD, and partial collections are available in NSW, AD and PERTH.

A preliminary survey of vegetative and inflorescence characters in representative species of the Podalyrieae was followed by selection of characters which either are constant within a genus or, in the case of *Pultenaea,* show variation between species. Observations on each species are tabulated in Sands (1966) together with descriptions of the inflorescence morphology characterising each genus or section thereof. Such data, summarised briefly below, provide the basis for the discussions on intergeneric and intrageneric relationships which follow.

Distribution

Species distributions have been assessed from the herbaria data, from State Floras and from the collections made during the course of this study.

OBSERVATIONS

Cytology

CHROMOSOME NUMBERS

Chromosome numbers for 25 Australian species in seven genera in the family Papilionaceae have been reported previously (Table 1).

In the present investigation chromosome numbers of 242 species of 22 of the 24 genera in Hutchinson's (1964) classification of the Podalyrieae are reported, together with numbers for a further 51 species of 13 genera in other tribes. These include the Bossiaeeae of Lee (1973), previously Genisteae, the Indigofereae, Coluteae and Tephrosieae of Hutchinson (1964), all previously Galegeae, and the Glycineae and Cajaneae which were classified by Bentham (1864) as Phaseoleae. The study has included an extensive sampling of *Pultenaea,* the largest genus in the Podalyrieae (Plate XVI). Full details of the chromosome number determinations

TABLE 1

Previous records of chromosome numbers in Australian species of the Papilionaceae, tribes according to Bentham (1864)

Species	2n	State	Author
Genisteae			
Platylobium obtusangulum	16	SA	Oram, R. N. (unpubl.)
Crotalaria juncea	16	SA	Darlington and Wylie (1955)
Galegeae			
Swainsona canescens	?24	WA	Humphries, A. W. (unpubl.)
S. occidentalis	32	WA	,, ,,
S. cyclocarpa	32	WA	,, ,,
S. stipularis	32	WA	,, ,,
Phaseoleae			
Hardenbergia comptoniana	22	WA	Silsbury, J. H. (unpubl.)
H. violacea (as *H. monophylla*)	22	NSW	Smith-White, S. (unpubl.)
Kennedia beckxiana	22	WA	Silsbury, J. H. (unpubl.)
K. carinata	22	WA	,, ,,
K. coccinea	22	WA	,, ,,
K. eximia	22	WA	,, ,,
K. microphylla	22	WA	,, ,,
K. nigricans	22	WA	,, ,,
K. prorepens	22	WA	,, ,,
K. prostrata	22	WA	,, ,,
K. rubicunda	22	NSW	Smith-White, S. (unpubl.)
K. stirlingii	22	WA	Silsbury, J. H. (unpubl.)
Podalyrieae			
Daviesia brevifolia	18	SA	Oram, R. N. (unpubl.)
D. corymbosa	18	SA	,, ,,
Pultenaea gunnii	14	Tas.	Curtis (1952)
P. daphnoides	16	NSW	,, ,,
P. daphnoides var. *obcordata*	16	Tas.	,, ,,
P. stricta	16	Tas.	,, ,,
P. tenuifolia	16	Tas.	,, ,,
P. juniperina var. *juniperina*	18, 27, 36	Tas.	,, ,,
P. juniperina var. *planifolia*	18, 27	Tas.	,, ,,

are given in the Appendix with authorities for species names. Chromosome numbers are summarised at the generic level in Table 2. Karyotype analysis is not practicable. The chromosomes are generally small and do not show distinctive morphological features.

MEIOTIC BEHAVIOUR

Meiotic behaviour is normally regular but aberrations were noted in a few species. Residual bridge and fragment formation, sometimes accompanied by formation of an additional microcyte, or by subterminal neocentric activity or by reduction in the quantity of viable pollen produced, were observed in *Phyllota phylicoides, Dillwynia juniperina, D. parvifolia* var. *trichopoda, Pultenaea canescens, P. villosa* and *P. procumbens,* all with $n = 7$. In one specimen of *Oxylobium ilicifolium* ($n = 8$) "stickiness" of second metaphase chromsomes and occasional bridge formation were observed. These examples of irregular meiotic behaviour were infrequent and no population analyses were made.

POLYPLOIDY

Polyploidy was found in 14 of the 242 species examined (Table 3). In *Pultenaea muelleri* var. *reflexifolia* the diploid and tetraploid plants were obtained from the one population but in the other species from

TABLE 2

Chromosome numbers of Australian genera of the Papilionaceae, following the classification of Hutchinson (1964)

Genus	No. of species studied	Total counts obtained	2n
Bossiaeeae ex Genisteae Benth. and Hook.f.			
Bossiaea	23	43	18
Goodia (Lee, 1973)	1	1	16
Hovea	9	28	18
Platylobium	1	7	16
Templetonia	1	3	16
Indigofereae ex Galegeae Benth. and Hook.f.			
Indigofera	3	11	16
Coluteae ex Galegeae Benth. and Hook.f.			
Swainsona	2	6	16, 32
Tephrosieae ex Galegeae Benth. and Hook.f.			
Tephrosia	1	1	16
Glycineae ex Phaseoleae Benth. and Hook.f.			
Glycine	1	3	20, 40
Hardenbergia	2	8	22
Kennedia	5	10	22
Cajaneae ex Phaseoleae Benth. and Hook.f.			
Rhynchosia	1	1	22
Podalyrieae			
Aotus	3	15	16
Brachysema	4	4	16
Burtonia	1	1	18
Chorizema	10	15	16, 32
Cupulanthus	1	1	16
Daviesia	28	65	18
Dillwynia	19	97	14, 28
Euchilopsis	1	2	14
Eutaxia	5	13	16, 32
Gastrolobium	18	29	16
Gompholobium	13	22	18
Isotropis	1	4	16, 32
Jacksonia	7	11	18
Latrobea	1	2	14
Leptosema	1	1	16
Mirbelia	11	27	16
Nemcia	7	14	16
Oxylobium	16	27	16
Pultenaea	89	283	8, 12, 14, 16, 18, 27, 28, 32
Phyllota	2	8	14
Sphaerolobium	3	4	18
Viminaria	1	2	18

different populations. In general a low frequency of multivalent formation at first metaphase was observed in tetraploid specimens. Pollen fertility was in the intermediate range wherever it could be assessed with the exception of complete pollen sterility in the single tetraploid determination of *P. linophylla.*

Twenty-two plants sampled in the only known population of *Dillwynia stipulifera* were all triploid. Meiotic material was not available but meiotic irregularity was suggested by the incidence of pollen sterility involving complete pollen breakdown. Fertility ranged from 5% to 90% with a mean of 30% for the 30 plants analysed. Re-establishment after fire suggested regeneration by root stocks. Insufficient plants survived

TABLE 3

*Incidence of polyploidy in the Podalyrieae**

Species	2n	4n	3n
Chorizema aciculare	1	1	
Dillwynia floribunda	8	3	
D. parvifolia var. *trichopoda*	4	3	
D. phylicoides	5	4	
D. prostrata		2	
D. retorta	5	2	
D. stipulifera			1
Eutaxia densifolia	1	1	
E. microphylla	6	1	
Isotropis cuneifolia	3	1	
Pultenaea dentata		1	
P. juniperina var. *juniperina*	1		
P. juniperina var. *planifolia*	4		4
P. linophylla	2	1	
P. muelleri var. *reflexifolia*	1	1	

* The figures in the body of the table represent the number of locations at which this particular level of ploidy was found.

and they were too small at the time of sampling to estimate the degree of variation within individual plants in the proportion of sterile pollen. For the same reasons the mechanism responsible for the high incidence of fertile pollen in some plants could not be investigated.

In the four collections of *Pultenaea juniperina* var. *planifolia* both diploid and triploid plants were obtained. The single plant of *P. juniperina* var. *juniperina* studied was diploid. Meiosis was regular in the diploid plants, but triploid plants showed considerable trivalent formation at first metaphase and lagging univalents at first and second anaphases. Pollen analysis of the populations near Sawpit Creek on the lower slopes of the Kosciusko Plateau showed that triploids had low pollen fertility but that there was a range of sterility among diploid plants greater than expected if meiosis had been completely regular (Table 4). Insect depredations thwarted study of seed set.

TABLE 4

Pollen analysis of three populations of Pultenaea juniperina *var.* planifolia*

% Fertility	Population K		Population M		Population J	
	2n	3n	2n	3n	2n	3n
100–90	7	—	3	—	—	—
89–70	2	—	1	—	—	—
69–50	3	—	3	—	1	—
49–30	1	—	2	—	—	—
29–10	2	2	1	—	3	2
9–0	1	3	4	—	3	12
No pollen	1	—	2	3	—	—

* The figures in the body of the table show the various pollen fertility ranges, with the number of 2n and 3n plants in each range.

Population K : Sawpit Creek walking track to Hatchery, 1·6 km from road.

Population M : Sawpit Creek track, 2·4–3·2 km from road, on opposite side of river.

Population J : Kosciusko roadside 1·6 km above Sawpit Creek, about 1,190 m.

TABLE 5

Chromosome and ovule numbers in the genera of the Podalyrieae, using the generic classification of Hutchinson (1964)

Chromosome base no.	No. of ovules	
	2	Variable 2–30
7	*Phyllota* *Euchilopsis* *Dillwynia* *Latrobea*	
8	*Eutaxia* *Aotus* *Gastrolobium*	*Oxylobium* *Nemcia* *Mirbelia* *Chorizema* *Isotropis* *Brachysema* *Cupulanthus* *Leptosema* *Jansonia*?
9	*Burtonia* *Sphaerolobium* *Jacksonia* *Viminaria* *Daviesia* *Erichsenia*?	*Gompholobium*
4, 6, 7, 8, 9	*Pultenaea*	

? denotes that generic relationships indicated by morphological studies have not yet been supported by cytological data for these monotypic genera.

Morphology in the Podalyrieae

The secondary taxonomic characters such as size and shape of organs and degree of pubescence were found to vary with age and within the environmental and geographical ranges of the species. Greater significance could be attached to features of the reproductive organs where character expression was much less altered by environment. These include inflorescence structure, the presence of floral leaves or of an involucre of sterile bracts, the form of the bract subtending each flower and of the bracteoles, pubescence of ovary and number of ovules.

The 24 Australian genera (Hutchinson, 1964) may be grouped according to the chromsome number and number of ovules characteristic of each genus (Table 5). Observations made on almost all species of the Podalyrieae are summarised below.

GENERIC GROUP I

A haploid complement of 9 chromosomes is found in six genera, all of which have 2 ovules and which comprise a great number of species. *Gompholobium,* also with $n = 9$, must be included with these on general morphological grounds despite its numerous ovules, as also must *Erichsenia,* although its chromosome number is not known.

The large genus *Daviesia* displays uniformity in many characters but diversity in leaf modifications and types of inflorescence. Its characteristic numerous bracts on the peduncles of all species and its scarious subtending bracts together with its typical pod shape and seed structure distinguish it from the monotypic *Viminaria* and *Erichsenia.* The three genera show similarities in the absence of bracteoles, orbicular floral standard, glabrous ovary with 2 ovules and strophiolate seeds.

Despite the varied modifications of cladode-type branches in *Jacksonia* which together with pod shape and thickness of ovule funicles separate it from *Gompholobium* and *Burtonia,* the 50 species of *Jacksonia* are relatively homogeneous in inflorescence and fruiting characters. These three genera all possess long calyx lobes, entire subtending bracts and bracteoles, and non-strophiolate seeds. *Gompholobium* and *Burtonia* can only be separated from each other by their differing number of ovules and direction of ovule funicles, both showing slight variability in other leaf and inflorescence characters. *Sphaerolobium* differs from *Jacksonia* mainly in habit, the form of the calyx lobes, glabrous ovary with style appendages and small stipitate globular pod. Interspecific differences are slight apart from variation in the style appendages.

Intrageneric uniformity appears to characterise this group of seven genera.

GENERIC GROUP II

With the exception of *Gompholobium,* genera possessing more than 2 ovules have a haploid complement of 8 chromosomes. The inclusion of *Gastrolobium* ($n = 8$ but 2-ovulate) in this complex is based on its similarity to *Oxylobium* series *Gastrolobioideae* (now the genus *Nemcia*), which has 4 or rarely 6 ovules. All species of both are similar in absence of bracteoles (neither bracteoles nor their scars were observed in *Gastrolobium* species, *contra* Bentham (1864)) and in seeds with strophioles. Some species in common possess similar inflorescence types, other trifid subtending bracts and stipulate leaves. In *Gastrolobium* series *Racemosae* leaves are stipulate and flowers in open or dense racemes or terminal clusters all have entire subtending bracts. In *Gastrolobium* series *Axillares,* however, while flowers are always in axillary clusters, one group of species has stipulate leaves and trifid subtending bracts (in a few species trifid lower bracts and entire bracts in the upper flowers of the inflorescence) and the other group has exstipulate leaves with entire subtending bracts.

Comparable patterns of overlapping variability are found within and between all the genera of this group. This is most evident in the large genus *Oxylobium*; the six series into which this genus was divided by Bentham (1864) show considerable similarities to other genera. *Oxylobium* series *Gastrolobioideae* (*Nemcia*) and series *Podolobieae* differ in the density of their racemes and in strophiolation of seeds but are distinct from the other four series in having 4 ovules and trifid subtending bracts, with bracteoles absent. *Oxylobium* series *Racemosae, Ericoideae, Callistachyae* and *Laxiflorae* have in common with *Mirbelia* the entire subtending bracts, bracteoles present with very few exceptions, and more numerous ovules which develop into nonstrophiolate seeds. The series may be separated on minor leaf and inflorescence characters, but while *Mirbelia* shows comparable diversity, it is consistently characterised by the false dissepiment dividing ovary and pod. *Chorizema* is also similar to these four *Oxylobium* series, but in some species has trifid subtending bracts reminiscent of the *Gastrolobium* trend, and shows leaf and stipule variation. Difference in habit, calyx form and size of pod distinguish this genus from *Isotropis.*

The monotypic *Jansonia* differs in a specialised bract arrangement, but is similar in its short narrow floral standard to the two sections of *Brachysema,* now defined by Hutchinson (1964) as three genera, namely, *Brachysema, Cupulanthus* and *Leptosema.* Despite lack of cytological confirmation, *Jansonia* must be included in this complex of genera. There is similarity between *Jansonia, Brachysema* section *Eubrachysema* (now *Brachysema sens. str.*) and *Oxylobium* series *Gastrolobioideae* (*Nemcia*), with stipulate leaves, trifid subtending bracts, lack of bracteoles and strophiolate seeds. By contrast, *Brachysema* section *Leptosema* (now *Leptosema*) resembles the four series of *Oxylobium* which have entire subtending bracts and bracteoles, and nonstrophiolate seeds.

It is evident that underlying the generic distinctions in this Group II, similar modifications in inflorescence structure occur repeatedly, giving rise to considerable morphological diversity at the intrageneric level. Interrelationships in the complex are close.

GENERIC GROUP III

Each genus in the third complex, characterised by 2 ovules, shows greater or less affinity with one of the groups of species in the large genus *Pultenaea*. Excluding the latter, the genera are similar in showing a trend towards solitary flowers, and in having an entire subtending bract and a pubescent ovary. Bentham's (1864) criterion of separation from *Pultenaea*, namely, absence of stipules, cannot be maintained, since vestiges of stipules are present in several species of *Eutaxia, Dillwynia, Aotus* and *Phyllota*.

Although many *Pultenaea* species have incurved or involute leaf margins, they are distinct, with their bracteoles adnate to or at the base of the calyx, from *Eutaxia, Dillwynia* and *Latrobea* with bracteoles attached below the calyx. The opposite leaves and haploid number of 8 of *Eutaxia* separate it from *Dillwynia* and *Latrobea* with alternate leaves and $n = 7$. The latter genera differ in size of calyx lobes and shape of the floral standard. Although there are minor differences between the two sections within each of these genera, there is considerable intrageneric uniformity in morphology.

Recurved and revolute leaf margins characterise other *Pultenaea* species and *Aotus, Phyllota* and the monotypic *Euchilopsis*. The latter, with $n = 7$, is distinct in size of calyx lobes. *Aotus*, with $n = 8$, scarious subtending bracts and lacking bracteoles, shows little specific diversification and is readily distinguished from *Phyllota* with $n = 7$ and leaf-like subtending bracts and bracteoles. There is integradation of the latter genus into a Western Australian group of *Pultenaea* species with $n = 7$ and exstipulate leaves, notably in leaf-margin curvature, union of staminal filaments with petals and reduction in number of flowers.

In this complex, morphological distinctions between genera with $n = 7$, or the two with $n = 8$, are greater than those between *Eutaxia* ($n = 8$) and *Dillwynia* ($n = 7$).

PULTENAEA IN GROUP III

The diversity of inflorescence structure in the very large genus *Pultenaea* is greater than that in any other genus of the Podalyrieae. Some significant features of the species are summarised in Tables 6 and 7. The infrageneric variability described below in these characters is of the same order as the differences which distinguish genera in the rest of the tribe.

Inflorescence Types

Where the stem continues growth during the flowering season, the inflorescence is frequently an open raceme with flowers so widely spaced as to appear solitary and axillary (Fig. 1a) or may be a shorter raceme with few flowers (Fig. 1c). In other species a compact raceme forms at the base of the new foliar growth or there may be axillary clusters

TABLE 6

Inflorescence characters, chromosome numbers and regional distribution of Pultenaea *species*

Group	Region	Inflor.	Invol.	Sub.br.	Br'ole	n	Ovary
I	E	LR	SL	SL	SL	8	Pu
II–1	W	,,	,,	,,	,,	—	,,
2	,,	,,	,,	SRL	En	—	,,
3	,,	,,	,,	En	,,	4	,,
III– 1	E	,,	,,	SL	,,	8	,,
a– 1	,,	,,	,,	,,	,,	8	,,
a– 2	,,	,,	,,	,,	,,	8	Tu
a– 3	,,	,,	,,	,,	,,	7	,,
a– 4	,,	,,	,,	,,	,,	7	Gl
b– 5	,,	,,	,,	,,	,,	9	Pu
b– 6	,,	,,	,,	SRL	,,	9	,,
b– 7	,,	DR	,,	,,	,,	8	,,
b– 8	,,	,,	SL–SRL	,,	,,	8	,,
b– 9	,,	,,	Tr	En	,,	8	,,
b–10	,,	,,	SL	SRL	,,	9	,,
b–11	,,	,,	SL–SRL	,,	,,	9	,,
c–12	,,	,,	,,	,,	Tr	8	,,
IV– 1	W	LR	SL	SL	SL	7	,,
2	,,	DR	,,	,,	SRL	7	,,
3	,,	,,	,,	,,	Tr	7	,,
4	,,	,,	,,	SRL	SRL	7	,,
5	,,	,,	SL–SRL	,,	En	7	,,
6	,,	,,	SRL	Tr	,,	7	,,
V– 1	,,	LR	SL	SL	SL	8	,,
2	,,	,,	,,	,,	,,	9	,,
3	,,	,,	,,	,,	En	—	,,
4	E	,,	,,	,,	,,	7	Tu
VI– 1	,,	,,	,,	,,	RSL	8	Pu
2	,,	,,	,,	,,	,,	7	,,
3	,,	,,	,,	,,	,,	7	Tu
4	,,	DR	,,	SRL	,,	8	,,
5	,,	,,	,,	,,	,,	8	Gl
VII–1	,,	LR	,,	SL	SL	7	Tu
2	,,	,,	,,	,,	SRL	7	,,
VIII	,,	DR	SL–SRL	SRL	En	8	Pu
IXa–1	,,	LR	SL	SL	,,	8	,,
a–2	,,	DR	,,	,,	,,	8	,,
a–3	,,	,,	,,	SRL	,,	8	,,
a–4	,,	,,	,,	Tr	,,	7	,,
a–5	,,	,,	SL–SRL	,,	,,	8	,,
b–6	W	,,	SL	SL	,,	—	,,
b–7	,,	,,	,,	SRL	,,	—	,,
b–8	,,	,,	Tr	En	En	—	,,
X–1	,,	,,	EL	EL	EL	7	,,
2	,,	LR	,,	,,	,,	7	,,

Key

I–X	Groups of *Pultenaea* species which are morphologically similar.
a–c	Subgroups of similar species in Groups III and IX.
1–12	Individual species or groups of species which are identical in the characters concerned.
E	Eastern Australia.
W	Western Australia.
Invol.	Involucre.
Sub.br.	Subtending bract.
Br'ole	Bracteole.
DR	Dense umbel-like raceme or few or solitary flowers surrounded by involucral bracts.
LR	Loose raceme, cluster or solitary flowers.
SL	Stipulate leaf.
SRL	Stipulate reduced leaf.
SL–SRL	Stipulate leaf on lower involucral bracts, stipulate reduced leaf on higher bracts.
RSL	Leaf with reduced stipules.
EL	Exstipulate leaf.
Tr	Trifid.
En	Entire.
Pu	Pubescent ovary.
Tu	Glabrous ovary with a tuft of apical hairs.
Gl	Glabrous ovary.
n	Haploid chromosome number ; (—) denotes number not determined.

Table 7

Species Groups in Pultenaea

Group I
P. trifida, P. quadricolor, P. d'altonii
Group II
1 *P. ochreata*
2 *P. aspalathoides*
3 *P. reticulata*
Group III
1 *P. tenuifolia, P. prolifera, P. fasciculata, P. teretifolia, P. canaliculata, P. trinervis, P. trichophylla, P. villifera, P. viscidula, P. graveolens, P. densifolia, P. patellifolia*
Subgroup (a)
1 *P. blakelyi*
2 *P. flexilis*
3 *P. campbellii*
4 *P. euchila, P. altissima, P. obovata*
Subgroup (b)
5 *P. acerosa, P. rigida, P. vrolandii*
6 *P. juniperina, P. costata*
7 *P. bauerlenii, P. subalpina*
8 *P. divaricata, P. echinula, P. largiflorens*
9 *P. involucrata, P. muelleri, P. prostrata*
10 *P. viscosa, P. mollis, P. angustifolia*
11 *P. hibbertioides*
Subgroup (c)
12 *P. incurvata, P. paludosa, P. cambagei, P. subumbellata*
Group IV
1 *P. empetrifolia*
2 *P. vestita*
3 *P. adunca*
4 *P. radiata*
5 *P. verruculosa*
6 *P. ericifolia, P. strobilifera*
Group V
1 *P. calycina*
2 *P. obcordata*
3 *P. tenella, P. rotundifolia, P. arida, P. cymbifolia, P. spinulosa*
4 *P. cunninghamii, P. subternata, P. spinosa*
Group VI
1 *P. laxiflora*
Subgroup (a)
2 *P. hispidula, P. recurvifolia, P. pubescens*
3 *P. villosa*
Subgroup (b)
4 *P. stipularis, P. aristata*
5 *P. glabra*
Group VII
1 *P. procumbens, P. boormanii, P. foliolosa, P. stuartiana, P. ferruginea, P. setulosa*
2 *P. canescens, P. elliptica, P. subspicata, P. parviflora, P. humilis, P. weindorferi*
Group VIII
P. dentata
Group IX
Subgroup (a)
1 *P. pedunculata, P. hartmannii, P. microphylla, P. scabra, P. milleri,*
2 *P. petiolaris*
3 *P. benthamii, P. selaginoides*
4 *P. gunnii*
5 *P. paleacea, P. myrtoides, P. capitellata, P. pycnocephala, P. stricta, P. maidenii, P. rosmarinifolia, P. daphnoides, P. mucronata, P. polifolia, P. linophylla, P. retusa, P. amoena, P. platyphylla*
Subgroup (b)
6 *P. skinneri*
7 *P. conferta, P. drummondii*
8 *P. pinifolia*
Group X
1 *P. capitata, P. dasyphylla, P. lycopodioides, P. andrewsii, P. georgei*
2 *P. neurocalyx*

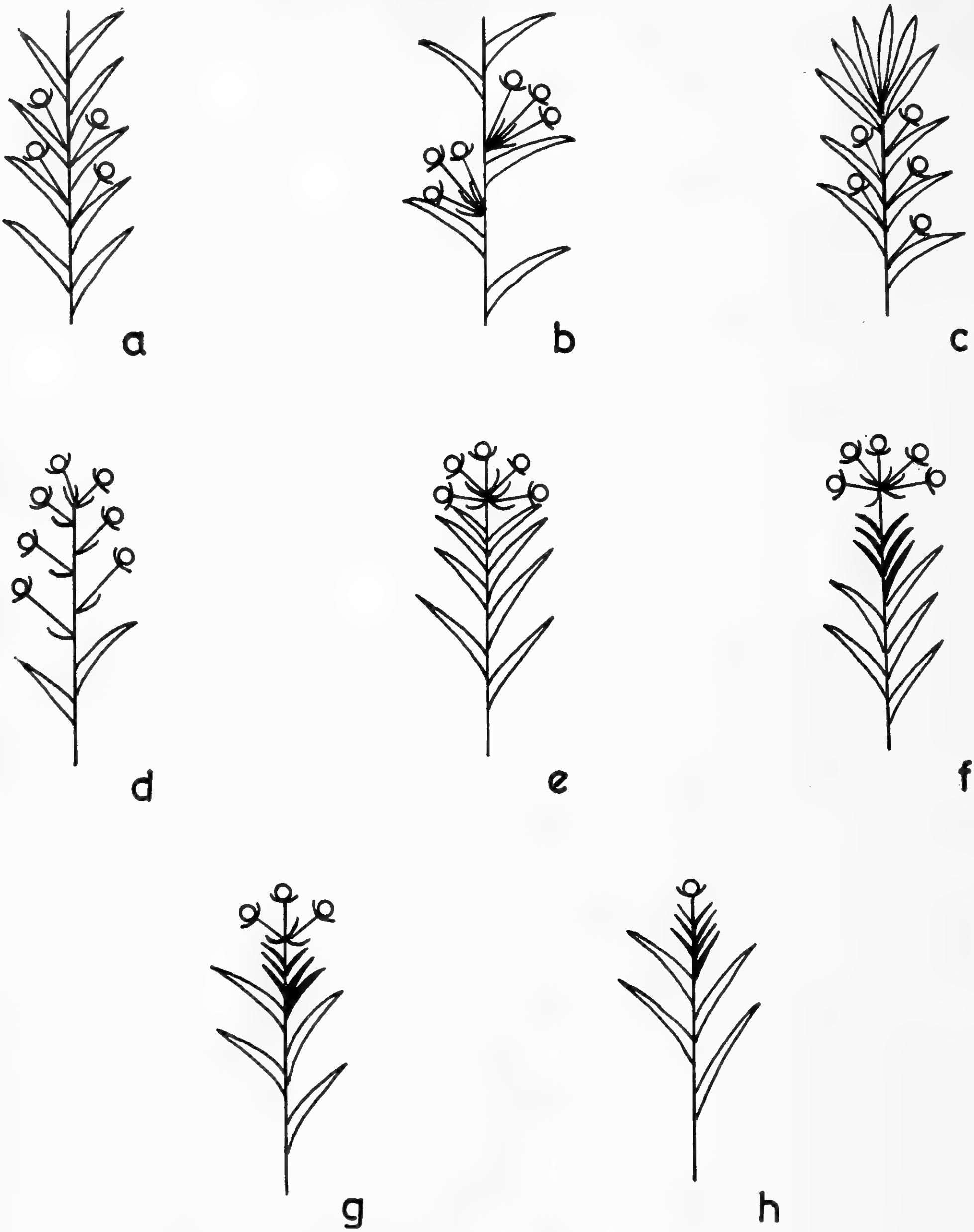

Fig. 1. Variations in inflorescence structure in *Pultenaea*. "Open" structure: a. Open raceme with stem growth continued during flowering season. b. Axillary clusters at the base of new foliar growth, sessile or terminal on short lateral shoots. c. Few-flowered raceme with dense foliar growth during flowering season. "Closed" structure: d. Loose terminal raceme with no stem growth during flowering season. e. Dense umbel-like terminal raceme surrounded by floral leaves. f. Dense terminal raceme surrounded by involucre of sterile bracts. g. Terminal cluster surrounded by involucre of sterile bracts. h. Solitary flower surrounded by involucre of sterile bracts.

(Fig. 1b) or solitary flowers. In all such inflorescences each flower is subtended by a normal stipulate leaf.

Where stem proliferation ceases with flowering, the inflorescence may be a more open terminal raceme (Fig. 1d), a dense terminal raceme with peduncles attached to the stem very close together giving an umbel-like appearance (Fig. 1e, f), or may be reduced to a cluster (Fig. 1g) or to solitary flowers (Fig. 1h). Whatever their form, such terminal inflorescences are surrounded either by a dense whorl of floral leaves (Fig. 1e) or in certain *Pultenaea* species, by an involucre of sterile bracts (Fig. 1f, g, h).

BRACTS AND BRACTEOLES

The normal stipulate leaf or bract subtending each flower is a "deckblatt" in the sense of Troll (1957) and Goebel (1931) and is called the "subtending bract" in this study.

Gradation of bract development prevents sharp distinction between those species of *Pultenaea* with floral leaves at the base of the inflorescence (Fig. 1e) and those with an involucre (Fig. 1f). In the latter the involucral bracts are consistently less modified than the subtending bracts of the flowers above. In all species of *Pultenaea* the floral leaves are inserted on the stem in closer proximity to one another than are the vegetative leaves and their stipules are enlarged and often coherent for almost their entire length. The reduction in stipules on vegetative leaves in some species is accompanied by comparable reduction on the subtending bracts (Fig. 2b). Other species entirely lack stipules in vegetative and floral leaves, subtending bracts and bracteoles (Fig. 2a).

Four species of *Pultenaea* have racemes or clusters of flowers surrounded by floral leaves, and both subtending bracts and bracteoles are normal leaves with enlarged stipules (Fig. 2d). More commonly, however, the floral or bract leaf is reduced to a pubescent lanceolate structure attached externally at the base of the large stipules (Fig. 2e), as is the normal leaf, or even higher up towards the point of cohesion of the stipules (Fig. 2f). The subtending bract may be similar to the floral leaf and the bracteoles either trifid and three-veined (Fig. 2g) or entire with only a mid-vein (Fig. 2h). Alternatively the subtending bract may be trifid and the bracteoles entire; in this case the involucre is normally separate from the leaves below. The three *Pultenaea* species which have only one to three flowers enclosed in a distinct involucre have trifid involucral bracts and entire, single-veined subtending bracts and bracteoles.

Pubescence

Consistency of pubescence within a species is observed only in the ovary. The surface may be densely pubescent, glabrous with an erect tuft of bristles on the more rounded side towards the apex, or entirely glabrous. Degree of pubescence sometimes differs between species with an otherwise close morphological relationship.

Distribution

With the exception of four monotypic genera, two larger genera and several sections of genera which are endemic to the west, species of the remaining genera of the Podalyrieae in Australia are distributed throughout the western and eastern Temperate regions and the borders of the southern Eremaean region. A few are found in refugial areas in the Tropical Zone and in Central Australia.

Discussion

Classification

Bentham's (1864) classification of the genera of the Podalyrieae is in accord with the karyological data (see Appendix) but the gross morphology of the inflorescence (Sands, 1966) supports the further generic divisions of *Oxylobium* and *Brachysema* proposed by Hutchinson (1964).

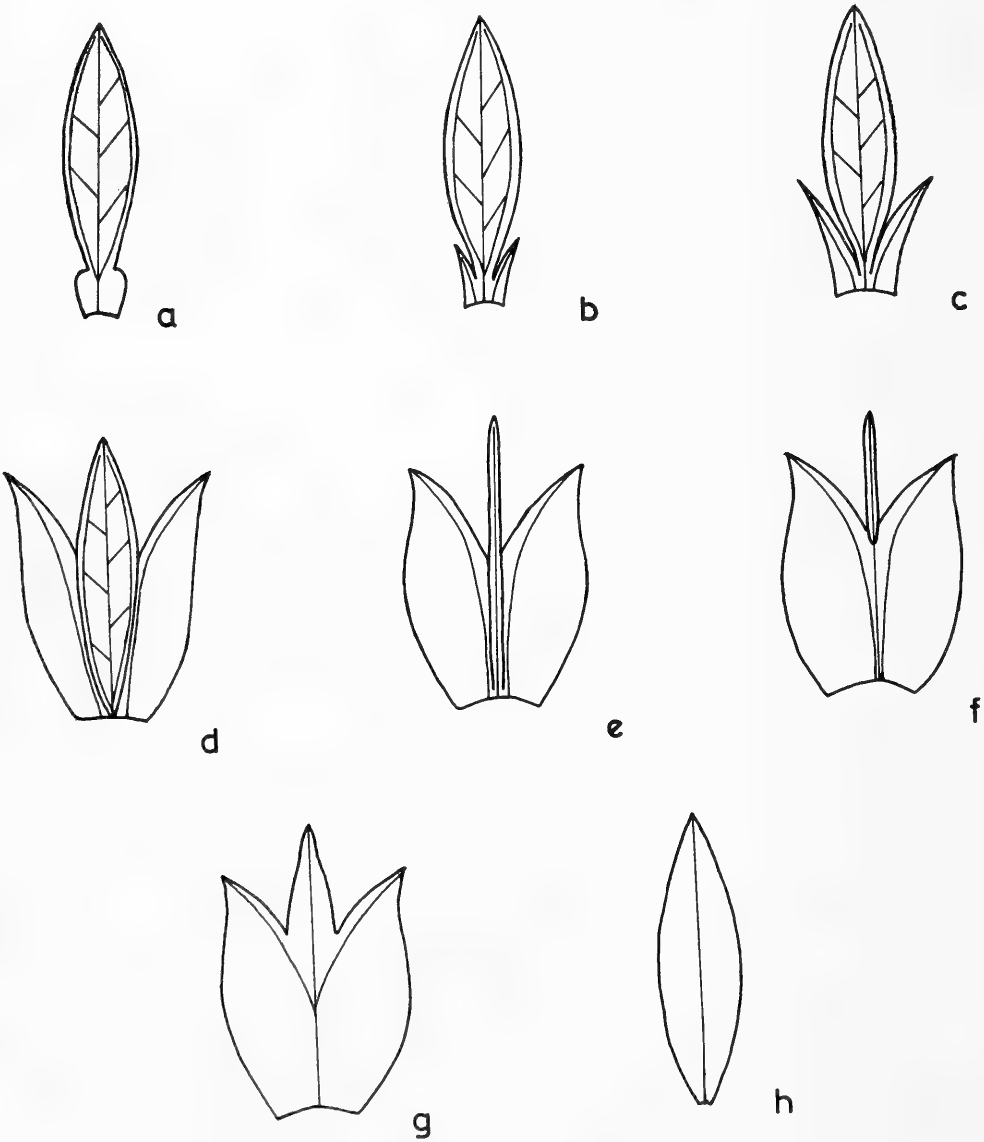

Fig. 2. Variation in bracts and bracteoles in *Pultenaea*. a. Extipulate leaf or bract (EL). b. Bract or bracteole with stipules reduced (RSL). c. Bract or bracteole with normal stipules (SL). d. Bract or bracteole with enlarged stipules (SL). e. Bract leaf reduced, attached basally to enlarged fused stipules (SRL). f. Bract leaf very reduced, attached near point of cohesion of fused stipules (SRL). g. Bract or bracteole trifid (Tr). h. Bract or bracteole entire, single-veined (En).

On the basis of these data it is possible to divide the tribe Podalyrieae into three major groups of genera:

Group I	*Gompholobium, Burtonia, Sphaerolobium, Jacksonia, Viminaria, Daviesia* and probably *Erichsenia.*
Group II	*Gastrolobium, Oxylobium, Nemcia, Mirbelia, Chorizema, Isotropis, Brachysema, Cupulanthus, Leptosema* and probably *Jansonia.*
Group III	*Pultenaea, Phyllota, Aotus, Euchilopsis, Eutaxia, Dillwynia* and *Latrobea.*

Pultenaea may only be distinguished from the remainder of the Podalyrieae by a number of characters, no one of which is sufficient alone for definition. The complexity of this genus with approximately 120 species is greater than suggested by Bentham's (1864) delineation of it into four sections. Leaf arrangement is consistent within each species and effectively distinguishes section *Euchilus,* while marked venation delimits section *Aciphyllum.* However, in his other two sections, *Coelophyllum* and *Eupultenaea,* curvature of leaf margins is of limited use as a criterion of distinction.

When such vegetative characters as Bentham (1864) employed are correlated with modifications in inflorescence and bracts, with degree of ovary pubescence and with chromosome number, ten groups of species may be distinguished (Table 7). There is overlap from one group to another in this integrading plexus of species and the discontinuity between any two groups rests on one character only (Table 6). The continuous variation of morphological characters confirms the taxonomic integrity of the genus.

Recognised Trends in Morphology

It is possible to analyse further the morphological variation between genera, and particularly between species of *Pultenaea,* in terms of the evolutionary trends recognised in other Angiosperm families and of the generally accepted principles of modification and advancement.

Sporne (1948) and Zimmerman (1959) consider that opposite or whorled leaves have generally been derived from spirally arranged or alternate leaves. Incurved leaves with exposed stomates presumably have lower selective value during times of increased aridity than do flat or recurved leaves, while involute leaves would be even less susceptible to environmental change. Physiological adaptability of vegetative organs is evident in the great range of leaf modifications in the Podalyrieae and must have permitted survival and diversification of these genera under variable and extreme conditions. This is demonstrated in the large and widespread genera *Daviesia, Jacksonia* and *Pultenaea.*

In recent decades the Ranalian concept of Angiosperm evolution has been widely accepted. In particular, the current consensus is that there has been progressive reduction in number of ovules (Stebbins, 1950; Bailey, 1954; Hutchinson, 1959; Barnard, 1961) and that the solitary-flowered condition has been derived from many-flowered inflorescences (Takhtajan, 1959), with compact inflorescences having greater selective value for efficiency of pollination.

Particular trends in development of racemose inflorescences are outlined by Troll (1957, 1964) and are clearly exemplified in the genus *Pultenaea.* He suggests that the "open" raceme with active growing point may by loss of this growth become a "closed" raceme. Sharp reduction in the number of flowers may lead to a short raceme or "in extreme cases can extend even to a solitary flower, as among the Papilionaceae". Alternatively, the floral stem internodes may be reduced to give a dense raceme resembling an umbel either with a proliferating apex or a terminal flower.

The species of *Daviesia* further illustrate such sequences. The unusual and consistent bract arrangement may indicate the ancestral inflorescence of the genus. Each flower in any type of inflorescence is subtended by a bract and below this on the peduncle are other small alternately placed bracts, often more closely clustered towards the base. These are never present on the pedicels of an umbel, raceme or axillary cluster, which suggests that loss of flowers from a primitive loose raceme or condensation of the upper peduncles gave rise to the existing modifications. The rudiments of subtending bracts may be observed opposite the bracts which subtend the solitary flowers in *Gompholobium* and following the interpretation of Troll (1957) may be taken to indicate earlier racemose structure. In all the genera except *Jansonia* and *Eutaxia* at least some of the species have the primitive racemose inflorescence, which therefore should be regarded as the basic inflorescence in the ancestral Podalyrieae stock.

Takhtajan (1959) considers that a gradation from a whorl of floral leaves to an involucre of sterile bracts surrounding the dense racemose heads of flowers, as found in many species of *Pultenaea,* indicates a trend from primitive to more advanced, as does the reduction of vegetative leaves to form bracts. In the three species with single flowers surrounded by involucral bracts there may have been loss of the basal flowers of a large raceme. This formation of an involucre occurs in *Pultenaea* species which show the greatest modification of subtending bracts and bracteoles. Without exception the subtending bracts are similar to or more modified, by reduction of parts, than the involucral bracts and the bracteoles are the same as or more reduced than the subtending bracts. In *Gastrolobium* series *Axillares* certain species show the same progression from trifid subtending bracts at the base of the inflorescence to entire bracts towards the apex.

The transition from a stipulate leaf to an entire, and at maturity, scarious bract, may have occurred by reduction of stipules to minute vestiges or to the point where the leaf was exstipulate. In the other direction, enlargement and cohesion of the stipules, allied with progressive reduction of the leaf and its fusion with the stipule structure as described by Takhtajan (1959), appears to have occurred in many species of *Pultenaea.*

In *Pultenaea* the open racemose, clustered or solitary-flowered conditions are associated with the less modified types of bracts and also with differences in the degree of ovary pubescence. The closed or umbel-like raceme, by contrast, is generally found together with reduced subtending bracts and bracteoles and with development of an involucre of sterile bracts. Species with this dense inflorescence are characterised by a pubescent ovary, thought by Stebbins (1950) to represent a more primitive condition.

Basic Chromosome Number

PAPILIONACEAE

A basic chromsome number of 4 was first suggested for this family by Wanscher (1934) using the doubtful evidence of secondary association. Senn (1938) contended that $x = 8$ was primitive because of its frequency of occurrence in the great proportion of species of all tribes of the Papilionaceae and emphasised the largely intergeneric nature of secondary change in the family. Stebbins (1966), Raven and Kyhos (1965), Ehrendorfer *et al.* (1968) and Raven *et al.* (1971) provide evidence in support of Darlington and Mather's (1949) postulate of 7 as the primitive haploid number of the Angiosperms, with aneuploid and polyploid derivation of higher numbers in many woody Angiosperm families.

The complement of 7 is well represented in the Papilionaceae but $x = 8$ and $x = 11$ are basic to the cytoevolution of certain tribes and series. The additional chromsome numbers obtained in this survey have not provided critical evidence in support of these hypotheses. They conform to the chromosomes numbers obtained for extra-Australian genera within their respective tribes with the exceptions of $n = 9$ in the numerous species of *Bossiaea* and *Hovea* (Bossieeae) $2n = 16$ for *Tephrosia* (Tephrosieae), and $n = 4$, 6, 7, 8 and 9 in the Podalyrieae. Cytological data is insufficient for the elucidation of the cytoevolution of the Papilionaceae.

PODALYRIEAE

Although Senn (1938) suggested that the Podalyrieae may have been derived from a primitive stock in the Sophoreae with the majority of its genera having a haploid complement of 9 chromosomes, he favoured $x = 8$ as the basic number of the Podalyrieae because of the preponderance of this number in several of the other tribes.

Of the eight genera of the Podalyrieae which occur in South Africa, Asia and North America, five, namely *Baptisia* Vent., *Anagyris* Linn., *Podalyria* Lam., *Piptanthus* Sweet and *Thermopsis* R. Br. ex Ait., are known to have a diploid complement of 18 chromosomes (Darlington and Wylie, 1955; Index to Plant Chromosome Numbers 1956–1964). This wide and disjunct distribution is probably indicative of their ancient origin and of the primitiveness of $x = 9$ but does not necessarily imply that this haploid number was basic to the evolution of the Australian genera. Polyphyletic origin of the tribe was suggested by Dormer (1945, 1946) following his study of the phyllotaxy and vascular systems of representatives from northern and southern hemispheres and comparison between the South African genera and a few of the Australian genera. This may be supported by the fact that all but one of the Australian genera with $x = 9$ have 2 ovules, while the extra-Australian genera have numerous ovules. It could be inferred, however, that early colonising stocks in Australia with 9 haploid chromosomes and numerous ovules were replaced by the derived species to which they gave rise.

It is evident that morphological and cytological study of the extra-Australian genera is required to elucidate the evolution of the tribe. Chromosome investigations and interpretation of the gross morphology in terms of accepted evolutionary trends indicate a monophyletic origin of the 24 Australian genera. Haploid complements of 7, 8 and 9 have been determined in these genera and with the exception of the genus *Pultenaea* there were no intrageneric differences in base number. It can be inferred that the base numbers were established prior to the origin of the other genera.

External morphology of the genera in Group I reveals a general uniformity of characters within genera associated with certain marked intergeneric discontinuities—a pattern indicative of age both of the genome and of the genera. Reduction in number of ovules to 2 must have occurred early in the differentiation of the genera. Group II genera have comparatively primitive inflorescence morphology with repeated occurrence of similar modifications. They show a morphological pattern with close relationships between genera and extensive specific diversification. This suggests a single origin of $x = 8$ prior to the development of the genera.

The lack of decisive non-overlapping distinctions between the Group III genera, with their reduced number of ovules and rather more advanced inflorescence characters, suggests a common ancestral stock. Chromosomal and morphological inter-relationships indicate multiple origins of the base numbers 7 and 8 within this complex. For example, *Phyllota* ($n = 7$) shows very close affinity to certain *Pultenaea* species with $n = 7$; *Eutaxia* ($n = 8$) is morphologically more similar to *Dillwynia* ($n = 7$) than to the other genera with $n = 8$. Excluding *Pultenaea,* differentiation between species within these four genera is not great and this lack of diversification at the level of both genera and species indicates either more recent origin or less potential for differentiation.

From these evolutionary patterns there is thus some evidence that 9 was the basic chromosome number of the Australian Podalyrieae, but $x = 8$ is clearly also very ancient. Reduction in number of ovules appears to have been basic to the development of the genera with 9 chromsomes, to have had considerable significance in one group of $x = 8$ genera and to be confined to one genus in the other group.

The geographic distribution of the tribe provides further indications of its development in Australia but not of its origin. The few known papilionaceous fossil types (Duigan, 1951; Cookson and Pike, 1954) do not provide significant information concerning past distribution. Present general east-west Temperate distribution in Australia suggests that the majority if not all the genera, and in consequence their 7–, 8– and 9–genomes, were in existence prior to the mid-Miocene isolation of east and west caused by the inundation of the Nullabor region (Crocker and Wood, 1947; David, 1950). The six species restricted to the South-West Province of Western Australia and of South Australia must be relics of this earlier broad distribution as also must certain other species with disjunct distribution across the north. Island movement of the winter rainfall belts into inland South Australia following the first Arid Phase may have permitted northern migration of the few species now isolated in Central Australia (Burbidge, 1960).

Pliocene uplift possibly provided a spur to differentiation in the west where with the exception of *Pultenaea* and *Dillwynia* all the genera show their major development. Species which were vegetatively adapted to relative dryness, e.g., *Jacksonia* and *Daviesia,* would be able more readily to tolerate the aridity of the Pleistocene and to take advantage of the subsequent denudation. In the eastern Temperate region *Dillwynia* and *Pultenaea* comprise some 60% of all species of Podalyrieae, and were more successful under the conditions brought about by the mountain building and coastal uplift of the late Pliocene and by later climatic changes.

PULTENAEA

Within the genus *Pultenaea* Curtis (1952) found base numbers of 7, 8 and 9, and the present work confirms her findings with the determination of eight species with $x = 9$, 48 with $x = 8$ and 31 with $x = 7$. In addition single species with $x = 6$ and $x = 4$, respectively, were found.

This range of chromosome numbers may be an example of development of secondary base numbers as described by Darlington (1937) and demonstrated in *Crepis* by Tobgy (1943) and others. The 4 haploid chromosomes of *P. reticulata* may be the end product of such a reduction series. Alternatively the complement could be primitive and $x = 8$ a secondarily derived tetraploid base number, which had an evolutionary potential for establishing a new diploid level. $x = 4$ may on the other hand be the product of a rare reversion of polyploidy (Kimber and Riley, 1963; Raven and Thompson, 1964; De Wet, 1971), a mechanism which would account for its preservation in a region where chromosome number change has been rife.

The great morphological variability in *Pultenaea* is associated with this change in chromosome number. In eastern species of *Pultenaea* $n = 8$ occurs with a considerable range of bract and inflorescence types whereas $x = 7$ and 9 are correlated with the more advanced or derived condition and with little alteration of flower or inflorescence other than in ovary pubescence. In the west, on the other hand, 7 is the haploid number most frequently observed in conjunction with all degrees of inflorescence development and modification of parts. Complements of 8 and 9 chromosomes occur only in the morphologically primitive species of Group V.

$x = 7$ appears to have been derived separately in eastern and western regions and is associated in all but one species with some modification of inflorescence structures in different sequences of morphological advancement rather on the periphery of the main evolutionary trends. $x = 9$ also is most frequently associated with morphological modifications and has certainly originated twice despite its sparse representation. These features indicate that the complements of 7 and 9 haploid chromosomes in *Pultenaea* were derived from a basic number of $x = 8$, this being associated generally with greater variability in a larger number of species, and with both primitive and advanced morphological features. Possibly the ancient complement of 8 represents an example of the cryptic polyploidy described by Stebbins (1950) for other families of the Angiosperms. Whatever the derivation of the $n = 4$ of *P. reticulata*, $x = 8$ was undoubtedly the most significant chromosome complement, whether as a primary or secondary base number, for the genus.

In *Pultenaea* there are distinct eastern and western sequences of morphological differentiation and several of the groups are confined to a single region. In addition, change of chromosome number has been more frequent in those regions where aridity had most profound effect. In the western representatives this is evidenced by complements of $n = 4$ in Group II, $n = 7$ in Group X, $n = 7$ and 8 in Group IV and $n = 8$ and 9 in Group V. In the east, $n = 7$ occurs predominantly among the generally more broad-leaved species of Queensland and New South Wales, i.e., Groups VI, VII and III(a), all morphologically distinct from the western groups with $n = 7$. $n = 9$ on the other hand is characteristic of Groups III and III(b), both found mainly in South Australia.

It appears that Victoria, which was less affected by climatic change, has been a centre of survival and dispersal for the majority of eastern species characterised by $x = 8$. Apart from a few species which are morphologically distinct and restricted in distribution, Victorian species are either closely related in primitive morphology to those occurring in neighbouring States or are represented there.

The effects of isolation and aridity on speciation in *Pultenaea* are evident in South Australia. The restriction of species to the coastal zones and mountain ranges in the 500 mm annual rainfall belt presumably followed the general dispersion during the moist subtropical climate of the Pliocene, the elevation of mountain ranges and of the Gulfs above sea level with colonisation of newly available habitats and the later resubmergence of the sunklands with isolation of species. The "Great" arid period of early Recent times (Crocker and Wood, 1947) destroyed all but a few relict species of this early broad distribution which were able to survive in these refugial areas, e.g. the 12 endemic species of *Pultenaea* at the western end of Kangaroo Island. Such refugia were doubtless centres of speciation during the differential separation of the peninsulas from the island (Wood, 1930), centres of survival during the arid phases and centres of dispersal during intermittent pluvial periods (Burbidge, 1960). This dispersal, together with waves of migration of species from Victorian refugia, is considered by Crocker (1959) to account for major recolonisation of south-eastern South Australia. Rapid separation would certainly be possibly following the relaxation of selection pressures as relict and migrant species extended over denuded areas (Wright, 1949), a situation of which *Pultenaea* appears to have taken advantage.

The Development of the Podalyrieae in Relation to other Australian Families

The pattern of evolutionary development in the Podalyrieae conforms to that outlined by Smith-White (1959) for five other Australian hardwood families of the Temperate Zone, namely, the Myrtaceae (Smith-White, 1950, 1954*a*), Epacridaceae (Smith-White, 1955*a*, 1959), Rutaceae (Smith-White, 1954*b*), Proteaceae (Ramsay, 1963) and Casuarinaceae (Barlow, 1959*a*, *b*). Geographical expansion and diversifaction during the Early Tertiary must have brought about the establishment of the present-day genera of the Podalyrieae across the continent since the great majority of genera are common to both eastern and south-western Australia. Chromsome number changes within each genus have been few since the mid-Miocene, a situation comparable to that in other hardwood families. However, to some extent polyploidy and aneuploidy have furthered evolutionary processes in the development of the Podalyrieae.

POLYPLOIDY

The occurrence of polyploidy in certain Australian herbaceous families, namely Lobeliaceae (James, 1963; McComb, 1968), Goodeniaceae (Peacock, 1962, 1963), Compositae (Smith-White *et al.*, 1970) and Graminae (Hayman, 1960; Brock and Brown, 1961), and to a lesser extent in hardwood genera such as *Casuarina* (Barlow, 1959*a*, *b*), *Cassia* (Rendell, 1970) and *Eremophila* (Barlow, 1969, 1971), has been interpreted as a response to geological and climatic changes during the late Tertiary or Quaternary. In the Podalyrieae polyploidy is of infrequent occurrence and is mainly or entirely intraspecific as in the above herbaceous families. Population sampling of the eastern species of *Dillwynia* which showed tetraploidy may reveal a geographic pattern of distribution of polyploid races similar to that in certain genera of the Goodeniaceae. It is clear however that polyploidy has been a recent specialisation in the Podalyrieae, making only a minor contribution to the evolution of genetic systems in the tribe.

An interesting sideline, of no profound evolutionary significance, is found in the two species in which a triploid system has developed and been maintained. In neither case is there any evidence of a permanent balanced triploidy comparable to that of the *Rosa canina* complex (Stebbins, 1950) or of *Leucopogon juniperinus* (Smith-White, 1955*b*), though in contrast to the restricted distribution of *Dillwynia stipulifera, Pultenaea juniperina* has widespread and disjunct distribution with diploids and triploids occurring together. Further study of these two species with regards to the origin and maintenance of the triploid condition, and of aberrant diploid behaviour in *Pultenaea juniperina,* is clearly warranted.

ANEUPLOIDY

The development of secondary base numbers appears to have been a most significant genetic mechanism in the cytoevolution of a number of Australian hardwood families. It is reported in Myrtaceae (Smith-White, 1950, 1954*a*), Boronieae of the Rutaceae (Smith-White, 1954*b*), Epacridaceae (Smith-White, 1955*a*), Casuarinaceae (Barlow, 1959*a*), Proteaceae (Ramsay, 1963), and in *Brachycome* of the Compositae (Smith-White *et al.,* 1970). A comparable aneuploid sequence involving $n = 9$, 8 and 7 appears to have preceded the origin of the genera in the Podalyrieae in Australia. And in more recent times the evolution of the largest genus in the tribe is correlated with aneuploidy.

The genus *Pultenaea,* with its many species having different chromosome numbers, is the notable exception to the intrageneric stability of chromosome numbers observed in the Podalyrieae. The greatest morphological diversification in *Pultenaea* appears to have occurred in regions which have suffered profound changes in environmental conditions, such as the Recent aridity in South Australia. Such changes would bring about plant migration, species diminution or extinction, survival in refugia, back-migration under more favourable conditions and recolonisation of denuded areas. Repeatedly, new biotypes would find themselves at the margin of a species range or in small isolated peripheral populations. If they possessed the potential to occupy new territory then the new adaptive biotypes could have been conserved by change of base number of chromosomes.

Aneuploidy is a mechanism by which the recombination rate may be lowered through the suppression of crossing-over and also by which reproductive isolation from the parental population could be achieved. Such a change in the genetic system will, if it has positive adaptive value so that it is selected for strongly, lead to speciation. Chromosome number differences are associated with morphological diversity in present-day species of *Pultenaea,* with multiple origins of haploid complements of 7 and 9 chromosomes being indicated by the differing patterns of morphological variability. Further, these species grow in regions where considerable climatic and geological changes have occurred since the Miocene Period. Aneuploidy must therefore have made a significant contribution to the evolution of this genus with its complex of intergrading species.

The evolution of the Group III(a) species of *Pultenaea* may provide an example of such a process. *P. flexilis* ($n = 8$) with glabrous ovary with tuft of apical hairs, exhibits considerable morphological diversity and *P. blakelyi* ($n = 8$) differs only in its pubescent ovary. The other four species with $n = 7$ show small size and shape variations and further reduction in ovary pubescence to tufted in *P. campbellii* and glabrous in *P. euchila, P. altissima* and *P. obovata.* The marginally overlapping geographic distribution of these species (Figure 3) resembles the pattern reported by Lewis (1962) for various species of *Clarkia.* He considers

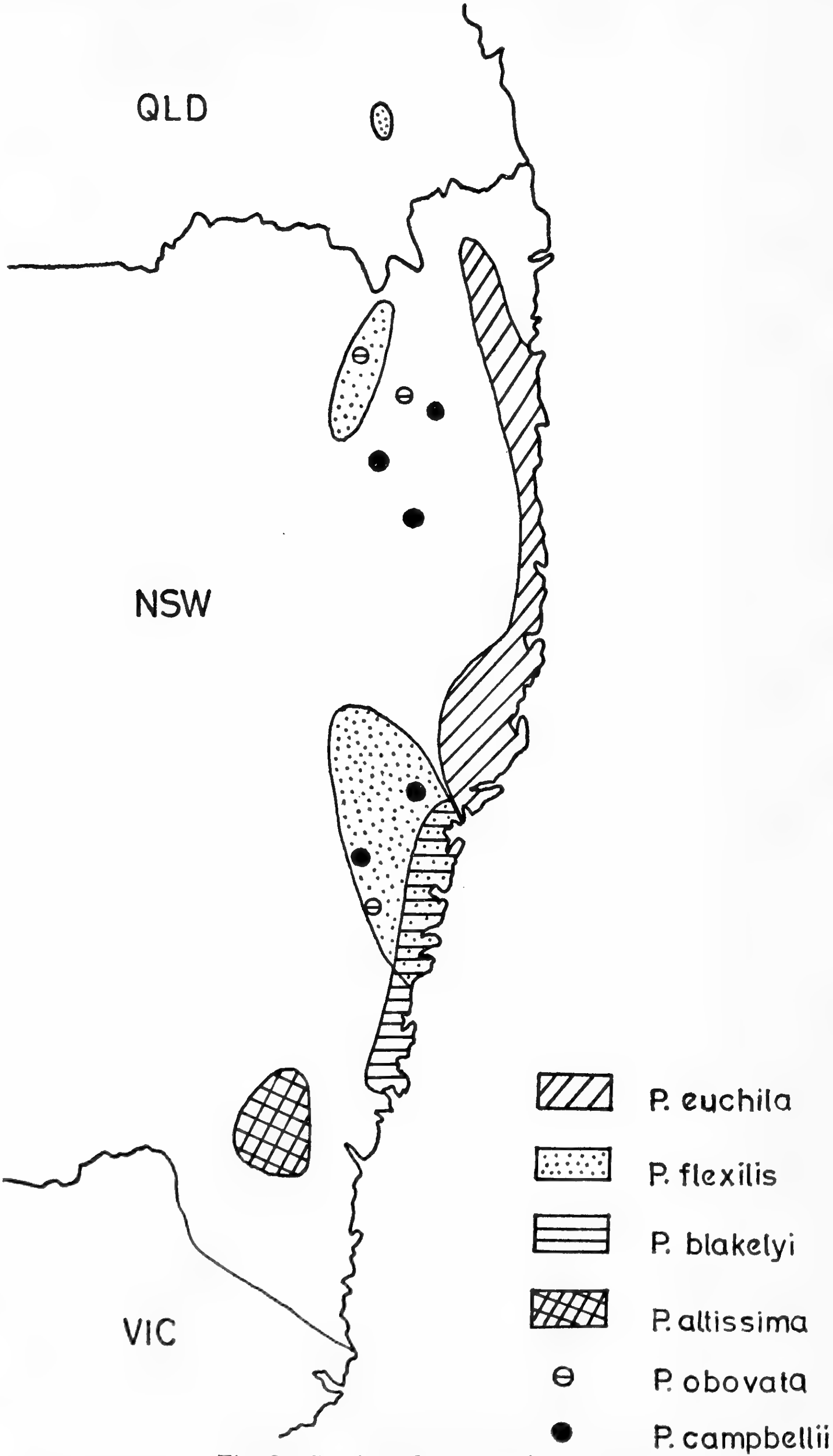

Fig. 3. *See legend on opposite page.*

that "the drastic alteration of genetic background in newly founded peripherally isolated populations has produced rapid speciation". Study of breeding mechanisms, incompatibilities, fertility of interspecific hybrids and karyotype analyses may reveal whether there are strong internal barriers to gene exchange between these *Pultenaea* species, which are not herbaceous as are all the examples quoted by Lewis (1962). If such barriers exist then the indications of rapid speciation noted by Stebbins (1950) are all in evidence.

Such "catastrophic" evolution may have been partially responsible for the evolutionary success of *Pultenaea* under conditions which decimated the more genetically inflexible genera in eastern Australia. Further, it may provide a model of the early evolution of the other genera of the Podalyrieae following the establishment of the tribe in Australia during the Cretaceous Period.

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Fig. 3. Distribution of certain species of *Pultenaea* Group IIIa in Queensland and New South Wales. *P. blakelyi*, $n = 8$, ovary pubescent; *P. flexilis*, $n = 8$, ovary glabrous with a tuft of apical hairs; *P. campbellii*, $n = 7$, ovary glabrous with a tuft of apical hairs; *P. euchila*, $n = 7$, ovary glabrous; *P. altissima*, $n = 7$, ovary glabrous; *P. obovata*, $n = 7$, ovary glabrous.

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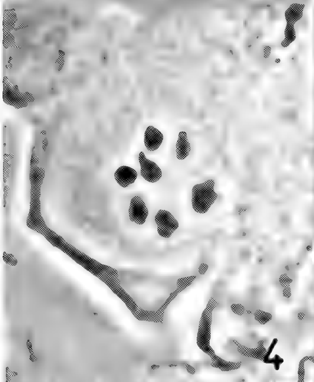
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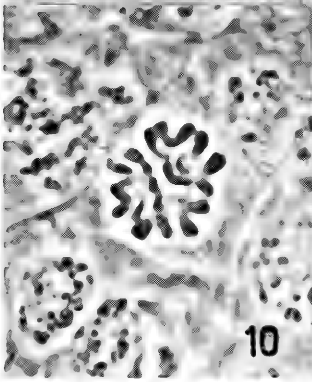
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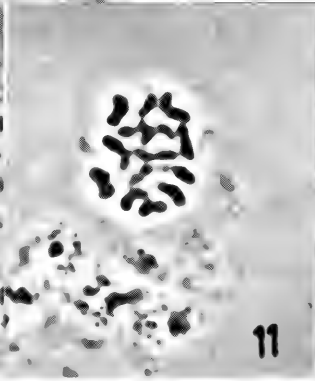
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EXPLANATION OF PLATE XVI

Representative species of *Pultenaea.*

1. *Pultenaea reticulata* P_I $n = 4$. 2. *P. reticulata* M_I $n = 4$. 3. *P. reticulata* M_{II} $n = 4$. 4. *P. boormanii* M_I $n = 7$. 5. *P. elliptica* M_{II} $n = 7$. 6. *P. fasciculata* P_I $n = 8$. 7. *P. microphylla* M_{II} $n = 8$. 8. *P. trinervis* M_I $n = 8$. 9. *P. vrolandii* M_I $n = 9$. 10. *P. euchila* mitosis $2n = 14$. 11. *P. canescens* mitosis $2n = 14$. 12. *P. acerosa* mitosis $2n = 18$.

APPENDIX

CHROMOSOME NUMBERS IN THE PAPILIONACEAE WITH ACCESSION NUMBERS AND LOCALITIES

Species	State	Locality	Coll. no.	Chromosome no.	
BOSSIAEEAE Benth. and Hook. f.					
Bossiaea aquifolium Benth.	W	Quindanning	638.7.3		18
	W	Karragullen	638.6.2		18
B. buxifolia A. Cunn.	N	Warrumbungle Ranges	628.10.1		18
	N	Goonoo Forest	628.17.6		18
	N	Varneys Range, 13 km E. Jindabyne	6211.1.4		18
B. disticha Lindl.	W	Deepdene	638.11.8		18
B. eriocarpa Benth.	W	Gingin to Mogumber	638.4.5		18
	W	8 km S.W. Northam	637.4.6		18
	W	Pinjarra	638.9.2		18
B. foliosa A. Cunn.	N	Goonoo Forest	619.10.6		18
	N	Kosciusko Rd	6211.2.6		18
B. heterophylla Vent.	N	National Park	635.2.2		18
	N	Hazelbrook	635.3.1		18
B. kiamensis Benth.	N	Belmore Falls	639.6.1		18
B. laidlawiana Tovey et Morris	W	Stewart Highway	638.12.6		18
B. lenticularis Sieber ex DC.	N	Colo Heights	627.1.9	9	
	N	Oakdale	628.20.7		18
B. linophylla R. Br.	W	Kojunup	638.8.4		18
B. obcordata (Vent.) Druce	N	5 km W. Penrith	628.21.7	9	18
	N	Faulconbridge	628.21.12		18
	N	Linden	619.1.5	9	
	N	Pennant Hills Reserve	618.1.4	9	
B. ornata (Lindl.) Benth.	W	Bannister	638.9.6		18
B. pedunculairs Turcz.	W	21 km N. Southern Cross	637.4.2		18
B. preissii Meissn.	W	21 km W. Lake Grace	638.19.10		18
	W	Cape Riche Rd, Green Ranges	638.14.25		18
	W	29 km E. Gnowangerup	638.16.5		18
B. prostrata R. Br.	N	Coxs River, Jenolan	6310.8.13		18
B. pulchella Meissn.	W	51 km S.W. Northam	637.4.17		18

Species	State	Locality	Coll. no.	Chromosome no.	
B. rhombifolia Sieber ex DC. ssp. *rhombifolia*	Q	Glenmorgan	628.4.19		18
	N	8 km N. Sackville	627.1.4	9	
	N	Lower Portland Ferry	619.3.2	9	
B. rhombifolia ssp. *concolor* (Maid. et Betche) A. Lee	Q	Moonie Hwy, 85 km E. St George	628.5.4	9	
	Q	Moonie Hwy, Westmar	628.5.5		18
	N	Pilliga Scrub	628.9.1	9	
B. riparia A. Cunn. ..	N	Yarrangobilly	6211.3.5		18
B. scolopendria Sm.	Q	Glenmorgan	628.4.20		18
	N	Warrah	628.13.4		18
B. stephensonii F. Muell. ..	N	8 km S. Port Macquarie	628.15.4		18
	N	National Park	627.2.1		18
	N	5 km N. Heathcote	6110.4.2		18
B. walkeri F. Muell. ..	Q	Glenmorgan	628.4.1		18
Bossiaea sp.	N	Goonoo Forest	628.17.6		18
Goodia lotifolia Salisb. ..	W	18 km N. Ravensthorpe	638.19.1		16
Hovea chorizemifolia (Sweet) DC.	W	Quindanning	638.7.4		18
	W	Brunswick Junction	638.8.1		18
H. elliptica (Sm.) DC. ..	W	Metricul Siding	638.11.4		18
	W	Alexandra Bridge	638.12.1		18
H. heterophylla A. Cunn. ..	Q	Condamine Hwy to Meandarra	628.4.23		18
	Q	16 km N.W. Stanthorpe	628.6.7		18
	N	Gibraltar Range State Forest	628.2.7		18
H. linearis R.Br.	N	8 km S. Port Macquarie	628.15.6		18
	N	Colo Heights	627.1.1		18
	N	National Park	627.2.3		18
H. longifolia R.Br.	Q	Kogan	628.3.1		18
	Q	Glenmorgan	628.4.9		18
	Q	Moonie Hwy, Westmar	628.5.1		18
	Q	48 km N.W. Stanthorpe	628.6.1		18
	Q	Jollys Falls, Stanthorpe	628.6.15		18
	N	Yetman	628.8.6		18
	N	Warrumbungle Ranges	628.10.10		18
	N	Goonoo Forest	628.12.2		18
	N	Kosciusko Rd	6211.2.7		18
H. longipes Benth.	Q	Glenmorgan	628.4.2		18
H. pungens Benth.	W	South of New Norcia	637.5.14		18
H. stricta Meissn.	W	Mogumber	638.4.4		18
	W	Yanchep	638.5.4		18
H. trisperma Benth... ..	W	Bindoon	638.4.2		18
	W	East Bullsbrook Rd	637.5.5		18
	W	48 km S.W. Northam	637.4.16		18
	W	Brookton Hwy, Gleneagle State Forest	638.6.3		18
	W	Brunswick Junction	638.8.2		18
Platylobium formosum Sm. ..	N	Warrah	618.8.2		16
	N	Sunny Corner State Forest	6110.3.1		16
	N	Neville	6110.3.2		16
	N	Wentworth Falls	628.21.19		16
	N	Waterfall	6110.4.8	8	
	N	Garie, National Park	637.2.4		16
	N	Huskisson	639.5.10		16
Templetonia aculeata (F. Muell.) Benth.	W	79 km E. Jerramungup	638.16.18		16
T. retusa (Vent.) R.Br. ..	W	Bunbury	626.1.1		16
	S	Pt Lincoln, (St Andrews Tce)	649.2.2		16
T. sulcata (Meissn.) Benth.	W	61 km W. Coolgardie	637.3.2		16
	W	3 km N. Southern Cross	637.4.1		16
	W	Tambellup	638.15.10		16
INDIGOFEREAE Benth. and Hook.f.					
Indigofera australia Willd. ..	Q	Glenmorgan	628.4.22		16
	Q	16 km N.W. Stanthorpe	628.6.9		16

Species	State	Locality	Coll. no.	Chromosome no.	
Indigofera australia Willd.—*continued*	N	Pilliga Scrub	628.9.3		16
	N	8 km S. Pt Macquarie	628.15.6		16
	N	Wellington	628.18.1		16
	N	56 km E. Queanbeyan	639.4.5		16
	N	Kosciusko Rd	6211.2.3		16
I. australia var *signata* F. Muell.	N	Warrumbungle Ranges	628.10.6	8	16
	N	Wellington	628.18.2		16
	N	6 km S. Talbingo	6211.3.7		16
I. coronillifolia A. Cunn ..	N	Goonoo Forest	619.10.7	8	
COLUTEAE Benth. and Hook.f.					
Swainsona galegifolia R.Br.	Q	Glenmorgan	628.4.3	8	16
	N	Warrumbungle Ranges	628.10.9		32
	N	Dripstone	628.16.2		32
	N	Wellington	628.18.3		16
	N	Kanangara	6111.2.2		32
	N	Jenolan Caves	6212.1.1		16
TEPHROSIEAE Benth. and Hook.f.					
Tephrosia purpurea Pers. ..	N	Dripstone	628.16.3	8	16
GLYCINEAE Benth.					
Glycine clandestina Wendl.	N	Warrumbungle Ranges	628.10.7		40
	N	Cronulla	6111.1.1		20
	N	Oakleigh	619.5.1		40
Hardenbergia comptoniana Benth.	W	Yanchep	638.5.2		22
H. violacea (Schneev.) Stearn	Q	Glenmorgan	628.4.5		22
	N	Pt Macquarie	628.1.2		22
	N	Neville	6110.2.1	11	
	N	Vittoria	619.9.1		22
	N	Sunny Corner State Forest	6110.3.2		22
	N	Cronulla	618.9.1	11	
H. violacea " var. *rosea* " ..	S	Adelaide	625.1.4	11	22
Kennedia coccinea Vent. ..	W	Kelmscott	638.6.1		22
	W	Porongorup Ranges	638.13.6		22
	W	Chillingup, Green Ranges	638.14.24		22
K. eximia Lindl.	W	16 km E. Gnowangerup	638.16.1		22
K. nigricans Lindl. ..	W	32 km N. Perth	625.1.2	11	22
K. prostrata R.Br.	N	16 km S. Bodalla	6210.1.9		22
	W	Wanneroo	637.5.3		22
	W	8 km S.W. Northam	637.4.7		22
K. rubicunda Vent.	N	Colo River	618.8.1		22
	N	Pearl Beach	619.3.1		11
CAJANEAE Benth. and Hook.f.					
Rhynchosia minima DC. ..	Q	32 km S. Warwick	628.2.15		22
PODALYRIEAE Benth.					
Aotus ericoides (Vent.) G. Don.	N	Heathcote	618.3.2		16
	N	National Park	627.2.6	8	
	N	27 km N. Nerriga	639.11.14		16
	N	40 km S. Nowra	639.5.6		16
	N	16 km N. Moruya	6210.1.7		16
	N	Junction Hume Hwy and Snowy Mtn Hwy	6210.2.1		16
	S	16 km S. Kimba, Eyre Peninsula	649.4.1		16
	W	Yanchep	638.5.6		16
	W	29 km W. Albany	628.12.11		16
	W	Manypeaks	638.14.1		16
A. preissii Meissn.	W	Mogumber to Gingin	638.4.6		16
	W	39 km E. Ravensthorpe	638.18.1		16
A. subglauca Blakely et McKie	Q	Wyberba National Park	628.7.4		16
	N	Pilliga Scrub	628.9.2		16

Species	State	Locality	Coll. no.	Chromosome no.	
A. subglauca var. *filiformis* Blakely et McKie	Q	Moonie Hwy, 85 km E. St. George	628.5.6	8	16
Brachysema lanceolatum Meissn.	Q	Glenmorgan, from W.A.	628.4.14	8	
B. latifolium R.Br.	W	Chillingup to Keerjanup West Rd	638.14.27		16
B. praemorsum Meissn.	W	Kojunup	638.8.5		16
B. sericea (Sm.) Domin.	W	Denmark	638.12.9		16
Burtonia scabra R.Br.	W	Green Ranges	638.14.14		18
Chorizema aciculare (DC.) Gardn.	W	Bannister	638.7.1		32
	W	18 km E. Gnowangerup	638.16.3		16
C. cordatum Lindl.	W	Arthur River	638.8.3		16
	W	Pinjarra	638.9.3		16
C. cytisoides Turcz.	W	Albany to Mt Barker	638.13.2		16
	W	Cape Riche Rd, Green Ranges	638.14.20		16
C. dicksonii Grah.	W	47 km S.W. Northam	637.4.15		16
C. ericifolium Meissn.	W	252 km N. Perth	638.1.2		16
C. glycinifolium (Sm.) Druce	W	16 km W. Albany	638.12.17		16
	W	19 km E. Ongerup	638.16.9		16
C. ilicifolium Labill.	W	Collie to Arthur River	638.8.3		16
	W	Pinjarra to Boddington	638.9.3		16
C. nervosum T. Moore	W	56 km E. Jerramungup	638.16.16		16
C. reticulatum Meissn.	W	Albany to Mt Barker	638.13.1		16
C. rhombeum R.Br.	W	Cape Riche Rd, Green Ranges	638.14.23		16
Cupulanthus bracteolosus (F. Muell.) Hutch.	W	South Stirlings	638.14.29		16
Daviesia acicularis Sm.	Q	Moonie Hwy, Westmar	628.5.2	9	
	Q	Jollys Falls, Stanthorpe	628.12.11		18
	N	Coonabarrabran	628.11.3		18
	N	Goonoo Forest	628.17.10		18
D. alata Sm.	N	National Park	629.2.1		18
D. brevifolia Lindl.	S	Fishery Bay Rd, S. Pt Lincoln	649.2.7		18
D. corymbosa Sm.	N	Wentworth Falls	628.21.20	9	
	N	Waterfall	6110.4.7		18
	N	Heathcote	618.4.7	9	
D. daphnoides Meissn.	W	18 km W. Lake Grace	638.19.9		18
D. divaricata Benth.	W	270 km N. Perth	638.1.4		18
	W	Bannister	638.7.2	9	
D. flexuosa Benth.	W	Stewart Hwy	638.12.4		18
D. genistifolia A. Cunn. ex Benth.	Q	16 km S. Warwick	628.2.14		18
	Q	Moonie Hwy, Westmar	628.5.3		18
	N	Pilliga Scrub	628.9.3	9	
	N	Warrumbungle Ranges	628.10.13		18
	N	Goonoo Forest	628.17.11	9	
	N	Buladelah State Forest	628.14.6		18
	S	Mt Shannon, 63 km S. Kimba	649.4.4		18
D. grahamii Ewart and White	W	18 km N. Bruce Rock	639.1.6		18
D. horrida Meissn.	W	Bullsbrook	638.4.8	9	
D. incrassata Sm.	W	Three Springs	638.2.3		18
	W	32 km S.W. Northam	637.4.12		18
	W	Mumballup	638.8.6		18
D. juncea Sm.	W	East Bullsbrook Rd	637.5.6		18
	W	37 km W. Wyalkatchem	637.4.5		18
D. latifolia R. Br.	Q	Wyberba National Park	628.7.3		18
	N	24 km E. Glen Innes	628.2.4		18
	N	Warrumbungle Ranges	628.10.12		18
	N	Vittoria	619.9.2	9	
	N	Waterfall	6110.4.7		18
D. mimosoides R.Br.	N	16 km S. Canberra	6210.2.6		18
	N	Kosciusko Rd	6211.2.4	9	
D. nematophylla (F. Muell.) Benth.	W	16 km N. Bruce Rock	639.1.7		18

Species	State	Locality	Coll. no.	Chromosome no.	
D. nudiflora Meissn.	W	Yanchep	638.5.3		18
	W	Wanneroo	637.5.1		18
D. pachyphylla F. Muell.	W	51 km E. Jerramungup	638.16.15		18
D. pectinata Lindl.	W	13 km S.W. Northam	637.4.8		18
	S	Fishery Bay Rd, S. Pt Lincoln	649.2.6		18
D. pubigera A. Cunn. ex Benth	N	Warrumbungle Ranges	628.10.1		18
	N	Goonoo Forest	628.17.7	9	
D. reversifolia F. Muell.	W	39 km E. Jerramungup	638.16.11		18
D. rhombifolia Meissn.	W	40 km S.W. Northam	637.4.13		18
	W	Gleneagle State Forest, Brookton Hwy	638.6.5		18
D. squarrosa Sm.	N	Gibraltar Range State Forest	628.2.12	9	18
	N	5 km W. Penrith	628.21.5		18
	N	16 km N. Batemans Bay	639.5.1		18
D. squarrosa var. *villifera* (A.cunn. ex Benth.) Benth.	Q	Helidon Hills	638.20.5		18
	N	Yetman	628.8.7	9	
D. striata Turcz.	W	Dandarragan	638.3.6		18
D. teretifolia Benth.	W	51 km E. Jerramungup	638.16.14		18
D. trigonophylla Meissn.	W	Green Ranges	638.14.19		18
D. ulicifolia Andr.	Q	Glenmorgan	628.4.21		18
	N	Yetman	628.8.1		18
	N	Goonoo Forest	619.10.10	9	
	N	Buladelah State Forest	628.14.7		18
	N	Lower Portland Ferry	619.3.7	9	
	N	7 km W. Kurrajong Heights	619.2.1		18
	N	Liverpool	619.4.3		18
	N	Kosciusko Road	6211.2.5		18
D. umbellulata Sm.	N	32 km S. Pt Macquarie	628.15.2	9	
D. uniflora D. A. Herbert	W	23 km W. Lake Grace	638.19.11		18
D. virgata A. Cunn. ex Hook.	N	Kings Plain	6110.2.4	9	
	N	8 km N. Goulburn	6210.3.2		18
Dillwynia acicularis Sieber ex DC.	N	Calga	6310.2.4		14
D. brunioides Meissn.	N	Kings Tableland	639.7.7		14
	N	Currarong Rd, 8 km S. Nowra	639.5.15		14
	N	11 km N. Nerriga	639.11.13	7	
	N	31 km N. Nerriga	639.11.15		14
D. cinerascens R.Br.	W	37 km S. New Norcia	637.5.8		14
	W	Brookton Hwy	638.6.10		14
	W	Dunsborough	638.11.2		14
D. dillwynioides Meissn.	W	Brockman Hwy	638.12.3		14
D. floribunda Sm.	Q	Pottsville	638.20.1		14
	Q	Currimundi	638.20.6		14
	N	Coonabarrabran to Mendooran	628.11.2	14	
	N	Wilberforce	627.1.11		14
	N	Colo	627.1.10		14
	N	Kings Tableland	639.10.6		14
	N	Woodford	639.10.3		14
	N	Warrah	618.8.6	14	28
	N	Warrah	628.13.5	14	14, 28
	N	Warrah	637.1.1	14	28
	N	Woronora Dam Rd	637.2.3		14
	N	National Park	627.2.5	7	14
	N	National Park	635.2.6	7	14
D. floribunda var. *teretifolia* (DC.) Blakely	N	Woy Woy	628.13.1		14
D. glaberrima Sm.	N	La Perouse	6110.6.4	7	
	N	Burrill Lakes	639.5.5		14
	V	Grampian Ranges	6310.5.15		14
D. hispida Lindl.	V	Kiata	6310.5.5		14
D. juniperina Lodd.	Q	48 km N.W. Stanthorpe on Inglewood Rd	628.6.2	7	14
	N	Mendooran	628.11.7		14
	N	Goonoo Forest	618.6.3		14

Species	State	Locality	Coll. no.	Chromosome no.	
D. juniperina Lodd.—*continued*	N	Goonoo Forest	628.12.3		14
	N	Lower Portland Ferry	619.3.5	7	
	N	14 km E. Penrith	619.1.2	7	
	N	Liverpool	619.4.2	7	
	N	5 km E. Queanbeyan	639.4.1		14
D. parvifolia R.Br.	N	2 km S. Batemans Bay	6210.1.5	7	14
	N	19 km S. Batemans Bay	639.5.3		14
	N	13 km N. Moruya	6210.1.8	7	14
D. parvifolia var. *trichopoda* Blakely Blakely	Q	Gurulmundi transplant to Glenmorgan	628.4.13	7	14
	N	Buladelah	628.14.2	7	
	N	1 km W. Morisset	639.8.7		28
	N	1 km W. Glenbrook	6110.9.4	14	
	N	Oakdale (prostrate form)	619.8.1	7	
	N	Oakdale (erect form)	628.20.2	7	
	N	Falls Creek turnoff to Huskisson	6210.1.2	14	28
D. peduncularis Benth.	Q	Stanthorpe	638.20.9		14
	N	Wollumbi	6310.2.3		14
	N	1 km E. Linden	6110.9.5		14
	N	3 km W. Faulconbridge	628.21.13		14
	N	De Burghs Bridge, Pymble	629.3.1		14
	N	29 km W. Batemans Bay	639.4.7		14
	S	8 km N.E. Warrow, Eyre Peninsula	649.4.5		14
D. phylicoides A. Cunn.	Q	Wyberba National Park	628.7.2	14	
	N	Gibraltar Range State Forest	628.2.11		14
	N	Warrumbungle Ranges	628.10.3,8,14	14	28
	N	Mullion Creek, 19 km N. Orange	628.19.3		28
	N	3 km E. Kings Plain	6110.2.5	7	
	N	5 km W. Bell	6310.8.4		14
	N	Jenolan Rd	6310.8.11		14
	N	2 km W. Hartley Vale	6310.4.5	7	
	N	Black Mountain, Canberra	639.3.4		28
D. prostrata, Blakely	N	Dry Plains, S. Adaminaby	6211.3.2		28
	N	27 km S. Talbingo	6211.3.4	14	
D. ramosissima Benth.	N	7 km N. Nerriga, Pigeon House Range	639.11.12		14
	N	Currarong Rd, 8 km S. Nowra	639.5.12		14
D. retorta (Wendl.) Druce	N	Warrah	618.8.11		14
	N	Kuring-gai	618.2.1	7	
	N	Pennant Hills Reserve	618.1.2	7	
	N	National Park near Audley	635.2.1,7		14
	N	National Park near Waterfall	6110.4.3		28
	N	La Perouse	6110.6.3		28
	N	Woronora Dam Rd	637.2.1		14
D. rudis Sieber ex DC.	N	Wollumbi	6310.2.1		14
	N	Bells Line of Rd	639.7.8		14
D. sericea A. Cunn.	N	45 km N. Dubbo to Mendooran	628.17.2		14
	N	Dubbo Arboretum	628.17.14		14
	N	Mullion Creek, 19 km N. Orange	628.19.2		14
	N	5 km E. Kings Plain	6110.2.3	7	
	N	Warragamba Dam	6210.4.2		14
	N	Monaro Hwy, 16 km S. Canberra	6210.2.4	7	14
	N	7 km E. Queanbeyan	639.4.3		14
	N	14 km E. Bungendore	639.11.2		14
	N	40 km W. Yass	639.3.2		14
	N	Cooma	6211.3.1	7	
	V	Grampians Ranges	6310.5.7		14
D. stipulifera Blakely	N	Dargans Creek, Clarence	6310.8.7		21
D. tenuifolia Sieber ex DC.	N	Bells Line of Rd, Kurrajong turnoff	6110.9.13	7	
	N	Linden to Woodford	639.7.5		14
D. uncinata (Turcz.) Gardn.	W	40 km W. Coolgardie	637.3.1		14
	W	24 km N. Ravensthorpe	638.19.3		14

Species	State	Locality	Coll. no.	Chromosome no.	
D. uncinata (Turcz.) Gardn.—*continued*	S	3 km N. Arno Bay turnoff, Eyre Peninsula	649.1.2		14
Euchilopsis linearis (Benth.) F. Muell.	W	East Bullsbrook Rd	637.5.7	7	
	W	3 km W. Albany	638.12.16		14
Eutaxia densifolia Turcz. ..	W	Green Ranges	638.14.12		16
	W	3 km E. Ongerup	638.16.8		32
E. epacridoides Meissn. ..	W	Brockman Hwy.	638.12.2		16
E. microphylla (R.Br.) Gardn.	V	Kiata	6310.5.4		32
	W	Bullfinch to Southern Cross	639.1.1		16
	S	3 km N. Arno Bay turnoff, Eyre Peninsula	649.1.1		16
	S	14 km S. Arno Bay turnoff, Eyre Peninsula	649.1.4		16
E. microphylla var. *diffusa* (F. Muell.) A. B. Court ..	S	St Andrews Tce to Sandspits, Pt Lincoln	649.2.3	8	
	S	Brownlaw Rd, 11 km from Kingscote to American River, Kangaroo Is.	649.5.1		16
	S	7 km S. Nhill to Winniam	649.6.4		16
E. parvifolia Benth. ..	W	58 km E. Jerramungup	638.16.17		16
E. virgata Benth.	W	42 km N. Bullfinch	639.1.4		16
	W	Capel	638.10.4		16
	W	29 km W. Albany	638.12.10		16
Gastrolobium bennettsianum Gardn.	W	11 km E. Wyalkatchem	639.1.10		16
G. bidens Benth.	W	335 km N. Perth	638.1.5		16
	W	252 km N. Perth	638.1.1		16
G. bilobum R.Br.	W	Albany	638.12.13	8	16
G. calycinum Benth. ..	W	130 km N. Perth	637.5.9		16
	W	Boddington	638.9.7		16
G. crassifolium Benth. ..	W	24 km E. Gnowangerup	638.16.4		16
G. hamulosum Meissn. ..	W	24 km W. Lake Grace	638.19.13		16
G. hookeri Meissn.	W	Brookton Hwy	638.6.8		16
	W	Pingelly	638.6.12		16
G. microcarpum Meissn. ..	W	16 km S.W. Northam	637.4.10		16
G. obovatum Benth.	W	29 km W. Wyalkatchem	637.4.4		16
G. parvifolium Benth. ..	W	11 km E. Yoting	639.1.9		16
	W	Brookton Hwy	638.6.11		16
G. polystachyum Meissn. ..	W	130 km N. Perth	637.5.10		16
G. pulchellum Turcz. ..	W	16 km S.W. Northam	637.4.11		16
G. reticulatum (Meissn.) Benth.	W	18 km E. Gnowangerup	638.15.2		16
G. spathulatum Benth. ..	W	S. New Norcia	637.5.15		16
G. spinosum Benth.	W	7 km N. Gingin	638.4.7		16
	W	13 km E. Yoting	639.1.8		16
	W	Stirling Ranges	638.15.3		16
	W	Ravensthorpe to Hopetoun	638.17.5		16
G. stowardii S. Moore ..	W	Eneabba	638.2.2		16
G. trilobium Benth.	Q	Glenmorgan	628.4.6		16
G. velutinum Lindl.	W	Stirling Ranges to Cranbrook	638.15.4		16
	W	Mt Barker to Porongorup Ranges	638.13.4		16
	W	66 km N. Ravensthorpe	638.19.6		16
G. villosum Benth.	W	South of New Norcia	637.5.16		16
	W	Brookton Hwy, Gleneagle State Forest	638.6.4		16
Gompholobium burtonioides Meissn.	W	Cape Riche Rd, Green Ranges	638.14.10		18
G. glabratum Sieber ex DC...	N	2 km E. Linden	619.1.4		18
	N	Waterfall	6110.4.13		18
G. grandiflorum Sm. ..	N	Warrah	618.8.4	9	
	N	Adelina Falls	6110.9.9		18
	N	Colo Heights	627.1.5		18

Species	State	Locality	Coll. no.	Chromosome no.	
G. huegelii Benth.	N	Kanangra	6111.2.1		18
	N	Mt Victoria Pass	6310.8.10		18
	N	Clarence	6310.8.8		18
G. knightianum Lindl.	W	Yanchep	638.5.5		18
	W	Green Ranges	638.14.16		18
	W	Ravensthorpe to Hopetoun	638.17.12		18
G. latifolium Sm.	N	Warrah	618.8.5	9	18
	N	Colo Heights	627.1.8		18
	N	Wentworth Falls	628.21.21	9	
G. marginatum R.Br.	W	Chester Pass, Stirling Ranges	638.15.2		18
G. minus Sm.	N	47 km N. Braidwood on Nerriga Rd	639.11.11		18
G. polymorphum R.Br.	W	Green Ranges	638.14.15		18
G. tomentosum Labill.	W	31 km E. Gnowangerup	638.16.6		18
G. uncinatum A. Cunn. ex Benth.	N	Mt Victoria Pass	6310.8.9		18
G. venustum R.Br.	W	Green Ranges	638.14.13		18
G. viscidulum Meissn.	W	Ravensthorpe to Hopetoun	638.17.4		18
Isotropis cuneifolia (Sm.) Domin.	W	373 km N. Perth	638.1.7		16
	W	246 km N. Perth	638.1.3		16
	W	Mandurah	638.10.12		32
	W	Green Ranges	638.14.17		16
Jacksonia cupulifera Meissn.	W	Moora	638.3.1		18
J. furcellata (Bonpl.) DC.	W	Yanchep	638.5.1		18
J. horrida DC.	W	Witchcliffe turnoff	638.11.5		18
J. racemosa Meissn.	W	47 km E. Ravensthorpe	638.18.3		18
J. scoparia R.Br.	Q	Glenmorgan	628.4.12	9	18
	Q	39 km N.W. Stanthorpe	628.6.6		18
	N	Dooralong Valley	639.8.4		18
	N	1 km E. Glenbrook	6110.9.2		18
J. sternbergiana Hueg.	W	Dandarragan	637.3.2		18
	W	Wanneroo	638.5.2		18
J. ulicina Meissn.	W	369 km N. Perth	638.1.6		18
Latrobea hirtella (Turcz.) Benth.	W	Mt Barker	638.13.3		14
	W	Green Ranges	638.14.18		14
Leptosema aphyllum Hook.	W	Three Springs	638.2.1		16
Mirbelia baueri (Benth.) J. Thompson	N	31 km N. Nerriga	639.11.16		16
M. depressa E. Pritzel	W	42 km N. Bullfinch	639.1.3		16
	W	Ravensthorpe to Hopetoun	638.17.1		16
M. floribunda Benth.	W	Dandarragan	638.3.5		16
	W	145 km N. Perth	637.5.12		16
M. ovata Meissn.	W	Stirling Ranges to Cranbrook	638.15.7		16
	W	Tambellup	638.15.8		16
	W	Gnowangerup	638.15.11		16
M. oxylobioides F. Muell.	N	Varneys Range, 13 km E. Jindabyne	6211.1.2	8	
	N	Kosciusko Road	6211.2.1	8	
M. platylobioides (DC.) J. Thompson	N	Kings Tableland	628.21.16		16
	N	Wallerawang	6110.3.3		16
	N	77 km E. Queanbeyan	639.4.6		16
M. pungens A. Cunn. ex G. Don.	Q	Kogan	628.3.4		16
	Q	Glenmorgan	628.4.8		16
	Q	16 km N.W. Stanthorpe	628.6.8		16
	N	Dubbo Arboretum	628.12.7	8	
	N	Goonoo Forest	628.17.9		16
M. rubiifolia (Andr.) G. Don.	N	32 km S. Pt Macquarie	628.15.1		16
	N	Kuring-gai Chase	6110.5.2		16
	N	5 km W. Penrith	628.21.2		16
	N	Waterfall	6110.4.9		16
M. speciosa Sieber ex DC.	Q	32 km S. Warwick	628.2.10		16
	N	Gibraltar Range State Forest	628.2.8		16

Species	State	Locality	Coll. no.	Chromosome no.	
M. spinosa Benth.	W	Bullfinch	639.1.2		16
	W	135 km N. Perth	637.5.11	8	
M. trichocalyx Domin.	W	87 km W. Coolgardie	637.3.3		16
Nemcia axillare Meissn.	W	Dandarragan	638.3.4		16
N. capitatum Benth.	W	Mogumber	638.4.3		16
	W	East Bullsbrook Road	637.5.4		16
	W	47 km S.W. Northam	637.4.14		16
	W	Brookton Hwy, Gleneagle State Forest	638.6.6		16
N. coriaceum (Sm.) Domin.	W	Cheyne Bay	638.14.6		16
N. cuneatum Benth.	W	Pinjarra	638.9.1		16
	W	Bannister	638.9.9		16
N. drummondii S. Moore	W	Boddington	638.9.8		16
	W	Cheyne Bay	638.14.3		16
	W	Cape Riche Rd, Green Ranges	638.14.11		16
N. melanocaule E. Pritzel	W	Stirling Ranges to Cranbrook	638.15.5		16
N. reticulatum Meissn.	W	Safety Bay	638.10.1		16
	W	Moora to Dandarragan	638.3.3		16
Oxylobium aciculiferum (F. Muell.) Benth.	N	Dooralong Valley	639.8.5		16
O. alpestre F. Muell.	N	5 km S. Kiandra	6211.3.3		16
O. arborescens Ait.f.	N	14 km N. Marulan	6310.6.3		16
O. atropurpureum Turcz.	W	Brookton Hwy, Gleneagle State Forest	638.6.7		16
O. cordifolium Andr.	N	La Perouse	6110.6.2	8	
O. ellipticum (Labill.) R.Br.	N	Brindabella Ranges	639.11.17		16
	N	63 km S. Canberra	6210.2.2	8	16
O. ilicifolium (Andr.) Domin.	N	Wauchope	628.1.3		16
	N	Tea Gardens	618.10.1	8	
	N	Colo Heights	627.1.2		16
	N	Kurrajong	627.1.3	8	
	N	5 km W. Penrith	628.21.4	8	
	N	Oakdale	628.20.3	8	
	N	Batemans Bay	6210.1.6	8	
O. microphyllum Benth.	W	18 km N. Ravensthorpe	638.19.15		16
O. parviflorum Benth.	Q	Glenmorgan	628.4.7	8	
	W	60 km W. Southern Cross	637.4.3		16
	W	Brookton Hwy	638.6.9		16
	W	Chillingup to Keerjanup West	638.14.26		16
O. procumbens F. Muell.	N	Varneys Range, 13 km E. Jindabyne	6211.1.3	8	
O. pulteneae DC.	N	Calga	6310.2.5		16
O. racemosum Turcz.	W	18 km N. Ravensthorpe	638.19.2		16
O. robustum J. Thompson	N	Harrington	6311.1.2		16
O. scandens (Sm.) Benth.	N	Batemans Bay	6210.1.4		16
O. spectabile Endl.	W	48 km E. Jerramungup	638.16.13		16
O. tetragonophyllum E. Pritzel	W	35 km E. Jerramungup	638.16.10		16
Oxylobium sp.	W	Gleneagle State Forest	638.6.7		16
Phyllota humifusa Benth.	N	13 km W. Mittagong	6210.4.1	7	14
P. phylicoides (Sieber ex DC.) Benth.	N	Warrah	628.13.6		14
	N	Kuring-gai	618.2.5	7	
	N	Windsor	627.1.12		14
	N	Kings Tableland	628.21.17		14
	N	Wentworth Falls	628.9.8		14
	N	National Park	627.2.2	7	
	N	32 km S. Nowra	639.5.7		14
Pultenaea acerosa R.Br.	S	Mt Lofty Railway Station	639.2.6	9	18
	S	Mt Lofty Ranges	6312.3.1		18
	S	Foreshore S. Port Lincoln	649.2.1		18
	S	Fishery Bay Rd, S. Pt Lincoln	649.2.8		18
	S	Flinders Monument Rd, S. Pt Lincoln	649.2.10		18
	S	Penneshaw Rd, 19 km from Kingscote, Kangaroo Is.	649.5.3		18

Species	State	Locality	Coll. no.	Chromosome no.	
P. acerosa var. *acicularis* H. B. Williamson	S	Vivonne Bay, Kangaroo Is.	649.5.13		18
P. adunca Turcz.	W	Ravensthorpe to Hopetoun	638.17.3		14
P. altissima F. Muell. ex Benth.	N	Corang River, 42 km N. Braidwood	639.11.10	7	
P. andrewsii C. A. Gardn.	W	53 km N. Ravensthorpe	638.19.4		14
P. angustifolia Benth.	V	Silverband Rd, Grampians Ranges	6310.5.8		18
	V	N. Halls Gap, Grampians Ranges	649.7.2		18
P. aristata Sieber ex DC.	N	Mullion Creek, 19 km N. Orange	628.19.1		16
	N	Darke Forest turnoff on Princes Hwy	639.6.6		16
P. benthamii F. Muell.	V	3 km up Mt William Rd, Grampians Ranges	649.7.12		16
P. blakelyi J. Thompson	N	Garie Beach Rd, National Park	637.2.2		16
	N	1 km before Belmore Falls	639.6.4		16
	N	Termeil State Forest, 24 km S. Milton	639.5.4		16
P. boormanii Williamson	N	Sutton, 19 km N. Canberra	6310.6.1	7	
	N	18 km E. end of Sturt Hwy	639.3.1	7	14
P. calycina (Turcz.) Benth.	W	Keerjanup West Rd, Green Ranges	638.14.28	8	16
P. campbelli Maiden et Betche	N	Bucketty, convicts' drinking pump	648.1.3	7	14
P. canaliculata F. Muell.	V	Portland	6310.5.19		16
P. canaliculata var. *latifolia* Williamson	S	8 km from Seal Bay turnoff, Kangaroo Is.	649.5.6	8	
	S	" Brookland Park ", Kangaroo Is.	649.5.10		16
P. canescens A. Cunn.	N	5 km E. Bell	6310.8.3		14
	N	Head of Dargans Creek, Clarence	6310.8.5		14
	N	3 km S. Marulan	6310.6.2	7	14
	N	2 km N. Goulburn	6210.3.1	7	14
P. capitellata Sieber ex DC.	N	Mt. Werong, S. Oberon	6411.3.1		16
	N	The Crater, below Mt Wilson	6411.1.1		16
P. costata Williamson	V	2 km S. Zumsteins, Grampians Ranges	649.7.1		18
	V	7 km N.W. Halls Gap, Grampians Ranges	649.7.4		18
	V	Silverband Rd, Grampians Ranges	649.7.8		18
P. cunninghamii (Benth.) Williamson	Q	Glenmorgan, from Helidon	628.4.17	7	
	N	Wollumbi	6310.2.2		14
	N	7 km S. Talbingo	6211.3.6	7	
P. d'altonii Williamson	V	Black Ranges Rd	649.7.16	6	12
P. daphnoides Wendl.	N	Woy Woy	618.8.8		16
	N	Moonie Moonie	639.8.3		16
	N	16 km S. Bodalla	6210.1.11		16
	S	3 km before Mylor, Mt Lofty Ranges	639.2.1		16
	V	7 km S.E. Daylesford on Trentham Rd	649.9.2		16
P. dasyphylla (Turcz.) C. A. Gardn.	W	42 km E. Newdegate	638.19.8		14
P. densifolia F. Muell.	S	2 km on Vivonne Bay Rd, Kangaroo Is.	649.5.5		16
P. dentata Labill.	V	Grampians Ranges	6310.5.17	16	32
P. divaricata Williamson	N	Sublime Point Rd, Blue Mountains	6310.4.2		16
	N	Head of Dargan's Creek, Clarence	6310.8.6		16
P. echinula Sieber ex DC.	Q	Glenmorgan, from Stanthorpe	628.4.16		16

Species	State	Locality	Coll. no.	Chromosome no.	
P. elliptica Sm.	N	5 km N. Morrisset	639.8.9		14
	N	Linden	639.10.2	7	
	N	Glenbrook	649.10.1		14
	N	3 km S. Audley, National Park	6110.8.1		14
	N	3 km S. Audley, National Park	635.2.3		14
	N	Bundeena Rd	635.2.11		14
	N	Jervis Bay	634.1.2		14
P. empetrifolia Meissn.	W	34 km E. Gnowangerup	638.16.7	7	14
	W	Chester Pass, Stirling Ranges	638.15.1	7	14
P. ericifolia Benth.	W	89 km E. Jerramungup	638.16.19		14
	W	55 km N. Ravensthorpe	638.19.5		14
P. euchila DC.	N	22 km W. Grafton on Glen Innes Rd	6410.1.3		14
	N	Freemans Waterholes, N. Toronto	639.8.14		14
	N	Freemans Waterholes, N. Toronto	648.1.2		14
P. fasciculata Benth.	N	Waste Point, Snowy Mountains	631.1.1	8	
P. ferruginea Rudge	N	Wisemans Ferry	6110.7.1	7	
	N	Lapstone Hill Reserve	648.4.2	7	
P. ferruginea var. *deanei* (R. T. Baker) Williamson	N	N. Berowra	639.8.1		14
	N	1 km S. northern exit of new Gosford Hwy	648.3.4	7	14
	N	Warrah	623.1.1		14
P. flexilis Sm.	Q	Helidon Hills	638.20.3		16
	N	Crows Nest	638.20.6		16
	N	Mt Wilson	6310.4.7		16
	N	Tinda Creek, Colo Heights	648.1.1		16
	N	Liverpool	619.4.1		16
P. foliolosa A. Cunn. ex Benth.	Q	48 km N.W. Stanthorpe, Inglewood Rd	628.6.4		14
	N	Yetman	628.8.3		14
	N	Coonabarrabran	628.11.6		14
	N	Goonoo Forest	619.10.8		14
	N	Dubbo Arboretum	628.17.12		14
P. georgei (Hensl.) Gardn.	W	18 km N. Bruce Rock	639.1.5	7	
P. glabra Benth.	N	Lone Pine Park, Leura	639.6.3		16
	N	Pool of Siloam, Leura	639.10.9		16
	N	Boddington Hill	639.7.6		16
	N	Wentworth Falls	648.4.3		16
	N	Adelina Falls	628.21.15		16
P. graveolens Tate	S	Mt Lofty Ranges	6310.3.2	8	16
	S	Ashton	6310.3.6	8	
P. gunnii Benth.	V	Trentham East to Bullengarook	649.9.3		14
P. hartmannii F. Muell.	Q	Wyberba National Park	628.7.6	8	16
	Q	39 km N.W. Stanthorpe, Inglewood Rd	628.6.5		16
	Q	Jollys Falls, N. Stanthorpe	628.6.13		16
	N	Gibraltar Ranges, 68 km E. Glen Innes	6410.1.2		16
P. hibbertioides Hook.f.	V	Mt Difficult Rd, Grampians Ranges	649.7.6		18
	V	Victoria Valley Rd, Grampians Ranges	649.7.9	9	
P. hispidula R.Br. ex Benth.	N	St Ives	6310.1.1		14
	N	Frenchs Forest	6310.1.2		14
	N	Loftus	648.2.2		14
P. humilis Benth.	V	North Grampians Ranges	639.9.2		14
	V	Wonderland, Grampians Ranges	649.7.5		14
	V	Black Ranges Rd	649.7.17		14
	V	Footsteppes of Mt Sturgeon, 7 km N. Dunkeld	6310.5.13		14

Species	State	Locality	Coll. no.	Chromosome no.	
P. humilis Benth.—*continued*	V	Footsteppes of Mt Sturgeon, 7 km N. Dunkeld	649.7.14	7	14
P. humilis var. *glabrescens* Williamson	V	Black Ranges	6310.5.18		14
P. incurvata A. Cunn. . .	N	Valley of the Waters, Blue Mountains	628.21.18		16
	N	Lone Pine Park, Leura	639.10.8		16
P. involucrata Benth. . .	S	Mylor, Mt Lofty Ranges	6310.3.3		16
P. juniperina var. *juniperina* Labill.	V	Mt Difficult Rd, Grampians Ranges	649.7.7		18
P. juniperina var. *planifolia* Williamson	N	2 km above Sawpit Creek, Kosciusko Rd	6211.2.8	9	18, 27
	N	Sawpit Creek Track, 2–3 km from Kosciusko Rd	6211.2.9		18, 27
	N	Two Sticks Rd, Brindabella Ranges	6310.7.1,2	9	27
P. largiflorens var. *latifolia* Williamson	S	Belair Hill, Mt Lofty Ranges	639.2.7		16
P. laxiflora Benth.	S	Upper Sturt Rd, 5 km S.W. Mt Lofty	6312.1.1		16
	V	2 km N.E. Lawloit	649.6.3		16
	V	Lowan Sanctuary, Kiata	649.6.5		16
	V	10 km S.W. Stawell	649.7.11		16
P. laxiflora var. *pilosa* Williamson	V	Kiata	6310.5.3		16
P. linophylla Shrad. . .	N	Eraring	639.8.10		32
	N	Lawson	639.10.4		16
	N	16 km N. Batemans Bay	639.5.2		16
P. lycopodioides (S. Moore) C. A. Gardn.	W	116 km W. Coolgardie	637.3.4	7	14
P. microphylla Sieber ex DC.	Q	39 km N.W. Stanthorpe, Inglewood Rd	628.6.5		16
	N	13 km N. Armidale	628.1.5	8	
	N	Walcha	628.1.4		16
	N	S. Coonabarrabran on Mendooran Rd	628.11.4	8	16
	N	Goonoo Forest	628.17.3, 4, 5	8	16
	N	Dubbo State Forest	628.17.13		16
	N	Dubbo Arboretum	628.12.6		16
	N	2 km E. Bell	6310.4.6		16
	N	19 km E. Penrith	628.21.1	8	16
	N	Rooty Hill	639.7.1		16
	N	14–19 km N. Braidwood on Nerriga Rd	639.11.7, 9		16
	N	5 km E. Queanbeyan	639.4.2		16
P. microphylla var. *cinerascens* (Maiden et Betche) Williamson	Q	48 km N.W. Stanthorpe, Inglewood Rd	628.6.3	8	
	N	Yetman	628.8.5		16
	N	Pilliga Scrub	628.9.7		16
	N	Warrumbungle Ranges	628.10.2		16
	N	S. Coonabarrabran on Mendooran Rd	628.11.1		16
P. mollis Lindl.	V	Footsteppes Mt Sturgeon, 7 km N. Dunkeld	649.7.15		18
P. mucronata F. Muell. . .	N	Junction of Blackheath and Shipley Rds	6310.8.14	8	16
P. muelleri Benth. var. *reflexifolia* J. H. Willis . .	V	5 km S.E. Daylesford on Trentham Rd	649.9.1		16, 32
P. myrtoides A. Cunn. . .	N	Karuah	649.10.2		16

Species	State	Locality	Coll. no.	Chromosome no.	
P. neurocalyx Turcz.	W	Daniels Rd, Ravensthorpe to Hopetoun	638.17.7		14
	W	46 km E. Ravensthorpe	638.18.2		14
P. obcordata (R.Br.) Benth.	W	Ravensthorpe to Hopetoun	638.17.6	9	
	W	11 km N. Esperance	638.18.4		18
P. obovata Benth.	Q	Mudjimbah	638.20.8	7	
P. paleacea Willd.	N	Eraring, 5 km N. Morisset	639.8.11		16
	N	Stockyard Creek near Rathmines	639.8.3		16
	N	Swansea	628.1.1		16
P. paleacea var. *robusta* Williamson	Q	Mudjimbah	638.20.7	8	
P. parviflora Sieber ex DC.	N	St Mary's	639.7.2		14
	N	St Mary's	648.4.1		14
P. patellifolia Williamson	V	Black Range Rd	649.7.18		16
P. pedunculata Hook.	S	Norton Summit, Mt Lofty Ranges	6310.3.5	16	
P. petiolaris A. Cunn. ex Benth.	Q	Helidon Hills	638.20.4		16
	Q	Kogan	628.3.3, 5		16
P. polifolia A. Cunn.	N	Dripstone, near Wellington	628.16.5		16
	N	2 km S. Talbingo	6211.3.8		16
P. procumbens A. Cunn.	N	Jenolan Rd above Coxs River	6310.8.12		14
	N	16 km S. Canberra	6210.2.3	7	
	N	2 km S. Talbingo	6211.3.8		14
	N	Waste Point to Sawpit Creek, Kosciusko Rd	6211.2.2	7	14
P. prolifera Williamson	V	3 km E. Mt. Richmond	649.8.3, 4		16
P. prostrata Benth.	V	24 km W. Horsham, Cooac Scrub	639.9.1		16
	V	7 km W. Dimboola	649.6.6		16
P. pycnocephala F. Muell. ex Benth.	N	Gibraltar Range State Forest, 61 km E. Glen Innes	628.2.8		16
	N	Gibraltar Range State Forest, 61 km E. Glen Innes	6410.1.1		16
P. quadricolor J. M. Black	S	1 km W. Mylor, Mt Lofty Ranges	6311.2.1, 2		16
P. recurvifolia (Benth.) Williamson var. *readeriana* (Williamson) Willis	V	Victoria Valley Rd, Grampians Ranges	649.7.10		14
	V	Grampians Ranges	6411.2.1		14
P. reticulata (Sm.) Benth.	W	Dunsborough, S. Busselton	638.11.1		8
	W	Yallingup, S. Siding Rd	638.11.3		8
	W	S. Witchcliffe turnoff	638.11.6	4	
	W	Brockman Hwy	638.12.5	4	
	W	Manjimup	638.12.7		8
	W	N. Walpole	638.12.8	4	
	W	Emu Point, Albany	638.12.12	4	
P. retusa Sm.	N	Buladelah State Forest	628.14.4, 5	8	16
	N	32 km S. Pt Macquarie	628.15.3		16
	N	16 km N. Newcastle	628.14.1		16
	N	Oakdale	628.20.5		16
	N	Currarong Rd, 8 km S. Nowra	639.5.14		16
	N	2 km W. Huskisson	639.5.9		16
	N	19 km W. Batemans Bay	639.4.8		16
	N	16 km S. Bodalla	6210.1.10		16
P. rosmarinifolia Lindl.	N	Woy Woy to Ocean Beach	628.13.3		16
	N	Glenorie	629.1.1		16
	N	Gosford Rd, S. Mt White	648.3.3		16
	N	3 km W. Huskisson	639.5.8		16
P. scabra R.Br.	N	Blaxland	628.21.10		16
	N	Blaxland	639.7.4		16
	N	2 km E. Blackheath	639.10.10		16
P. scabra var. *biloba* (R.Br.) Benth.	N	Colo	627.1.7		16
	N	Lower Portland Ferry	619.3.6		16

Species	State	Locality	Coll. no.	Chromosome no.	
P. scabra var. *biloba* (R.Br.) Benth.—*continued* . .	N	1 km S. Lower Portland turnoff	627.1.6		16
	N	1 km E. Woodford	619.1.10		16
	N	Oakdale	628.20.1		16
	N	3 km E. Nelligen	639.4.10		16
	N	5 km N. Naroona	6210.1.12		16
P. scabra var. *montana* (Lindl.) Benth.	V	Silverband Rd, Grampians Ranges	6310.5.9		16
	V	3 km S. Zumsteins, Grampians Ranges	649.7.3		16
P. setulosa Benth.	N	Pilliga Scrub	628.9.4		14
P. spinosa (DC.) Williamson	Q	Childers, cultivated at Glenmorgan	628.4.15	7	
P. stipularis Sm.	N	Princes Highway, S. Waterfall	6110.4.4		16
	N	Princes Highway, S. Waterfall	647.1.1	8	
	N	Oakleigh Park	648.2.1		16
P. stricta Sims.	V	2 km S. Heywood	649.8.1		16
P. strobilifera Meissn. . .	W	16 km E. Newdegate	638.19.7		14
	W	Cape Riche Rd, Green Ranges	638.14.9		14
P. subalpina Druce	V	Near summit Mt William	6311.3.1		16
	V	Near summit Mt William	649.7.13		16
P. subspicata Benth. . .	N	18–22 km E. Bungendore	639.11.3, 4	7	14
	N	37 km E. Bungendore	639.11.5	7	14
	N	19 km N. Braidwood on Nerriga Rd	639.11.8		14
	N	2 km W. Hartley Vale	6310.4.4	7	
P. subternata Williamson . .	N	Mullion Creek, 19 km N. Orange	628.19.4		14
P. tenuifolia R.Br.	S	Stenhouse Bay, Yorke Peninsula	6310.3.9		16
	S	19 km S. Kimba, Eyre Peninsula	649.4.2		16
	S	10 km N. Tooligie, Eyre Peninsula	649.3.4, 5		16
	S	8 km N.E. Warrow, Eyre Peninsula	649.4.6		16
	S	14 km S. Arno Bay turnoff, Eyre Peninsula	649.1.3	8	
	S	Road to Flinders Monument, Pt Lincoln	649.2.9		16
	S	16 km W. Coonalpyn	649.6.2		16
P. tenuifolia var. *glabrescens* Williamson	S	48 km E. Tailem Bend	649.6.1		16
P. teretifolia Williamson . .	S	Mt Shannon, 63 km S. Kimba	649.4.3	8	
	S	7 km Mt Drummond, Eyre Peninsula	649.3.3		16
	S	7 km S. Coulter, Eyre Peninsula	649.3.2		16
	S	11 km E. Warrow, Eyre Peninsula	649.4.8		16
	S	Sandspit area, Pt Lincoln	649.2.5	8	16
P. trifida J. M. Black . .	S	Shackle Road, 10 km N. Rocky River Homestead, Flinders Chase, Kangaroo Is.	649.5.9		16
	S	" Brookland Park ", Kangaroo Is.	649.5.12		16
P. trinervis J. M. Black . .	S	Mylor, Mt Lofty Ranges	6310.3.4	8	
	S	11 km E. Warrow, Eyre Peninsula	649.4.7		16
	S	Coffin Bay Road, 13 km W. Pt Lincoln	649.3.1		16
	S	Sandspit area, Pt Lincoln	649.2.4		16
P. verruculosa Turcz. . .	W	3 km W. Albany	638.12.14		14
	W	Cape Riche, Green Ranges	638.14.8		14
	W	Chillingup	638.14.21		14
	W	Old Saltbush Rd to Cranbrook	638.15.6	7	
	W	Cheyne Bay	638.14.2	7	14

Species	State	Locality	Coll. no.	Chromosome no.	
P. verruculosa var. *brachyphylla* Benth.	W	45 km E. Jerramungup	638.16.2		14
P. vestita R.Br.	S	Stenhouse Bay, Yorke Peninsula	6310.3.7		16
P. villifera Sieber ex DC. ..	N	Jervis Bay	652.1.1		16
P. villosa Willd.	Q	Near Nerang	638.20.2		14
	N	22 km W. Grafton	6410.1.4		14
	N	State Forest N. Buladelah	628.14.3		14
	N	2 km N. Myuna Bay	638.8.12		14
	N	5 km N. Heathcote	6110.4.1		14
	N	Oakdale	628.20.5	7	
	N	2 km before Belmore Falls	639.6.2	7	
	N	Nowra	6210.1.1		14
	N	S. Ulladulla	6210.1.3		14
	N	19 km W. Batemans Bay	638.4.9	7	14
P. viscidula Tate	S	South West River Rd, Kangaroo Is.	649.5.7		16
	S	Western River Rd, Kangaroo Is.	649.5.8		16
P. viscosa R.Br. ex Benth. ..	N	Sublime Point Rd, Leura	639.10.7		16
	N	1 km before Belmore Falls	639.6.3, 5		16
P. vrolandii Maiden ..	N	13 km N. Braidwood on Goulburn Rd	639.11.6	9	18
Sphaerolobium alatum Benth.	W	3 km W. Albany	638.12.15		18
S. medium R.Br.	W	Cheyne Bay	638.14.5		18
S. vimineum Sm.	N	Morisset	639.8.8		18
	N	Waterfall	6110.4.12		18
Viminaria juncea (Schrad.) Hoffmgg.	N	Waterfall	6110.4.10	9	
	N	La Perouse	6110.6.1	9	

THE FIRST RECORD OF STENOPSOCIDAE (PSOCOPTERA) FROM NEW GUINEA WITH DESCRIPTIONS OF NEW SPECIES

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Synopsis

Seven species of the family Stenopsocidae are recorded from Papua-New Guinea-West Irian area. These include five new species of *Taeniostigma* Enderlein as well as *T. perkinsi* Banks and *Stenopsocus albipileus* Smithers, both previously known from north-eastern Australia.

Introduction

Seven species of the family Stenopsocidae are here recorded from Papua New Guinea and West Irian for the first time; six species belong to the genus *Taeniostigma* Enderlein and one to *Stenopsocus* Hagen.

Taeniostigma Enderlein was erected for *Psocus elongatus* Hagen from Ceylon and has since been recorded from several other localities in Indo-Malaya. Subsequently several additional species have been described from the Oriental and Australian Regions, but none from the Papua-New Guinea-West Irian area. Five new species are described below and new records given for *T. perkinsi* Banks, a species previously known only from Australia.

Stenopsocus albipileus Smithers, for which new records are given below, was also previously known only from Australia. The genus has not been previously recorded for New Guinea.

Taeniostigma Enderlein 1901

(Type species: *Psocus elongatus* Hagen 1858)

Taeniostigma baiyerensis sp. n.

Figs 1–6

FEMALE

Coloration (in alcohol). A distinctively marked species. Top of head, except for a narrow brown triangle in front of ocellar tubercle, pale yellowish. Genae, postclypeus and area between eyes and antenna bases very dark brown. Labrum and mouth parts, including maxillary palps, very pale, almost colourless. Antennae very dark brown with only slight suggestion of paling in proximal halves of flagellar segments. Dorsum of thorax anterior to mesothoracic wing bases very dark brown; no median pale area on antedorsum; sutural areas dark; thorax otherwise pale. Legs pale, except for pale brown distal tarsal segments. Fore wings (fig. 1) with area near wing base and cell IA very pale brown, otherwise hyaline.

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Pterostigma opaque. Wing membrane faintly tinged with brown near nodulus. Veins pale brown with r, r_1, $m + cu$ and cu_1 beyond separation from m darker. Hind wings (fig. 2) hyaline, veins brown.

Morphology. Length of body: 5·0 mm. Median epicranial suture distinct. Epicranial plates fairly flat with an occasional tiny seta. Frons with sparse, but larger, setae. Postclypeus and genae setose. Lengths of flagellar segments: f_1 : 2·16 mm; f_2 : 1·5mm. Antennae stout and very hairy. Eyes fairly large. IO/D : 1·8; PO : 0·85. Ocellar tubercle small. Lacinia (fig. 3). Measurements of hind legs: F : 1·5 mm; T : 2·4 mm; t_1 : 0·75 mm; t_2 : 0·20 mm; rt : 3·75 : 1; ct : 28, 0. Legs long and slender, femora almost parallel-sided for most of length. Fore wing length: 7·0 mm; fore wing width: 2·4 mm. Fore wings broad, with broadly rounded apex. Vein r_1 (hind margin of pterostigma) almost straight, with only slight anterior curvature near wing margin so that the pterostigma is very narrow. Free section of m between $rs + m$ confluence and $m + cu_{1a}$ confluence 1·45 times as long as $rs + m$. Areola postica tall with narrow apex. Veins and margin (except from wing base to nodulus) setose. Setae on cu_2 up to 0·117 mm. Hind wing length: 4·6 mm; hind wing width: 1·4 mm. Veins setose except for $r + m$, r and rs basad of fusion with m. Vein r_{2+3} in the right wing of the type specimen has an adventitious, short, branch. Margin setose except anterior margin from wing base to r_1. Epiproct simple with semicircular hind margin, setose in distal third, without papillae. Paraproct rounded, strongly setose in distal half with large, round, trichobothrial field but no papillae. Gonapophyses (fig. 4). Ventral valve on long stalk; both valves fairly broad with strong median, chitinized bar with delicate fleshy flanges; hardly tapering except close to apex. Subgenital plate (fig. 5) with rounded hind margin, setose.

MALE

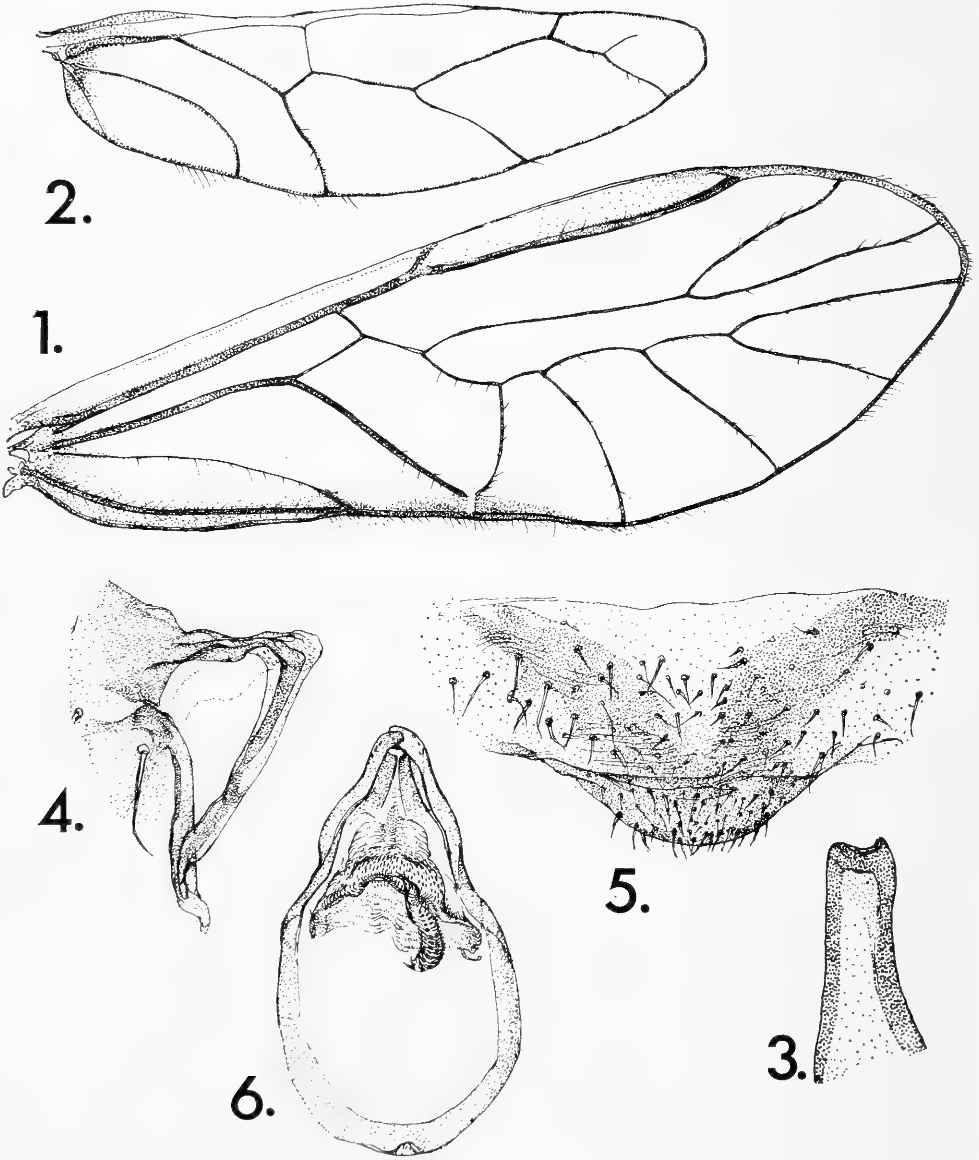
Coloration (in alcohol). As in female but brown area at base of wing and in cell Cu_2 paler.

Morphology. Length of body: 4·2 mm. Length of flagellar segments: f_1 : 1·56 mm; f_2 : 1·24 mm. Antennae stout and setose as in female. Eyes very large. IO/D : 0·84; PO : 0·84. Measurements of hind leg: F : 1·36 mm; T : 2·16 mm; t_1 : 0·76 mm; t_2 : 0·16 mm; rt : 4·8 : 1; ct : 25, 1. Fore wing length: 5·1 mm; fore wing width: 1·8 mm. Venation as in female; free section of m between $rs + m$ confluence and $m + cu_{1a}$ confluence 1·7 times as long as $rs + m$. Apex of areola postica narrow. Fore wing with all veins and margin (except nodulus to wing base) setose. Hind wing with all veins and margin (except r_1 to wing base) setose. Hind wing length: 3·6 mm; hind wing width: 1·1 mm. Epiproct simple, very lightly sclerotised, setose. Paraprocts with large, almost circular trichobothrial field, otherwise lightly sclerotised and setose; one large, exceptionally long seta arises just posterior to trichobothrial field. Hypandrium simple, setose, lightly sclerotised medially, a little more heavily sclerotised and setose laterally. Phallosome (fig. 6).

Material Examined. New Guinea: 1 ♀ (holotype), Baiyer River Sanctuary, August 28, 1970 (C. N. Smithers and I. W. B. Thornton); 1 ♀, 1 ♂, Baiyer River, NE., Western Highlands, 1150 m, October 18, 1958 (J. L. Gressitt).

Holotype in Australian Museum, Sydney (AM); allotype and paratype in Bishop Museum, Hawaii (BPBM).

Discussion. *Taeniostigma baiyerensis* and *T. phaeostigma* Smithers and Thornton are the only two species from New Guinea with the characteristic head and thoracic pattern in which the top of the head is pale and the anterior part of the pterothoracic dorsum is dark and sharply demarcated from the posterior paler part at the level of the fore wing bases. This pattern is quite distinctive.



Figs 1–6. *Taeniostigma baiyerensis* sp. n. 1. ♀, forewing. 2. ♀, hindwing. 3. ♀, lacinia. 4. ♀, gonapophyses. 5. ♀, subgenital plate. 6. ♂, phallosome.

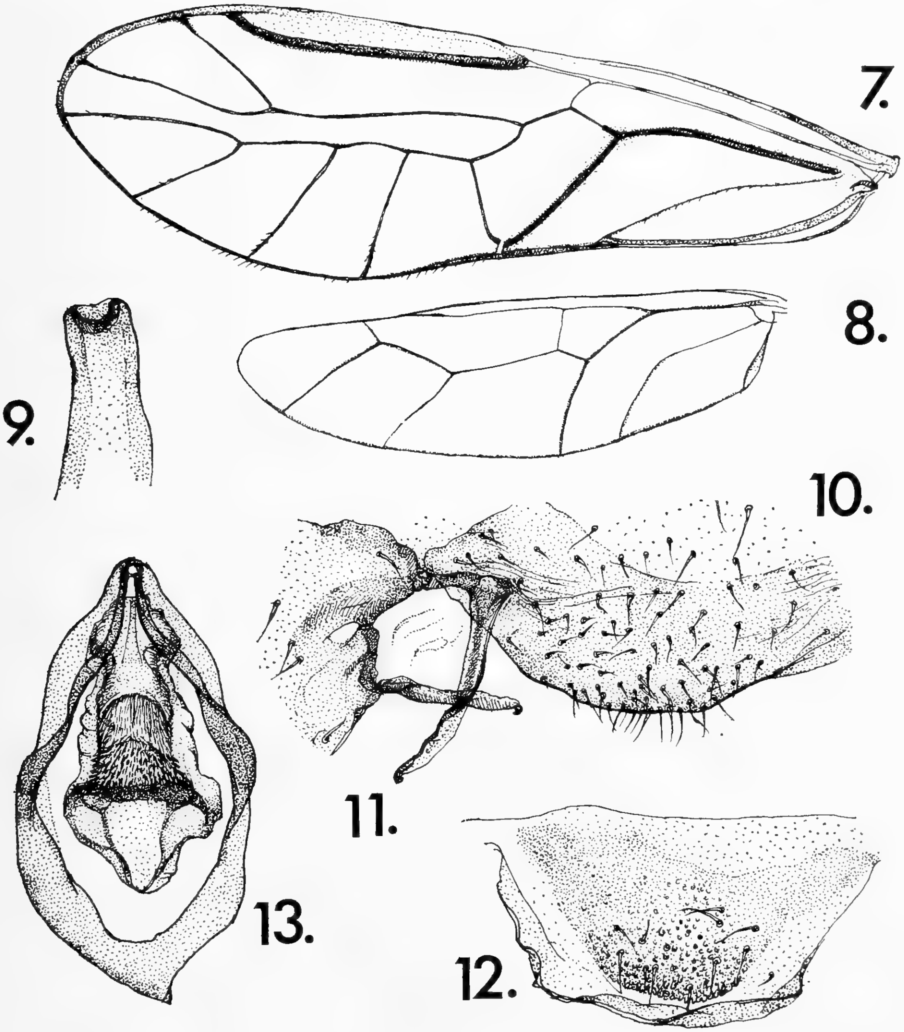
In *T. baiyerensis* the posterior part of the pterostigma is narrowly dark whereas in *T. phaeostigma* there is a strong dark band running along r_1.

Taeniostigma nigricornis sp. n.

Figs 7–13

FEMALE

Coloration (in alcohol). Head and body entirely pale brownish yellow except for very dark flagellar segments, black eyes, small black ocellar tubercle and brown distal tarsal segments. Fore wings (fig. 7), hyaline, veins pale except for dark brown $m + cu_1$, and cu_1 before areola postica; hind margin of pterostigma with narrow brown band. Hind wing (fig. 8).



Figs 7–13. *Taeniostigma nigricornis* sp. n. 7. ♀, forewing. 8. ♀, hindwing. 9. ♀, lacinia. 10. ♀, subgenital plate. 11. ♀, gonapophyses. 12. ♂, epiproct. 13. ♂, phallosome.

Morphology. Length of body: 5·0 mm. Length of flagellar segments: f_1 : 1·64 mm; f_2 : 1·20 mm. Eyes small. IO/D : 2·1; PO : 0·75. Ocelli small on a small tubercle. Lacinia (fig. 9). Measurements of hind leg: F : 1·48 mm; T : 2·2 mm; t_1 : 0·68 mm; t_2 : 0·20 mm; rt : 3·4 : 1; ct : 28, 0.

Fore wing length: 6·0 mm; fore wing width: 2·0 mm. Vein r_1 diverging very slightly from costal margin of wing where it forms the hind border of the pterostigma; $rs + m$ fusion fairly long; cu_{1a} fused with m for a fairly long length, that is, apex of areola postica broad. Free section of m between $rs + m$ confluence and areola postica 1·3 times $rs + m$. Veins (including cu_2) and margin setose except for margin from nodulus to wing base. Setae on cu_2 up to 0·090 mm. Hind wing length: 4·0 mm; hind wing width: 1·2 mm. Epiproct simple. Subgenital plate (fig. 10) setose. Gonapophyses (fig. 11, distorted in preparation).

MALE

Coloration (in alcohol). As in female.

Morphology. Length of body: 4·0 mm. Length of antennal segments: f_1 : 1·38 mm; f_2 : 0·84 mm. Eyes larger than in females. IO/D : 1·0; PO : 0·93. Measurements of hind leg: F : 1·2 mm; T : 2·00 mm; t_1 : 0·64 mm; t_2 : 0·20 mm; rt : 3·2 : 1; ct : 25, 0. Fore wing length: 4·7 mm; fore wing width: 1·6 mm. Venation and setae as in female. Free section of m between $rs + m$ confluence and areola postica 1·5 times $rs + m$. Setae on cu_2 up to 0·098 mm. Hind wing length: 3·3 mm; hind wing width: 0·9 mm. Epiproct (fig. 12) with seven symmetrically arranged setae in a field of papillae. Paraproct with large circular trichobothrial field and papillate area as usual in males of the genus. Phallosome (fig. 13).

Material Examined. NEW GUINEA: 1 ♀ (holotype), 1 ♂ (allotype), Wau, September 5, 1970 (C. N. Smithers and I. W. B. Thornton); 1 ♀, Kassem Pass, September 1, 1970 (C. N. Smithers and I. W. B. Thornton); 1 ♀, Wau, October 5, 1962 (J. Sedlacek).

Holotype, allotype and paratype in the Australian Museum, Sydney; paratype in Bishop Museum, Hawaii.

Discussion. This is the only species of *Taeniostigma* with an entirely pale brownish yellow body, without any darkening of the antedorsum and lateral lobes of the thorax; the antennae, however, have very dark, almost black, flagellar segments which contrast strongly with the body colour.

Taeniostigma sibilensis sp. n.

Figs 14–18

FEMALE

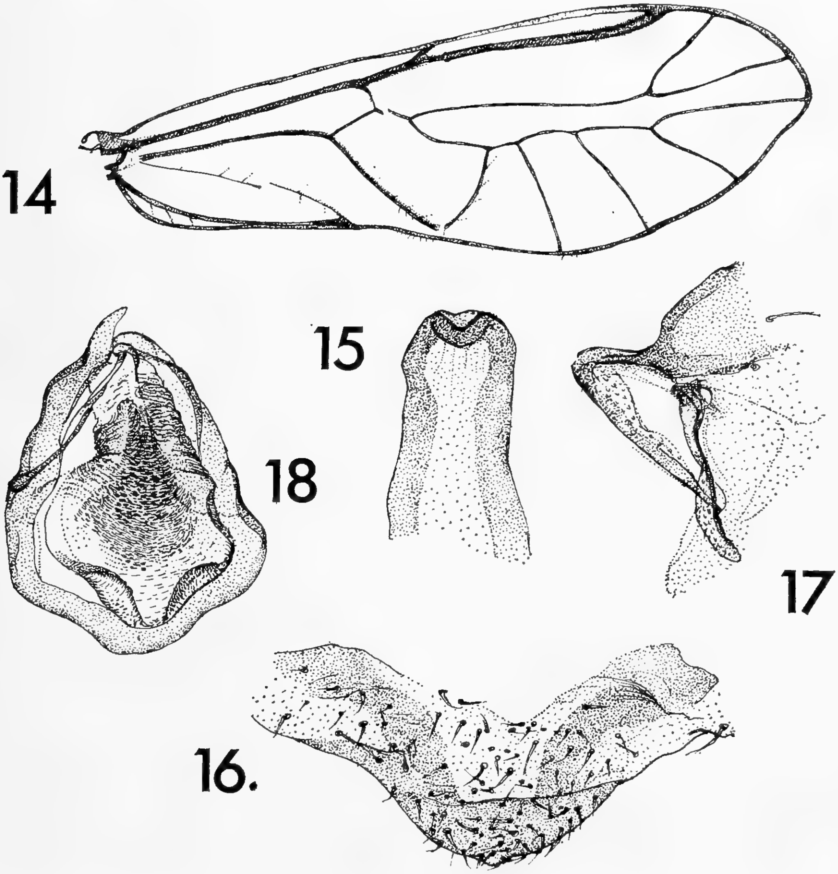
Coloration (in alcohol). Head dark brown with a paler spot on each epicranial plate and pale between ocellar tubercle and antenna base. Labrum and mouthparts pale brown. Antenna with scape, pedicel and first flagellar segment very dark, almost black; remainder of flagellum dark brown. Eyes black. Ocellar tubercle black. Maxillary palp pale brown. Antedorsum and lateral lobes of mesothorax dark brown with at most a trace of a median pale line on antedorsum. Femora pale with dark distal fifth; tibiae pale, dark at each end; tarsi brown. Wings hyaline. In fore wings (fig. 14) pterostigma with a narrow dark brown band along r_1. Veins brown.

Morphology. Length of body: 5·0 mm. Median epicranial suture very distinct. Other features as in *T. baiyerensis*. Eyes moderately large. IO/D : 2·0; PO : 0·83. Ocelli of almost equal size. Lacinia (fig. 15). Measurements of hind leg: F : 1·2 mm; T : 1·92 mm; t_1 : 0·60 mm; t_2 : 0·20 mm;

rt : 3 : 1; ct : 21, 1. Fore wing length: 5·2 mm; fore wing width: 1·8 mm. Veins $m + cu$ and cu_1 beyond separation from m only a little thickened. Free section of m between $m + cu_{1a}$ and $rs + m$ about 1·8 times as long as $rs + m$. Areola postica with fairly narrow apex. Radial fork opposite origin of m_2. Setae on cu_2 up to 0·140 mm. Paraproct with double cone on hind margin very well developed with a small adjacent seta; ventral to the cone is a large marginal seta. Trichobothrial field large, rosette bases of setae small and not touching each other. Subgenital plate (fig. 16). Gonapophyses (fig. 17).

MALE

Coloration (in alcohol). As in female but dark posterior margin to pterostigma less conspicuous.



Figs 14–18. *Taeniostigma sibilensis* sp. n. 14. ♀, forewing. 15. ♀, lacinia. 16. ♀, subgenital plate. 17. ♀, gonapophyses. 18. ♂, phallosome.

Morphology. Length of body: 4·0 mm. Lengths of flagellar segments: f_1 : 1·28 mm; f_2 : 1·00 mm. Eyes large than in female. IO/D : 1·5; PO : 1·0. First flagellar segment slightly curved near base. Measurements of hind leg: F : 1·28 mm; T : 2·08 mm; t_1 : 0·64 mm; t_2 : 0·20 mm; rt : 3·2 : 1; ct : 25, 0. Fore wing length: 5·7 mm; fore wing width: 1·9 mm. Free section of m between $rs + m$ and areola postica 1·6 times as long as $rs + m$. Apex of areola postica a little broader than in female. Setae on cu_2 up to 0·084 mm. Hind wing length: 3·8 mm; hind wing width: 1·2 mm. Epiproct with semicircular hind margin; sparsely setose with a large field of small papillae. Paraproct with large trichobothrial field. Marginal double cone well developed, large papillar area in distal half of paraproct. Hypandrium simple. Phallosome (fig. 18).

Material Examined. WEST IRIAN: 1 ♀ (holotype), Star Mountains, Sibil Valley, 1,245 m; October 18 to November 8, 1961 (S. and L. Quate); 1 ♀, 1 ♂, Wisselmeren, 1,700 m, Waghete, Tigi Lake, August 17, 1955 (J. L. Gressitt). NEW GUINEA: 1 ♂ (allotype), Daulo Pass, 2,400 m, June 15, 1955 (J. L. Gressitt); 1 ♂ Kubor Range, 2,950 m, May 23, 1961 (J. L. Gressitt); 1 ♂, Mount Wilhelm, 3,000 m, July 4, 1955 (J. L. Gressitt).

Holotype, allotype and paratypes in Bishop Museum.

Discussion. *Taeniostigma sibilensis* differs from *T. phaeostigma, T. baiyerensis, T. nigricornis* and *T. perkinsi* Banks in having a dark head with a paler area on each epicranial plate. *Taeniostigma iriana* Smithers and Thornton has a dark epicranium with a pale frons and a pale area behind the dark ocellar tubercle.

Taeniostigma phaeostigma sp. n.

Figs 19–22

FEMALE

Coloration (in alcohol). Very similar to *T. baiyerensis.* Pterostigma much more extensively marked with brown (fig. 19) but veins r and r_1 paler than $m + cu_1$.

Morphology. Length of body: 4·6 mm. General features as in *T. baiyerensis.* Lengths of flagellar segments: f_1 : 2·0 mm; f_2 : 1·32 mm. Antennae stout and strongly setose. Eyes hemispherical. IO/D : 1·8; PO : 0·73. Lacinia (fig. 20). Measurements of hind leg: F : 1·48 mm; T : 2·40 mm; t_1 : 0·68 mm; t_2 : 0·18 mm; rt : 3·8 : 1; ct : 26, 0. Fore wing length: 6·4 mm; fore wing width: 2·0 mm. Fore wing with $m + cu_1$ thickened. Free section of m between $m + cu_{1a}$ and $rs + m$ about as long as $rs + m$ or a little longer. Setae on cu_2 up to 0·112 mm. Hind wing length: 4·0 mm; hind wing width: 1·2 mm. Epiproct simple, rounded behind, setose. Paraproct as in *T. baiyerensis.* Subgenital plate (fig. 21). Gonapophyses (fig. 22).

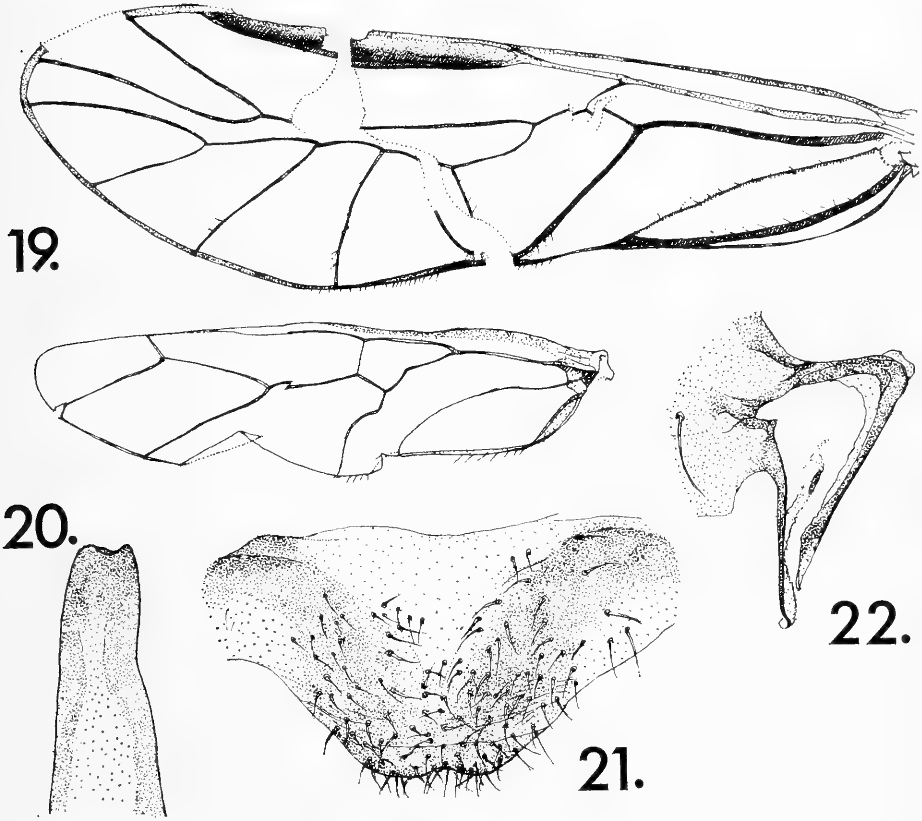
MALE

Unknown.

Material Examined. WEST IRIAN: 1 ♀ (holotype), Hollandia area, W. Sentani, Cyclops Mountain, 150–250 m, June 18, 1959 (J. L. Gressitt); 1 ♀, same locality, June 22, 1959 (T. C. Maa); 1 ♀, Waris, S. of Hollandia, 450–500 m, August 24 to 31, 1959 (T. C. Maa); 5 ♀, Bodem, 11 km S.E. of Oeberfaren, 100 m, July 7 to 17, 1959 (T. C. Maa). NEW GUINEA: 1 ♀, Finisterre Range, Saidor, Gabumi Village, June 24 to 30, 1958 (W. W. Brandt).

Holotype and paratypes in Bishop Museum.

Discussion. Taeniostigma phaeostigma differs from other New Guinea species of the genus, except *T. baiyerensis,* in having the dorsum of the pterothorax sharply demarcated into a dark brown anterior part and a paler posterior part, with the top of the head pale. From *T. baiyerensis* it differs in having a well developed dark band in the pterostigma along r_1.



Figs 19–22. *Taeniostigma phaeostigma* sp. n. 19. ♀, fore and hindwing. 20. ♀, lacinia. 21. ♀, subgenital plate. 22. ♀, gonapophyses.

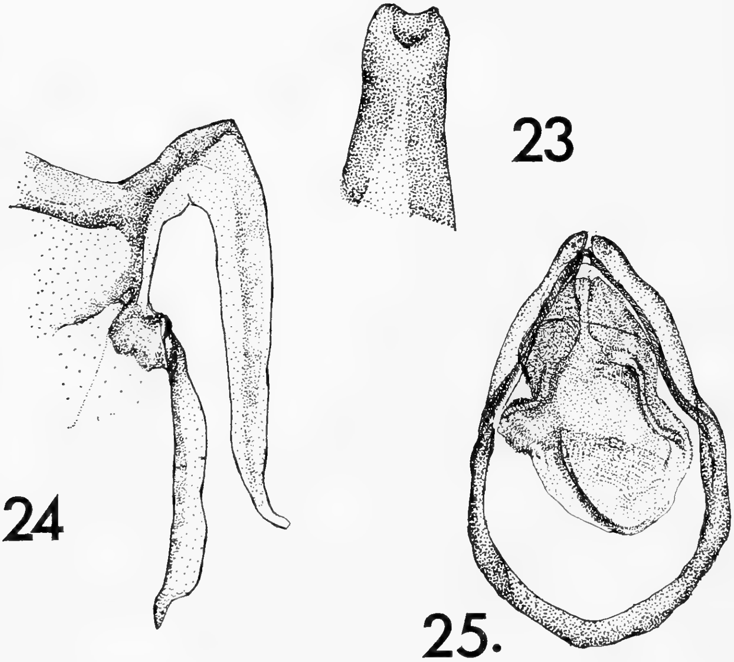
Taeniostigma iriana sp. n.

Figs 23–25

FEMALE

Coloration (in alcohol). Head dark brown, with a paler frons and a paler area behind the dark ocellar tubercle. Genae posteriorly pale. Labrum pale brown. Antennae very dark brown. Eyes black. Maxillary palps pale with distal half of fourth segment brown. Antedorsum and lateral lobes of mesothorax dark brown, sutures and areas adjacent to them very pale; scutellum pale. Femora pale, a little darker towards distal end. Tibiae pale brown, tarsi brown. Fore and hind wings hyaline; veins pale; r_1 well curved and bordered with brown. Abdomen pale except for the brown epiproct and paraprocts.

Morphology. Length of body: 4·0 mm. Median epicranial suture distinct. Lengths of flagellar segments: f_1 : 1·36 mm; f_2 : 1·00 mm. Eyes small. IO/D : 2·1; PO : 0·63. Lacinia (fig. 23). Measurements of hind leg: F : 1·28 mm; T : 1·96 mm; t_1 : 0·64 mm; t_2 : 0·2 mm; rt : 3·2 : 1; ct : 24, 0. Fore wing length: 5·4 mm; fore wing width: 2·0 mm. Fore wings broad, apex broadly rounded. Vein r_1 (hind margin of pterostigma) diverging slightly from costal margin before distinctly curving to meet costa; the pterostigma is, therefore, very slightly broadened in distal half. Free section of *m* between $rs + m$ confluence and $m + cu_{1a}$ confluence 1·5 times as long as $rs + m$. Areola postica tall, $m + cu_{1a}$ fairly short. All veins and margin (except hind margin from nodulus to wing base) setose. Setae on cu_2 up to 0·14 mm. Hind wing length: 3·5 mm; hind wing width: 1·2 mm. Veins setose except for $m + r$, *r* and *rs* basad of fusion with *m*. Wing margin setose except for anterior margin basad of r_1. Epiproct semicircular, setose in distal third. Paraproct rounded, strongly setose posteriorly with a large round trichobothrial field. Posterior margin with two large setae between which lies a double cone and one small adjacent seta. Subgenital plate sparsely setose, the setae fine, hind margin almost straight. Gonapophyses (fig. 24).



Figs 23–25. *Taeniostigma iriana* sp. n. 23. ♀, lacinia. 24. ♀, gonapophyses. 25. ♂, phallosome.

MALE

Coloration (in alcohol). As in female but with only two dark spots (trichobothrial fields) at the end of the abdomen.

Morphology. Length of body: 3·1 mm. Smaller than female. Eyes large, much larger than in female. IO/D : 0·66; PO : 1·0. Measurements of hind leg: F : 1·08 mm; T : 1·44 mm; t_1 : 0·48 mm; t_2 : 0·18 mm;

rt : 2·7 : 1; ct : 14, 0. Fore wing length: 4·9 mm; fore wing width: 1·8 mm. Fore wings similar to those of female. Free section of *m* between $rs + m$ confluence and $m + cu_{1a}$ confluence 1·7 times as long as $rs + m$. Setae as in female. Hind wing length: 3·2 mm; hind wing width: 1·0 mm. Epiproct simple, sparsely setose. Hypandrium simple, setose except for a small median area near hind margin. Phallosome (fig. 25).

Material Examined. WEST IRIAN: 4 ♀ (including holotype), 2 ♂ (including allotype), Waris, S. of Hollandia, 450–500 m, July 27 to 30, 1959 (T. C. Maa); 2 ♀, 1 ♂, Vogelkop, Kebar Valley, W. of Manokwari, 550 m, May 4 to 31, 1962 (S. and L. Quate).

Holotype, allotype and paratype in Bishop Museum.

Discussion. *Taeniostigma iriana* differs from *T. baiyerensis, T. phaeostigma, T. perkinsi* and *T. nigricornis* in having a dark epicranium. *T. sibilensis* has a pale central area on each epicranial plate.

Taeniostigma perkinsi Banks 1918

Material Examined. PAPUA: 1 ♂, Doa Estate, 80 km from Port Morseby, July 22, 1962; 1 ♂, same locality, September 9, 1962 (R. Straatman). (BPBM). NEW GUINEA: 1 ♀, Mount Missim, 7°15′S, 146°48′E, 1,600 m, May 27, 1966 (J. L. Gressitt) (BPBM); 2 ♀, Gauka, S. of Minj, August 27, 1970 (C. N. Smithers and I. W. B. Thornton) (AM); 1 ♀, Kamang, near Minj, 1,840 m, May 21, 1966 (J. L. Gressitt) (BPBM); 1 ♂, 2 ♀, Nondugl, July 8-9, 1955 (J. L. Gressitt) (BPBM); 1 ♂, ex *Araucaria cunninghamii,* Wau, September 5, 1970; 1 ♀, McAdam Park, Wau, September 5, 1970 (C. N. Smithers and I. W. B. Thornton) (AM); 1 ♀, Wau, May 20, 1965; 1 ♀, Wau, October 13, 1965; 1 ♀, Wau, September 10?; 1 ♀, Wau, no date (J. and M. Sedlacek) (BPBM); 1 ♀, Sinofi, 1,590 m, 30 km S. of Kainantu, September 30, 1959 (T. C. Maa) (BPBM).

This species has previously been recorded from north-eastern Australia (Smithers, 1974*a*).

Stenopsocus Hagen 1866

(Type species: *Psocus immaculatus* Stephens 1836)

Stenopsocus albipileus Smithers (1974)

Material Examined. NEW GUINEA: 1 ♂, Laiagam Village, near Tambul, August 29, 1970; 1 ♂, Paigona, Tomba, August 30, 1970; 1 ♀, Kundiawa, August 24, 1970; 1 ♀, Jimi Highway, Sepik Wangi Divide, 2,200 m, August 30, 1970 (C. N. Smithers and I. W. B. Thornton) (AM); 1 ♂, Upper Chimbu Valley, 2,200 m, July 5, 1955; 1 ♀, Nondugl, 1,600 m, July 9, 1955; 1 ♀, Ahl Valley, Nondugl, 1,750 m, July 8, 1955; 1 ♀, Mount Missim, 600 m, April 28, 1966; 2 ♀, Mount Otto, 2,200 m, June 21-23, 1955; 2 ♀, Nimbu, Upper Chimbu Valley, July 5, 1955 (L. G. Gressitt) (BPBM). PAPUA: 1 ♂, Bisianumu, 150 m, near Port Moresby, June 19, 1957 (D. E. Hardy) (BPBM). WEST IRIAN: 1 ♂, Central Mountains, Archbold Lake, 760 m, November 26 to December 3, 1961 (L. W. Quate) (BPBM).

This species has previously been recorded from north-eastern Australia (Smithers, 1974*b*).

ACKNOWLEDGEMENTS

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————, 1974*b*.—A new Australian species of *Stenopsocus* (Psocoptera: Stenopsocidae). *Aust. Ent. Mag.*, 2: 21-23.

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MORPHOLOGY AND DISTRIBUTION OF *BASSIA BIRCHII* (F. MUELL.) F. MUELL.

B. A. Auld* and P. M. Martin†

(Plate XVII)

[Accepted for publication 23rd July 1975]

Synopsis

Bassia birchii, an unpalatable native shrub, is widespread in semi-arid eastern Australia. Its early history and errors in previous descriptions are discussed. A new description of the species is presented and a spineless form of the species is also noted; some other variations in morphology are attributed to insect attack. Apart from these variations no consistent differences were found in specimens grown from seeds collected from a wide area. Specimens of the typical form from two widely separated areas in New South Wales and the spineless form all had the somatic chromosome number $2n = 18$ and there was no evidence of polysomaty. The range of the plant in eastern Australia is described and the occurrence of serious infestations in New South Wales is surveyed. Distribution is discussed in relation to seasonality of rainfall, winter temperatures and soil type.

INTRODUCTION

Bassia birchii (F. Muell.) F. Muell. is a widespread native shrub which is of considerable economic importance to the sheep grazing industry in semi-arid eastern Australia. It is not usually eaten by stock and in some situations it is so prolific as to exclude useful herbs and grasses. In spite of its importance the species has not been adequately described and the history of its spread and present distribution is poorly documented.

The aim of the present paper was to write a new description of the species, to record its present geographic range and to survey areas of serious infestation in New South Wales. Studies of the ecology and weed status of *B. birchii* are to be reported in future publications.

EARLY HISTORY OF THE SPECIES

Mueller (1874, p. 163) first described the species as *Anisacantha birchii* F. Muell. but in 1882 (Mueller, 1882, p. 30) he re-established the genus *Bassia* All. uniting under it nine genera including *Anisacantha* R. Br. Domin (1921) transferred the type species of *Anisacantha* (*A. divaricata* R. Br.) to *Sclerolaena* R. Br. and placed *A. birchii* in the subgenus *Anisacantha* under the genus *Sclerolaena* (*cf.* Ulbrich, 1934). Anderson revised the Australian species of the genus *Bassia* in 1923 and provided a new description of *B. birchii.*

The species was first collected in 1874 at Bowen Downs (22°28′S, 145°00′E) in Queensland. Bowen Downs was a large station of over 3,500 km^2 and at the time was wholly owned by the Scottish Australian Company Limited. On the station, a township of nearly 60 people was a focal point for a very wide area and

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an important stage on the route to the Gulf of Carpentaria (Macmillan, 1963). The next record of the species is from Morven in Queensland in 1890. There are six other records of the plant in Queensland before it was first recorded in New South Wales in 1916 on a property north-west of Wee Waa. It may be more than coincidental that the Scottish Australian Company had " runs " in this area, to which it moved sheep on at least one occasion (1868) from Bowen Downs (Macmillan, 1963). Early specimens of " *B. birchii* " in South Australia which were recorded by Black (1915, 1916) from Glen Ferdinand in 1915 and Minnipa in 1916 appear to have been later determined as another species by Black or to have been lost ; from Black's descriptions the former appears likely, and it seems probable that the specimens were *B. cornishiana* F. Muell. A report of *B. birchii* by Tate (1896) in the record of the Horn scientific expedition to central Australia is also suspect. Tate observed the plant at Illipa at the base of the Belt Range, but there is no herbarium record of *B. birchii* from that locality.

Anderson (1923) cites specimens in the New South Wales National Herbarium, representing six localities in New South Wales : Wee Waa (1916) ; Walgett (1918) ; Narromine (1920) ; Parkes (1921) ; Gunnedah (1922) and Wingham (?), (dates from herbarium specimen sheets, N.S.W. National Herbarium). The discovery of the plant at Wingham on the north coast of New South Wales seems improbable in view of later records. Inspection of all *B. birchii* material at N.S.W. National Herbarium revealed that all the specimens collected prior to 1923 had been noted by Anderson, with one exception. There is one (NSW 79069) from Wingen, a town on the New England Highway between Murrurundi and Scone, dated 1921. There is no specimen from Wingham. It appears likely that the two place names were confused in the preparation and printing of Anderson's paper.

Whether the plant is native to New South Wales and Queensland or to Queensland alone is uncertain. The first record of the plant is nearly 160 km north of any area where it is now common. Although there are earlier records of related species in New South Wales, the early records of *B. birchii* are not sufficiently comprehensive to establish its origin with confidence. Anderson (1923) did not discuss the origin of the plant. White (1925) was of the opinion that it was native to both States and Blake (1935) believed that its exact geographic origin could not be determined, but neither author discussed relevant evidence.

There is some evidence to suggest that *B. birchii* was a problem weed in Queensland before it became one in New South Wales. A specimen of the species from Wingen, New South Wales (NSW 79069), sent from the Scone Shire Clerk to the Government Botanist in 1921, contains the following note :

> " Inspector Higgins (Inspector of Noxious Plants) says the plant was known twenty years ago as ' Galvanised Roly Poly ' and is a bad one on Goodooga, St. George and Castlereagh country and takes possession of any rich lands if allowed to grow ".

Furthermore, a letter held in the Queensland Herbarium (BRI) dated 11 January 1918, from the Government Botanist to the Shire Clerk at Miles, Queensland, indicates that it was very common on the " [Darling] Downs and western country ".

Yet there is a distinct possibility that the plant had been present in New South Wales perhaps in small quantities prior to 1916 but had been confused with other *Bassia* species. Anderson (1923) in his revision of the genus stated that " this is probably the most unsatisfactorily defined species of the genus ". He noted also that the type specimen " came very close to what I had regarded as a very robust form of *B. quinquecuspis* var. *villosa* ". He also stated that the species *B. quinquecuspis* " is one of the most variable within the genus ". Anderson also confused *B. cornishiana* with *B. birchii*. He stated that from all the material labelled as *B. birchii* at the Melbourne Herbarium three distinct species were present : (i) *Bassia birchii* (represented by the type specimen only) (ii) *Bassia convexula* and (iii) *B. cornishiana.*

Mueller (1890) had suggested that *B. cornishiana* be made a variety of *B. birchii.* The plate labelled *B. birchii* in his *Iconography of Australian salsolaceous plants* (1891, Pl. 72) depicts both *B. birchii* and *B. cornishiana.* Anderson (1923) recognised the shorter branch in the plate as *B. cornishiana*, probably by the six spines on the fruits (*cf.* five for *B. birchii*). However Anderson considered that figs 7–10 (Mueller, 1891, Pl. 72), which are depicted below the branch of *B. cornishiana*, represented the type of *B. birchii.* It will be shown below that this latter judgement was itself in error and further confused the situation.

Morphology

The morphology of the mature fruiting perianth has been used as a key distinguishing character in the genus (Anderson, 1923 ; Ising, 1964) but it has not been adequately described, nor have the flowers been described.

Flowers in *B. birchii* are solitary and axillary. Floral development is protogynous. The flowers are four merous with the spines alternate with perianth lobes. The single style is short and divides into three white bristle-like stigmata (Pl. XVIIB), or occasionally into two or two with one branched, especially in immature plants. There are four stamens which have white translucent filaments and yellow versatile anthers.

The authors have used the term " mouth " to describe the opening of the perianth cavity and " throat " to describe the constricted area immediately below it (Pl. XVIIC). In young plants and sometimes in unhealthy specimens " juvenile " flowers are produced in which stamens remain in a partially developed form within the fruiting perianth (Pl. XVIIA). In some cases in the youngest flowers the perianth remains closed over the tube and no mouth or throat is developed, the differentiation of the style and ovary is limited and no anthers or spines form. In normal mature plants stigmata emerge several days before the anthers are visible above the hairs surrounding the mouth. The anthers remain immediately above the mouth for approximately 24 hours. The filaments then elongate in a few hours and the anthers burst (Pl. XVIIB) with at least one anther usually coming into direct contact with a stigma. Pollination is thus autogamous but the plant is not an obligate self pollinator. Successful cross pollination of a number of flowers was made and normal embryos and seedlings were produced. There are no nectaries and no insect visitors to flowers were observed. It is quite common for one anther (sometimes two) to become caught in the throat of the tube. Those anthers usually burst and spread pollen on the style and lower parts of the stigmata.

The shape of the tube of the fruiting perianth is rather irregular and variable. It is broadly tubular to ovoid or turbinate and shortly convex on its summit at the mouth of the tube (cf. *B. cornishiana* in which the summit is flat). The base is obliquely attached and the fruit is difficult to remove from the stem.

Ising (1964) in his key to the genus *Bassia* uses the orientation of spines as a distinguishing character. The orientation of spines on *B. birchii* is described as " ± horizontal ", but in fact they are usually in two distinct planes. The fruiting perianth has five divergent acicular spines, two of which occur close together (Anderson's " bifid " spine), adjacent and obliquely parallel to the stem (Pl. XVIIC). The other three spines radiate divergently, obliquely perpendicular to the stem, arising from an equatorial position on the fruiting perianth (in *B. cornishiana* the spines are all approximately in the same plane). The three spines obliquely perpendicular to the stem in *B. birchii* are usually longer than the other two, although one of the three is often reduced (this may vary on adjacent fruits on the same stem). The developing perianth spines have a large number of hairs which senesce as the spines become woody. The base of the hairs (Pl. XVIID) may harden and form a barb which is usually reflexed. The hardening of the base of the hairs appears to be very variable and may be influenced by environmental conditions at the time at which the hairs senesce. Such barbs would considerably increase the tenacity of the propagules in wool and aid in dispersal.

In his key to the genus, Anderson (1923) uses the position of the seed in the fruiting perianth as a principal distinguishing feature and erroneously states that in *B. birchii* it is " usually obliquely horizontal ". Bisalputra (1961) makes the same mistake. Plate XVIIC shows a mature fruiting perianth with one side cut away to reveal the seed, placed almost parallel to the stem and thus lying vertical to obliquely vertical. This is also true for all the specimens from New South Wales which Anderson cited. Moreover, it is true for the seeds and seed cavities in the type, represented by one fruit at Sydney (NSW 61508) and by the Melbourne specimen (C. W. Birch MEL holotype). The source of Anderson's error is probably twofold. First, he regarded figs 7–10 of Mueller (1891, Pl. 72) as representing *B. birchii*. These figures show a horizontally placed seed but they represent *B. cornishiana*. Figure 7 of Mueller's Plate 72 is a median vertical section through a fruiting perianth of *B. cornishiana* which shows cotyledons of the embryo to the left and the radicle to the right with perisperm (see Hindmarsh (1966)) between. Fig. 10 of the same plate is a longitudinal section of the same seed. A median vertical section of a fruiting perianth of *B. birchii* bisects the embryo symmetrically. Secondly, a number of sections of fruiting perianths on the type specimen have been made by previous workers which are not at right angles to, or parallel to, the stem. It would have been difficult, in these cases, to determine the orientation of the seed or seed cavity, particularly as many fruits are squashed. Mueller's original description (1874) did not refer to the position of the seed. Bailey (1901, pp. 1258–60) noted that the seed was vertical in the genus *Anisacantha*, following Bentham's (1870, p. 198) description in *Flora Australiensis*.

Using Anderson's key, *B. birchii* is readily confused with *B. quinquecuspis* ; Anderson noted that *B. birchii* " resembles very closely a robust form of *B. quinquecuspis* var. *villosa* Benth." He also noted that *B. quinquecuspis* was " probably the most common species of *Bassia* in New South Wales " and " one of the most variable within the genus ". Its seed position may be " truly vertical, oblique, or almost horizontal, but the oblique condition is most common ". Although Anderson described the leaves of *B. quinquecuspis* as linear-lanceolate (cf. obovate to broadly lanceolate for *B. birchii*), the species includes the variety *semiglabra* (which was not described until 1964 by Ising) which has obovate leaves. *B. birchii* differs from *B. quinquecuspis* var. *semiglabra* most conspicuously in that its leaves are tomentose on both surfaces, whereas the latter has leaves with a glabrous adaxial surface.

Anderson (1923) has noted that the type differs slightly from most other material referred to *B. birchii.* The type specimen was collected from the northern margin of the range of the species. It is thus not surprising that it displays characteristics of many young and physiologically weak plants observed by one author (B.A.A.) in the field and in specimens grown from seed in the garden in Sydney. These plants generally differ from most *B. birchii* in having more linear shaped leaves, reduced development of fruits, longer internodes, and narrower stems. An examination of the type showed that it has been squashed flat and many of the fruits are now compressed. Evidence of the immaturity of the plant is found in the juvenile flower remnants at lower nodes. Most flowers have failed to develop seeds, fruiting perianths are small and leaves are smaller and more linear than those of a mature, healthy plant.

Variation within the Species

Some apparent morphological differences between specimens can be attributed to insect attack. Symptoms similar to the well-known " witches broom " condition in lucerne, *Medicago sativa* L., attributed to the eriophyid mite *Aceria medicaginis* Keifer appear on some *B. birchii* plants over most of its range. They appear to be the result of attack by another eriophyid bud mite, *Aculops bassiae* Keifer. On affected plants internode lengths are short, leaves are small and linear and flowers remain immature or are absent.

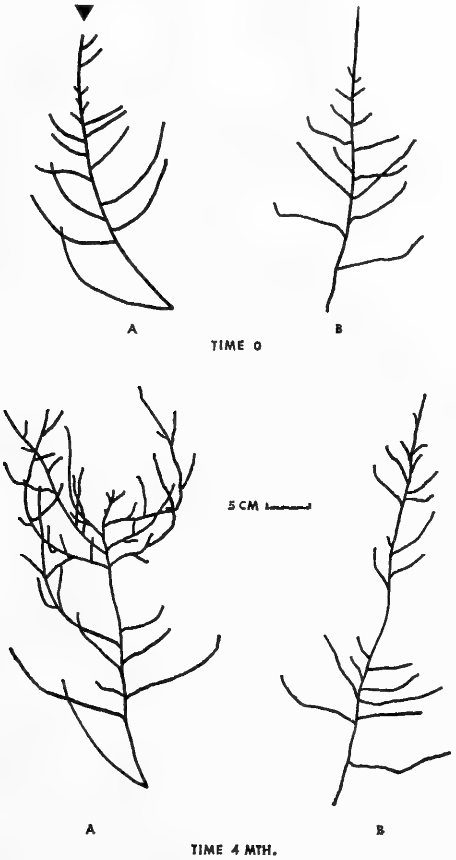

Fig. 1. Gross morphology of *Bassia birchii* ; shoots only. The effect of removal of the apical one cm of the leading shoot of a plant (A) compared with an untreated plant (B) after four months growth in a glasshouse. ▼ indicates point of removal of shoot tip. Scale is for length of shoots only.

Shoot tips are also often attacked by an undescribed tunnelling lepidopterous larva (*Mixodetis* sp. (Cosmopterigidae)). The tips become structurally weakened and eventually fall off. The effect of artificial pruning is quite dramatic ; the removal of apical dominance stimulates branching and the resulting plant has quite a different shape from that of an untreated plant. (Figure 1 compares the effect of removal of the apical one cm of shoot from the leading shoot of one plant with an untreated matched plant after four months growth in a glasshouse.) It is assumed that the effect of the larvae is similar to this artificial pruning and that differential attack by the insect may partly account for differences in shape of mature bushes. Larvae were not found on plants at the southern extreme of the range of *B. birchii* on the Riverine plain, and this may be the reason for a difference in shape between mature plants in that region and those from northern areas.

A spineless form of *B. birchii* was collected near Ivanhoe by Watson in 1970 (NSW 120365). It differs from normal *B. birchii* only in a reduced development of the perianth. In the field the spineless form is restricted to an area of approximately four hectares and occurs with normal spined plants. Seed from the spineless plants produced fertile spineless plants.

Apart from these variations in morphology, there did not appear to be any consistent differences in *B. birchii* over its range of occurrence in the field. Plants were raised in a glasshouse from seed collected over a wide area of the species' range and no consistent differences between plants from different sites were observed.

NEW DESCRIPTION OF BASSIA BIRCHII (F. MUELL.) F. MUELL.

A densely branched robust perennial undershrub, up to one m high, stems clothed in a white tomentum. Leaves alternate obovate to oblanceolate, shortly petiolate, woolly on both surfaces ; generally, 4–7 mm wide and 12–18 mm long. Flowers solitary, axillary, sessile, hermaphrodite. Perianth hypogynous, turbinate and shortly convex on its woolly summit, the narrow opening (mouth) of the throat bordered by four irregular lobes, densely tomentose, hard when in fruit, obliquely attached at the base, with five acicular spines (± reflexed barbs), alternate with perianth lobes, two proximal at the summit of similar length (1–3 mm), adjacent to and generally obliquely parallel to the stem and three longer radiating divergently from an equatorial position obliquely perpendicular to the stem, either all three approximately the same length (8–15 mm) or one reduced (2–3 mm long). Stamens four, filaments flattened translucent, anthers versatile yellow. Style short, persistent, branching into usually three setaceous white stigmatic branches. Ovary superior monocarpellary and unilocular, ovule campylotropus. Fruit enclosed in the perianth, compressed, ovoid, brown, vertical to obliquely vertical. Embryo annular, green ; radicle and cotyledons erect, perisperm white, containing starch ; pericarp and testa membraneous.

Differs from *B. cornishiana* in orientation of spines, position of seed, shape of perianth, and usually in number of spines. *B. cornishiana* usually has six spines but may have five.

Differs from *B. convexula* in leaf shape and size and orientation of spines.

Differs from *B. quinquecuspis* in leaf shape, except for some specimens of var. *semiglabra* which can be readily distinguished from *B. birchii* by their lack of hairs on the adaxial surface of the leaf and by their generally less woolly tomentum and thinner branches.

Generally, only young or weak *B. birchii* have leaves of more linear shape than usual and only these could be confused with *B. convexula* or *B. quinquecuspis*. Care must be exercised in assessing perianth shape and spine orientation from herbarium specimens, as these may become distorted in pressing.

CYTOLOGY

Introduction

Wulff (1937) found variation in the somatic number of chromosomes in root tips of several Chenopodiaceae, including three *Bassia* species. He found the normal diploid number of chromosomes in the dermatogen and plerome regions but tetraploid as well as diploid cells in the periblem region. He noted similar variation in the Australian *Atriplex* species, *A. semibaccata* R. Br. and *A. spongiosa* F. Muell. Polysomaty was first recorded in the Chenopodiaceae by

Stomps (1910). It is defined as that condition wherein one or more tissues of diploid organism contain some cells of varying degrees of polyploidy. The polyploid condition arises by double reproduction of the chromosomes and at least one mitotic division always intervenes between two successive double reproductions (Witte, 1947). Witte suggested that the length of the meristematic region may be a factor in determining the degree of polyploidy in root tips of *Atriplex*.

Methods

B. birchii material from within the largest continuous area of infestation in New South Wales at Miandetta and from a southern infestation at Hay (Fig. 3) as well as the spineless form from Ivanhoe was examined. Seedlings were raised in petri dishes at 20°C in darkness (following germination in light).

Two days after germination the amount of free water in the petri dishes was gradually decreased. Root tips were removed after four days from germination and placed in 0·05% colchicine for 90 minutes at 25°C. The material was fixed in Bradley's fixative (4 chloroform : 1 glacial acetic acid : 3 alcohol ; by volume) for 60 minutes. Root tips were then macerated in 1M HC1 at 60°C for 60 seconds. Aceto-orcein was used to stain the material on a microscope slide for 15 minutes. Tips were then gently warmed for a few seconds with a spirit burner, squashed with a coverslip and tapped. The squashes were examined by phase contrast microscopy.

Results

The chromosome number in all the material examined was $2n = 18$, which is the same as that recorded for three European *Bassia* species by Wulff (1937). The same diploid number is common throughout the family (Darlington and Wylie, 1955) and, indeed, the base number nine runs through all the European genera (Heslop-Harrison, 1953).

There was no evidence of polysomaty in *B. birchii* with or without colchicine pre-treatment. Divisions were only observed in the plerome region (in unsquashed root tips) ; the meristematic region was of very short length.

DISTRIBUTION

Introduction

Herbarium records indicate that the species is generally restricted to central western areas of New South Wales and Queensland between latitudes 21°S and 36°S and the 300 and 700 mm average annual rainfall isohyets (Fig. 2). However there are records of the species from Jamestown (1944), Yongala (1964) and Balaklava (1972) in South Australia. There are also specimens from six localities in the Northern Territory which were collected between 1955 and 1973 (Fig. 2).

The occurrence of the plant in New South Wales has been the cause of particular concern to the grazing industry and it has been proclaimed noxious in most shires in the State for over 30 years. Although the species has been the subject of a number of unpublished preliminary investigations, the areas of serious infestation have not been clearly defined. The species was also the subject of unpublished mail questionnaire surveys to State and local government officers by Dodd (1934) and by the New South Wales Department of Agriculture and the Council of Scientific and Industrial Research in 1948. Beadle (1943) also mapped the distribution of several plant species, including *B. birchii*, in western New South Wales using counties as mapping units.

The object of the present survey was to define the limits of serious infestations within New South Wales as an aid to further study of the species.

Methods

There are a number of survey techniques for the estimation of abundance of plant species. Brown (1954) reviewed several methods, but these techniques are not directly applicable to surveying one or a few species over an extensive area.

Cover, expressed as the percentage of ground occupied by the perpendicular projection of the aerial parts of the subject species, is probably the most useful measure in the present case. It is particularly suited to large scale pasture weed surveys where the subject species forms a clumped or contagious distribution. Cover is independent of sampling unit size and comparatively easily assessed visually. It directly relates to the effect of many weeds (including *B. birchii*) whose main undesirable property is their occupation of useful space, and cover can usually be regarded as an integrating measure of competitive ability.

Fig. 2. Range of *Bassia birchii*. Unbroken line indicates main range of the species ; broken line indicates areas of isolated collections.

The assessment of cover may be simplified by using discrete classes and in the case of a plant which restricts stock movement, such as *B. birchii*, the area rendered inaccessible by the presence of plants, as well as the area actually covered, can validly be included in the area recorded as " covered ". *B. birchii* occurs on land of widely differing agricultural potential, and since small areas of dense stands are characteristic of the species and occur over its entire range, more than one minimum limit of the size of serious infestations was required. Cover was divided into two classes : (i) equal to or greater than 3% (serious infestations) and (ii) less than 3% (the other areas within its range). East of the 500 mm average annual rainfall isohyet (Fig. 3) the minimum size of a serious infestation was set at 40 hectares ; west of the 500 mm isohyet the minimum size of a serious infestation was set at 80 hectares. Because of fluctuating numbers in this species it would be impractical to show each individual infestation at any particular time. A map was prepared to show, as far as could practically be determined, the limits of serious infestations over the period 1970–73.

Results

Serious infestations are concentrated in the northern semi-arid rangeland region where neither crops nor pastures are usually sown (Fig. 3). There are small areas of serious infestation on agricultural land to the north-east of Coonamble and near Gilgandra, Narrabri and Boggabilla. Serious infestations to the south near Hay were not recorded in previous unpublished surveys.

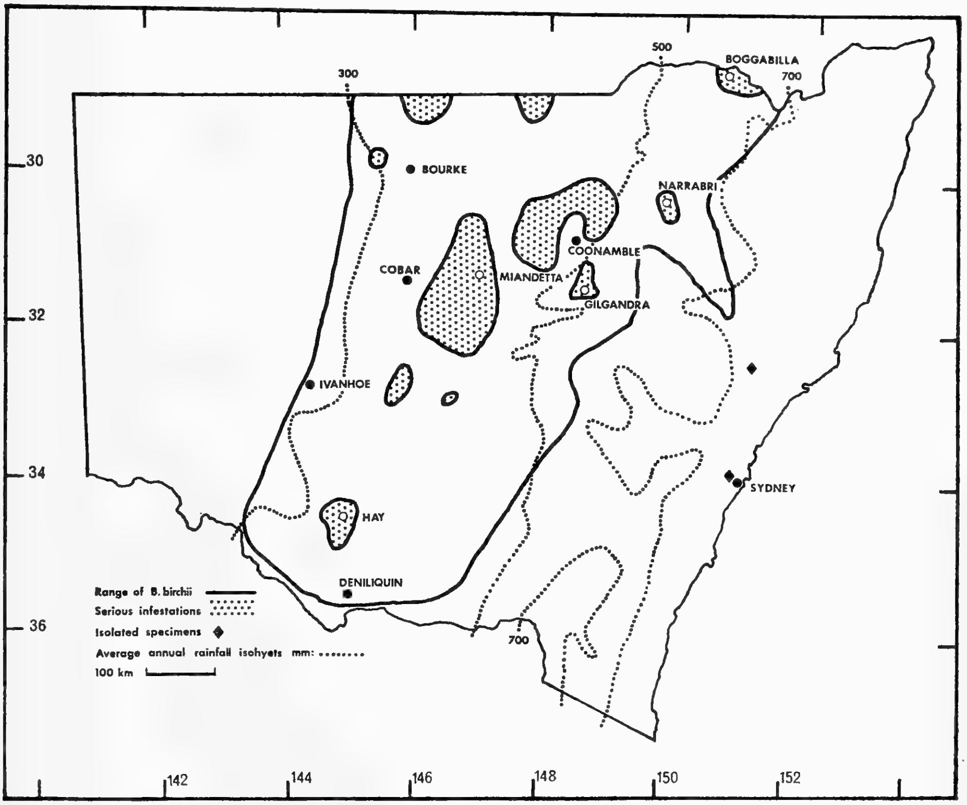

Fig. 3. *Bassia birchii* in New South Wales.

Throughout its range the species is restricted to soils of light surface texture. In northern areas it occurs chiefly on soils with gradational texture profiles: gravelly and non-gravelly neutral red earths (Gn 2.12) (Northcote, 1960) and sandy alkaline red earths (Gn 2.13), as well as on duplex texture profile soils: red brown earths (Dr 2.33) and solodised solonetz soils (Dy 5.43). In the Hay area to the south it generally occurs on the sands and loamy sands associated with prior stream courses.

Discussion

This species was first collected south of latitude 34°S in New South Wales in 1948 at Urana (35°18′S, 146°18′E). Although it was recorded as a rare plant or in small quantities in the questionnaire surveys there is no corresponding herbarium record and Beadle (1943) did not record it south of 34°S. Moreover, the species has apparently only assumed serious problem proportions in this region since the end of the drought of the mid 1960's. It appears that a gradual build up of " infection potential " took place in the period 1948–1968, which allowed the recent success of the species.

Seasonality of rainfall has probably restricted the colonisation of southern areas. Winter dominance of rainfall increases to the south in New South Wales and there is a high probability of very low rainfall in western areas during late spring, summer and early autumn (White, 1955). *Bassia birchii* has a requirement for extended period of high soil moisture conditions to establish a tap root and survive periods of moisture stress on gradational and duplex texture profile soils (Auld and Martin, unpublished data).

The requirement for an extended period of high soil moisture for establishment would also restrict westerly spread and northerly spread in Queensland into the more markedly summer dominant rainfall areas.

The faster growth rate of temperate plant species adapted to the moister environment to the east undoubtedly restricts the ability of this species to compete successfully and spread in that direction. However the range of the species extends to the foot of the tablelands areas and it is likely that low winter temperatures are the ultimate barrier to further easterly spread. Cambage (1914) has discussed the effect of the Great Dividing Range on vegetation. He stated that the Range produced three distinct climates in eastern Australia : " humid " to the east of the range, " dry " to the west, and " cold " on the range, and that the cold area acts as a barrier to intermingling of the humid and dry floras. He also noted certain gaps in the barrier effect, where western vegetation intruded into humid areas because there was no " cold " barrier. The upper Hunter region is the only such gap in northern New South Wales, and this is an area in which *B. birchii* has been collected a number of times since 1921. It has also been collected at the former Flemington stock sale yards in Sydney since 1968 where it has presumably been brought as fruits on stock from infested areas. Experimental evidence for the influence of low temperatures on distribution has been presented by Auld (1974).

The inability of the species to colonise soils of heavy surface texture may be related to an inability of *B. birchii* radicles to penetrate soils of high mechanical strength ; especially as soil strength increases with decreasing moisture content. Taylor and Burnett (1964) have demonstrated the important influence of soil strength on root development and Campbell (1972) has found large differences between species in regard to the ability of their radicles to penetrate soils of various strengths. The physiological and anatomical bases for such differences have not been investigated. *Bassia* species could be useful experimental material to investigate this phenomenon, as certain other species, including *B. quinquecuspis* var. *quinquecuspis* and *B. bicornis*, are generally restricted to soils of heavy surface texture.

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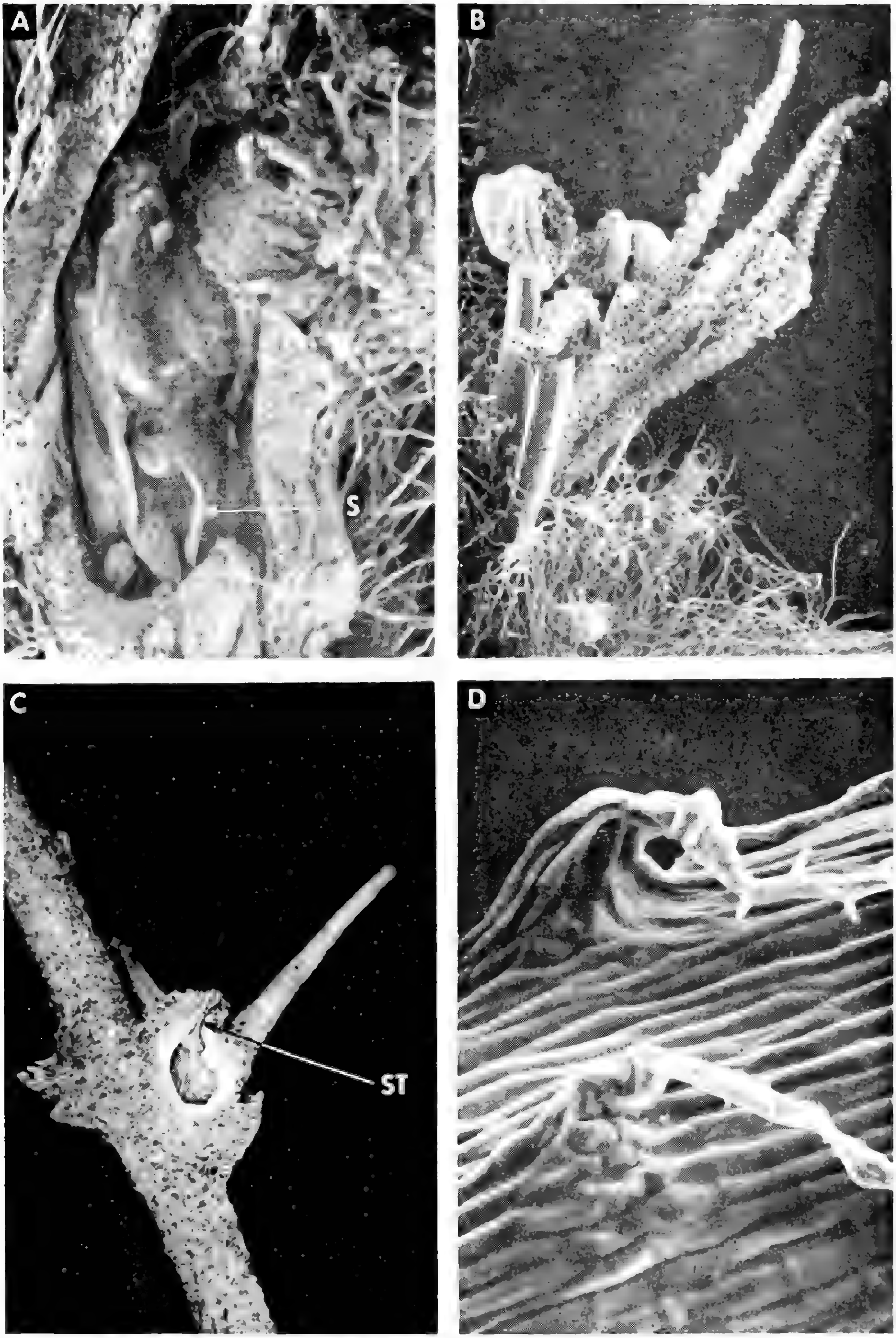
PLATE XVII



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EXPLANATION OF PLATE

PLATE XVII

Bassia birchii (F. Muell.) F. Muell. Fig. A. Juvenile flower. Perianth tube partly removed to reveal arrested development of stamen (s). Dried specimen, scanning electron micrograph. ×50. Fig. B. Normal flower. Note three stigmatic branches and four stamens. Fresh specimen, scanning electron micrograph. ×40. Fig. C. Mature fruiting perianth; one side pared away to reveal the vertical orientation of the seed. Note persistent style tissue (st) in perianth throat and orientation of spines; largest spine is one of three of similar length and orientation. ×7. Fig. D. Base of spine hairs on a young flower. Fresh specimen, scanning electron micrograph. ×1200.

APPENDIX

List of specimens of Bassia birchii *examined*

NEW SOUTH WALES. J. Mitchell : NSW 61590 : Angledool. B. A. Auld : NSW 134540 : Ashford. B. A. Auld : NSW 134552 : Collarenebri. B. A. Auld : NSW 134551 : Bingara. L. Jones : NSW 61593 : Walgett. M. R. Rupp : NSW 61591 : Wee Waa. B. A. Auld : NSW 134549 : Narrabri. S. Helms : NSW 61517 : Gunnedah. B. A. Auld : NSW 134541 : Gulargambone. B. A. Auld : NSW 134547 : Gulargambone. B. A. Auld : NSW 134545 : Gulargambone. J. C. Morrow (158) : NSW 88804 : Cobar. A. Morris : ADW 1284 : Hermidale. A Morris : NSW 61595 : Hermidale. B. A. Auld : NSW 134544 : Miandetta. B. A. Auld : NSW 134543 : Miandetta. B. A. Auld : NSW 134542 : Miandetta. Higgins : NSW 79069 : Wingen. J. W. Sutherland : NSW 61500 : Narromine. B. O'Neill : NSW 61499 : Narromine. P. Hurn : NSW 61520 : Ravensworth. J. Heel : NSW 61502 : Parkes. Shire Clerk : NSW 61503 : Cudal. E. J. McBarron : NSW 88771 : Flemington. G. R. Sainty (148) : NSW 81627 : Griffith. Stock Inspector : NSW 61504 : Narrandera. G. R. Godden : NSW 61599 : Berrigan.

NORTHERN TERRITORY. M. Lazarides : NSW 61506 : 40 km SSW. Napperby Station. D. J. Nelson : NT 10867 : 21 km E. Haasts' Bluff homestead. G. Chippendale : NSW 61507 : 31 km NW. Gosses' Bluff. G. Chippendale : NT 814 : 19 km E. Stokes' Yard. N. M. Henry : NT 38348 : Petermann Bore area, Tempe Downs Station. A. J. Mahood : NT 8748 : 19 km W. Hermannsburg.

QUEENSLAND. S. T. Blake : NSW 61509 : Longreach. C. T. White : NSW 61510 : Barcaldine. J. L. Boorman : NSW 61512 : Jericho. C. W. Birch : MEL (Holotype) : NSW 61508 : Bowen Downs, 1874. S. T. Blake : NSW 61513 : Blackall. B. A. Auld : NSW 134546 : Bollon.

SOUTH AUSTRALIA. R. Kain : ADW 29364 : Yongala. F. Humphris : ADW 5133 : Jamestown. G. Carmody : ADW : Balaklava.

ASPECTS OF THE SILURIAN RUGOSE CORAL FAUNA OF THE YASS REGION, NEW SOUTH WALES

R. A. McLean*

(Plates XVIII–XXI)

[Accepted for publication 19th February 1975]

Synopsis

The biostratigraphic distribution of rugose corals in the Yass region is tabulated. The rugosans *Palaeocyathus australis* Foerste, *Entelophyllum yassense yassense* (Etheridge), *Entelophyllum yassense patulum* (Foerste) and *Zelolasma*? *praecox* (Hill) are revised. *Rhizophyllum brachiatum* sp. nov., a colonial form from the Barrandella Shale, is described.

INTRODUCTION

The rugose corals of the Yass area in southern New South Wales have been for many years the best known of any Silurian rugosans in Australia, primarily through the work of Hill (1940). Recent study of the stratigraphy and conodont faunas of the sequence in the area and a more precise determination of its age (Link, 1970; Link and Druce, 1972) has prompted reappraisal of the biostratigraphy of the Rugosa of this classic succession. In addition several forms inadequately known previously are revised herein and a new species described.

Text-fig. 1 illustrates the stratigraphic range of species here recognised, with proposed generic assignments. It is based on the work of Hill (1940), Brown (1941), Link and Druce (1972) and collections of the present writer.

SYSTEMATIC PALAEONTOLOGY

Specimen numbers in the University of Sydney Palaeontological Collections have the prefix SUP. Fossil numbers in the Australian Museum, Sydney, bear the prefix AM.F. Fossil numbers of the Geological and Mining Museum, Sydney, have the prefix MMF.

Family DENSIPHYLLIDAE Dybowski, 1873

Genus PALAEOCYATHUS Foerste, 1888

1852 *Streptelasma* (*part.*); Hall, p. 3 (*non* Hall, 1847)
1869 *Petraia*; Safford, p. 320 (*non* Münster, 1839)
1874 *Streptelasma*; Hall, p. 114
?1879 *Streptelasma* (*part.*); Hall, p. 106
1887 *Streptelasma*; Hall and Simpson, p. 1
1888 *Cyathophyllum* (*part.*); Foerste, p. 128 (*non* Goldfuss, 1826)
?1890 *Cyathophyllum*; Foerste, p. 341.
?1890 *Streptelasma* (*part.*); Foerste, p. 345
1900 *Enterolasma* Simpson, p. 203
1901 *Streptelasma* (*part.*); Lambe, p. 107
1909 *Enterolasma*; Brown, p. 58
1909 *Enterolasma*; Brown, p. 65
1940 *Streptelasma*; Hill, p. 409
1949 *Enterolasma*; Amsden, p. 103

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HORIZON SPECIES	Cliftonwood Limestone	Euralie Limestone Mbr	Bowspring Limestone Mbr	Barrandella Shale Mbr	Hume Limestone Mbr	Yarwood Siltstone Mbr	Rainbow Hill Marl Mbr
Palaeocyathus australis							X
Phaulactis shearsbyi	X	X	X	X	X		
Entelophyllum yassense yassense			X	X	X		
E. yassense patulum				X	X	X	
Zenophila ? walli					X		
Zelolasma ? praecox			X	X			
Australophyllum spongophylloides			X	X	X		
A. ? shearsbii			X	X			
Yassia enormis			X				
Mucophyllum liliiforme			X	X			
M. crateroides				X	X		
Pycnostylus congregationis				X			
P. dendroides			X	X			
Tryplasma lonsdalei		X	X	X	X		
T. delicatulum				X			
T. derrengullenense				X			
Cystiphyllum cf. siluriense bohemicum			X				
C. sp.				X			
Holmophyllum multiseptatum	X						
H. colligatum			X				
Rhizophyllum interpunctatum	X			X			
R. robustum	X						
R. yassense				X			
R. brachiatum				X			

Text-fig. 1. Stratigraphic distribution of rugose coral species in the Yass region.

1952 *Orthopaterophyllum* Nikolaeva *in* Bulvanker, p. 7
1960 *Orthopaterophyllum* ; Nikolaeva *in* Bulvanker *et al.*, p. 221
1965 *Enterolasma* ; Sutherland, p. 22
1965 *Enterolasma* ; Kullmann, p. 143
1971 *Enterolasma* ; Dubatolov and Spasskiy, p. 81

Type species. *Cyathophyllum* (*Palaeocyathus*) *australe* Foerste, 1888. Rainbow Hill Marl Member, Yass region. Late Ludlow.

Diagnosis (based on diagnosis of "*Enterolasma*" by Sutherland, 1965). Corallum solitary, small, trochoid or ceratoid. Major septa long, with irregular carinae or tubercles on their sides. Axial edges of major septa lobed, forming irregular, open-meshed axial structure having appearance of twisted rods. Tabulae complete or incomplete, dissepiments lacking.

Discussion. Foerste (1888, p. 129) suggested *Palaeocyathus* as a subgeneric name for his species *Cyathophyllum australe* (1888, p. 128) from the Yass area. It was subsequently considered a synonym of *Streptelasma* Hall by Hill (1940). Study of further, more complete material of *Palaeocyathus* (see below) has shown its distinction from *Streptelasma* on the basis of having a loose axial structure and weak development of carinae or tubercles on the septa. These features ally the form to *Enterolasma* Simpson, 1900. According to Simpson (1900, pp. 204–5) *Enterolasma* is characterised by a pseudocolumella of twisted septal lobes and the presence of numerous carinae or tubercles on the sides of the septa. The Yass species has only sparsely developed carinae or tubercles, but according to Brown (1909, p. 59) *Streptelasma caliculum* Hall, 1852, included in *Enterolasma* by Simpson (1900), possesses a weakly developed *Enterolasma*-type axial structure, but lacks the tubercles on the septa. Hence the major diagnostic feature of *Enterolasma* would appear to be the peculiar axial structure and as this feature is clearly developed in *Palaeocyathus* (herein, Pl. XVIII, figs 3, 7), *Enterolasma* is here regarded as junior synonym of *Palaeocyathus*.

The writer has followed Weyer (1974) in placing "*Enterolasma*" (=*Palaeocyathus*) in the family Densiphyllidae Dybowski, characterised according to Weyer by forms bearing the peculiar axial structure of twisted septal lobes and lamellae (" axial synapticulae " of Weyer) found in *Palaeocyathus*. The genus *Rhegmaphyllum* Wedekind, 1927, as revised by Weyer (1974) and included also in the Densiphyllidae, is closely similar to *Palaeocyathus*, differing mainly in showing a markedly shortened cardinal septum and fossula, together with a more weakly developed axial structure.

Of the North American forms listed as belonging to "*Enterolasma*" by Bassler (1950), only three have been studied and illustrated in thin section. "*E.*" *strictum* (Hall, 1874), the type species of "*Enterolasma*" from the early Devonian (Helderbergian) New Scotland Limestone of New York (Oliver, 1960), has been illustrated by Hall and Simpson (1887, Pl. 1, figs. 1–10), Simpson (1900, Figs 11, 12) and Brown (1909, p. 66, Figs 1, 2). "*E.*" *waynense* (Safford, 1869) from the Brownsport Formation (Ludlow) of Tennessee has been illustrated by Sutherland (1965, Pl. 30, figs 1–3 ; Pl. 31, figs 4, 5). "*E.*" *caliculum* (Hall, 1852) from the " Niagara Formation " of New York and Ontario has sections illustrated by Lambe (1901, Pl. VII, figs 4a, b) and Brown (1909, Figs 11–26). This species has been recorded from many localities in the Silurian of North America (Bassler, 1950). The other species of "*Enterolasma*" listed by Bassler (1950) include "*E.*" *radicans* (Hall, 1879, p. 106, Pl. 5, figs 1–4) from the Waldron Shale (Upper Wenlock) of Indiana and "*E.*" *facetum* (Foerste, 1890, p. 341, Pl. IX, fig. 8) and "*E.*" *geometricum* (Foerste, 1890, p. 345, Pl. IX, figs 7, 12, 13), both from the Brassfield Limestone (?Middle-Upper Llandovery) of Ohio. These three forms are recorded as having " crenulated septa ", but their inclusion in *Palaeocyathus* cannot be confirmed without thin-section study.

The synonymy of the genus *Orthopaterophyllum* Nikolaeva *in* Bulvanker, 1952 with "*Enterolasma*" has been suggested by Ivanovskiy (1965*b*), Kullmann (1965), Dubatolov and Spasskiy (1971) and Weyer (1974). In view of their comparable septal and axial structures, these genera are regarded as synonymous here also and consequently *Orthopaterophyllum* becomes a junior synonym of *Palaeocyathus*. Several forms attributed to "*Orthopaterophyllum*" ("*O.*" *kasachstanicum* Nikolaeva, "*O.*" *cornuformis* Nikolaeva and "*O.*" *tschernyshewi* Spasskiy) require description of their tabular structure, but their inclusion in *Palaeocyathus* on the basis of septal structure would seem beyond doubt.

Protosyringaxon primitivum Ivanovskiy, 1963 from the Upper Llandovery of the River Moyero, Siberian Platform, was listed as a representative of "*Enterolasma*" by Ivanovskiy (1970). However, it has been illustrated only in external view (Ivanovskiy, 1963*b*, Pl. VI, fig. 3) and its affinities cannot be certain.

The genus *Paterophyllum* Počta, 1902 has been included by some authors as a synonym of "*Orthopaterophyllum*" or "*Enterolasma*" (e.g. Nikolaeva *in* Bulvanker *et al.*, 1960; Kullmann, 1965; Dubatolov and Spasskiy, 1971). However, the original material of Počta (1902) from the early Devonian of Bohemia requires detailed study before this synonymy can be confirmed.

It would appear that many of the species of *Palaeocyathus* can be separated into two distinct morphological groups. First there are forms having markedly thickened septa in the ephebic stage, the septa having pronounced tubercles or carinae on their sides. Included in this group are *P. strictus* (Hall, 1874) and *P. waynense* (Safford, 1869). Also showing this morphology are *P. tschernyschewi* (Spasskiy *in* Bulvanker *et al.*, 1960) and possibly *P. cornuformis* (Nikolaeva *in* Bulvanker *et al.*, 1960). A second group of species tends to show slender septa in the ephebic stage with tubercles of varying dimensions, although generally small, on the septa. Included among these forms are *P. australis* Foerste, 1888, *P. caliculus* (Hall, 1852), *P. conicus* (Nikolaeva *in* Bulvanker, 1952), *P. ibericus* (Kullmann, 1965) and possibly *P. kasachstanicus* (Nikolaeva *in* Bulvanker *et al.*, 1960). When all material referable to *Palaeocyathus* is adequately studied, and if this separation of species groups is found to be widely applicable, then it may be advisable to regard the groups as subgenera of *Palaeocyathus*.

Range. Llandovery of Ontario, Newfoundland, Indiana, ?Ohio; Late Llandovery-early Wenlock of New York, Ontario; Wenlock of Podolia, New York, Ontario, Ohio, Wisconsin, ?Indiana, ?Maine; Ludlow of N.S.W., New York, Ontario, Quebec, Missouri, Tennessee, Indiana, Oklahoma; ?Pridoli of New York; Late Silurian or early Devonian of Kazakhstan; Lower Devonian of Northern Spain, Kazakhstan, north-eastern America; ?Eifelian of south-west Siberia.

Palaeocyathus australis Foerste, 1888

Pl. XVIII, figs 1–7; Text-fig. 2

1888 *Cyathophyllum australe* Foerste, p. 128, Pl. XIII, figs 12–14.
1940 *Streptelasma australe* (Foerste); Hill, 1940, p. 410.

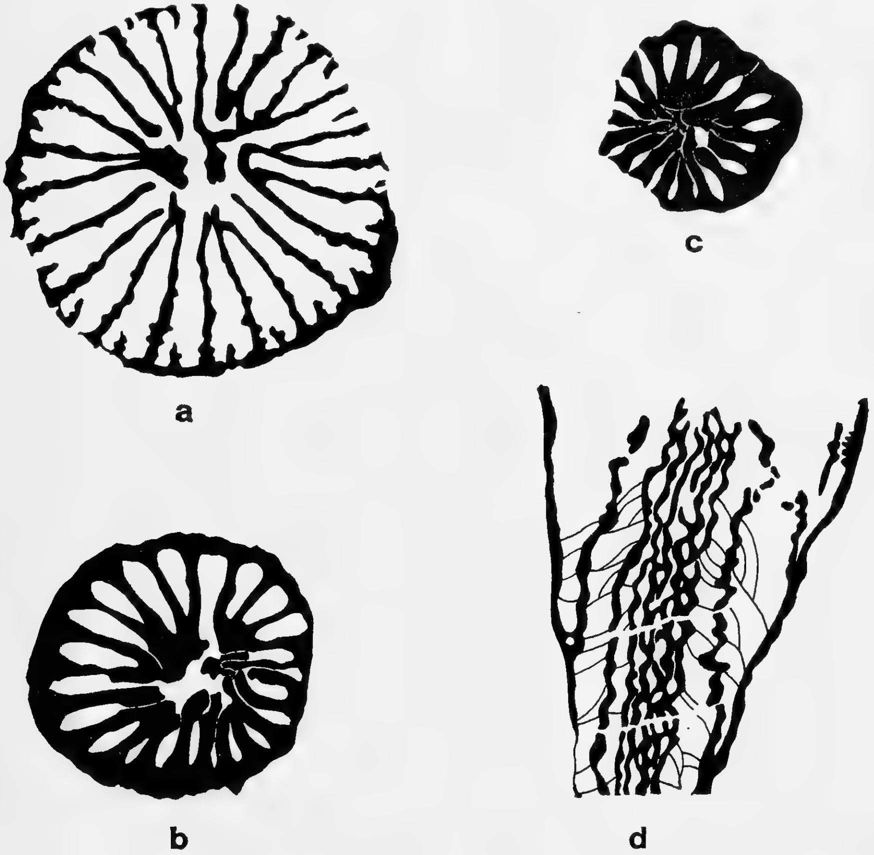
Lectotype. (chosen Hill, 1940) R 26519, British Museum (Nat. Hist.). "Hardened grey-brown shales east of Bowning Hill" (Hill, 1940, p. 410).

Present material. SUP 69227–69229, 74224–74227, Rainbow Hill Marl Member, Derringullen Creek; SUP 74221–74223, 74235–74241, Rainbow Hill Marl Member, near Black Range Road, "Belle Vale", Yass region. Late Ludlow.

Diagnosis. *Palaeocyathus* with septa dilated in neanic stage, slender in ephebic stage, with weak lateral "tubercles" or carinae. Axial structure clearly developed; peripheral stereozone weak in ephebic stage. Tabulae incomplete, strongly arched.

Description. Corallum solitary, trochoid to ceratoid, with extremely deep calice. Corallite diameter ranges up to 35 mm in largest specimen observed, with average diameter 8–10 mm at base of calice.

In neanic stage, septa are moderately dilated, particularly at periphery and axis (Pl. XVIII, figs 1, 2 ; Text-fig. 2c). Minor septa are not developed in this stage. In ephebic stage, septa are generally slender showing lateral extensions to a varying degree (Pl. XVIII, fig. 6), but it is not clear in available material if continuous carinae are developed. Their axial ends are frequently dilated and in contact, but peripheral stereozone is very narrow. Major septa range in number commonly from 23 to 26 in late ephebic stage (base of calice). Major septa slightly withdrawn from axis at base of calice, with minor septa, if developed, extending only up to 0·2 of length of major septa. Axial structure clearly apparent in longitudinal section, comprising loosely entwined septal lobes. Tabulae are incomplete, forming strongly arched floors, with average spacing 0·5–0·7 mm.



Text-fig. 2a–d. *Palaeocyathus australis* Foerste. a. SUP 69228, transverse section, ephebic stage, ×6. b. SUP 69227, transverse section, late neanic stage, ×6. c. SUP 74236a, transverse section, neanic stage, ×6. d. SUP 74239, longitudinal section, ×4.

Remarks. The slender septa of *P. australis* in the ephebic stage ally it to the second group of *Palaeocyathus* discussed above.

P. caliculus (Hall, 1852) would appear to be quite similar to *P. australis*, especially in the ephebic stage (see Lambe, 1901, Pl. VII, fig. 4 ; Brown, 1909, Figs 11–26). *P. caliculus* differs in having generally weaker dilation of septa in the neanic stage and a rather wider stereozone in the ephebic stage. *P. conicus* (Nikolaeva *in* Bulvanker, 1952) from the Kitaygo Horizon (Wenlock) of Podolia shows similarities to *P. australis* in septal number, thin, weakly tuberculate septa, narrow peripheral stereozone and arched tabulae. However, the former may be distinguished by its rather more open, irregular axial structure in longitudinal section (Bulvanker, 1952, Pl. V, fig. 2 ; Pl. VI, fig. 6a), possibly more weakly dilated septa in the neanic stage (Bulvanker, 1952, Pl. VI, fig. 6v) and apparently more widely spaced tabulae.

Family ARACHNOPHYLLIDAE Dybowski, 1873

Genus ENTELOPHYLLUM Wedekind, 1927

1927 *Entelophyllum* Wedekind, p. 22
1927 *Xylodes* Lang and Smith, p. 461
?1930 *Petrozium* Smith, p. 307
1933 *Xylodes* (*? part.*) ; Smith, p. 513
1939 *Cyathophyllum* ; Shrock and Twenhofel, p. 250 (*non* Goldfuss, 1826)
1939 *Xylodes* (*part.*) ; Weissermel, p. 47
1940 *Entelophyllum* ; Hill, p. 411 (*cum syn.*)
1949 *Cyathophyllum* (*part.*) ; Amsden, p. 108
1951 *Entelophyllum* (*part.*) ; Schouppé, p. 244
1952 *Entelophyllum* ; Sytova, p. 137
1958 *Petrozium* ; Kaljo, p. 114
1959 *Entelophyllum* ; Ivanovskiy, p. 137
?1963*a* *Entelophyllum* ; Ivanovskiy, p. 85
1963*b* *Entelophyllum* (*part.*) ; Ivanovskiy, p. 83 (*cum. syn.*)
1965 *Entelophyllum* ; Sutherland, p. 26
1965 *Petrozium* ; Zheltonogova, p. 40
1971*a* *Entelophyllum* (*? part.*) ; Lavrusevich, p. 71
?1972 *Petrozium* ; Merriam, p. 37
?1973*a* *Petrozium* ; Merriam, p. 47
1973*a* *Entelophyllum* (*? part.*) ; Merriam, p. 48
1973*b* *Entelophyllum* (*? part.*) ; Merriam, p. 38 (*cum syn.*)
non 1952 *Xylodes* ; Bulvanker, p. 31
non 1962 *Entelophyllum* ; Flügel, p. 290
non 1965 *Entelophyllum* ; Zheltonogova, p. 41
non 1971 *Entelophyllum* ; Tcherepnina, p. 90

Type species. *Madreporites articulatus* Wahlenberg, 1821. " Upper Silurian ", Gotland

Diagnosis. Corallum ?solitary and colonial. Septa thin, often weakly carinate, major septa generally extending nearly to axis. Dissepiments mainly small, globose ; tabulae typically arched.

Discussion. Several Silurian genera show close similarities to *Entelophyllum*. *Stereoxylodes* Wang, 1944 and its possible synonym *Carinophyllum* Strelnikov, 1964 are both strongly carinate forms and their affinities with *Entelophyllum* have been discussed by McLean (1975). The position of the lonsdaleoid form *Strombodes* Schweigger, 1819 and its likely synonym *Evenkiella* Soshkina, 1955, has also been reviewed by McLean (1975). The genus *Micula* Sytova, 1952, was considered by Sutherland (1965) to differ from *Entelophyllum* only in its solitary growth form and thickening of the septa at the periphery. It may well be a synonym of *Entelophyllum*.

The systematic position of the genus *Petrozium* Smith, 1930 is not clear. According to the original description of Smith (1930, p. 307), the genus differs from *Entelophyllum* in having the axial ends of some of the major septa reinforced with sclerenchymal tissue so as to form a thin axial structure. Whether such a distinction, which is developed to varying degrees, is of generic importance is doubtful, Ivanovskiy (1965*a*, *b*), for example, regarding *Petrozium* as simply a synonym of *Entelophyllum*. Some species of *Petrozium* described by other authors (Kaljo, 1958 ; Zheltonogova, 1965) apparently lack the axial structure and are regarded as representatives of *Entelophyllum* (see Kaljo, 1970 and Hill, 1967). Two species described by Merriam (1972, 1973*a*) from North America have incipient development of an axial structure. *Petrozium* is here tentatively regarded as a synonym of *Entelophyllum*.

Forms of *Entelophyllum* like *E. rugosum* (Smith, 1933), *E. angulare* (Amsden, 1949), *E. medius* Ivanovskiy, 1963*a*, *E. nikolaievae* Lavrusevich, 1971*a* and *E. engelmanni* Merriam, 1973*a*, with a rather narrow dissepimentarium and uniseriate tabularium of flat or sagging tabulae, would appear to be significantly different to the type species of *Entelophyllum*, *E. articulatum* (Wahlenberg, 1821). This species is characterised by a wide dissepimentarium and biseriate or triseriate tabularium comprising generally strongly arched floors. The atypical species of *Entelophyllum* show closer similarities to the genus *Strephophyllum* Lavrusevich, 1971*a* (type species *S. princeps* Lavrusevich, 1971*a*, Horizon K—Lower Wenlock—Tadzhikistan), which differs from *Entelophyllum* in having generally sagging tabulae in a uniseriate tabularium. They could perhaps be considered congeneric with *Strephophyllum* or at least as intermediate between *Entelophyllum* and *Strephophyllum*.

The Devonian cyathophyllid *Cyathophyllum* (*Radiophyllum*) Hill, 1942 shows very close similarities to *Entelophyllum*, as noted by Hill (1942) and Jell and Hill (1969), emphasing a close affinity between the Cyathophyllidae and Silurian Arachnophyllidae. Judging by the illustrations of the type species, *C.* (*R.*) *arborescens* (Hill and Jones, 1940) from the Garra Formation (late Lochkovian to Pragian, A. E. H. Pedder, pers. comm. 1975) of N.S.W., given by Strusz and Jell (1970), it may be distinguished in having weak peripheral dilation of septa (although this feature is very variable) and a rather more irregular arrangement of the tabulae, although the basic entelophyllid style is recognisable. *Amaraphyllum* Pedder, 1970 (type species *A. amoenum* Pedder, 1970, Timor Limestone—Givetian—N.S.W.) appears very closely comparable to *Entelophyllum*, as mentioned by Pedder (*in* Pedder, Jackson and Ellenor, 1970, pp. 252–3). It shows greater similarity to *C.* (*Radiophyllum*) however, particularly to *C.* (*R.*) *arborescens*, in the slight peripheral septal dilation and more irregular spacing of tabulae, and is probably a representative of that subgenus. "*A.*" *amoenum* would not appear to belong to *Disphyllum*, contrary to the assertion of Rozkowska and Fedorowski (1972). *Entelophyllum devonicum* Tcherepnina, 1971 from the early Devonian Remnev Beds of the Altai would appear also to show closer affinities with *C.* (*Radiophyllum*) than with *Entelophyllum*.

Range. Upper Llandovery of Sweden, Siberian Platform, Tadzhikistan ; Wenlock of England, Gotland, Czechoslovakia, Urals, Siberian Platform, Tadzhikistan, Kazakhstan, north-east USSR, ?Indiana-Kentucky ; Ludlow of Norway, Gotland, Estonia, Urals, Podolia, Turkey, ?Tennessee, ?Oklahoma, ?Indiana-Kentucky ; Upper Silurian (undifferentiated) of Maine, Nevada.

Petrozium is recorded in the Middle Llandovery of Estonia ; Upper Llandovery of England ; Lower Wenlock of California ; Upper Wenlock of south-west Siberia and Upper Wenlock-Ludlow of California.

Entelophyllum yassense yassense (Etheridge, 1892)

Pl. XVIII figs 8–10 ; Pl. XIX fig. 1 ; Text-fig. 3

1892 *Heliophyllum yassense* Etheridge, p. 170, Pl. XI, fig. 8, Pl. XII, figs 1–3

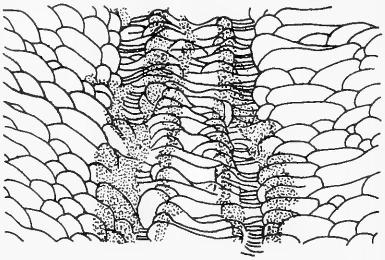
1936 *Xylodes yassense* (Etheridge) ; Jones, p. 56, Pl. VII, figs 3, 4 (*non* fig. 5)
1940 *Entelophyllum yassense* (Etheridge) ; Hill, p. 412, Pl. XIII, figs 11, 12

Type material. Missing (see Jones, 1936, p. 56).

Additional material. SUP 74253–74257. Barrandella Shale, Limestone Creek, " Silverdale "-" Allview " area, Yass region. Middle Ludlow.

Diagnosis. Corallum fasciculate. Septa very slender, weakly carinate, wavy. Minor septa up to 0·5 of length of major septa. Tabularium narrow, divided into axial arched series and periaxial concave series with tabulae very closely spaced.

Description. See Hill (1940, p. 412).



Text-fig. 3. *Entelophyllum yassense yassense* (Etheridge). SUP 74253c, longitudinal section, ×4.

Remarks. E. yassense yassense shows the tabular structure of the *E. articulatum* group of species i.e. a peripheral, distally concave series and an axial, arched series. This feature distinguishes it from the group of " *E.* " *rugosum* with mainly horizontal tabulae, mentioned above. The wide dissepimentarium and very closely spaced tabulae of the periaxial series serve to distinguish this form from other described species.

Entelophyllum yassense patulum (Foerste, 1888)

Pl. XIX, figs 2–6 ; Pl. XX, figs 1–3

1888 *Cyathophyllum patula* Foerste, p. 129, Pl. XIII, figs 9–11.
1940 *Entelophyllum yassense* var. *patulum* (Foerste) ; Hill, p. 413, Pl. XIII, figs 13*a*, *b*.

Type material. Missing (possibly in British Museum—Hill, 1940, p. 413). Yarwood Siltstone Member, Bowning (=" Lower trilobite bed, Bowning " of Hill, 1940, p. 413).

Additional material. SUP 69222–69226, 74248–74252. Barrandella Shale, Limestone Creek. " Silverdale "-"Allview " area, Yass region. Middle Ludlow.

Diagnosis. E. yassense with patellate corallum, either solitary or with calicinal offsets. Septa very numerous, thin, major septa extending to axis.

Description. Corallum is generally solitary, but at least three calical offsets have been observed in larger specimens (Pl. XIX, figs 3, 4). Parent corallum is patellate, expanding very rapidly after initiation of growth. Corallum height reaches at least 25 mm, with diameter up to 75 mm. Coralla are frequently asymmetrical. Septa are very thin, wavy, with very fine zigzag carinae. Major septa extend 0·5–0·6 of corallite radius. Septa range in number up to 170 in larger specimens. Formation of septa of offsets from major septa of parent corallite is illustrated in Pl. XIX, fig. 4 (note distortion of septa immediately prior to increase, Pl. XIX, fig. 6).

Tabulae and dissepiments are similar in structure to those of *E. yassense yassense.*

Remarks. This form, regarded here as a subspecies of *E. yassense*, is illustrated in thin-section for the first time and may be distinguished from *E. yassense yassense* by its patellate growth form and very numerous septa. It should be noted that *E. yassense yassense* occurs together with *E. yassense patulum* and that early growth stages of the nominate subspecies are closely similar to small *E. yassense patulum*, the latter tending to expand rather more rapidly.

Family DISPHYLLIDAE Hill, 1939

Genus ZELOLASMA Pedder, 1964

?1937 *Acervularia* (*part.*) ; Soshkina, p. 62 (*non* Schweigger, 1820)
?1940 *Disphyllum* ; Hill, p. 398 (*non* de Fromentel, 1861)
1964 *Zelolasma* Pedder, p. 364
1965 *Zelolasma* ; Strusz, p. 534
1970 *Zelolasma* ; Pedder, Jackson and Philip, p. 232 (*cum syn.*)
1971*c* *Zelolasma* ; Lavrusevich, p. 85

Type species. Diphyphyllum gemmiformis Etheridge, 1902. Cavan Limestone, Taemas Bridge, Murrumbidgee River, N.S.W. Lower Devonian (Late Pragian, A. E. H. Pedder, pers. comm. 1975).

Diagnosis. Corallum phaceloid to subcerioid. Septa generally subequal in length, thin, often wavy or weakly carinate and may show slight axial dilation. Dissepimentarium narrow, with globose dissepiments in several rows. Tabulae commonly complete, approximately flat and widely spaced.

Discussion. Oliver (1974) has distinguished the family Craspedophyllidae Dybowski (particularly subfamily Craspedophyllinae Oliver) from the Disphyllidae Hill on the basis of members of the former family having attenuate septa and well developed carinae, while those of the latter have septa thickened peripherally and lacking marked carinae. Under this interpretation, the genus *Zelolasma* Pedder, having attenuate septa peripherally but lacking carinae, would be intermediate in structure between representatives of the two families. It is tentatively left in the Disphyllidae for the present, equivalent to the classification adopted by Pedder (1964), Strusz (1965) and Jell (1969). *Zelolasma* may be distinguished from typical members of the Cyathophyllidae Dana in having a narrow dissepimentarium and more widely spaced, simpler tabulae.

The genus *Acinophyllum* McLaren, 1959 appears closely similar to *Zelolasma*, having a narrow dissepimentarium, short major septa and generally lacking tabellae. Pedder (1964) considered *Zelolasma* to differ in lacking the connecting processes between corallites of *Acinophyllum*, but these processes are not always developed clearly in the latter genus (McLaren, 1959) and do not appear to be of generic significance. Carinae are developed to a rather variable extent in *Acinophyllum* according to McLaren (1959) and Scrutton (1968), but Oliver (1974), after a thorough review of the genus, considered them to be generally strongly developed and this interpretation is followed here.

Some Silurian genera show similarities to *Zelolasma*. *Diplophyllum* Hall, 1852, reviewed by Oliver (1963), has a narrow dissepimentarium of globose dissepiments and broad tabularium of mainly complete tabulae similar to *Zelolasma.* It may be distinguished from the latter by having the septa strongly dilated at the tabularial margin to form an inner wall and it generally has longer major septa. The genus *Columnaria* Goldfuss, 1826 has both Devonian and Silurian representatives ; the Silurian forms most probably belonging to the genus have been reviewed by Norford (1962). They may be distinguished from *Zelolasma* by having the dissepiments in their single rank strongly elongate, as opposed to the globose forms of *Zelolasma.*

Zelolasma has not been previously recorded in strata older than Devonian, but several Silurian species may be representative of the genus. *Disphyllum praecox* Hill, 1940, discussed below, is here regarded as possibly belonging to *Zelolasma*. " *Diphyphyllum caespitosum* " (Hall, 1852) of Lambe (1901, Pl. XIII, fig. 3) is not congeneric with Hall's original material, the type of *Diplophyllum*, as mentioned by Oliver (1963). With a single row of globose dissepiments, mainly complete tabulae and short septa, Lambe's material could be representative of *Zelolasma*. " *Entelophyllum caespitosum* " (Hall) of Ivanovskiy (1963*a*, Pl. I, fig. 2 and 1963*b*, Pl. XXIV, fig. 1) seems to be conspecific with Lambe's " *Diphyphyllum caespitosum* " and hence may also belong to *Zelolasma*. These two forms would appear to be the oldest representatives of *Zelolasma* if confirmed, being of Middle to Upper Llandovery age.

Acervularia luxurians var. *breviseptata* Weissermel, 1894 described by Soshkina (1937, p. 63, Pl. XVII, figs 1, 2) from the ?Upper Silurian of the Urals may also be a representative of *Zelolasma*, being especially similar in dissepimental and tabular structure. It is not the same as Weissermel's form (Weissermel, 1894, p. 608, Pl. XLIX, figs 4, 5). Lavrusevich (1971*c*) considered Soshkina's material to be conspecific with *Z. gemmiforme*, but regarded it as being Lower Devonian rather than Upper Silurian in age.

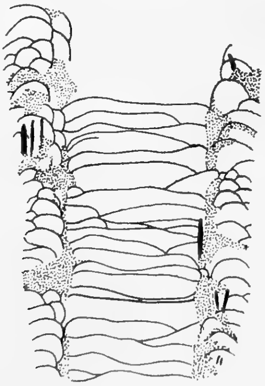
?*Diphyphyllum* sp. illustrated by Nikolaeva (1936, Pl. II, figs 6, 7) from the ?Middle or Upper Silurian of the River Kolyma area, north-east USSR, appears similar to *Zelolasma*, again particularly in dissepimental and tabularial characters, but there is some evidence of development of an inner wall and it may possibly be assigned more properly to *Diplophyllum*.

Range. Middle Llandovery of ?Anticosti Island ; Upper Llandovery of ?Siberian Platform, ?Anticosti Island ; Ludlow of ?N.S.W. ; ?Upper Silurian or early Devonian of ?the Urals ; Lower Devonian of Tadzhikistan and N.S.W.

Zelolasma? *praecox* (Hill, 1940)

Pl. XX, fig. 4 ; Pl. XXI, figs 5–7 ; Text-fig. 4

1940 *Disphyllum praecox* Hill, p. 398, Pl. XI, figs 15–17.



Text-fig. 4. *Zelolasma*? *praecox* (Hill) AM 603, longitudinal section, × 6.

Material. Holotype AM.F 9709 with thin-sections, AM 745, probably from the Barrandella Shale, Limestone Creek, near Bowning-Wargeilo road crossing, Yass region. Middle Ludlow. Paratypes—see Hill, 1940, p. 399. Additional specimen—AM.F 8505 with thin-sections AM 603, horizon uncertain, portion 35, Parish of Derringullen (Limestone Creek, near " Allview ").

Diagnosis. Corallum subphaceloid with connecting processes. Major septa withdrawn from axis, minor septa at least half length of major septa. Tabulae mainly complete, flat or weakly domed ; dissepiments in 1–3 rows, very strongly globose.

Description. See Hill, 1940, p. 398.

Remarks. "*Disphyllum*" *praecox* Hill, 1940 differs from *Disphyllum* in lacking the peripheral dilation of the septa characteristic of that genus, as well as lacking tabellae. These features ally it with *Zelolasma*, although it lacks the subequal major and minor septa and axial dilation of the septa in that genus. Hence it is only tentatively assigned here to *Zelolasma.* Both Hill (1940) and Pedder (1964) have noted the close similarity of "*D.*" *praecox* and *Z. gemmiforme.*

Z.? praecox differs from *Acinophyllum* McLaren in having only weakly developed carinae, but is otherwise closely similar to that genus. Wang (1947, p. 178) considered *Z? praecox* to be related to *Phacellophyllum* Gürich, but it lacks the grouped horseshoe dissepiments of that genus. Ivanovskiy (1965*b*, p. 98) listed the species as a representative of *Entelophyllum*, and while showing some similarities to this genus, more especially the doubtfully included forms with flattened tabulae and narrow dissepimentarium mentioned above, the typically short septa, very narrow dissepimentarium with generally horizontal dissepimental layers, and flat, complete, widely spaced tabulae clearly distinguish it from *Entelophyllum.*

Family GONIOPHYLLIDAE Dybowski, 1873

Genus RHIZOPHYLLUM Lindström, 1866

1974 *Rhizophyllum* McLean, p. 29 (*cum syn.*)

Type species. Calceola gotlandica Roemer, 1856 Eke, Hemse Beds (Ludlow), Gotland.

Diagnosis, Discussion and Range. See McLean (1974).

Rhizophyllum brachiatum sp. nov.

Pl. XXI, figs 1–4 ; Text-figs 5, 6

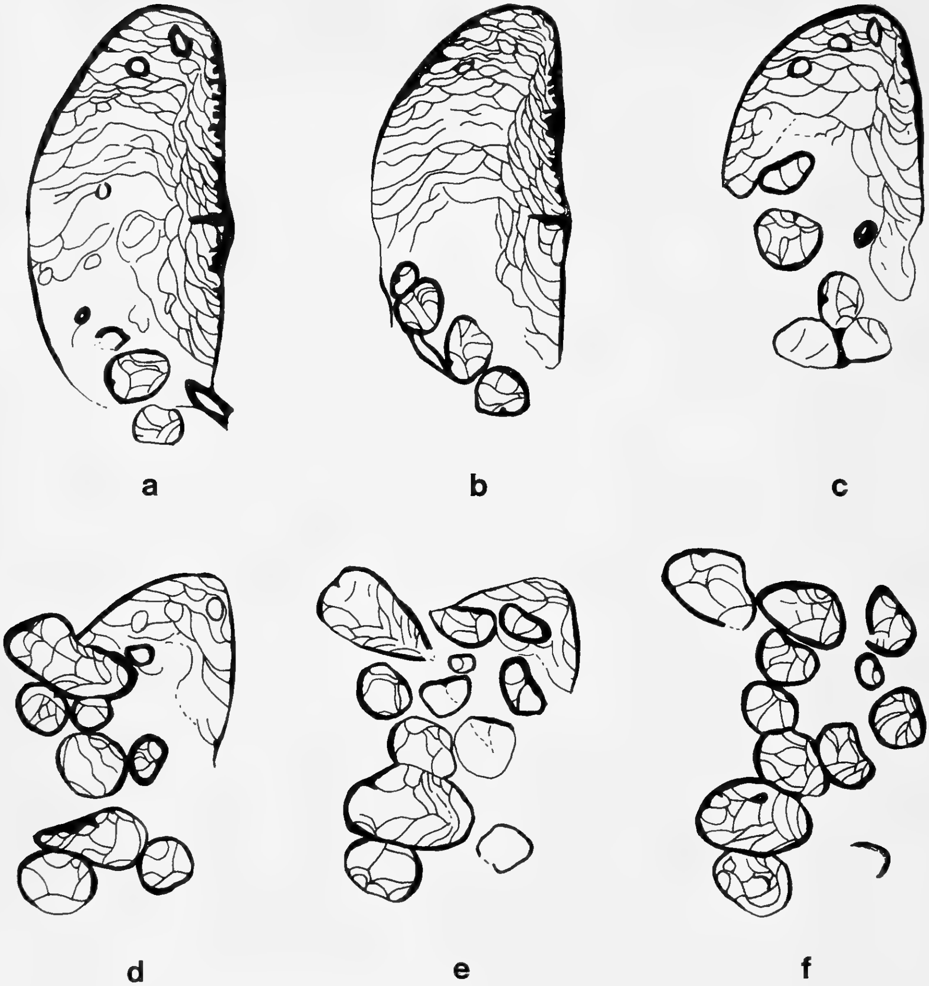
Derivation of name. Latin brachiatus = branching.

Material. Holotype MMF 12981. Fragmented colony. Barrandella Shale, "Silverdale", Yass region. Middle Ludlow.

Diagnosis. Corallum fasciculate with very long slender, subparallel corallites. Increase calicinal, parricidal. Septa irregularly developed, occurring on flat wall only. Zone of smaller dissepiments occurs adjacent to flat wall.

Description. Corallum fasciculate, colony (fragmented) attaining large size. Corallites very long, slender, frequently scolecoid, subparallel. Increase is calicinal, apparently parricidal with at least 12 offsets from the one calice (Text-fig. 5). Increase apparently occurs uncommonly after initial growth period of corallum, the many offsets from the one calice generally forming very long corallites that often extend throughout remainder of corallum. No apparent relationship is evident between orientation of counter septum of parent corallite and offsets, although some rotation of daughter corallites during growth is evident (Text-fig. 5). Hollow rootlets with transverse structures are abundantly developed for support between adjacent corallites, most commonly at angles but also on flat wall of corallites (Text-fig. 6). There is no clear development of an axial pit in calice.

Mature corallite diameter reaches 12 × 7·5 mm with angles slightly rounded. Corallite height ranges to at least 10 cm. Counter septum clearly developed except in earliest growth stages (Pl. XXI, fig. 2 ; Text-fig. 5) where corallites have



Text-fig. 5a-f. *Rhizophyllum brachiatum* sp. nov. MMF 12981, transverse serial sections (5a is the most proximal section) illustrating progressive formation of calical offsets with elimination of the parent corallite. Approximately 1 cm of corallum growth is covered by the series of sections; traced from photographs of acetate peels. ×4.

Text-fig. 6. *Rhizophyllum brachiatum* sp. nov. MMF 12981, transverse section showing rootlets. Note transverse structures in broken rootlet. ×5.

not attained typical calceoloid shape. Counter septum is long and slender but other septa are irregularly and weakly developed, occurring only in mature corallites. They range in number to approximately 20–26, with major and minor septa not clearly distinguishable. Septa are confined to flat wall only.

Dissepiments in septal zone adjacent to flat wall are small, strongly elongate, in partial arched series approximately 0·3 of corallite diameter (Pl. XXI, fig. 3). Tabellae or dissepiments occupying remainder of corallite are larger, in moderately sagging series.

Vertical tube-like structures are commonly developed growing parallel to corallite wall and occurring just within curved rim of corallite (Pl. XXI, figs 1, 3, 4). These tubes have common diameter of 0·5–0·6 mm, with wall thickness of 0·08–0·1 mm. Sagging transverse plates, widely spaced, may be sporadically developed.

Remarks. Colonial representatives of *Rhizophyllum* include *R. elongatum* Lindström, 1883 from the Eke Beds (Middle Ludlow) of Gotland and the Kunzhak Horizon (? Lower Devonian) of central Tadzhikistan (Lavrusevich, 1971*b*) and *R. attenuatum* (Lyon, 1879) from the Louisville Limestone (late Wenlock—early Ludlow) of Indiana—Kentucky. In addition from the Wenlock or Ludlow of north-western California, Oliver (1964) recorded "*Rhizophyllum* sp. C." which, though poorly preserved, is probably a colonial form.

R. attenuatum has not been illustrated in thin section, but it can be distinguished from *R. elongatum* and *R. brachiatum* by having lateral rather than calical increase (Lindström, 1883, Pl. III, fig. 17). *R. brachiatum* may be differentiated from *R. elongatum* by the former having a clearly differentiated zone of smaller dissepiments adjacent to the flat wall and generally much longer corallites. *R. elongatum* however requires more illustration of thin sections.

It seems likely from the section illustrated in Text-fig. 6 that rootlets were formed as a type of lateral bud, with transverse structures internally. They apparently were then specialised as supporting structures. In structure the earliest stage of an offset does not appear distinguishable from a rootlet.

The tube-like structures occurring within the horizontal skeletal tissue of *R. brachiatum* are of problematical origin. Among the goniophyllids, similar structures are apparent in *R. elongatum* (Lindström, 1883, Pl. II, fig. 17 and Pl. IV, fig. 5) and the Devonian *Calceola sandalina* (Linnaeus, see Lafuste and Semenoff-Tian-Chansky, 1968). Plusquellec (1968*a*, *b*) has reviewed the occurrence of comparable structures in representatives of Palaeozoic corals and stromatoporoids, attributing them to commensal organisms of uncertain affinities. References to previous work on these structures may be obtained from Plusquellec's works.

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EXPLANATION OF PLATES

PLATE XVIII

Figs 1–7. *Palaeocyathus australis* Foerste. 1. SUP 74221b, transverse section, late neanic stage, ×6. 2. SUP 74236a, transverse section, neanic stage, ×6. 3. SUP 74224, longitudinal section, ×4. 4. SUP 69229, transverse section, ephebic stage, ×6. 5. SUP 74221a, transverse section, ephebic stage, ×6. 6. SUP 69228, transverse section, ephebic stage, ×6. 7. SUP 74239, longitudinal section, ×4.

Figs 8–10. *Entelophyllum yassense yassense* (Etheridge). 8. SUP 74254f, transverse section, early growth stages, ×3. 9. SUP 74253c, longitudinal section, ×3. 10. SUP 74254c, transverse section, ×2.

PLATE XIX

Fig. 1. *Entelophyllum yassense yassense* (Etheridge). SUP 74254d, transverse section, ×3.

Figs 2–6. *Entelophyllum yassense patulum* (Foerste). 2. SUP 69222, transverse section, ×1·5. 3. 69226a distal transverse section, ×1·5. 4. SUP 69226a, transverse section of axial region showing offsets. 5. SUP 69224, transverse section showing offset, lower right, ×1·5. 6. SUP 69226b, transverse section slightly more proximal than that in Fig. 3, showing distortion of septa near axis prior to formation of offsets.

PLATE XX

Figs 1–3. *Entelophyllum yassense patulum* (Foerste). 1. SUP 69222b, longitudinal section, ×3. 2. SUP 69223 longitudinal section showing offset at right ×3. 3. SUP 69226c transverse section prior to formation of offsets, ×1·5.

Fig. 4. *Zelolasma*? *praecox* (Hill). AM 745, holotype, transverse section, ×4.

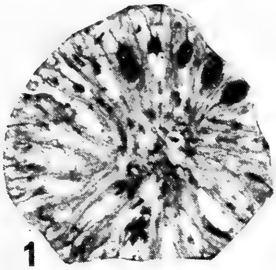
PLATE XXI

Figs 1–4. *Rhizophyllum brachiatum* sp. nov. MMF 12981, ×6. 1. transverse section, ephebic stage. 2. transverse section, neanic stage (note long counter septum). 3. longitudinal section (flat wall at right). 4. transverse section, ephebic stage.

Figs 5–7. *Zelolasma*? *praecox* (Hill). 5. AM 603, transverse section, ×8. 6. AM 603, longitudinal section, ×6. 7. AM 3317 (AM.F 9879), paratype, longitudinal section, ×6.

Corrigendum

PROC. LINN. SOC. N.S.W., 99: 94. Pl. X, fig. 7, *read* SUP 39184b, transverse section, ×7.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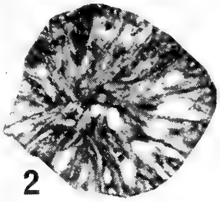
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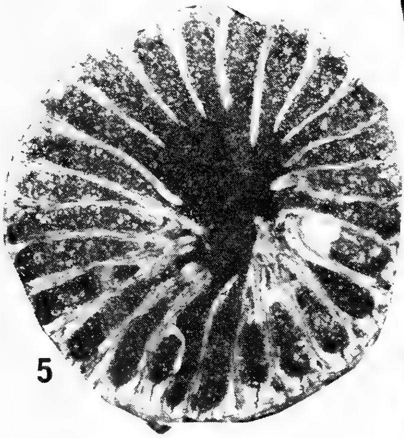
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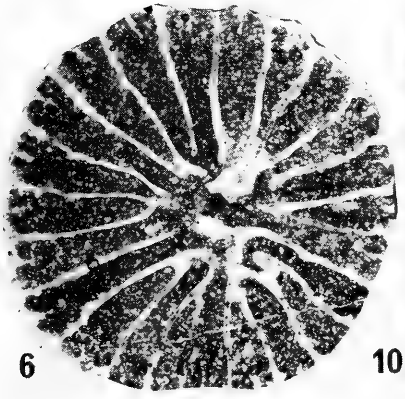
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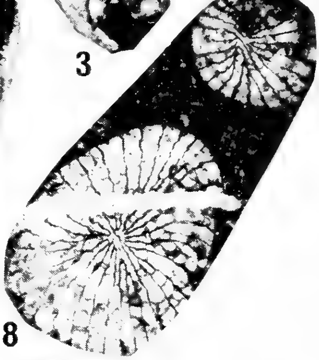
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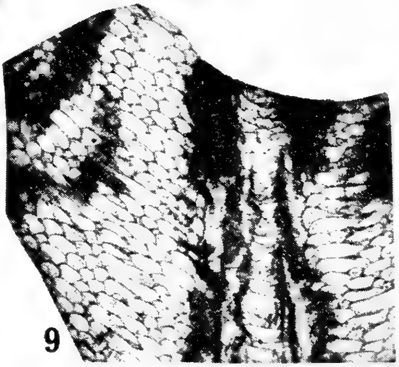
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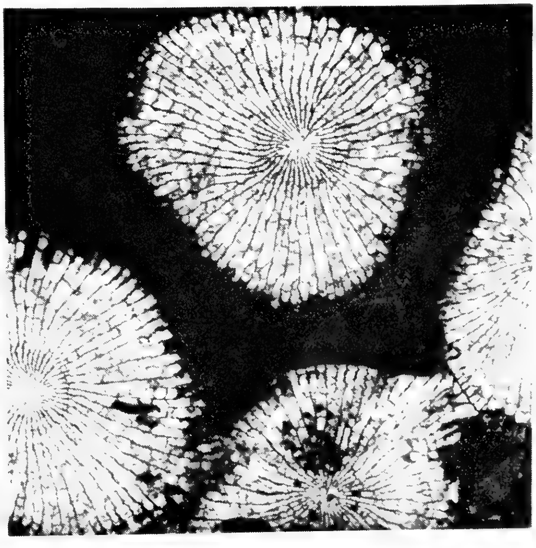
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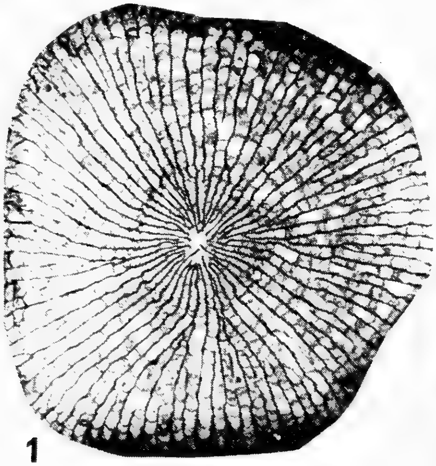

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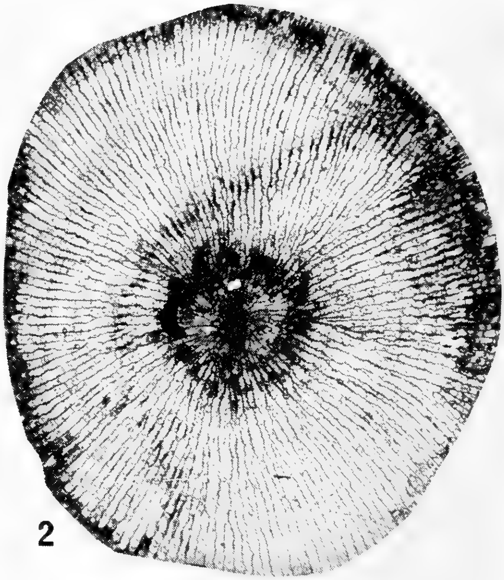

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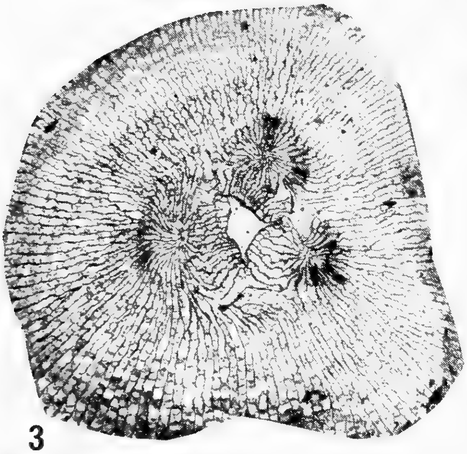

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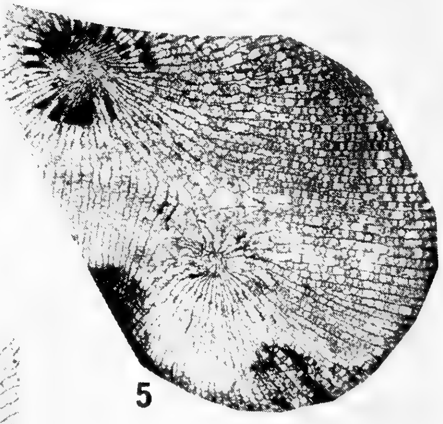

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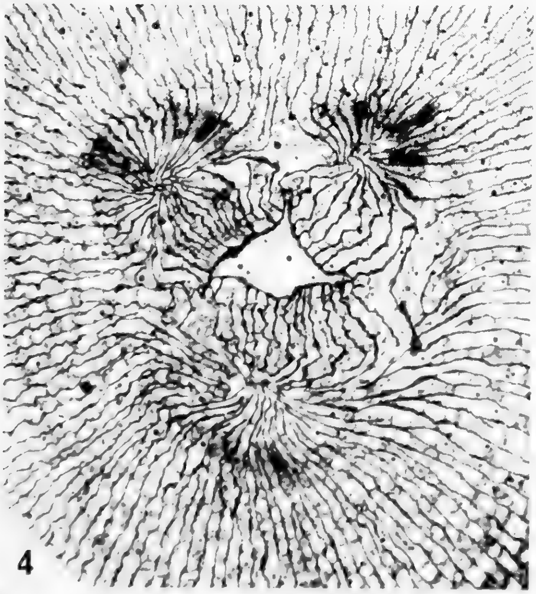

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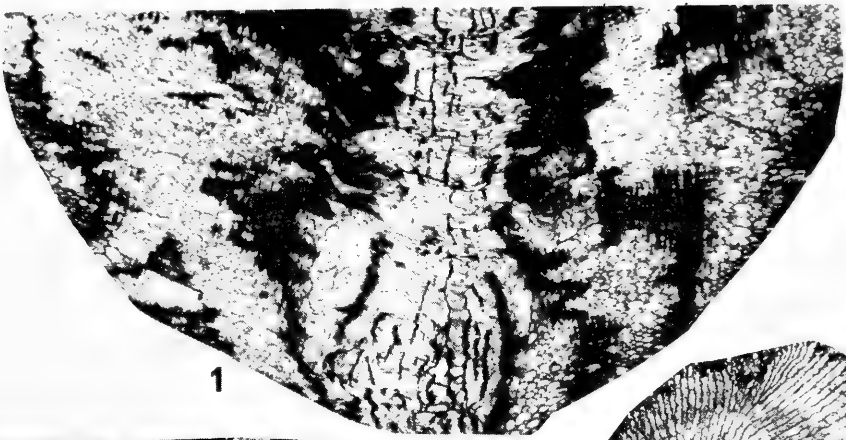

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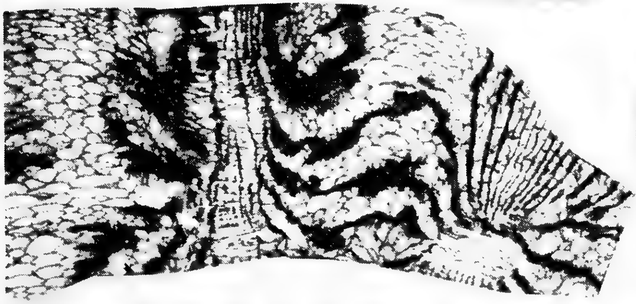

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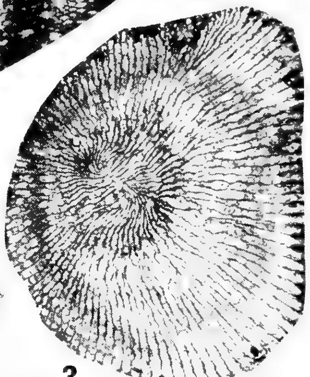

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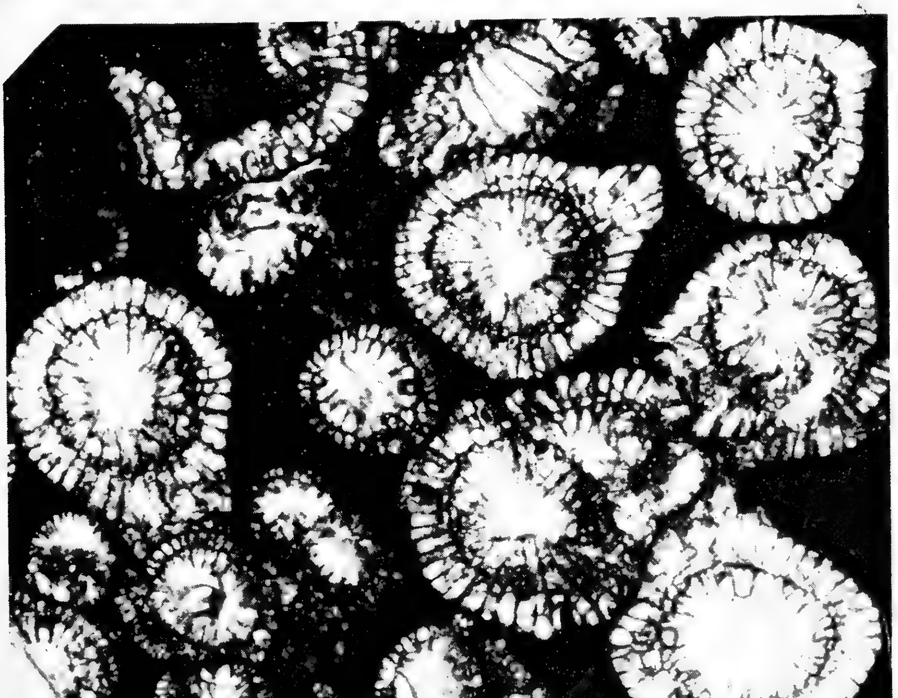

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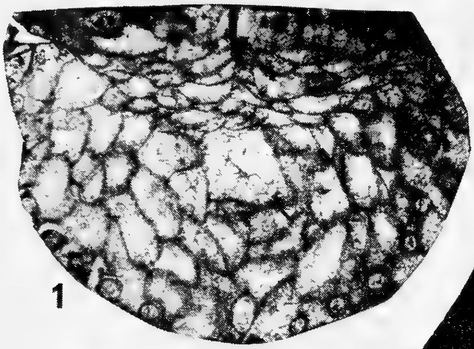
PLATE XXI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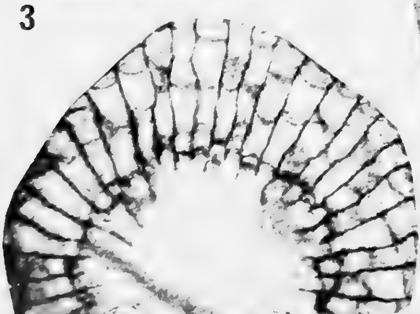
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SOURCES OF RESISTANCE TO *HETERODERA AVENAE* WOLL. IN NEW SOUTH WALES

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[Accepted for publication 23rd July 1975]

Synopsis

Australian cultivars of wheat, oats, barley and rye and European cereal cultivars and lines resistant to various European pathotypes were tested over four years for resistance to the pathotype of the cereal cyst nematode, *Heterodera avenae*, present in New South Wales. Amongst the Australian cultivars three of 42 wheats, eleven of 15 oats, none of 11 barleys and two of 3 ryes showed resistance. The European barleys Marocaine 079 and Morocco and the Cc 4658 line of *Avena sterilis* were resistant. New South Wales nematode populations resemble Victorian populations in their reactions on the European cereals. Australian populations resemble mixtures of certain European pathotypes in their reactions on European barleys, but differ in their reaction on Loros wheat.

Introduction

Heterodera avenae Woll., the cereal cyst nematode, attacks winter cereals throughout Europe, in Australia (New South Wales, South Australia, Victoria, Western Australia), Canada (Ontario), Israel, Morocco, South Africa, Japan and India (Kort, 1972). By growing isogenic lines of barley differing only in the presence of a single gene for resistance to *H. avenae*, Cotten (1967*a*), in Britain,

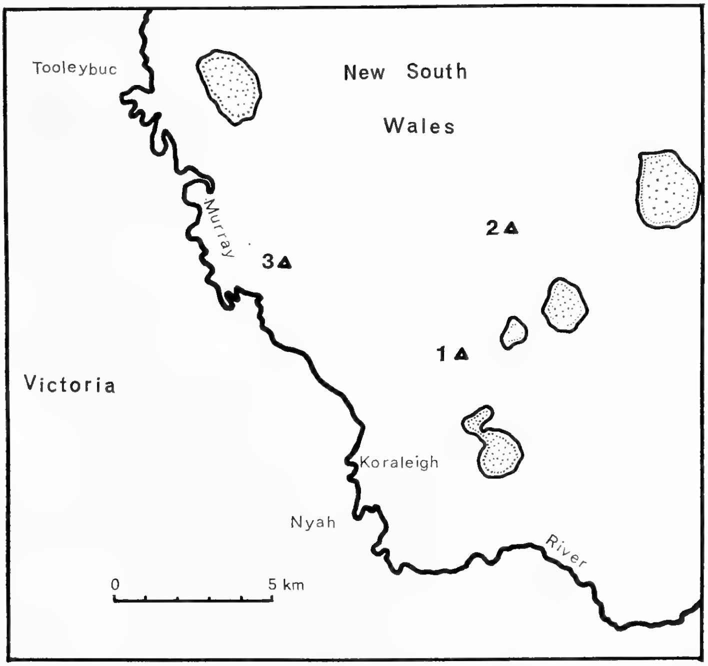

Fig. 1. Sites where soil was collected and field trials were carried out. These sites enclose the area known to be infested with *H. avenae* in New South Wales.

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showed that this nematode can reduce yield by 20% on heavily infested land. Dixon (1970) showed that for every ten eggs of *H. avenae* per g of soil before sowing, yield of oats fell 376 kg/ha, yield of wheat 188 kg/ha and yield of barley 75 kg/ha. The only practical control on infested land is to grow other crops or cereal cultivars which do not allow the nematode to multiply (resistant cultivars). Resistant cultivars not only outyield susceptible ones in heavily infested soil (Cotten 1967*a*, 1970 ; Mukhopadhyaya *et al.*, 1972) but also the yield of following susceptible cultivars (Cotten, 1967*a* ; Williams, 1970) is increased because nematode numbers are reduced. In Europe at least six pathotypes have been distinguished on the basis of host resistance (Cook and Williams, 1972). In Victoria, Brown (1969) has found a single pathotype which differs from those described elsewhere. Thus it is necessary to determine what pathotypes occur in a newly discovered infested area before cultivars incorporating resistance and adapted to the area can be bred.

In New South Wales, *H. avenae* is found over a very small area (McLeod, 1973 ; Fig. 1). However, ready access to sources of resistance effective against local populations would be advantageous should the nematode spread. The present work was done in New South Wales with the aims of (i) identifying the pathotype present by testing cereal cultivars and lines known to be resistant to European pathotypes and (ii) locating sources of resistance amongst Australian cultivars used or of potential use in New South Wales.

TABLE 1

Origin of seed and reactions of European cultivars and lines to pathotypes of Heterodera avenae

Cultivar or line	Origin of seed	Recorded reactions to pathotypes	
Wheat			
Loros Aus 2897	Burnley, Victoria	**R**	D1, D2*
		S	V
Avena sterilis			
Cc4658	Wageningen, The Netherlands		Resistant to all pathotypes tested†
Barley			
7187CoSS	Rothamsted, England		Susceptible to all pathotypes tested
Drost	Rothamsted, England	**R**	D1, NA, NB, ND, B1‡
		S	D2, NC, B2,‡ V
191	Rothamsted, England	**R**	D1, D2, NA, NC, ND‡
		Rp	V
		S	NB, B3‡
No. 14	Rothamsted, England	**R**	NA, NB, B1‡
		Rp	B2,‡ V
		S	NC, ND‡
Marocaine 079 Morocco	Wageningen, The Netherlands	**R**	NA, NB, NC, ND, B1, B2,‡ V
		S	B3‡

Aus = prefix for accessions in the Australian Wheat Collection.
R = resistant; **Rp** = partially resistant; **S** = Susceptible.
D1, D2 = Danish pathotypes.
NA, NB, NC, ND = Netherlands pathotypes.
B1, B2, B3 = British pathotypes.
V = pathotype in Victoria (Brown, 1969 ; Brown and Meagher, 1970).
* Nielsen (1966).
† Cook and Williams (1972).
‡ Hayes and Cotten (1971).

MATERIALS AND METHODS

European cultivars and lines used in pathotype testing and their known reactions are shown in Table 1. Ten single plants of each variety were grown in pots of 800 g of soil in a glasshouse. Soil from three sites, enclosing the known infested area in New South Wales (Fig. 1) was tested. Tests were started in May each year in 1970, 1971 and 1972. After 12 weeks, new white cysts on roots and in the soil in each pot were counted, using the method of Cotten (1963), except that cysts collected on the 300 μm-aperture sieve were counted directly by placing it in a tray of water.

Australian cultivars were tested in the field at site 1 (Fig. 1). The soil in this district is a sandy solonised brown soil (Mallee soil) (Stace *et al.*, 1968). Seed was sown in May 1971, 1972, 1973 and 1974 in drill rows 100 m long and 36 cm apart. District rainfall was 416 mm (18% above average) in 1971, 260 mm (27% below average) in 1972, 684 mm (94% above average) in 1973 and 730 mm (104% above average) in 1974 (Australian Bureau of Meteorology, 1971–74). In September each year, 20 plants were dug randomly from each row, freed of excess soil, washed carefully and the number of cysts on the roots counted. Cultivars which were obviously susceptible, with an average of more than four cysts per plant, were not sown in following years, except that Festiguay wheat, which had an average of eight cysts per plant in 1971, was sown in succeeding years and Dural and Duramba wheats, which had averages of five and nine cysts per plant respectively in 1973, were sownagain in 1974.

RESULTS AND DISCUSSION

Results of tests with European lines and cultivars are shown in Table 2 and with Australian cultivars in Table 3.

TABLE 2

Production of cysts on European cereal cultivars and lines by Heterodera avenae *from Koraleigh, New South Wales*

Number of cysts on ten plants as a percentage of number on ten susceptible control plants

Cultivar	Site 1			Site 2		Site 3	Reaction
	1970	1971	1972	1971	1972	1970	
Wheat							
Loros Aus 2897*	—	447	307	200	537	—	S
*Avena sterilis** (Cc4658)	1	1	0	0	0	0	R
Barley							
7187CoSS†	135	584	740	127	1250	130	
Drost	100	100	100	100	62	100	S
191	16	15	12	6	10	12	Rp
No. 14	12	16	15	12	5	19	Rp
Marocaine 079	3	9	5	0	2	0	R
Morocco	0	5	5	5	0	1	R

R=resistant; Rp=partly resistant; S=susceptible.

* Number of cysts on ten plants shown.

† Control susceptible cultivar, number of cysts on ten plants shown.

Uniformity of eastern Australian populations

Tests of the European cultivars and lines in soil from different sites and in different years gave similar results (Table 2) and provide no evidence for more than one pathotype. The reactions are in agreement with those reported in Victoria (Brown, 1969). Twenty-five Australian cultivars tested both in Victoria and New South Wales have reacted similarly (Table 3). It is concluded that New South Wales and Victorian populations of *H. avenae* belong to the one pathotype, as is to be expected from the geographical position of the infested areas.

TABLE 3

Numbers of cysts of Heterodera avenae *on Australian cultivars of wheat, oats, barley and rye grown in naturally infested soil at Koraleigh, New South Wales*

Cultivar	Number of cysts per plant (mean of 20 and standard error)			
	1971	1972	1973	1974
Wheats				
Bencubbin	—	—	>20*	—†
Bokal	—	—	>20	—
Condor	—	25±5	—	—
Darkan	—	—	>20	—
Dural	—	—	5±1	7±3
Duramba	—	—	9±2	9±5
Eagle	18±3	—	—	—
Egret	—	16±1	—	—
Emblem	—	—	>20	—†
Falcon	11±3	—	—	—
Festiguay	8±·5	1±·4	2±·5	5±1
Gabo	—	—	15±1	—†
Gamut	16±2	—	—	—
Gatcher	14±3	—	—	—
Glenwari	—	—	>20	—†
Glaive	11±2	—	—	—
Halberd	—	—	>20	—
Heron	26±6	—	—	—†
Insignia	—	—	>20	—†
Isis	—	—	>20	—†
Kite	—	14±1·4	—	—
Mendos	—	—	>20	—
Mengavi	—	—	14±1	—
Mersey	—	—	>20	—
Olympic	18±3	—	—	—†
Pinnacle	32±3	—	—	—†
Robin	21±5	—	—	—
Spica	13±3	—	—	—
Summit	24±2	—	—	—†
Sun 17 I	—	—	—	13±4
Sun 17 L	—	—	—	>20
Tarsa	—	38±5	—	—
Teal	>20	—	—	—
Timgalen	16±2	—	—	—
Winglen	20±8	—	—	—
Winter DARF	—	—	>20	—
Winter Heron	—	—	—	>20
Wren	19±3	—	—	—
Zenith	—	—	—	>20
WW 33	—	—	>20	—
WW 97–2	—	—	—	>20
IIB	—	—	—	>20
Oats				
Acacia	·9±·3	0	·5±·2	0†
Algerian	1±·4	2±·1	1·5±·6	0†
Avon	·1±·06	·2±·1	0	0†
Bundy	2±·5	2±·3	3±1	0†
Cassia	—	>20	—	—
Cooba	·7±·4	·5±·2	·2±·1	0
Coolabah	>20	—	—	†
Fulghum	7±1	—	—	—†
Irwin	—	—	—	0
Klein 69B	·6±·3	·1±·07	0	0
Mugga	5±·6	—	—	—†
Swan	—	—	—	2±·4
P4315	2±·8	·4±·2	1±·3	0

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* All plants with more than 20 cysts.

† Tested in Victoria by Brown and Meagher (1970) with similar results.

TABLE 3—*continued*

Numbers of cysts of Heterodera avenae *on Australian cultivars of wheat, oats, barley and rye grown in naturally infested soil at Koraleigh, New South Wales*

Cultivar	Number of cysts per plant (mean of 20 and standard error)			
	1971	1972	1973	1974
P4319	—	2±1	0	·5±·6
M1354	—	—	·6±·2	2±·3
Barley				
Abyssinian	15±3	—	—	—
Beecher	37±4	—	—	—†
Bussell	11±2	—	—	—
Clipper	14±3	—	—	—†
Dampier	11±2	—	—	—†
Ketch	—	13±2	—	—
Lara	—	13±1·5	—	—
Noyep	6±1	—	—	—†
Prior	11±3	—	—	—†
Resibee	14±1	—	—	—†
Weeah	10±2	—	—	—†
Rye				
South Australian	0	0	0	—†
Strain 8	6±1	—	—	—†
Weethalle	·4±·1	0	0	—

* All plants with more than 20 cysts.

† Tested in Victoria by Brown and Meagher (1970) with similar results.

Relation of Australian and overseas pathotypes

Most of the wheat cultivars tested proved susceptible whereas the majority of oat varieties were resistant (Table 3). A similar situation occurs in Victoria (Brown and Meagher, 1970). However, in Europe, most commercial oat cultivars are susceptible (Cook and Williams, 1972). Whether this is due to genetic differences between European and Australian oat cultivars or to nematode differences is not clear. Franklin (1951) and Cotten (1967*b*) found oat cultivars which were resistant or partly resistant when tested in Australia (Millikan, 1938 ; Brown and Meagher, 1970) but susceptible when tested in England. This suggests differences between nematode populations rather than host differences.

The partial resistance of 191 barley and the susceptibility of Loros wheat (Table 2) rule out the presence of Danish pathotypes 1 and 2 (Table 1). The susceptible reaction of Drost and partial resistance of 191 could be explained by the presence of a mixture of two European pathotypes. For example Netherlands C, able to form cysts on Drost, mixed with a smaller number of Netherlands B, able to form cysts on 191 (Table 1), could give this reaction. Further, Netherlands C forms more cysts on Drost than on No. 14 (Kort, personal communication) as do New South Wales populations (Table 2). However, no line of Loros wheat has been found susceptible to C (Kort, personal communication) whereas both Victorian and New South Wales populations form cysts freely on the line of Loros wheat used in these tests (Brown, 1969 ; Table 2). British pathotype 2 mixed with a smaller number of 3 could give a susceptible reaction on Drost and a partially resistant reaction on 191 and No. 14 (Table 1). British pathotype 3, however, would form as many cysts on Marocaine 079 and Morocco as on 191 (Cook and Williams, 1972) but this is not so for the New South Wales nematode. Thus, although there are resemblances, there are important differences which indicate that Australia has a pathotype differing from any known in Europe.

The results perhaps indicate a relationship with the pathotype in Rajasthan, India, where Gill and Swarup (1971) report that Drost is susceptible and 191 is only partly resistant. However, the Indian pathotype reproduces on *Zea mays* L. (Gill and Swarup, 1971 ; Yadav and Verma, 1971) but our population failed to form cysts on this host in glasshouse tests in which Drost barley plants had an average of 88 cysts per plant.

Sources of resistance for use in New South Wales

Only three of the Australian wheat varieties tested–Festiguay, Dural and Duramba–showed a degree of resistance (Table 3). Festiguay is a cross between Festival and an introduction from Uruguay, Uruguay C10837 (Macindoe and Walkden Brown, 1968). Resistance has evidently come from the Uruguay introduction since Festival is susceptible in Victoria (Brown and Meagher, 1970). This cultivar is suited to conditions in the north-western wheat belt of New South Wales, but it is being replaced by the susceptible Tarsa (Matheson, 1972). Its resistance could be introduced into other cultivars more suited to the southern wheat belt. Dural and Duramba are drum wheats (cultivars of *Triticum durum* Desf.) and their resistance would be more difficult to use. Millikan (1938) found that *T. durum* cultivars were, on the whole, more resistant than *T. aestivum* L. cultivars at Nhill in Victoria.

The resistance of Cooba oat is fortunate because it is the most widely grown oat in New South Wales (Walkden Brown and Fitzsimmons, 1972). Coolabah is a new cultivar suitable for the marginal rainfall areas where the nematode now occurs but it has the disadvantage of being susceptible. The susceptibility of Cassia is also disadvantageous since this is now recommended as a gradual replacement for resistant Avon (Komoll and Fitzsimmons, 1973), the third most widely grown oat in New South Wales. A further possible source of resistance in oats is that available in the Cc4658 of *Avena sterilis* L. (Table 2).

All of the Australian barley cultivars tested (Table 3) allowed too many cysts to develop to be considered resistant. However, two of the European test cultivars, Marocaine 079 and Morocco, were resistant (Table 2) and could be used as sources for introducing resistance into locally adapted cultivars. Barley 191, the source used in breeding resistant barleys in Britain (Hayes and Cotten, 1971), would be less effective than these since in all but one test it supported considerably more cysts (Table 2).

South Australian rye and Weethalle rye, a selection of the former, are highly resistant as has been found in Victoria (Brown and Meagher, 1970). These could be used directly to prevent population build-up.

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TYPE SPECIMENS IN THE MACLEAY MUSEUM, UNIVERSITY OF SYDNEY
VII. THE HOLOTYPE OF *GRYLLUS SPINULOSUS* JOHANSSON (INSECTA : ORTHOPTERA : TETTIGONIOIDEA)

G. P. Whitley* and P. J. Stanbury†

(Plates XXII and XXIII)

[Accepted for publication 18th June 1975]

Synopsis

Specimen of an insect, labelled 1756, in The Macleay Museum, Sydney, is identified as the holotype of *Gryllus spinulosus* Johansson 1763.

Introduction

The Macleay Museum at the University of Sydney contains a comprehensive zoological collection including a number of type specimens. Lists of types of insects (Hahn, 1962), fish (Stanbury, 1968), reptiles (Goldman *et al.*, 1969), birds (Stanbury, 1969*a*), mammals (Stanbury, 1969*b*) decapod crustaceans (Griffin and Stanbury, 1970) and mollusca (Ponder and Stanbury, 1972) have been published.

This paper describes the oldest dated specimen in the Macleay Museum.

Gryllus spinulosus

The specimen is a female orthopteran insect 7·5 cm long, belonging to the superfamily Tettigonioidea, family Tettigoniidae. It formed part of Alexander Macleay's original collection which he brought to Sydney in 1825. It is pinned to a circular label, dating from the eighteenth century, which reads : " A curious insect from Barbary, the only one known of its kind in England. Geo. Edwards, 1756 ". It has been figured by Anderson (1965) and exhibited by Whitley (1975), but its specific identity has not hitherto been fully determined.

A figure and description (Anonymous, 1799), apparently of this specimen, were recently noticed in *The naturalist's pocket magazine*, a rare, anonymous work, in seven volumes, published between 1798 and 1803, without numbers on its pages or plates. Bibliographical particulars of this publication, which also contains early paintings of Australian animals and plants, have been provided by Hindwood (1933, 1968). The anonymous author (who may have been George Shaw of the British Museum) did not give a scientific name to the insect but called it " Whistle Insect " without explanation. The locality was given as Santa Crux in Barbary.

George Edwards (1694–1773), mentioned on the Macleay Museum label, was a celebrated ornithologist who illustrated not only birds but also plants, insects and mammals on his published plates (Edwards, 1751, 1758). In Edwards' rare book *Gleanings.* (Edwards, 1758, Vol. 2 : 160, Pl. 285, figs 3–5) the " Whistle Insect " is figured from three aspects–dorsal, ventral and lateral.

Plate XXII shows the 1758 illustration and Pl. XXIII the specimen in the Macleay Museum. In both *Gleanings* and *The naturalist's pocket magazine* the

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* The Australian Museum, Sydney. *Deceased, July 1975.*

† The Macleay Museum, University of Sydney, New South Wales, 2006.

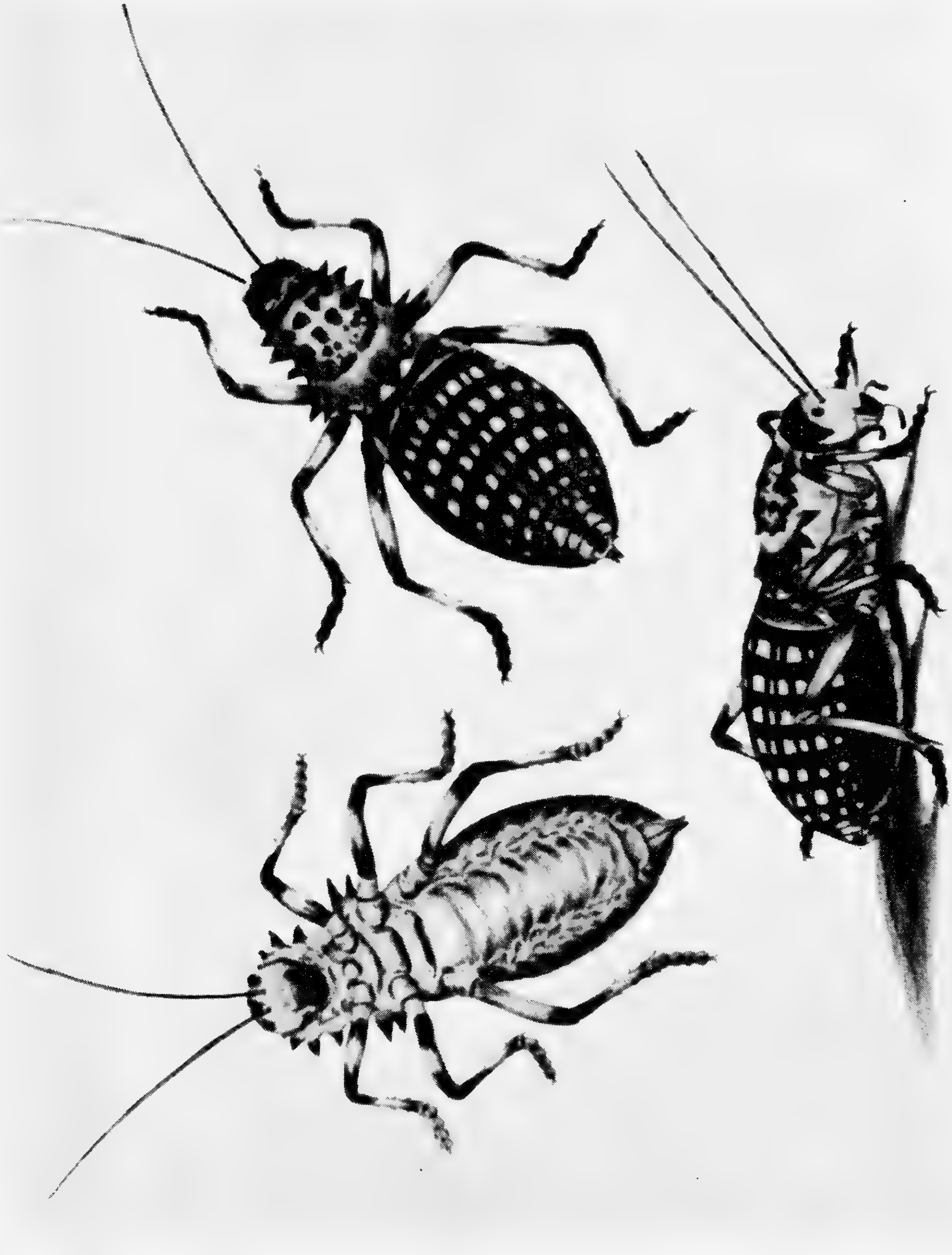

PLATE XXII
A black and white photograph of the coloured illustration of the "Whistle Insect" in G. Edwards, *Gleanings of natural history* . . . London, Royal College of Physicians, 1758.

PLATE XXIII

Gryllus spinulosus Johansson. The specimen in the Macleay Museum, photographed in 1975. Its length is 54 mm, head to tail, excluding antenna. (The dorsal and ventral views have been photographed at a slightly lower magnification than the lateral view.)

antennae are long, but it is hardly surprising that the specimen in the Macleay Museum has lost parts of the antennae over more than two centuries.

Edwards' text (1758, pp. 161–162) is mostly descriptive of the specimen but reads in part :

> " The Whistle-Insect is shown in three different views at the bottom of the plate. The head is made like that of a locust . . . [full description follows] . . . the horns are brown.
> " The Whistle-Insect was brought from Santa Crux in Barbary, by my good friend Capt. John Dobson, because it very nearly agrees with another insect found in Africa, of which the natives make whistles to call their cattle together : these whistles consist of the whole outer cover of the insect ; the head, legs and end of the tail being taken off, and the inward parts taken out ; which shells, hardened and dried for the purpose, were found hanging about the necks of the natives of Africa, on the coast over-against Madagascar. The figures of them are shewn in my History of Birds, &c. plate 178. I do not know what tribe or genus of insects to class this last with : I believe it hath not till now been figured or described ".

The Oxford English Dictionary entry under *whistle insect* is : " 1760 G. Edwards *Glean. Nat. Hist. II.* The head is made like that of a locust : the . . . thorax is surrounded with many sharp points ; . . . I have called it the Whistle-Insect, because it very nearly agrees with another insect found in Africa, of which the natives make whistles to call their cattle together : these whistles consist of the whole outer cover of the insect ".

Plate 178 of George Edwards' *Natural history of birds* (Vol. 3, 1751) shows, associated with a bird called the Grenadier, several insects, drawn in 1751. Amongst them are the dorsal, lateral and ventral views of another genus of insects (minus legs), perhaps a large weevil, and obviously the true Whistle Insect from Africa.

Such a well illustrated species as the Santa Crux Whistle Insect would have received a scientific name. Edwards' date of publication was too late for it to be noticed in Linnaeus' tenth edition of his *Systema naturae* (1758), but inspection of Gmelin's edition (1789) and a check with Fabricius (1793) showed that Edwards' Whistle Insect had been named *Gryllus spinulosus* by Linnaeus.

In Linnaeus' *Amoenitates academicae* (1763, p. 398), the following entry appears :

> " 35. *GRYLLUS spinulosus* L., thorace Ipinis muricato cinctoque, corpore aptero.
> *Edw. av.* 2.p. 161.t.285.f.3. 4. 5.
> *Habitat in* Indiis
> *Gryllos in maximos numberandus.* Antennae *filiformes, longitudine fere corporis.* Thorax *testaceus, spinis numberosis muricatur & postice margine spinoso cinctus.* Abdomen *supra nigrum maculis testaceis tesselatum. Alae nulla* ".

The evidence presented above suggests that the specimen in the Macleay Museum is the one collected by Edwards in 1756 ; described and illustrated by him in 1758 ; and first identified under Linnaeus' name in 1763.

Gryllus spinulosus is now known as *Eugaster spinulosus* (Kirby, 1906), or more correctly as *Eugaster spinulosa* (Johansson), with the specific name having a feminine ending to agree in gender with *Eugaster*. Johansson is the correct author of the name as *Amoenitates academicae* was published under Linnaeus' general authorship, with contributions from other biologists.

Another label was added to the specimen in 1975. The new label reads *Eugaster spinulosa* (Johansson). For the history of this specimen see this paper.

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THE LARVAL DEVELOPMENT AND METAMORPHOSIS OF THE ASCIDIANS *PYURA PRAEPUTIALIS* (HELLER) AND *PYURA PACHYDERMATINA* (HERDMAN) (PLEUROGONA, FAMILY PYURIDAE)

D. T. Anderson,* B. M. White* and E. A. Egan*

[Accepted for publication 23rd July 1975]

Synopsis

Pyura praeputialis and *P. pachydermatina* are self-fertile hermaphrodites. In the Sydney region, artificial fertilisation (self or cross) yields larvae of *P. praeputialis* in April, May and September, and of *P. pachydermatina* in May, June and July. Larvae cannot be obtained by this method at other times of the year.

The egg of *P. praeputialis* is 0·23 mm in diameter, that of *P. pachydermatina*, 0·25 mm. At 20–23°C, the tadpole larvae of both species hatch within 12 hours of fertilisation. The trunk of the larva in both species is relatively large and yolky. In *P. pachydermatina*, the anterior adhesive papillae are long and prominent.

Tadpoles of both species begin to settle and metamorphose within 1–2 hours of hatching. Settlement occurs readily on glass. Degenerative changes in the larval tail begin at the distal end. Muscular contractions break up the tail structures in *P. pachydermatina* but not in *P. praeputialis.*

Ampullae develop on the zooid after settlement. In *P. praeputialis*, the 8 ampullae function in attachment and as a support for the tunic. The 4 ampullae of *P. pachydermatina* do not function in attachment. The attachment stalk of *P. pachydermatina* develops in the region of the adhesive papillae.

Siphons are developed in both species within 20 hours of settlement. By this time the zooid has begun to differentiate the pharynx, intestine and other adult structures, though subsistence on yolk continues for several days.

In comparison with other pyurids, although the eggs of *P. praeputialis* and *P. pachydermatina* are among the larger eggs in the family, embryonic development is rapid and the free-swimming larval stage is brief. The rudiments of the permanent organs show no differentiation until after settlement.

INTRODUCTION

Larval development and metamorphosis have been described for several species of Pyuridae (*Boltenia echinata*, *B. hirsuta*, Berrill, 1929, 1948 ; *Pyura squamulosa*, *P. microcosmus* Millar, 1951, 1954 ; *Herdmania pallida*, Sebastian, 1953 ; *Halocynthia pyriformis*, Berrill, 1929, 1935 ; *Halocynthia roretzi*, Hirai, 1941, 1968 ; see also Berrill, 1950, 1955). All of these species are oviparous and fall within the range of ascidian species categorised by Berrill (1935) as having small eggs, 0·26 mm or less in diameter, with a basal yolk/cytoplasm ratio and an unspecialised mode of development.

The pyurid fauna of the New South Wales coast includes two large species in abundance, *Pyura praeputialis* (Heller) and *Pyura pachydermatina* (Herdman). The mode of development of these species has not hitherto been known. *P. praeputialis* has generally been referred to in Australia as *P. stolonifera*, e.g. by Dakin (1952), Kott (1952) and Endean (1955), but has more recently been separated by Millar (1963) from the closely related *P. stolonifera* of South Africa. Millar's ruling, accepted by Goddard (1972), has been followed by the present authors.

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* School of Biological Sciences, University of Sydney, New South Wales, 2006.

Goddard (1972) investigated the seasonal changes in gonad weight relative to body weight in *P. praeputialis* and determined probable breeding seasons. The seasonal cycle of *P. pachydermatina* has not been investigated. In the present work, Goddard's results on the seasonal cycle of *P. praeputialis* are confirmed, the seasonal cycle of *P. pachydermatina* is established and the development of both species is described.

MATERIALS AND METHODS

Specimens of *Pyura praeputialis* and *P. pachydermatina* were collected at monthly intervals from February 1973 to January 1974. All of the specimens used in this study were obtained from intertidal rock platforms in the Sydney area, either on the open coast (Cape Banks at the entrance to Botany Bay) or in the lower reaches of Port Jackson (Dobroyd Point and Balmoral on the northern shore ; Bottle and Glass Rocks on the southern shore). *P. praeputialis* is common on the lower littoral zone at these localities. *P. pachydermatina* is found at the lower littoral margin, accessible on spring low tides. No specimens of the estuarine form of *P. praeputialis* were examined in the present study.

In the laboratory, each animal was removed from its test and opened to expose the gonads. The state of maturity of the gonads was assessed by visual inspection and was then tested by attempting artificial fertilisation. Eggs were released from the gonad by separating off portions of ovarian tissue and slicing the tissue finely in filtered sea water. The eggs were then teased free, washed in four changes of filtered sea water and dispensed into glass Petri dishes in sufficient numbers to provide an even, slightly spaced distribution on the bottom of the dish. A sperm suspension was obtained by slicing portions of testis in a Petri dish of filtered sea water. Approximately 2 ml of sperm suspension was added to each dish of eggs. After 30 minutes, the water was changed to remove excess sperm. In dishes in which development ensued, the water was changed at three-hourly intervals to prevent the infestation of the embryo cultures by protozoans. All cultures were maintained at 20–23°C.

At each attempted artificial fertilisation, both self-fertilisation and cross-fertilisation were tested for individuals of each species. When ripe gametes were available, both methods yielded larvae. No differences in development were observed between embryos obtained by self-fertilisation and those obtained by cross-fertilisation. Natural spawning was not observed in the laboratory for either species.

When development was obtained, embryos and larvae were removed from the culture dishes at intervals and fixed in 5% formalin-seawater for subsequent examination. Representative fixed specimens were embedded in paraffin (M.P. 56°C), sectioned at 7 μm and stained with Harris' haematoxylin and eosin.

RESULTS

SEASONAL CYCLES

In this investigation, the occurrence of normal development following artificial fertilisation was taken as evidence that the animals contained mature eggs and sperm and were potentially capable of spawning. The question of whether spawning in the field is coincident with these times, or has a more restricted occurrence, was not investigated.

Pyura praeputialis : Using this criterion, the gonads of many individuals of *P. praeputialis* were found to contain mature eggs and sperm during the late autumn months, April and May. At this time, the ovarian portions of the gonads were distended with olive green eggs and the testicular portions were swollen and white. Many of the eggs released by dissection had a layer of follicle cells attached to the external surface of the chorion (Fig. 1A), and sperm suspensions showed a high level of activity. Artificial fertilisation yielded embryonic development followed by the hatching of larvae which settled and underwent metamorphosis.

In June, July and August, the winter months, the gonads and gametes of *P. praeputialis* retained the same appearance as in April and May, but the results of artificial fertilisation were different. The June and July tests yielded some early development of the eggs, many reaching the gastrula stage, but development usually became arrested at this stage. A few eggs completed embryonic development, but the tadpoles that hatched were abnormal and died soon after hatching. The August tests produced a few cases of early cleavage only, with no development beyond this stage.

In the September samples, some specimens of *P. praeputialis* showed a reversal of this condition, with normal embryos and larvae resulting from artificial fertilisation. By October, however, only a few abortive larvae could be obtained, and from November to March, no development was observed in any of the monthly tests using artificial fertilization. In November, December and January, the gonads were small and lacked the distinctive coloration of ripe gonad tissue. This coloration, olive green in the ovarian portions and white in the testicular portions, reappeared in some individuals in February and March, but the gametes extracted during these months showed signs of immaturity. The eggs had no follicle cells attached to the chorion, and the sperm, although active, had vacuoles attached to their tails. Artificial fertilisation tests using these gametes yielded no more than a few abortive early cleavage divisions.

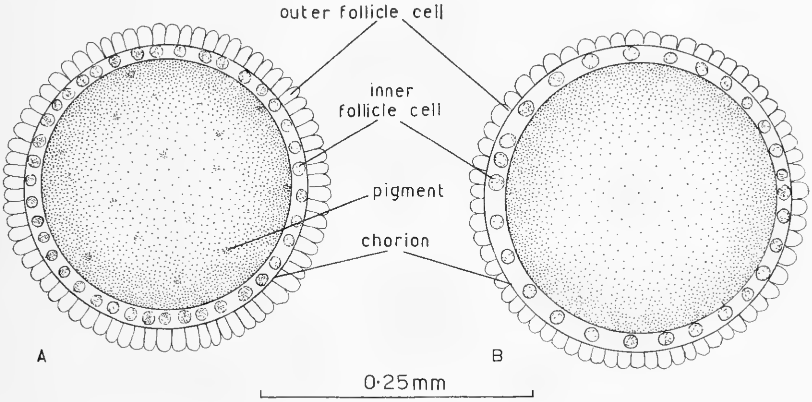

Fig. 1. Unfertilised eggs. A. *Pyura praeputialis.* B. *Pyura pachydermatina.*

In summary, therefore, the occurrence of mature gametes capable of yielding normal development after artificial fertilisation is confined in *P. praeputialis* to the months of April and May, with a minor resurgence in September.

Pyura pachydermatina : The seasonal changes in the gonads and gametes of *P. pachydermatina* are more sharply defined than those of *P. praeputialis.* During February and March and also in April immature gametes were plentiful but no eggs of mature size were found in the gonads of any individual examined. Sperm were obtained from some individuals during these months, but were not fully active and had vacuoles attached to their tails. In May, June and July, in contrast, the gonads of all individuals in each sample were distended, ovarian portions being olive green and testicular portions white. Artificial fertilisation resulted in embryonic development, normal hatching, settlement and metamorphosis.

During August, September and October, the gonads in *P. pachydermatina* remained superficially unchanged, but artificial fertilisation yielded only abortive embryonic development, with no hatching. Active resorption of gametes was evident in the November sample and, by December, none of the individuals examined had large gonads. Proliferation of immature gametes in the gonads was resumed in January.

P. pachydermatina in the vicinity of Sydney, therefore, has mature gametes in intertidal individuals of the population only in the late autumn to winter months, May, June and July.

Development

Gametes

The mature eggs of both species are spherical and yolky, with an external chorion and a layer of small follicle cells. Both are olive green in general coloration, but the egg of *P. praeputialis* is 0·23 mm in diameter and has small, reddish pigment spots scattered over its surface, while the egg of *P. pachydermatina* is 0·25 mm in diameter and lacks surface pigment spots. The chorion of an egg freshly removed from the ovary is attached to the egg surface, but lifts off after immersion of the egg in seawater, leaving a perivitelline space 30 μm wide. Inner follicle cells are visible in this space.

The sperm of *P. praeputialis* is about 50 μm long, with a rod-shaped head 7·5 μm long. That of *P. pachydermatina* is about 40 μm long, with a rod-shaped 5·0 μm head.

Embryonic Development

Development of the embryo follows the same general timetable in *P. praeputialis* and in *P. pachydermatina.* The first two cleavage divisions are completed within one hour after fertilisation and the next four divisions follow during the second hour. Cleavage is total, equal and radial (Fig. 2). Histological sections of cleaving eggs reveal a yolk-free cytoplasmic halo around each nucleus and a uniform distribution of yolk throughout the remainder of each cell. One pole of the 2-cell stage contains a cluster of large, refractile granules. By the 4-cell stage, the distribution of these granules has changed. In *P. praeputialis* the granules are now grouped around the nucleus in all four cells. In *P. pachydermatina* they are grouped around the nucleus in two cells only. The same pattern of peripheral yolk and central nucleated cytoplasm with associated granules persists in the 8-cell and later stages of cleavage, but the significance of the refractile granules is not known.

The hemispherical gastrula stage is attained in both species within 3 hours of fertilisation (Figs 2D, 4A). The ectoderm cells are still large and yolky, but most of the yolk is now located in the large endoderm cells lining the archenteron. With the completion of gastrulation, the archenteron is obliterated.

The tail rudiment becomes visible by 5–6 hours (Fig. 3) and completes its elongation to encircle the body of the embryo by 8–10 hours. The yolk reserves now lie mainly in the mass of endoderm cells in the trunk rudiment. The ectoderm cells are smaller than in the gastrula, but still contain some yolk granules (Fig. 4B). The notochord cells are also yolky, but the large muscle cells of the tail are now yolkless and basophilic. The otolith and ocellus are visible in the trunk by this time and the anterior adhesive papillae are beginning to develop.

The Tadpole Larva

In embryo cultures maintained under continuous illumination, hatching in both species begins about 12 hours after fertilisation. The tadpole larvae of the two species are easily distinguished (Fig. 5).

The larva of *P. praeputialis* (Fig. 5A) is 1·0–1·1 mm long. The trunk is 0·30 mm long and 0·24 mm deep, with three short, slightly tapered papillae at the anterior end. The tail is 0·70–0·80 mm long. The larva of *P. pachydermatina* (Fig. 5B) is 0·9–1·0 mm long, with a trunk 0·30 mm long and 0·17 mm deep. The anterior papillae are more prominent than in *P. praeputialis*, being longer, thicker and set more widely apart. The tail is 0·60–0·70 mm long. The dorsal

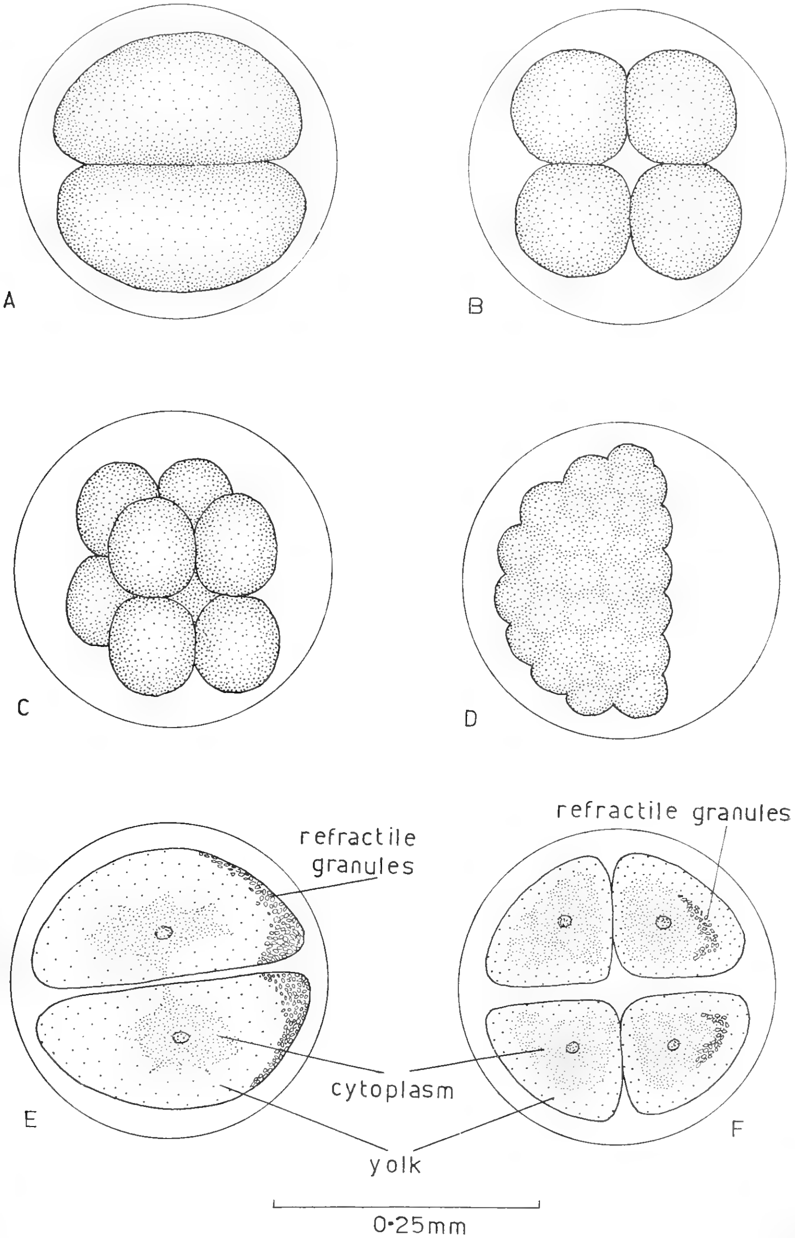

Fig. 2. *Pyura pachydermatina*. A. 2-cell stage. B. 4-cell stage. C. 8-cell stage. D. gastrula. E. 2-cell stage in section. F. 4-cell stage in section.

and ventral tail fins of *P. praeputialis* are larger, more regularly shaped and more distinctly striated than those of *P. pachydermatina*, but no differences in swimming activity were observed between the two species. Both tadpoles swim about randomly in short bursts and are negatively phototropic.

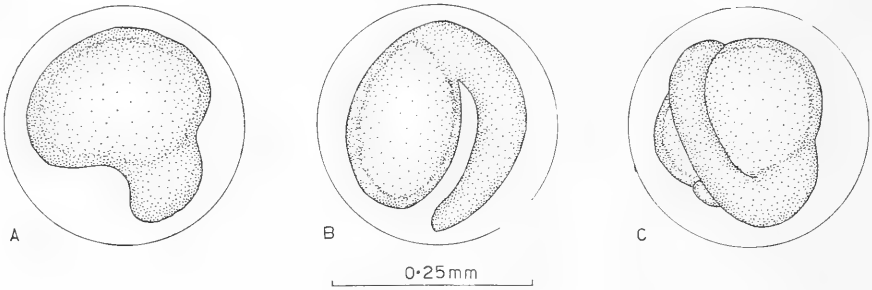

Fig. 3. *Pyura pachydermatina*, stages in development of the tail. A. 5–6 hours. B. 7–8 hours. C. 8–10 hours.

Histological examination (Fig. 6) shows that the ectoderm cells of the larval trunk, though small, still contain some yolk. The anterior papillae are protrusions of ectoderm, with a few mesoderm cells in the interior. The ectodermal cells of the papillae are enlarged and glandular. The dorsal ectoderm shows no sign of the invagination of the rudiment of the peribranchial sacs.

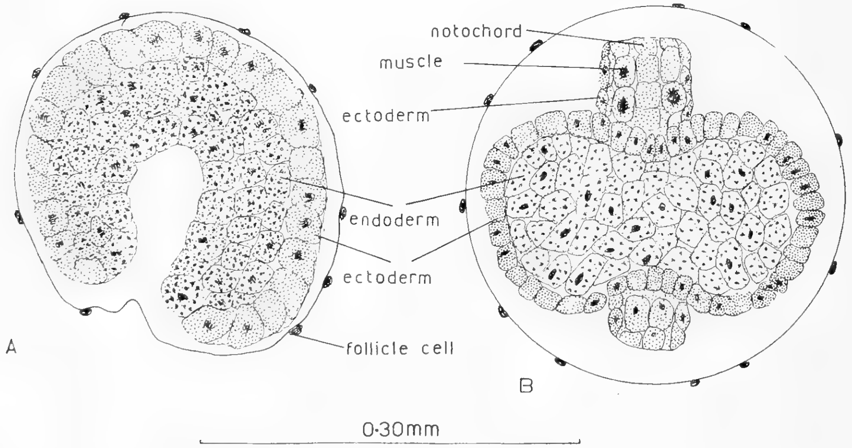

Fig. 4. *Pyura praeputialis*. A. gastrula in section. B. 8–10 hour embryo in transverse section.

Inside the trunk, the endoderm remains a mass of yolky cells, with no development of a central lumen or epithelial arrangement. The cerebral vesicle with its otolith and ocellus is embedded dorsally in the endodermal mass. Posteroventral to the endoderm is a compact mass of small, darkly staining mesoderm cells, clustered around the anterior end of the notochord.

In the tail, the larval muscle cells are similar in both species but the notochord of each is distinctive. In *P. praeputialis*, the anterior face of each notochord cell is concave, leaving a disc-shaped vacuole between successive cells. The nucleus

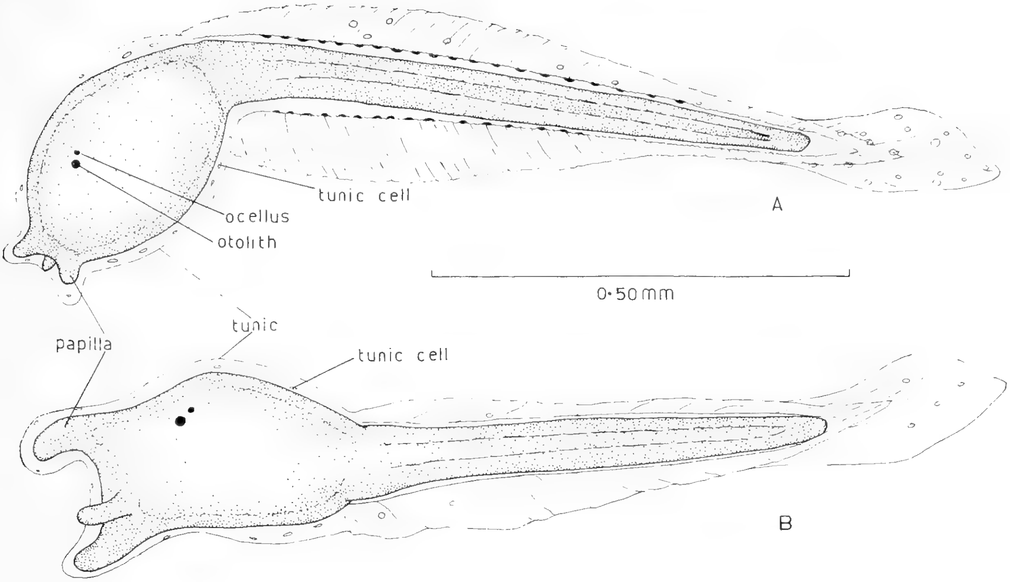

Fig. 5. A. larva of *Pyura praeputialis*. B. larva of *Pyura pachydermatina*.

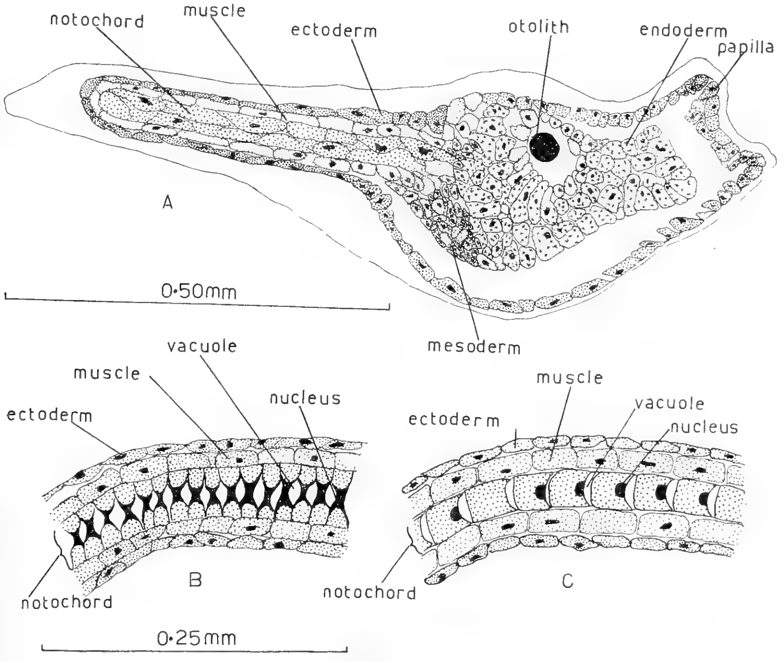

Fig. 6. A. longitudinal section of the larva of *Pyura pachydermatina*. B. frontal section of the larval tail of *Pyura pachydermatina*. C. frontal section of the larval tail of *Pyura praeputialis*.

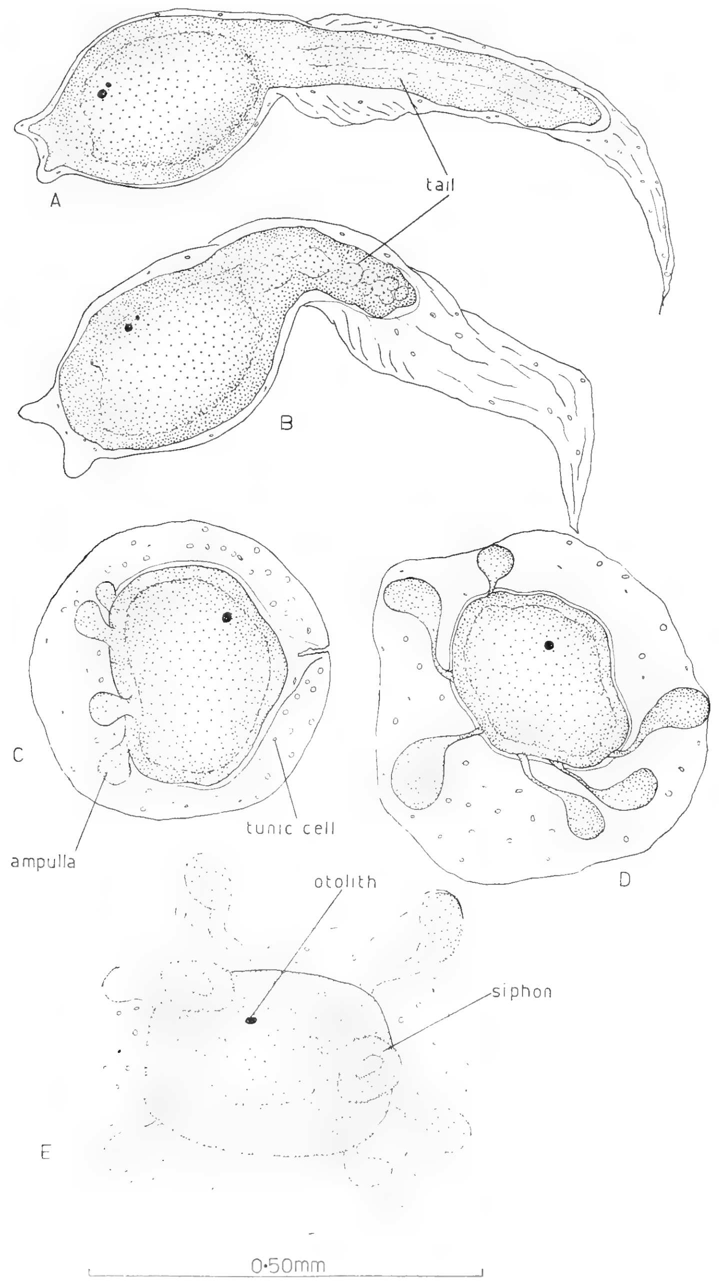

Fig. 7. Metamorphosis of *Pyura praeputialis*. A–B. stages in tail resorption. C–D. development of ampullae. E. development of siphons.

is ovoid and lies at the anterior end of the cell (Fig. 6C). The notochord cells of *P. pachydermatina* are concave on both faces, leaving lens shaped vacuoles between the cells (Fig. 6B). The nucleus occupies the narrow central region of the cell and is irregular in form.

Settlement

Within 2 hours of hatching, the tadpole in both species has settled and begun to metamorphose. Attachment to the substratum occurs in the usual manner by the anterior papillae and swimming activity then ceases. Following attachment, the papillae withdraw from the tunic, leaving the latter attached to the substratum. The tadpoles settled readily on the glass of their containers. Metamorphosis also began in tadpoles which did not become attached to the substratum, but was not completed in these individuals.

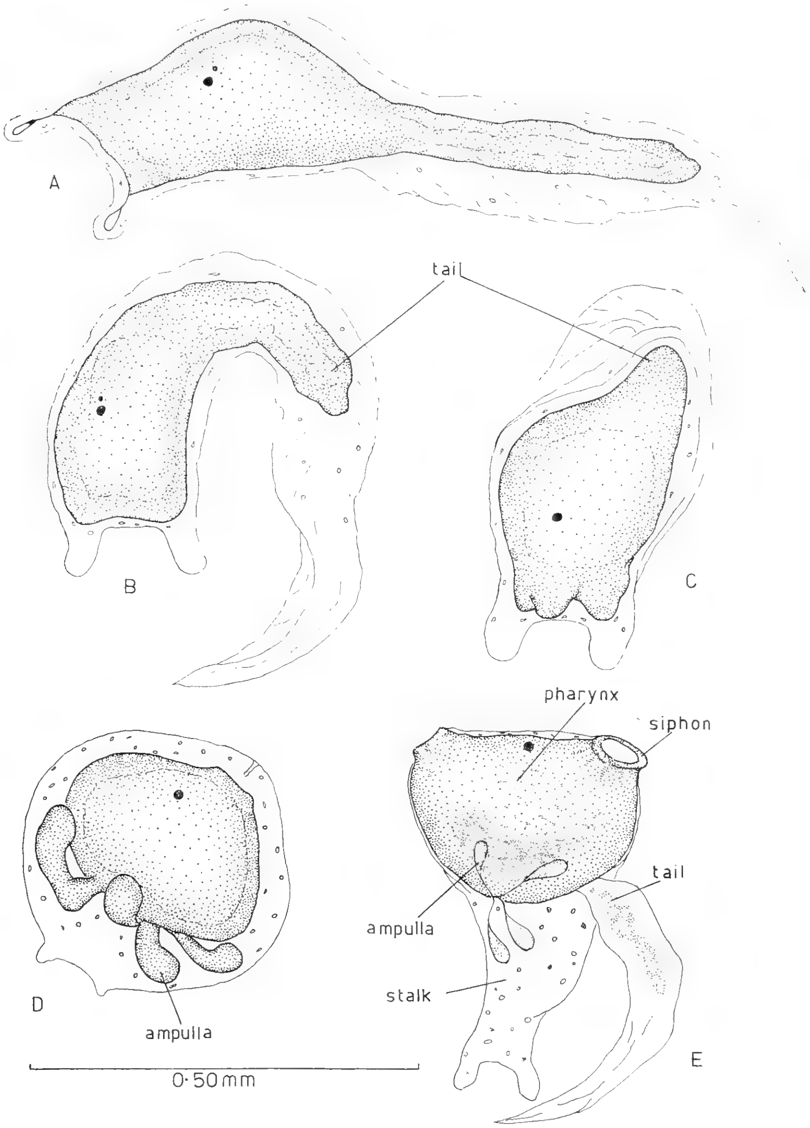

Fig. 8. Metamorphosis of *Pyura pachydermatina*. A–B. stages in tail resorption. C–D. development of ampullae. E. development of stalk and siphons.

Metamorphosis

The first external change in the metamorphosis of both species is reduction of the tail (Figs 7 and 8). In *P. praeputialis*, this change is accompanied by expansion of the space between the trunk and tunic. The resorption of the tail tissues begins at the tip, where the notochord and muscle cells round up and become vacuolated. In *P. pachydermatina*, muscular contractions play a part in breaking up the tail tissues and pulling them into the trunk. These contractions do not occur in *P. praeputialis*. The tunic of the tail remains intact during resorption of the tail tissues and often persists into post-larval stages. The tail is fully resorbed 4–6 hours after settlement.

As the tail is resorbed, the trunk becomes more spherical. *P. praeputialis* develops a ring of eight ampullae arising from a central point. The ampullae extend into the space between the trunk and tunic, becoming long and thin. Some of the ampullae grow down towards the substratum and appear to have an attachment function. Others project upwards and may have a role in supporting the tunic. *P. pachydermatina* develops four ampullae, which do not have an attachment function. Initial attachment in this species is followed by extension of the tunic at the site of attachment, to form the stalk. The ampullae are folded back against the surface of the trunk during their early growth and do not project into the stalk region. They become thin and vessel-like in later settled stages with functional siphons (Fig. 8E).

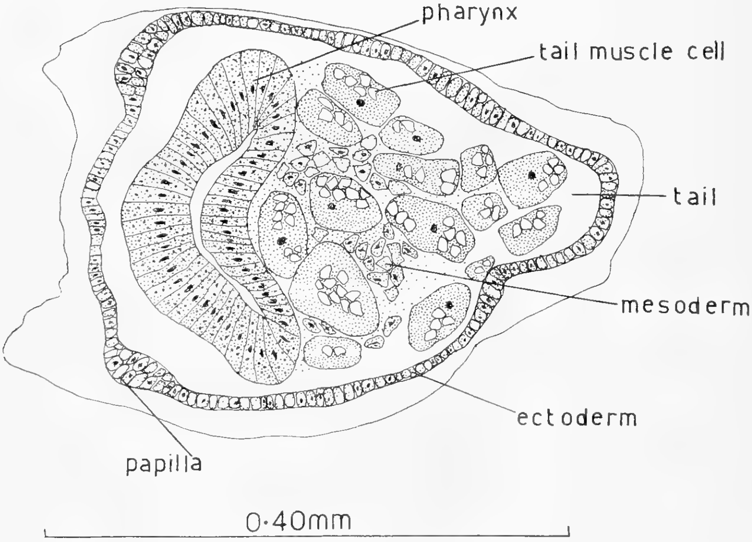

Fig. 9. *Pyura praeputialis*. Longitudinal section through a stage intermediate between Figs 7B and 7C.

The ampullae develop as ectodermal projections, but do not contain mesoderm cells. The endoderm is still a mass of yolky cells in the early settled stages of both species, but then becomes organised as an epithelium around a central lumen (Fig. 9). The vacuolated, degenerating tail cells can be seen in the body cavity of postlarval stages, surrounded by small cells derived from the mesoderm of the larval trunk. The otolith and ocellus remain visible in early settled stages, but the ocellus disappears as the ampullae become well developed.

The zooid in both species has developed oral and atrial apertures 15–20 hours after settlement. *P. praeputialis* shows regular contractions of the siphonal musculature 2 days after settlement. The otolith remains visible between the siphons. Contractions of the siphons in *P. pachydermatina* are first seen approximately 4 days after settlement, by which time contractions of the heart and ciliary action in the pharynx are also visible.

The timing of development of *P. praeputialis* and *P. pachydermatina* at 20–23°C can be summarised as follows :

First and second cleavage divisions	½–1 hour
Later cleavage divisions	1–2 hours
Gastrula	3 hours
Tail rudiment forming	5–6 hours
Tail fully developed	8–10 hours
Hatching	12 hours
Settlement	13–14 hours
Tail resorbed	18–19 hours
Ampullae developing	20–24 hours
Oral and atrial apertures present	28–34 hours
Siphons contracting (*P. praeputialis*)	2½ days
Siphons contracting (*P. pachydermatina*)	4½ days

DISCUSSION

SEASONALITY

The results obtained by Goddard (1972) indicated that *Pyura praeputialis* has a major breeding season in the autumn and a minor breeding season in the spring. The present study has confirmed this finding. *P. pachydermatina*, in contrast, has a single breeding season in the late autumn to early winter.

Among other pyurids, a similar restricted breeding season has been demonstrated by Sugawara *et al.* (1968) for *Halocynthia roretzi* in Japanese waters. Breeding in this species commences in the winter months, December to January, and continues for about two months. Several pyurid species of the northern hemisphere are known to breed in the summer (*Boltenia echinata*, *B. hirsuta*, Berrill, 1929, 1948 ; *Pyura squamulosa*, *P. microcosmus*, Millar, 1951, 1954 ; *Herdmania pallida*, Sebastian, 1953 ; *Halocynthia pyriformis*, Berrill, 1929, 1935) but the duration of the breeding season has not been established.

EMBRYONIC AND LARVAL DEVELOPMENT

The egg diameter, the duration of embryonic development and the duration of larval swimming are now known for a number of species of pyurid ascidians (Table 1). Table 1 shows that the egg diameters of *Pyura praeputialis* and *P. pachydermatina* fall towards the upper end of the range of the family. It might therefore be expected, following Berrill (1935), that the duration of embryonic development and the length of free-swimming larval life in these species would be in general similar to those of *Halocynthia roretzi* and *H. pyriformis*, with eggs of similar diameter. Clearly this expectation is not fulfilled by the results of the present work. Even taking into account the temperature differences involved, *Pyura praeputialis* and *P. pachydermatina* develop to hatching and attain settlement with unusual rapidity. *Herdmania pallida* is the only species among those so far studied that has a similar rapid development, but the results quoted for this species (Sebastian, 1953) were obtained at exceptionally high temperatures and still include a longer free-swimming period than in *P. praeputialis* and *P. pachydermatina*.

An explanation of how *P. praeputialis* and *P. pachydermatina* attain settlement and the onset of metamorphosis with such rapidity can be suggested in terms of the mode of development of their larval and permanent organ rudiment. It has long been known (Berrill, 1931, 1935, 1955) that these two sets of rudiments in an ascidian embryo show considerable independence in development. In all the pyurids that have been investigated, apart from *P. praeputialis* and *P. pachydermatina*, the rudiments of the permanent organs at hatching have already undergone some organogenesis and include a pharyngeal sac, an intestinal rudiment and sometimes a peribranchial invagination. Some further development of these rudiments takes place during the free-swimming period, and is then followed by the functional differentiation of the permanent organs after settlement has been attained.

In *P. praeputialis* and *P. pachydermatina*, however, the rudiments of the permanent organs do not reach this level of development in the embryo or larva. The endoderm remains a mass of yolky cells without a lumen. The mesoderm is a simple cluster of cells. The ectoderm cells retain yolk granules and there is no peribranchial invagination. In the period between the end of gastrulation and the completion of settlement, including the brief larval period, the rudiments of the permanent organs undergo almost no development. This brief time is devoted entirely to the development and functioning of the larval organisation. The further development and functional differentiation of the permanent organisation is delayed in these species until after settlement.

TABLE 1

Egg diameters and development in Pyuridae

Species	Egg diameter (mm)	Hatching at (hrs)	Free swimming (hrs)	Temperature (°C)	Reference
Pyura squamulosa	0·16	22	10	18–20	Millar, 1951
Boltenia echinata	0·18	34	10	16	Berrill, 1929, 1935, 1948
Boltenia hirsuta	0·18	34	10	16	
Herdmania pallida	0·19	8	3	26–29	Sebastian, 1953
Pyura microcosmus	0·20	24	24	18–20	Millar, 1954
Pyura praeputialis	0·23	12	1–2	20–23	this paper
Pyura pachydermatina	0·25	12	1–2	20–23	
Halocynthia roretzi	0·25	46	24	13–14	Hirai, 1941, 1968
Halocynthia pyriformis	0·26	60	—	16	Berrill, 1935

A simple change in the developmental relationship between the larval and permanent organisations therefore accounts for the brevity of embryonic development and larval life in *P. praeputialis* and *P. pachydermatina*. It does not, of course, explain why this brevity should have evolved in the two species. There may be advantages in a shortened duration of vulnerable free stages in the life cycle of an oviparous sessile species, but much more will have to be known about their population biology before this question can be answered.

METAMORPHOSIS

In spite of the lesser degree of development of the permanent organs at settlement, the metamorphosis of *Pyura praeputialis* and *P. pachydermatina* also proceeds at a faster rate than those described for other Pyuridae, e.g. *Pyura squamulosa* and *P. microcosmus* (Millar, 1951, 1954). Resorption of the larval tail and development of the ampullae is completed within 12 hours of settlement in *P. praeputialis* and *P. pachydermatina* at 20–23°C, in contrast to 1–2 days in the two British species at 18–20°C. The development of functional siphons within 2½ days of settlement, as compared with 6–9 days, and the onset of feeding at 4 days, as compared with 12 days, are further indications of a generally faster rate of development after settlement in *P. praeputialis* and *P. pachydermatina* as compared with *P. squamulosa* and *P. microcosmus*.

The general pattern of metamorphosis and development of the permanent organs described by Millar (1951, 1954) for *Pyura squamulosa* and *P. microcosmus* is retained in *P. praeputialis*. The resorption of the tail and rounding up of the trunk are accompanied by the development of a ring of eight ampullae which serve temporarily in facilitating attachment of the test to the substratum. The ampullae are still prominent when the siphons become functional, and the otolith remains visible between the siphons. Metamorphosis in *P. pachydermatina* differs in several details. Only four ampullae are formed and they do not play a direct part in the growth of the attachment stalk of this species. By the time that the siphons are prominent, the ampullae in *P. pachydermatina* have become vestigial. The development of four ampullae rather than eight is a feature of *Boltenia echinata* and *Halocynthia pyriformis* (Berrill, 1929, 1948). A second feature of metamorphosis which *Pyura pachydermatina* shares with *Boltenia villosa*, but which does not occur in *Pyura praeputialis*, is the muscular contractile activity that plays a part in resorption of the larval tail (Barrington, 1968).

ACKNOWLEDGEMENT

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DEFENSIVE BEHAVIOUR OF THE NEW GUINEA STICK INSECT *EURYCANTHA* (PHASMATODEA : PHASMATIDAE : EURYCANTHINAE)

G. O. BEDFORD*

(Plates XXIV and XXV)

[Accepted for publication 17th September 1975]

Synopsis

A description is given of presumed defensive behaviour in New Guinea phasmatids of the genus *Eurycantha*, which inhabit hollow tree trunks and stumps. When disturbed, adult males raise the abdomen in an S-shape and strike together the metathoracic legs which are heavily armed with spikes. Any restraining object tends to be grasped by these legs and impaled on the spikes by the closure of the femoro-tibial joints. The male copulatory organ is repeatedly everted, releasing an odour. Females show similar, though weaker, grasping movements, as their metathoracic legs are thinner and less armed with spikes.

INTRODUCTION

Adult males of New Guinea Phasmatids of the genus *Eurycantha* have very large spikes on the metathoracic legs ; the use of these spikes in the behaviour of the insect was first noted briefly by Montrouzier (1855).

An opportunity was taken recently to restudy this matter ; the present paper describes the behaviour in considerably more detail than was given by Montrouzier and includes new aspects. Knowledge of the biology of the insect, of its morphological adaptations and of the circumstances in which the behaviour to be described occurs, suggests that this behaviour is defensive. But in the absence of experimental tests with predators it should strictly be referred to as *presumed* defensive behaviour (Robinson, 1969) ; however for convenience the word *presumed* is omitted.

MORPHOLOGICAL DETAILS

Montrouzier (1855) described his *Eurycantha* material as *Karabidion horrida* ; however the generic component of this name is a synonym for *Eurycantha*, the name *Eurycantha horrida* Boisduval, 1835, having priority. The morphology was discussed by Gurney (1947) and brief mention is made here only of certain morphological details which are important to the description of the defensive behaviour. Both sexes are of a dark chocolate brown colour, measure 11–13 cm long and approximately 2 cm wide, and are apterous. The femora of the metathoracic legs of the males are much larger and heavier than those of the other legs, and bear four backwardly directed sharp spikes which are absent from the other legs. The third spike is approximately 1·1 cm long, the others 0·3–0·4 cm. The hind tibia bears a conspicuous ventral tooth approximately 1 cm from the femoro-tibial joint. The tenth abdominal tergite bears a small roughly triangular tooth at each side and the eleventh forms the median triangular epiproct. The posterior edge of the ninth sternite also bears a median tooth.

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* FAO Rhinoceros Beetle Project, c/– Koronivia Research Station, Nausori, Fiji.

The females are thick bodied, with the metathoracic femora much thinner than in the males and all the spikes much smaller, being only approximately 0·25 cm long.

The related *Eurycantha calcarata* Lucas 1872 is similar to *E. horrida* in most characters, differing principally in lacking the ventral tooth on the hind tibiae.

Occurrence in the Field

Eurycantha horrida or *E. calcarata* occurred in groups inside hollows in the bases of living trees and specimens were collected in these habitats in the forest near Lowlands Agricultural Experiment Station, Keravat, New Britain (Pl. xxiv, fig. a). At the time these collections were made the distinction between the two species was not realised. So it is not possible to state whether both species occurred together in the same habitats or whether they occurred in unispecific groups. In a hollow in one tree were one male and eighteen adult females, also four male and six female nymphs. Other trees contained respectively three male adults and ten female adults, one female nymph and the remains of a dead female adult ; one male ; one male and one female ; two males and two females ; one male.

In a garden, two adult females of *E. horrida* were found inside a hollow pipe and were forced to emerge when water was poured in. There were feeding marks on nearby ornamental croton plants (*Codiaeum variegatum* L. Blume var. *pictum*). Presumably the insects emerge from the hollow tree trunks or shelters at night to feed on foliage, but this was not checked by observation.

At Panameko, New Ireland, three males of *E. calcarata* were found in the axils of fronds of young coconut palms.

Rearing and Maintenance in the Insectary

Eurycantha could be maintained readily in cages with branches of croton foliage in jars of water as the food plant. During the day the insects lay dormant in a mass on top of each other on the floor of the cage (Pl. xxiv, fig. b). At night they became active, moving about and feeding. The cages were kept in an insectary, the diurnal temperature of which ranged from 21–35°C.

Defensive Behaviour

Eurycantha horrida and *E. calcarata* were similar in their behaviour. When an adult male was disturbed by being prodded, the abdomen was raised and curled up over the back and the one lower and three upper " teeth " at the end of the abdomen resembled open jaws. The ventral surface of the abdomen was then seen to have a series of white transverse segmental bands (Pl. xxiv, fig. c). The metathoracic legs were lifted clear of the ground and extended wide apart. If the insect was further stimulated or picked up, the metathoracic legs were swung together in a grasping motion. If a finger was held in their path, it was caught in the spikes and then locked within the angle of the femur and tibia either of the one leg by the closing together of femur and tibia like a nutcracker, or of both legs acting together in the same way. The femoral spikes were thus driven into the flesh and locked there so powerfully that blood was drawn, causing a very painful sensation. If however nothing was in their path, the legs were swung together two or three times, or once following each stimulation.

If the insect standing on the ground was touched on the antennae, it swung part way round so that the upraised abdomen and extended metathoracic legs were brought partially to face the source of the disturbance. At the moment the defensive behaviour was given, the membraneous copulatory (phallic) organ, dark purple in colour, was repeatedly everted and a noticeable odour was emitted. A very small amount of brown liquid could be collected by dabbing the everted copulatory organ with filter paper ; the liquid had the same odour as was noted during the defensive reaction. A specimen in which the copulatory organ has been pulled into the everted position is shown in Pl. xxv, fig. a. Some specimens were dissected and traces of material with the characteristic odour could be obtained from the interior of the infolded copulatory organ (Pl. xxv, fig. b).

When an adult *Eurycantha* female was disturbed, the abdomen was raised vertically, displaying a large white band representing the tergosternal membrane down each side and a series of white transverse segmental bands representing the intersegmental membranes (Pl. xxv, fig. c). The metathoracic legs were raised clear of the ground and struck together several times, or once each time the abdomen was touched. If a finger was inserted, the tibiae would close on the femora, but since these legs were much thinner and the spikes much smaller than in the males, the spiking effect was much weaker. No odour was noted during the defensive reaction of the females. At times when disturbed the insects simply walked away with abdomen upraised.

After stimulation of both sexes for two or three minutes the insects became unresponsive and walked away.

Discussion

The circumstances in which the behaviour of *Eurycantha* described here occurs, strongly suggest that it is defensive in function. The behaviour is given only when the insects are molested and is not seen if they are left undisturbed. It has not been seen to be given prior to mating, as a means of attracting the opposite sex. Robinson (1969) suggested that insect anti-predator adaptations could be classified into two broad functional categories :

1. Primary defence systems which reduce the probability of a predator initiating a prey-capture attempt (adaptations which conceal the insect or which advertise its real or apparent unsuitability as food).

2. Secondary defence systems which operate after the initiation of a prey-capture attempt and which reduce the probability that the attempt will be successful (systems of active escape, anti-predator displays, defensive chemical secretion, flash coloration and death feigning).

The defensive behaviour of *Eurycantha* includes both these defence systems. The primary defence consists of cryptic behaviour, the insects hiding inside hollow tree trunks during the day. Procrypsis may be aided by the brown colour. The heavily indurated, spiny character of the integument of the whole body must also be regarded as protective. If a prey-capture attempt is made, the secondary defences come into play in two successive phases. First comes the display—the rearing up of the end of the abdomen, the rapid working of the copulatory organ with the emission of the odour in the males, and the striking together of the metathoracic legs. If the attack persists and the insect is seized, then the final defensive phase is active counter-attack with the spikes of the metathoracic legs.

The use of the legs in defensive behaviour is not very common in phasmatids. Two Australian species, *Eurycnema goliath* Gray and *Tropidoderus childrenii* Gray strike the metathoracic legs together during pseudaposematic startling displays (Bedford and Chinnick, 1966). The Panamanian species *Onctophasma martini* Griffini, if seized, flexes the posterior legs at the femoro-tibial joint and thus drives the femoral spines into the restraining object (Robinson, 1968) in the same way as *Eurycantha horrida.* The wingless *Dryococelus* (formerly *Karabidion*) *australis* Montrouzier, which once occupied Lord Howe Island and is closely related to *Eurycantha*, sheltered during the day in groups in hollows inside living trees. When captured, males used the large spines on the hind femora in conjunction with the strongly curved tibiae (Lea, 1916) again in a manner similar to *Eurycantha.*

Curvature of the abdomen dorsally occurs during defensive behaviour in *E. goliath* and *T. childrenii* (Bedford and Chinnick, 1966), and in *O. martini*, in reference to which Robinson (1968) considers the display to resemble to some extent the movements made by scorpions prior to stinging. In males of the mantid *Angela guianensis* Rehn, the abdomen during display is swept forwards (dorsally) towards the head in a series of bowing movements, and at the same time the foliaceous anal cerci are opened outwards, revealing their previously concealed yellow inner surface in a conspicuous way (Robinson, 1969). In *E. horrida* males, the abdomen is reared dorsally in an S-shape and at the same time the copulatory organ is worked rapidly in and out, the whole perhaps resembling the rearing of a serpent's head with opened jaws and flickering tongue.

Referring to *O. martini*, Robinson (1968) stated that " if the display and the use of the femoral armature are to be regarded as defensive, it is necessary to explain why they are most highly developed in males and almost absent in females ". He suggested that males may wander considerable distances in search of females and so may be more exposed to predation ; thus they could have been the subject of selection pressure favouring the evolution of stronger lines of defence. Similar reasoning may apply to *Eurycantha*. Very occasionally, dead intact males have been seen lying on the ground in the open where they must have been moving about, whereas dead females were not seen. There is another possibility : the occurrence of both sexes together with immature stages in groups or " colonies " inside discrete shelters such as hollow stumps and tree trunks, could mean that the presence of the males confers some " protection " on the less endowed females and immatures, the males acting as " defenders " of the " colony " as a whole if danger threatens.

The fact that *Dryococelus australis* almost became extinct on Lord Howe Island following the introduction of rats (Smithers, 1970) emphasises the fact that a defensive mechanism may fail against a predator better equipped than those in whose presence it was evolved.

ACKNOWLEDGEMENTS

I am grateful to Dr. K. H. L. Key and Dr. J. L. Readshaw of CSIRO Division of Entomology, Canberra, for helpful comments on the manuscript. Mr. B. G. M. Kamp helped photograph some of the specimens and Mr. M. Wanariu assisted in the rearing of them.

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EXPLANATION OF PLATES

Plate xxiv

Fig. a. Felled hollow tree trunk at Keravat, New Britain, in which *Eurycantha* were found.

Fig. b. *Eurycantha* adults dormant on cage floor during daytime.

Fig. c. *Eurycantha horrida* male in defensive posture.

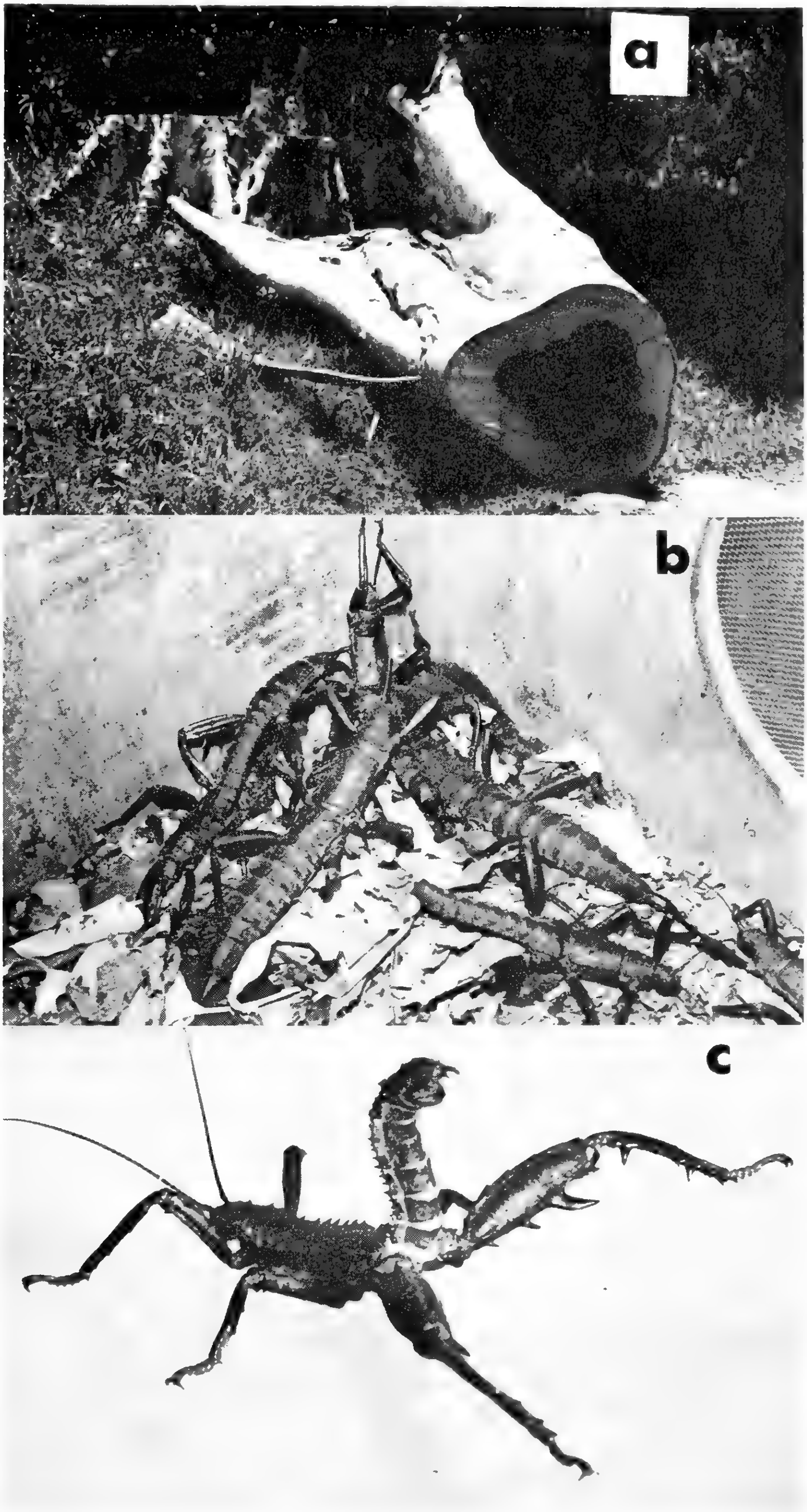
Plate xxv

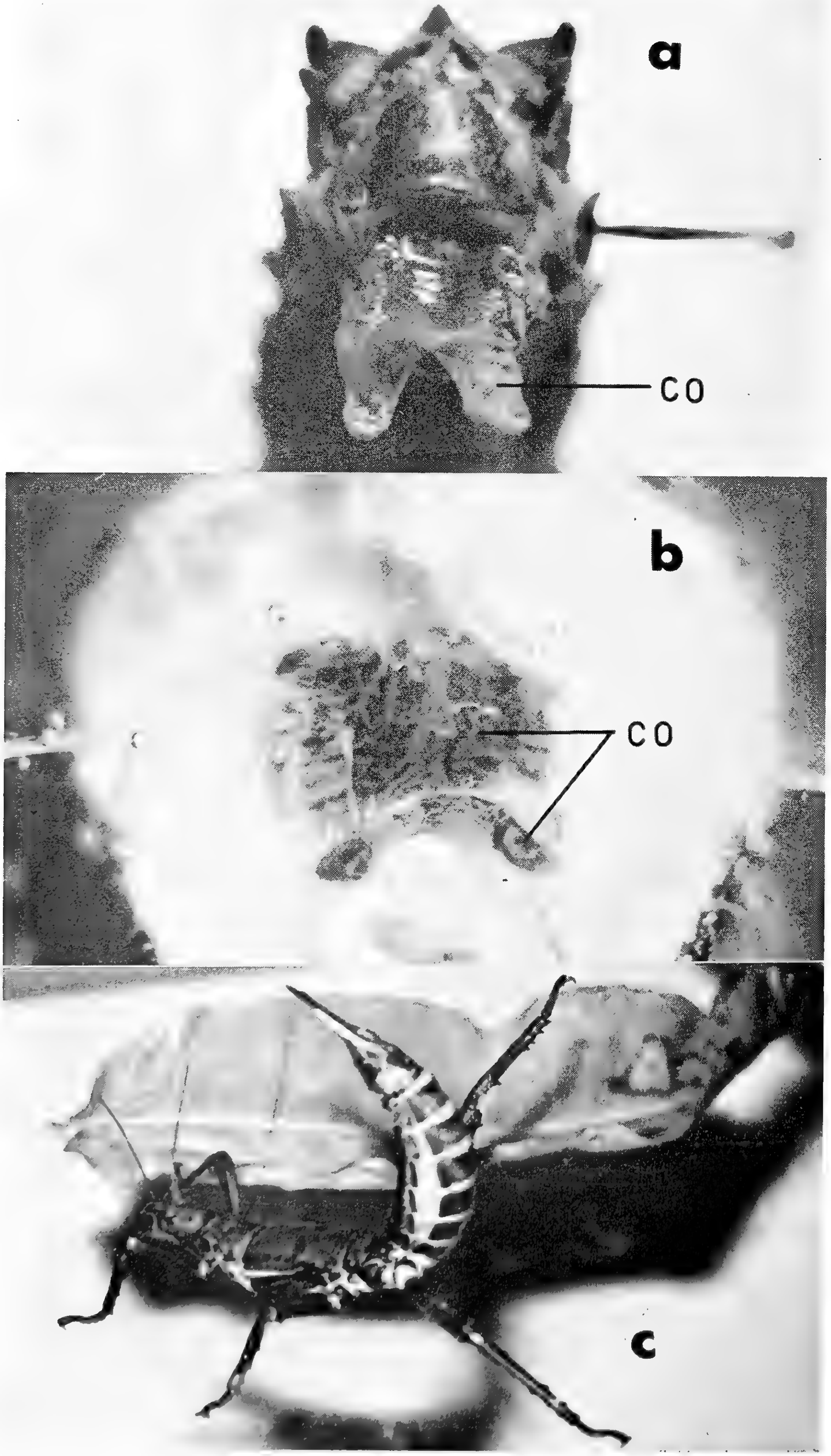
Fig. a. End of abdomen of freshly dead *Eurycantha* male with copulatory organ (CO) pulled out.

Fig. b. Dorsal dissection of *Eurycantha* male showing infolded copulatory organ (CO).

Fig. c. *Eurycantha horrida* female in defensive posture.

PLATE XXIV

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THREE NEW SPECIES OF *QUESTOPOGON* DAKIN AND FORDHAM (DIPTERA : ASILIDAE) FROM AUSTRALIA

G. DANIELS[*]

[Accepted for publication 19th November 1975]

Synopsis

The genus *Questopogon* Dakin and Fordham is recorded from eastern Australia for the first time. Three new species are described : *Q. lineatus* from Queensland and New South Wales ; *Q. guttatus* from Western Australia ; and *Q. affinis* from South Australia and Western Australia. The male of *Q. clarkii* Dakin and Fordham is also described.

INTRODUCTION

Questopogon clarkii Dakin and Fordham, 1922, type of the monotypic genus *Questopogon* Dakin and Fordham, was described from two females collected at Cunderdin, Western Australia. Hardy (1926, p. 308) recorded two female specimens in South Australian Museum from South Australia which he doubtfully placed in *Questopogon*. Material supplied by Mr. G. F. Gross from the South Australian Museum's collection does not contain these specimens. Hardy (1930, p. 255) also records a female from Denman, New South Wales, in the J. S. Mann collection ; the specimen is likely to be *Q. lineatus* sp.n.

The genus is readily distinguished from other Asilid genera by the presence of an apical pair of stout, spine-like, ventral bristles on the fore tibia (Figs 6–8), an apical pair of down-turned, spine-like, ventral bristles on the mid tibia (Fig. 9) and the curved hind basitarsus (Fig. 5).

Collections in which examined material is located are indicated by the following abbreviations : AM Australian Museum, Sydney ; ANIC Australian National Insect Collection, CSIRO, Canberra ; BM British Museum (Natural History), London ; GD author's collection ; NMV National Museum of Victoria, Melbourne ; SAM South Australian Museum, Adelaide ; WAD West Australian Department of Agriculture, Perth.

Key to species of Questopogon

1.	Tergites with a greyish yellow stripe along lateral margins	2.
	Tergites with golden-yellow spots on posterior corners ..	3.
2.	Fronto orbital hairs distinctly yellow-orange ; tarsii black, sharply contrasting with red tibiae ; hind femur and tibia red, of uniform colour	*Q. lineatus* sp.n.
	Fronto orbital hairs dark or pale rufous ; tarsi at most only slightly darker than tibiae ; tibiae becoming indistinctly darker apically	*Q. affinis* sp.n.
3.	Claws black ; hind basitarsus redish, rarely blackish ; tergites densely covered with golden-yellow hairs, forming tesselated " plates "	*Q. clarkii* Dakin and Fordham
	Claws yellow, only the apices black ; hind basitarsus black ; dense yellow hairs only at sides of tergites, without tesselated " plates " ; greater part of tergites shining ..	*Q. guttatus* sp.n.

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Questopogon clarkii Dakin and Fordham

Figs 1, 5, 6, 11, 12, 16

Questopogon clarkii Dakin and Fordham, 1922 : 525–528, figs 2B, 5, 6, Pl. XV.

Material Examined. WESTERN AUSTRALIA : 1♂ (ANIC), 1♀ (WAD), Mullewa, September, L. J. Newman ; 1♂ (ANIC), Erady, 8 September 1926, F. W. Ferguson ; 1♂, 1♀ (ANIC), Morawa, 12 September 1952, McIntosh and Calaby ; 1♂, 1♀ (ANIC), Pinjara, no date, Goerling ; 1♀ (ANIC), Canna, 16 August 1953, T. Lee.

Holotype ♀ and paratype ♀ in BM : Cunderdin, W.A., July–August 1915, presented by Dakin and Fordham.

MALE

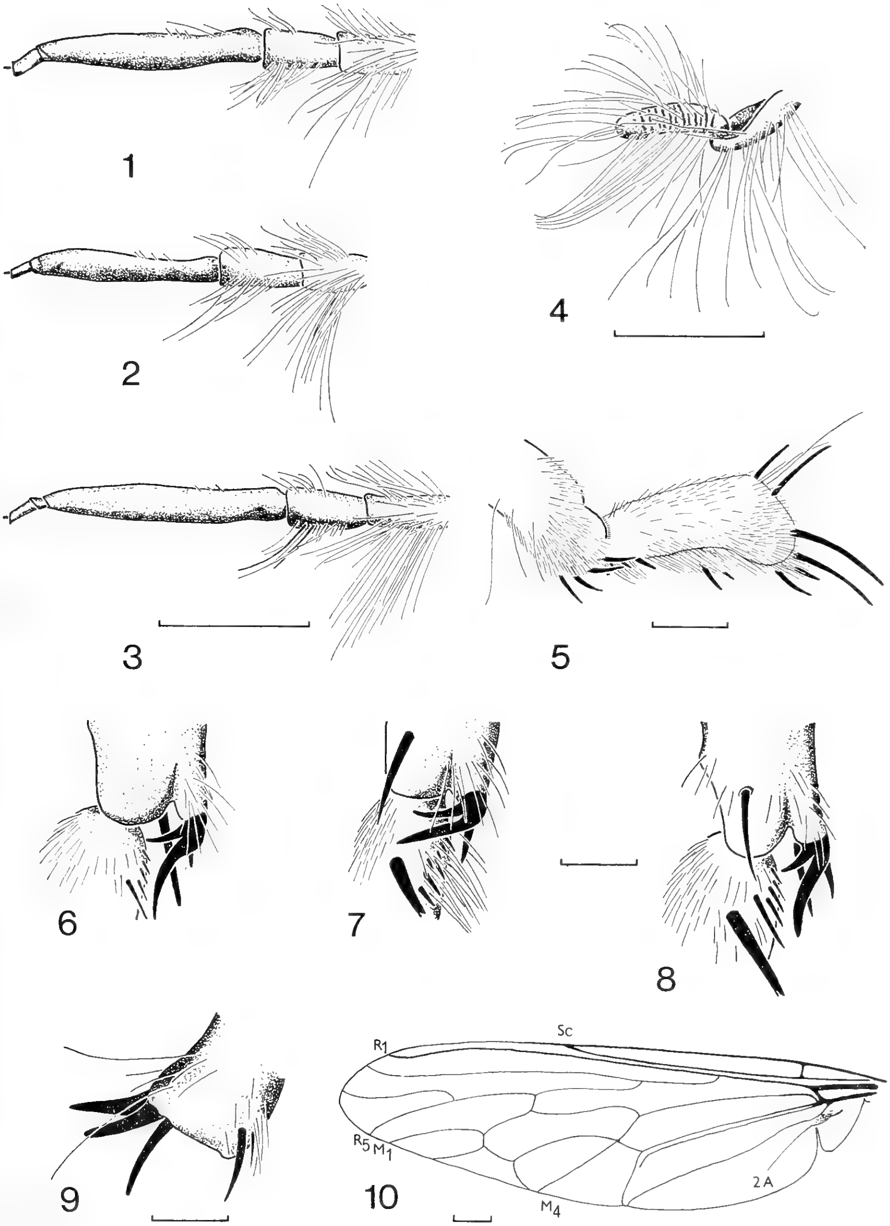
Head. Width 1·7–1·8 height. Frons at narrowest 0·3 width of head. Face well developed and convex, oblique from ventral epistomal margin to base, covered with golden micropubescence. Mystax with numerous, long, stiff, irregularly disposed yellowish hairs, lower elements stouter and erect. Occiput following contour of posterior eye margin to about mid point of eye, then becoming narrower until obliterated by vertex ; occipital pile long, yellowish below and at vertex, with some black pile at middle. Proboscis approximately two-thirds length of eye, shining black with long fine white hairs on basal one-half. Palpi black, corrugated ; segment 1 with yellowish ventral hairs ; segment 2 with black hairs and a few white hairs basally and ventrally ; slightly longer than segment 1 and held distinctly at an angle. Antennae (Fig. 1) black with extremely fine yellow micropubescence ; slightly longer than eye ; attached at upper one-third of head ; segments 1 and 2 sub equal ; segment 3 1·4–1·5 combined lengths of segments 1 and 2, of uniform width for about two-thirds its length then narrowing to width of its base ; bearing a short microsegment, its length being one-third maximum width of segment 3 and followed by a longer, conical truncate, spine tipped microsegment ; segment 1 with numerous stout black hairs on all surfaces, becoming longer ventrally ; segment 2 sub apically with 3 or 4 black dorsal hairs and several longer, stouter, black hairs ventrally ; segment 3 micropubescent, sometimes with a few short fine hairs arising at basal one-third. Frons narrowed level with base of antennae, covered with yellowish micropubescence, with a group of black hairs at base of antennae. Ocellar tubercle with long divergent black bristles.

Thorax. Mesoscutum black, sometimes with an indistinct yellowish, longitudinal, medial line extending to suture ; covered with fine erect black pile ; a yellow pollinose line extends along lateral slopes from pronotum to postalar callus ; 2–4 black notopleurals ; 1 or 2 black or yellow supraalars ; 4 or 5 yellow postalars. Scutellum black with yellow pollinose rim ; 6 or 7 pairs of yellow convergent marginal bristles. Metanotal callosity micropubescent. Lateral slopes of thorax yellow-grey pollinose. Anepisternite, sternopleuron, pleural tergite and meropleuron with long, dense, fine yellowish hairs. Halteres yellow.

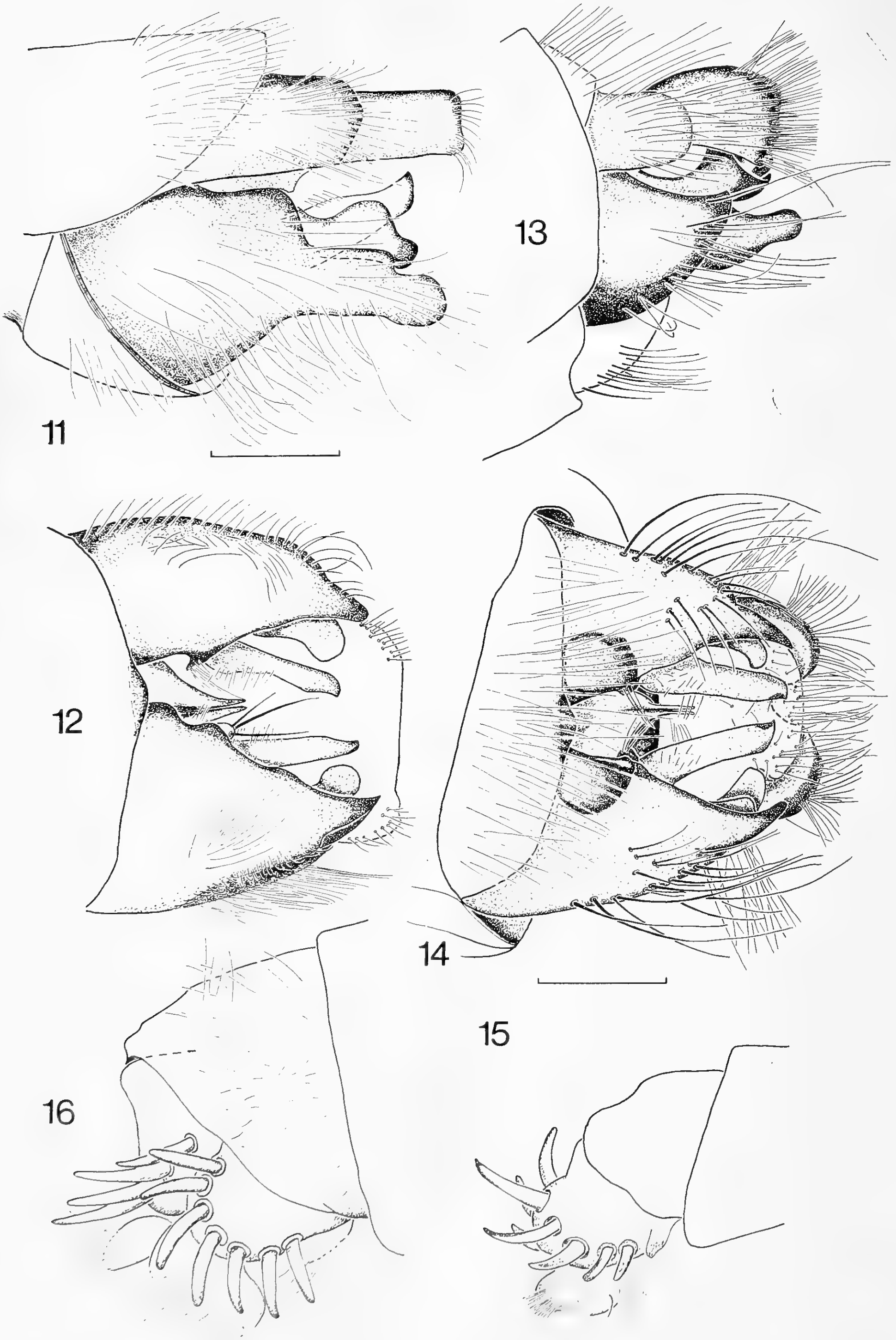
Legs. Coxae black, densely yellow pollinose, with very long yellowish hairs. Femora red-brown with long, fine, erect yellowish hairs, and shorter scattered black elements ; fore and mid femora black dorsally on basal three-quarters and one-half respectively. Tibiae red-brown with black dorsal and yellow ventral hairs ; bristles mostly yellow with black apical elements ; fore tibia black dorsally on apical one-half, apically with a ventral red tubercle bearing 2 strong, twisted black spurs. Fore and mid tarsi black ; hind tarsi with at least basitarsi reddish. Pulvilli yellow. Claws long and black.

Wing. Hyaline with brown suffusion along veins ; basal one-third of marginal cell suffused brown ; basal costal cell brownish. Venation similar to *Q. lineatus*.

Abdomen. Long and broad, black and shining, tapering regularly towards apex. Tergites with long fine yellowish hairs ; tergite 1 with depressed hairs, outwardly



Figs 1–10. Scales = 1·00 mm. Figs 1–3. Antennae. 1. *Q. clarkii.* 2. *Q. lineatus.* 3. *Q. guttatus.* Fig. 4. Palpi, *Q. lineatus.* Fig. 5. Hind basitarsus, *Q. clarkii.* Figs 6–8. Fore tibiae. 6. *Q. clarkii.* 7. *Q. lineatus.* 8. *Q. guttatus.* Fig. 9. Mid tibia, *Q. guttatus.* Fig. 10. Wing, *Q. lineatus.*



Figs 11–16. Scales = 0·5 mm. Figs 11–12. Male genitalia, *Q. clarkii*. 11. laterally. 12. ventrally. Figs 13–14. Male genitalia, *Q. lineatus*. 13. laterally. 14. ventrally. Figs 15–16. Female genitalia, laterally. 15. *Q. clarkii*. 16. *Q. lineatus*.

directed medially, but normal at sides ; tergites 2–5 with anterior hairs depressed laterally towards median line, hairs in middle slightly erect, posteriorly depressed from median line towards the sides, producing a chequered appearance, depending upon the angle from which abdomen is observed ; tergites 6 and 7 with similar hairs but directed towards the sides ; lateral margin of tergites 2–7 each with a sharply defined golden yellow pollinose spot. Sternites yellow-grey pollinose with long white pile ; sternites 1–5 with a variable shining black medial spot. Terminalia small, reddish with pale hairs ; tergite 8 reduced and recessed into segment 7 with terminalia. Aedeagus bifid.

FEMALE

Differing from the male in the following characters : one specimen with brown suffusion along veins and in wing cells entirely lacking ; tergites 2–6 with lateral spots ; tergites 6 and 7 bare and shining ; tergite 7 reddish, tergite 6 partly so ; terminalia reddish, recessed into segment 7 ; acanthophorites bearing reddish blunt spines.

DIMENSIONS. Body length, excluding antennae, ♂ 22–24 mm, ♀ 17–26 mm. Length of thorax, ♂ 6·5–8·0 mm, ♀ 6·5–9·0 mm. Length of wing, ♂ 18·5–20·0 mm, ♀ 16·0–23·5 mm.

Questopogon guttatus sp. nov.

Figs 3, 8, 9

Holotype. ♀ (ANIC), Pithara, W.A., 3 October 1933, M. Fuller.

FEMALE

Similar to *Q. clarkii* in most characters and differing principally as indicated below.

Head. Width 1·7 height. Mystax with a few scattered dark hairs dorsally. Proboscis about as long as eye, orange on apical margin.

Thorax. Mesoscutum black, without yellowish medial line. Three black notopleurals ; 2 black supraalars ; 4 or 6 yellow postalars. Scutellar margin with 6 pairs of yellow convergent bristles.

Legs. Tibiae with at least basal one-half black. Tarsi completely black. Pulvilli yellowish. Claws yellow, apical one-third black.

Wings. Hyaline with narrow yellowish suffusion along veins ; veins black to deep rufous. Marginal cell entirely hyaline ; basal costal cell with indistinct yellowish suffusion.

Abdomen. Tergites with long fine yellow hairs, becoming longer on lateral slopes, without chequered appearance ; tergites 2–5 with golden pollinose spots on posterior corners ; tergite 1 with greyish yellow pollinosity on lateral margin ; tergites 6 and 7 black, shining ; tergite 8 shining black, recessed into segment 7. Six pairs of blunt reddish spines on acanthophorites.

DIMENSIONS. Body length, excluding antennae, 24 mm. Length of thorax, 8·5 mm. Length of wing, 20·5 mm.

MALE

Unknown.

Questopogon lineatus sp. nov.

Figs 2, 4, 7, 10, 13, 14, 15

Holotype. ♂ (ANIC), 17 miles SSW. Bohema, Pilliga Scrub, N.S.W., 7 April 1951, Key and Chinnick.

Paratypes. QUEENSLAND : 1♂, 1♀ (AM), Carnarvon Range, February and March 1944, N. Geary ; 1♂ (GD), Carnarvon Gorge, 7 September 1971, M. S. Moulds ; 1 ♂ (ANIC), 27 miles SSE. Tambo, 2 March 1957, Key and Chinnick.

NEW SOUTH WALES : 1 ♀ (GD), 5 miles S. Mendooran, 1 April 1972, G. Daniels ; 1 ♂, 6 ♀ (GD), 3 miles SW. Mount Tomah, Blue Mountains, 2 March 1974, G. Daniels.

MALE

Head. Width 1·3–1·7 height. Frons narrowed level with antennal base, at this point 0·2–0·3 head width, with a group of orange-yellow hairs above antennal bases. Face well developed and convex, oblique from ventral epistomal margin to base ; golden micropubescent. Mystax with numerous long stiff irregularly disposed yellowish hairs ; lower elements stouter, white and erect. Occiput following contour of posterior margin of eye to about mid point, then becoming narrower until obliterated at vertex ; occipital pile long, pale yellow, and below not as fine as *Q. clarkii*, moderately dense at vertex, reaching almost to eye margin. Proboscis almost as long as eye. Palpi 2 segmented, black with pale yellow hairs ; segment 2 strongly corrugate, slightly longer than segment 1 and held distinctly at an angle, with offset attachment. Antennae slightly longer than eye, attached at upper one-third of head ; black with yellowish micropubescence ; hairs pale yellow ; segments 1 and 2 sub equal ; segment 3 1·4–1·5 combined lengths of segments 1 and 2, of uniform width for about two-thirds its length, then narrowed to almost one-third its maximum width ; bearing a short microsegment followed by a longer conical, truncate, spine tipped microsegment ; segment 1 with numerous stout yellow hairs on all surfaces, being longer ventrally ; segment 2 with yellow dorsal hairs and several longer, stouter yellow hairs ventrally ; segment 3 micropubescent only. Ocellar tubercle with long divergent black bristles ; 5–8 slightly shorter black hairs in vertex.

Thorax. Mesoscutum black, shining, with yellowish medial and sub medial stripes extending to scutellar suture ; covered with fine erect black pile ; a yellow pollinose band extends along lateral slopes to scutellum. Three or 4 notopleurals ; 2 or 3 supraalars and 3–5 postalar bristles, dark yellow to black. Scutellum yellow pollinose, with 4–6 pairs of convergent yellow marginal bristles. Metanotal callosity micropubescent. Halteres yellow.

Legs. Coxae grey pollinose. Tibiae and femora red. Fore femur with a large black stripe on basal two-thirds, covering anterior to posterior surfaces ; apical spines twisted towards dorsal surface. Tarsi black. Pulvilli yellow. Claws yellow, apical one-half black. Bristles on legs red.

Wing. Hyaline. Basal costal cell yellow.

Abdomen. Shining, blue-black, elongated and as wide as mesoscutum. Tergal pile long, pale yellow, not dense, sub erect ; lateral slopes of tergites 1–7 with a narrow uninterrupted stripe of greyish yellow dusting ; tergite 8 reduced, shining black, concealed by tergite 7. Sternites grey pollinose, with long suberect white pile, and with a distinct, narrow, black medial longitudinal line. Terminalia yellowish, recessed into segment 7. Aedeagus bifid.

FEMALE

Differing from male in the following characters : head width 1·6–1·7 height; antennal segment 3 1·3–1·5 combined lengths of segments 1 and 2 ; 2–4 supraalars ; 4–6 postalars ; 3–5 pairs scutellar bristles ; tergites 1–5 with narrow uninterrupted stripe ; tergites 6 and 7 completely shining black ; terminalia tawny, partly recessed into segment 7 ; acanthophorites each with 7 or 8 comparatively stout blunt spines.

DIMENSIONS. Body length, excluding antennae, ♂ 23·0–29·0 mm, ♀ 20·5–26·5 mm. Length of thorax, ♂ 6·0–8·0 mm, ♀ 7·0–9·0 mm. Length of wing, ♂ 14·5–19·0 mm, ♀ 15·5–21·0 mm.

Habitat. Specimens from Mount Tomah were taken in a clearing amongst dry sclerophyll forest where they frequently rested on the ground. The Mendooran specimen was taken in dry sclerophyll forest, flying amongst low dry grass.

Questopogon affinis sp. nov.

Holotype. ♂ (NMV), Booyana, W.A., November 1932, Miss Baesjou.

Paratype. ♀ (SAM), Kimba, S.A., no date, E. Broomhead.

MALE

Very similar in most characters to *Q. lineatus* and agreeing with the description given for that species except as indicated below.

Head. Width 1·8 height. Frons 0·3 width of head. Face with fulvous micropubescence. Antennae slightly shorter than length of eye; segment 1 with numerous stout yellowish hairs, with a few black elements scattered throughout; segment 2 with 4–6 black dorsal hairs on apical one-half and ventrally with several longer stouter black hairs. Frons with an irregular row of dark rufous fronto-orbital hairs and a group of dark rufous hairs arising from an indistinct gibbosity above antennal bases. Ocellar tubercle with long, divergent, dark rufous hairs.

Thorax. Mesoscutum black, with a greyish yellow pollinose line along lateral margin extending from humeral callus to postalar callus; an indistinct brownish, longitudinal sub-medial line extends from anterior margin for about one-third mesoscutal length; a greyish dorsocentral triangle borders sub-medial line for its length; 3 or 4 black notopleurals; 4 black supraalars; 3 yellow postalars. Scutellum black with yellowish micropubescence; 6 pairs of yellow convergent marginal bristles.

Legs. Femora with long, erect, fine yellow hairs. Tibiae indistinctly darkened apically. Fore tibia with a darkened tubercle bearing a pair of dark red spines. Tarsi black. Claws yellow, apical one-half black.

Wing. Hyaline with narrow yellow suffusion along veins. Veins reddish to black. Marginal and basal costal cells hyaline.

Abdomen. Tergites with long fine yellowish sub appressed hairs; lateral margin of tergites 1–7 with a greyish yellow pollinose line. Sternites grey pollinose, with sub appressed white pile, with a distinct narrow, black medial longitudinal line. Terminalia deep rufous, recessed into segment 7.

FEMALE

Differing from the male in the following characters: Head width 1·7 height; hairs above antennal bases mainly pale rufous with a few black elements dorsally; occipital pile whitish; mesoscutum dull black with indistinct brownish submedial lines; legs uniform red-brown; tarsi becoming slightly darker apically; basal costal wing cell hyaline; abdomen shining, brownish black.

DIMENSIONS. Body length, excluding antennae, ♂ 26·5 mm, ♀ 26·0 mm. Length of thorax, ♂ 8·5 mm, ♀ 6·5 mm. Length of wing, ♂ 20·5 mm, ♀ 16·8 mm.

The female is paler than the male, but agrees structurally, in pattern, and in hairing of the abdomen, is obviously immature and is probably placed correctly here. It also bears the label " Type. *Questopogon vittatus*, n. sp. F. M. Hull "; this appears to be a manuscript name only.

Acknowledgements

Reference has been made to the manuscript of the late Dr. S. J. Paramonov, held in CSIRO Division of Entomology, Canberra. The author thanks the Curators of various Australian museums for the loan of material in their charge,

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UPPER ORDOVICIAN RUGOSE CORALS OF CENTRAL NEW SOUTH WALES

R. A. McLean* and B. D. Webby†

(Plates XXVI–XXX)

[Accepted for publication 18th June 1975]

Synopsis

Ten species of rugose corals are described and illustrated from the Upper Ordovician (Caradoc) limestones of central New South Wales. They include the new genera *Bowanophyllum* (type species *B. pilatum*) and *Rhabdelasma* (type species *R. exigua*), and four other new species, *Palaeophyllum jugatum, P. arrectum, Palaeophyllum*? *patulum* and *P.*? *laxum*. *Rhabdelasma* is one of the earliest rugosans to show rhabdacanths, occurring in an horizon of probably early Bolindian (late Caradoc) age. The New South Wales Ordovician fauna also exhibits representatives of *Helicelasma, Streptelasma*? and *Grewingkia*.

Introduction

Although the rugose corals are numerically subordinate to the tabulate corals in the Ordovician limestones of central New South Wales, they nevertheless constitute one of the more important groups for use in establishing biostratigraphic subdivision of the succession. Aspects of the stratigraphic distribution of the rugosoans have been previously outlined by Webby (1971, 1972, 1975). The distribution of the whole fauna is summarised in Text-fig. 1. *Hillophyllum* is the earliest form to appear, occurring in Fauna I of probable Gisbornian (early Caradoc) age. It is the earliest rugosoan to exhibit monacanthine septa. *Palaeophyllum* makes its appearance in Fauna II (early Eastonian), and is the first to show " laminar " septa. It becomes, by the late Eastonian (Fauna III), the most abundant and, at the species level, most diverse element of the New South Wales Ordovician rugosoan fauna. In Fauna III there is also the first appearance of solitary streptelasmatids (*Helicelasma* and *Streptelasma*?) and cerioid *Favistina*. Fauna IV (early Bolindian) is characterised by *Rhabdelasma*, the earliest form to exhibit rhabdacanths, *Bowanophyllum* and *Grewingkia*.

Stratigraphic Distribution

It now appears that there are two stratigraphically distinct Ordovician limestones in the region west of Parkes (Webby, in press). The lower is the Billabong Creek Limestone (Packham 1967 ; Sherwin 1970, 1973), which contains representatives of Fauna II, including the corals *Hillophyllum priscum*, *H.* sp., *Tetradium cribriforme*, heliolitids and the stromatoporoid *Ecclimadictyon*. It is succeeded by probable Eastonian graptolitic shales (Campbell and Durham 1970 ; Sherwin 1973) and by an unnamed limestone, presently included in the lower part of the Goonumbla Volcanics. The unnamed limestone crops out just north of Gunningbland and exhibits a rich coral fauna, including *Streptelasma*?

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sp., *Palaeophyllum jugatum*, *Favistina* sp., *Plasmoporella inflata* and other heliolitids, and the stromatoporoid *Cliefdenella etheridgei*. It is considered to be a Fauna III assemblage of late Eastonian age.

CORAL/STROMATOPOROID SCHEME	FAUNA I	FAUNA II			FAUNA III				FAUNA IV
FORMATION / DISTRIBUTION OF RUGOSA	Cliefden Caves Limestone (lower part)	Cliefden Caves Limestone (upper part)	Quondong Formation	Billabong Ck. Limestone	Cargo Creek Limestone (middle-upper part)	Canomodine Limestone (upper part)	Clearview Limestone Mbr, Ballingoole Formation	Limestone unit, Goonumbla Volcanics (lower part)	Limestone unit & breccia, Malachi's Hill Beds (uppermost part)
Helicelasma sp.					X				
Streptelasma ? sp.								X	
Grewingkia sp.									X
Palaeophyllum ? *patulum*							X		
P. ? *laxum*						X			
Palaeophyllum proliferum		X^{2}	X^{2}						
P. jugatum								X	
P. crassum					X				
P. aff. *crassum*					X				
P. arrectum						X			
P. macrocaule									X
Favistina spp.					X	X		X	X
Hillophyllum priscum	X^{1}	X	X	X					
H. sp.		X	X	X					
Bowanophyllum pilatum									X
B. sp									X
Rhabdelasma exigua									X^{3}

Text-fig. 1. Diagram showing distribution of Late Ordovician (Caradoc) rugose corals in central New South Wales. Coral/stromatoporoid faunas I-IV of Webby (1969; 1972). First appearances of particular septal types are shown by numerals 1–3. 1. earliest form with monacanthine septa; 2. earliest species with "laminar" septa; 3. earliest with confirmed rhabdacanths.

The occurrence of *Cliefdenella etheridgei* was originally taken to be a diagnostic element of Fauna II (Webby, 1969). However, it has recently been found in a stratigraphically higher level (Fauna III) of the Cargo Creek Limestone (Stevens, 1950, 1957), and clearly has a more extended upward range. *Helicelasma* sp.

and *Palaeophyllum crassum* are associated with *Quepora calamus* and *Cliefdenella etheridgei* in beds of the Cargo Creek Limestone underlying the main fossiliferous units of the upper part of the succession. These latter contain *P.* cf. *crassum*, *Favistina* sp. and favositids. From equivalent horizons in the upper part of the Canomodine Limestone (Stevens, 1950; Ryall, 1965) on the south bank of the Belubula River, east of Cranky Rock, *Palaeophyllum*? *laxum*, *Favistina* sp. and *Halysites praecedens* have been found, and near Rockdale, *Palaeophyllum arrectum*, *Favistina* sp., and abundant favositids have been collected.

In the Clearview Limestone Member of the Ballingoole Formation (Bowan Park Group), *Palaeophyllum*? *patulum* is associated with a varied tabulate coral and stromatoporoid fauna (Semeniuk, 1973), also a Fauna III assemblage. *Favistina* is not recorded, but *Halysites praecedens* and *Palaeofavosites* make their first appearance in the Bowan Park succession, towards the top of the member. The Malachi's Hill Beds (Semeniuk, 1970) succeed the Bowan Park Group, and contain, in limestone breccia and a massive limestone unit at the top of the sequence, a rich and diverse coral fauna (Fauna IV). The limestone breccia has yielded *Grewingkia* sp., and the overlying limestone unit, *Palaeophyllum macrocaule*, *Favistina* sp., *Bowanophyllum pilatum*, *B.* sp., and *Rhabdelasma exigua*. Tabulate elements of the fauna include *Catenipora* sp., *Quepora* sp., *Palaeofavosites* spp., *Plasmoporella* sp., and *Heliolites* sp.

Systematic Descriptions

Genus HELICELASMA Neuman 1969

Type species. *H. simplex* Neuman 1969.

Discussion. The redefinition of the genus *Streptelasma* by Neuman (1969) has been discussed by McLean (1974*a*, p. 38). Included now in *Helicelasma* Neuman are many forms earlier thought congeneric with the type species of *Streptelasma*, *S. corniculum* Hall. Neuman regarded the following species as representative of *Helicelasma*: *Streptelasma fossulatum* Wang, 1948; *S. whittardi* Smith, 1930; *S. corniculum* Cox, 1937; *S. rusticum* (Billings, 1858) and *Helicelasma simplex* Neuman, 1969. The position of '*S.*' *rusticum* (Billings) is not certain. The transverse section figured by Lambe (1901, Pl. VII, fig. 3) shows a wide axial structure of intertwined septal lobes and lamellae, a characteristic feature of the genus *Grewingkia* Dybowski, 1873. However the species, as illustrated by Cox (1937, Pl. II, figs 11–13) shows a weak axial structure and all features characteristic of *Helicelasma*. Unfortunately the types are lost (Cox, 1937, p. 12) but the thorough study of widespread material of the species made by Cox would appear to give a good basis for interpreting the form as a representative of *Helicelasma*. The species has been recorded from numerous localities of Richmond age in North America (see Bassler, 1950), but thin-section analysis is required for verification. *Streptelasma poulseni* Cox, 1937 from the Cape Calhoun Formation of north-western Greenland (Richmond) would also appear to be a representative of *Helicelasma*. As mentioned by McLean (1974*a*), *Streptelasma ruttneri* Saleh *in* Flügel and Saleh, 1970 from the Llandovery of north-east Iran shows typical characteristics of *Helicelasma* and is included here in that genus.

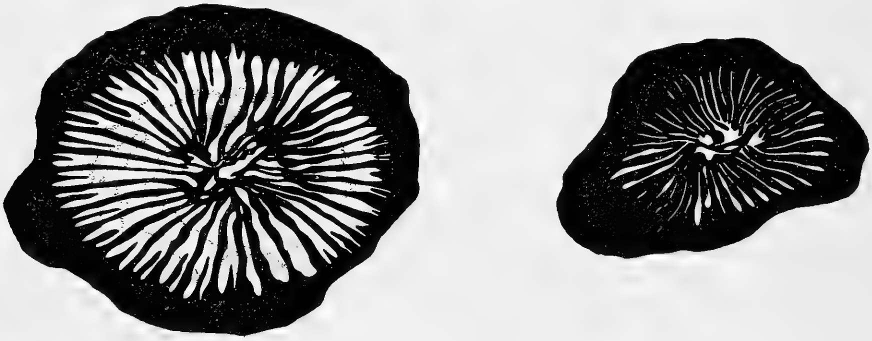
Helicelasma sp.

Pl. XXVI, figs 6–8; Text-fig. 2

Material. SUP 75160–75162 from middle-upper part of the Cargo Creek Limestone; tributary south-east of Canomodine Creek.

Description. Corallum solitary, of indeterminate growth form owing to incompleteness of material; only late neanic and ephebic growth stages preserved. Corallum up to 25 mm in diameter, with calice deep, at least 10 mm depth. Septa are strongly dilated in peripheral stereozone in ephebic stage, this zone being

0·15–0·2 of radius of corallite. Major septa have a maximum number of 41 in largest, most complete specimen (Pl. xxvi, fig. 6); gradually tapering towards axis in ephebic stage, with a few dilated lobes and traces of free lamellae in axial zone. Minor septa are short and of variable length; extending inwards generally only to about 0·3 of corallite radius. In late neanic stage, septa are strongly dilated being almost in lateral contact; major septa extend to axis. Owing to the fragmentary material, only a few tabulae were observed in section; they are strongly arched, apparently mainly complete, with a broad, central flattened region; spacing is approximately 0·8–1·2 mm apart.



Text-fig. 2. *Helicelasma* sp., transverse sections, ×2·5. SUP 75160b, ephebic stage (left); SUP 75161, neanic stage (right).

Remarks. The above described form bears close resemblances to "*Streptelasma corniculum*" of Cox (1937) and Lambe (1901) characteristic of the Trenton of North America. Following the revision of Hall's material by Neuman (1969) it is evident their material is not conspecific with that of Hall (1847) and is representative of *Helicelasma*. The material of Cox (1937, Pl. i, fig. 2*b*) from strata of Trenton age in Cornwall, Ontario appears to have a more strongly developed ephebic axial structure than that of the N.S.W. specimens. However the ephebic section of Lambe (1901, Pl. vi, fig. 7*b*) from the Trenton of Ottawa, Ontario has a very weak axial structure more comparable to that of the N.S.W. form. The North American species would thus appear to be quite variable and the material from the Cargo Creek Limestone may be conspecific with it. More complete specimens from Cargo Creek are required, however, before definite synonymy can be established. A new specific name for the North American form must also be selected.

Genus STREPTELASMA Hall, 1847

Type species. *S. corniculum* Hall, 1847.

Streptelasma? sp.

Pl. xxvi, figs 1–5

Material. SUP 75195, 77267, from unnamed limestone in lower part of Goonumbla Volcanics; "Currajong Park", just north of Gunningbland.

Description. Corallum solitary, straight, subcylindrical. Specimen SUP 75195 is incomplete but a height of at least 70 mm is represented, with diameter reaching 28 mm. Calice straight-sided with depth of approximately 16 mm. A wide peripheral stereozone is present throughout visible ontogeny, although early growth stages are lacking; it reaches a width of approximately 0·3 of corallite radius at base of calice. In ephebic stage major septa are thin, tapering, withdrawn from axis, extending approximately 0·7–0·8 of corallite radius. Septal lamellae occur in the axial region but no axial structure is developed. Septal number cannot be determined owing to incompleteness of material, but is estimated to be approximately 56 major septa at base of calice. Minor septa are short, barely protruding beyond peripheral stereozone. In the late neanic stage (Pl. XXVI, fig. 3), major septa are only weakly dilated and extend to corallite axis where they may be slightly twisted. Tabulae are incomplete, forming strongly arched series with flattened central zone. Average spacing is 2 mm towards the periphery, whereas it is only 0·3–1·0 mm axially.

Remarks. Since these specimens are incomplete, generic determination is uncertain. They seem most likely to be representatives of *Streptelasma* because the septa do not appear to have become greatly dilated in early growth stages, and the major septa of the ephebic stage are somewhat withdrawn from the axis with rather irregular axial ends.

Genus GREWINGKIA Dybowski, 1873

Type species. *Clisiophyllum buceros* Eichwald, 1856.

Grewingkia sp.

Pl. XXVI, figs 9–12

Material. SUP 75223 from the limestone breccia underlying the limestone lens in the uppermost part of the Malachi's Hill Beds; northeast of Malachi's Hill.

Description. Corallum small, solitary, growing in association with tabulate coral *Catenipora.* Attains maximum diameter of 5·4 mm. Broad peripheral stereozone composed of dilated septa to a width of approximately 1 mm. Major septa taper markedly inside peripheral stereozone; extend unbroken up to 0·6 of corallite radius and frequently show lateral " tubercles " and axial lobes (Pl. XXVI, fig. 9). Minor septa may project slightly beyond stereozone. Axial region of corallite occupied by dense structure (approximately 2 mm in diameter) of anastomosing septal lobes and lamellae. Earlier growth levels show axial structure to be rather smaller and slightly more open. Nature of tabulae unknown.

Remarks. The species is distinguished from all previously described species of *Grewingkia* in exhibiting at the ephebic stage dilated septa and an axial structure with strongly dilated septal lobes and lamellae. It may be related to *Densigrewingkia* (type species, *D. pyrgoidea* Neuman 1969) but differs in lacking strong sclerenchymal thickening of the axial structure. *Grewingkia* is represented by two species in the late Lower or early Middle Llandovery of central New South Wales (McLean, 1974*a*), but this is the first record of the genus in the Ordovician of Australia. Another smaller Ordovician species of *Grewingkia* (SUP78210) with much less dilated septa has recently been found by I. Percival (pers. comm.); it is associated with *Halysites* sp. in a limestone lens of the Angullong Tuff (locality CO.1/50 of Smith, 1966).

Genus *Palaeophyllum* Billings, 1858

Type species. *P. rugosum* Billings 1858.

Discussion. For synonymy and previous discussion of this genus, see Webby (1972) and McLean (1975). The species *P. jugatum*, *P.* aff. *crassum* and *P. arrectum* are regarded as typical representatives of *Palaeophyllum*, but *P.? patulum* and *P.? laxum* because of their " pseudo-colonial " habit are only tentatively assigned to the genus.

Palaeophyllum jugatum sp. nov.

Pl. XXVII, figs 1–7; Text-fig. 3A–B

Material. Holotype SUP 74258; paratypes SUP 43261–43262, 75150–75157, 74259–74269. Unnamed limestone in lower part of the Goonumbla Volcanics; " Currajong Park ", just north of Gunningbland.

Description. Corallum is phaceloid (less commonly dendroid). Increase is axial and parricidal, with up to four (or five?) offsets from one calice. Corallite diameter ranges from 3·5 to 4·5 mm in mature specimens. Calice relatively deep (up to 3·5 mm), steep-sided, with pronounced axial boss often present. Peripheral stereozone ranges from 0·2–0·5 mm in width. Septa of two orders; major septa are moderately dilated, tapering only slightly from stereozone towards axis; range in number from 19 to 22. Individual corallites of a single corallum may exhibit major septa of markedly differing lengths; in some they extend inwards to form a solid axial structure up to 1 mm wide, in others only one or two septa elongate to form an axial element (usually blade-like), and still others may not reach the axis. Owing to the indifferent preservation of specimens, it proves difficult to elucidate nature of the much thickened axial structure. However, in one slightly better preserved specimen (SUP 75151), the axial structure seems to be formed of fused to partially fused septal lobes. Minor septa, where discernible, are short and barely protrude inwards beyond the peripheral stereozone. Tabulae are usually complete, moderately to strongly updomed; they have a spacing of up to 12 in 5 mm.

Remarks. This species differs from *P. proliferum* " in having more widely spaced corallites and much less prominent budding " (Webby, 1972, p. 153), and also by exhibiting, in many corallites, the development of a solid axial structure. The only other New South Wales species to show conspicuous coalescence of inner ends of septa to form an axial structure is *P. macrocaule*, Webby, 1972. However, it has larger corallite dimensions, more conspicuous minor septa, and shows a different mode of budding. An axial structure has also been described in *P. aggregatum* Nicholson and Etheridge 1878 from the Craighead Limestone of Girvan, Scotland (Nicholson and Etheridge, 1878, p. 71; Wang, 1948, p. 101), but it tends to be a more loosely formed structure than in *P. jugatum*. *Palaeophyllum aggregatum* exhibits few other resemblances to *P. jugatum*. Thin sections of *P. aggregatum* in Sydney University palaeontological collections (SUP 77268–69, 78150) show it to have larger corallite dimensions, much more dilated septa peripherally, a marked denticulation on inner edges of the septa, and much longer minor septa.

Two species from the Late Ordovician of the Altai Mountains show some development of an axial structure. In *P. lebediensis* (Čherepnina, 1960) this structure is rather weak and formed by fusion of axial ends of a few septa, without significant dilation (Čherepnina, 1960, Pl. O–X, figs 4, 5; Ivanovskiy, 1969, Pl. X, fig. 1). *Palaeophyllum virgulta* (Čherepnina, 1960) may show a tendency to form a more pronounced axial structure (Čherepnina, 1960, Pl. O–XI, fig. 2b) but differs from *P. jugatum* in having a more open axial structure, greater corallite diameter and lateral rather than axial increase.

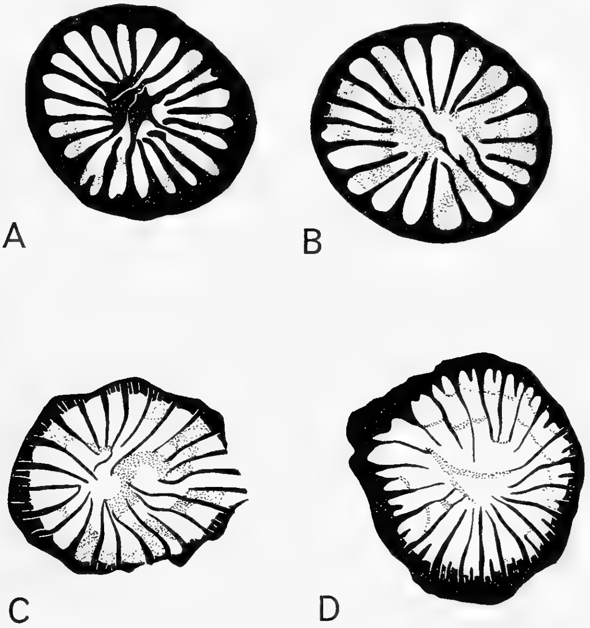
Palaeophyllum aff. *crassum* Webby 1972

Pl. XXVI, fig. 13; Text-fig. 3D

Material. SUP 75159, from the upper part of the Cargo Creek Limestone (associated in an horizon with *Favistina*); tributary on the south-east side of Canomodine Creek.

Comparative description. Corallum is phaceloid, in part fragmented by post-burial alteration (mainly pressure solution). Corallite diameter ranges from 7–9 mm. Septal number varies from 44 to 48 in mature corallites. Major septa are somewhat withdrawn from the axis; weakly dilated in the 0·4–0·5 mm wide peripheral stereozone, tapering rapidly inside stereozone, and more gradually towards axial ends. Minor septa are short, extending up to twice width of stereozone. Tabulae are complete, generally strongly arched periaxially and deeply sagging axially, but occasionally exhibiting flatter, less updomed or sagging forms. Peripheral spacing of tabulae ranges from 4–7 in 5 mm.

This form has been collected from the Cargo Creek Limestone in the same tributary of Canomodine Creek as *P. crassum* Webby 1972, but from a slightly higher horizon. It compares closely with *P. crassum* differing only in having a slightly smaller corallite size, and more widely spaced tabulae, with more pronounced axial sag and periaxial updoming. It may eventually prove to be conspecific with *P. crassum* when more specimens are found to enable the range of variability of the species to be more fully assessed.



Text-fig. 3. A–B. *Palaeophyllum jugatum* sp. nov., SUP 74258a, holotype, ×8.
C. *Palaeophyllum arrectum* sp. nov., SUP 75158c, holotype, ×4.
D. *Palaeophyllum* aff. *crassum* Webby 1972, SUP 75159a, ×4.

Palaeophyllum arrectum sp. nov.

Pl. XXVII, figs 8–9 ; Pl. XXVIII, figs 1–2 ; Text fig. 3C

Material. Holotype SUP 75158, from the upper part of the Canomodine Limestone, near " Rockdale ".

Description. Corallum phaceloid ; also damaged by pressure solution. Corallite diameter ranges from 6·0–7·5 mm. Major septa are slender, tapering slightly from peripheral stereozone towards axis ; mostly reaching to about 0·7 of corallite radius ; vary in number from 20 to 24. Minor septa are generally only very rarely visible, and then virtually confined to narrow (0·4 mm average width) peripheral stereozone. Tabulae are complete or rarely incomplete, slightly to moderately arched, occasionally with a broad, flattened axial region, or a weak axial depression. Spacing of tabulae ranges from 6–8 in 5 mm.

Remarks. Of the New South Wales Ordovician forms, only *P. crassum* and *P.* cf. *crassum* closely resemble this species. However, they both differ in exhibiting more pronounced axial sag of the tabulae, and more clearly recognisable minor septa.

Palaeophyllum? *patulum* sp. nov.

Pl. XXVIII, figs 3–7

Material. Holotype SUP 75194 ; paratypes SUP 29131, 75182–75190. Clearview Limestone Member of the Ballingoole Formation (Bowan Park Group) at Malachi's Hill.

Description. Corallum is solitary-dendroid ; the many single individuals probably include both original solitary coralla and fragments broken off dendroid colonies. Mode of budding unknown. Corallites are subcylindrical ; some surrounded by encrusting clathrodictyid stromatoporoid ; with diameter ranging from 10 to 14 mm. Narrow peripheral stereozone varies from 0·4–0·8 mm in width ; composed mainly of lamellar sclerenchyme with septa only slightly dilated. Septa range in number from 52 to 64 in mature corallites. Major septa generally rather slender, tapering slightly towards axis, and extending up to approximately 0·7 of corallite radius. In earlier growth stages, major septa may extend to axis (though an axial structure is not developed), or they may be slightly withdrawn ; but in later stages may be still more strongly withdrawn. Minor septa of variable length, usually short, but may reach inwards up to twice the width of the stereozone. Tabulae are complete and incomplete ; steeply inclined upward adjacent to stereozone, with broad flat to gently sagging axial region. Spacing of tabulae from 4–6 in 5 mm.

Remarks. This species is only tentatively assigned to *Palaeophyllum* because it does not show the typical fasciculate growth habit of the genus. It has been referred to previously by Semeniuk (1970, p. 21 ; 1973, p. 84) as a " *Streptelasma* ". Webby (1972, p. 154) has noted already the differences between this species and *P. crassum*.

Palaeophyllum? *laxum* sp. nov.

Pl. XXVIII, figs 8–10 ; Pl. XXIX, figs 1–3

Material. Holotype SUP 75163 ; paratypes 43264, 75164–75175, 75177–75180. Upper part of the Canomodine Limestone, south bank of Belubula River, east of " Cranky Rock ".

Description. Corallum fasciculate to possibly solitary ; poorly preserved with recrystallisation and some distortion of specimens. Lateral, non-parricidal increase exhibited by holotype. Corallites sub-cylindrical, with diameter ranging up to 13 mm. Peripheral stereozone ranges from 0·8 to 1·5 mm in width, composed of dilated septa, but little or no differentiation of lamellar sclerenchyme. Septa vary in number from 62 to 66 in mature corallites, strongly dilated in stereozone but tapering rapidly towards axis. Major septa usually extent inward to approximately 0·6–0·7 of corallite radius, but in some specimens (Pl. XXIX, fig. 2) they reach the axis, forming a very loose aggregation of septal ends ; no apparent septal lobes. Recrystallized calcite infilled areas in the centres of some corallites (Pl. XXVIII, fig. 8 ; Pl. XXIX, fig. 1) do not represent solid axial structures. Minor septa are long, usually 0·4–0·5 of corallite radius. Tabulae are mainly incomplete or partly coalescing ; very steeply inclined peripherally, with highly arched periaxial ridge and deep axial depression. Spacing of tabulae is highly variable, from 0·5 to 2·5 mm apart.

Remarks. Although only one corallum exhibits definite offsets, the general abundance and association of specimens in the one sampled horizon east of " Cranky Creek " suggest that they belong to a colonial rather than a solitary species.

Both *P.*? *laxum* and *P.*? *patulum* have a similar solitary-fasciculate habit, but in other respects are markedly different. *P.*? *laxum* has more dilated septa in the peripheral stereozone, longer minor septa, and the tabulae more steeply inclined peripherally with more prominent downflexing in the axial region.

Genus BOWANOPHYLLUM gen. nov.

Type species. Bowanophyllum pilatum sp. nov.

Diagnosis. Corallum solitary, usually ceratoid ; calice very deep, funnel-shaped. Interior of corallum, even axially, almost entirely filled by dense tissue of long, rod-like trabeculae of uncertain original microstructure set in lamellar sclerenchyme. Septa not clearly differentiated into major and minor. Tabulae limited to one or two complete, flat to gently sagging elements just beneath calice and at points of rejuvenescence. No dissepiments.

Discussion. This new genus appears very closely similar to *Rhabdocyclus* Lang and Smith 1939 (*pro Acanthocyclus* Dybowski 1873), a mainly Silurian form. *Rhabdocyclus* is characterised by having a patellate-trochoid form, two orders of dimorphacanthine septa and usually lacks tabulae. However, a few tabulae have been recorded in one specimen of the type species, *R. fletcheri* (Edwards and Haime), by Hill (1936, p. 202) and from specimens of *R.* aff. *transiens* Hill (1936, p. 204). By comparison, *Bowanophyllum* is typically a ceratoid form, the septal spines are much longer and more closely packed, apparently only of the holacanthine type, and lacking differentiation into major and minor presumably because of extreme length of the minor ; the tabulae are restricted to one or two at points of rejuvenescence and at the base of the calice, possibly related to pauses in growth of the corallum. This latter feature is also seen in *Tryplasma primum* Hill 1936, a transitional member of the *Rhabdocyclus–Tryplasma* lineage of the British Wenlock Shales (Hill, 1936, p. 199, fig. 23, Pl. 30, figs 43–44), and a species Ivanovskiy (1969, p. 48) regards as representative of *Rhabdocyclus. Bowanophyllum* is distinguished from this species on the basis of having more closely spaced coarser trabeculae forming septa seemingly of one order only.

The only recorded Ordovician species of *Rhabdocyclus* are the Estonian *R. aequispinatus* Reiman, 1958 from the Vormsi horizon (late Upper Caradoc) and *R. atavus* Kaljo, 1958 from the Rakvere horizon (early Upper Caradoc). These two species, regarded as synonymous by Ivanovskiy (1969, p. 50), are clearly distinguishable from *Bowanophyllum.* They have a trochoid growth form and short septal spines, the densely occupied area of septal spines and lamellar sclerenchyme is confined to lower and outer parts of the corallum, and they lack tabulae.

Also showing similarities to *Bowanophyllum* is the Ordovician genus *Coelostylis* Lindström 1880, as interpreted by Neuman (1967). The latter has closely spaced, long septal spines as exhibited by *Bowanophyllum*, but they are monacanthine and lack wrapping of lamellar sclerenchyme. *Coelostylis* also differs in possessing a marked axial structure and calical boss of partially fused septal spines, and in lacking tabulae. However the dense structure of septal spines apparent in transverse sections of *Coelostylis compactum* (Hill, 1953, Pl. I, figs 4a–b) from the Middle Caradoc Sphaeronite Limestone of Norway is very closely comparable to that shown by *Bowanophyllum.* Weyer (1973) interpreted *Coelostylis* as having septal pores, although they are not apparent in the type species figured by Neuman (1967). There is no evidence of septal pores in *Bowanophyllum*, all intertrabecular loculi being filled with lamellar sclerenchyme.

Bowanophyllum pilatum sp. nov.

Pl. XXIX, figs 4–11 ; Pl. XXX, fig. 1

Material. Holotype SUP 75197, paratypes SUP 75196, 75198–75207 ; from limestone unit in the uppermost part of Malachi's Hill Beds, north-east of Malachi's Hill.

Description. Corallum solitary, usually ceratoid, frequently showing rejuvenescence (Pl. XXIX, figs 6–7). Corallite diameter ranges to common maximum of 15–17 mm, with corallite height unknown, but estimated to be at least 50 mm. Calice is very deep and inverted funnel-shaped. Septa are formed of series of long, close spaced trabeculae of indeterminate original microstructure, extending inwards to axis and wrapped in lamellar sclerenchyme; lack of differentiation between major and minor septa presumably due to extreme length of minor; virtually the entire lumen, even axially, is filled with a dense tissue composed of acanthine septa and associated lamellar sclerenchyme; typically the septa are not in contact, and the lamellar sclerenchyme fills the spaces between them. The predominant continuity of layering of the lamellar sclerenchyme between adjacent septa and around discrete trabeculae of a single septum suggests it represents real growth lamellae, rather than a diagenetically-formed microstructure. The few observed discontinuities in the layering of the lamellar sclerenchyme and the very rare occurrences of sutures between individual septa may best be interpreted as the result of pressure solution selectively disrupting or exsolving portions of the original lamellar sclerenchyme. The case for inferring the layering as secondary pseudo-lamellar tissue (Oekentorp, 1974) is unconvincing. Trabeculae have common diameter of 0·25–0·35 mm, and usually gently inclined (20–30°) upwards in outer parts of corallum, steepening to almost vertical near axis. Whether the presently structureless trabeculae originated by replacement from rhabdacanths is uncertain, but there is no trace of rhabdacanthine septa in corallum. Septal number is difficult to determine in transverse sections, but there is up to 86 in mature corallites. Horizontal skeletal elements are rarely evident, except at points of rejuvenescence and at the base of the calice. At these levels, one or two wide spaced, flat or slightly sagging tabulae may occur (Pl. xxx, fig. 5).

Remarks. A number of specimens (Pl. xxx, figs 2–4) from the same horizon and locality as the type species seem likely to represent a smaller species of *Bowanophyllum*, although the possibility that they comprise early growth stages of *B. pilatum* cannot be entirely ruled out. They are solitary, ceratoid, up to 7·0 mm in diameter, and exhibit an occasional rejuvenescence. Septa are acanthine. Only at a rejuvenescence (Pl. xxx, fig. 2) are septa shown to be weakly differentiated into major and minor, but some of the ‘ minor ’ septa seem to be as prominent as the major in extending towards the axis. Up to 24 ‘ major ’ septa occur. Very broad, dense peripheral stereozone occupies almost two-thirds of the corallite diameter. Area of tabularium almost entirely filled with axial ends of acanthine septa. Only a very rare occurrence of flat to sagging complete tabulae (Pl. xxx, fig. 4).

Genus RHABDELASMA gen. nov.

Type species. *Rhabdelasma exigua* sp. nov.

Diagnosis. Corallum small, solitary (usually ceratoid) and possibly dendroid; with rhabdacanthine septa and broad peripheral stereozone. Septa of two orders; both break down into discrete spines, the major near the axis and the minor just inside the peripheral stereozone. Tabulae are mainly incomplete, markedly sagging in the outer part of the tabularium, and gently updomed axially. No dissepiments.

Discussion. The majority of Ordovician rugosoans with acanthine septa that have been studied in terms of their septal microstructure have been shown to have monacanthine trabeculae (Neuman, 1967; Webby, 1971; Weyer, 1973). The only forms for which rhabdacanthine trabeculae have been confirmed are *Tryplasma antiqua* Reiman, 1958 and *Rhabdocyclus aequispinatus* Reiman 1958 (regarded as having dimorphacanths by Ivanovskiy, 1969), both from the Vormsi horizon (late Caradoc) of Estonia. *Tryplasma antiqua* differs from *Rhabdelasma* in having shorter septa and a narrower stereozone (Reiman, 1958, Pl. II, figs 9–10). *Rhabdelasma aequispinatus* has even shorter septa, and lacks tabulae (Reiman, 1958, Pl. II, figs 12–13). *Rhabdocyclus atavus* Kaljo 1958, considered synonymous with *R. aequispinatus* by Ivanovskiy (1969), comes from a lower stratigraphical level—from the Rakvere horizon (early Upper Caradoc) of Estonia—but its septal microstructure has not been described. If in fact *R. atavus* eventually proves to exhibit rhabdacanths, it will be the earliest form to show this microstructure. *Rhabdelasma*, in coming from an horizon of approximately Upper Caradoc age (see earlier discussion), certainly no older than that containing *Rhabdocyclus atavus* and no younger than that with *T. antiqua* and *R. aequispinatus*, represents one of the earliest forms to exhibit rhabdacanths.

Weyer (1973) described several new genera including *Lambelasma* (probably a junior synonym of *Lambeophyllum* Okulitch, 1938) and *Coelolasma*, and substantially reinterpreted *Coelostylis* Lindström 1880. He based these descriptions on material collected from Pleistocene glacial erratics in North Germany and Poland, supposedly derived from the Baltoscandian Macrourus Limestone of Middle Caradoc age. These forms are characterised by monacanthine trabeculae, although in high levels of the calice, Weyer considers rhabdacanths to be developed. This latter observation, however, is based on the shape of inner edges of the septa, rather than on the internal structure of the trabeculae; hence the presence of rhabdacanths is not proven. Weyer also regarded the presence of septal pores as diagnostic of these forms. *Rhabdelasma exigua* exhibits some discontinuities in individual septa, as seen in transverse section. These may reflect septal pores especially as the breaks often occur between groups of trabeculae, rather than between individual trabeculae, as in cystiphyllids, e.g., *Holmophyllum* Wedekind 1927 (McLean, 1974*b*). However, no definite septal pores could be confirmed in longitudinal sections. *Rhabdelasma* should be assigned to the family Tryplasmatidae (Etheridge, 1907) rather than to Weyer's (1973) Lambelasmatidae.

Rhabdelasma shows some similarities to the genus *Neotryplasma* Kaljo, 1957. However the type species of the latter, *N. longiseptata* Kaljo, 1957 (Vormsi Horizon, Estonia: Late Caradoc) lacks the broad peripheral stereozone of *Rhabdelasma* and there is some development of a loose axial structure of grouped septal spines (Kaljo, 1957, Pl. XVI, figs 9–12; Shurygina, 1973, Pl. XXVIII, figs 1–3). *Neotryplasma codonophylloides* Kaljo, 1957 (Porkuni Horizon, Estonia: Upper Ashgill) apparently has greater development of a peripheral stereozone and may be more closely related to *Rhabdelasma*. Unfortunately there is no record of the nature of the septal microstructure in any described specimens of *Neotryplasma*. Shurygina (1973) has also recorded *Neotryplasma* from the Cherdinsk, Typylsk and Rassokhinsk Horizons of the central and northern Urals (Middle-Upper Caradoc).

Rhabdelasma exigua sp. nov.

Pl. XXX, figs 5–11

Material. Holotype SUP 75212, paratypes SUP 75213–75220, 75222; from limestone unit at the top of Malachi's Hill Beds, north-east of Malachi's Hill.

Description. Corallum usually solitary, but possible lateral budding (with corallites growing together in a cluster) is shown by more than one specimen (Pl. XXX, figs 5 and 8). Growth form is ceratoid, with maximum diameter of 5–7 mm. Peripheral stereozone broad at all growth stages, from 0·4–0·6 of corallite radius, composed of dilated septa and set in a tissue composed either of true primary lamellar sclerenchyme or, possibly, of secondary pseudolamellar material. It is difficult to resolve the nature of the microstructure in the peripheral stereozone owing to poor preservation. However, it is apparent that the septa, rather than being closely linked along sutures, are separated by spaces filled with lamellar tissue. Septa are of two orders, ranging from a total of 32 to 40 in mature corallites; each is composed of a single row of rhabdacanthine trabeculae. Rhabdacanths consist of discrete dark bundles of radiating fibres set in lamellar tissue (Pl. xxx, fig. 11). Minor septa are largely confined to peripheral stereozone; where they protrude inside the border, form discrete spines. Major septa extend to axis or may be slightly withdrawn; towards axial ends become discrete spines but no axial structure present. Occasional disruptions in the plane of the septum between groups of trabeculae, as seen in transverse section (Pl. xxx, figs 7 and 10), may represent septal pores, but have not been confirmed in available longitudinal sections. Throughout ontogeny, septa usually well separated, but in an early stage of one specimen (SUP 75213) septa are closely spaced together. Tabularium sharply differentiated from peripheral stereozone; tabulae usually seen to be incomplete; strongly sagging peripherally, and gently arched in axial region, although disrupted by trabeculae (Pl. xxx, fig. 9). Spacing of tabulae is extremely variable; 0·6–1·5 mm apart in available material. No dissepiments seen.

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EXPLANATION OF PLATES

PLATE XXVI

Figs 1–5. *Streptelasma*? sp., unnamed limestone north of Gunningbland, ×2·5. 1. SUP 75195a, transverse section, late ephebic stage. 2. SUP 75195d, transverse section, ephebic stage. 3. SUP 75195f, transverse section, neanic stage. 4. SUP 75195h, longitudinal section. 5. SUP 77267, transverse section.

Figs 6–8. *Helicelasma* sp., middle-upper part of Cargo Creek Limestone, south-east tributary of Canomodine Creek, ×2·5. 6. SUP 75160a, transverse section, ephebic stage. 7. SUP 75160c transverse section, early ephebic stage. 8. SUP 75162c, longitudinal section.

Figs 9–12. *Grewingkia* sp., limestone breccia, uppermost part of Malachi's Hill Beds, north-east of Malachi's Hill; specimen associated with *Catenipora* sp.; transverse sections, ×5. 9. SUP 75223a. 10. SUP 75223b. 11. SUP 75223c. 12. SUP 75223d.

Fig. 13. *Palaeophyllum* aff. *crassum* Webby 1972, upper part of Cargo Creek Limestone, south-east tributary of Canomodine Creek, transverse and longitudinal sections, ×3. SUP 75159b.

PLATE XXVII

Figs 1–7. *Palaeophyllum jugatum* sp. nov., unnamed limestone north of Gunningbland. 1–2. holotype. 1. SUP 74258a, ×3, showing quadripartite division. Note two corallites (one with solid axial structure) towards bottom margin of figure are those depicted in Text-fig. 2A–B. 2. SUP 74258b, ×4, longitudinal section exhibiting calice. 3. SUP 43261, paratype, ×3. 4. SUP 74262b, paratype, ×3, transverse section showing axial, parricidal division of one corallite which also exhibits prominent minor septa. 5. SUP 74262a, paratype, ×4, transverse section exhibiting four or five? buds. 6. SUP 75152a, paratype, ×4, longitudinal section showing axial, parricidal increase. 7. SUP 74259b, paratype, ×4, longitudinal section.

Figs 8–9. *Palaeophyllum arrectum* sp. nov., upper part of Canomodine Limestone near "Rockdale", holotype, ×3. 8. SUP 75158a, transverse section. 9. SUP 75158e, longitudinal section.

PLATE XXVIII

Figs 1–2. *Palaeophyllum arrectum* sp. nov., upper part of Canomodine Limestone near "Rockdale", holotype, ×3. 1. SUP 75158k, transverse section. 2. SUP 75158n, longitudinal section showing occasional incomplete tabulae.

Figs 3–7. *Palaeophyllum*? *patulum* sp. nov., Clearview Limestone Member (Ballingoole Formation) at Malachi's Hill. Figs 3–4 exhibit "pseudo-colonial" form ; others may be solitary. 3. SUP 29131, ×2·5, paratype, transverse section. 4. SUP 75194b, ×2·5, holotype, longitudinal section. 5. SUP 75186b. ×3, paratype, transverse section. Note short minor septa. 6. SUP 75187a, ×2·5, paratype, longitudinal section. 7. SUP 75182b, ×3·5, paratype, transverse section of corallite surrounded by clathrodictyid stromatoporoid, *Plexodictyon*? sp.

Figs 8–10. *Palaeophyllum*? *laxum* sp. nov., uppermost part of Canomodine Limestone, Belubula River east of "Cranky Rock". 8. SUP 75163d, ×3, holotype, transverse section. 9. SUP 43264, ×1·5, paratype, transverse section. 10. SUP 75169, ×2·5, paratype, longitudinal section.

PLATE XXIX

Figs 1–3. *Palaeophyllum*? *laxum* sp. nov., uppermost part of Canomodine Limestone, Belubula River east of "Cranky Rock". 1. SUP 75163b, ×3, holotype, transverse section. 2. SUP 75168, ×3, paratype, transverse section. 3. SUP 75164, ×2·5, paratype, longitudinal section.

Figs 4–11. *Bowanophyllum pilatum* gen. et sp. nov., unnamed limestone at top of Malachi's Hill Beds, north-east of Malachi's Hill. 4. SUP 75197c, ×3, holotype, transverse section. 5. SUP 75198b, ×3, paratype, longitudinal section showing deep calice partitioned at the base by two complete tabulae. 6. SUP 75195c, ×2, paratype, longitudinal section exhibiting rejuvenescence with associated tabulae. 7. SUP 75198a, ×3, paratype, transverse section showing rejuvenescence. 8. SUP 75202b, ×8, paratype, transverse section in calical region showing trabeculae of uncertain original microstructure set in lamellar sclerenchyme. 9. SUP 75206, ×3, paratype, transverse section exhibiting spinose character of septa. 10. SUP 75200d, ×2·5, paratype, oblique longitudinal section showing rows of inclined trabeculae. 11. SUP 75200c ×2·5, paratype, transverse section.

PLATE XXX

All specimens come from unnamed limestone at top of Malachi's Hill Beds, north-east of Malachi's Hill.

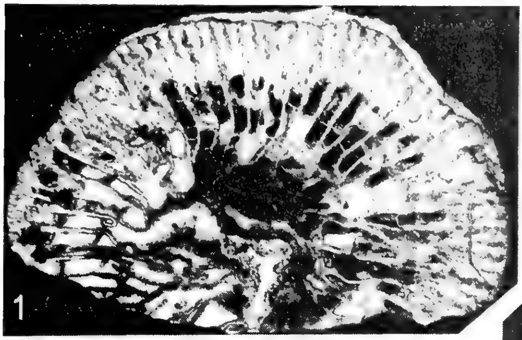
Fig. 1. *Bowanophyllum pilatum* gen. et sp. nov., SUP 75197a, ×8, holotype, transverse section showing solid tissue of long, rod-like trabeculae of uncertain original microstructure draped in lamellar sclerenchyme. Note elongate, light-coloured area midway between outer wall and axis which represents only open space in otherwise dense tissue.

Figs 2–4. *Bowanophyllum* sp., ×4. 2. SUP 75210b, transverse section showing weak differentiation of minor septa at rejuvenescence. 3. SUP 75208a, transverse section. 4. SUP 75208b, longitudinal section exhibiting tabularial area filled with dense septal tissue except for a single open space bounded by two tabulae.

Figs 5–11. *Rhabdelasma exigua* gen. et sp. nov. 5. SUP 75214a, ×5, paratype, transverse section exhibiting two corallites in contact. 6. SUP 75213a, ×5, paratype, transverse section. 7. SUP 75213c, ×5, paratype, transverse section. 8. SUP 75214b, ×5, paratype, transverse section showing three corallites in contact. Larger corallite situated towards top margin of figure exhibits two very tiny, possible lateral buds. 9. SUP 75212b, ×5, holotype, longitudinal section. Note small part of an associated favositid colony at top left. 10. SUP 75217b, ×5, paratype, oblique transverse section of large specimen. 11. SUP 75215b, ×10, paratype, tangential longitudinal section of curved specimen showing rhabdacanthine character of septa in peripheral stereozone breaking down into discrete spines in tabularium.

Corrigenda

PROC. LINN. SOC. N.S.W., 100 : 184, line 5, *read* Kitaygorod ; 186, *for* Major septa extend 0·5–0·6 of corallite radius, *read* Minor septa extend 0·5–0·6 of length of major septa.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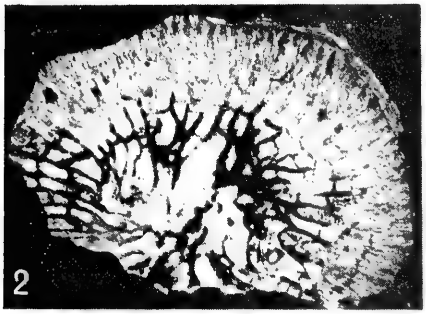
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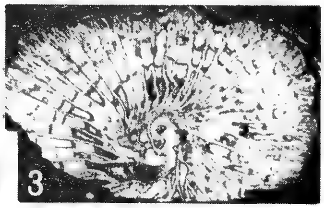
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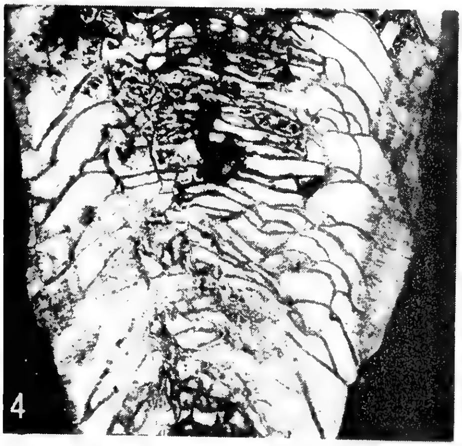
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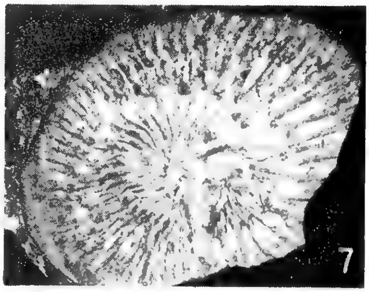
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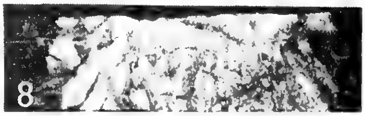
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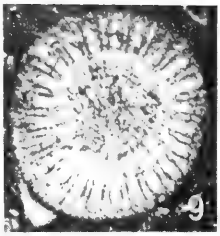
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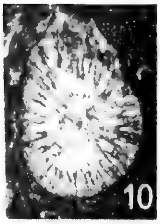
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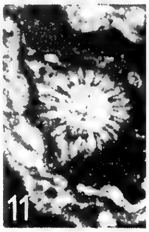
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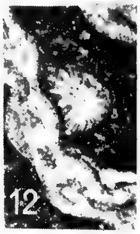
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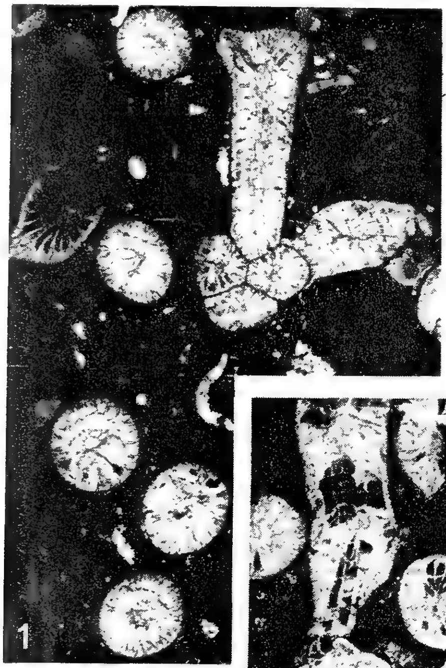
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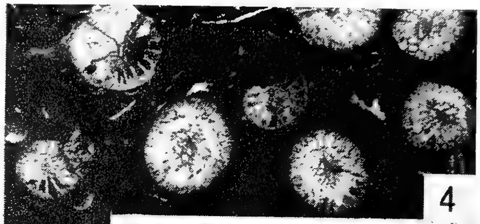
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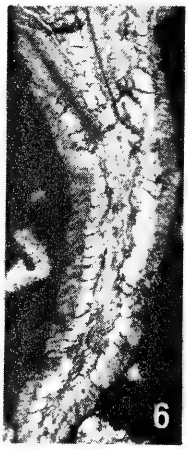
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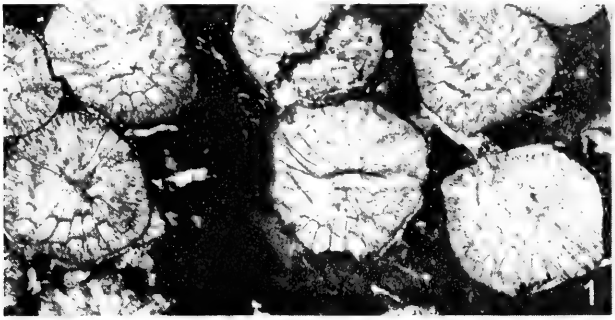
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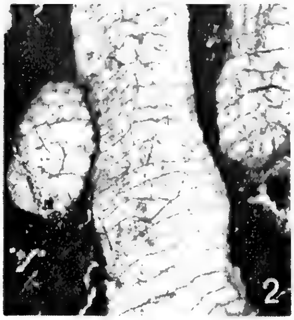
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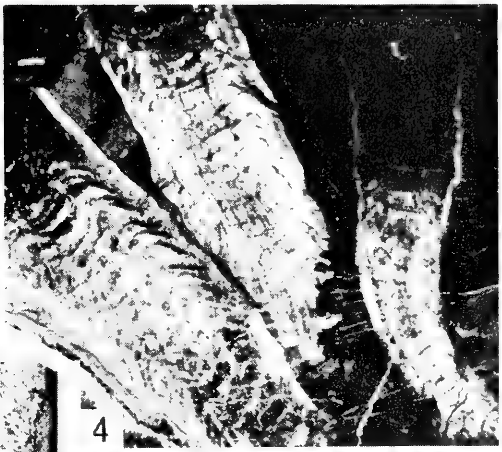
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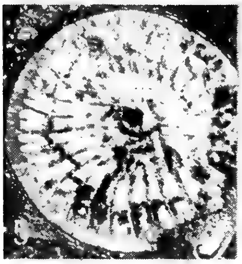


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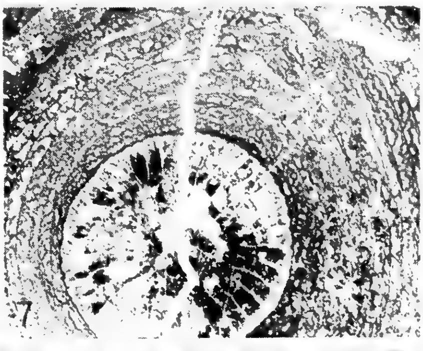
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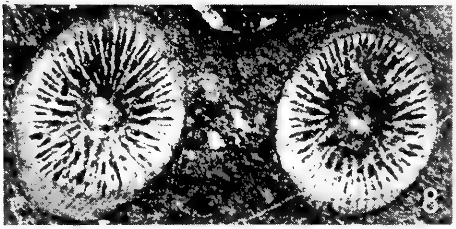
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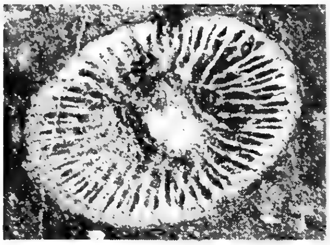

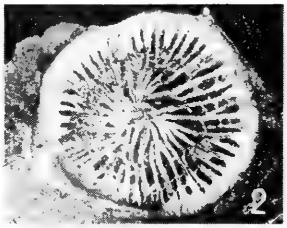

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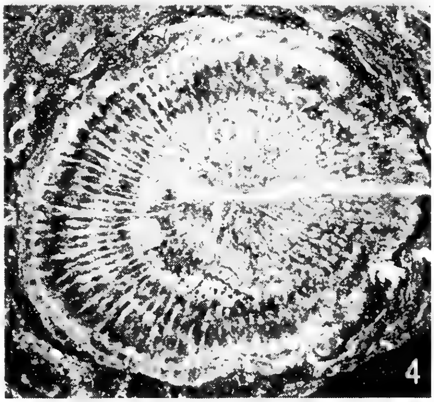

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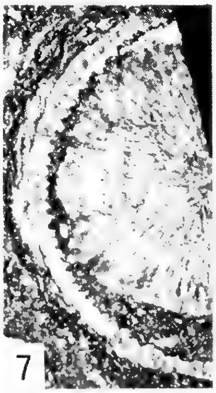

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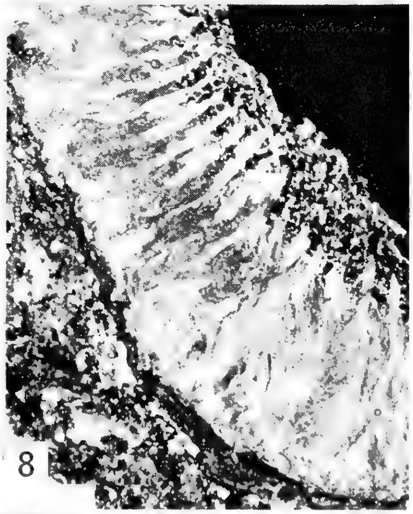

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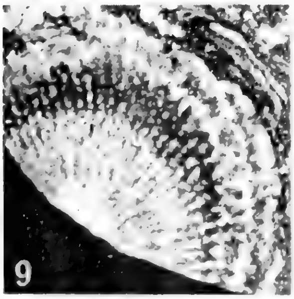

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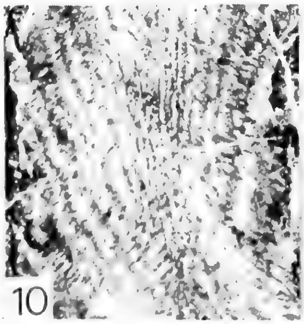

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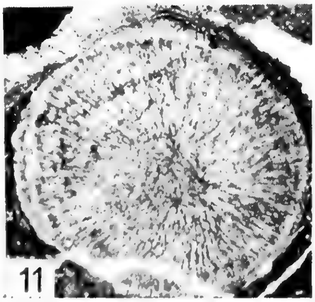

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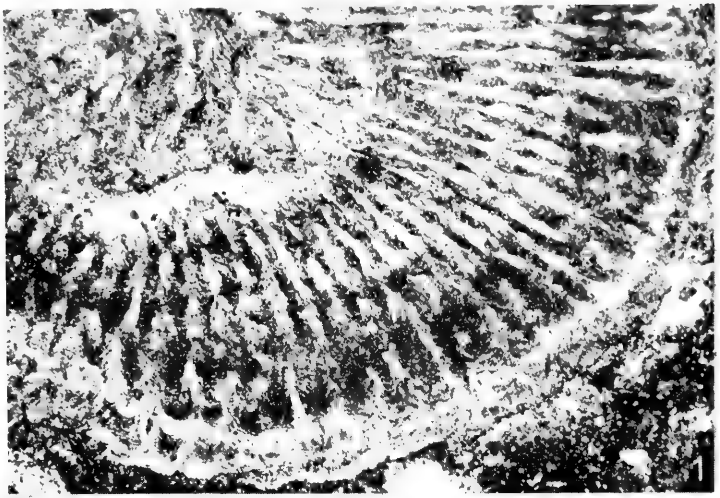
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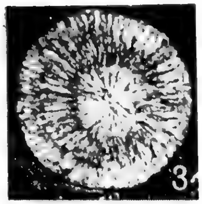
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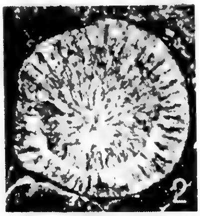
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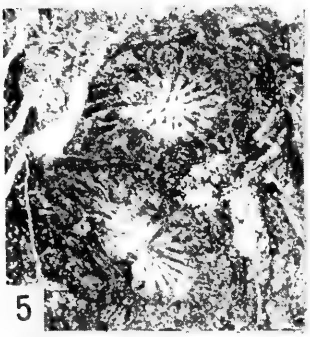
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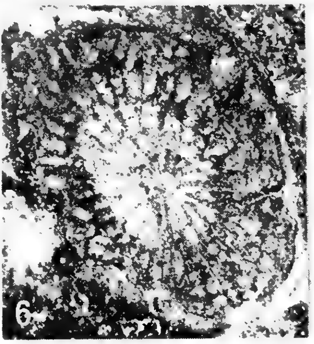
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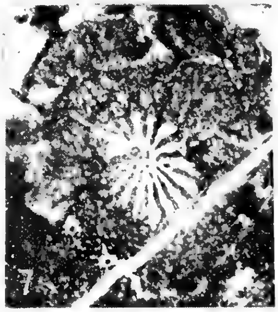
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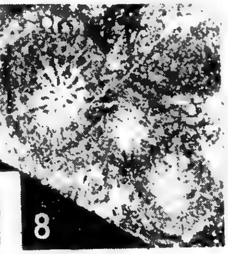
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